

RESEARCH ARTICLE

Functional Ecology



Tracking temperate fish reveals their relevance for plant seed dispersal

Andrea J. E. Mulder^{1,2} | Roland van Aalderen³ | Casper H. A. van Leeuwen¹

¹Department of Aquatic Ecology,
Netherlands Institute of Ecology (NIOO-
KNAW), Wageningen, The Netherlands

²Wildlife Ecology and Conservation Group,
Wageningen University (WUR), Wageningen,
The Netherlands

³Royal Dutch Angling Association, Bilthoven,
The Netherlands

Correspondence

Casper H. A. van Leeuwen
Email: c.vanleeuwen@nioo.knaw.nl

Funding information

H2020 Marie Skłodowska-Curie Actions,
Grant/Award Number: 750240

Handling Editor: Shawn Leroux

Abstract

1. Seed dispersal is a fundamental process for plant communities, especially now that our changing world demands rapid colonization of new habitats. Long-distance dispersal is especially important for plant population persistence and range expansions.
2. The contribution of fishes to plant seed dispersal in aquatic ecosystems (ichthyochory) has long been overlooked. Although we know fish disperse seeds, it is largely unknown where, when and how far—especially in temperate regions. Here we studied the potential of fish to disperse seeds locally and over long distances, specifically hypothesizing that (a) dispersal by fish depends on the season, (b) individual fish contribute differently to seed dispersal and (c) water-regulating structures (barriers) inhibit seed dispersal.
3. We tested our hypotheses by acoustically tracking 71 common carp *Cyprinus carpio* with 21 hydrophones in a 38-km long study system for >2 years in the Netherlands. We calculated potential seed dispersal throughout this system by combining nearly 1.5 million location registrations with experimentally assessed retention times of seeds after ingestion (i.e. time between ingestion and egestion).
4. Seed dispersal on local scales was quantitatively most important during summer and autumn, with high dispersal potential in a range of 4 km from the location of seed ingestion. Long-distance dispersal up to 16 km was possible at low probabilities in spring. In winter, most seeds were egested within two km. Maximum and median dispersal distances varied widely among individuals, emphasizing variation in effectiveness among individual fish for seed dispersal. Less than two per cent of all fish movements reached beyond sluices and weirs, indicating that anthropogenic barriers in freshwater systems strongly reduced the potential of common carp to disperse seeds to these areas.
5. This study shows that common carp can locally disperse plant seeds with high probabilities, and over distances up to 16 km with low probabilities throughout temperate ecosystems. This can contribute to restoration and maintenance of plant community diversity. However, this ecosystem function of fish to plants

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2021 The Authors. *Functional Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society

requires intact fish populations—because not all individual fish contribute equally to dispersal—and unrestricted connectivity throughout aquatic ecosystems.

KEYWORDS

acoustic transmitter, barriers, *Cyprinus carpio*, endozoochory, ichthyochory, intraspecific variation, seasonality, seed dispersal kernel

1 | INTRODUCTION

Seed dispersal is a key process in determining the spatial extent of plant communities, and geographical distributions, range dynamics and the genetic structure of plant populations (González-Varo et al., 2013; Levine & Murrell, 2003; Nathan & Muller-Landau, 2000). Global changes—including an increased fragmentation of landscapes, introductions of non-native species and rapid changes in local habitat suitability—make seed dispersal vital for plant population persistence (McConkey et al., 2012). If plant migration rates are lower than the rates of global changes, a ‘migration-lag’ can result in the decrease or loss of species (Corlett & Westcott, 2013; Ozinga et al., 2009). Predictive power to assess the dispersal potential of both endangered and non-native plant species is therefore of fundamental and applied concern.

Plants can disperse their seeds via multiple vectors, including water flow, wind and animals (Soomers et al., 2013; Van Leeuwen et al., 2012). The ultimate dispersal distance depends on the combination of vectors a seed uses (Van Leeuwen et al., 2017; Vittoz & Engler, 2007). Most seeds are generally deposited close to the parent plant and dispersal becomes less frequent over long distances (long-distance dispersal, LDD; Nathan et al., 2008). However, LDD is especially crucial in facilitating a link between habitat fragments and influencing the geographic distribution of species through range expansion (Cain et al., 2000; Mokany et al., 2014; Nathan, 2006). Animal-mediated seed dispersal (zoochory) often disperses seeds fast and directionally towards suitable habitat—which contributes importantly to local processes via dispersal over shorter distances, but may also occasionally lead to LDD.

The most common form of zoochory is endozoochory, which involves seed ingestion, a time period of gut passage with seeds remaining in an animal's digestive system and seed egestion (Pollux, 2011). The spatial extent of seed dispersal by endozoochory can be estimated by combining data on seed gut passage time with data on the distance moved by the animal during this gut passage time (Rehm et al., 2019). Reliable estimates of seed dispersal distances—and therefore the importance of an animal vector for either local dispersal or LDD—can be calculated from the combination of data on movement of the disperser animal (Rehm et al., 2019) and seed retention times (Yoshikawa et al., 2019). This combination is increasingly used to improve estimations of the importance of seed dispersal by birds and mammals (Kleyheeg et al., 2019; Russo et al., 2006; van Leeuwen et al., 2020; Wehncke et al., 2003; Westcott et al., 2005). However, reliable estimates for seed-dispersing taxa such as reptiles and fish

are still lacking (Horn et al., 2011; Piazzon et al., 2012; Pollux, 2011; Valido & Olesen, 2019). This creates a bias in our knowledge on plant seed dispersal and on the importance of plant–animal interactions.

Freshwater fish have long been overlooked as potentially important seed dispersal vectors (Correa et al., 2007; Horn et al., 2011), partly because their movements are notoriously difficult to study. Seeds dispersed by fish (ichthyochory) are generally from riparian or water plants, and the main mechanism is by endozoochory. The importance of fish-mediated dispersal is mainly documented in studies in the Neotropics (Correa et al., 2015; VonBank et al., 2018), with limited knowledge for temperate regions (Correa et al., 2015; VonBank et al., 2018). There are, however, a number of fish species recognized with potential for seed dispersal, notably in the order of the Cypriniformes (e.g. carps and minnows; Horn et al., 2011). Multiple cyprinids consume and egest vascular plant seeds in experimental setups and field situations (Boedeltje et al., 2015, 2016, 2019).

Several aspects of ichthyochory have remained understudied due to lack of knowledge on where and how far temperate fish species may move after potential ingestion of plant seeds. First of all, many fish species show seasonal variation in their intensity of local movements and feeding, and/or perform migrations during certain seasons (for e.g. spawning). Knowledge is needed on how the timing of more local and long-distance movements may correspond to the timing of seed availability in the habitat. Secondly, for many animal species—including fish—it is still unknown how variability among individuals affects their contribution to seed dispersal (Zwolak et al., 2020). Space use, movement and habitat occupation can all differ consistently among individual fish within a population (Brodersen et al., 2012; Chapman et al., 2011). Individual fish can differ in how effective their digestive systems digest seeds (Pollux, 2017) and can differ in their seasonal and daily movements (Chapman et al., 2012). How this may impact fish-mediated seed dispersal is largely unknown. Finally, seed dispersal depends strongly on the spatial extent that fish can cover in their habitat, which we have only more recently started to document with more accurate tracking technologies. Anthropogenic activities increasingly fragment river- and lake systems, which prevent fish from accessing spawning, nursing and feeding habitats (Baumgartner et al., 2014; Van Leeuwen et al., 2018). There is a need to better understand how river fragmentation may affect plant dispersal (Jones et al., 2020). Inhibited movement of fish may also impact seed dispersal potential, if physical barriers such as dams, sluices and culverts restrict movements.

The aim of this study was to quantify the importance of fish in temperate freshwater ecosystems, with regard to the spatial extent of seed dispersal. To do so, we combined for the first time detailed

fish movement data with seed retention time data in a temperate fish species (Van Leeuwen et al., 2016). We selected the common carp *Cyprinus carpio* L. (hereafter referred to as 'carp') as our study species, because this is considered an important seed-dispersing fish in temperate regions (Horn et al., 2011; VonBank et al., 2018). We tested three hypotheses: (a) carp show seasonal differences in their potential to disperse plant seeds, (b) individual carp differ in their importance for seed dispersal and (c) seed dispersal is affected by physical structures in the habitat. Our expectations were that (a) seed dispersal would mostly occur during late spring or summer when carp most actively move and forage (Wilt & Emmerik, 2008), and seeds are available in highest quantities (Miao & Zou, 2009; Russi et al., 1992); (b) a small proportion of all individuals within a carp population would be responsible for a large part of the seed dispersal events, as bolder individuals are likely to move more and over longer distances (Chapman et al., 2011; Fraser et al., 2001; Klefoth et al., 2017) and (c) physical structures in habitats—like sluices and weirs—are barriers for fish and negatively affect seed dispersal.

2 | MATERIALS AND METHODS

2.1 | Study species

The common carp *C. carpio* L. (Cyprinidae) is a widely distributed and well-studied freshwater fish (Pollux, 2011; Van Leeuwen et al., 2016). Carp are omnivores that frequently ingest plant seeds (VonBank et al., 2018), although ingestion may occur unintentionally (Horn et al., 2011). Carp can cover long distances in search of suitable spawning habitat or when foraging (Bajer et al., 2010), which is why movements during summer are largely determined by food availability (Lubinski et al., 1986). The species spawns in spring in vegetated shallow flooded areas when water temperatures reach 15–16°C (Crivelli, 1981).

2.2 | Study location

This study was performed in the Noord-Willems canal and its connecting waterways, which is located in the North of the Netherlands (Figure 1). The canal is used for both commercial shipping and seasonally recreational boats. The water level is regulated by sluices and weirs, and the depth of the canal and its connecting waterways varies between 1 and 4 m. The water supply comes from the canal Drentse Hoofdvaart, and indirectly from river the River IJssel, and runoff is northwards towards the intertidal zone of the Waddensea via the Eems canal (van Aalderen et al., 2018). Water residence time in the 38-km long Noord-Willems canal is relatively low: on average between 5 and 8 days (H. Klomp 2020, personal communication, 7 February 2020).

Water temperatures for Noord-Willems canal and connecting waterways (river Deurzerdiep, river Drense Aa, canal Winschoterdiep and lake Zuidlaardermeer) were measured monthly from Jan 2015

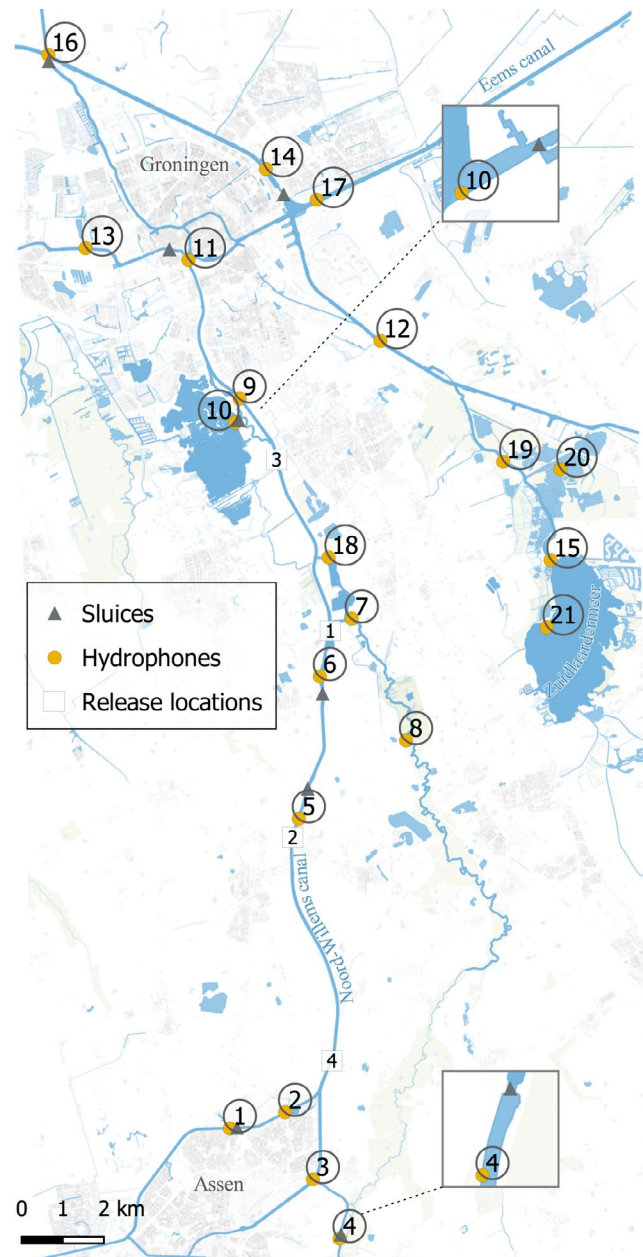


FIGURE 1 A map of the study area of the Noord-Willems canal and connecting waterways between the cities Assen and Groningen in the north of the Netherlands, showing the locations of the hydrophones, release locations and barriers

to June 2017. We used these data to derive a daily average water temperature over the 3 years in the study system by averaging the measurements with equal dates, and visualized this with smoothed conditional means.

2.3 | Tracking study in the field

In the study system we released 486 common carp that were supplied by Carpfarm B.V. from their fish farm in La Brenne, France. There were two supplies of carp: one in 2015 (246 individuals) and

one in 2016 (240 individuals). From these groups the Royal Dutch Angling Association chose a representable sample to be inserted with acoustic transmitters manufactured by Vemco Ltd (Vemco V13/1L). This procedure included anaesthetizing the fish by placing them in a separate tank with a benzocaine 100 ppm solution. When the fish no longer showed muscle tension, we placed the fish upside down in a cradle with a tube with flowing benzocaine 50 ppm solution in their mouth. After positioning the carp we made a mid-ventral incision in the body cavity and closed the fish with two separate sutures (soluble Vicryl from Ethicon) after inserting a V13 acoustic transmitter (following Jepsen et al., 2002). Thirty-six fish (mean body mass 1,894 g [293 SD]) were tagged in 2015 and 35 in 2016 (mean body mass 1,774 g [422 SD]), leading to a total of 71 tagged common carp with a mean weight of 1,835 g (368 SD, range: 1,120–2,924 g). The fish were released at four different locations along the Noord-Willems canal; roughly nine carp at each location both years (Figure 1).

The movements of the fish equipped with acoustic transmitters were monitored via a network of hydrophones (Vemco VR2W) at 21 locations (Figure 1). Hydrophones are submerged acoustic receivers that register signals they receive from transmitters inserted in fish. Whenever these fish come within a 200–500 m range (mean detection range in the study system: 245 m) of the receiver, it is registered with a unique code. All registrations are transmitter-specific and timestamped, and can therefore be used to analyse the carp movements. The study duration was from 28/02/15 until 11/05/17 (van Aalderen et al., 2018) with the V13-transmitters programmed to send an acoustic signal every 1.5 min—leading to an expected battery life of 1,264 days. An overview of the obtained data is visualized in Supporting Information Figure S1.

2.4 | Seed retention time experiments

To quantify the seed dispersal potential by common carp, we combined the data obtained on fish movement with previously experimentally estimated seed retention times in the digestive tract of carp after the moment of ingestion. Seed retention times of common carp were previously studied experimentally by placing the fish in a flume tank with low-, medium- and high-speed water flows (Van Leeuwen et al., 2016). In short, eight fish were fed pellets with known amounts of seeds from two sedge species (*Carex acuta* and *Carex riparia*), and seed egestion was monitored hourly for up to 15 hr. The carp selected for this study (mean fork length 28 cm [1.7 SD] and mean body mass 535.9 g [73.5 SD]) originated from the Aquatic Research Facilities of Wageningen University and Research Centre, the Netherlands (ARF-WUR). These experimental fish were substantially smaller than the fish used in the tracking study, and body mass can affect intestine mass, length and seed passage rates. Generally, gut passage times of larger fish will be longer than that of smaller fish (Yoshikawa et al., 2019), hence, our estimates of maximum dispersal distances are conservative.

2.5 | Data selection

The raw data consisted of >1.8 million registrations, with each timestamp consisting of the fish and hydrophone identity linked to its location in the study system. The data calculations and statistics were performed on a selection of all available data. Firstly, we assumed an acclimation period for the tagged fish after release before starting the study by deleting the first 30 days of registrations (Jenkins et al., 2014; Jepsen et al., 2002). Secondly, to correct for possible biases due to variation in the time each carp was monitored, we selected exactly one or exactly two year(s) of data for each carp; from the first registration after the acclimation period up to exactly 365 or 730 days later. Carp without at least 1 year of data were excluded from the analyses ($n = 17$ carp discarded). Discrepancy in the amount of data generated per individual carp is due to a stop in registration, which could have had multiple causes, e.g. death, disappearance from the study area, inactivity or only very local activity of the carp beyond the reach of a hydrophone or malfunctioning of the transmitter. Thirdly, we detected many false registrations on hydrophones 1 and 4, of which the transmitter signals had passed through the doors of two sluices but the fish did not. The number of registrations over time was—except for three cases—too low for a carp to have passed through the sluices. We include these registrations as movements of the carp to the area, but not as connectivity beyond the sluices. The remaining data consisted of nearly 1.5 million registrations of 45 carp (in total 62 carp-years, Figure S1).

To calculate potential seed dispersal from the combination of seed retention time and movement data we made three basic assumptions: (a) a dispersal event was considered when a fish moved between hydrophones, (b) a dispersal event would last 15 hr, based on the seed retention time and (c) seeds were uniformly available in the environment.

2.6 | Data analyses

All analyses were conducted in R (version 4.0.2; R Core Team, 2020). To test our first hypothesis we (a) compared the monthly carp activity, and (b) calculated realistic dispersal distance kernels, that estimated seed deposition probabilities by moving fish in our study system. Carp activity was measured in total distance moved per week in kilometres, and the monthly activity was compared by using a Kruskal–Wallis analysis and Dunn test. To calculate the dispersal kernels, we used the experimentally assessed chances of seed egestion over time, measured as hourly seed egestion probabilities calculated during trials with carp swimming at medium (0.25 m/s) and high (0.40 m/s) water velocities (Van Leeuwen et al., 2016). Data of both velocities were merged to get an estimation of digestive activity during normal gait transition speeds of carp (Tudorache et al., 2007). Data from the two plant species were not significantly different (Van Leeuwen et al., 2016) and were therefore merged to obtain a general estimation.

We constructed four seed dispersal distance kernels—one for each season—by combining all dispersal events in each season as follows. First, we ran through the data chronologically for each individual fish, and started 0–15 hr intervals when a fish moved from one (source) hydrophone to a next (destination) hydrophone (indicating movement). The last registration at the source hydrophone was assumed as the moment of ingestion of 100 seeds, and the start of a 15-hr time interval (termed ‘dispersal event’) at which these ingested seeds could potentially be egested. Based on the timing of arrival at a next hydrophone, we calculated distances moved over these 0–15 hr time intervals. If a fish moved to more than one station within this 15-hr interval or returned to the source hydrophone, distances were corrected accordingly. In total we constructed 1,044 movement trajectories.

Secondly, we combined this spatio-temporal data with experimentally assessed seed survival and egestion probabilities over time since ingestion (Van Leeuwen et al., 2016). Each calculated distance away from a source hydrophone had a corresponding time since ingestion, i.e. a retention time in the fish after ingestion. This resulted in a database in which each of the 100 seeds that were ingested at the source hydrophones and survived digestion obtained an assigned dispersal distance. Dispersal distances that matched exact distances between pairs of hydrophones were strongly overrepresented in the obtained distributions, because fish were always assumed to be moving when they were not within reach of a hydrophone. However, they could be stationary for several hours at exact positions of hydrophones. To avoid this bias in the distance distributions we removed all distances that exactly matched the distances between pairs of hydrophones, to obtain distributions that were independent of the chosen hydrophone setup as much as possible.

Thirdly, we fitted probability density functions to the four obtained distributions to mathematically describe the seed dispersal kernels for each season (Nathan et al., 2012) using the function ‘fitdist’ in package FITDISTRPLUS (Delignette-Muller & Dutang, 2015). Informed by the shape of the distributions we selected four likely one- or two-parameter density functions (i.e. exponential, log-normal, Gamma and Weibull) to the data and estimated the parameters of each distribution based on maximum-likelihood estimations. We selected the best fitting model for each season based on the Akaike information criterion (Burnham & Anderson, 2002), and calculated Kolmogorov–Smirnov (KS) statistics to assess model accuracy. Lastly, we compared the distance distributions among seasons using Kruskal–Wallis and Dunn tests (Table S1).

To test our second hypothesis, i.e. to assess if individual carp differed in their importance for seed dispersal, we plotted the distributions of maximum dispersal distances and the median dispersal distances per individual fish. The ranges of these distributions indicate the variation among individuals in their contribution to seed dispersal. We used general linear models to test possible external effects on the (natural log-transformed) dispersal distances. In a first model we tested the possible effect of body mass upon release (as continuous explanatory variable) and its initial release location (as factor with four levels) on 43 carp with at least 1 year of data. In a

second model we tested for a possible effect of the year after release (as factor: 1st or 2nd year after release), on $n = 14$ carp for which we had 2 years of data.

To test our third hypothesis, i.e. the potential effect of fragmentation in the study system, we assessed the connectivity within the study area. The number of times carp moved between two hydrophones was assumed to reflect the connectivity between two neighbouring hydrophones. For this analysis we worked with the full dataset including 69 carp (two tagged carp were never registered after release), because we expected effects of barriers to be independent of a possible acclimatization period or exact duration of fish tracking. We calculated for each pair of neighbouring hydrophones how many fish moved directly between them, which identified areas in the study system with low and higher connectivity. We defined low connectivity as when fish moved <10 times between neighbouring hydrophones, and analysed whether they were related to possible anthropogenic barriers by means of a Wilcoxon rank sum test with continuity correction.

3 | RESULTS

We detected a total of 1,044 movement trajectories by carp—with which we simulated the dispersal of 75,529 seeds throughout the study system. Median dispersal distance of these seeds was 1,207 m, ranging from zero to 16.1 km from the place of assumed ingestion. Mean movements of common carp (calculated per week) differed significantly per month (Figure 2; $\chi^2(11) = 38.256$, $p < 0.001$). April, May, June, July and October were the months in which the fish

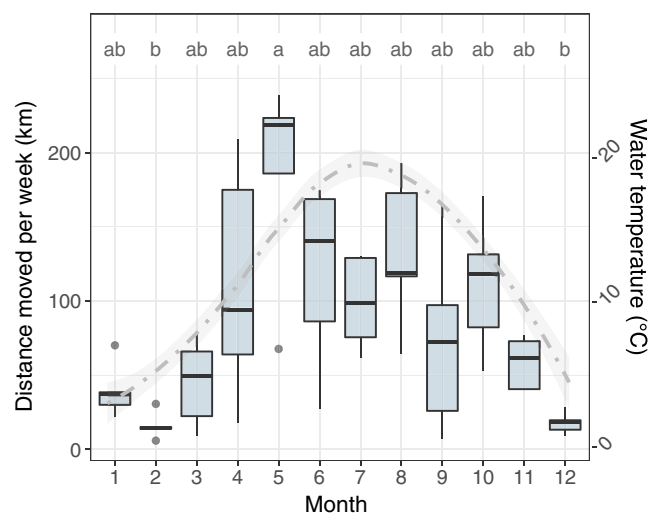


FIGURE 2 Box and whisker plots showing the distance moved per week in kilometres by all carp ($n = 45$ carp) for each month of the year. The letters indicate a significant difference between groups; months that do not share a common letter are significantly different from each other. The curve is the smoothed average water temperature of the study area waters in °C, measured at five locations (Noord Willemskanaal, Deurzerdiep, Drense Aa, Winschoterdiep and Zuidlaardermeer)

covered the longest distances. December and February showed very little movement.

The seed dispersal kernels all looked relatively similar, starting with high dispersal probabilities in a radius of 2–4 km from the locations of seed ingestion, and a decline of this probability at distances between 4 and 7 km (Figure 3; Figure S2). The best mathematical descriptions for the probability density functions for spring, summer and winter were Gamma distributions, and the Weibull distribution best fitted the data for autumn (all KS-statistics <0.1, Figure S3). Seasonal differences—under the assumption of constant seed ingestion probabilities year-round—were notably that (a) in winter there is a relatively high probability for short distance dispersal but a low long-distance dispersal potential, (b) in spring there is the greatest potential for LDD with a fat tail until 7 km, and a maximum beyond 16 km, (c) in summer and autumn there are high probabilities until 4 km and moderate probabilities for seed dispersal until 7 km (Table 1). Although summer and autumn differed in the number of

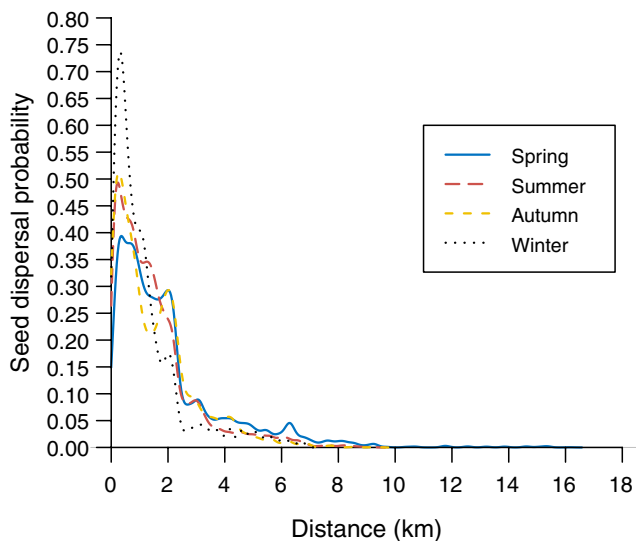


FIGURE 3 Dispersal distance kernels for each season, visualizing how the seed dispersal probability depends on distance from the location of assumed seed ingestion. Probabilities of seed survival, seed ingestion and the pattern of seed egestion over time were assumed constant year-round. Hence, seasonal differences in dispersal kernels are only due to differences in fish movements ($n = 45$ common carp). For separate kernels per season including confidence intervals see Figure S2

dispersal events, they did not significantly differ in their dispersal distances (Dunn test, $p = 0.46$), while all other season combinations did (Kruskal–Wallis chi-squared $\chi^2(3) = 1876.2$, $p < 0.001$, Table S1). The top 1% of all dispersal distances, indicative as a criterion for LDD (Cain et al., 2000), occurred once during autumn, twice during summer and eight times during spring (Table 1).

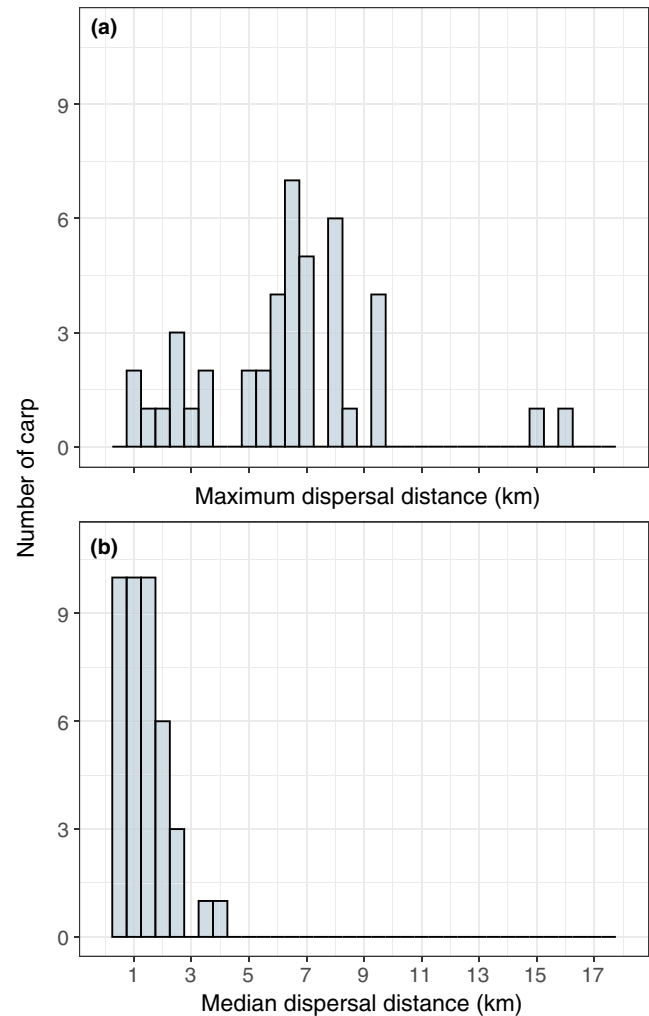


FIGURE 4 Histograms of the distributions of dispersal distances for each individual common carp in kilometres: (a) depicts the maximum dispersal distance per individual, and (b) the median dispersal distance ($n = 45$ carp)

Season	Dispersal events						
	Top 10%		Top 5%		Top 1%		100%
	<i>n</i>	km	<i>n</i>	km	<i>n</i>	km	<i>n</i>
Winter	5	8.90–6.74	2	6.67–6.73	0	—	79
Spring	54	5.41–16.14	29	6.55–16.14	8	8.76–16.14	376
Summer	35	5.61–9.27	15	6.58–9.27	2	8.35–9.27	392
Autumn	11	5.64–9.26	7	6.56–9.26	1	9.26	197
Total	105		53		11		1,044

TABLE 1 Overview of all simulated dispersal events with their corresponding distances. The table indicates how many of the longest dispersal events occurred during each season (n) for the top 10%, 5% and 1% of longest events, and how long these distance intervals were (km)

Individual carp varied in their potential contribution to seed dispersal (Figure 4; Figure S4). The distribution of median and maximum dispersal distances both showed gradients within the population, reflecting variation in an order of magnitude between individual carp. Variation in contribution to seed dispersal among individuals ranged from dispersal within 1 km to individuals dispersing seeds >16 km. Individual maximum dispersal distances

were independent of the four different release locations of the individuals (linear model $F_{3,1039} = 1.81$, $p = 0.14$). Fish initially released with the highest body masses dispersed seeds maximally 577 m farther than fish with the lowest body masses, indicating only a minor influence of body mass on the dispersal kernels ($F_{1,1039} = 11.90$, $p < 0.001$, Figure S4). For the 14 individuals that were monitored for 2 years, some moved more during the first year

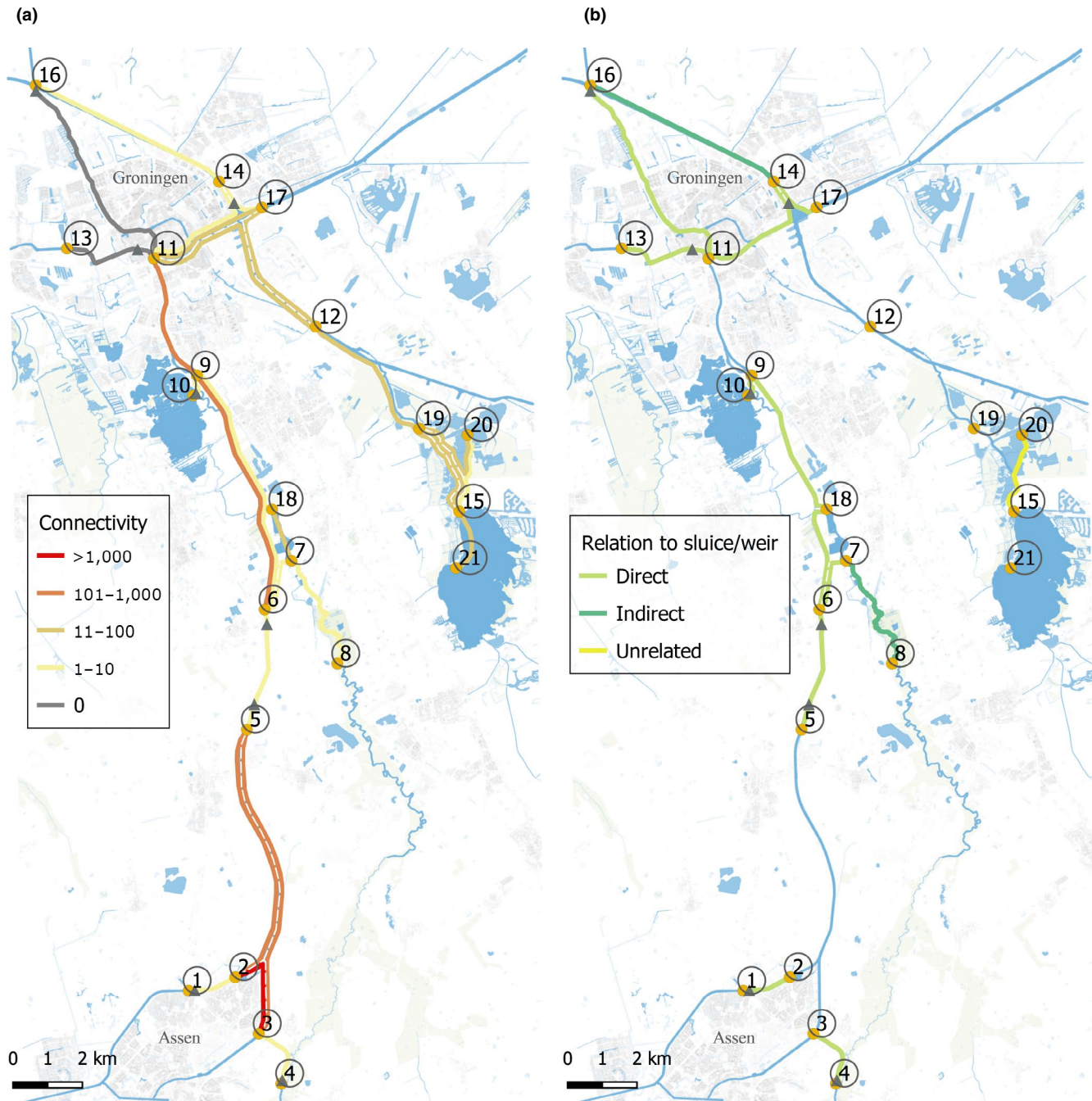


FIGURE 5 (a) Figure showing the connectivity of the study area. The lines connect pairs of neighbouring hydrophones, and are coloured according to the number of times a carp travelled between the two hydrophones. The connectivity ranges from zero (grey) to low (yellow), moderate (orange), high (dark orange) and intense (red). More information can be found in Table S2. (b) Figure with only the 14 pairs of neighbouring hydrophones that had restricted connectivity (<10 movements), with colours indicating their relation to a sluice or weir. Eleven pairs were directly separated by a sluice or weir (light green), and two pairs (dark green) indirectly: meaning that carp had to cross a sluice or weir to reach this pair of hydrophones. Low connectivity unrelated to sluices or weirs was only observed once (yellow)

of monitoring and some moved more during the second year—but the year of monitoring did not consistently affect the contribution of fish to seed dispersal (Figure S5).

The analysis of fish movements showed where carp have and have not moved (Figure 5a). We identified 14 pairs of neighbouring hydrophones with <10 fish movements in 2 years, and of these nine were separated by sluices and four by overshot weirs (Figure 5b). Of the in total 2,048 recorded movements among neighbouring hydrophones (Table S2), 27 movements (1.3%) occurred across a barrier. Mean number of movements among connected hydrophones (144 ± 291) was significantly higher than among hydrophones separated by barriers (2 ± 2 , Wilcoxon rank sum test with continuity correction: $W = 1$, $p < 0.001$).

4 | DISCUSSION

This study provides quantitative predictions on how far, when and how often temperate fish species may disperse wetland plant seeds. We show that seed dispersal by common carp is quantitatively most important during summer and autumn, when available seeds are locally dispersed commonly up to 4 km. There is potential for LDD up to 16 km during spring, but only for those seeds that are by this time still available in the habitat for ingestion. The contribution of individual fish to seed dispersal varied among individuals and within individuals by year, which emphasizes the importance of preserving all fish in populations to preserve the ecosystem services that a population provides. Sluices and weirs formed barriers in our study system that restricted fish movement, and strongly reduced the potential for ichthyochory.

4.1 | Seasonal difference in seed dispersal potential

Freshwater fish are known to move for various reasons, including search for food, avoidance of predators and migration to spawning areas (Brönmark et al., 2014). We observed the most movement in the common carp in the month of May, which coincided with rising water temperatures in spring towards above 15°C: the beginning of movement towards suitable spawning habitat in carp (Crivelli, 1981, Figure 2).

Monthly differences in activity translated into varying contributions to potential seed dispersal, as illustrated in the simulated dispersal kernels that show differences in quantity and extent of seed dispersal among the seasons. In summer and autumn the fish showed frequent dispersal events and good potential for seeds to be transported over several kilometres from their location of ingestion. The farthest movements—possibly resulting in LDD—occurred in spring. However, this likely does not coincide with maximum seed availability in the habitat nor with times that fish consume most seeds (Boedeltje et al., 2019). Seed availability across all wetland species is generally lower in spring due to degradation during winter (VonBank et al., 2018) and germination in spring (Leck & Simpson, 1987). These

factors combined lead us to deduce that seed dispersal over moderate distances by common carp is quantitatively most important during summer and autumn (i.e. between June and November), as these are times that freshwater fish such as carp move often and seeds are available for consumption.

4.2 | Individual differences in seed dispersal potential

Intraspecific differences among seed dispersers are in need of more attention (Zwolak et al., 2020). Our study showed considerable variation within the carp population for dispersal distances by individuals, for both maximum and median distances. Some of the individuals that we tracked for 2 years also showed different behaviour in these 2 years. This indicates that (a) under similar circumstances different individuals can contribute differently to seed dispersal, and that (b) the same individual in a different situation can contribute differently to seed dispersal. This observed variation in disperser quality among individuals supports our hypothesis that within a certain year only a portion of all individuals in a fish population is responsible for the majority of long-distance dispersal events. With only 2 years of data per individual we cannot yet assess whether some individuals may always contribute more to seed dispersal than others—but consistent life strategy differences between individuals have been documented in carp (Klefoth et al., 2017). This intraspecific variation in movements can sometimes even exceed interspecific variation (Harrison et al., 2019).

The probability for seed dispersal is thus not only dependent on the fish and plant species, but also to a large extent on the individuals within each species. Consistent variation in movement within a species is not always ascribed to animal personality (Fraser et al., 2001), but can in some studies be explained by gender (Stehfest et al., 2014) or related to weight (Anderson et al., 2011). In our study we did not have information on the sex of the carp, and the effects of body mass on maximum dispersal distances were only weak. Hence, we here document variation with the aim of stimulating future studies to detect potential underlying causes.

4.3 | Sluices and weirs as barriers for seed dispersal

The connectivity analysis suggested that water-regulating structures in the study area inhibited carp movement and its consequential seed dispersal. While a sluice is mostly closed and opens its gates occasionally, a weir is a permanent one-directional passage. Both can inhibit movement of fish (Baumgartner et al., 2014; Harris et al., 2017). To date, no study had assessed how endozoochorous dispersal may be affected by barriers (Jones et al., 2020), but our study signifies how river fragmentation by barriers may have direct consequences for fish as well as indirect consequences for the ecosystem services they can fulfil.

4.4 | Variation among fish and plant species

For this study we selected common carp as our model species because it is an opportunistic omnivore that is known to regularly ingest large numbers (>1,000) of plant seeds and invertebrate resting eggs in temperate habitats (Crivelli, 1981; Pollux, 2011). For common carp, we showed potential to disperse seeds over several kilometres, focusing on *Carex* sp. plant seeds for which detailed retention time data were available. These results provide indications for the ichthyochory potential of omnivorous cyprinids, however, we should note that ichthyochory is known to vary extensively among both fish and plant species (Brodersen et al., 2012). For instance, variation in feeding strategy among freshwater cyprinids can lead to variation in the plant species each fish species can disperse (Boedeltje et al., 2019).

Previous experimental work has shown that seed retention times—and therefore potential dispersal distances of surviving seeds—vary less among seeds with different morphologies than their survival (Boedeltje et al., 2015, 2016). This implies that the shapes of the here obtained dispersal kernels (Pollux et al., 2006)—resulting from only fish movements and retention times—could be interpreted more broadly, as these distributions (Gamma, Weibull) are also in line with what is common in zoochory. However, the magnitude of the here calculated seed dispersal probabilities will likely vary extensively depending on seed morphologies (e.g. soft, large seeds rather than small, hard seeds) and may be much lower or higher for fish species with different digestive systems (Boedeltje et al., 2019; Pollux, 2011; Pollux et al., 2006).

5 | CONCLUSIONS

This study showed that freshwater cyprinids can potentially disperse seeds over several kilometres in temperate regions, that dispersal quantitatively depends on the season, and that individual fish can differ substantially in their contribution to dispersal. This variation calls for conservation of intact fish populations throughout the annual cycle. Potential dispersal distances exceeded 16 km, except for when anthropogenic barriers were present. Together this implies that conservation of fish and restoring connectivity in underwater landscapes will aid to preserve a potentially important service fish provide to the functioning of ecosystems.

ACKNOWLEDGEMENTS

The authors thank Hermen Klomp from Waterschap Hunze en Aa's for providing records of the monthly water temperature for Noord-Willems canal and connecting waterways (Deurzerdiep, Drense Aa, Winschoterdiep and Zuidlaardermeer) and Jesper Lysgaard Rasmussen for help with data analyses. This study was supported by Marie S-Curie Actions–H2020 grant 750240 of the EU to C.H.A.v.L. The research plan of the tracking study (VA2014_38 versie2) by the Royal Dutch Angling Association was approved by the animal experiment committee The Animal Science Group (ASG)-Lelystad of

Wageningen UR. This is publication number 7135 of the Netherlands Institute of Ecology (NIOO-KNAW). We thank Janny Bosman for providing the photo for the Plain Language Summary.

AUTHORS' CONTRIBUTIONS

C.H.A.v.L., R.v.A. and A.J.E.M. conceived the ideas and designed methodology; C.H.A.v.L. collected the experimental seed retention time data and R.v.A. collected all fish tracking data; A.J.E.M. and C.H.A.v.L. analysed the data with help of R.v.A.; A.J.E.M. and C.H.A.v.L. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.x3ffbg7hh> (Mulder et al., 2020).

ORCID

Casper H. A. van Leeuwen  <https://orcid.org/0000-0003-2833-7775>

REFERENCES

- Anderson, J. T., Nuttle, T., Rojas, J. S. S., Pendergast, T. H., & Flecker, A. S. (2011). Extremely long-distance seed dispersal by an overfished Amazonian frugivore. *Proceedings of the Royal Society B: Biological Sciences*, 278, 3329–3335. <https://doi.org/10.1098/rspb.2011.0155>
- Bajer, P. G., Lim, H., Travaline, M. J., Miller, B. D., & Sorensen, P. W. (2010). Cognitive aspects of food searching behavior in free-ranging wild Common Carp. *Environmental Biology of Fishes*, 88, 295–300. <https://doi.org/10.1007/s10641-010-9643-8>
- Baumgartner, L., Zampatti, B., Jones, M., Stuart, I., & Mallen-Cooper, M. (2014). Fish passage in the Murray-Darling Basin, Australia: Not just an upstream battle. *Ecological Management & Restoration*, 15, 28–39. <https://doi.org/10.1111/emr.12093>
- Boedeltje, G., Jongejans, E., Spanings, T., & Verberk, W. C. E. P. (2016). Effect of gut passage in fish on the germination speed of aquatic and riparian plants. *Aquatic Botany*, 132, 12–16. <https://doi.org/10.1016/j.aquabot.2016.03.004>
- Boedeltje, G., Klutman, B., Schaap, M., Sollman, P., de Vos, M., Lenssen, J. P. M., & Verberk, W. C. E. P. (2019). Plant dispersal in a temperate stream by fish species with contrasting feeding habits: The role of plant traits, fish diet, season, and propagule availability. *Frontiers in Ecology and Evolution*, 7, <https://doi.org/10.3389/fevo.2019.00054>
- Boedeltje, G., Spanings, T., Flik, G., Pollux, B. J. A., Sibbing, F. A., & Verberk, W. C. E. P. (2015). Effects of seed traits on the potential for seed dispersal by fish with contrasting modes of feeding. *Freshwater Biology*, 60(5), 944–959. <https://doi.org/10.1111/fwb.12550>
- Brodersen, J., Nilsson, P. A., Chapman, B. B., Skov, C., Hansson, L.-A., & Bronmark, C. (2012). Variable individual consistency in timing and destination of winter migrating fish. *Biology Letters*, 8, 21–23. <https://doi.org/10.1098/rsbl.2011.0634>
- Brönmark, C., Hulthén, K., Nilsson, P. A., Skov, C., Hansson, L. A., Brodersen, J., & Chapman, B. B. (2014). There and back again: Migration in freshwater fishes. *Canadian Journal of Zoology*, 92, 467–479. <https://doi.org/10.1139/cjz-2012-0277>
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed., pp. 1–488). Springer.
- Cain, M. L., Milligan, B. G., & Strand, A. E. (2000). Long-distance seed dispersal in plant populations. *American Journal of Botany*, 87, 1217–1227. <https://doi.org/10.2307/2656714>

- Chapman, B. B., Hulthén, K., Blomqvist, D. R., Hansson, L. A., Nilsson, J. Å., Brodersen, J., Anders Nilsson, P., Skov, C., & Brönmark, C. (2011). To boldly go: Individual differences in boldness influence migratory tendency. *Ecology Letters*, 14, 871–876. <https://doi.org/10.1111/j.1461-0248.2011.01648.x>
- Chapman, B. B., Skov, C., Hulthén, K., Brodersen, J., Nilsson, P. A., Hansson, L. A., & Brönmark, C. (2012). Partial migration in fishes: Definitions, methodologies and taxonomic distribution. *Journal of Fish Biology*, 81, 479–499. <https://doi.org/10.1111/j.1095-8649.2012.03349.x>
- Corlett, R. T., & Westcott, D. A. (2013). Will plant movements keep up with climate change? *Trends in Ecology & Evolution*, 28, 482–488. <https://doi.org/10.1016/j.tree.2013.04.003>
- Correa, S. B., Costa-Pereira, R., Fleming, T., Goulding, M., & Anderson, J. T. (2015). Neotropical fish–fruit interactions: Eco-evolutionary dynamics and conservation. *Biological Reviews*, 90, 1263–1278. <https://doi.org/10.1111/brv.12153>
- Correa, S. B., Winemiller, K. O., Lopez-Fernandez, H., & Galetti, M. (2007). Evolutionary perspectives on seed consumption and dispersal by fishes. *BioScience*, 57, 748–756. <https://doi.org/10.1641/B570907>
- Crivelli, A. J. (1981). The biology of the common carp, *Cyprinus carpio* L. in the Camargue, southern France. *Journal of Fish Biology*, 18, 271–290. <https://doi.org/10.1111/j.1095-8649.1981.tb03769.x>
- Delignette-Muller, M. L., & Dutang, C. (2015). fitdistrplus: An R package for fitting distributions. *Journal of Statistical Software*, 64, 1–34.
- Fraser, D. F., Gilliam, J. F., Daley, M. J., Le, A. N., & Skalski, G. T. (2001). Explaining leptokurtic movement distributions: Intrapopulation variation in boldness and exploration. *The American Naturalist*, 158, 124–135. <https://doi.org/10.1086/321307>
- González-Varo, J. P., López-Bao, J. V., & Guitián, J. (2013). Functional diversity among seed dispersal kernels generated by carnivorous mammals. *Journal of Animal Ecology*, 82, 562–571. <https://doi.org/10.1111/1365-2656.12024>
- Harris, J., Kingsford, R., Peirson, W., & Baumgartner, L. (2017). Mitigating the effects of barriers to freshwater fish migrations: The Australian experience. *Marine and Freshwater Research*, 68, 614–628. <https://doi.org/10.1071/MF15284>
- Harrison, P. M., Keeler, R. A., Robichaud, D., Mossop, B., Power, M., & Cooke, S. J. (2019). Individual differences exceed species differences in the movements of a river fish community. *Behavioral Ecology*, 30, 1289–1297. <https://doi.org/10.1093/beheco/arz076>
- Horn, M. H., Correa, S. B., Parolin, P., Pollux, B. J. A., Anderson, J. T., Lucas, C., Widmann, P., Tjui, A., Galetti, M., & Goulding, M. (2011). Seed dispersal by fishes in tropical and temperate fresh waters: The growing evidence. *Acta Oecologica-International Journal of Ecology*, 37, 561–577. <https://doi.org/10.1016/j.actao.2011.06.004>
- Jenkins, J. A., Bart Jr., H. L., Bowker, J. D., Bowser, P. R., MacMillan, J. R., Nickum, J. G., Rachlin, J. W., Rose, J. D., Sorensen, P. W., & Warkentine, B. E. (2014). Guidelines for use of fishes in research—Revised and expanded, 2014. *Fisheries*, 39, 415–416.
- Jepsen, N., Koed, A., Thorstad, E. B., & Baras, E. (2002). Surgical implantation of telemetry transmitters in fish: How much have we learned? *Hydrobiologia*, 483, 239–248.
- Jones, P. E., Consuegra, S., Börger, L., Jones, J., & García de Leaniz, C. (2020). Impacts of artificial barriers on the connectivity and dispersal of vascular macrophytes in rivers: A critical review. *Freshwater Biology*, 65(6), 1165–1180. <https://doi.org/10.1111/fwb.13493>
- Klefoth, T., Skov, C., Kuparinen, A., & Arlinghaus, R. (2017). Toward a mechanistic understanding of vulnerability to hook-and-line fishing: Boldness as the basic target of angling-induced selection. *Evolutionary Applications*, 10, 994–1006. <https://doi.org/10.1111/eva.12504>
- Kleyheeg, E., Fiedler, W., Safi, K., Waldenström, J., Wikelski, M., & van Toor, M. L. (2019). A comprehensive model for the quantitative estimation of seed dispersal by migratory mallards. *Frontiers in Ecology and Evolution*, 7. <https://doi.org/10.3389/fevo.2019.00040>
- Leck, M. A., & Simpson, R. L. (1987). Seed bank of a freshwater tidal wetland: Turnover and relationship to vegetation change. *American Journal of Botany*, 74, 360–370. <https://doi.org/10.1002/j.1537-2197.1987.tb08618.x>
- Levine, J. M., & Murrell, D. J. (2003). The community-level consequences of seed dispersal patterns. *Annual Review of Ecology and Systematics*, 34, 549–574. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132400>
- Lubinski, K., Van Vooren, A., Farabee, G., Janecek, J., & Jackson, S. (1986). Common carp in the upper Mississippi River. *Hydrobiologia*, 136, 141–153. <https://doi.org/10.1007/BF00051511>
- McConkey, K. R., Prasad, S., Corlett, R. T., Campos-Arceiz, A., Brodie, J. F., Rogers, H., & Santamaria, L. (2012). Seed dispersal in changing landscapes. *Biological Conservation*, 146, 1–13. <https://doi.org/10.1016/j.biocon.2011.09.018>
- Miao, S., & Zou, C. B. (2009). Seasonal variation in seed bank composition and its interaction with nutrient enrichment in the Everglades wetlands. *Aquatic Botany*, 90, 157–164. <https://doi.org/10.1016/j.aquabot.2008.08.006>
- Mokany, K., Prasad, S., & Westcott, D. A. (2014). Loss of frugivore seed dispersal services under climate change. *Nature Communications*, 5, 1–7. <https://doi.org/10.1038/ncomms4971>
- Mulder, A. J. E., van Aalderen, R., & Van Leeuwen, C. H. A. (2020). Data from: Tracking temperate fish reveals their relevance for plant seed dispersal. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.x3ffbg7hh>
- Nathan, R. (2006). Long-distance dispersal of plants. *Science*, 313, 786–788. <https://doi.org/10.1126/science.1124975>
- Nathan, R., Klein, E., Robledo-Arnuncio, J. J., & Revilla, E. (2012). Dispersal kernels: Review. In J. Clobert, M. Baguette, T. G. Benton, & J. M. Bullock (Eds.), *Dispersal ecology and evolution* (pp. 187–210). Oxford University Press.
- Nathan, R., & Muller-Landau, H. C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, 15, 278–285. [https://doi.org/10.1016/S0169-5347\(00\)01874-7](https://doi.org/10.1016/S0169-5347(00)01874-7)
- Nathan, R., Schurr, F. M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., & Tsoar, A. (2008). Mechanisms of long-distance seed dispersal. *Trends in Ecology & Evolution*, 23, 638–647. <https://doi.org/10.1016/j.tree.2008.08.003>
- Ozinga, W. A., Romermann, C., Bekker, R. M., Prinzing, A., Tamis, W. L. M., Schaminée, J. H. J., Hennekens, S. M., Thompson, K., Poschlod, P., Kleyer, M., Bakker, J. P., & van Groenendaal, J. M. (2009). Dispersal failure contributes to plant losses in NW Europe. *Ecology Letters*, 12, 66–74. <https://doi.org/10.1111/j.1461-0248.2008.01261.x>
- Piazzon, M., Larrinaga, A. R., Rodríguez-Pérez, J., Latorre, L., Navarro, L., & Santamaria, L. (2012). Seed dispersal by lizards on a continental-shelf island: Predicting interspecific variation in seed rain based on plant distribution and lizard movement patterns. *Journal of Biogeography*, 39, 1984–1995. <https://doi.org/10.1111/j.1365-2699.2012.02718.x>
- Pollux, B. J. A. (2011). The experimental study of seed dispersal by fish (ichthyochory). *Freshwater Biology*, 56, 197–212. <https://doi.org/10.1111/j.1365-2427.2010.02493.x>
- Pollux, B. J. A. (2017). Consistent individual differences in seed disperser quality in a seed-eating fish. *Oecologia*, 183, 81–91. <https://doi.org/10.1007/s00442-016-3749-4>
- Pollux, B. J. A., De Jong, M., Steegh, A., Ouborg, N. J., Van Groenendaal, J. M., & Klaassen, M. (2006). The effect of seed morphology on the potential dispersal of aquatic macrophytes by the common carp (*Cyprinus carpio*). *Freshwater Biology*, 51, 2063–2071. <https://doi.org/10.1111/j.1365-2427.2006.01637.x>
- R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org>
- Rehm, E., Fricke, E., Bender, J., Savidge, J., & Rogers, H. (2019). Animal movement drives variation in seed dispersal distance in a plant–animal

- network. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20182007. <https://doi.org/10.1098/rspb.2018.2007>
- Russi, L., Cocks, P., & Roberts, E. (1992). Seed bank dynamics in a Mediterranean grassland. *Journal of Applied Ecology*, 29(3), 763–771. <https://doi.org/10.2307/2404486>
- Russo, S. E., Portnoy, S., & Augspurger, C. K. (2006). Incorporating animal behavior into seed dispersal models: Implications for seed shadows. *Ecology*, 87, 3160–3174.
- Soomers, H., Karssenberg, D., Soons, M. B., Verweij, P. A., Verhoeven, J. T. A., & Wassen, M. J. (2013). Wind and water dispersal of wetland plants across fragmented landscapes. *Ecosystems*, 16, 434–451. <https://doi.org/10.1007/s10021-012-9619-y>
- Stehfest, K. M., Patterson, T. A., Barnett, A., & Semmens, J. M. (2014). Intraspecific differences in movement, dive behavior and vertical habitat preferences of a key marine apex predator. *Marine Ecology Progress Series*, 495, 249–262. <https://doi.org/10.3354/meps10563>
- Tudorache, C., Viaenen, P., Blust, R., & De Boeck, G. (2007). Longer flumes increase critical swimming speeds by increasing burst–glide swimming duration in carp *Cyprinus carpio*, L. *Journal of Fish Biology*, 71, 1630–1638. <https://doi.org/10.1111/j.1095-8649.2007.01620.x>
- Valido, A., & Olesen, J. M. (2019). Frugivory and seed dispersal by lizards: A global review. *Frontiers in Ecology and Evolution*, 7. <https://doi.org/10.3389/fevo.2019.00049>
- van Aalderen, R. A. A., Romeijn, W., & Wijmans, P. A. D. M. (2018). *Migratie-onderzoek karper Noord-Willemskanaal*. Sportvisserij Nederland.
- Van Leeuwen, C. H. A., Beukeboom, R., Nolet, B. A., Bakker, E. S., & Pollux, B. J. A. (2016). Locomotion during digestion changes current estimates of seed dispersal kernels by fish. *Functional Ecology*, 30, 215–225. <https://doi.org/10.1111/1365-2435.12485>
- Van Leeuwen, C. H. A., Dalen, K., Museth, J., Junge, C., & Vøllestad, L. A. (2018). Habitat fragmentation has interactive effects on the population genetic diversity and individual behaviour of a freshwater salmonid fish. *River Research and Applications*, 34, 60–68. <https://doi.org/10.1002/rra.3226>
- Van Leeuwen, C. H. A., Lovas-Kiss, Á., Ovegård, M., & Green, A. J. (2017). Great cormorants reveal overlooked secondary dispersal of plants and invertebrates by piscivorous waterbirds. *Biology Letters*, 13, 20170406. <https://doi.org/10.1098/rsbl.2017.0406>
- Van Leeuwen, C. H. A., Tella, J. L., & Green, A. J. (2020). Editorial: Animal-mediated dispersal in understudied systems. *Frontiers in Ecology and Evolution*, 7. <https://doi.org/10.3389/fevo.2019.00508>
- Van Leeuwen, C. H. A., Van der Velde, G., Van Groenendael, J. M., & Klaassen, M. (2012). Gut travellers: Internal dispersal of aquatic organisms by waterfowl. *Journal of Biogeography*, 39, 2031–2040. <https://doi.org/10.1111/jbi.12004>
- Vittoz, P., & Engler, R. (2007). Seed dispersal distances: A typology based on dispersal modes and plant traits. *Botanica Helvetica*, 117, 109–124. <https://doi.org/10.1007/s00035-007-0797-8>
- VonBank, J. A., DeBoer, J. A., Casper, A. F., & Hagy, H. M. (2018). Ichthyochory in a temperate river system by common carp (*Cyprinus carpio*). *Journal of Freshwater Ecology*, 33, 83–96.
- Wehncke, E. V., Hubbell, S. P., Foster, R. B., & Dalling, J. W. (2003). Seed dispersal patterns produced by white-faced monkeys: Implications for the dispersal limitation of neotropical tree species. *Journal of Ecology*, 91, 677–685. <https://doi.org/10.1046/j.1365-2745.2003.00798.x>
- Westcott, D. A., Bentrupperbaumer, J., Bradford, M. G., & McKeown, A. (2005). Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. *Oecologia*, 146, 57–67. <https://doi.org/10.1007/s00442-005-0178-1>
- Wilt, R. D., & Emmerik, W. V. (2008). *Kennisdocument karper: Cyprinus carpio (Linnaeus, 1758)*. Kennisdocument 22. Sportvisserij Nederland.
- Yoshikawa, T., Kawakami, K., & Masaki, T. (2019). Allometric scaling of seed retention time in seed dispersers and its application to estimation of seed dispersal potentials of theropod dinosaurs. *Oikos*. <https://doi.org/10.1111/oik.05827>
- Zwolak, R., & Sih, A. (2020). Animal personalities and seed dispersal: A conceptual review. *Functional Ecology*, 34(7), 1294–1310. <https://doi.org/10.1111/1365-2435.13583>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Mulder AJE, van Aalderen R, van Leeuwen CHA. Tracking temperate fish reveals their relevance for plant seed dispersal. *Funct Ecol*. 2021;00:1–11. <https://doi.org/10.1111/1365-2435.13757>