

Network analyses reveal intra- and interspecific differences in behaviour when passing a complex migration obstacle

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Summary

1. Network theory offers new perspective on movement data by evaluating the relationships between animal movements (links) and detection locations (nodes) in spatially complex systems, including human-altered landscapes.
2. We applied network analyses to intra- and interspecific movement patterns in the migration behaviour and dam passage success of two anadromous fish species, Pacific lamprey *Entosphenus tridentatus* Gairdner and Chinook salmon *Oncorhynchus tshawytscha* Walbaum, when moving through a large multifishway hydroelectric project (Bonneville Dam, USA).
3. Network analyses revealed greater variation in movement for Pacific lamprey compared with Chinook salmon. Salmon that passed the dam had networks consisting of more direct passage routes with fewer overall movements compared with lamprey that passed the dam. Lamprey that did not pass the dam exhibited a wide range of behaviours, from approaching only one fishway site to testing all possible passage routes. Accounting for the time spent in the network improved the ability to detect biological differences in network structure for lamprey that did and did not pass the dam.
4. The movement patterns likely resulted from different behavioural responses to complex environmental and internal factors affecting a philopatric species (Chinook salmon) vs. a non-philopatric species (Pacific lamprey) when moving through an engineered environment designed primarily for salmon.
5. *Synthesis and applications.* Our case study highlights the potential for network analyses to link questions of basic movement ecology with monitoring of movement and behaviour in human-altered landscapes. Network analyses can thus serve as a valuable tool for describing movement and behaviour in the face of environmental change and assessing the effectiveness of mitigation efforts at spatially complex obstacles to animal movement.

Key-words: altered landscapes, animal movement, barriers, fish passage, lamprey, migration, network analyses, salmon, spatial dynamics, telemetry

Introduction

Recent advancements in biotelemetry have improved the ability to track and quantify animal movements, which has been critical for elucidating new patterns of animal behaviour (Cooke *et al.* 2004; Cagnacci *et al.* 2010). Technological advances have also spurred development of new conceptual approaches for analysing movement (e.g. Nathan *et al.* 2008). However, variability is a hallmark of animal movement and telemetry data sets can often be

large and difficult to analyse with traditional statistical techniques that may leave potentially valuable biological information underutilized (Jacoby *et al.* 2012; Bestley *et al.* 2013). As a result, the application of new mathematical and statistical approaches has provided novel opportunities for ecologists to interpret movement data more comprehensively, particularly for species that move over large spatiotemporal scales or through complex landscapes (Schick *et al.* 2008; Morales *et al.* 2010; Finn *et al.* 2014).

In the last decade, ecologists have begun using network theory to quantify spatial movements. Network theory is a component of graph theory, which characterizes the size, connectivity and topology of spatial systems based

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on interactions between network components. A network is composed of nodes and edges, where nodes represent a location, population or individual, while an edge represents an interaction between nodes (Wey *et al.* 2008; Eros *et al.* 2012; Jacoby *et al.* 2012). Network analyses have been applied to various ecological questions such as understanding metapopulation structure (Fortuna, Gomez-Rodriguez & Bascompte 2006) and the influence of landscape connectivity on habitat conservation (Galpern, Manseau & Fall 2011). Network analyses have also recently been used to describe animal movements at the individual level (Jacoby *et al.* 2012; Finn *et al.* 2014). To our knowledge, network analyses have not been used to summarize individual movement patterns at the population level or for direct hypothesis testing, both of which are crucial for identifying the mechanisms that explain larger patterns of movement (Cagnacci *et al.* 2010). The purpose of this study was to explore the application of network analyses for evaluating movement behaviour within and between two migratory fish species at a migration obstacle (a hydroelectric dam with upstream passage facilities) as a case example.

Pacific lamprey and Chinook salmon share semelparous and anadromous life histories (Spice *et al.* 2012; Keefer & Caudill 2014). The two taxa also exhibit important differences in migration behaviour and passage ability that make them good models for a comparative application. Whereas Pacific salmonids generally exhibit a strong philopatric migration strategy with high motivation to overcome barriers and reach upstream spawning sites (i.e. natal homing; Keefer & Caudill 2014), evidence suggests that Pacific lamprey do not home to natal streams (Spice *et al.* 2012) and that migration distance is influenced by a combination of body size and genetics (Keefer *et al.* 2009; Hess *et al.* 2014). On the Columbia River, Chinook salmon pass large dams much faster (<2 days; Keefer *et al.* 2004) than Pacific lamprey (4–6 days; Moser *et al.* 2002) and dam passage success is nearly twice as high for Chinook salmon compared with Pacific lamprey (>95% vs. *c.* 50%, respectively; Moser *et al.* 2002; Keefer *et al.* 2013).

In order to determine the potential for network analyses to monitor movements in altered landscapes, we evaluated both interspecific (i.e. Chinook salmon vs. Pacific lamprey) and intraspecific (i.e. morphological traits) patterns in movement to test hypotheses about the complex set of mechanisms causing differences in passage at a migration obstacle. Since Pacific lamprey exhibit non-philopatric behaviours and have lower passage rates, we hypothesized that lamprey would exhibit greater variation in their movement patterns at the dam compared with Chinook salmon (i.e. that they would 'mill' while searching for a suitable passage route). We also evaluated how the movement patterns of fish differed based on body size, migration timing and dam passage outcome (passed or did not pass). We conclude by discussing potential applications of network analyses in animal movement studies of human-altered landscapes.

Materials and methods

STUDY SITE AND DATA COLLECTION

We monitored the movements of Pacific lamprey and Chinook salmon at Bonneville Dam (45.6°N, 121.9°W) on the lower Columbia River, USA. The dam is the first hydropower project on the Columbia River [river kilometre (rkm) 235 from the Pacific Ocean] encountered by anadromous fishes during upstream spawning migrations. The dam has two powerhouses and one spillway, each separated by islands (Fig. 1a). Below the dam is a 1–2 km long tailrace with relatively turbulent conditions associated with outflow from the spillway and turbines. The fishways at Bonneville Dam are complex because there are multiple, branched routes for ascending the dam. Notably, all passage routes had similar lower fishway sections with low gradient (entrance-collection channel-transition area), a steeper (1 : 10 slope) gradient pool-and-weir fish ladder, and an upper fishway section with counting stations, vertical slot weirs and exits.

The dam has a total of eight primary fishway entrances, four primary passage routes and two exits. Powerhouse 1 (PH1) has two entrances leading to the Bradford Island fishway (Fig. 1c). There are two entrances flanking the spillway channel (SP). The south entrance of the spillway is adjacent to Bradford Island and leads to the fishway exit on the Oregon shore, while the north entrance adjacent to Cascades Island leads fish to the Washington shore fishway exit (Fig. 1d). Powerhouse 2 (PH2) has four entrances leading to the Washington shore fishway (Fig. 1b).

Tagging protocols have been described previously for both Pacific lamprey (Moser *et al.* 2002; Johnson *et al.* 2012) and Chinook salmon (Keefer *et al.* 2004; Caudill *et al.* 2007). Briefly, Pacific lamprey were collected at night from May to August of 2010 using traps situated adjacent to fishway weirs in the Adult Fish Facility (AFF) on the Washington shore ladder. Lamprey were anesthetized using eugenol (4–5 mL solution per 50 L water) and were measured for body length, weight and girth. A small incision was made on the ventral side of the body nearly parallel to the first dorsal fin. A radiotransmitter (8 mm by 18 mm and 2.1 g; Lotek Wireless, Newmarket, ON, Canada) was inserted into the body cavity, and incisions were closed with sutures. Lamprey were allowed to recover in holding tanks for 8–12 h before being released at dusk approximately 3 km downstream of Bonneville Dam at two sites, one on the Washington and one on the Oregon shore.

Chinook salmon were sampled at the Washington shore AFF during April–July of 2010. Salmon were anesthetized using eugenol (22 mL solution L⁻¹ water) and measured for total length, weight and sex, and identified as either natural or hatchery origin based on presence/absence of adipose fins (hatchery = 155, wild = 85). Preliminary analyses revealed that sex and origin were not significantly associated with network structure and were excluded from further analyses. Salmon were gastrically implanted with a radiotransmitter (8.3 cm by 1.6 cm and 29 g; Lotek Wireless) and recovered (4–8 h) in a 2275-L oxygenated tank prior to release approximately 7 km downstream of Bonneville Dam at sites on the Washington or Oregon shore.

Fish movements were monitored using an extensive array of aerial and underwater radioreceivers at the dam and at downstream receiver 'gates' in the tailrace. Radiotransmitters emitted digital signals every 5–8 s that were unique to individual fish.

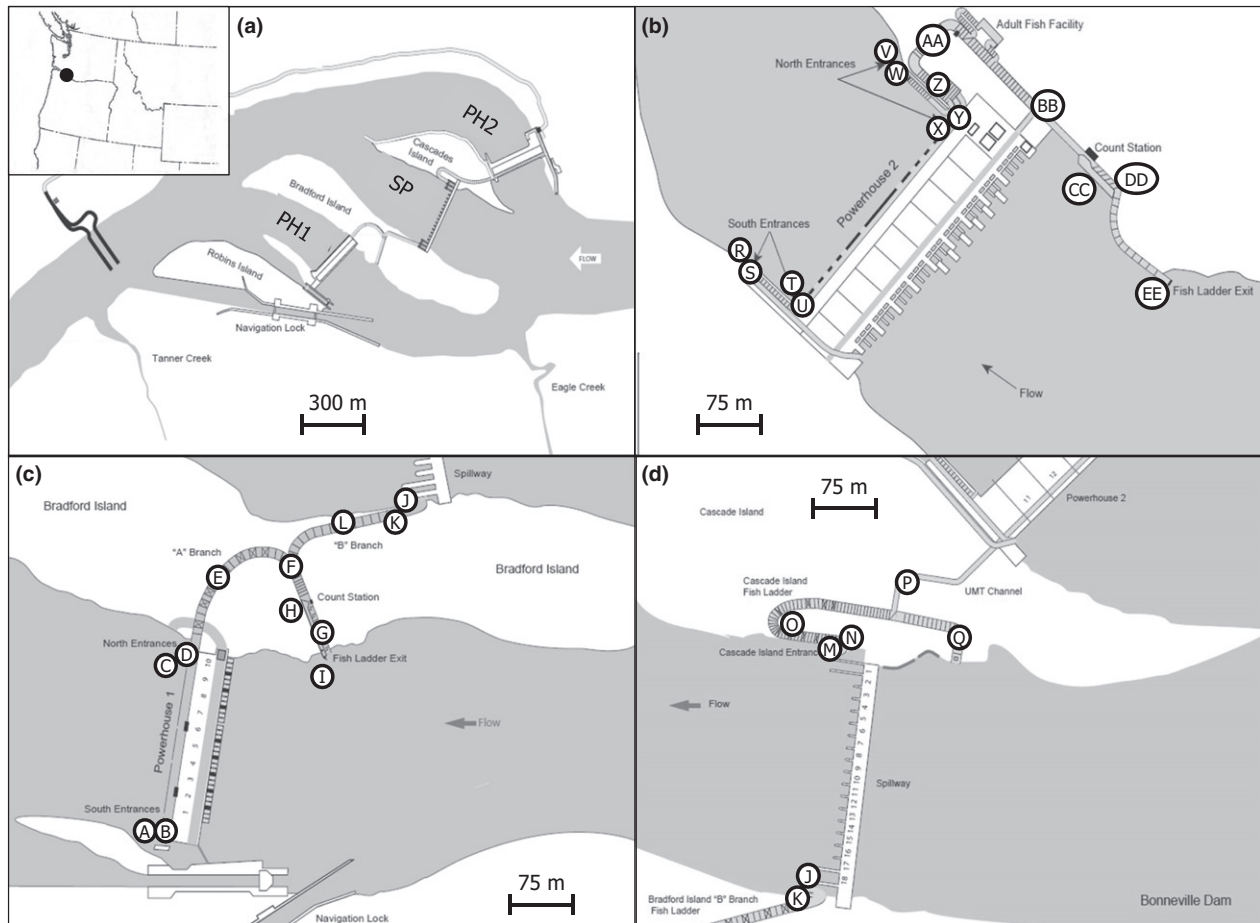


Fig. 1. Map of (a) Bonneville dam on the Columbia River border of Washington-Oregon showing all of the monitored locations in the (b) Washington shore Powerhouse-2 (PH2), (c) Bradford Island Powerhouse 1 (PH1) and (d) Cascade Island fishway.

Multiple receivers along fishway segments produced detection efficiencies of 95–100% for each site (Keefer *et al.* 2004). However, any missed detections that could be reasonably inferred were subsequently entered (e.g. movements along linear pathways). Detection histories of individual fish at each receiver were assigned a time-stamped activity code to describe the behaviours at each site (e.g. approach at a fishway entrance, first fishway entrance). The movements between sites were defined as either upstream (entrance towards exit), downstream (exit towards entrance) or between fishway entrances (entrance to entrance). Outcomes of all passage histories were classified as either ‘Pass’ or ‘Did not pass’.

We calculated the ‘time in network’ of individual fish to compare the spatial movements at Bonneville Dam with a temporal element of movement. We also aimed to statistically control for the time fish spent in the network since we expected measures of network size and connectivity to increase with increasing time in the network. Time in network for fish that passed the dam was calculated from the time of first approach at a fishway entrance until the time of last detection (i.e. passage time). Time in network for fish that did not pass the dam was conservatively calculated from the time of first approach until the time of last known detection. Any fish that passed and were subsequently redetected downstream of Bonneville Dam were classified as ‘fallbacks’ (Boggs *et al.* 2004), and only movements from the first upstream passage event were included.

NETWORK ANALYSES

Two hundred and fifty-five Pacific lamprey and 240 Chinook salmon were randomly selected for analysis from a sample of 285 lamprey and 600 salmon in a 2010 radiotelemetry study. The subsample of lamprey excluded 30 individuals with no records at Bonneville Dam, a rate typical for Pacific lamprey radiotelemetry studies (Moser *et al.* 2002), and the subsample of salmon was selected to provide an approximately balanced sample size. The system of fishways at Bonneville Dam was treated as the network of interest. In this study, monitored fishway locations were defined as nodes and fish movements were defined as edges, which were classified as either upstream, downstream or between entrances.

The network included 30 nodes for salmon, with one node representing the release locations, 28 nodes at fishway locations and one node indicating successful passage or not. The network for lamprey was identical with the exception of three nodes, which monitored flow-control areas that had lamprey passage structures (LPS; Moser *et al.* 2011) at the top of each fishway. The LPSs provided a short, alternative ‘branch’ for lamprey to exit compared with the traditional exit, which meant lamprey had networks with 33 total nodes. Although 25.4% of lamprey passing Bonneville Dam used the LPS route (30 of 118 passing lamprey), analyses censoring lamprey using these routes revealed no significant differences in network structure that would confound our

comparisons between species. Note for both species, the network became increasingly constrained moving upstream (i.e. only a single upstream and downstream edge was possible in the upper fishways).

Fish detection histories were analysed using CYTOSCAPE (version 2.8.3, developed by the Institute for Systems Biology, Seattle, WA, USA), an open-source network program designed for molecular and bioinformatics use, but applicable to other network analyses (Shannon *et al.* 2003; Smoot *et al.* 2011). Network maps were constructed, and we visually reviewed the movement paths for all fish individually to ensure accuracy in network construction. The 'network analysis' plugin (Shannon *et al.* 2003) was then used to calculate quantitative metrics of network structure for individual fish.

We selected five metrics to characterize individual movements at the dam. Each metric described a particular element of either network size or network connectivity relevant to the movements of fish. The first metric, *diameter*, was the path length with the greatest number of edges between any two nodes in the network (Wey *et al.* 2008; Jacoby *et al.* 2012). Diameter was an estimate of network size and described the route length of fish.

The second and third metrics described very similar elements of connectivity and were related to the total number of edges (i.e. total number of connections between nodes) exhibited across the network. The *average number of neighbours* was defined as the number of edges for each node in the network divided by the total number of nodes in the Bonneville Dam network (Smoot *et al.* 2011), which measured the average connectivity of each node and served as an indicator of the number of movements exhibited across sites. Similarly, *network density* was the number of edges in the network divided by the total number of edges possible in the network (Wey *et al.* 2008), which also served as an indicator for the extent of travel across the network.

The fourth metric, the *number of multi-edge node pairs*, was the number of node pairs in the network that shared more than one edge (Smoot *et al.* 2011). This metric described the linearity of movements (i.e. $A \rightarrow B \rightarrow C$ vs. $A \leftrightarrow B \leftrightarrow C$) and how frequently fish moved between the same sites (e.g. moving upstream to a new site, then downstream to the previous site). This metric was not only associated with higher rates of connectivity and movement, but also indicated possible milling behaviours between adjacent sites.

Finally, we calculated an *edge to diameter ratio* (number of edges divided by the network diameter) for individual fish that compared the number of movements standardized by a measure of path length. Higher ratios were indicative of passage routes composed of more movements and thus indicated potential exploration or milling behaviours. Important to note is that although individual fish may have made the same movements between the same nodes multiple times, network metrics did not account for multiple movements along the same path and thus may underestimate milling.

STATISTICAL ANALYSES

We used analysis of variance (ANOVA) to test for differences in network metrics for the passage outcomes of each species (Chinook salmon that passed the dam, Pacific lamprey that passed the dam, Pacific lamprey that did not pass the dam). Chinook salmon that did not pass the dam were excluded due to a small sample size ($n = 4$). *Post hoc* Tukey's 'honestly significant

difference' (HSD) tests were used to test for further mean differences between the three outcome groups.

We also employed multiple regression analysis to test whether biological covariates within each species were associated with network metrics. The multiple regression model for Pacific Lamprey was:

$$\text{Metric} = \text{outcome} + \text{body length} + \text{tag date} + \text{time in network} + \text{outcome} \times \text{time in network}$$

where a separate analysis was run with the same model for each of the five metrics. We included lamprey body length in our model because larger lamprey reach upstream sites more frequently (Keefer *et al.* 2009; Hess *et al.* 2014). The model also included tag date (indicator of migration timing and seasonal environmental conditions) and \log_e (time in network) to control for potential variation in these factors. The outcome \times time in network interaction tested whether metrics increased at the same rate with time in network for the different outcome groups. The model for Chinook salmon was similar, but excluded outcome and the outcome \times time in network given the low number of salmon that did not pass the dam. Variance inflation factors (VIF) indicated acceptable levels of collinearity among the selected predictor variables (all VIF's were < 3 ; Zuur, Ieno & Elphick 2010). Network metrics were \log_e -transformed to meet the assumption of normality in the residuals. All analyses were completed using generalized linear models in R, version 3.0.3 (R Development Core Team 2014), and the significance level for all tests was set at $\alpha = 0.05$.

Results

A movement path for a single Pacific lamprey is provided in Fig. 2 to illustrate the complexity of movements exhibited by fish at Bonneville Dam. Additional movement paths of two Pacific lamprey and two Chinook salmon, all of which are representative of the average body size and migration timing for these species, are provided in the supporting information to illustrate how these network metrics captured different patterns of movement (see Fig. S1, Table S1, Supporting information).

Variation in movement was higher for Pacific lamprey compared with Chinook salmon, and movement patterns were associated with passage outcome for each species. Of the 240 salmon that were detected approaching a fishway entrance, 236 passed the dam (98.3%). The four salmon that did not pass had similar network characteristics composed of short path lengths and very few movements (i.e. few edges; Fig. 3a,c). In contrast, only 118 of the 255 lamprey that approached an entrance passed the dam (46.3%) and the variation in network diameter and number of edges was high for the 137 lamprey that did not pass (Fig. 3b,d).

Movements were more frequent, and passage routes were more circuitous for lamprey that passed the dam compared with salmon. Mean network diameter differed between the three groups ($F_{2,488} = 261.40$, $P < 0.001$) with salmon and lamprey that passed having longer passage routes than lamprey that did not pass (Fig. 4a), partially

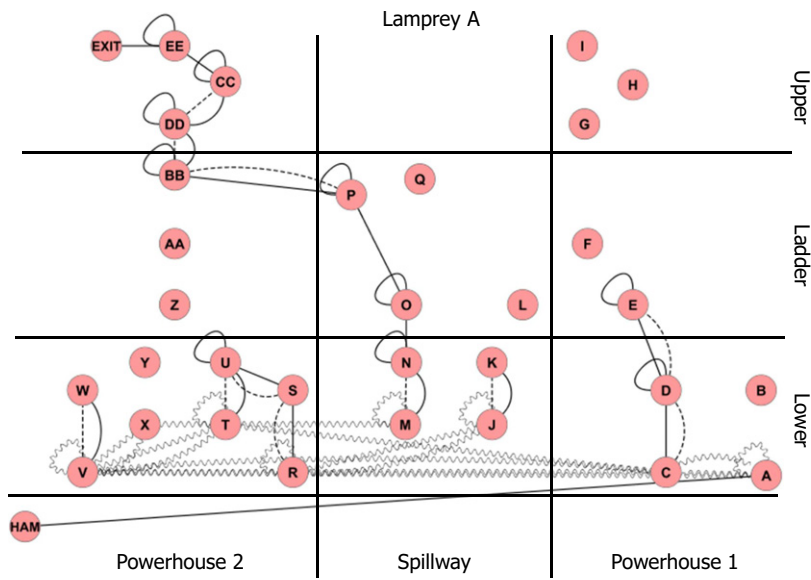


Fig. 2. Top-down illustration of a Pacific lamprey movement path through Bonneville dam. Black lines separate the three channels at Bonneville Dam (Powerhouse 1, Spillway, Powerhouse 2) and the fish-way sections (lower, ladder, upper). HAM represents the release location downstream of the dam, and EXIT indicates the last detection at the dam. Solid edges indicate upstream movements, dashed edges indicate downstream movements, and sinusoidal edges indicate between-entrance movements. Loops at each site indicate locations where fish were repeatedly detected more than once. [Colour figure can be viewed at wileyonlinelibrary.com]

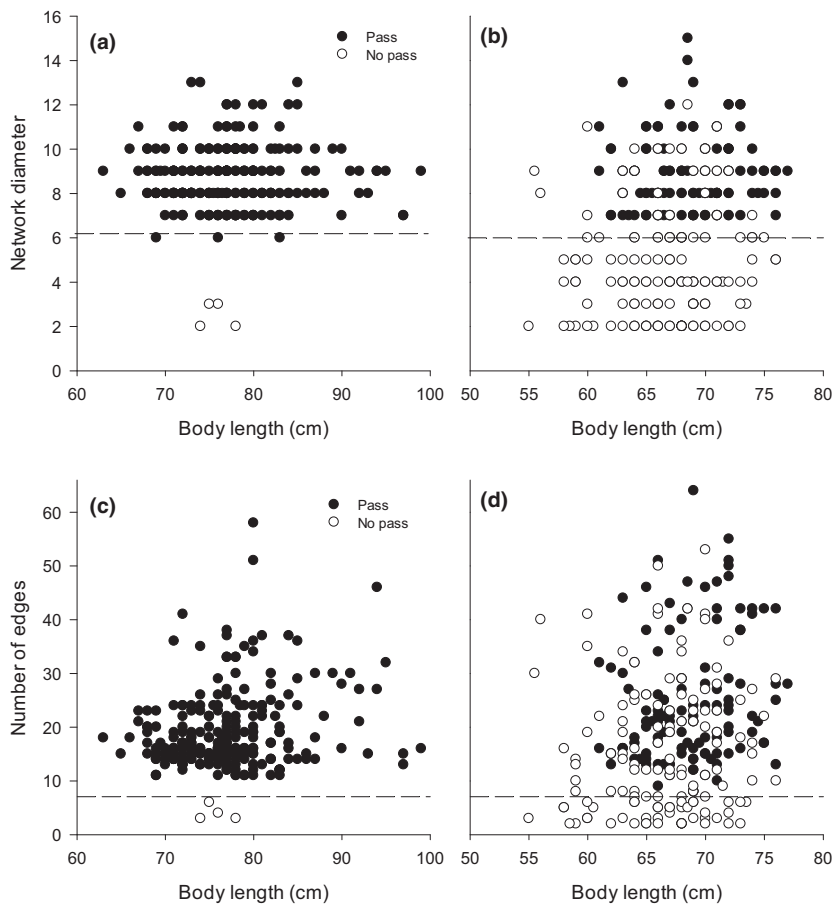


Fig. 3. Relationships between network diameter, number of edges and body length for Chinook salmon (a and c) and Pacific lamprey (b and d) sorted by fish that passed and did not pass Bonneville Dam. Dashed horizontal lines indicate the minimum number of movements and the minimum diameter required to pass the dam.

because successful passage required a higher minimum diameter. Average number of neighbours ($F_{2,488} = 66.23$, $P < 0.001$) and network density ($F_{2,488} = 77.17$, $P < 0.001$) indicated more movements across sites for lamprey that passed and salmon compared with lamprey that did not pass (Fig. 4c), again a potential artefact of larger networks

being required for successful passage. The mean number of multi-edge node pairs differed between all three groups ($F_{2,488} = 13.34$, $P < 0.001$) with lamprey that did pass the dam having more circuitous routes, while salmon exhibited more direct passage routes across the dam (Fig. 4b). Finally, the edge: diameter ratio differed between the three

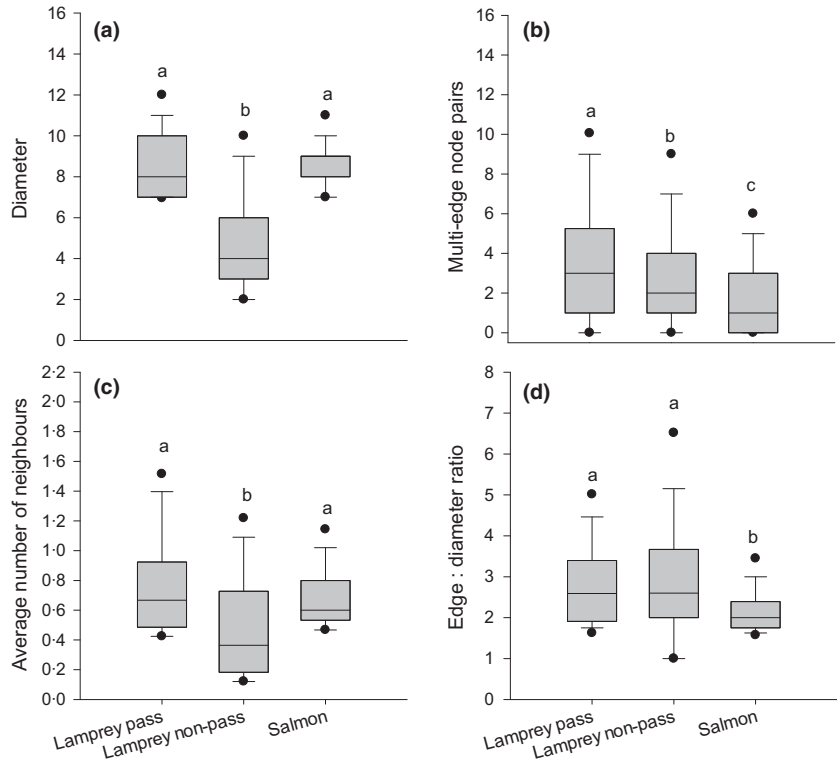


Fig. 4. Comparison of (a) network diameter, (b) multi-edge node pairs, (c) average number of neighbours and (d) edge to diameter ratio for Chinook salmon, Pacific lamprey that passed Bonneville Dam and Pacific lamprey that did not pass Bonneville Dam. Letters indicate significantly different groups based on Tukey’s honestly significant difference ($P < 0.05$). Box plots show 5th, 10th, 25th, 50th, 75th, 90th and 95th percentiles.

groups ($F_{2,488} = 17.28$, $P < 0.001$) with ratios lower for salmon compared with lamprey of both outcome groups (Fig. 4d). The coefficient of variation in the edge: diameter ratio was also lower for salmon ($CV = 0.31$) compared with lamprey that did ($CV = 0.40$) and did not pass ($CV = 0.53$), indicating greater consistency in Chinook salmon movements.

Comparisons within Pacific lamprey revealed passage outcome was a significant predictor for models with all five network metrics (all $P \leq 0.007$; Table 1) and that models explained anywhere from 28% to 62% of the

observed variation. Time in network was a significant predictor for all network metrics (all $P < 0.001$), indicating that longer times at the dam corresponded to higher network metrics. Interestingly, the direction of the effect switched for several metrics after accounting for the time in network, which improved the ability to detect biological patterns within outcome groups. For example, the effect of outcome on the number of multi-edge pairs and the edge: diameter ratio was reversed for the multiple regression results (metrics were higher for lamprey that did not pass; Table 1). Specifically, the outcome \times time

Table 1. Multiple regression results (β = coefficient, P = whether β was significantly different from 0 at $\alpha = 0.05$) for five network metrics and the predictor variables (outcome, body length, tag date, time in network) for Pacific lamprey and Chinook salmon. Outcome comparison is passed: did not pass (i.e. positive coefficient indicates higher metric values for lamprey that passed)

	Network metrics									
	Diameter		Network density		Average number of neighbours		Multi-edge node pairs		Edge: diameter ratio	
	β	P	β	P	β	P	β	P	β	P
Pacific lamprey ($n = 255$)										
Outcome	0.283	<0.001	0.144	<0.001	0.162	<0.001	-0.413	0.007	-0.648	0.005
Length	-0.001	0.746	<0.001	0.931	0.001	0.808	-0.002	0.884	0.021	0.260
Date	0.001	0.173	<-0.001	0.377	<-0.001	0.327	-0.001	0.946	-0.007	0.036
Time	0.095	<0.001	0.134	<0.001	0.141	<0.001	0.388	<0.001	0.525	<0.001
Outcome \times Time	-0.027	0.301	0.032	0.390	0.019	0.606	0.528	<0.001	0.218	0.303
Chinook salmon ($n = 236$)										
Length	-0.001	0.200	<0.001	0.470	<0.001	0.490	0.009	0.304	0.013	0.038
Date	0.001	<0.001	0.002	<0.001	0.002	<0.001	0.015	<0.001	0.059	<0.001
Time	0.005	<0.001	0.015	<0.001	0.014	<0.001	0.065	<0.001	0.013	<0.001

Bolded values are significant ($P < 0.05$).

in network interaction indicated that individuals who did not pass and had very short times in network (<3 h) were frequently observed moving between many locations within the lower fishway (Fig. 5). Hence, many non-passing lamprey had passage histories with a high degree of activity (i.e. ‘milling’ behaviours) while spending only a short time in the network. Contrary to expectations, lamprey body size was not a significant predictor for network metrics (all $P \geq 0.260$).

Multiple regression models for each network metric of Chinook salmon had lower explanatory power compared with Pacific lamprey ($0.13 \leq R^2 \leq 0.34$), partially because behaviours were less variable overall. Salmon body size was not statistically associated with network metrics, except for the edge: diameter ratio ($P = 0.038$), where smaller bodied salmon had passage routes composed of shorter path lengths and fewer movements compared with larger salmon. Time in network and tag date also had significant, positive relationships with all network metrics (all $P < 0.001$; Table 1), whereby late-migrating salmon exhibited more movements across sites compared with early-migrating salmon.

Discussion

We evaluated the behaviours of two migratory fish species to demonstrate the strength of network analyses for developing population-level inferences about movement with an example from a human-altered landscape. One of the most frequently cited threats to migratory fish are anthropogenic barriers, and the installation of fish passage systems at dams world-wide has been a primary mediation tool for this problem (Clay 1995). Although monitoring of migratory fish at dams is common, dams can be complex spatial systems and traditional metrics to monitor passage, such as ‘efficiency’ or ‘passage time’ may overlook important elements of passage behaviour (Boggs *et al.* 2004; Caudill *et al.* 2007; Bunt, Castro-Santos &

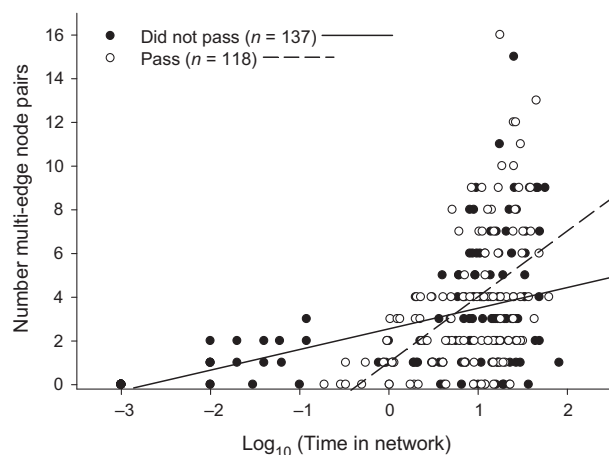


Fig. 5. Relationship between the number of multi-edge node pairs and log-transformed time in network for Pacific lamprey that passed and did not pass the dam.

Haro 2012; Piper *et al.* 2015). In particular, spatial elements of passage behaviours are not well captured by traditional metrics and spatial analyses of movement may provide new insight into behaviour at these and other obstacles to movement.

Network analyses provided new metrics for quantifying elements of migration behaviour associated with low rates of passage for Pacific lamprey. Previous studies have shown that performance-related mechanisms associated with limited swimming capacity (e.g. burst-swimming speed), structural impediments and environmental factors may explain the low passage rates observed for Pacific lamprey at Columbia River dams compared to salmon (Keefer *et al.* 2010, 2013; Johnson *et al.* 2012; Kirk *et al.* 2015). While large variation has been previously documented in the migration rates and passage times of Pacific lamprey (Moser *et al.* 2002, 2013), the variability in movement reported herein was directly associated with outcome, whereby non-passing lamprey had networks of smaller size and fewer movements, contrary to expectations for higher milling by unsuccessful individuals.

Migration involves a complex interplay of factors, including effects of both environment and internal condition (Dingle & Drake 2007). Thus, a number of mechanisms may have contributed to the observed differences in movement patterns, including differences in migration behaviour, mortality, predation susceptibility, movements out of the study system and observational error. While the challenging monitoring environment left the final fate of non-passing lamprey ambiguous, some non-passing lamprey do move downstream to spawning tributaries. For instance, 6.1% of non-passing lamprey herein were detected at the largest downstream spawning tributary in this study (Willamette River) and recent monitoring has revealed lamprey overwintering below lower Columbia River dams prior to moving downstream and into spawning tributaries in the following spring (Noyes 2013). Although potential predation by white sturgeon (see Kirk *et al.* 2015) and marine mammals is unknown and may have been responsible for non-passage of some lamprey, most pinniped predators depart prior to the lamprey migration and application of rates observed for salmon (Keefer *et al.* 2012) cannot fully account for the number of observed non-passing lamprey. Future biotelemetry studies (see Cooke *et al.* 2004) are warranted to refine the final fate of non-passing lamprey and determine how movement at dams and passage ‘failure’ is related to these additional mechanisms.

Nonetheless, the observed variation in network structure between lamprey and salmon likely results in part from interspecific differences in the migration behaviours in response to internal and external cues during passage. The non-philopatric behaviour of lamprey may confer greater plasticity in the behavioural processes that determine migratory decisions (Waldman, Grunwald & Wirgin 2008; Spice *et al.* 2012). This behavioural plasticity could be associated with traits responding to previous passage

experiences (e.g. tagging effects), maturation status, boldness or predation risk (Sih, Bell & Johnson 2004; Chapman *et al.* 2011; Mittelbach, Ballew & Kjelson 2014). In contrast, Chinook salmon exhibited less variation in their movement patterns with most individuals having direct passage routes. These patterns are likely a result of (i) the fishways being optimized for salmonids (Clay 1995; Bunt, Castro-Santos & Haro 2012) and (ii) the majority of salmon sharing high motivation to reach upstream spawning grounds due to their philopatric behaviour and interspecific responses to environmental cues (Keefer & Caudill 2014). From a management perspective, network analyses may be used to quantitatively address *a priori* predictions or generate mechanistic hypotheses about movement in human-impacted landscapes. In this example, the complex responses exhibited by Pacific lamprey in fishways likely result from a combination of both behaviour and environment and that a greater understanding of the behavioural processes acting on lamprey during upstream migration will aid efforts to improve passage for this species.

An important caveat is that some of the differences between outcome groups may have been an analysis artefact rather than a biological result because the minimum network size for fish that did not pass the dam would always be lower compared with fish that passed the dam. Nonetheless, additional network metrics suggested significant biological differences in movement were still occurring despite potential confounding effects between outcome and network size, which emphasize the utility of using multiple metrics. The number of multi-edge node pairs and the edge: diameter ratio were significantly higher for lamprey that did not pass the dam compared with salmon that passed the dam, despite salmon having larger networks. Furthermore, controlling for time in network revealed that lamprey not passing the dam still exhibited high movement rates and milling behaviours despite having small networks. Future studies should carefully consider both potential artefacts when classifying movement behaviours within a network context and carefully select metrics that best match hypothesized impacts or monitoring needs of the study.

Similarly, developing a monitoring array *a priori* is critical to ensure limited measurement error and generating meaningful results that are compatible with the question of interest. The outcome of network analyses for any telemetry data depends on the structure of monitoring locations (Papastamatiou *et al.* 2013; Finn *et al.* 2014). Missed detections or limited spatial coverage can lead to incorrect inferences, which will require a clear understanding of both detection range and detection efficiency (Cagnacci *et al.* 2010). The selection of monitoring sites in this study was a logical outcome of how fishways were designed at Bonneville Dam, and the majority of missed detections in our study could be reasonably inferred due to the linear nature of fishways and the large number of receivers used in this study. However, applying similar analyses to habitats like the pelagic zone of lakes or

marine systems will require careful consideration of the scale of movements relative to the spacing of nodes in the network of interest (Schick *et al.* 2008; Finn *et al.* 2014).

Inclusion of biological covariates, like body size, also highlights the potential to test process-based hypotheses about movement and behaviour using network analyses. For example, past studies have shown that Pacific lamprey passage and migration distance are associated with body size in the Columbia River (Keefer *et al.* 2009; Hess *et al.* 2014). However, lamprey body size was not associated with any network metrics in our study. We would predict larger lamprey to make more passage attempts and have higher performance in overcoming local passage challenges within fishways. The lack of a body size effect in network metrics suggests while size selection occurs at the dam-wide scale, size-selectivity is weak at local scales (this study; Keefer *et al.* 2013). It may also be that these size-selective processes are associated with genotype (Hess *et al.* 2014) or the behavioural mechanisms discussed above. More importantly however, network analyses provide empirically derived metrics for describing movement that can be statistically compared among individuals or groups, which traditional movement models (e.g. random walks, state-space) typically overlook (Morales *et al.* 2010). Similar models could be used to test for the influence of individual traits on movement behaviours.

Looking beyond large dams, roads, highways and culverts are similar obstacles to movement that can alter animal behaviours and may be suitable for network analyses. Even though these obstacles are not totally impassable for some animals, studies have shown that many exhibit strong avoidance to these obstacles (Coulon *et al.* 2008; Shepard *et al.* 2008; Beyer *et al.* 2014). Mitigation techniques for reducing mortality at road crossings have received much attention and prioritization of where to improve habitat connectivity is critical. Network analyses have the potential to identify road crossings with high connectivity to fragmented habitat patches via node-removal manipulations (Eros *et al.* 2012; Jacoby *et al.* 2012). Given that movements patterns are believed to be largely environmentally controlled (Fahrig 2007; Avgar *et al.* 2013), future applied applications of network methods would be most valuable within the context of a before-and-after, control-impact (BACI) experimental design. Such evaluations could include evaluating the impacts of local-scale mitigation efforts (Dodd, Barichivich & Smith 2004; Naughton *et al.* 2007; Johnson *et al.* 2012) or ecosystem development (Fahrig 2007; Kim *et al.* 2012; Piper *et al.* 2015) on patterns of movement and space use.

Animals often exhibit altered movement patterns in human-modified landscapes (reviewed in Fahrig 2007). Incorporation of spatial information, such as patterns of network structure, should provide a more complete view of potential fitness consequences during an individual's migration experience (Morales *et al.* 2010). Although 'delay' at anthropogenic barriers has been frequently cited as a critical threat to migratory species (Caudill *et al.* 2007;

Marschall *et al.* 2011; Keefer *et al.* 2013), most of the fitness-related consequences have been evaluated using time-based metrics (i.e. passage time). This is because movement times are easier to analyse than the larger and more complex elements of data associated with space use (Zabel 2002; Jacoby *et al.* 2012). Since energy expenditure is a function of both time and distance, future inclusion of both spatial and temporal dynamics should provide more accurate assessments on whether certain movement behaviours are adaptive and how an animal perceives the surrounding landscape (Fahrig 2007; Schick *et al.* 2008). Overall, network analyses are likely to be most useful in circumstances where habitat changes are hypothesized to alter movement patterns.

In summary, network analyses provide a promising tool for both basic and applied ecologists to gain a better understanding of animal movements. As shown here, network analyses can be used to statistically test for population-level effects, while testing for environmental or biological covariates. These analyses also can serve as a valuable tool for describing animal movement and behaviour in the face of environmental change and assessing the effectiveness of mitigation efforts, particularly in spatially complex ecosystems. Whether the intended use is exploratory, descriptive or inferential, we believe that the application of network analyses to individual movement data can provide ecologists with a fresh view for characterizing animal movements in their system of interest.

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Data accessibility

Data for the network properties and biological traits of Chinook salmon and Pacific lamprey are available online at the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.724mk> (Kirk & Caudill 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Traits and network metrics for three Pacific lamprey and two Chinook salmon selected for visual representation.

Fig. S1. Movement paths of additional Pacific lamprey and Chinook salmon through the network of Bonneville Dam fishways.