



Patterns and predictors of fish dispersal in rivers

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Abstract

Quantifying fish dispersal and identifying its general predictors is key for understanding temporal patterns in population dynamics, emigration and immigration, meta-community dynamics, many ecological processes and predicting recovery time or population responses to environmental changes. This is the first comprehensive quantitative meta-analysis of heterogeneous freshwater fish movement, aiming to determine mobile and stationary shares of fish communities, their dispersal distances and key predictors of dispersal patterns. By reviewing and analysing 160 empirical data sets from 71 studies covering 62 fishes in streams, it goes beyond previous studies of salmonids' heterogeneous movement. Based on fitted leptokurtic dispersal kernels, the movement distances of (i) a stationary component (σ_{stat}) and (ii) a mobile component (σ_{mob}) as well as the (iii) share of each component (p) were calculated. The median movement distance of the stationary and mobile component of a fish population was 36.4 and 361.7 m, respectively. The share of the stationary individuals was high (median = 66.6%), but unrelated to movement distance. Single and multiple linear regressions as well as mixed-effects models revealed movement distances positively related to fish length, aspect ratio of the caudal fin, stream size and duration of the study. Furthermore, movement distance differed between taxonomic families. The quantitative parameters of heterogeneous fish movement provided are prerequisite to estimate time lags in fish response to river rehabilitation, temporal patterns in species dispersal, and minimum effective size of potential founder populations for species conservation and stock recovery based on minimum numbers of specimen to disperse.

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Introduction

Spawning migrations of fish and the seasonality of spawning runs have been recognized for hundreds of years, and most of the early work has concentrated on distance, triggering factors and the philopatry of fish migration (Harden Jones 1968). More recently, perception and studies emerged of non-spawning movements in fish. After some early attempts of measuring fish movement at various spatial and temporal scales (Thompson 1933), fish movement has been controversially discussed mainly pinned on the central question of how mobile or resident fish are. The argumentation ranged from Gerking's (1959) 'restricted movement paradigm' (RMP; sensu Gowan *et al.* 1994) to consider fish as totally mobile (Linfield 1985).

The seminal works of MacArthur and Wilson (1963, 1967) on island biogeography have especially fuelled the science on species dispersal, because of the central role of emigration and immigration in species turnover. Later on metapopulation biology provides the concept for the dynamics of migration among local populations (reviewed by Hanski 1998) with particular interests in effective migrants and migration rates between subpopulations as determinants of gene flow between and genetic diversity within subpopulations (Wright 1978). The observed geographic orientation in genetic lineages within natural populations finally resulted in the growth of phylogeography as scientific discipline to elucidate dispersal and colonization processes at very large temporal and spatial scales (Avise *et al.* 1987).

Dispersal acts as a key determinant in population dynamics and interactively links ecology, behaviour, genetics and evolution (Lidicker and Stenseth 1992; McMahon and Matter 2006). Especially fish dispersal is a fundamental process, taking place in stream networks along linear and branched dimensions (Fagan 2002; Lowe and Likens 2006). Dispersal has been defined as a one-way movement away from a certain site (Lidicker and Stenseth 1992), which arises from behavioural decisions at the level of individuals in various

life stages of fish and at different temporal and spatial scales (Fausch *et al.* 2002).

Despite of its well-known ecological importance for gene flow (Wright 1978; Hanski 1998; Heggnes *et al.* 2006), distribution of species, species turnover and recolonization of newly available habitats (Detenbeck *et al.* 1992; Albanese *et al.* 2009), information on the spatial and temporal patterns of fish movement are surprisingly limited. Deeper knowledge on the amount of dispersal, its distances or speed and on the share of mobile dispersal-relevant individuals on the population is widely lacking. This makes it especially challenging to predict species range shifts in response to global environmental changes, the invasion success and speed of non-native species or the recolonization potential, respectively, recovery time of endangered species following conservation efforts (Kokko and Lopez-Sepulcre 2006).

In recent years, the concept of heterogeneous movement was steadily developed (Skalski and Gilliam 2000; Rodríguez 2002), which considers fish populations consisting of both stationary and mobile components. The stationary component is reflected by a high peak in a leptokurtic dispersal kernel and can be linked to the concept of home range. In contrast, the mobile part of a population is characterized by a remarkably wider spread and higher ability to move and becomes apparent in a leptokurtic dispersal kernel as typical fat tail. Although it could be shown that the spatiotemporal pattern of dispersal is very sensitive to the shape of the dispersal kernel (Kot *et al.* 1996), there is only sparse information on leptokurtic dispersal kernels for fish and its appropriate movement parameters. The mobile component of each population is hypothesized as being responsible for individuals exchange between populations and thus decisive for dispersal, colonization and recolonization. Accordingly, the number of mobile individuals determines the successful spread into new habitats, and their proportion becomes a proxy to predict the minimum total size of a potential founder population suitable for species' recovery and recolonization of restored habitats. Estimating the average share of mobile individuals

within populations allows for assessing (i) time lags between river rehabilitation and fish response in relation to distance and size of the nearest founder population, (ii) species-specific invasion potential of and faunal homogenization by exotics and (iii) the average time frame needed by species to respond to environmental changes by range shifts. In particular, the latter becomes relevant due to the predicted global environmental changes within the next decades (e.g. Cox *et al.* 2000; Döll and Zhang 2010).

Therefore, the main objective of this study was to synthesize the current knowledge and to refit empirical data sets to leptokurtic dispersal kernels to obtain species-specific estimates for fish movement parameters and their spatial and temporal patterns. If movement constitutes a response to internal (e.g. genetic, ontogenetic, physiologic, homing) and external cues (e.g. habitat-suitability, light, temperature, hydrology, water quality, population density) as suggested by Lucas and Baras (2001), then also dispersal kernels shall strongly depend on the fish studied as well as on the environmental characteristics of the studied rivers. Therefore, the second objective of this study was to identify and to analyse factors that determine the mobile component of a fish population and their dispersal abilities. It was hypothesized that the movement parameters depend on (i) fish length, (ii) aspect ratio of the caudal fin, both as proxies for swimming performance, (iii) the size of the studied stream [discharge, stream width and stream order] reflecting habitat availability and home range and (iv) the duration of the study determining the temporal patterns of dispersal. Finally, this study aimed in providing vital quantitative information on fish movement and its predictors for future applications such as in dispersal models, species conservation, river rehabilitation or water management.

Methods

Data acquisition

In a first step, field studies of heterogeneous fish movement have been collected from peer reviewed and 'grey' literature using the electronic search engines ISI Web of knowledge, Scopus and Google Scholar. In a second step, additional reports that were cited in the retrieved studies were sourced and included in the survey. Only those studies

were selected for analyses (i) which were conducted in rivers, (ii) reported a number or percentage of fish recaptured or detected in more than three distance classes and (iii) were not specifically conducted to analyse obligatory life cycle migrations (e.g. spawning migrations; see references indicated with asterisks).

A leptokurtic dispersal kernel most accurately describes heterogeneous fish movement (Skalski and Gilliam 2000; Rodríguez 2002). Consequently, the reported data were either directly extracted from the text or measured from provided graphs and subsequently transformed to percentages of fish recaptured per distance class to obtain comparable movement parameters based on leptokurtic movement. The data points were then used to derive mathematical equations which relate cumulative percentages to a certain area defined by distance class limits under the dispersal curve. These mathematical equations were then used as conditions to optimally fit the function of the dispersal kernel (Equation 1) by minimizing the errors in the conditional equations. In contrast to other statistical methods based on absolute or relative counts per distance class, this mathematical method allowed for both exactly defining the area of recapture (upper and lower limit of each distance class instead of class means) and incorporating data with open distance classes (e.g. y % of the population moves further than x metres) into the analysis.

The fitted dispersal kernel basically consists of two superimposed normal distributions and provides a probability of occurrence of an individual as a function of the distance (x) from the source population:

$$F(x) = p \times \frac{1}{\sqrt{2\pi\sigma_{\text{stat}}^2}} \times e^{-\frac{(x-\mu)^2}{2\sigma_{\text{stat}}^2}} + (1-p) \times \frac{1}{\sqrt{2\pi\sigma_{\text{mob}}^2}} \times e^{-\frac{(x-\mu)^2}{2\sigma_{\text{mob}}^2}} \quad (1)$$

where σ_{stat} represents the mean movement distance of the stationary component, σ_{mob} of the mobile component and p the share of the stationary component on the total population.

All curve-fitting calculations were performed using the least square fit from the optimize package of Scipy (Jones *et al.* 2001) which allows using equations as fitting conditions instead of data points only. Upstream and downstream movement was not distinguished as some studies

only provided one-directional movement data, and no common directional bias was clearly observable. Accordingly, μ in dispersal function was set to zero for simplicity. For all fitted solutions, the relative errors in the sum of squares were below 1.49012×10^{-8} . Data sets that could not be successfully optimized as their parameter estimates were not converging were not considered for further analysis.

Besides the movement parameters, potential explanatory variables were collected for each data set comprising (i) fish morphometry (length and aspect ratio), (ii) river characteristics (stream order, discharge and stream width) and (iii) the time duration of the study.

If a fish length frequency was provided in the original paper, the mean fish length was used as reported or calculated. In cases where only a size range was reported in the original paper, a mean size between minimum and maximum was used. If no fish length was given ($n = 42$), the common length was used reported in fishbase.org (Froese and Pauly 2011). As a second morphometric parameter and a proxy for swimming performance, the aspect ratio of the caudal fin was extracted for each fish species from fishbase.org (Froese and Pauly 2011), which is related to the typical swimming mode of a species (Webb 1984).

Many of the analysed studies already provided information on stream order (Strahler 1957), mean stream width and/or mean discharge. If one of these parameters was not reported, retrieving cited descriptive papers, enquiring to the original authors or asking national hydrological agencies for additional information, have completed it. In addition, the mean stream width was measured from the freely available Google Earth mapping service [version 6.0.1.2032 (beta)], unless it was already reported in the original source. For the time duration of study, the maximum reported time between marking and recapture was considered, respectively, the time between two consecutive sightings. This represents the time interval where all fish (even far dispersing fish) were recaptured at least once.

Data analysis

First, it has been analysed whether there is any correlation between the three movement parameters. Thus, a simple correlation matrix for σ_{stat} , σ_{mob} and p and the ratio between σ_{mob} and σ_{stat} was calculated.

Second, linear regressions were used to analyse the single relationships between the movement parameters (σ_{stat} , σ_{mob} and p) and fish length, aspect ratio, stream order, discharge, stream width and study time. To meet the assumptions for linear models, the response variable was firstly log-transformed and the predictor variable subsequently transformed (log or square root transformation) if indicated by a Box–Cox test. In addition, data were stratified subsampled, because pseudo replications among data collected in the same water body would bias the results. Therefore, a single data set per species per study reach was randomly selected and regressions repeatedly calculated (999 replicates). For each regression, a mean for R^2 , the P -value and the regression parameter estimates can be retrieved.

Third, multiple linear regression models were fitted for four different predictor variable sets: one complete model including all parameters (fish length, aspect ratio, stream order, discharge, stream width and time) and three models each include only one of the three proxies for stream size, because stream order, discharge and width are highly correlated. As for the single models, the subsample approach was used to eliminate the influence of pseudo replicates. Furthermore, only complete data sets (all predictor variables known) were considered for the multiple linear models. Finally, the parameter estimates and measures of the goodness of fit [adjusted R^2 , Akaike's information criterion (AIC)] were calculated for all four models for σ_{stat} and σ_{mob} .

To evaluate potential irregularities in the linear trends of the multiple regression model, regression trees (recursive partitioning) were calculated for a model initially including all predictor variables for σ_{stat} and σ_{mob} . Trees were pruned by selecting a tree size that minimizes the cross-validated error to avoid overfitting. Moreover, for the visualization of any irregularities, a LOESS curve (locally weighted scatterplot smoothing, R package 'GGPLOT2' – `geom_smooth`) is provided in addition to the plots of the single regression models.

To evaluate potential effects of the study method and the taxonomic family on movement parameters, the model's residuals of both multiple σ_{stat} and σ_{mob} -models were plotted (boxplots) for visual inspection. Furthermore, an ANCOVA with a *post hoc* Tukey HSD test was run including all main predictors as well as taxonomic family and study method to test for any significant effect of the latter two.

Finally, mixed-effects models were calculated to disentangle any confounded species-specific or study-related patterns. The same predictor variable sets used for the multiple linear regressions were set as fixed effects and variability within and between families, study method, species nested within families, and the study itself were included as additive random effects.

Based on the results of the multiple regression models, the R package 'FISHMOVE' was programmed that calculates dispersal parameters for a new set of the input variables (fish length, aspect ratio, stream order and time). The package will be available for download from the CRAN repository and its documentation is also provided as Supporting Information (see Data S2).

All statistical analyses were conducted in R statistical software version 2.15.2 (R Development Core Team 2011) using the packages 'CAR' (version 2.0-12, Fox and Weisberg 2011) for Box-Cox tests, 'LME4' (version 0.999999-0, Bates *et al.* 2012) for calculating linear mixed-effects models, 'RPART' (version 4.1-0, Therneau *et al.* 2012) for calculating regression trees and 'GGPLOT2' (version 0.9.2.1, Wickham 2009) for most of the illustrations.

Results

A total of 160 data sets from 71 studies could be extracted and parameter estimates for movement obtained (see Data S1, Supporting information). The studies were conducted in 16 countries spread over five continents and described the movement of 62 species from 12 families. As the largest groups, salmonids, cyprinids and centrarchids accounted for 56, 31 and 25 data sets and 12, 15 and 10 species, respectively. Three different experimental designs were used: mark recapture ($n = 119$), telemetry ($n = 31$) and traps ($n = 10$). Total fish length ranged between 39 and 810 mm (median = 192.5 mm), and aspect ratio of the caudal fin ranged between 0.51 and 2.29 (median = 1.43).

The analysed streams ranged from 1st order to 9th order (median = 3) while low-order streams with stream order ≤ 3 represented the majority of 61% ($n = 83$) data sets. Only seven data sets (5%) derived from larger rivers with stream orders ≥ 7 . Accordingly, the majority of the streams had an average discharge $\leq 15 \text{ m}^3 \text{ s}^{-1}$ (81%) and a stream width $< 10 \text{ m}$ (62%; median = $1.4 \text{ m}^3 \text{ s}^{-1}$, respectively, 6.9 m). Time

duration of the studies ranged between 0.25 and 3285 days (median = 150.5 days).

The movement distance varied between families (Fig. 1a) and ranged between 0.01 and 39 760 m (median = 36.36 m) for the stationary component (σ_{stat}), respectively, between 2.22 and 166 400 m (median = 361.70 m) for the mobile component (σ_{mob}). The share of the stationary component (p) ranged between 13.28 and 97.62% (median = 66.61%; Fig. 1b).

Although no significant relation between any distance parameter estimates (σ_{stat} and σ_{mob}) and p could be detected, a strong correlation was found between movement distances of the stationary and the mobile component (log-log, $r = 0.91$, $P < 0.001$, Fig. 2). Furthermore, the movement distance σ_{mob} was 13.67 times longer (median value, 7.78–28.33 IQR) than σ_{stat} .

Single regressions between $\log(\sigma_{\text{stat}})$, respectively, $\log(\sigma_{\text{mob}})$ and fish length ($\log L$), aspect ratio (AR), stream order ($\text{SO}^{1/2}$), discharge ($\log D$), river width ($\log W$) and time of the study ($\log T$) revealed throughout significantly positive relations ($P < 0.01$; Fig. 3a–f). Detailed information on the single regression parameter estimates are given in Table 1. From the single parameters, total fish length accounts for the highest explanation ($R^2 = 0.46$, respectively, 0.44, both $P < 0.001$) while aspect ratio showed the least but still significant relation ($R^2 = 0.09$, respectively, 0.07, $P < 0.01$). In contrast, no significant predictor was found for p , except for a weak effect of fish length ($R^2 = 0.03$, $P = 0.06$).

A Pearson correlation analysis of the transformed explanatory variables indicated stream order, stream width and discharge as highly inter-correlated ($r = 0.78$ – 0.86 , $P < 0.001$) and further correlated with fish length ($r = 0.43$ – 0.54 , $P < 0.001$). The aspect ratio was correlated with fish length ($r = 0.22$, $P < 0.01$) too and with discharge ($r = 0.19$, $P < 0.05$).

The multiple regression models using all predictor variables performed best in predicting σ_{mob} (adjusted $R^2 = 0.78$), but not σ_{stat} which was best explained by the four-parameter multiple regression model including only stream order as proxy for stream size (adjusted $R^2 = 0.65$). Detailed information on the single regression parameter estimates is given in Table 2. All models showed similar explanatory values for the two movement components σ_{mob} and σ_{stat} . However, the values for the σ_{mob} -models (adjusted $R^2 = 0.76$ – 0.78 , AIC = 37.31–

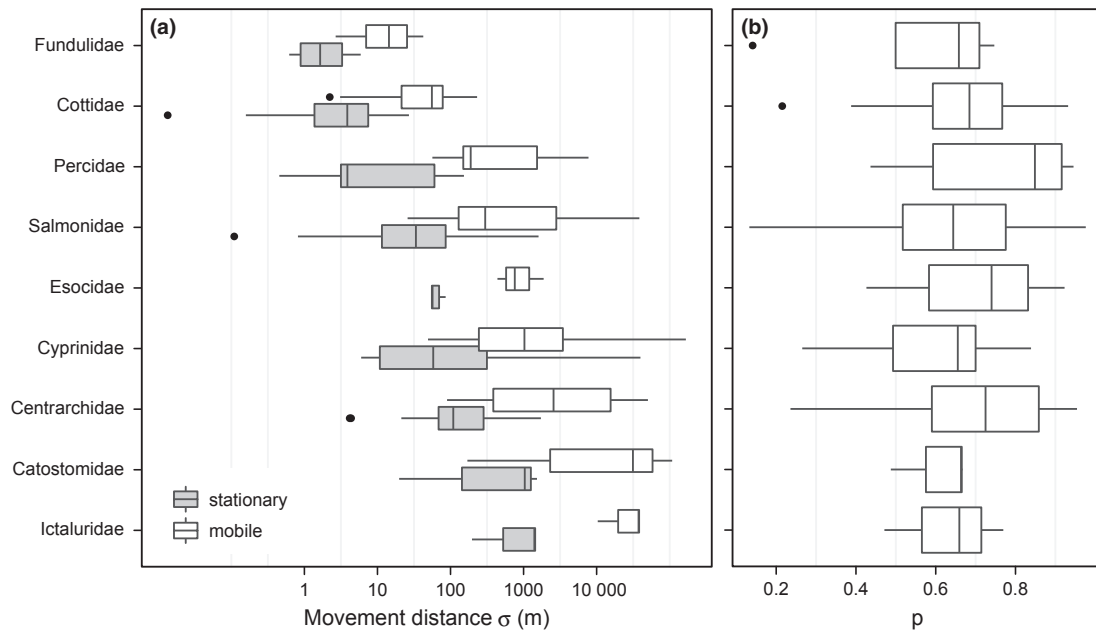


Figure 1 Characteristics of movement parameters across families ($n > 2$): (a) Movement distance σ of the stationary (grey boxes) and mobile (white boxes) component. (b) Share of the stationary component (p).

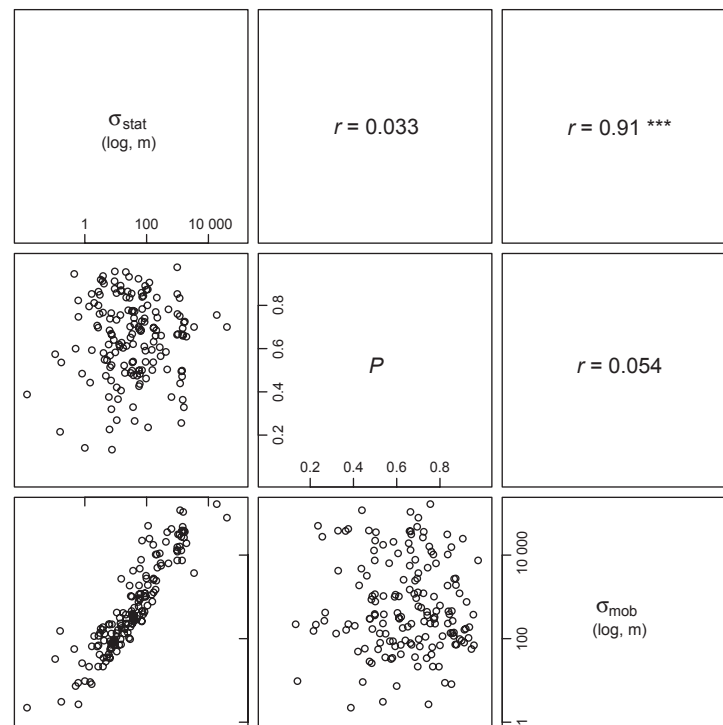


Figure 2 Scatterplot matrix of movement parameters: movement distance of the stationary (σ_{stat}) and mobile (σ_{mob}) component and share of the stationary component (p). Pearson's product moment correlation coefficient $^{***}P\text{-value} < 0.001$.

42.62) were typically higher than for the σ_{stat} -models (adjusted $R^2 = 0.62\text{--}0.65$, AIC = 84.83–91.31). The regression slopes (coefficient β) for fish length

and aspect ratio were higher in all σ_{stat} -models, while in contrast, the slopes β for stream size and time were higher in the σ_{mob} -models.

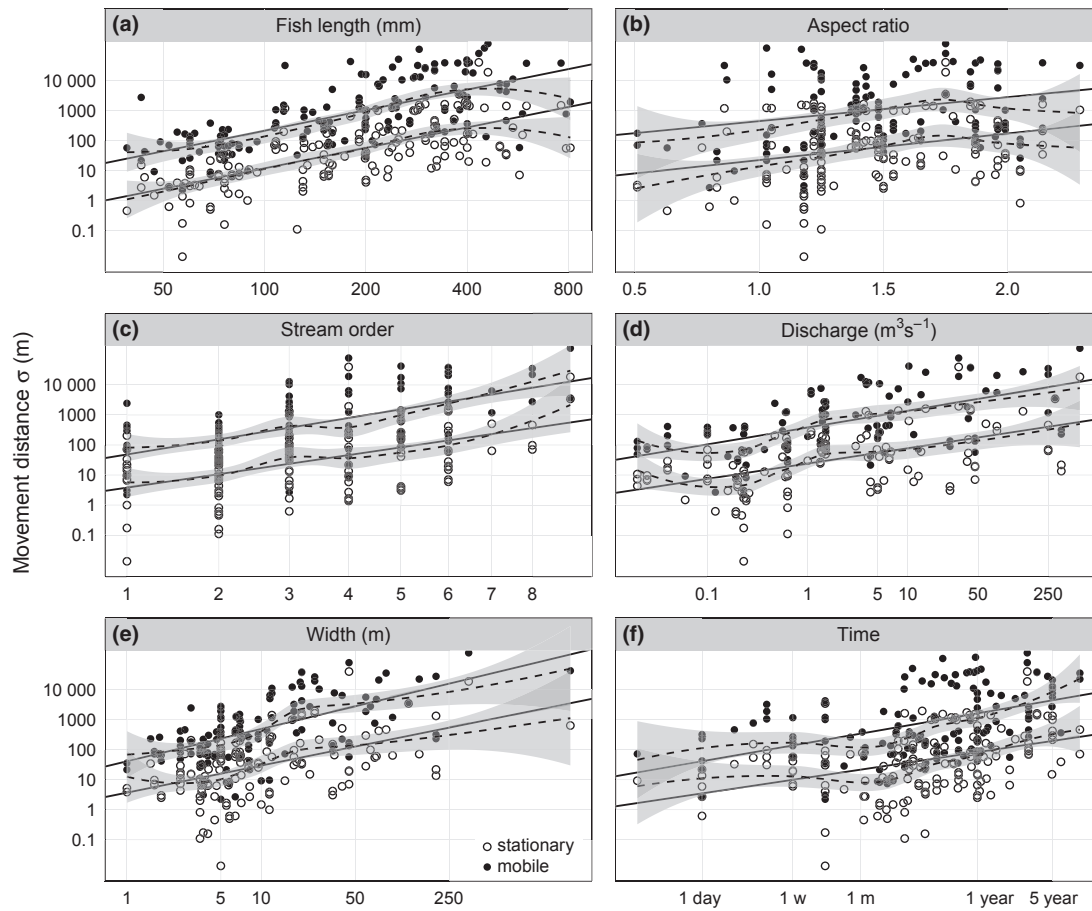


Figure 3 Movement distance σ of stationary component (σ_{stat} , open circles) and mobile component (σ_{mob} , closed circles) in relation to (a) fish length, (b) aspect ratio of the caudal fin, (c) stream order, (d) discharge, (e) stream width and (f) time. Solid lines indicate linear regressions. Dashed lines illustrate fitted LOESS curves, corresponding standard errors in grey.

The regression tree analysis (pruned tree) of the stationary component σ_{stat} detected two terminal nodes produced by a single split at a fish length of 424.5 mm (Fig. 4b). All other variables were dropped from the model. In contrast, the pruned regression tree of the mobile component σ_{mob} yielded four terminal nodes produced by three splits (Fig. 4a): The data were firstly partitioned at a fish length of 273.5, then at a study time of 62.5 days and finally at a fish length again of 424.5 mm. The relative errors of the regression tree models ($1-R^2$) were 0.89 (σ_{stat}) and 0.61 (σ_{mob}).

Contrasting the residuals of both models by the taxonomic family revealed that cottids showed less movement than the average (negative residuals) and fundulids more (positive residuals; Fig. 5). Differences between families were found for σ_{stat}

(ANCOVA $F_{8,70} = 2.38$, $P < 0.05$) and σ_{mob} (ANCOVA $F_{8,70} = 2.75$, $P < 0.05$). The σ_{mob} -model was nearly significantly different between cottids and cyprinids (Tukey HSD test, $P < 0.1$), while all other pair-wise comparisons were not significant ($P > 0.01$).

The field methods (mark recapture, telemetry or traps) had no detectable effect on the results. Neither σ_{stat} (ANCOVA $F_{3,70} = 1.52$, $P > 0.1$) nor σ_{mob} (ANCOVA $F_{3,70} = 1.47$, $P > 0.1$) were significantly influenced by the study method.

Table 3 provides detailed information on the estimates for the linear mixed models. The model including all predictor variables performed best in predicting σ_{stat} (AIC based on log-likelihood = 331.62) and σ_{mob} (AIC based on log-likelihood = 285.99). Similar to the multiple linear regressions, all models performed similarly well with

Table 1 Results of the linear regressions between movement distance and fish morphometrical parameters, stream size and time.

Predictor	Model $\log(\sigma_{\text{stat}}) \sim$ $\log(\sigma_{\text{mob}}) \sim$	α	Regression coefficients β						n	R^2	P -value
			$\log(L)$	AR	$SO^{1/2}$	$\log(D)$	$\log(W)$	$\log(T)$			
Fish length (mm)	$\alpha + \beta \log(L)$	-7.95	2.26						128	0.46	<0.001
		-5.12	2.27						128	0.44	<0.001
Aspect ratio	$\alpha + \beta \text{AR}$	1.05		2.04					116	0.09	0.002
		4.24		1.84					116	0.07	0.005
Stream order	$\alpha + \beta SO^{1/2}$	-1.17			2.50				106	0.25	<0.001
		1.08			2.80				106	0.34	<0.001
Discharge ($\text{m}^3 \text{s}^{-1}$)	$\alpha + \beta \log(D)$	3.21				0.50			100	0.27	<0.001
		5.96				0.56			100	0.34	<0.001
Width (m)	$\alpha + \beta \log(W)$	1.30					0.90		108	0.23	<0.001
		3.70					1.08		108	0.35	<0.001
Time (days)	$\alpha + \beta \log(T)$	1.25						0.54	128	0.17	<0.001
		3.71						0.62	128	0.22	<0.001

n = number of subsampled data sets included in regression analyses; σ_{stat} = movement distance of the stationary component; σ_{mob} = movement distance of the mobile component.

Table 2 Results of the multiple linear regressions between movement distance and fish morphometrical parameters, stream size and time.

Model $\log(\sigma_{\text{stat}}) \sim$ $\log(\sigma_{\text{mob}}) \sim$	α	Regression coefficients β						n	R^2 adj	AIC	AIC (logLik)
		$\log(L)$	AR	$SO^{1/2}$	$\log(D)$	$\log(W)$	$\log(T)$				
$\alpha + \beta_1 \log(L) + \beta_2 \text{AR} +$ $\beta_3 SO^{1/2} + \beta_4 \log(T)$	-10.57	1.64	0.97	1.14			0.43	96	0.65	85.86	360.30
	-7.48	1.45	0.58	1.51			0.55	96	0.77	36.73	311.16
$\alpha + \beta_1 \log(L) + \beta_2 \text{AR} +$ $\beta_3 \log(D) + \beta_4 \log(T)$	-8.25	1.61	0.83		0.20		0.44	90	0.63	84.38	341.79
	-4.74	1.44	0.47		0.27		0.57	90	0.76	42.53	299.94
$\alpha + \beta_1 \log(L) + \beta_2 \text{AR} +$ $\beta_3 \log(W) + \beta_4 \log(T)$	-9.72	1.73	0.99			0.29	0.44	98	0.63	91.67	371.79
	-6.32	1.53	0.63			0.53	0.53	98	0.76	42.65	322.77
$\alpha + \beta_1 \log(L) + \beta_2 \text{AR} +$ $\beta_3 SO^{1/2} + \beta_4 \log(D) +$ $\beta_5 \log(W) + \beta_6 \log(T)$	-9.59	1.54	0.90	1.02	0.08	-0.08	0.44	88	0.63	85.49	337.23
	-6.40	1.33	0.57	0.84	0.02	0.30	0.56	88	0.77	38.96	290.70

L = fish length (mm); AR = aspect ratio of the caudal fin; SO = stream order; D = discharge ($\text{m}^3 \text{s}^{-1}$); W = stream width (m); T = time (days); σ_{stat} = movement distance of the stationary component; σ_{mob} = movement distance of the mobile component; R^2 adj = adjusted R^2 ; AIC = Akaike's information criterion; AIC(logLik) = AIC based on log-likelihood.

higher levels for σ_{stat} (AIC based on log-likelihood = 331.62–368.61) than for σ_{mob} (AIC based on log-likelihood = 285.99–316.12). The four-parameter model including only one proxy for stream size with the lowest AIC was the model using discharge followed by that using stream order. The random effects

showed highest variation (on the intercept) for the study itself (0.95–1.36) with higher values for σ_{stat} than for σ_{mob} . The other random effects varied between 0.06–0.40, 0.03–0.16 and 0.00–0.1 for family, sampling method and species within families, respectively.

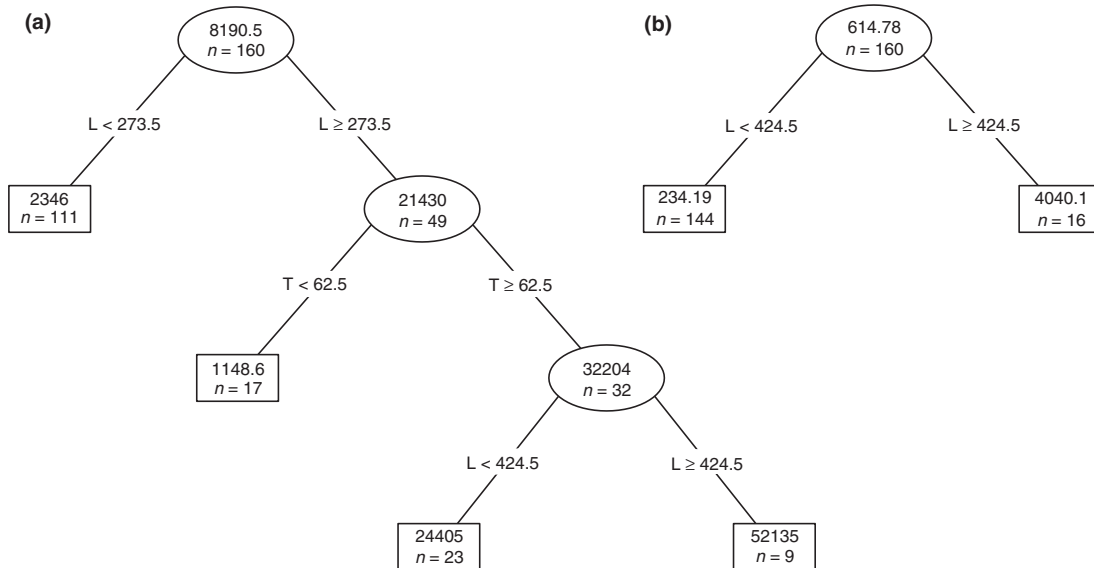


Figure 4 Pruned regression trees initially considering all parameters for the prediction of (a) σ_{mob} and (b) σ_{stat} . L = fish length (mm); T = time (days).

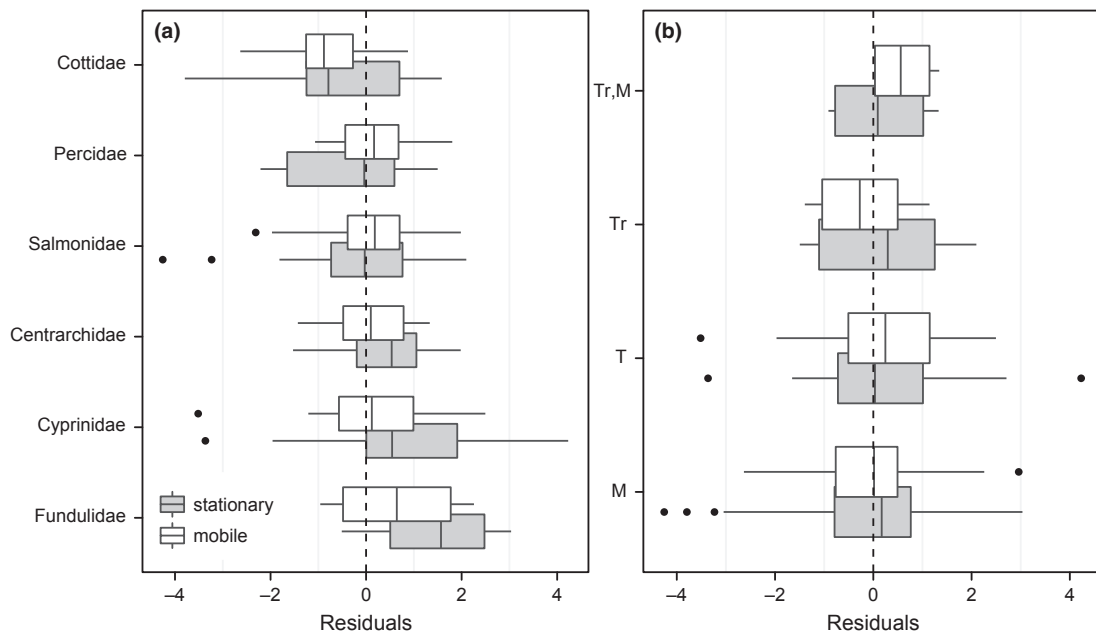


Figure 5 Residuals of the four-parameter (fish length, aspect ratio, stream order, time) multiple regression model (a) across families ($n > 5$) and (b) across study methods (M = mark-recapture, T = telemetry, Tr = traps) for σ_{stat} (white boxes) and σ_{mob} (grey boxes).

Discussion

This study reinforces the importance of considering fish populations as heterogeneous consisting of a stationary and a mobile dispersal-relevant component demonstrated by leptokurtic dispersal ker-

nels. In contrast to most previous reviews considering fish populations as homogeneous and independent from temporal scales (Minns 1995; Woolnough *et al.* 2009), fish were found partly spatially constrained to a core range in their immediate environment, but also straying to dis-

Table 3 Results of the linear mixed model showing estimates for fixed effects (fish morphometrical parameters, stream size and time) and random effects (family, species, study method and study).

Model $\log(\sigma_{\text{stat}}) \sim$ $\log(\sigma_{\text{mob}}) \sim$	Fixed-effects coefficients β							Random effects variance					AIC (logLik)
	α	log (L)	AR	SO ^{1/2}	log (D)	log (W)	log (T)	Fam	Sp: Fam	Met	Stu	<i>n</i>	
$\alpha + \beta_1 \log(L) + \beta_2 \text{AR} + \beta_3 \text{SO}^{1/2} +$	-9.18	1.45	1.10	0.92			0.42	0.12	0.02	0.10	1.36	96	354.36
$\beta_4 \log(T) + b_1 \text{Fam} +$	-6.79	1.34	0.87	1.34			0.52	0.06	0.04	0.05	0.95	96	307.36
$b_2 \text{Sp:Fam} + b_3 \text{Met} + b_4 \text{Stu}$													
$\alpha + \beta_1 \log(L) + \beta_2 \text{AR} + \beta_3 \log(D) +$	-6.39	1.28	0.87		0.22		0.44	0.17	0.06	0.11	1.42	90	334.02
$\beta_4 \log(T) + b_1 \text{Fam} +$	-3.19	1.12	0.70		0.31		0.54	0.40	0.00	0.04	1.08	90	289.60
$b_2 \text{Sp:Fam} + b_3 \text{Met} + b_4 \text{Stu}$													
$\alpha + \beta_1 \log(L) + \beta_2 \text{AR} + \beta_3 \log(W) +$	-8.16	1.48	1.03			0.19	0.45	0.18	0.01	0.16	1.26	98	368.61
$\beta_4 \log(T) + b_1 \text{Fam} +$	-5.14	1.28	0.78			0.50	0.52	0.09	0.10	0.11	0.86	98	316.12
$b_2 \text{Sp:Fam} + b_3 \text{Met} + b_4 \text{Stu}$													
$\alpha + \beta_1 \log(L) + \beta_2 \text{AR} + \beta_3 \text{SO}^{1/2} +$	-6.92	1.26	0.93	0.54	0.26	-0.22	0.42	0.16	0.03	0.06	1.54	88	331.62
$\beta_4 \log(D) + \beta_5 \log(W) +$	-4.63	1.09	0.75	0.60	0.15	0.19	0.53	0.20	0.01	0.03	1.05	88	285.99
$\beta_6 \log(T) + b_1 \text{Fam} +$													
$b_2 \text{Sp:Fam} + b_3 \text{Met} + b_4 \text{Stu}$													

L = fish length (mm); AR = aspect ratio of the caudal fin; SO = stream order; D = discharge ($\text{m}^3 \text{s}^{-1}$); W = stream width (m); T = time (days); Fam = taxonomic family; Sp:Fam = species nested within family; Met = study method; Stu = study; σ_{stat} = movement distance of the stationary component; σ_{mob} = movement distance of the mobile component; AIC(logLik) = AIC based on log-likelihood.

tant locations and exploring new habitats. This long-distance dispersal might be an important factor for genetic exchange within metapopulations.

Three movement parameters (σ_{stat} , σ_{mob} , p) have been calculated for a broad range of different freshwater fishes, and the hypotheses have been tested that dispersal distance is related to (i) stream size, (ii) fish length, (iii) aspect ratio of the caudal fin and (iv) time duration. All four hypotheses were supported by the results presented, and a multiple regression model was developed to predict the shape of leptokurtic dispersal kernels based on these four parameters.

Share of the mobile component

Former studies emphasized the size of the source population (abundance) and the specific dispersal parameters as decisive for genetic exchange and recolonization processes (Albanese *et al.* 2009). In addition, this study considered especially the share of the mobile component as crucial for these exchange processes between metapopulations. Correspondingly, empirical studies have shown that the movements of such highly mobile

and far dispersing individuals explain recolonization patterns to a higher degree than the overall mean movement of a population (Roghair and Dolloff 2005). However, it must be stated that the affiliation of an individual to both the stationary and the mobile component is not fixed and may temporally change (Harcup *et al.* 1984; Aparicio and De Sostoa 1999; Knaepkens *et al.* 2004, 2005).

The share of the dispersal-relevant mobile component was determined on average one-third of the population, but reached values over 85%. This share was slightly higher than a comparable value observed by Rodríguez (2002) solely for salmonids (19%). However, no conclusive predictor was found for the share of the mobile component on the population except a weak relation with body size. Similarly, other studies have identified fish size and growth (Skalski and Gilliam 2000) but also individual behaviour such as boldness (Fraser *et al.* 2001) as important factors for explaining heterogeneity, respectively, leptokurtosis in fish movement. Corresponding to the observations by Rodríguez (2002), the share of the stationary component (p) determined showed high variation

among studies. Unfortunately, the data did not allow for more detailed analyses of this phenomenon. It was assumed that p might be related to environmental differences in habitat structures or complexity not covered by stream type. Other studies have shown that less favourable and less complex habitats were associated with increased exploratory behaviour showing higher degrees in mobile fish (Winker *et al.* 1995; Albanese *et al.* 2004; McMahon and Matter 2006).

Surprisingly, this study revealed a very constant ratio between the movement distance of stationary and the mobile component, with a mobile component that moves 14 times further than the stationary component. Correspondingly, a comparable ratio (18 times) between these two components has been reported for salmonids (Rodríguez 2002).

The parameter estimates for σ_{stat} and σ_{mob} and an average share of 30% mobile individuals can be used to predict dispersal kernels, which provide probabilities of long-distance dispersal (probability of individuals in the tails of the distribution kernel) after a given time step (an example is given in

Fig. 6). This probability together with an estimate of the founder population size might serve to roughly estimate the time lag after which the mobile individuals of a known source population might have reached a new river stretch or habitat. For example, according to the very simple and still criticized 50/500 rule for the minimum size of a viable population, a population needs at least 50 spawners (Soule 1980) or 500 adults (Franklin 1980) to persist in the long term. Applying this concept to successful recolonization of a river reach would mean a mobile component of 50 effective migrants reaches the spot with the probability 1 which translates to a minimum of 150 spawners in the founder population or even more if the probability of moving a certain distance is lower.

Fish length

A strong relation was found between the movement distance and fish length explaining approximately 45% of the variance. This supports existing

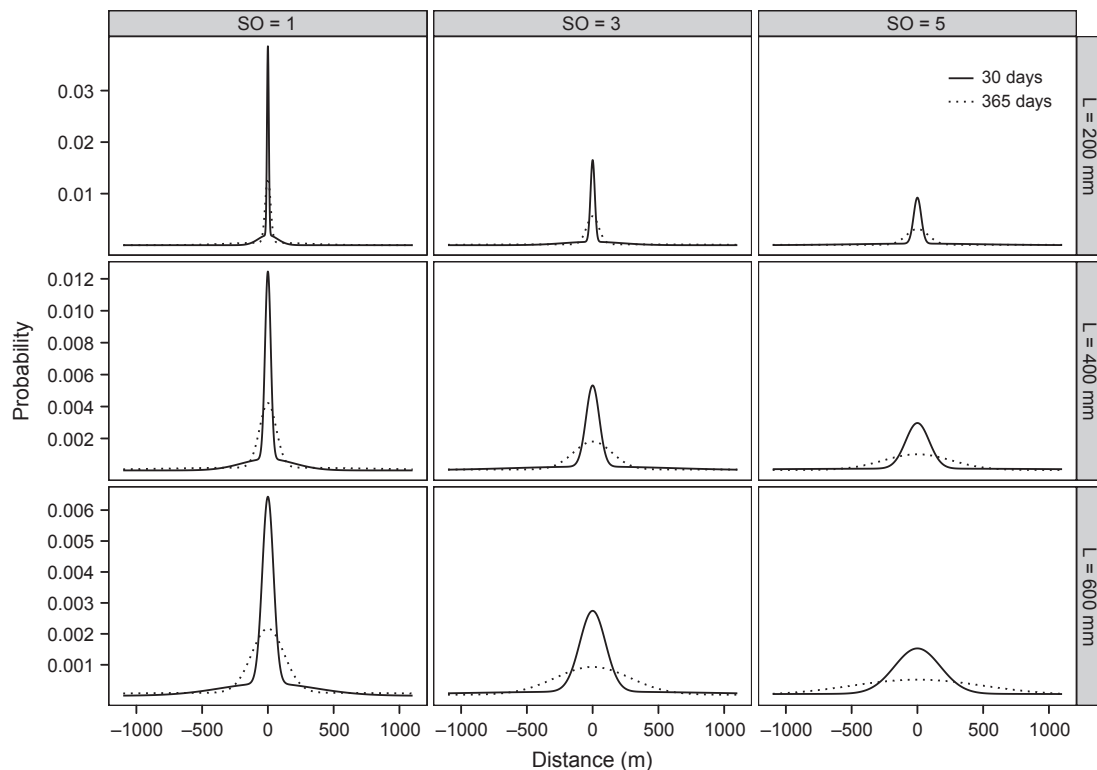


Figure 6 Example for leptokurtic dispersal kernel for Brown trout (*Salmo trutta fario*) predicted from the multiple regression model (aspect ratio = 1.25 and $P = 0.64$). Comparisons across size classes (L = fish length), stream sizes (SO = stream order) and time intervals [30 days (solid line), 365 days (dotted line)].

theory that both movement and home range of animals generally increase with body size (Peters 1983). Correspondingly, Minns (1995) reported home ranges increasing with body size for 18 fish species in 25 rivers and calculated the following relationships for riverine fish: home range approximately $-2.91 \times \text{length}^{1.65}$. Compared to the regression slope reported by Minns (1995), the length exponents obtained here were higher in the single regression model, but very similar in the multiple regression models considering also other factors (time, stream size and aspect ratio).

The finding that fish length was positively correlated with the stream size underlined the implication that larger rivers contain larger fish and large-bodied fish species (Matthews 1998). However, the split in the σ_{stat} data set at 42.5 cm total length (Fig. 4) and the corresponding drop in the LOESS curve (Fig. 3a) indicated a rather asymptotic relation between fish length and dispersal distance. Above a certain threshold length, here 42.5 cm, larger fish tend to disperse less than smaller fish in relation to their body length.

Beside the statistical analyses of species dispersal here, empirical studies of the size effect at the species level are still inconsistent. While some authors revealed a relation between body size and movement distance for certain species (Gatz and Adams 1994), others could not detect such relations (Smithson and Johnston 1999; Albanese *et al.* 2004).

Stream size

As predicted, the results show that the dispersal distance strongly depends on the size of the river expressed as stream order, stream width or discharge. By comparing fish abundance and richness measures between sites and relating them to the network topology, Hitt and Angermeier (2008) found that larger main stem rivers exhibit faster recolonization and support higher degrees in local dispersal than headwaters. Similarly, the home range of fish increased proportionally to the size of a water body (Woolnough *et al.* 2009), and the probability of fish to emigrate was negatively related to the distance from the main channel (Albanese *et al.* 2004). This notion was supported by the presented results that stream order, according to Strahler (1957) well depicts the characteristics of stream size to predict fish movement distance. In large water bodies, larger movement distances of

the stationary component necessarily lead to increased movement distances of the mobile component due to the determined fixed overall distance ratio between both components discussed above.

Aspect ratio of the caudal fin

This study showed for the first time that the aspect ratio of the caudal fin affects dispersal distances (σ_{stat} and σ_{mob}) although its explanatory value was the lowest among all considered predictors. This proxy was chosen to cover additional species-specific traits and fitness correlates which are linked to swimming performance too, but were typically not measured or estimated in fish migration studies and thus could not be disentangled in their effects on dispersal.

Beside fish length, the shape of the caudal fin is a main feature in locomotion of most freshwater fish (Lindsey 1978) and the mode of locomotion relates to primary feeding traits (Webb 1984). For example, fish species with slender shaped caudal fins (high aspect ratio, e.g. Scombridae) are considered specialists in cruising and commonly pelagic predators, while those with higher relative surface of the caudal fin (low aspect ratio) are specialists in accelerating and typically sit and wait predators (e.g. *Esox Lucius*, Esocidae; Webb 1984). Correspondingly, the aspect ratio is considered as broad index of metabolism and activity in fish, which is correlated with food consumption (Palomares and Pauly 1989), natural mortality, longevity, red muscle content, gill area and growth performance (Pauly 1989).

For example, it has been documented that riverine cyprinid species exhibited a higher critical swimming performance (Wolter and Arlinghaus 2004) and showed also higher recolonization potential than other families (Hitt and Angermeier 2008). Analysing the effects of families on movement distances further revealed that cyprinids and fundulids showed slightly elevated dispersal distances, while cottids moved lower distances. These findings were consistent with earlier observations concerning limited cottid movement (Petty and Grossman 2004; Hudy and Shifflet 2009; Ovidio *et al.* 2009) which might be related to the poorer swimming ability of small-bodied benthic species (Knaepkens *et al.* 2004; Chaumot *et al.* 2006).

The regression models related both predictors, fish length and aspect ratio, positively to dispersal distance. This finding on the one hand underlined

the well-known additional contribution of other factors than length to swimming performance. On the other hand, it suggested the aspect ratio as a well-suited proxy for the species-specific type of locomotion and related metabolic and fitness factors.

Time

While monitoring studies on restoration efforts focus on the re-establishment of target species, little is known about the ability of fish to disperse to newly rehabilitated habitats within a given time-frame. In contrast to studies that did not analyse any time effect and considered movement as static home ranges of fish (Minns 1995; Woolnough *et al.* 2009), a significant positive relation was found between study time duration and movement distance using the maximum time interval between mark and recapture or two consecutive detections.

Thompson (1933) has already documented time dependence in fish movement for 12 fish species. He found that the distance fish moved increases proportionally to the square root of the time. If time-dependent movement is regarded as redistribution of fish for single time steps, it can mathematically be described as convolution of the corresponding distribution kernel. Moreover, theoretical studies have shown that the resulting variance in convoluted normal distributions equals the sum of the variance in the single distributions (Vinga and Almeida 2004). This implies that the variance in the movement distance linearly increases with time, at least for normal distributed dispersal kernels. So far, there were no studies available that explicitly relate these theoretical findings to heterogeneous dispersal kernels with leptokurtic characteristics. Nevertheless, Skalski and Gilliam (2000) showed that the variance in the leptokurtic movement distribution (comparable to σ_{stat} and σ_{mob}) of chub species increased with a constant rate over time. In contrast to the initial hypotheses and expectations, the distance of the stationary component increased at a similar rate as the distance of the mobile component in time.

Implications and conclusions

The final dispersal kernel consists of three parameters: the share of the stationary/mobile component, the movement distance of stationary and the movement distance of the mobile component. The

dispersal distances could be well predicted by four parameters, while the ecological correlates with the share of the mobile component still remain a question that needs further empirical examination, especially if the affiliation of individuals to both components may frequently shift. Considering the latter, the main finding of this study that fish populations form a mobile and a stationary component with movement distances increasing in time, raises the question whether or not the home range concept is still applicable for fish. Crook (2004) has drawn similar conclusions as he also stressed the importance of addressing fish as heterogeneous, a distinction not considered by the rather static term 'home range'.

In their study on stream salmonids Gowan and Fausch (1996) already fundamentally questioned the RMP by showing salmonid populations as heterogeneous comprising mobile components. This study goes even further beyond and for the first time shows the universality of this concept: within all populations among various families and taxa, there is a moving component and fish cannot at all be considered as sedentary. Fish assemblages are constantly subjected to emi- and immigration processes and individual range shifts partly at very large spatial scales. In contrast to previous empirical demonstrations of the validity of the heterogeneous populations' concept (Gowan and Fausch 1996), this study more generally related that pattern to biotic and abiotic predictors. The findings presented should encourage more detailed studies on primary triggers for mobility but also serve in planning future movement studies in regard to spatial design (Fig. 6).

The general relationships between the dispersal components as well as their predictors allow analogous conclusions and thus provide also valuable estimates of movement parameters for species with no or little information on their movement behaviour, as it is typical for rare or endangered species.

Regardless of fishes' dispersal abilities, recolonization or genetic exchange might only take place if a fish can move without barriers. Thus, any successful dispersal process is closely linked to habitat connectivity. This meta-analysis has initially excluded all studies of fish movements at barriers or with a potential effect of a barrier in the study reach reported. However, habitat fragmentation by all kinds of human-caused migration barriers like dams, weirs, culverts, sluices, tidal barrages, pumping stations, and many more is one of the

most common and most significant impacts on riverine ecosystems (Gough *et al.* 2012).

One advantage of the leptokurtic dispersal kernels and its predictors is their nearly universal ability of being implemented in all kinds of individual-based or species distribution models in a geo-referenced context based on dendritic river networks, which can also account for the effects of any existing movement barriers. Moreover, the dispersal kernels might become proportionally truncated (Pépin *et al.* 2012) according to already known more or less successful fish passage at a barrier (compare Noonan *et al.* 2012; Roscoe and Hinch 2010). This might further contribute to assess quantitative effects of habitat fragmentation on fish and preferably the improvement of fish populations by weir removal, migration facilities and river rehabilitation.

The results serve determining the size and maximum distance of a source population and time for successful recolonization as well as support theoretical research by quantifying emigration and immigration rates with particular interest in metapopulation dynamics. They might be further used for predicting range limitations, time lags and potential range shifts of species in response to climate change in relation to the available migration corridors.

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Supporting Information

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

Data S1. Characteristics of original data sets ($n = 160$) from literature with fish length (L), aspect ratio of the caudal fin (AR), stream order (SO, *sensu* Strahler (1957)), stream width (W), discharge (D), time (T).

Data S2. R Package ‘FISHMOVE’ reference manual. Version 0.0-1FAF.