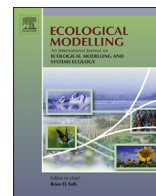




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Applying network methods to acoustic telemetry data: Modeling the movements of tropical marine fishes

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ABSTRACT

Modeling animal movements is fundamental to animal ecology as it provides the foundation for further exploration into mechanisms affecting individual and population-level processes. In the last few decades, biotelemetry has enabled scientists to track the movements of marine life across a variety of scales. However, the use of such technology is progressing faster than the analytical techniques for modeling movement patterns. In summer 2012, we deployed an acoustic telemetry array around Culebra, Puerto Rico, consisting of 48 remote receivers that can detect coded transmissions sent by tags implanted in fish. We surgically implanted transmitters in bonefish ($n = 28$), great barracuda ($n = 2$) and permit ($n = 1$) as part of a multi-year study. In January 2013, we downloaded over 850,000 detections from 39 receivers for 31 fish (several receivers had zero fish detections, and two receivers were not downloaded), and used that six-month data set to explore how graph theory and network analysis can be used to model the movement ecology of the tagged fish. We analyzed this data as two types of graphs. First, a bipartite graph was constructed by linking each fish with an edge weighted by the number of detections of that fish by that receiver. Bipartite graphs are not explicitly spatial, but rather represent which fish associate with which receivers. Second, spatial movement graphs for individuals were built by linking receivers (nodes) by edges with the number of times each fish moved along that edge as weights. The bipartite graph identified groups of fish visiting the same sites, and groups of sites visited by the same fish. Of the six community detection algorithms used, Multilevel, Fast-Greedy, and Walk-Trap performed best, with similar module partitions and modularity scores. All three of these algorithms produced modules (groups) that appear to reflect working hypotheses related to the coastal bathymetry, habitat types, and associated movement ecology of the tagged species. Spatial movement graphs were very different for each fish examined and reflect behavioral differences. Fish exhibited various movement patterns, some showing the pattern of a central place forager (bonefish), while others cruised along a territory (great barracuda and permit).

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1. Introduction

Animal movements are physiological and behavioral responses to fitness tradeoffs, influenced by how individuals interact with and perceive their condition as well as their abiotic and biotic environment (Dingle, 1996). Movements in space and time can be related to a vast suite of factors such as competition among conspecifics for

territories (Ostfeld, 1990), foraging strategies (Wilson et al., 2012), predator avoidance (Lima and Dill, 1990), and seasonal reproductive migrations (Danylchuk et al., 2011). Regardless of the scale, being able to quantify animal movements can lead to significant insights into phenomena that shape the evolution of life histories, drive population-level processes (e.g., demography, gene flow) and distributions, and are the result of associations among populations within communities and across landscapes (Schick et al., 2008). This greater understanding can thus play an important role in advancing basic ecology as well as the conservation and management of wild animals.

Quantifying animal movements relies on being able to repeatedly observe the location of individuals in spatially structured landscapes through time (Nathan, 2008). In aquatic systems, observing fish and other aquatic life can be particularly challenging

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since researcher time underwater is limited. Conventional tags and the recapture of tagged individuals are often used to quantify fish movements, but studies may not offer the resolution to allow for quantifying detailed movement patterns, while repeat capture of tagged focal animals could potentially elicit undue stress and alter behavior (Lucas and Baras, 2000; reviewed in Cooke et al., 2012). Technological advances in biotelemetry in aquatic systems have increased the capacity to track animal movements, particularly in the marine environment via the use of acoustic transmitters and receivers (Cooke et al., 2012; Heupel and Webber, 2012). Manual tracking of acoustically-tagged fish began in the 1970s (Ireland and Barlow, 1978; Kanwisher et al., 1974) with passive fixed-receiver techniques evolving in the late 1980s (Klimley and Butler, 1988; McKibben and Nelson, 1986). It is now possible to track fish movements on a variety of spatial and temporal scales ranging from ocean basins across years to fine-scale (sub meter) movements over minutes. This revolution in animal tracking technology has provided insight into the spatial ecology of fish that was previously unattainable.

Although there has been an increase in the use of acoustic telemetry to quantify the movement of marine life (see Heupel and Webber, 2012), the application of this technology is progressing faster than the analytical techniques for interpreting and modeling movement. Acoustic telemetry can generate an enormous amount of data that can be challenging to quantitatively analyze to reveal spatial patterns at the individual and population-levels (Jacoby et al., 2012). While a decade ago the novelty of the technology was sufficient to warrant publication with basic descriptive summary statistics, today there is both an opportunity and expectation to apply rigorous and sophisticated analytical approaches, although examples for marine fish are still rare (but see Jacoby et al., 2012; Simpfordorfer et al., 2002). Analysis of telemetry data with network methods is increasing in ecology (Dale and Fortin, 2010; Fang and Huang, 2013; Urban et al., 2009) and is beginning to be used for marine species (Jacoby et al., 2012). Network analysis is embedded in the much larger discipline of graph theory; a body of mathematics dealing with connectivity, flow, and routing in networks. Given the parallels between graph theory and basic ecological and evolutionary processes (such as connectivity), network approaches have much potential to elucidate the mechanistic basis of animal movements and social interactions (Krause et al., 2011; Pinter-Wollman et al., 2013).

An acoustic telemetry system deployed in the coastal waters of the island of Culebra, Puerto Rico, in the Caribbean Sea, provided an opportunity to explore novel analytical approaches for acoustic telemetry data. The aim of this study was to explore a range of network analysis methods to model the movement patterns of the focal project species (bonefish, *Albula vulpes*). Specifically, we attempted to employ community detection algorithms on bipartite graphs, to identify groups (modules) of fish and sites more tightly connected to each other than to the rest of the acoustic array. As additional data across multiple years and sites are collected, it is expected that the network analyses explored here will be particularly effective in documenting home ranges, site fidelity, social interactions (within and among species), and spawning-related movements. Earlier work on bonefish in Florida (Humston et al., 2005) and The Bahamas (Danylchuk et al., 2011; Murchie et al., 2013) has provided some information on the spatial ecology of bonefish, however, the habitats were qualitatively different than those in Culebra (i.e., Culebra has fringing coral reef flats as opposed to flats directly connected to the shoreline) and analytical approaches were rather descriptive. We also tagged two other species (permit, *Trachinotus falcatus*, and great barracuda, *Sphyrna barracuda*) as part of a pilot examination of their connectivity among coastal marine habitats surrounding Culebra. Acoustic telemetry of great barracuda has previously been conducted in

The Bahamas (O'Toole et al., 2011) that has a different coastal bathymetry than the waters around Culebra. No previous acoustic telemetry has been conducted on permit.

2. Methods

2.1. Data

Acoustic tags were surgically implanted in 28 bonefish, 1 permit, and 2 great barracuda between July and early August 2012 (bonefish and permit – Vemco V13-1L, 69 kHz, 13 mm diameter, 36 mm long, 6.0 g in air, min and max delay times 45–135 s; great barracuda – Vemco V16-1L, 69 kHz, 16 mm diameter, 54 mm long, 19 g in air, min and max delay times 60–180 s; Vemco Inc., Halifax, NS, Canada). An array of 48 autonomous fixed acoustic receivers (V2RW receivers, Vemco Inc., Halifax, NS, Canada) was placed around the island (Fig. 1). Receivers were moored close to the substrate as per methods described in Murchie et al. (2012). The receivers were deployed concentrated on the southeast portion of the island where several shallow reef flats provide habitat typically used by bonefish. One portion of the array around the reef crest in Las Pelas (Fig. 1) consisted of 25 closely spaced V2RW receivers. This deployment design comprises a VPS (Vemco V2RW Positioning System) array that allows more refined X-Y positions because a single coded transmission can be detected by two or more receivers (Espinoza et al., 2011). Although the VPS is a part of the larger study, we do not use the refined X-Y positions for this modeling exercise, but rather explore the fact that the VPS was nested within a broader-scale array of receivers deployed as nodes.

In January 2013, we downloaded data from all but two of the receivers (because of unfavorable weather conditions). Of the 46 receivers downloaded, 39 contained detections from fish we had tagged six months earlier. For the purposes of this exercise, we excluded fish (tags) with fewer than 1000 detections (5 fish were excluded with this rule). We did not filter the detections further, although detections of phantom tag numbers were eliminated by the above rule. All analyses were done in R 2.15.2 (R Core Team, 2012) using the igraph package (Csardi and Nepusz, 2006).

2.2. Use metrics

Number of detections is one index of use of a receiver (site). It is better to determine other use metrics such as number of distinct visits, or time spent at a site (Pautzke et al., 2010) but these require knowing when the fish has 'left' the site. However, we have yet to develop a decision rule for these metrics and simply analyzed the number of detections at each receiver.

2.3. Bipartite graphs

Linking fish to the sites they visit produces a 'bipartite' graph (two kinds of nodes or vertices; Dale and Fortin, 2010) of fish (tags) connected to receivers (sites). In our bipartite graphs, all fish are linked to each receiver by an edge (arrow) weighted by the number of detections as an indicator of the use of each receiver by each fish. The layout of the graph was determined by the Fruchterman–Reingold force-directed layout algorithm (Fruchterman and Reingold, 1991). This method balances repulsive forces among all nodes with attractive forces between adjacent nodes, the attractive force being proportional to the weight of the edges connecting adjacent nodes (Tamassia, 2010). Therefore, as a null model, the repulsive forces alone (without any edge connections) would cause the nodes to arrange themselves equidistant from their nearest neighbors within a circle.

The number of edges connecting to a node (vertex) is called that node's degree. The distribution of degree for all vertices in

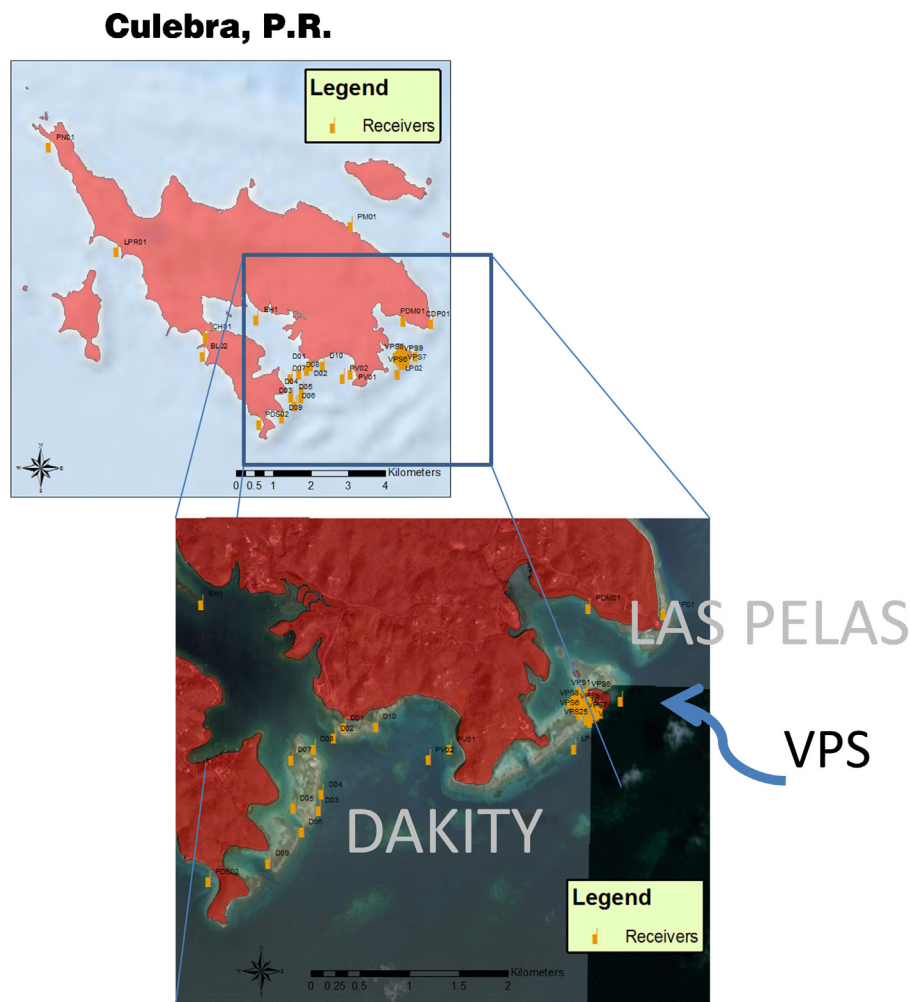


Fig. 1. Map of acoustic array network around the Island of Culebra, Puerto Rico. Inset shows an enlarged view of the southeast portion of the array, including the dense VPS array in Las Pelas.

a network often follows a power or exponential law (Boccaletti et al., 2006; Milo et al., 2002), although some bipartite graphs do not (Chakrabarti and Faloutsos, 2006; Montgomery and Faloutsos, 2001). For the bipartite graph, we looked at the degree distribution for fish and receivers separately. A fish that visits many sites (i.e., has a high degree) is wide-ranging, while a fish that visits only a few sites (i.e., has low degree) either has a small home range or its home range only partially overlaps our receiver array. Similarly, a receiver that is visited by many fish is attractive for some reason (e.g., as a corridor, a foraging habitat, or a spawning site), while a receiver that is visited by only a few fish is less attractive or representative of more transient behavior. We plotted the degree distribution of the graph.

2.4. Community detection

Groups of nodes with tighter connections to each other than to the rest of the graph are called 'communities'. We used network community detection algorithms to try to identify: home ranges of individual fish, groups of fish that visited the same receivers, differences between fish species, etc. We tested several community detection algorithms including 'Leading-Eigenvector' (Newman, 2006), 'Walk-Trap' (Pons and Latapy, 2006), 'Fast-Greedy' (Newman and Girvan, 2004; Clauset et al., 2004), 'Spin-Glass' (Reichart and Bornholdt, 2006), 'Label-Propagation' (Raghavan et al., 2007), and 'Multilevel' (Blondel et al., 2008). The

Leading-Eigenvector method looks at groups based on eigenvectors of the modularity matrix of the graph (Newman, 2006). The Walk-Trap method simulates many short random walks on the graph and identifies groups of nodes where such walks get trapped (Pons and Latapy, 2006). The Fast-Greedy method (a faster version of the greedy algorithm) is a hierarchical agglomerative method (Clauset et al., 2004; Newman and Girvan, 2004). The Spin-Glass algorithm is an optimization method relying on an analogy between the statistical mechanics of networks and physical Spin-Glass models (Reichart and Bornholdt, 2006). The Label-Propagation algorithm (Raghavan et al., 2007) initially assigns each node a unique label. Then, iterative rounds of label assignment re-label nodes based on the label spread most in the neighborhood of each node. The algorithm stops when a condition is met; for example, no further label changes. The Multilevel algorithm is an agglomerative, hierarchical approach based on modularity (Blondel et al., 2008). Initially, each vertex is assigned to a unique community. In every step, vertices are re-assigned to communities in a local, greedy way: each vertex is moved to the community with which it achieves the highest contribution to modularity. When no vertices can be reassigned, each community is considered a vertex on its own, and the process starts again with the merged communities. The process stops when there is only a single vertex left or when the modularity cannot be increased any more in a step. Orman and Labatut (2009) compared five community detection algorithms (all of the above except Multilevel), using generated graphs containing 1000 nodes with varying

means and maximum degrees, and concluded that Spin-glass and Walk-Trap are the most robust.

For each set of ‘communities’ or modules detected, we evaluated the quality of the modules detected in two ways. First, we calculated modularity (Newman and Girvan, 2004), a measure of the quality of a particular division of a network. Modularity is defined as the proportion of edges within the given groups minus the expected such proportion if edges were distributed randomly, given the degree (number of edges) of each node. Second, for each node in an identified module, we counted the number of links to members of the same module (in-degree) and the number of links to nodes outside the module (out-degree). We then used a Wilcoxon sum-rank test on all nodes in each module to test whether the members in a module are linked more to each other than to the rest of the network (Song and Singh, 2013). This test can confirm that the proposed community has significantly more links within it than outside it, that it is not significant, or that it is an ‘anti-community’ having significantly more connections with other modules than within itself. Anti-communities occur when a ‘module’ has strong connections to the rest of the network, but moving any single node to another module reduces modularity of the graph as a whole.

2.5. Spatial movement graphs

By placing receivers (nodes) in their actual (x, y) locations, we were able to construct a directed spatial graph with edges weighted by the number of movements. These graphs enabled us to visualize the movement patterns of individual fish and how they used space. For example, the spatial graph of a central-place forager might look like a hub with spokes, while an individual that regularly patrolled a home range boundary might look like a donut. We produced spatial graphs for a great barracuda (GB5) and a bonefish, as examples, and overlaid them on a benthic habitat map (Kendall et al., 2001).

3. Results

3.1. Acoustic array data

In January 2013, we downloaded 46 receivers (out of 48 in the array). Following our detection criteria, data for 23 bonefish, one permit, and two great barracuda were used in the model analyses (26 of the 31 fish we had tagged). Total occurrences for these fish ranged from 1121 to 183,426 detections, with a total of over 850,000 detections.

3.2. Bipartite graphs

Fig. 2A shows a bipartite graph (with a Fruchterman–Reingold layout) of fish with greater than 1000 detections and the receivers that heard them. Node size is relative to the ‘degree’ (number of edges entering or leaving each node). In this graph (Fig. 2A), fish (tags) are white and receivers (sites) are green (or gray). Fish nodes are located close to the sites they visited and site nodes are located

close to the fish that visited them. This procedure separated the VPS array into forereef (receivers V18–25) and lagoon (receivers V1–17) portions of the reef flat. The Dakity area (Fig. 1) exhibits a looser clustering of receivers on the right of Fig. 2A, with receivers D9, and D5–7 being the core, and receivers D1, D2, D8 and D10 on the periphery. Four bonefish (B3, B8, B9 and B11) are primarily associated with the Dakity cluster.

The degree (number of edges for each node) for fish in this graph ranges from 2 to 31 (visits to a possible 46 receivers in the graph), while the degree for receivers ranges from 3 to 22 (visits from a possible 26 fish). The degree distribution for fish (Fig. 3A, left) is W-shaped, with the maximum frequency being vertices with about 16 edges, and a large number of vertices with medium to high degree. The low degree fish might be fish whose home ranges only partially overlap our receiver array. The degree distribution for receivers has 40% of the receivers at the high end of the range, and relatively few low numbers (although 7 receivers not included in the graph were not visited by any fish; degree of zero).

Part of the reason for this degree distribution may be the fact that within the VPS array, a single coded signal from a tag may be heard by multiple receivers. If we group the receivers in the VPS array into a lagoon portion (receivers V1–V17 are merged into VL) and a forereef portion (receivers V18–V25 are merged into VFR), then we can mostly remove this effect from the degree distribution (although edge weights are still uncorrected) (Fig. 2B). The two grouped portions of the VPS array are now next to one another in the center of the graph (Fig. 2B), the Dakity cluster is now split in two (receivers D5–7 and D9; and receivers D1, D2, D8 and D10), and a group of fish has formed around receiver PDM1 (bonefish B14–19).

The degree distributions for the graph of the contracted receiver array (26 fish nodes and 16 receiver nodes) are shown in Fig. 3B. For fish nodes, degree now ranges from 1 to 10 with a mode around 4, and for receiver nodes it ranges from 1 to 21 with a mode of 5 (Fig. 3B).

3.3. Community detection

We wanted to find a less subjective way of interpreting groups of receivers and fish in our bipartite graph (Fig. 2A). Modules (communities) were found using each of six community detection algorithms (Table 1). Of the six detection algorithms used on our bipartite graph, two (Multilevel and Fast-Greedy, Fig. 4) produced identical module partitions and had the best modularity scores (0.396, Table 1). A third (Walk-Trap) produced a similar partition to the first two (Table 2; Fig. 5), with only a slightly lower modularity score (0.343, Table 1). The Spin-Glass and Label-Propagation methods performed slightly worse, and the Leading-Eigenvector method had the lowest modularity score (Table 1). Communities detected by the Fast-Greedy and Multilevel methods (5 modules, Fig. 4), and the Walk-Trap method (6 modules, Fig. 5) were similar (see cross-tabulation of the assignment of nodes to modules in Table 2).

Table 1
Statistics for different community detection algorithms applied to the Culebra bipartite graph (26 fish, 39 receivers, no contraction). Modularity is a measure of how good a division is, or how separated the different vertex types are from each other (Newman and Girvan, 2004). Significant modules had significantly more connections to nodes within a module than outside a module ($p > 0.05$, according to a Wilcoxon sum-rank test). If there were significantly more connections to outside the module than within it ($p > 0.05$, according to a Wilcoxon sum-rank test), then that module is called an anti-module.

Community detection algorithm	Modularity	Modules detected	Significant modules	Significant anti-modules
Fast-Greedy	0.396	5	1	2
Multilevel	0.396	5	1	2
Walk-Trap	0.343	6	2	0
Spin-Glass	0.333	10	0	5
Label-Propagation	0.332	6	1	1
Leading-Eigenvector	0.187	5	1	1

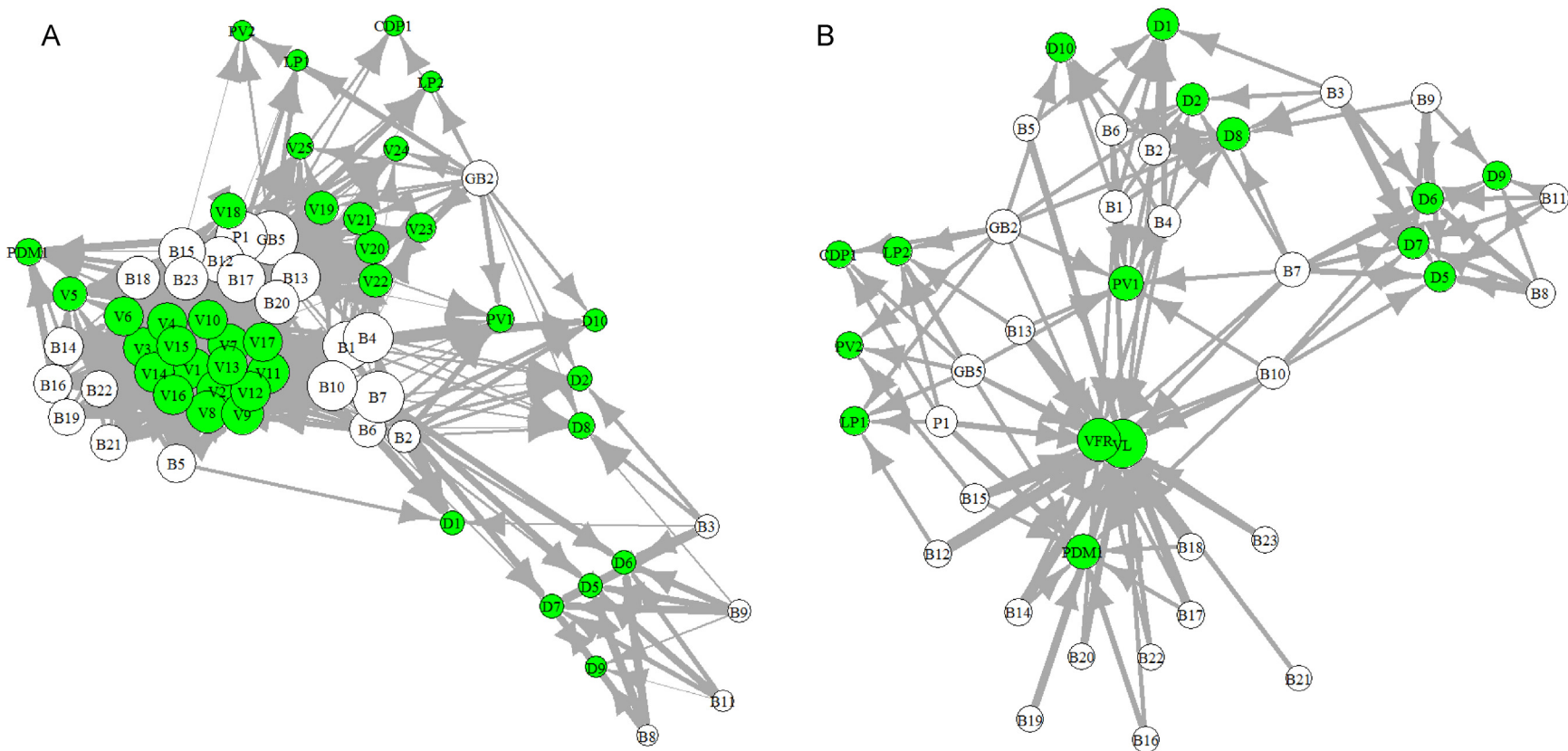


Fig. 2. Bipartite graph of fish-receiver network in Culebra, Puerto Rico. (A) Network links fish tags (green nodes) with the receivers they visit (white nodes). The width of the edges (links) is proportional to the number of detections at each receiver. The size of each node is proportional to its degree (the number of links entering or leaving that node). (B) Network after lumping the 25-receiver VPS array into a lagoon node (VL) and a foreereef node (VFR). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

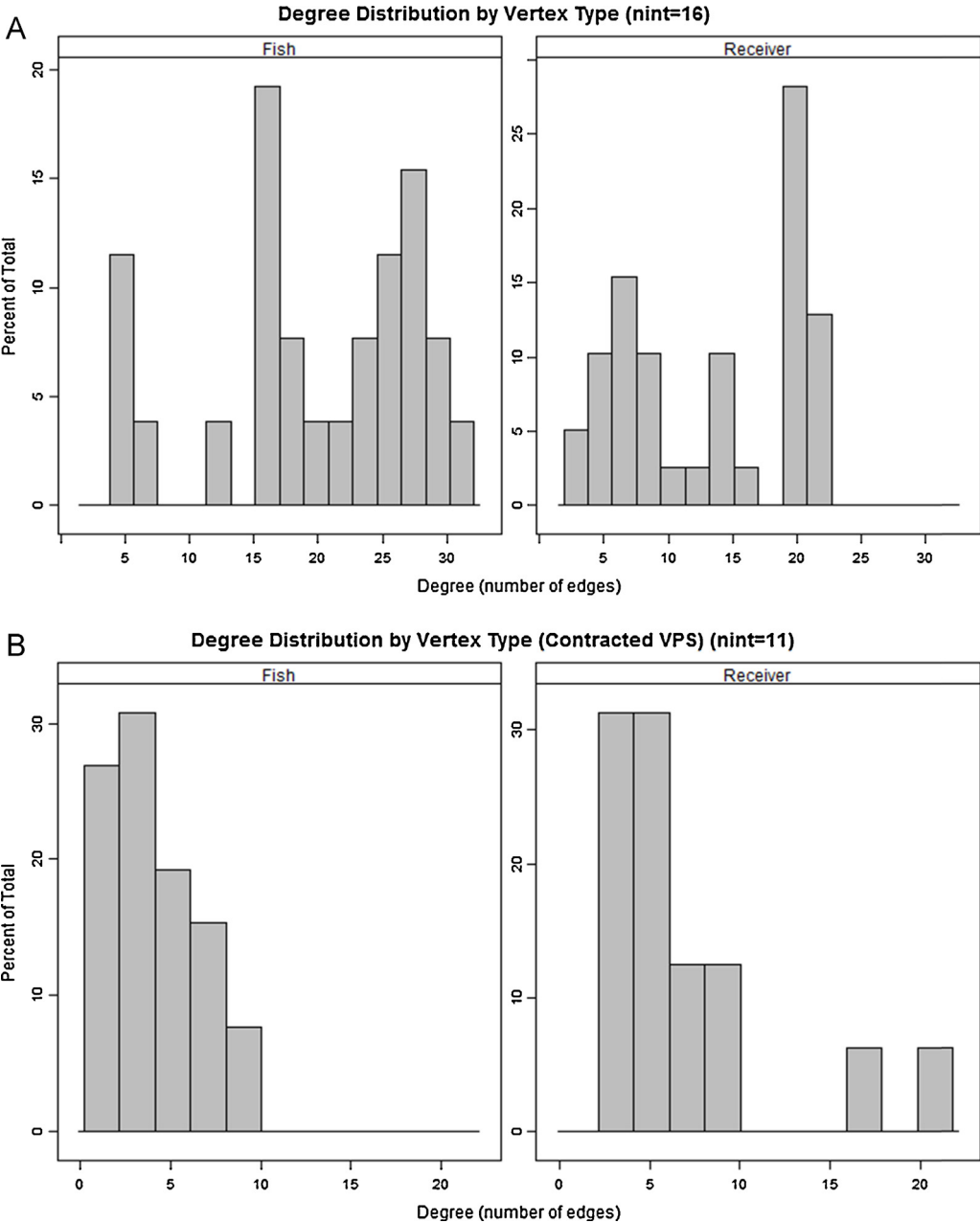


Fig. 3. Degree distribution by vertex type for the bipartite graphs in Fig. 2. (A) Histogram of frequency of degree (number of edges per vertex) for graph in Fig. 2A. (B) Histogram of frequency of degree (number of edges per vertex) for graph with lumped VPS in Fig. 2B.

The Fast-Greedy and Walk-Trap results can also be displayed as dendrograms (Appendix Figs. A1 and A2). The Fast-Greedy and Walk-Trap methods both identified the same module of 5 bonefish and 5 receivers in the Dakity area

($p = 0.013$, Wilcoxon sum rank test; module #2 in Fig. 4 and module #6 in Fig. 5; Table 2). This module contains receiver nodes D5–9 and bonefish nodes B3, B7–9 and B11. The Walk-Trap algorithm split Fast-Greedy module #1 (Fig. 4) into Walk-Trap modules #2 and #5

Table 2
Cross-tabulation of nodes assigned to modules by the Fast-Greedy/Multilevel and Walk-Trap community detection algorithms. Each element in the table represents the number of nodes in each of the 6 Walk-Trap modules present in each of the 5 Fast-Greedy/Multilevel modules. Fast-Greedy/Multilevel module #2 had significantly higher links to nodes within it than outside it ($p = 0.013$) and two modules were significant 'anti-communities', having more connections outside the module than within it (#3, $p = 0.012$; #5, $p < 0.0001$). Walk-Trap modules #1 and #6 were significant communities (#1, $p < 0.0001$; #6, $p = 0.013$).

		Walk-Trap modules					
		1	2	3	4	5	6
Fast-Greedy/Multilevel modules	1	0	3	0	0	4	0
	2	0	0	0	0	0	10
	3	22	0	0	0	0	0
	4	0	0	3	7	0	0
	5	16	0	0	0	0	0

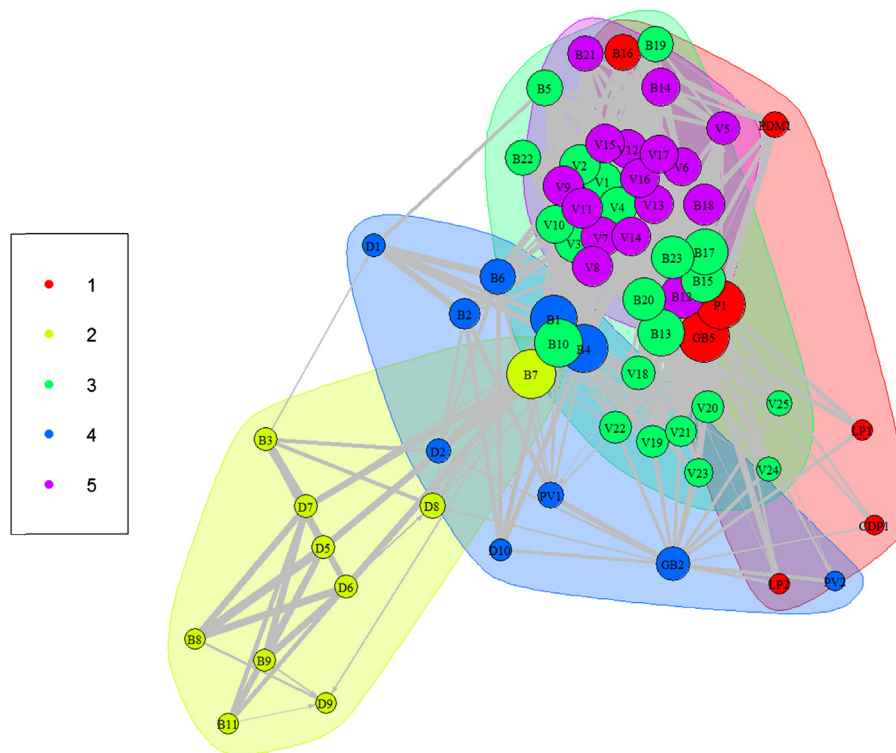


Fig. 4. Bipartite graph of Culebra fish network with five communities identified by both Multilevel and Fast-Greedy algorithms.

(Fig. 5), and Fast-Greedy module #4 (Fig. 4) into Walk-Trap modules #3 and #4 (Fig. 5). Finally, Walk-Trap lumped Fast-Greedy modules #3 and #5 (Fig. 4) into module #1 composed of all 25 receivers in the VPS array and 13 bonefish (Fig. 5; $p < 0.0001$, Wilcoxon sum rank test). The Fast-Greedy/Multilevel modules lumped by the Walk-Trap method were significant 'anti-communities', meaning that

there were significantly more connections to nodes outside each module than to nodes within them (Fig. 4, module #3, $p = 0.012$ and module #5, $p < 0.0001$). The Walk-Trap partition separated each great barracuda (GB2 and GB5) into their own modules (#5 and #3, respectively; Fig. 5) on different sides of the reef crest, and put the permit and a single bonefish together with a single receiver on the

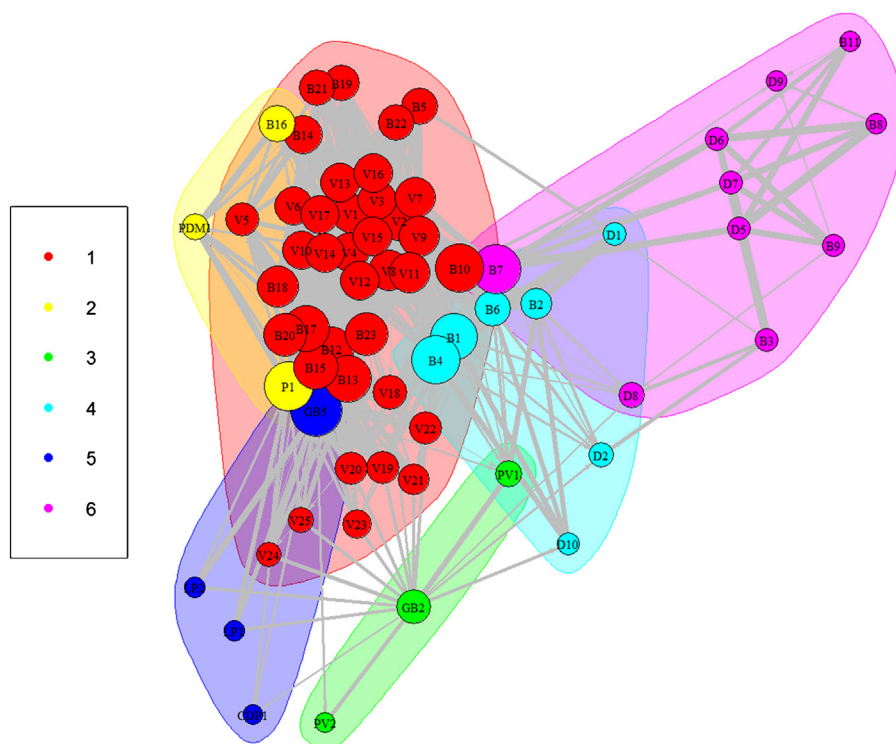


Fig. 5. Bipartite graph of Culebra fish network with six communities identified by the Walk-Trap algorithm.

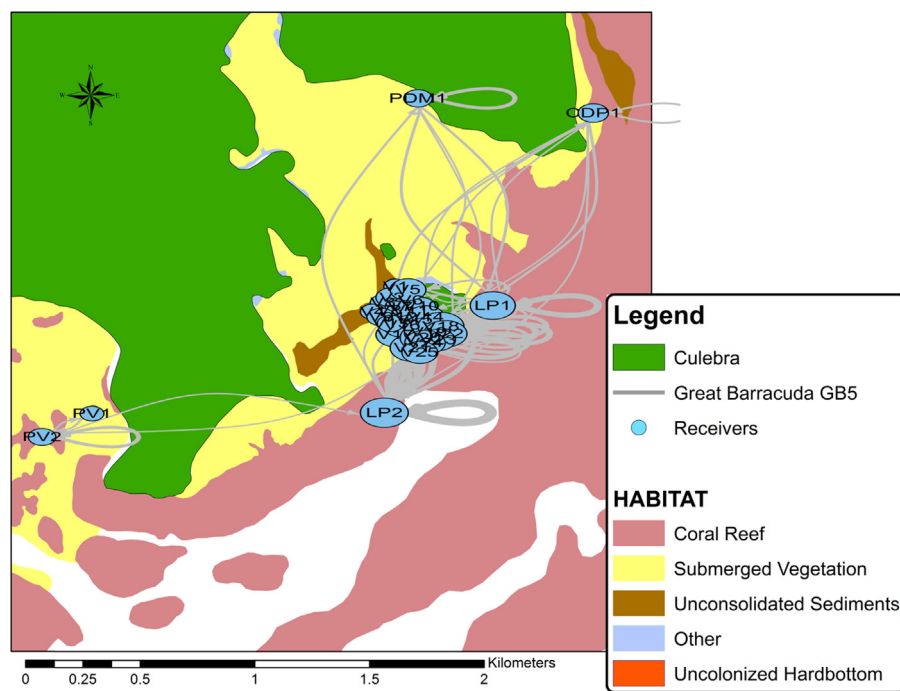


Fig. 6. Spatial graph for movement of a great barracuda (GB5) between receivers overlaid on coral reef habitat map. Circles (nodes) represent receivers (a node's size is proportional to its degree) and are placed according to their spatial location (UTM coordinates), and arrows (edges) represent movements between receivers (edge thickness is proportional to the number of movements). Edges that start and end at the same receiver represent two sequential detections at the same receiver. Habitat map is from Kendall et al. (2001).

north side of the lagoon (PDM1, Fig. 1). In the Walk-Trap partition there were two significant modules with no 'anti-community' modules, while the Fast-Greedy/Multilevel partition had a single significant module and two significant 'anti-community' modules. However, the Fast-Greedy/Multilevel partition had a higher modularity score (Table 1).

3.4. Spatial movement graphs

Fig. 6 shows movements of a great barracuda (GB5) over 6 months on the SE side of Culebra overlaid on a map of habitat (Kendall et al., 2001). The arrows correctly display direction of movement, but not the path (some paths appear to go overland). Arrows that loop from a node back to the same node indicate that the fish was detected next at the same receiver. It spent most of its time at receivers LP2 and LP1, and made forays to other sites. For example, it moved directly from both Las Pelas stations (LP1 and LP2) to station PDM1 but returned directly only to LP1 (and the VPS array; Fig. 6). It also made a single excursion from the VPS array to receivers PV2 and PV1 and then moved back to LP2. Fig. 7 shows a bonefish (B1) inhabiting the Dakity area for 194 days (Fig. 7A) and then moving to the VPS array on the Las Pelas reef flat for the last 5 days (Fig. 7B) before we downloaded the receivers. Unlike the great barracuda, bonefish B1 was not seen in areas further from shore (receivers D3, D4 and PV2 in the Dakity area [Fig. 7A] and receivers LP1 and LP2 in Las Pelas [Fig. 7B]).

4. Discussion

4.1. Degree distribution

Three types of graphs have different degree distributions (Dale and Fortin, 2010): (i) randomly connected networks have a binomial (or Poisson) degree distribution; (ii) scale-free networks,

including the world wide web and some social networks, have a degree distribution that follows a power law ($P(k) \sim k^{-\gamma}$, where γ is a constant); and (iii) small-world networks have an exponential degree distribution. Bipartite graphs (such as actors connected to the films they appear in) may also follow a Poisson degree distribution, but exceptions occur. Spatial networks are less likely to be 'small-world' networks, with long right-tailed degree distributions (i.e., many nodes with few edges and a few nodes, 'hubs', with a very high number of edges), and more likely to resemble regular graphs: each pixel (node) connected to its nearest neighbors (Urban et al., 2009). In this kind of network, most (if not all) of its nodes have a few connections (4 or 8), with no highly connected 'hubs' at all.

Many networks discussed in the literature of social network analysis are considerably larger than the receiver-tag network we have examined here. We had to contract our network in order to remove the effect of the VPS array on the degree distribution of the bipartite graph (Fig. 2). The degree distribution did not follow a binomial or Poisson distribution (Fig. 3), but the small number of nodes precluded testing more esoteric distribution models (e.g., Newman et al., 2001). The degree distributions for our network showed a complex pattern of peaks for both fish and receiver nodes (Fig. 3A), although the distribution for the graph with the VPS array lumped into two nodes was smoother, and almost Poisson. These were not regular graphs since the nodes were not regularly spaced throughout the study area.

4.2. Community detection

Of the six detection algorithms used on our bipartite graph, Multilevel and Fast-Greedy produced identical module partitions and had the best modularity scores (0.396, Table 1). The Walk-Trap algorithm produced a similar partition to the first two (Table 2; Figs. 4 and 5), with only a slightly lower modularity score (0.343, Table 1). All three of these algorithms produce modules that appear

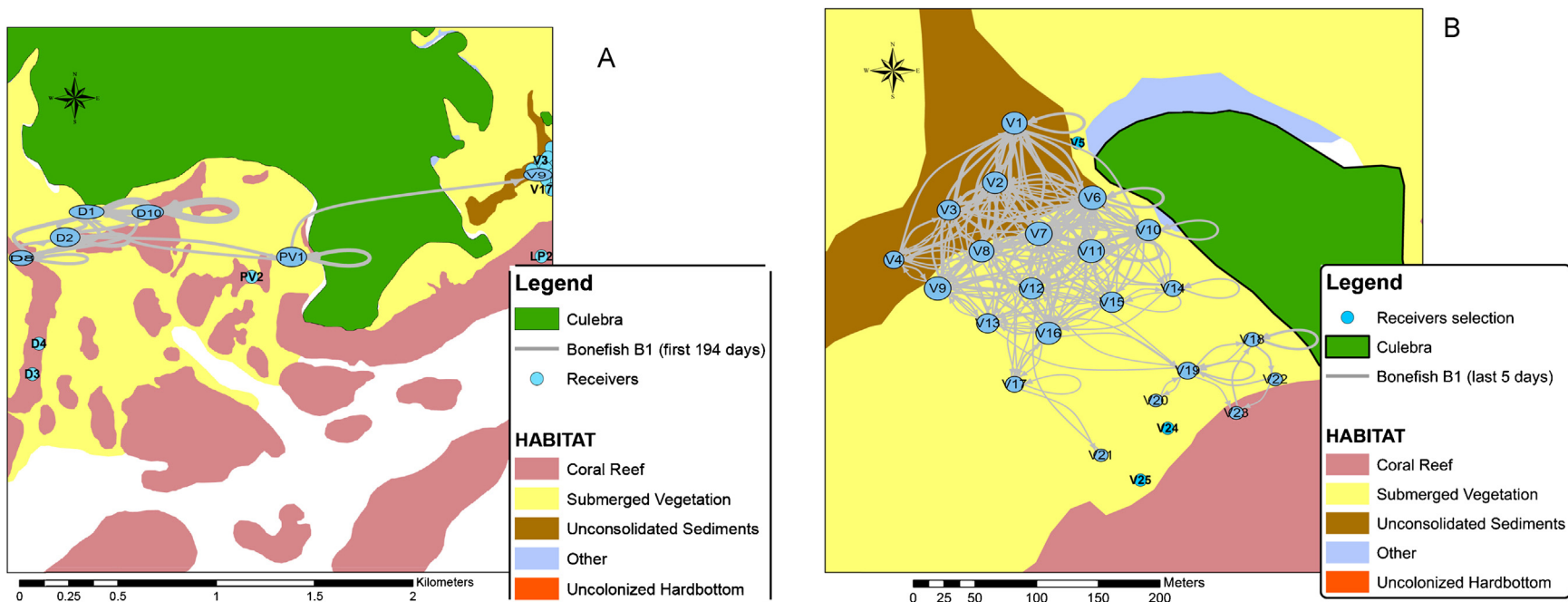


Fig. 7. Spatial graphs for movement of a bonefish (B1) between receivers overlaid on coral reef habitat map. (A) Graph of first 194 days tagged. (B) Graph of last 5 days tagged before data download. Circles (nodes) represent receivers (a node's size is proportional to its degree) and are placed according to their spatial location (UTM coordinates), and arrows (edges) represent movements between receivers (edge thickness is proportional to the number of movements). Edges that start and end at the same receiver represent two sequential detections at the same receiver. Habitat map is from Kendall et al. (2001). Receivers with no arrows entering or leaving did not detect this fish.

to reflect working hypotheses related to the coastal bathymetry, habitat types, and associated movement ecology of the tagged species. For instance, for bonefish, the Multilevel and Fast-Greedy algorithms produced module partitions (modules #2, #3 and #5, Fig. 4) that represent isolated reef flats where this species likely spends much of its time foraging. The products of these algorithms could also be used to demonstrate that there is potentially high site fidelity for bonefish at each of these reef flats. The Multilevel and Fast-Greedy algorithms also separated the bonefish detected by the VPS into primarily forereef (module #3) and lagoon (module #5) zones (module #3 lumps 5 lagoon receivers with the eight forereef receivers; Fig. 4). Significant anti-communities (modules #3 and #5) are revealed by the partitioning of the forereef and lagoon modules. Bonefish may also migrate to deeper habitats for seasonal spawning activities (Danylchuk et al., 2011), but this has only been documented in The Bahamas where the coastal bathymetry is quite different than that around the islands of the Caribbean basin. For permit and great barracuda, Multilevel, Fast-Greedy, and Walk-Trap generated module partitions that suggest somewhat different spatial ecologies for these species when compared to bonefish. Previous studies on great barracuda (O'Toole et al., 2011) as well as anecdotal information on permit indicate that these species have a greater likelihood of use of deeper coastal habitats on a regular basis, which may be the reason behind the associated module partitions (e.g., module #1 in Multilevel and Fast-Greedy, Fig. 4; modules #2 and #3 in Walk-Trap, Fig. 5). Based on our modeling exercise, the two great barracuda roamed over the same areas along the reef crest, but GB2 spent most of its time at receivers PV1 and PV2 and GB5 (Fig. 6) spent its time at the VPS array and at stations LP1, LP2 and CDP1. The permit (P1) spent its time in the VPS array and at PDM1 (similar to bonefish B16).

4.3. Technical challenges

Several technical challenges remain to be overcome. First, a different use metric, one that is more stable than detections (e.g., number of visits, or length of stay for each visit), might reduce effects of noise level differences between habitats. Determining when a fish has left the array (i.e., is not within range of any receiver) is essential in determining length of stay or number of separate visits. To illustrate the problem, if we look only at apparent non-movements (i.e., a fish was detected by the same receiver twice in a row) we get distributions of the apparent time spent at each receiver. Appendix Figures A3, A4 and A5 show the distribution of the length of stays at each receiver for a great barracuda (GB5), a bonefish (B1) and a permit (P1). The great barracuda had modes of times between detections at a node (Fig. A3) of less than 6 min for all stations except CDP1, with a mode of about 15 h. For the bonefish, the modes of times between sequential detections were all less than 30 min (Fig. A4). The permit had high modes of times between sequential detections for stations CDP1 and V25, over 4 h, while for the rest of the stations the modes were less than 15 min. If detection probability were constant, we could set a time threshold for when a fish must be heard in order to be considered still staying at a site. Unfortunately, detection probability changes with environmental conditions and the number of other tags in the neighborhood (Gjelland and Hedger, 2013). There is daily information in the receiver record on the number of tag signal collisions each receiver discarded that may help determine these probabilities (Espinoza et al., 2011). Future efforts should incorporate detection efficiency measures and adjust detection probabilities accordingly (Kessel et al., 2013).

The VPS array may detect a single coded pulse at several stations almost simultaneously. This allows exact X-Y location of the tag for that pulse. However, we need to treat the VPS array differently from the rest of the acoustic array in order to make the edge

weights mean the same thing for both VPS and other receivers. Assigning each precise X-Y fix to the closest receiver would remove the multiple counting of detections now in the data and allow all VPS receivers to be treated as a node within the broad scale array, as well as be used for fine-scale positioning.

Additional information is contained in these fish location data that we have not taken advantage of yet. For example, it may be possible to identify when fish are 'together', that is, at the same receiver simultaneously. A togetherness matrix would identify which individuals are together and when, and may allow analysis of association patterns as is done in social network analysis (e.g., Jacoby et al., 2012; Montgomery and Faloutsos, 2001). This may require the finer resolution VPS X-Y data, rather than the raw acoustic receiver data.

4.4. Landscape connectivity

The spatial graphs we produced for individual fish used receivers as nodes. More realistically, habitat patches would be nodes and edges would be the connections between patches actually observed to be used by the fish (Dale and Fortin, 2010; Grober-Dunsmore et al., 2009; Urban et al., 2009). Driezen et al. (2007) used telemetry data for hedgehog movement back to their home range after displacement to compare actual movement paths to paths predicted by a least cost model. Fletcher et al. (2012) looked at how well two social network models, a sender-receiver model (Hoff, 2005) and a latent space model (Hoff et al., 2002), predict landscape connectivity for two examples of observed movements. Both models predicted about 30% of the observed links, and did about as well with half or more of the data removed (our sampling of the full network of bonefish, barracuda and permit movement around Culebra is surely even sparser than that).

Biotelemetry tools are enabling ecologists to ask unique questions about social networks and interactions across a variety of spatial and temporal scales (Krause et al., 2013). How networks change through time and how to analyze such networks is an area of great interest both for ecologists (Blonder et al., 2012; Polansky et al., 2010) and social network analysts (Dorogovtsev and Mendes, 2002; Kossinets and Watts, 2006). For fish, the movement network may change because of patterns of wind, waves and tides that vary daily, monthly, seasonally and over the long term. The analytical techniques needed to advance the visualization and interpretation of telemetry-derived animal movement data exist but are only now beginning to be applied to marine fish data (Krause et al., 2013). The suite of analyses presented in this paper highlights the utility of network methods for revealing distinct patterns of habitat use and animal interaction, yet these patterns will still need to be evaluated based on their relevance to life history and ecological phenomena. Moving forward, we also encourage that the use of such models be linked to a priori hypotheses about the spatial ecology of marine fishes.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2013.12.014>.

References

- Blondel, V.D., Guillaume, J.-L., Lambiotte, R., Lefebvre, R., 2008. Fast unfolding of communities in large networks. *J. Stat. Mech.*, P10008.
- Blonder, B., Wey, T.W., Dornhaus, A., James, R., Sih, A., 2012. Temporal dynamics and network analysis. *Methods Ecol. Evol.* 3, 958–972.
- Boccaletti, S., Latora, V., Moreno, Y., Chavez, M., Hwang, D., 2006. Complex networks: structure and dynamics. *Phys. Rep.* 424, 175–308.
- Chakrabarti, D., Faloutsos, C., 2006. Graph mining: laws, generators, and algorithms. *ACM Comput. Surv.* 38, A1–A69.
- Clauset, A., Newman, M.E.J., Moore, C., 2004. Finding community structure in very large networks. *Phys. Rev. E* 70, 066111.
- Cooke, S.J., Hinch, S.G., Lucas, M.C., Luttcavage, M., 2012. Biotelemetry and biologing. In: Zale, A.V., Parrish, D.L., Sutton, T.M. (Eds.), *Fisheries Techniques*, third edition. American Fisheries Society, Bethesda, MD, pp. 819–860 (Chapter 18).
- Csardi, G., Nepusz, T., 2006. The igraph software package for complex network research. *InterJournal Complex Syst.* 1695, <http://igraph.sf.net> (15.07.13).
- Dale, M.R.T., Fortin, M.J., 2010. From graphs to spatial graphs. *Annu. Rev. Ecol. Evol. Syst.* 41, 21–38.
- Danylchuk, A.J., Cooke, S.J., Goldberg, T.L., Suski, C.D., Murchie, K.J., Danylchuk, S.E., Shultz, A.D., Haak, C.R., Brooks, E.J., Oronti, A., Koppelman, J.B., Philipp, D.P., 2011. Aggregations and offshore movements as indicators of spawning activity of bonefish (*Albula vulpes*) in The Bahamas. *Mar. Biol.* 158, 1981–1999.
- Dingle, H., 1996. *Migration: The Biology of Life on the Move*. Oxford University Press, New York.
- Dorogovtsev, S.N., Mendes, J.F.F., 2002. Evolution of networks. *Adv. Phys.* 51, 1079–1187.
- Driezen, K., Adriansen, F., Rondinini, C., Doncaster, C.P., Matthysen, E., 2007. Evaluating least-cost model predictions with empirical dispersal data: a case-study using radiotracking data of hedgehogs (*Erinaceus europaeus*). *Ecol. Modell.* 209, 314–322.
- Espinosa, 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. *Fish. Res.* 108, 364–371.
- Fang, Q., Huang, S., 2013. A directed network analysis of heterospecific pollen transfer in a biodiverse community. *Ecology* 94, 1176–1185.
- Fletcher, R.J., Acevedo, M.A., Reichert, B.E., Pias, K.E., Kitchens, W.M., 2012. Social network models predict movement and connectivity in ecological landscapes. *PNAS* 108, 19282–19287.
- Fruchterman, T., Reingold, E., 1991. Graph drawing by force-directed placement. *Softw. Pract. Exp.* 21 (11), 1129–1164.
- Gjelland, K.O., Hedger, R.D., 2013. Environmental influence on transmitter detection probability in biotelemetry: developing a general model of acoustic transmission. *Methods Ecol. Evol.* 4, 665–674.
- Grober-Dunsmore, R., Pittman, S.J., Caldwell, C., Kendall, M.S., Frazer, T.K., 2009. A landscape ecology approach for the study of ecological connectivity across tropical marine seascapes. In: Nagelkerken, I. (Ed.), *Ecological Connectivity among Tropical Coastal Ecosystems*. Springer Science+Business Media, Dordrecht, the Netherlands, pp. 493–530.
- Heupel, M.R., Webber, D.M., 2012. Trends in acoustic tracking: where are the fish going and how will we follow them? In: McKenzie, J., Parsons, B., Seitz, A., Kopf, R.K., Mesa, M., Phelps, Q. (Eds.), *Advances in Fish Tagging and Marking Technology*. American Fisheries Society, Symposium 76, 560 pp.
- Hoff, P.D., 2005. Bilinear mixed-effects models for dyadic data. *J. Am. Stat. Assoc.* 100, 286–295.
- Hoff, P.D., Raftery, A.E., Handcock, M.S., 2002. Latent space approaches to social network analysis. *J. Am. Stat. Assoc.* 97, 1090–1098.
- Humston, R., Ault, J.S., Larkin, M.F., Luo, J., 2005. Movements and site fidelity of bonefish (*Albula vulpes*) in the northern Florida Keys determined by acoustic telemetry. *Mar. Ecol. Prog. Ser.* 291, 237–248.
- Ireland, L.C., Barlow, R.B., 1978. Tracking normal and blinded *Limulus* in the ocean by means of acoustic telemetry. *Biol. Bull.* 155, 445–446.
- Jacoby, M.P., Brooks, E.J., Croft, D.P., Sims, D.W., 2012. Developing a deeper understanding of animal movements and spatial dynamics through the application of network analyses. *Methods Ecol. Evol.* 3, 574–583.
- Kanwisher, J., Lawson, K.D., Sundes, G., 1974. Acoustic telemetry from fish. *Fish Bull. U.S. Wildl. Serv.* 72, 251–255.
- Kendall, M.S., Monaco, M.E., Buja, K.R., Christensen, J.D., Krueger, C.R., Finkbeiner, M., Warner, R.A., URL: <http://ccma.nos.noaa.gov/products/biogeography/benthic/htm/manual.pdf>. Also available on U.S. National Oceanic and Atmospheric Administration. National Ocean Service, National Centers for Coastal Ocean Science Biogeography Program. 2001. (CD-ROM). Benthic Habitats of Puerto Rico and the U.S. Virgin Islands. Silver Spring, MD: National Oceanic and Atmospheric Administration 2001. (On-line). Methods Used to Map the Benthic Habitats of Puerto Rico and the U.S. Virgin Islands.
- Kessel, S.T., Cooke, S.J., Heupel, M.R., Hussey, N.E., Simpfendorfer, C.A., Vagle, S., Fisk, A.T., 2013. A review of detection range testing in aquatic passive acoustic telemetry studies. *Rev. Fish. Biol.* <http://dx.doi.org/10.1007/s11160-013-9328-4>, Published online 6 October.
- Klimley, A.P., Butler, S.B., 1988. Immigration and emigration of a pelagic fish assemblage to seamounts in the Gulf of California related to water mass movements using satellite imagery. *Mar. Ecol. Prog. Ser.* 49, 11–20.
- Kossinets, G., Watts, D.J., 2006. Empirical analysis of an evolving social network. *Science* 311, 88–90.
- Krause, J., Wilson, A.D.M., Croft, D.P., 2011. New technology facilitates the study of social networks. *Trends Ecol. Evol.* 26, 5–6.
- Krause, J., Krause, S., Arlinghaus, R., Psorakis, I., Roberts, S., Rutz, C., 2013. Reality mining of animal social systems. *Trends Ecol. Evol.* 28, 541–551.
- Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68, 619–640.
- Lucas, M.C., Baras, E., 2000. Methods for studying spatial behaviour of freshwater fishes in the natural environment. *Fish. Fish.* 1, 283–316.
- McKibben, J.N., Nelson, D.R., 1986. Patterns of movement and grouping of gray reef sharks, *Carcharhinus amblyrhynchos*, at Enewetak, Marshall Islands. *Bull. Mar. Sci.* 38, 89–110.
- Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D., Alon, U., 2002. Network motifs: simple building blocks of complex networks. *Science* 298, 824–827.
- Montgomery, A.L., Faloutsos, C., 2001. Identifying web browsing trends and patterns. *IEEE Comput. Sci.* 34 (7), 94–95.
- Murchie, K.J., Danylchuk, A.J., Cooke, S.J., O'Toole, A.C., Shultz, A., Haak, C., Brooks, E., Suski, E.C.D., 2012. Considerations for tagging and tracking fish in tropical coastal habitats: lessons from bonefish, barracuda, and sharks tagged with acoustic transmitters. In: *Handbook of Fish Telemetry*. American Fisheries Society Special Publication, Bethesda, MD, pp. 389–412.
- Murchie, K.J., Cooke, S.J., Danylchuk, A.J., Danylchuk, S.E., Goldberg, T.L., Suski, C.D., Philipp, D.P., 2013. Bonefish (*Albula vulpes*) movement patterns in tidal creeks and coastal waters of Eleuthera, The Bahamas. *Fish. Res.* 147, 404–412.
- Nathan, R., 2008. An emerging movement ecology paradigm. *PNAS* 105, 19050–19051.
- Newman, M.E.J., 2006. Finding community structure using the eigenvectors of matrices. *Phys. Rev. E* 74, 036104.
- Newman, M.E.J., Girvan, M., 2004. Finding and evaluating community structure in networks. *Phys. Rev. E* 69, 026113.
- Newman, M.E.J., Strogatz, S.H., Watts, D.J., 2001. Random graphs with arbitrary degree distributions and their applications Part 2. *Phys. Rev. E (Statistical Non-linear Soft Matter Physics)* 2, 026118.
- Orman, G.K., Labatut, V., 2009. A comparison of community detection algorithms on artificial networks. In: Gama, J., Santos Costa, V., Jorge, A., Brazdil, P. (Eds.), *Discovery Science, Lecture Notes in Computer Science*, vol. 5808, pp. 242–256.
- Ostfeld, R.S., 1990. The ecology of territoriality in small mammals. *Trends Ecol. Evol.* 5, 411–415.
- O'Toole, A.C., Danylchuk, A.J., Goldberg, T.L., Suski, C.D., Philipp, D.P., Brooks, E., Cooke, S.J., 2011. Spatial ecology and residency patterns of adult great barracuda (*Sphyrnaea barracuda*) in coastal waters of The Bahamas. *Mar. Biol.* 158, 2227–2237, <http://dx.doi.org/10.1007/s00227-011-1728-1>.
- Pautzke, S.M., Mather, M.E., Finn, J.T., Deegan, L.A., Muth, R.M., 2010. Seasonal use of a New England estuary by foraging contingents of migratory striped bass. *Trans. Am. Fish. Soc.* 139, 257–269.
- Pinter-Wollman, N., Hobson, E.A., Smith, J.E., Edelman, A.J., Shizuka, D., de Silva, S., Waters, J.S., Prager, S.D., Sasaki, T., Wittemyer, G., Fewell, J., McDonald, D.B., 2013. The dynamics of animal social networks: analytical, conceptual, and theoretical advances. *Behav. Ecol.* <http://dx.doi.org/10.1093/beheco/art047>.
- Polansky, L., Wittemyer, G., Cross, P.C., Tambling, C.J., Getz, W.M., 2010. From moonlight to movement and synchronized randomness: Fourier and wavelet analyses of animal location time series data. *Ecology* 91, 1506–1518.
- Pons, P., Latapy, M., 2006. Computing communities in large networks using random walks. *J. Graph Appl.* 10, 191–218.
- Raghavan, U.N., Albert, R., Kumara, S., 2007. Near linear time algorithm to detect community structures in large-scale networks. *Phys. Rev. E* 76, 036106.
- Reichart, J., Bornholdt, S., 2006. Statistical mechanics of community detection. *Phys. Rev. E* 74, 016110.
- R Core Team, 2012. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0 <http://www.R-project.org/>
- Schick, R.S., Loarie, S.R., Colchero, F., Best, B.D., Boustany, A., Conde, D.A., Halpin, P.N., Joppa, L.N., McClellan, C.M., Clark, J.S., 2008. Understanding movement data and movement processes: current and emerging directions. *Ecol. Lett.* 11, 1338–1350.
- Simpfendorfer, C.A., Heupel, M.R., Hueter, R.E., 2002. Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. *Can. J. Fish. Aquat. Sci.* 59, 23–32.
- Song, J., Singh, M., 2013. From hub proteins to hub modules: the relationship between essentiality and centrality in the yeast interactome at different scales of organization. *PLOS Comput. Biol.* 9 (2), e1002910.
- Tamassia, R., 2010. *Handbook of Graph Drawing and Visualization*. Chapman and Hall, London.
- Urban, D.L., Minor, E.S., Tremblay, E.A., Schick, R.S., 2009. Graph models of habitat mosaics. *Ecol. Lett.* 12, 260–273.
- Wilson, R.P., Quintana, F., Hobson, V.J., 2012. Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proc. Royal Soc. B* 279, 975–980.