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Social network analysis as a tool to inform anguillid eel conservation and management

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Abstract

Eel Management Plans demand European silver eel (*Anguilla anguilla*) escapement to the sea of at least 40% of that expected historically in the absence of human impacts. Landlocked lentic waterbodies, such as drinking water reservoirs, host substantial numbers of eel, which could represent a significant contribution to catchment-based conservation targets. To optimize netting strategies for eel management policies, information on their aggregation behaviour is currently needed but lacking. We performed a fine-scale acoustic tracking study to monitor the movements of 86 European eel in a UK reservoir. Social network sampling and sensitivity analyses were used to assess whether eel aggregate at scales relevant for current capture techniques. European eel were found to aggregate at spatial and temporal scales of 50 m and 2 days, respectively, which complements current capture methodologies and recommendations. Aggregations were not driven by fixed resources, indicating that other factors, such as sociality, may drive aggregation behaviour. Results also show that current netting practices could be optimized by increasing netting lengths from 50 to 80 m. In addition to aiding conservation and management protocols, these results provide an ecological foundation for exploring the role of social behaviour in this Critically Endangered species.

Keywords: aggregation; *Anguilla*; behaviour; ecology; freshwater; lentic; network; reservoir

Introduction

The European eel (*Anguilla anguilla*) is one of 19 species/subspecies in the genus *Anguilla* and is classified as Critically Endangered on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Jacoby et al. 2015, Pike et al. 2020). Since the 1980s, the recruitment of eel into European rivers has declined by 90%–99% (Jacoby et al. 2015, Drouineau et al. 2018, Righton et al. 2021). Recent International Council for the Exploration of the Sea (ICES) advice states that European eel status remains critical and recommends that all fisheries- and non-fisheries-related anthropogenic mortalities should be halted (ICES 2022). Numerous potential factors may be driving this population decline, including climate-driven alteration to oceanic conditions, anthropogenic barriers to migration, habitat loss, pollution, invasive species, and unsustainable exploitation (Jacoby et al. 2015, Drouineau et al. 2018). As such, the European Union (EU) established the Eel Regulation (Council Regulation 1100/2007/EC) in 2007, requiring member states to develop Eel Management Plans (EMPs). The objective of EMPs are to reduce anthropogenic mortality to enhance silver eel unimpeded escapement to the sea by at least 40% of that expected historically in the absence of human impacts (eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=CELEX:32007R1100). Increased escapement may be achieved through directly limiting catch, or through other methods, such as barrier easement or removal, restocking inland waters with juveniles, or assisted migration of juveniles as well as silver eel through the trapping and transportation of individuals directly to the sea (De Meyer et al. 2020, ICES 2022).

Although primarily studied in lotic systems (Béguer-Pon et al. 2018), European eel can also be found in lentic habitats, such as lakes, ponds, and reservoirs (Williamson et al. 2023). Landlocked lentic waterbodies, such as drinking water reservoirs, can hold substantial numbers of European eel, which typically enter through pumped inputs or via climbing spillways as juveniles (Bašić et al. 2019, Piper et al. 2020), but also may be stocked in these waterbodies as part of management plans (Froehlicher et al. 2023). Such waterbodies could therefore represent a significant contribution to the 40% escapement target if migratory silvering eel from these landlocked populations were able to reach the sea. However, in many of these systems, there is limited opportunity for natural escapement. 'Trap and Transport' (henceforth referred to as T&T), also known as 'trap and haul', where fish are captured and translocated to sites with good seaward connectivity, is a common management strategy to facilitate fish passage over impassable structures, such as hydroelectric dams (Ward et al. 1997, McDougall et al. 2013, Harris et al. 2019, Weigel et al. 2019). However, it is primarily used in linear, lotic systems, such as rivers, where target species are moving unidirectionally and capture probability is relatively high.

Management strategies, such as T&T, rely on efficient capture of target species to be effective (Peterson and Dunham

2003, Hardie et al. 2006, Lintermans 2016). The viability of management strategies in nonlinear systems, where capture can be unpredictable, is poorly understood. Efficiency of capture and netting is dependent not only on the temporal and spatial thresholds of capture techniques, but also on the ecology of the target species, such as aggregation behaviour. In large lakes, European eel are predominantly caught using fyke nets (O'Leary et al. 2020, Williamson et al. 2023), with probability of capture ranging from 0.2 to 0.9 and primarily dependent on the size of eel (Jellyman and Graynoth 2005). Although the number of fyke nets used can be dependent on the size of the waterbody, it is currently recommended that either 10 single (length = 5 m, width = 1 m) or 5 double fyke nets (length = 10 m, width = 1 m) are deployed (total of 10 cod ends), netting a fish corridor and trapping footprint of 50 m × 1 m, and checked after 24–48 h (Chisnall and West 1996, Environment Agency 2016, 2019, Piper et al. 2020). However, whether individuals occur, associate, or aggregate, within 50 m of one another in the same two days, and whether these are the optimal spatial and temporal thresholds for capture, is unknown.

Many life stages of anguillid eel possess a tendency to aggregate and can, at times, be highly gregarious (Sorensen 1986, Tesch 2003, Geffroy et al. 2014). Anguillid eel are typically observed aggregating around natural or human-made impediments during brief periods before both upstream and downstream migration (Todd 1981, Tesch 2003, Bruijs and Durif 2009, Burgerhout et al. 2013, Schabetsberger et al. 2013, Sandlund et al. 2017, Noda et al. 2021). Like other fish, eel aggregations might be driven by resource use, such as for habitat or feeding (Spiegel et al. 2016, Teitelbaum and Mueller 2019), and such drivers can be fixed or dynamic in space and time (Lewison et al. 2015, Spiegel et al. 2016, Hazen et al. 2018). With few predators of eel in these lentic systems, it is unlikely that aggregations serve antipredator functions, so another hypothesis is that aggregations may be the result of active social preferences between individuals (Jacoby et al. 2012, Armansin et al. 2016) or a combination of multiple spatial and social influences, which can be challenging to disentangle (Spiegel et al. 2016). Yet, information on whether European eel aggregate, the drivers of these aggregations, and to what extent this behaviour is predictable in space and time could be applied to optimize capture methodologies. For example, if eel aggregations are driven by fixed resources, such as environmental structures or specific habitat, netting and capture could be concentrated in those areas to optimize effort, improving the efficacy of management techniques and aiding eel conservation and management.

Hanningfield reservoir is an artificially made waterbody located in Essex, UK. Water is abstracted from nearby rivers into the reservoir, and prior to recent screening has allowed fish to enter the reservoir, but not to leave. As such, it contains significant populations of fish species, including European eel (Bašić et al. 2019). The aim of this study is to investigate whether the spatial and temporal netting thresholds defined by current management practices are suitable for capturing eel association and aggregation behaviour and to vary these thresholds to explore sensitivity to changes in these practices. This study utilizes fine-scale acoustic telemetry data from this site and proximity-based social networks to achieve the following objectives: (i) assess if yellow and silver European eel form nonrandom aggregations at scales relevant to common management practices (net length of 50 m and over 2 days); (ii) determine whether aggregations are driven by fixed resources such as habitat; and (iii) assess whether current thresholds for netting and capture are optimized for effort.

Materials and methods

Study area and telemetry array

Hanningfield reservoir covers an area of 402.9 ha (Fig. 1) and is owned and run by Essex and Suffolk Water Ltd. It consists of a main fishing area and a nature reserve, which is classified as a site of special scientific interest due to important bird populations. An array of 31 receivers (Vemco VR2W V5–180 kHz) were deployed at the site between 29 July 2015 and 14 December 2016. As boat traffic from fishing and sailing activities occurs on the main part of the reservoir, potentially disrupting the long-term deployment of acoustic receivers, only the nature reserve was used as a study area (Fig. 1). Range tests by Bašić et al. (2019) determined that 98.89% of tags were detected at a range of 120 m at the edge of the reservoir. However, near the intakes, detection efficiency over similar distances was reduced to 39.29%, which could be due to the acoustic noise created from the intakes or the acoustic reflection from the concrete walls of the reservoir. As such, 31 acoustic receivers were situated within a 150 m range of each other to provide sufficient overlap for fine-scale positioning using the VEMCO Positioning System (VPS system) (Fig. 1). Receivers were anchored to the bottom by 10 kg weights at a mean depth of 6.1 ± 0.5 m (SE) (Bašić et al. 2019) and connected to a surface float for easy recovery and data downloads. They were deployed in vertical alignment with the hydrophone towards the water surface and ~1 m from the reservoir bed.

Eel tagging and 2D acoustic positioning system

European eel were captured and tagged using the method outlined in Bašić et al. (2019), and all tagging was carried out in compliance with UK Home Office regulations under licence PPL70/7958. Eel were anaesthetized in 2-phenoxyethanol solution (2–2.5 ml^{-1}) and measured for total length, weight, vertical and horizontal eye measurements, lipid percentage, and length of pectoral fin. Subsequently, eel were moved onto a V-shaped foam support and acoustic tags were surgically implanted. The procedure took <5 min per animal after which the fish were placed in an oxygenated water until complete recovery and released at the initial location of capture. Sampling was carried out in two separate seasons between August and December in 2015 and June and August in 2016, resulting in 36 and 68 eel tagged with individual coded 180 kHz acoustic transmitters (VEMCO V5-2X-180 kHz-0; repeat cycle: 50–100 s), respectively. Eel were tracked during two periods: August 2015 until February 2016 and from June 2016 until November 2016. (The receivers had to be removed in both years to prevent disruption to protected bird species.) The receiver array remained the same during both tracking periods. The Innovasea (formerly VEMCO) Positioning System was used to calculate individual locations of eel from raw detection data (Andrews et al. 2011, Roy et al. 2014, Orrell and Hussey 2022). Downloaded data were postprocessed by Innovasea using proprietary software (Armansin et al. 2016). Data returned included latitude, longitude, projected Cartesian coordinates, and an estimate of the error for each loca-

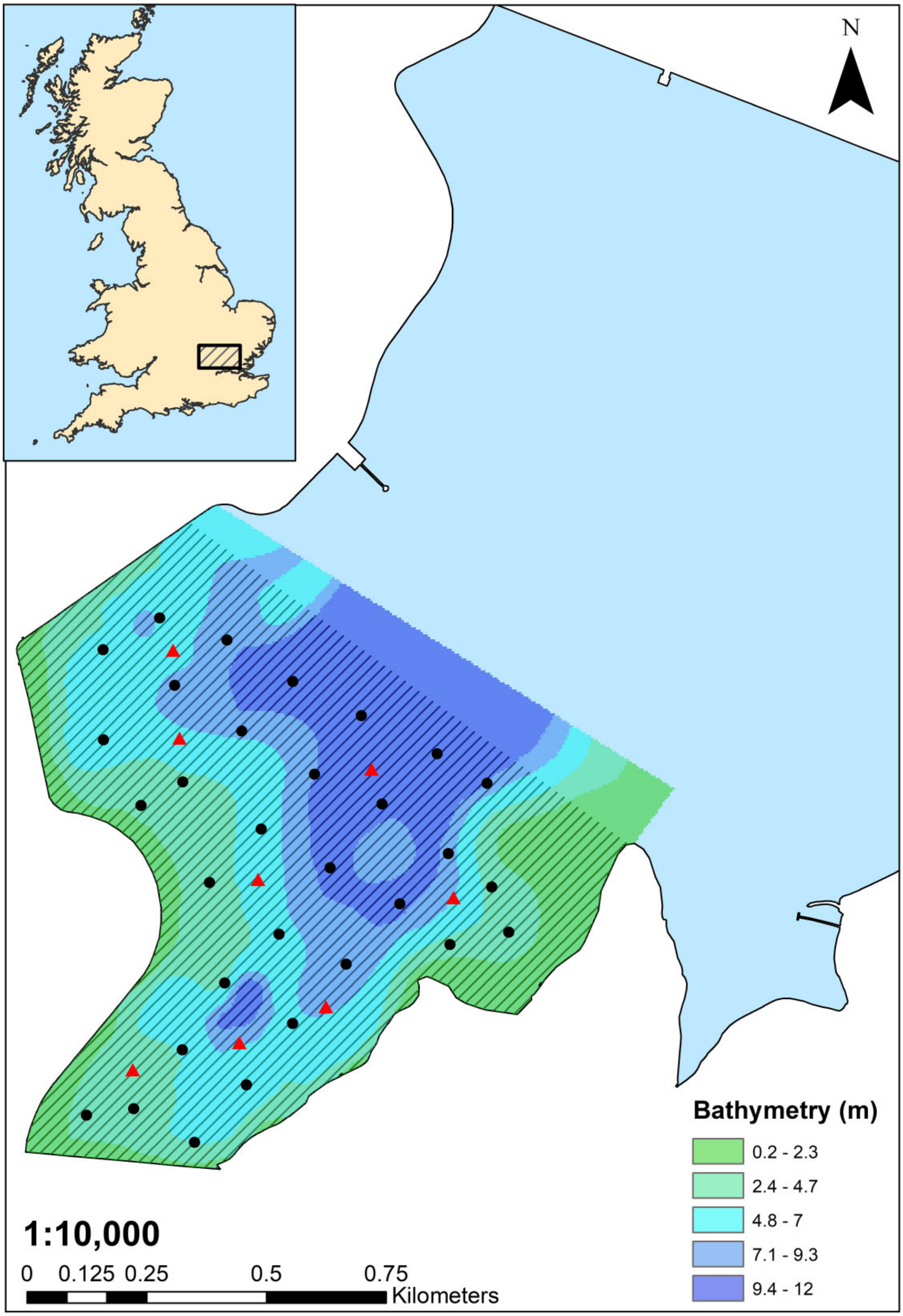

Figure 1. Maps showing the study site, Hanningfield reservoir position in the UK (inset Ordnance Survey 2005), study site location inside the reservoir (hashed area), bathymetry (depth profiles), and position of the receivers and synctags (filled circles), and synctags only (triangles) (bottom right)) used for monitoring movement of European eel (*Anguilla anguilla*). Figure adapted from Bašić et al. (2019).

tion, which was used to filter the data for positional precision (Supplementary Appendix S1).

Defining eel aggregations under standard netting thresholds

To test whether yellow and silver European eel aggregate at current spatial and temporal thresholds used for netting (length of 50 m, 2 days) and whether this is driven by fixed resources, such as environmental structures, where netting and capture efforts could be concentrated, three metrics of aggregation were calculated from our observed data. We argue that the efficiency with which eel can be captured will be dependent on both group size and how connected individuals are in the population, with larger, more densely connected aggregations (i.e. aggregations where a high percentage of individuals associate with many or most other group members) translating into more efficient netting. As such, we calculated three metrics, typically used in social network analyses of animal aggregations: mean group size, edge density, and node degree. Mean group size is the average group size within an aggregation. Edge density, which ranges between 0 and 1, is a social network metric that defines the proportion of associations within a network relative to the total number of associations possible. Node degree is a social network metric that quantifies how many other individuals an animal has associated with across the network. Mean node degree was calculated for the network. All metrics were calculated at 50 m and 2 days.

In order to maximize the numbers of tagged individuals available for detection, eel location data were filtered into two periods: (i) those consisting of locations from a 24-day period in late 2015 (8 December 2015 to 1 January 2016) (henceforth called 2015 group data) and (ii) those consisting of locations obtained in summer 2016 from a 48-day period (14 July 2016 to 31 August 2016) (henceforth called 2016 group data) (Supplementary Fig. S1). The data for these periods include locations of 23 eel and 63 eel, respectively, and as such reflect datasets of low (2015) and high eel density (2016). The R package *spatsoc* (Robitaille et al. 2019) was used to group eel VPS locations and aggregation metrics calculated from these observed data (Supplementary Appendix S2). This package was also used to build null models to test whether associations within aggregations (defined by our aggregation metrics) were nonrandom in their structure (Farine and Whitehead 2015, Robitaille et al. 2019, Aspillaga et al. 2021) (Supplementary Appendix S2). Observed aggregations may reflect associations resulting from the presence/absence of resources, the structure of the environment, or social responses to conspecifics (Spiegel et al. 2016). Null models were generated by randomizing the temporal order of individual daily trajectories but maintaining the spatial structure of an animal's path (i.e. the places an individual visits remain the same), having the effect of decoupling synchronization among individuals. This allows comparison of observed associations between individuals with those expected by chance, given the explicit space use of each individual (Spiegel et al. 2016). This method, therefore, provides information on whether associations between individuals are primarily driven by fixed resources, or by other reasons such as social factors, or potentially short-term dynamic resource use. Significance was calculated by comparing the observed test statistic against the null distribution to generate a *P*-value (Veech 2012, Farine 2017). Significance (two-tailed) was determined if the test statistic fell within the upper or lower 2.5 percentile of the null distribution (Veech 2012, Farine 2017).

Sensitivity analysis of optimal spatial and temporal netting thresholds

The optimal spatial and temporal thresholds of an aggregation for netting may vary depending on the drivers of the aggregation (Grünbaum and Okubo 1994, Parrish and Edelstein-Keshet 1999). It has yet to be tested whether the current standard spatial and temporal thresholds (net length of 50 m and 2 days) for netting and management are optimal. To assess this, a sensitivity analysis was undertaken. Our three metrics of eel aggregation from both the low- and high-density datasets were calculated (Supplementary Appendix S2) across a range of temporal (6 h to 2 days) and spatial thresholds (10–100 m, representing 1–10 fyke nets) relevant for management practices (Supplementary Appendix S3). Optimal thresholds where diminishing returns are no longer worth the additional cost can be identified by calculating 'elbow points' on a curve (Hart et al. 2022, Guy et al. 2023), where the second derivative on the curve reaches the maximum value (Zhao et al. 2017, Coffey et al. 2019, Shade and Stopnisek 2019). As such, data were plotted, and points of diminishing returns calculated using elbow point analyses to indicate the optimum length of net required for different lengths of sample periods. This assesses the optimal thresholds for netting and capture of European eel at different population densities, given a range of different spatial and temporal scenarios.

Results

Following filtering of the data, 13 342 and 86 475 positions were calculated from 23 (19 silver, 4 yellow) and 63 (36 silver, 27 yellow) animals for the low (2015)-density and the high (2016)-density datasets, respectively. Detailed metadata for each tagged individual used in the final analysis can be found in Supplementary Table S1.

Eel aggregations under standard netting thresholds

For the low-density data, mean group size at this site was 3.2 +/− 2.3 (SD), with a maximum group size of 15 and minimum group size of 2. Mean node degree was 13.8 +/− 6.3 (SD), ranging between 0 and 19. As edge density is a whole network descriptor, only a single value was calculated. Edge density of the 2015 data was 0.63, suggesting that 63% of all possible associations between tagged eel were formed at least once during the course of the 2015 dataset. For the high-density (2016) data, mean group size was 7.1 +/− 8.9 (SD), with a maximum group size of 37 and minimum group size of 2. Mean node degree was 49.2 +/− 11.4 (SD), ranging between 21 and 62. Edge density of the 2016 data was 0.79, suggesting that ∼80% of all possible associations were formed at least once during the course of the 2016 dataset.

The two-tailed test revealed that observed mean group size, mean node degree, and edge density were significantly larger than expected from the null model at both low and high densities (Supplementary Figs S2 and S3), using spatial and temporal thresholds of 50 m and 2 days, respectively. Fewer than 2.5% of random values were greater than observed values for all aggregation metrics from all years (2015—mean group size, $P < .001$; edge density, $P < .001$; mean node degree, $P < .001$; 2016—mean group size, $P < .001$; edge density,

$P < .001$; mean node degree, $P < .001$). This indicates that eel at Hanningfield were observed in greater numbers, interacted with more individuals, and the population was more connected than expected by chance when controlling for explicit space use.

Are current thresholds optimal?

Sensitivity analysis curves of aggregation metrics at each spatial and temporal threshold are shown in Fig. 2, for both low- and high-density populations. Aggregation metrics were larger at the higher density and with increasing temporal period, which confirms the expectation that eel may be netted in greater numbers when nets are placed for longer at sites with higher population densities (Fig. 2). Elbow points varied depending on both spatial and temporal thresholds (Fig. 2, Supplementary Table S2). However, optimal spatial thresholds were found to be mostly greater than the current standard netting length of 50 m, for both low- and high-density populations, indicating that ~7–8 double fyke nets (length of 80 m; Fig. 2) may be required to optimize netting practices for management methods across all temporal periods used for netting.

Discussion

Drinking water reservoirs potentially contain substantial number of European eel that could help countries reach Eel management plan targets (Bašić et al. 2019, Piper et al. 2020, Williamson et al. 2023). However, escapement from these systems is limited. This study aimed to evaluate if European eel aggregate at scales appropriate to current management protocols, as well as investigating the potential drivers of aggregations in these systems, to aid conservation and management of this threatened species. This study found that European eel in a UK reservoir do aggregate at spatial and temporal scales of 50 m net lengths and 2 days, respectively, in line with current netting methodologies and recommendations. European eel were found to aggregate in greater numbers, and were more connected, than would otherwise be expected compared to resource explicit null models, suggesting that European eel aggregations in these systems are not primarily driven by fixed resources. In addition, current netting practices could be optimised by increasing netting lengths from 50 to 80 m by increasing the number of nets. This information could help aid conservation and management techniques, such as T&T, to increase escapement of eel from these waterbodies.

Our study not only indicates quantitatively that yellow and silver European eel aggregate, but that aggregations are not primarily driven by fixed resource use. Drivers of these aggregations could therefore be driven by social factors or by short-term dynamic resource use. Despite it being noted that many life stages of European eel aggregate (Sorensen 1986, Tesch 2003), very little research into aggregations and sociality in European eel has been undertaken (Sandlund et al. 2017). Evidence in other diadromous fish, such as Atlantic salmon (*Salmo salar*), suggests that social interactions between individuals may play an important role in migration aggregations (Berdahl et al. 2016). Sociality has been seen in captive European glass eel and social cues linked to synchronizing their locomotor activity (Bolliet et al. 2007, Geffroy et al. 2014). In addition, social cues may play an important role in aggregation and movement in yellow and silver eel, with migration in silver eel triggered by other conspecifics moving (Sandlund et al. 2017), and river colonization by yellow eel has been linked to positive density dependence (Edeline et al. 2009).

This study, therefore, implies that sociality might be an important factor in European eel behaviour, and the timing of associations in this species will likely be an interesting avenue for future research. However, resources can also be dynamic in space and time, and as such our results may also reflect the responses of individuals to environmental changes over short time-scales (Spiegel et al. 2016). To disentangle the impacts of social drivers and short-term dynamic resource use, conducting randomizations with variable temporal windows, as conducted by Spiegel et al. (2016), allows the decoupling of temporal dependencies of movements of eel while accounting for more gradual temporal dynamics. A number of factors in the current study meant that this method was inappropriate for this dataset. In this study, eel were tagged in small batches according to their capture frequencies, which limited the maximum number of tagged eel in the system simultaneously, and reduced the temporal range over which changing environmental factors could be assessed. In addition, for logistic reasons, the array was kept to a confined area, and as a result, tagged eel could move out of the range of the array. Finally, previous work on the movement patterns of eel at this site indicated that eel had large home ranges and went relatively long periods between detections, with long return times to previously visited locations (Bašić et al. 2019).

In the future, conducting randomizations with variable temporal windows using long-term, reservoir wide arrays and higher resolution technologies (Lennox et al. 2023, Orrell et al. 2023, Sanderson et al. 2023), and with greater temporal overlap of tagged individuals, will help to further disentangle the social and environmental drivers of European eel behaviour in reservoir systems. This will also help identify the temporal and spatial scale that constitutes biologically meaningful aggregation and association behaviour in eel, which was beyond the scope of this paper. Range testing work at the site has indicated that some areas had lower tag detection efficiency than others (Bašić et al. 2019). Variability of detection efficiency within the array has potential to influence the estimation of aggregation metrics. However, these lower detection rates only occurred in a highly localized area around the reservoir input and, as such, would not have had a large impact on our results. However, in future studies, a receiver wide array would also mitigate the impacts of lower detection efficiency on a small number of receivers within an array.

Due to welfare considerations for European eel, nets have a maximum active fishing period of 48 h before being checked (Environment Agency 2016, 2019). Here, we analysed aggregation metrics at temporal periods up to 2 days, and at spatial scales of 10–100 m representing deployment of 1–10 double fyke nets. There are trade-offs when considering the duration of netting time, with deployments of shorter durations requiring more nets and surveyed area (with subsequent increase in effort). Our results indicate that netting spatial scales could be optimized across all durations of deployment by increasing the number of nets deployed and spatial area of survey, from five fyke nets (50 m length) to eight (80 m length). Although the current standard length of 50 m is probably optimal for 2 day sampling at higher density populations (Fig. 2), our results show that increasing the number of nets when sampling at this temporal threshold may result in greater numbers of

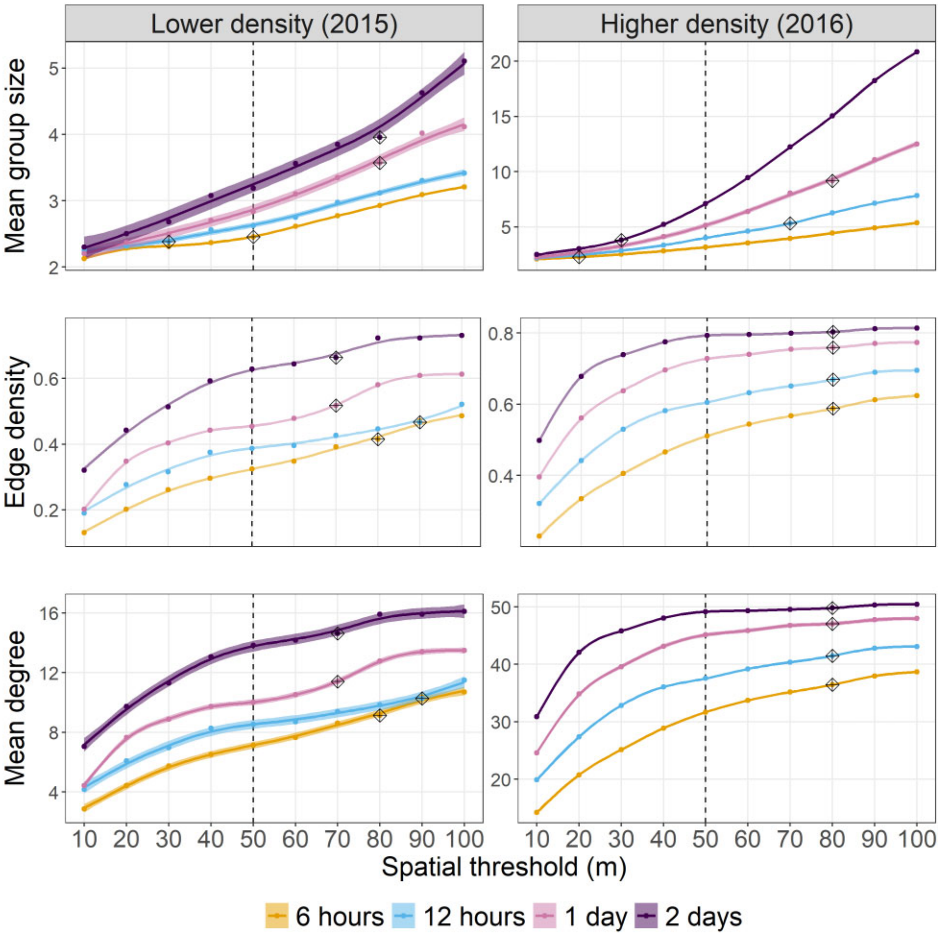

Figure 2. Sensitivity analysis of spatial and temporal thresholds for mean group size, edge density, and mean degree in European eel (*Anguilla anguilla*) for both 2015 and 2016 group data. Mean values with standard error bars are included. The dashed vertical line indicates the common spatial netting length of 50 m. Crossed, diamonds denote elbow points, points of diminishing returns on the curve. Note that data points at 2 days indicate common temporal threshold for netting and *y*-axes are not standardized between different metrics and years.

eel caught. As such, where feasible we recommend deploying eight fyke nets to optimize capture of European eel in lentic systems.

Optimal does not necessarily mean 'best'. Increasing netting lengths does come with increased equipment, labour, and effort costs. This sensitivity analysis is not aimed to be definitive, but more to be used by managers to aid and assess how different deployment durations and spatial thresholds could be utilized to capture eel in their systems. We also acknowledge that our method of calculating elbow points is relatively coarse due to the categorial nature of the data. To find the optimal periods for netting European eel, more comprehensive data from several different sites containing alternative habitats and population densities, followed by *in-situ* sampling over multiple periods, are required.

Knowledge of spatial and temporal thresholds of animal aggregations can greatly aid conservationists and managers. For example, Oppel et al. (2018) identified the management approaches, such as Marine Protected Area establishment or reduction in fishing effort, which are most likely to be effective, given aggregation size and the geographic scale over which the threats to specific species should be addressed. Spatial and temporal identification of multispecies aggregations also allows protection, which can yield disproportionately high benefits for conservation (Erisman et al. 2017, Carlson et al. 2023). Despite the abundant information on fish aggregations in the literature, relative to other taxa (Bauer et al. 2009), these data had been, until recently, rarely used to inform conservation and management (Tobin et al. 2013, Erisman et al. 2017). As such, directed conservation of threatened fish species that aggregate has started to be developed (Daly et al. 2018, Chollett et al. 2020, Ostrega et al. 2023). The results of our sensitivity analysis on eel aggregations can help optimize netting procedures to maximize eel numbers while minimizing netting time, or balance risk reward during netting and sampling for Critically Endangered European eel. Moving forward, further research on both the social and environmental drivers of eel aggregations will be vital to the conservation and management of this Critically Endangered species.

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Author contributions

Michael J. Williamson (Conceptualization [equal]), (Methodology [equal]), (Investigation [equal]), (Formal analysis [lead]), (Data curation [equal]), (Visualization [lead]), (Writing—original draft [lead]), (Writing—review & editing [lead]), David M. P. Jacoby (Conceptualization [equal]), (Methodology [equal]), (Writing—review & editing [supporting]), Tea Bašić (Investigation [equal]), (Writing—review & editing [supporting]), Alan Walker (Investigation [equal]), (Writing—review & editing [supporting]), (Supervision [equal]), (Funding acquisition [equal]), and Adam T. Piper (Investigation [equal]), (Methodology [supporting]), (Writing—review & editing [supporting]), (Supervision [equal]), (Funding acquisition [equal])

Supplementary data

Supplementary material is available at *ICESJMS* online.

Conflict of interest : The authors report that there are no conflict of interests to declare.

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Data availability

The raw data used in this study are available from the corresponding author upon reasonable request. The R code used for analyses are available from the Zenondo Digital Repository: https://zenodo.org/records/10246102.

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