



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



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ARTICLE INFO

Article history:

Available online 10 January 2014

Keywords:

Acoustic tagging
Fish movement
Social network analysis
Bipartite graphs
Directed graphs

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, *Sphyræna 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

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