Modelling fish dispersal in catchments affected by multiple anthropogenic pressures

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Abstract

The colonisation of rivers by fishes is directly linked to abiotic habitat conditions but often impaired by dispersal abilities of fishes and movement constraints such as barriers. Despite the relevance of dispersal, comprehensive knowledge and in particular quantitative information or models on fish dispersal in rivers considering fish populations as differently mobile consisting of stationary and mobile components has not been available yet.

The first part of this thesis provides the first comprehensive compilation and quantitative analysis of freshwater fish movement while considering each fish population consisting of differently mobile specimens. Main objectives of the study were to determine movement distances of stationary and dispersal relevant mobile components of fish populations and identifying determining factors for dispersal distances. The review yielded 160 empirical datasets from 71 studies on the movement of 62 riverine fish species which were evaluated, completed and analysed in a standardised way based on refitted leptokurtic probability-densitiy functions (dispersal kernels). A share of one third and two thirds emerged as a general pattern of the mobile and stationary component of a fish population, respectively. Moreover, four variables were identified primarily determining dispersal distances: fish length, aspect ratio of the caudal fin, river size and time.

In the second part of the thesis, the novel fish dispersal model FIDIMO is introduced. FIDIMO provides a tool for predicting and simulating spatio-temporal patterns of fish dispersal in dendritic river networks considering movement barriers with a real integration of GIS. The fish dispersal model FIDIMO links conceptual considerations on dispersal modelling with empirically observed leptokurtic fish movement patterns and the strengths of geographically explicit modelling in Free and Open Source GIS.

In the third part of the thesis, FIDIMO was applied for modelling dispersal of multiple fish species in an anthropogenically impacted North-German river catchment. A main objective of the study was to disentangle and quantify the single and joint contributions of habitat suitability, dispersal constraints and network fragmentation (barriers) on the distribution patterns of 17 fish species. The results show significant positive effects of both, local-scale habitat quality and species-specific dispersal ability on the distribution of river fishes, whereas no significant effect of barriers influencing the presence of a species could be found. Furthermore, over longer time periods the importance of dispersal decreased in favour of habitat suitability becoming relatively more relevant in determining species' presence.

Overall, this thesis contributes to an improved understanding of fish dispersal abilities and patterns and points out its importance in the colonisation of river networks. Moreover, the presented dispersal model FIDIMO allows predicting spatio-temporal colonisation patterns and estimating time lags in fish response to river rehabilitation and changed network connectivity, predicting temporal patterns of (invasive) species spread and estimating maximum distance between stepping stone habitats. Based on the findings, it can be emphasised that the prioritisation of connectivity measures (e.g. opening new suitable habitat patches) and the restoration of stream reaches might be most efficient if the spatial arrangement of source populations, their position in relation to barriers and the dispersal ability of fishes are considered.

Zusammenfassung

Die Besiedlung von Gewässern, z.B. durch Fische, ist neben den abiotischen Lebensraumbedingungen auch davon abhängig, inwieweit Individuen den jeweiligen Fließgewässerabschnitt erreichen können. Diese Erreichbarkeit bzw. Besiedelbarkeit der Gewässer ist wiederum maßgeblich vom verfügbaren Artenpool, der artspezifischen Ausbreitungsfähigkeit der Fischarten sowie dem Vorhandensein von Wanderhindernissen abhängig. Ungeachtet der höchst relevanten und immensen Bedeutung der Ausbreitungsfähigkeit von Fischen, gibt es bisher kaum quantitative Daten und keine anwendbaren Modelle zur Mobilität von Fischen, die darüber hinaus noch speziell berücksichtigen, dass Fischpopulationen unterschiedlich mobil sind und sich aus stationären und mobilen Komponenten zusammensetzen.

Der erste Teil dieser Arbeit bietet die erste umfangreiche Zusammenstellung und quantitative Analyse von Ausbreitungsmustern und -distanzen von Süßwasserfischen unter Berücksichtigung unterschiedlich mobiler Komponenten einer Fischpopulation. Ein Hauptziel dieser Studie war es, die Ausbreitungsdistanzen der stationären und der mobilen, ausbreitungsrelevanten Komponente zu bestimmen und Schlüsselfaktoren zu identifizieren die diese Ausbreitungsdistanzen beeinflussen. Aus der Fachliteratur wurden 160 empirische Datensätze aus 71 wissenschaftlichen Studien zur Ausbreitung von 62 Fischarten in Flüssen extrahiert und mittels einer standardisierten Methode an leptokurse Wahrscheinlichkeits-Dichte-Funktionen (Dispersal kernel) angepasst. Grundsätzlich konnte bei Fischpopulationen zwischen einer stationären Komponente (ca. 2/3) und einer mobilen Komponente (ca. 1/3) unterschieden werden. Die Ausbreitungsdistanz beider Komponenten ist dabei hauptsächlich von vier Faktoren abhängig: der Fischlänge, der Form der Schwanzflosse, der Fließgewässergröße und der betrachteten Zeitspanne.

Der zweite Teil dieser Arbeit widmet sich dem neu entwickelten Fischausbreitungsmodell FIDIMO. FIDIMO ist ein geographisch explizites Softwareprogramm (implementiert in GIS) zur Modellierung, Vorhersage und Simulation der räumlichen und zeitlichen Ausbreitungsmuster von Fischen in Fließgewässern unter Berücksichtigung von Wanderhindernissen. Dabei verknüpft FIDIMO konzeptionelle Überlegungen zu Ausbreitungsmodellen in verzweigten Fließgewässernetzwerken mit empirisch bestimmten leptokursen Fischausbreitungskurven unter ausschließlicher Verwendung von Freier und Offener (Free and Open Source) Software.

Im dritten Teil der Arbeit wurde das Fischausbreitungsmodell FIDIMO zur Modellierung der Ausbreitung von insgesamt 17 Fischarten in einem stark anthropogen beeinflussten Einzugsgebiet in Norddeutschland angewendet. Hauptziel dieser Studie war es, sowohl die einzelnen als auch den gemeinsamen Einfluss von drei Faktoren auf die Besiedlungsmuster der präsenten Fischarten zu bestimmen und zu quantifizieren: Habitatqualität, Ausbreitungsfähigkeit von Fischen und Fließgewässer-Fragementierung durch Wanderhindernisse. Die Ergebnisse zeigen, dass sowohl die kleinräumige artspezifische Habitatqualität als auch die artspezifische Ausbreitungsfähigkeit die Besiedlung von Flusshabitaten maßgeblich bestimmen. Dagegen wurde kein signifikanter Einfluss von Barrieren auf das Vorkommen einer Art gefunden. Darüber hinaus konnte gezeigt werden, dass über längere Zeiträume der Einfluss von Fischausbreitung auf das lokale Vorkommen einer Fischart sinkt während die Habitatqualität relativ wichtiger wird.

Zusammenfassend trägt diese Arbeit zu einem verbesserten Verständnis von Fischausbreitung und Ausbreitungsmustern bei und unterstreicht deren Wichtigkeit für die Besiedlung von Fließgewässernetzwerken. Zudem ermöglicht das neu entwickelte Modell FIDIMO die Modellierung von räumlich und zeitlich variablen Ausbreitungs- und Besiedlungsmustern sowie die Prognose der Wirkung von Maßnahmen zur Verbesserung der Durchgängigkeit, der Ausbreitung invasiver Arten oder der Bestimmung maximaler Abstände zwischen Trittstein-Biotopen. Basierend auf den Ergebnissen kann davon ausgegangen werden, dass die Priorisierung von Maßnahmen zur Verbesserung der Durchgängigkeit (z.B. Zugang zu neuen Habitaten) sowie die Renaturierung von Fließgewässerabschnitten dann die größten Erfolge zeigt, wenn auch die räumliche Verteilung von Quellpopulationen, deren relative Lage in Bezug zu Wanderhindernissen und fischspezifische Ausbreitungsfähigkeiten berücksichtigt werden.

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General Introduction

1 Dispersal and habitat

It has long been recognised that the distribution of species is determined by two factors, its dispersal abilities and its habitat requirements. As early as the nineteenth century, these factors were driving research investigating the distribution of species (Wallace 1876). In aquatic organisms Guppy (1893) in particular explored species *powers of dispersal* on the one hand and their *dependence on special conditions to its existence* on the other hand.

Regarding the former, Lidicker and Stenseth (1992) defined dispersal as an one-way movement away from an animals home-range (site). Moreover, dispersal is a highly complex ecological system (Fig. 0.1), acts as a key determinant of population dynamics and interactively links the disciplines of ecology, behaviour, genetics and evolution (Lidicker and Stenseth 1992). Due to conflicting terms in this scientific field, this work will adhere to Lidicker and Stenseth's (1992) definition of dispersal or will use the more general term 'movement', both different from life-cycle related and often directed movements with return phenomenons such as fish' spawning migrations.

Regarding the latter, the ecological area inhabited by an organism, its habitat, is tightly associated with its movement. This becomes more obvious when looking at the three stages of dispersal: (i) leaving (emigration), (ii) travelling (movement) and (iii) arriving (colonisation) (Lidicker and Stenseth 1992). All three steps encompass behavioural decisions on individual level at different temporal and spatial scales, are affected by the fish's surrounding habitat and have consequences on population level.

McMahon and Matter (2006) provide a conceptual model of how resource availability and habitat features are linked to the exploratory behaviour of movement

Figure 0.1: Google Scholar wordcloud illustrating the complexity of fish dispersal/movement. Higher color intensity and larger font size represent relatively higher frequency in titles of scientific articles. Search term: "allintitle: fish dispersal OR movement", 874 hits (June 7, 2013), wordcloud based on titles solely. Radinger (2013), DOI: 10.6084/m9.figshare.718144.

and emigration (as a form of dispersal movement) away from a local habitat, which has direct consequences on population dynamics. Moreover, they postulate that fish might leave their home range and emigrate from their immediate environment once the resources' needs at this habitat reach are not met which in turn might be governed by fish' internal factors (McMahon and Matter 2006). So, fish are like other highly mobile species in that they can actively move away from an unsuitable area and disperse to a newly available or better-suited habitat but are restricted to the river network as a dispersal pathway.

2 Rivers affected by multiple pressures

Rivers are one of the most impacted ecosystems (Malmqvist and Rundle 2002; Vörösmarty et al. 2010) and often susceptible to multiple pressures as a consequence of the conflicting priorities of the multiple ecosystem services they provide. This increased anthropogenic use of rivers and their surrounding catchment led to severe alterations of rivers concerning (i) the degradation of physical in-stream habitats (e.g. Malmqvist and Rundle 2002; Muhar et al. 2000), (ii) water quality issues caused by diffuse and point source pollution (e.g. Behrendt 1996), (iii) river impoundment and disconnection from floodplain areas (e.g. Ward et al. 1999), (iv) loss of riparian vegetation (e.g. Bunn et al. 1999), (v) altered flow regimes (e.g. Bunn and Arthington 2002; Poff and Zimmerman 2010).

Historically, the core focus of research on riverine fish has to analyse relationships between a species and its habitat requirements. Consequently, numerous empirical, statistical and modelling studies relate fish distributions to environmental parameters of the physical in-stream habitat at a river reach scale, the catchment-scale land-use, climatic conditions and hydraulic regimes. Furthermore, the strong link between in-stream hydraulic variables such as depth and flow velocity and the associated presence of fish led to the development and the continually extensive use of micro-scale habitat suitability tools. Consequently, river management and restoration projects mainly focus on the question of how to improve the local habitat suitability to e.g. increase local biodiversity or to re-establish a target species. However, such projects which only focus on the local scale of stream reaches rather than a stream network approach might show weaker ecological responses than might be expected (Altermatt 2013).

The ecological response of aquatic biota after local-scale site rehabilitations is often inconsistent and evaluations often show no or no immediate response (Haase et al. 2012; Lepori et al. 2005; Stoll et al. 2013). A key reason for this failure might simply be the time lag specimen need to reach a newly available habitat from nearby or more distant source populations or barriers that limit species from dispersing. Thus, beside catchment, local habitat and biotic constraints, dispersal constraints are increasingly recognised to be a main cause for the lack of success of stream ecological restoration (Parkyn and Smith 2011; Stoll et al. 2013).

Detenbeck et al. (1992) evaluated the recovery of stream fish assemblages from disturbances and found that besides site-specific (e.g. habitat quality, stream size, refugia) and species-specific factors that affected the recovery rate, time delays caused by existing barriers to migration and the proximity of source populations were important factors influencing recovery rates. Similarly, Stoll et al. (2013) and Sundermann et al. (2011) found that the local fish species richness in restored sites was positively affected by the regional species pool within in a distance of 5 km.

While the number of river restoration projects is increasing (Palmer et al. 2005), little is known about the fish's ability to disperse to these newly rehabilitated habitats. Hence, successful re-colonisation depends on factors affecting the fish's dispersal away from a source habitat (decision to move) as well as on factors for the decision to remain at and eventually re-colonise at a new site (habitat quality) (Albanese et al. 2004). Thus, profound knowledge of dispersal mechanisms and species-specific movement patterns, as well as appropriate dispersal models are increasingly important.

However, the need for dispersal models is not only limited to an application in the context of restoration ecology. Indeed, such models might also be highly valuable in other applied fields related to anthropogenically impacted river ecosystems as (i) the spread and potential establishment of (non-native and/or invasive) species, (ii) the assessment of the connectivity of dendritic stream networks, (iii) the impact assessment of barriers, (iv) the assessment of long-term colonisation patterns and (v) the modelling of potential range shifts in response to changes of habitats and climate. Quantifying dispersal processes and specific dispersal models might also serve theoretical research such as the assessments in relation to genetic exchange between (sub)populations (Wright 1978) and the determination of emi- and immigration processes as a driving factor in insular biogeography (MacArthur and Wilson 1963) and meta population dynamics (Hanski 1998) as well as the associated determination of minimum viable population sizes (Lehmkuhl 1984; Shaffer 1981) and maximum distances of source populations (stepping stone ecology, e.g. Saura et al. 2014).

Consequently, a mechanistic and spatially explicit dispersal model which can be combined with dynamic and spatially explicit population models and/or habitat suitability models can help to gain meaningful insights into these complex ecological processes and might be highly valuable for future efforts in the management of river ecosystems.

3 Modelling fish dispersal

In general, *modelling* is the approach to simplify and generalise complex systems like ecological systems and to construct a formal theory that describes and explains it. Therefore, a model is always an abstract representation of a 'real world' system and typically contains only some selected key factors sufficient to meaningfully describe and facilitate insights e.g. how species interact with their environment (Breckling et al. 2011) and to make predictions based on these described patterns.

Models are also often used to explore more factors than can be controlled in an experiment carried out under laboratory conditions or in the field (Saltelli et al. 2001). However, as natural systems are highly complex, it is impossible to accurately predict them in every aspect of space and time in a single model, which led to Levins' (1966) principle that only two out of three model properties (generality, reality and precision) can be improved simultaneously (Guisan and Zimmermann 2000) (see Fig. 0.2). Thus, gains in two of the properties are accompanied by losses in the third remaining but also desired property.

So far fish dispersal models have mainly provided conceptual frameworks and equations (i) to describe fish movements as drivers of meta-population dynamics (e.g. Auerbach and Poff 2011; Gotelli and Taylor 1999), (ii) to describe individual based movements (e.g. Ovaskainen and Hanski 2004; Patterson et al. 2008; Railsback 1999; Schönfisch and Kinder 2002), (iii) to test effects of dendritic networks on metacommunity models (e.g. Muneepeerakul et al. 2008), (iv) to formulate habitat-mediated diffusion models (e.g. Ovaskainen 2004) (v) to assess spawning runs in diadromous fish (e.g. Åström and Dekker 2007; Rivinoja 2005), (vi) to describe empirical dispersal patterns (e.g. Rodríguez 2002; Skalski and Gilliam 2000), (vii) to quantify the permeability of structural barriers (e.g. Pépino et al. 2012), (viii) to analyse sub-population structures according to the isolation by distance hypothesis (e.g. Bradbury and Bentzen 2007; Pinsky et al. 2010; Puebla et al. 2009), (ix) to analyse the interactions of source and sinks in dispersal (e.g. Gundersen et al. 2001; Kristan III 2003; Schick and Lindley 2007) and (x) to describe

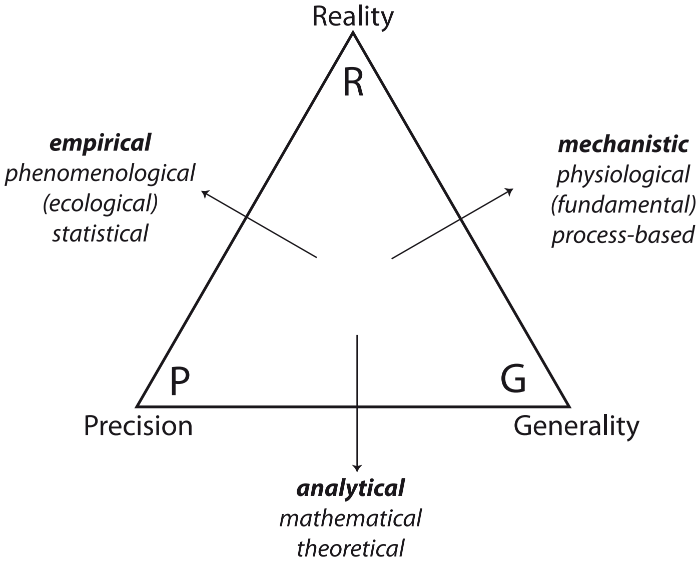

Figure 0.2: Classification scheme of models based on three model properties: generality, reality and precision. After Guisan and Zimmermann (2000) and Levins (1966)

the drift of larvae and recruitment of commercially important species in marine systems (e.g. Huret et al. 2007; Pelc et al. 2010; Sundelöf and Jonsson 2012).

Habitat patterns as well as dispersal processes are both spatially determined and thus, are well suited to be modelled with geographical information systems (GIS). Indeed, most of the state-of-the-art GIS software programs already provide tools for modelling the spread and dispersal of species in a spatially discrete (lattice-like, based on raster grid cells) framework by mainly considering two-dimensional radial dispersal (e.g. Gaussian diffusion). In mathematical ecology and for many spatial dispersal models so-called dispersal kernels are used to formally describe the probability of specimen of a population to spread from one to another location as a function of distance and time (Kot et al. 1996).

In contrast to this typically radial spread of terrestrial species, fish dispersal in rivers differs by two factors, (i) the specific leptokurtic spread of fish species and (ii) the restriction of active dispersal to dendritic (tree-shaped and branching) river networks as movement corridors.

3.1 The leptokurtic characteristic of fish dispersal and movement

It is of special interest to our understanding which individuals are dispersing and why, meaning what are the cues triggering animals to move to a new habitat. These movement motivations can be viewed from an ultimate (evolutionary) and from a proximate (environmental triggers) perspective (Lidicker and Stenseth 1992) and thus dispersal is a highly complex topic affecting many fields in ecological research (Fig. 0.1). A movement response is an outcome of internal (genetic and ontogenetic factors, hunger, homing) and external cues (habitat-suitability, light, temperature, hydrology, water quality, population density) (Lucas and Baras 2001). Although recent technologies result in increased measurements of the movements of freshwater fish (Lucas and Baras 2000), little is known about generality and prevalence of dispersal patterns among the fishes. Indeed, spatial and temporal estimates of fish dispersal distances and information on the share of mobile dispersal-relevant individuals is widely lacking.

After some early attempts of measuring fish movement across various temporal and spatial scales (Thompson 1933), fish movement has mainly been discussed around the question of how mobile or resident fish are. In this context, Gerking (1959) stated that stream fish are sedentary and spend their entire life in a very restricted area. Conversely, Stott (1961) found that a roach population in the River Thames consisted not only of a stationary component but also of a mobile component that has a wider range of movement, which provides an explanation for the fast re-colonisation of waterways (Stott 1961). Moreover, a review on stream salmonids showed the substantial importance of fish movement and thus disproves Gerkin's restricted movement paradigm (Gowan et al. 1994).

Spatial behaviour and movements are now considered as norm, rather than the exception and are recognised as a fundamental process in the various life stages of fish (Lucas and Baras 2001). In recent years the concept of heterogeneous movement (Rodríguez 2002; Skalski and Gilliam 2000) developed, considering fish populations consisting of stationary and mobile components (Fig. 0.3). The stationary component is reflected by a high peak of the dispersal kernel, the mathematical formulation of the spread of a species, while the mobile component is characterised

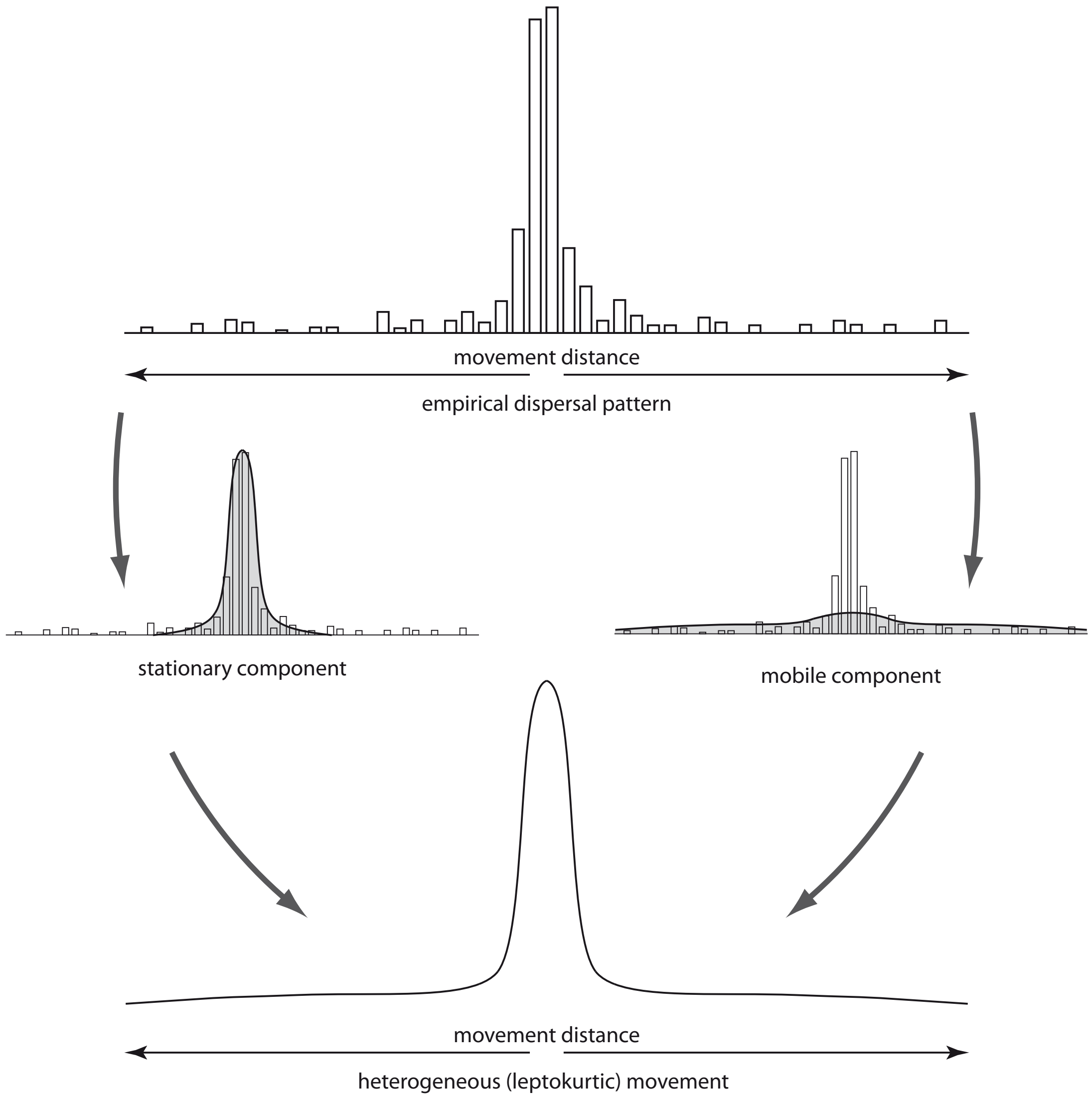

Figure 0.3: Schematic illustration of a leptokurtic dispersal kernel derived from empirical e.g. mark-recapture studies. The leptokurtic shape describes the typically heterogeneous movement of fish populations consisting of stationary (high peak) and mobile components (fat tails).

by a remarkably wider spread and becomes apparent in the kernel as typically fat tails. Such heterogeneous dispersal kernels describe with most accuracy, the patterns of the spread of fish previously observed by Stott (1961). This leptokurtic movement pattern accounts for individuals that are often considered as sedentary and only move in their home range, but also considers that some individuals of a population are highly mobile and move far distances within short time periods, a pattern that is highly decisive for approaching and (re-)colonising newly available and distant habitats (Kot et al. 1996). Consequently, this state-of the art understanding of fish dispersal as a heterogeneous and leptokurtic pattern will be used throughout this thesis.

3.2 Rivers – dendritic and fragmented ecosystems

Rivers are dendritic ecosystems, are hierarchical in nature, similar in structure to a tree and consisting of typically many first order (head water branches) and less main stems or lower order streams. Previously, rivers have mainly been viewed either from a very localised viewpoint analysing processes that occur on the reach-scale (species-habitat interactions) or from a (linear) longitudinal perspective. The River Continuum Concept (RCC, Vannote et al. 1980) in particular subscribed to this viewpoint. The RCC, which significantly changed the perception of rivers in the 1980s viewed these systems as gradually changing systems from the source to the mouth but mainly ignored the existence of abrupt changes in the continuum such as confluences and the branching structure of rivers.

However, rivers are network structures of pathways (river reaches) and nodes (confluences): this is increasingly acknowledged in recent studies (e.g. Altermatt 2013; Grant et al. 2007). Futhermore, river confluences are points of mixtures in downstream perspective (e.g. of temperatures or chemical composition) but also depict decision points as fish move in upstream direction. As a consequence, active fish dispersal is generally restricted to movements along the river corridors considering the dendritic structure (nodes) of river networks, this makes it fundamentally different from other two dimensional, lattice-like (e.g. terrestrial) dispersal.

In addition, some rivers are highly fragmented ecosystems (Dynesius and Nilsson 1994). So besides natural barriers (e.g. waterfalls), the presence of technical or structural barriers such as weirs, dams, etc. inhibit the free movement of fish in river networks. The impact of barriers on the free movement of migratory fish has been the focus of extensive research work in the literature (e.g. Meixler et al. 2009; Ovidio and Philippart 2002). Furthermore, it has been shown that barriers exhibit varying permeability in up and downstream directions (Noonan et al. 2012) and their species-specific passability strongly depends on their technical structure and hydraulic characteristics as well as on the actual discharge level (Powers and Orsborn 1984). In recent years, various assessment methods for evaluating the passability of barriers have been made available (Bourne et al. 2011; Kemp and O'Hanley 2010) and frameworks how to include passability rates of barriers into dispersal processes were provided (Pépino et al. 2012). However, explicit species and barrier specific passability rates and the mechanistic process of network dispersal of fish is yet to be combined in a comprehensive spatial (e.g. GIS) model.

4 Objectives and aims

The success of recolonisation of newly available habitats is directly linked to habitat conditions but often impaired by dispersal constraints. Despite the relevance of dispersal, comprehensive knowledge and in particular quantitative information on fish dispersal in rivers considering its leptokurtic nature (stationary and mobile components) has not yet been available. This lack of quantitative information has also impeded the development of software tools and analysis frameworks to spatially explicitly model fish dispersal. Consequently, assessments of the effects of fish dispersal under the consideration of multiple pressures such as habitat degradation and river fragmentation have been rather limited. This was further compounded by limited information on the dispersal abilities of riverine species and the lack of appropriate models/software tools.

Therefore, the first main objective was to synthesise current knowledge of riverine fish dispersal abilities and to obtain species-specific movement parameters from empirical studies to describe the spatial and temporal patterns of heterogeneous fish movement considering stationary and mobile components of a population. Furthermore, environmental and fish internal key predictors should be identified and related to the specific movement patterns and abilities. I hypothesised that the species-specific movement parameters depend on fish length, river size, aspect ratio of the caudal fin (as a proxy for species-specific swimming abilities) and duration of the studies.

The second objective was to apply these species-specific dispersal patterns in a mechanistic and predictive fish dispersal model (FIDIMO, FIsh DIspersal MOdel). Thus, the synthesised results on leptokurtic fish dispersal parameters should be combined with and applied to dendritic river networks considering movement barriers as dispersal constraints. FIDIMO should be developed as a software tool for Geographical information system (GIS) entirely using free and open source software.

The third objective was to demonstrate the usability of the newly developed dispersal model FIDIMO and to apply it for modelling dispersal of multiple fish species in an anthropogenically impacted (habitat degradation, catchment land use, migration barriers) river catchment (German River Treene). Moreover, a modelling framework to disentangle and quantify the single effects of dispersal and habitat quality on the occurrence of fish species should be provided. It was hypothesised that the discontinuous distribution of river fish is jointly governed by species' dispersal abilities, species-specific habitat suitability and the impacts of migration barriers and that the importance of dispersal decreases in time in favour of the increasing importance of habitat suitability.

4.1 List of papers

This thesis was conducted as part of the IWRM-Net Project IMPACT (`http://www.impact.igb-berlin.de/`, BMBF grant number 02WM1134) and is a cumulative work based on three research papers (1-3). Each paper, thus forms a separate part including an introduction, methods, results, discussion and references section. The papers are either reprinted with permission of the publisher (Part 1 and Part 2) or submitted/under review to a peer-reviewed journal (Part 3). The text has been reformatted and figures and tables were renumbered for a coherent layout throughout the thesis. Finally, a synthesis following the single research papers provides the connection to previous findings, identifies present knowledge gaps and points out future directions of research.

Part 1:	**Radinger, J.** and Wolter, C. (2013). Patterns and predictors of fish dispersal in rivers. *Fish and Fisheries*, 1-18. in press. DOI: 10.1111/faf.12028
Part 2:	**Radinger, J.**, Kail, J. and Wolter, C. (2013). FIDIMO – A Free and Open Source GIS based dispersal model for riverine fish. *Ecological Informatics*, 1-10. in press DOI: 10.1016/j.ecoinf.2013.06.002
Part 3:	**Radinger, J.** and Wolter, C. (submitted). Disentangling the effects of habitat suitability, dispersal and fragmentation on the distribution of river fishes

Chapter 1

Patterns and predictors of fish dispersal in rivers

Patterns and predictors of fish dispersal in rivers

Johannes Radinger and Christian Wolter

Fish and Fisheries, DOI: 10.1111/faf.12028

Quantifying fish dispersal and identifying its general predictors is key for understanding temporal patterns in population dynamics, emi- 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 datasets 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 m 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.

Keywords: fish dispersal, fish movement, leptokurtic dispersal, mobile component, movement distance, stationary component

1 Introduction

Spawning migrations of fish and the seasonality of spawning runs have been recognised 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 colonisation 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 et al. 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 (Hanski 1998;

Heggenes et al. 2006; Wright 1978), distribution of species, species turnover and recolonization of newly available habitats (Albanese et al. 2009; Detenbeck et al. 1992), 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 (Rodríguez 2002; Skalski and Gilliam 2000), 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 characterised 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 hypothesised as being responsible for individuals exchange between populations and thus decisive for dispersal, colonisation 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 homogenisation 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 synthesise the current knowledge and to refit empirical datasets 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 hypothesised 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.

2 Methods

2.1 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 (iv) 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 (Rodríguez 2002; Skalski and Gilliam 2000). 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 (Equ. 1.1) by minimising 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 meters) 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:

$$F(x) = p * \frac{1}{\sqrt{2\pi\sigma_{stat}^2}} * e^{-\frac{(x-\mu)^2}{2\sigma_{stat}^2}} + (1-p) * \frac{1}{\sqrt{2\pi\sigma_{mob}^2}} * e^{-\frac{(x-\mu)^2}{2\sigma_{mob}^2}} \tag{1.1}$$

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 optimise 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. Datasets that could not be successfully optimised as their parameter estimates were not converging were not considered for further analysis.

Besides the movement parameters potential explanatory variables were collected for each dataset 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.

2.2 Data analysis

First, it has been analysed if there is any correlation among 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, since pseudo replications among data collected in the same water body would bias the results. Therefore, a single dataset 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, 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 minimises the cross-validated error to avoid overfitting. Moreover, for the visualisation 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 which 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 Appendix A.2). 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.

3 Results

A total of 160 datasets from 71 studies could be extracted and parameter estimates for movement obtained (see Appendix, Table A.1). 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 datasets 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 % ($n = 83$) datasets. Only seven datasets (5 %) derived from larger rivers with stream orders ≥ 7. Accordingly the majority of the streams had an average discharge ≤ 15 m^3s^{-1} (81 %) and a stream width <10 m (62 %) (median = 1.4 m^3s^{-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. 1.1a) and ranged between 0.01 m and 39 760 m (median = 36.36 m) for the stationary component (σ_{stat}) respectively between 2.22 m 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. 1.1b).

Although no significant relation between any distance parameter estimates (σ_{stat}

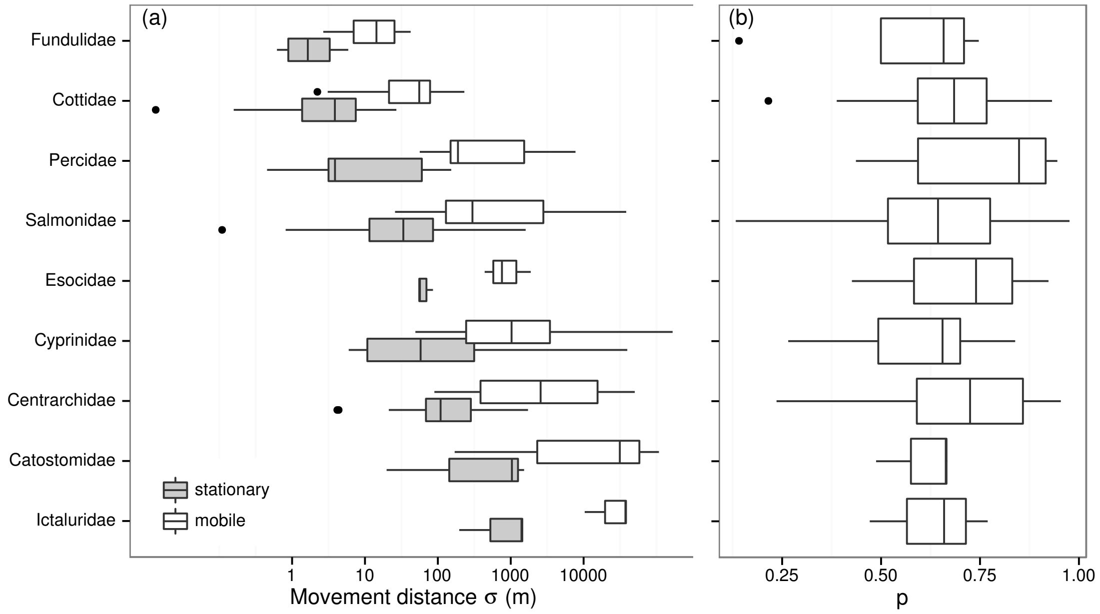

Figure 1.1: Characteristics of movement parameters across families ($n > 2$): (a) Movement distance σ of the stationary (grey boxes) and mobile (white boxes) component. (b) Share of the stationary component (p).

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. 1.2). Furthermore, the movement distance σ_{mob} was 13.67 times longer (median value, 7.78-28.33 IQR) than σ_{stat}.

Single regressions between $\log(\sigma_{stat})$ respectively $\log(\sigma_{mob})$ and fish length (log L), aspect ratio (AR), stream order ($SO^{\frac{1}{2}}$), discharge (log D), river width (log W) and time of the study (log T) revealed throughout significantly positive relations ($P < 0.01$) (Fig. 1.3a-1.3f). Detailed information on the single regression parameter estimates are given in Table 1.1. 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 intercorrelated ($r = 0.78$-

Table 1.1: Results of the linear regressions between movement distance and fish morphometrical parameters, stream size and time.

Predictor	Model		Regression coefficients β								
	$\log(\sigma_{stat}) \sim$ $\log(\sigma_{mob}) \sim$	α	log(L)	AR	$SO^{\frac{1}{2}}$	log(D)	log(W)	log(T)	n	R^2	P-value
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	$\alpha + \beta$ AR	1.05		2.04					116	0.09	0.002
		4.24		1.84					116	0.07	0.005
Stream order	$\alpha + \beta\ SO^{\frac{1}{2}}$	-1.17			2.50				106	0.25	<0.001
		1.08			2.80				106	0.34	<0.001
Discharge (m^3sec^{-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 (d)	$\alpha + \beta \log(T)$	1.25						0.54	128	0.17	<0.001
		3.71						0.62	128	0.22	<0.001

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

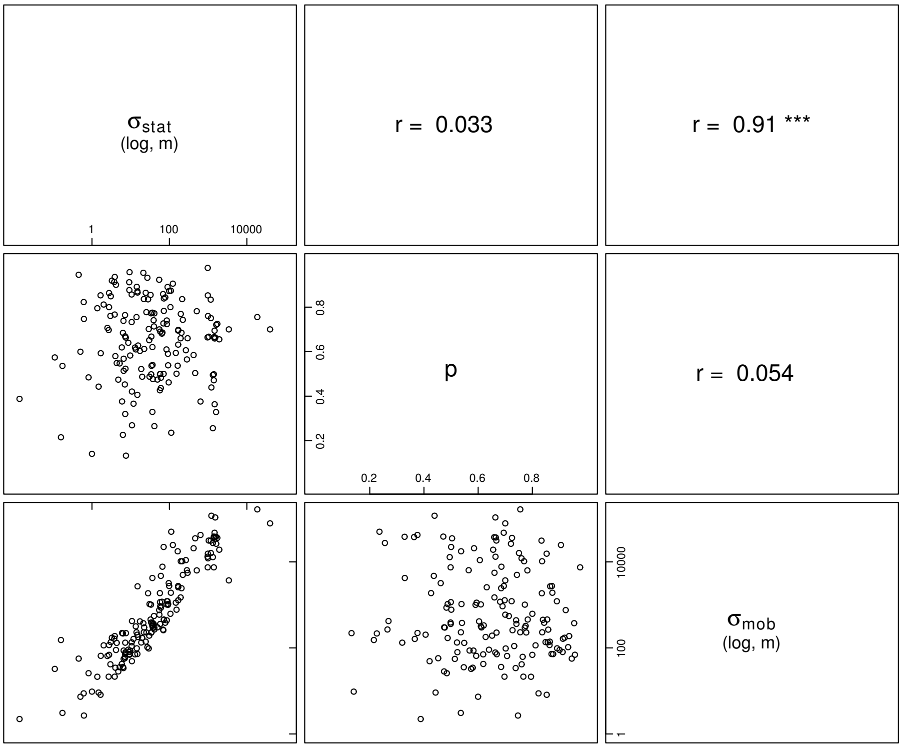

Figure 1.2: Scatterplot matrix of movement parameters: Movement distance of the stationary (σ_{stat}) and mobile (σ_{mob}) component and share of the stationary component (p). Pearson's product moment correlation coefficient ***P-value <0.001.

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 are given in Table 1.2. All models showed similar explanatory values for the two movement components σ_{mob} and σ_{mob}. However, the values for the σ_{mob}-models (adjusted $R^2 = 0.76$-0.78, $AIC = 37.31$-42.62) were typically higher than for the σ_{stat}-models (adjusted $R^2 = 0.62$-0.65, $AIC = 84.83$-91.31). The regression slopes (coefficient β) for fish length and aspect ratio were higher in all

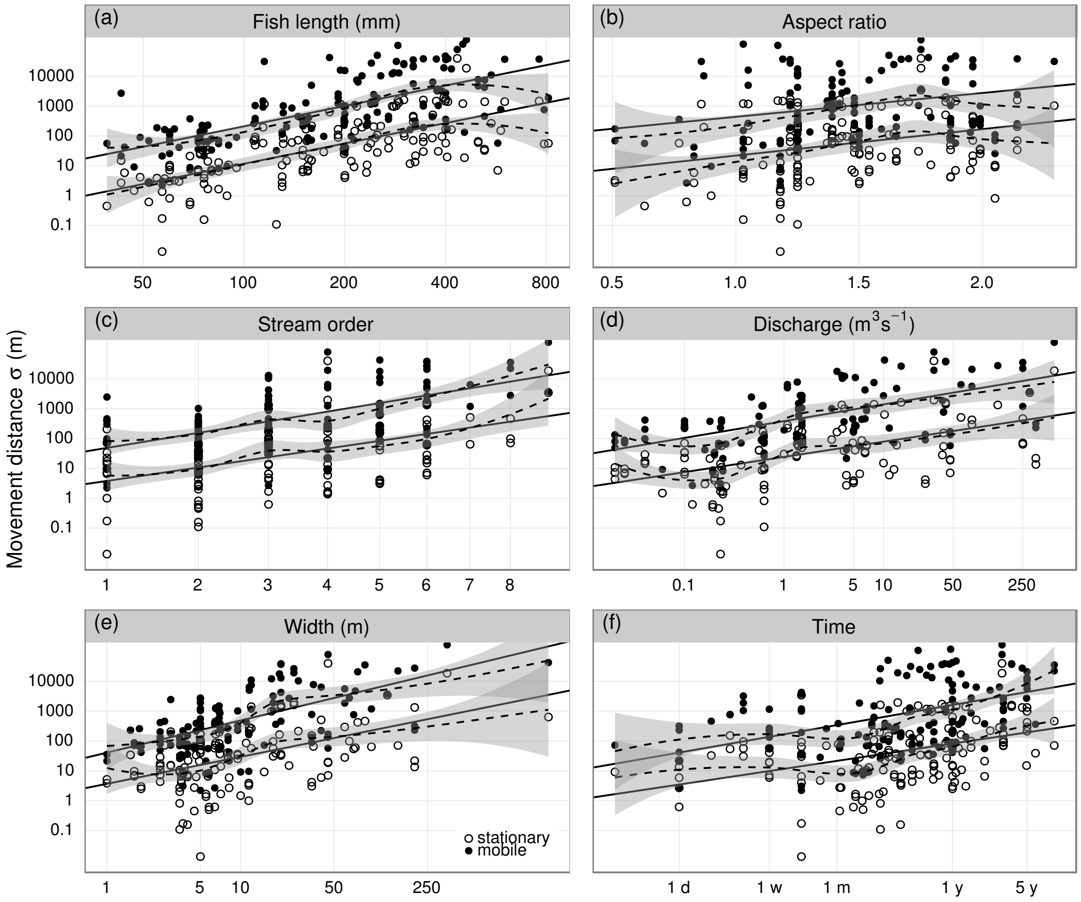

Figure 1.3: Movement distance σ of stationary component (σ_{stat}, open circles) and mobile component (σ_{mob}, closed circles) in relation to (a) fish length, (b) aspect ratio of the caudal fin, (c) stream order, (d) discharge, (e) stream width and (f) time. Solid lines indicate linear regressions. Dashed lines illustrate fitted LOESS curves, corresponding standard errors in grey.

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

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. 1.4b). 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. 1.4a): The data were firstly partitioned at a fish

Table 1.2: Results of the multiple linear regressions between movement distance and fish morphometrical parameters, stream size and time.

Model		Regression coefficients β									
$\log(\sigma_{stat}) \sim$ $\log(\sigma_{mob}) \sim$	α	log(L)	AR	$SO^{\frac{1}{2}}$	log(D)	log(W)	log(T)	n	R^2adj	AIC	AIC(logLik)
$\alpha + \beta_1\log(L) + \beta_2AR +$	-10.57	1.64	0.97	1.14			0.43	96	0.65	85.86	360.3
$\beta_3SO^{\frac{1}{2}} + \beta_4\log(T)$	-7.48	1.45	0.58	1.51			0.55	96	0.77	36.73	311.16
$\alpha + \beta_1\log(L) + \beta_2AR +$	-8.25	1.61	0.83		0.2		0.44	90	0.63	84.38	341.79
$\beta_3\log(D) + \beta_4\log(T)$	-4.74	1.44	0.47		0.27		0.57	90	0.76	42.53	299.94
$\alpha + \beta_1\log(L) + \beta_2AR +$	-9.72	1.73	0.99			0.29	0.44	98	0.63	91.67	371.79
$\beta_3\log(W) + \beta_4\log(T)$	-6.32	1.53	0.63			0.53	0.53	98	0.76	42.65	322.77
$\alpha + \beta_1\log(L) + \beta_2AR +$	-9.59	1.54	0.9	1.02	0.08	-0.08	0.44	88	0.63	85.49	337.23
$\beta_3SO^{\frac{1}{2}} + \beta_4\log(D) +$	-6.4	1.33	0.57	0.84	0.02	0.3	0.56	88	0.77	38.96	290.7
$\beta_5\log(W) + \beta_6\log(T)$											

L = Fish length (mm); AR = Aspect ratio of the caudal fin; SO = Stream order; D = Discharge (m^3sec^{-1}); W = Stream width (m); T = Time (d); σ_{stat} = Movement distance of the stationary component; σ_{mob} = Movement distance of the mobile component; R^2adj = Adjusted R^2; AIC = Akaike information criterion, AIC(logLik) = AIC based on log-likelihood.

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}).

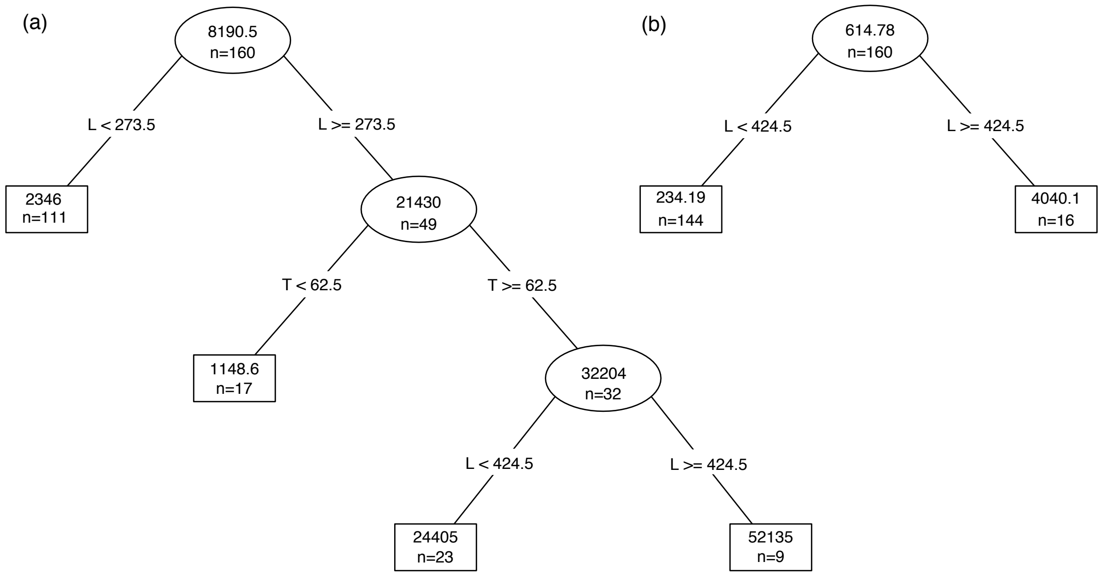

Figure 1.4: Pruned regression trees initially considering all parameters for the prediction of (a) σ_{mob} and (b) σ_{stat}. L = fish length (mm); T = Time (d).

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. 1.5). 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} (ANCOV $F_{3,70} = 1.52$, $P > 0.1$) nor σ_{mob} (ANCOVA $F_{3,70} = 1.47$, $P > 0.1$) were significantly influenced by the study method.

Table 1.3 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 per-

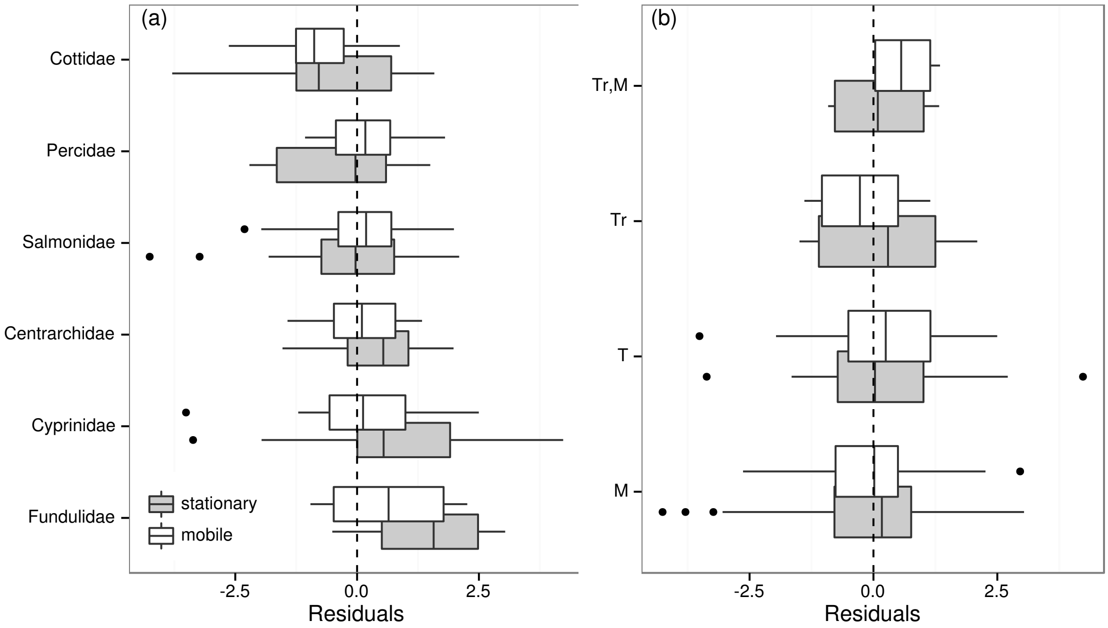

Figure 1.5: Residuals of the four-parameter (fish length, aspect ratio, stream order, time) multiple regression model (a) across families ($n > 5$) and (b) across study methods (M = mark-recapture, T = telemetry, Tr = traps) for σ_{stat} (white boxes) and σ_{mob} (grey boxes).

formed similarly well with 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.

4 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 kernels. In contrast to most previous reviews con-

Table 1.3: 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		Fixed effects coefficients β						Random effects variance					
$\log(\sigma_{stat}) \sim$ $\log(\sigma_{mob}) \sim$	α	log(L)	AR	$SO^{\frac{1}{2}}$	log(D)	log(W)	log(T)	Fam	Sp:Fam	Met	Stu	n	AIC(logLik)
$\alpha + \beta_1\log(L) + \beta_2 AR + \beta_3 SO^{\frac{1}{2}} +$	-9.18	1.45	1.1	0.92			0.42	0.12	0.02	0.1	1.36	96	354.36
$\beta_4\log(T) + b_i Fam +$	-6.79	1.34	0.87	1.34			0.52	0.06	0.04	0.05	0.95	96	307.36
$b_i Sp{:}Fam + b_i Met + b_i Stu$													
$\alpha + \beta_1\log(L) + \beta_2 AR + \beta_3\log(D) +$	-6.39	1.28	0.87		0.22		0.44	0.17	0.06	0.11	1.42	90	334.02
$\beta_4\log(T) + b_i Fam +$	-3.19	1.12	0.7		0.31		0.54	0.4	0	0.04	1.08	90	289.6
$b_i Sp{:}Fam + b_i Met + b_i Stu$													
$\alpha + \beta_1\log(L) + \beta_2 AR + \beta_3\log(W) +$	-8.16	1.48	1.03			0.19	0.45	0.18	0.01	0.16	1.26	98	368.61
$\beta_4\log(T) + b_i Fam +$	-5.14	1.28	0.78			0.5	0.52	0.09	0.1	0.11	0.86	98	316.12
$b_i Sp{:}Fam + b_i Met + b_i Stu$													
$\alpha + \beta_1\log(L) + \beta_2 AR + \beta_3 SO^{\frac{1}{2}} +$	-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	0.6	0.15	0.19	0.53	0.2	0.01	0.03	1.05	88	285.99
$\beta_6\log(T) + b_i Fam +$													
$b_i Sp{:}Fam + b_i Met + b_i Stu$													

L = Fish length (mm); AR = Aspect ratio of the caudal fin; SO = Stream order; D = Discharge ($m^3 sec^{-1}$); W = Stream width (m); T = Time (d); 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.

sidering 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 distant locations and exploring new habitats. This long distance dispersal might be an important factor for genetic exchange within meta-populations.

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.

4.1 Share of the mobile component

Former studies emphasised 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 meta-populations. 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 (Aparicio and Sostoa 1999; Harcup et al. 1984; Knaepkens et al. 2005, 2004).

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 (Albanese et al. 2004; McMahon and Matter 2006; Winker et al. 1995).

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. 1.6). 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 populations might have reached a new river stretch or habitat. For example, according to the very simple and still criticised 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.

4.2 Fish length

A strong relation was found between the movement distance and fish length explaining approximately 45% of the variance. This supports existing theory that both movement and home range of animals generally increase with body size (Pe-

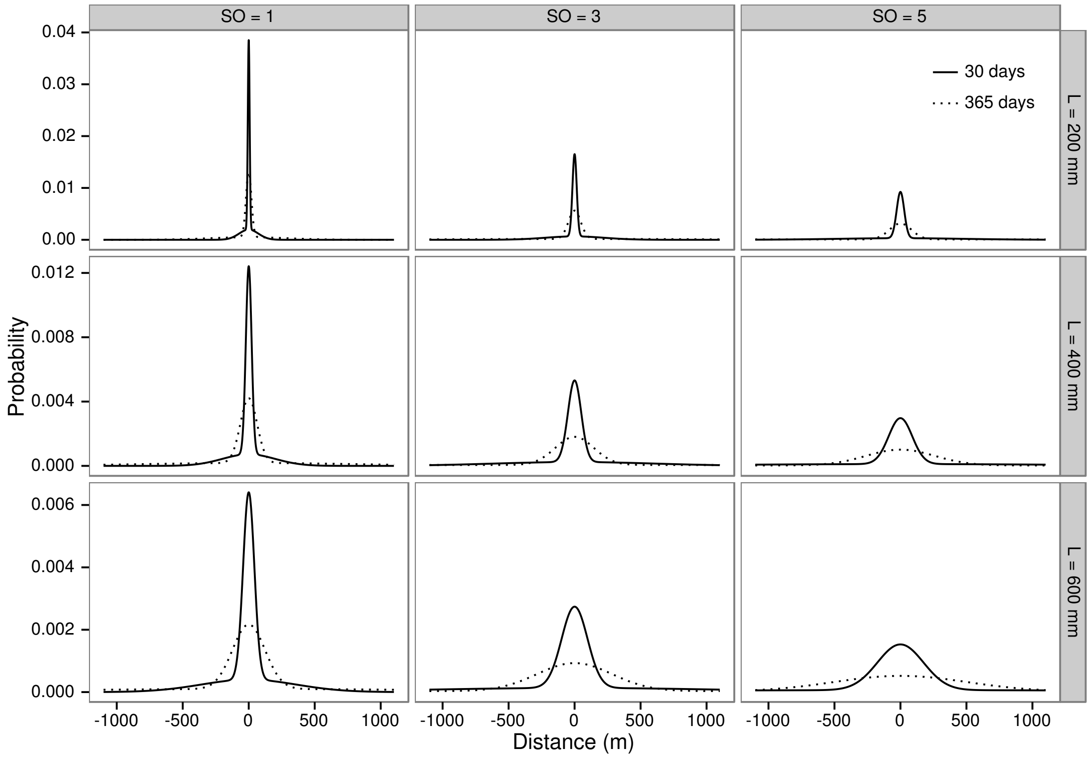

Figure 1.6: Example for leptokurtic dispersal kernel for Brown trout (*Salmo trutta fario*) predicted from the multiple regression model (aspect ratio = 1.25 and p = 0.64). Comparisons across size classes (L = fish length), stream sizes (SO = stream order) and time intervals (30 days (solid line), 365 days (dotted line)).

ters 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 $\sim$ -2.91 $\times$ 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. 1.4) and the corresponding drop in LOESS curve (Fig. 1.3a) 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 (Albanese et al. 2004; Smithson and Johnston 1999).

4.3 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.

4.4 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 (Hudy and Shiflet 2009; Ovidio et al. 2009; Petty and Grossman 2004) which might be related to the poorer swimming ability of small bodied benthic species (Chaumot et al. 2006; Knaepkens et al. 2004).

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

4.5 Time

While monitoring studies on restoration efforts focus on the reestablishment of target species, little is known about the ability of fish to disperse to newly rehabilitated habitats within a given timeframe. 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 by 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 proportional 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 kernels. Moreover, theoretical studies have shown that the resulting variance of convoluted normal distributions equals the sum of the variance of the single distributions (Vinga and Almeida 2004). This implies that the variance of 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.

5 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 for 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 restricted movement paradigm 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. 1.6).

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 (Pépino 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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Chapter 2

FIDIMO – A free and open source GIS based dispersal model for riverine fish

FIDIMO – A free and open source GIS based dispersal model for riverine fish

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Dispersal is a key process in community ecology and dynamics that comprises not only various movement processes, but also behavioural components and large-scale spatio-temporal patterns. Modelling fish dispersal further has to consider the species-specific dispersal abilities and the branching, dendritic nature of river networks.

With FIDIMO (Fish Dispersal Model) a tool is provided for predicting and simulating spatio-temporal patterns of fish dispersal in river networks with a real integration of GIS for the first time. The model has been written in Python programming language as open source add-on for GRASS GIS. The model has been developed to apply the characteristics of heterogeneous, species and size class specific fish movement on a rasterised river network including migration barriers. Fish dispersal is modelled as a leptokurtic diffusion process spreading from spatially predefined source populations consisting of stationary and mobile components each. The fish dispersal model FIDIMO links conceptual considerations on dispersal modelling with empirically observed fish movement patterns and the strengths of geographically explicit modelling in FOSS GIS. It can be used for different species and any river network meeting the input requirements.

As main results FIDIMO yields probabilities of occurrence of fish species in river raster cells based on empirically derived dispersal kernels after the time step of interest modelled.

The model output serves to understand and predict time lags and spatio-temporal patterns of recolonization events, the related success of river rehabilitation but also the spread of invasive species. The

consequent use of open source programs allows free access to the code and facilitates easy modifications, adoptions and improvements of the model.

Keywords: GRASS GIS; fish dispersal; dispersal modelling; raster GIS; leptokurtic dispersal; dispersal time lags

Abbreviations: GIS, Geographic Information Systems; FOSS, Free and Open Source Software; FIDIMO, Fish Dispersal Model; GRASS, Geographic Resources Analysis Support System; UTM, Universal Transverse Mercator projection; WGS84 World Geodetic System 1984; nad27, North American Datum of 1927; GUI, Graphical User Interface; GNU, GNU's Not Unix; WFD, Water Framework Directive; IWRM-net, Regional and National research programs network on Integrated Water Resource Management; IMPACT, Developing an integrated model to predict abiotic habitat conditions and biota of rivers for application in climate change research and water management;

1 Introduction

The dispersal of animals is the movement of individuals away from their home range (Turchin 1998). It is a key process in community ecology that governs the exchange between subpopulations, the emi- and immigration as well as the (re-)colonisation of new habitats and strongly influences the spatio-temporal distribution and abundance of species. Fish dispersal is a complex process that depends on many different factors: Triggering factors that cause individuals to leave their home range (e.g. immediate environment, food availability, hydrological variables), variables that influence the movement and the distance moved (e.g. fish size, stream size, movement barriers) and factors that cause individuals to colonise a new habitat (e.g. habitat features, depth, flow velocity, food availability) (e.g. Lucas and Baras 2001; McMahon and Matter 2006).

Like for other ecological processes, modelling (i) can improve our understanding by generalising and simplifying such complex systems to a small set of key components (Breckling et al. 2011) best depicting the patterns e.g. of movement at the population level and (ii) can be used for predictions. So far fish dispersal modelling studies have mainly provided conceptual frameworks and equations (i) to describe fish movements as driver of meta-population dynamics (e.g. Auerbach and Poff 2011; Gotelli and Taylor 1999), (ii) to assess spawning runs in diadromous fish (Åström and Dekker 2007; Rivinoja 2005), (iii) to statistically support the occupancy – abundance relationship hypothesis in macroecology (Rose and Leggett 1991; Winters and Wheeler 1985), (iv) to formulate empirically derived dispersal kernels (e.g. Radinger and Wolter 2013; Rodríguez 2002; Skalski and Gilliam 2000), (v) to analyse sub-population structures according to the isolation by distance hypothesis (e.g. Bradbury and Bentzen 2007; Pinsky et al. 2010; Puebla et al. 2009) and (vi) to describe drift of larvae and recruitment of commercially important species in marine systems (e.g. Pelc et al. 2010).

These conceptual frameworks and equations can be used to describe and quantify riverine fish dispersal but comprehensive modelling tools to apply these equations in a specific river network and geographical setting, i.e. the implementation in a fish dispersal modelling software are lacking (e.g. Bonhommeau et al. 2009; Wolter and Sukhodolov 2008). Such dispersal models, however, may greatly contribute to mapping and predicting movement patterns of fish populations in relation to (i) success and time lags in recolonization of e.g. restored habitats, (ii) spread of invasive species and (iii) temporal patterns in population dynamics.

To fully capture and model riverine fish dispersal two key aspects have to be considered: The species-specific movement patterns and the linear structure of river networks. Concerning the movement patterns, empirical studies revealed a highly leptokurtic dispersal of fish populations due to a large stationary component which only shows local small-scale movements and a smaller mobile component showing long distance dispersal (Rodríguez 2002; Skalski and Gilliam 2000). This characteristic is reflected in the shape of the probability density functions describing how fish disperse, the so-called dispersal kernels, which show a high central peak (stationary component) and typically fat tails (mobile component).

In species dispersal modelling, the speed of organisms' spread is highly sensitive to the shape of this dispersal kernel especially to the characteristics of the tails of the distribution (Kot et al. 1996). This leptokurtic pattern can be described with a heterogeneous model combining the distribution kernel of both components and its relative share on the total population. In an extensive review and meta-analysis of empirical studies on riverine fish dispersal of over 60 fish species, Radinger and Wolter (2013) found out that the movement distance of both components is positively related to fish length, aspect ratio of the caudal fin, stream size and time and provided corresponding movement parameters.

The second key aspect is that the active spread of freshwater fish is restricted to river networks often described as dispersal corridors. From an ecological perspective these river networks are linear and dendritic structures with a main stem and branches that hierarchically decrease in size and increase in numbers in upstream direction (Grant et al. 2007). At confluences of rivers and tributaries, so-called network nodes, the upstream moving fish have to be apportioned to the main stem and the tributary. Thus, modelling dispersal along linear and hierarchically branching river networks differs fundamentally from the radially modelled terrestrial spread (Pitt 2008). A growing number of studies underscore the importance of viewing rivers as networks at the landscape level and the needs to link local demographic processes with the spatial scales of networks (Benda et al. 2004; Fausch et al. 2002; Lowe et al. 2006) to fully capture dynamics in stream ecology. However, most river networks are heavily fragmented and longitudinal connectivity is commonly altered by movement barriers (e.g. dams and weirs) (e.g. Dynesius and Nilsson 1994; Nilsson et al. 2005; Poff et al. 2007). Fragmentation affects population dynamics and thus, needs to be considered in developing a comprehensive dispersal model.

Both key aspects of riverine fish dispersal – leptokurtic spread and dispersal along network corridors – are spatially determined, which means that they depend on the geographical and topographical setting. For example, the structure of river networks primarily depends on geology, climate and topography (Knighton 1998) and hence, differs between regions. Moreover, the number and type of migration barriers differs locally (Nilsson et al. 2005). Furthermore, the leptokurtic dispersal function depends on river size besides fish-specific variables (Radinger and Wolter 2013).

Geographical Information Systems (GIS) are capable to analyse spatially varying data like dendritic river ecosystems and leptokurtic fish movement patterns, and hence, seemed predestinated to model fish dispersal. Especially the enhanced computational capabilities and the on-going improvement and development of appropriate GIS tools can facilitate the analyses, processing, management and visualisation of spatial ecological data. The usefulness and strengths of GIS have been outlined for instance in large-scale analyses of biodiversity and conservation planning (e.g. Ferrier et al. 2002; Jones et al. 1997), of vegetation (e.g. Goodchild 1994; Kent et al. 1997), entomology (e.g. Dminic et al. 2010) and in aquatic ecology (e.g. Johnson and Gage 1997; Sowa et al. 2007). Recent studies have also shown the successful application of GIS to model species dispersal e.g. of terrestrial insects (e.g. Pitt et al. 2009), invasive plants (e.g. Fox et al. 2007) and marine fish larvae (e.g. Fischer et al. 2011). However, due to licensing policies, proprietary GIS does not allow for free accessibility as well as easy modifications and the implementation of newly developed models, particularly to accomplish the dispersal needs of aquatic species. Thus, free and open source software GIS (FOSS GIS) becomes increasingly important to develop complex integrated spatial models and can be considered an integrative part of spatial ecology (Rey 2009).

Here we present the fish dispersal model FIDIMO (GRASS command r.fidimo), as a new tool for GRASS GIS (Neteler and Mitasova 2007), which has been developed to predict the movement and dispersal of riverine fish species at the river network scale. It combines the consideration of leptokurtic fish dispersal in fragmented stream networks with the modelling strengths of freely available FOSS GIS tools for assessing the spatial and temporal (re)-colonisation potential of fish in a raster-GIS environment.

2 Model description

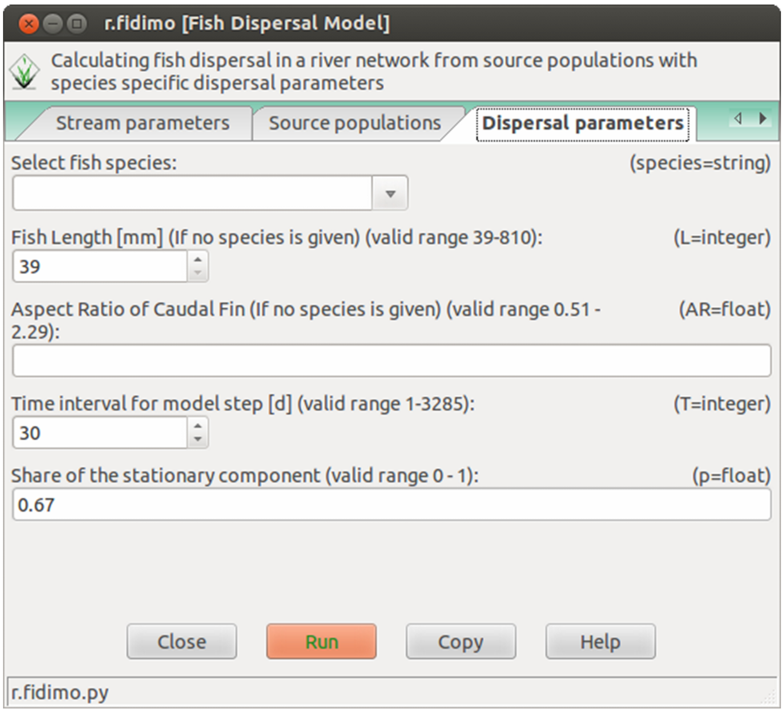
In general, dispersal comprises three phases: (1) leaving a home range, (2) travelling or movement and (3) colonising a new suitable river reach (Lidicker and Stenseth 1992). In FIDIMO, the central process of dispersal, the movement of the species (phase 2) is modelled from source populations to adjacent raster cells, i.e. from the source to the sink. Therefore the geographical locations of the source populations in the river network have to be provided prior to the modelling.

In FIDIMO, a leptokurtic function consisting of two superimposed normal distributions is used as the core model since it most adequately describes fish dispersal (Rodríguez 2002; Skalski and Gilliam 2000). This diffusion-based dispersal kernel describes the probability of occurrence of the fish species as a function of the distance (x) from the source population and is applied to each source population on a distance raster map in GIS:

$$F(x) = p * \frac{1}{\sqrt{2\pi\sigma_{stat}^2}} * e^{-\frac{(x-\mu)^2}{2\sigma_{stat}^2}} + (1-p) * \frac{1}{\sqrt{2\pi\sigma_{mob}^2}} * e^{-\frac{(x-\mu)^2}{2\sigma_{mob}^2}} \tag{2.1}$$

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

FIDIMO requires certain input parameters to parameterise the leptokurtic dispersal function and to apply it to a specific river network, which have been arranged in the GUI in four sections: (i) stream parameters, (ii) source populations, (iii) dispersal parameters and (iv) output and optional settings (Fig. 2.1).



r.fidimo [Fish Dispersal Model]

Calculating fish dispersal in a river network from source populations with species specific dispersal parameters

Select fish species: (species=string)

Fish Length [mm] (If no species is given) (valid range 39-810): (L=integer)
39

Aspect Ratio of Caudal Fin (If no species is given) (valid range 0.51 - 2.29): (AR=float)

Time interval for model step [d] (valid range 1-3285): (T=integer)
30

Share of the stationary component (valid range 0 - 1): (p=float)
0.67

r.fidimo.py

Figure 2.1: Graphical user interface (GUI) for FIDIMO, section “Dispersal parameters”.

2.1 Input and output

Stream parameters

The river network needs to be provided in the GRASS raster format. This raster map is further used for calculating stream flow directions and stream topological features. Its resolution defines the grid cell size for the final model output. A river network in vector format has to be rasterised and thinned first to ensure a unique identification of the flow direction. Each input cell may neighbour only one upstream and one downstream cell, except for cells that represent nodes in the network. Especially for highly meandering rivers with narrow river bends it is appropriate to smooth the river in advance (e.g. GRASS command v.generalize) and check the result for any undesired artefacts.

Additionally, the latitudinal and longitudinal coordinates of the outflow pour-point must be provided in a simple text file in comma-separated format ("X, Y") in the coordinate system of the actual GRASS location.

Despite all efforts in building fish passage facilities, movement barriers such as weirs continue to substantially affect fish movement in fragmented landscapes depending on the type of barrier and the fish species (reviewed by Noonan et al. 2012). Thus, descriptive data on the geographic location and passability of movement barriers are an optional input of FIDIMO. The text file with the coordinates and passability rates (ranging from 0 = impassable to 1 = all fish can pass) must be formatted after the default GRASS command v.in.ascii in which each line refers to a barrier (|-separated: "X|Y|passability value").

Source populations

In population ecology, source habitats are typically of good quality fostering population growth and the emission of specimens, i.e. they serve as potential source populations (Dias 1996). Here, the source population provides the starting point in FIDIMO, which is in principal freely definable depending on the research question of interest. Mostly, potential source populations should be directly determined from empirical survey data using species occurrences, e.g. the nearest population of a target species in assessing restoration success. Alternatively, potential sources could be assessed from the distribution of high quality habitats based on species distribution models or set at potential entering points of recolonizing or invading species, e.g. at the mouth of a river network or at harbours and urban centres in case of exotic species.

The geographical location of source populations (as starting points for applying the dispersal kernel) must be provided as a raster map indicating the presence or abundance of a certain fish species. Such empirical data are rarely available at the catchment or river network scale, but species distribution models can be developed prior to the modelling of fish dispersal in FIDIMO and can provide reasonable input maps. In relation to that, Elith and Leathwick (2009) provided a review on the ability of various models to predict species distributions respectively how to improve them. Alternatively, either specifying an absolute number of cells or a percentage of cells of the river network randomly sets source populations in the entire catchment (e.g. for simulations).

Dispersal parameters

The dispersal parameters σ_{stat} and σ_{mob} of the leptokurtic function (1) are set based on information on fish length, aspect ratio of the caudal fin, stream order, and time (Radinger and Wolter 2013). Fish length and the species-specific aspect ratio of the caudal fin (Pauly 1989) can be automatically derived from the R package 'FISHMOVE' for so far 43 fish species in a predefined list. Alternatively, a specific length and aspect ratio can be provided manually. The stream order is extracted from the river network, and the time interval for a model run is by default set to 30 days but can be changed manually. There is no significant predictor for p (share of the stationary component) and hence, this dispersal parameter is by default set to the median value of 0.67 reported by Radinger and Wolter (2013), but it can be also set manually (Fig. 2.1). A detailed description of the input parameters for fish dispersal is provided in the manual for the R-package 'FISHMOVE', which accompanies a comprehensive review on freshwater fish dispersal patterns (Radinger and Wolter 2013).

Neither the FIDIMO model nor the underlying dispersal review (Radinger and Wolter 2013) includes information about hydrology or in-stream hydraulics which considerably vary throughout the year (e.g. Poff et al. 2007). Therefore, it is recommended to apply the model either to rather short (less than one year) time intervals of average flow conditions or even better to substantially larger time scales which cover the entire variability of a hydrological year within one modelling step.

Output and optional settings

The output of FIDIMO is a raster GRASS GIS map containing probabilities of occurrence of fish per cell. In addition, if any statistical interval has been selected, FIDIMO creates raster maps for the fitted mean value and for the upper and lower bounds (confidence or prediction interval) of the 'FISHMOVE' output. The optional settings include any retention and savings of temporary files created during the model runs. Moreover, a kernel truncation criterion can be set that specifies where the theoretically infinite dispersal kernel is truncated to achieve reasonable computation times.

2.2 Description of FIDIMO

The model itself can be divided in two main parts, (i) the pre-processing and (ii) the core model. These can be further subdivided into single sub-processing steps where each step is associated with one or several GRASS GIS commands that run partly in computation loops. All central computation steps are commented in the Python script of FIDIMO and shown in Fig. 2.2.

Pre-processing

First, FIDIMO sets up the GRASS region configured by the river raster input and an SQlite database connection. All vector attribute tables are stored in the SQlite database of the running GRASS location providing the advantage to loop easily over single vector items (e.g. source population points) using SQL.

Furthermore, FIDIMO converts the stream from raster to vector format (GRASS command r.to.vect) and breaks the stream at network nodes and locations of movement barriers into linear stream segments representing the processing units for later computational steps. The optionally imported barrier points are internally snapped to the nearest cell of the river raster beforehand. Subsequently, the broken river vector is transformed back to raster format (GRASS command v.to.rast)

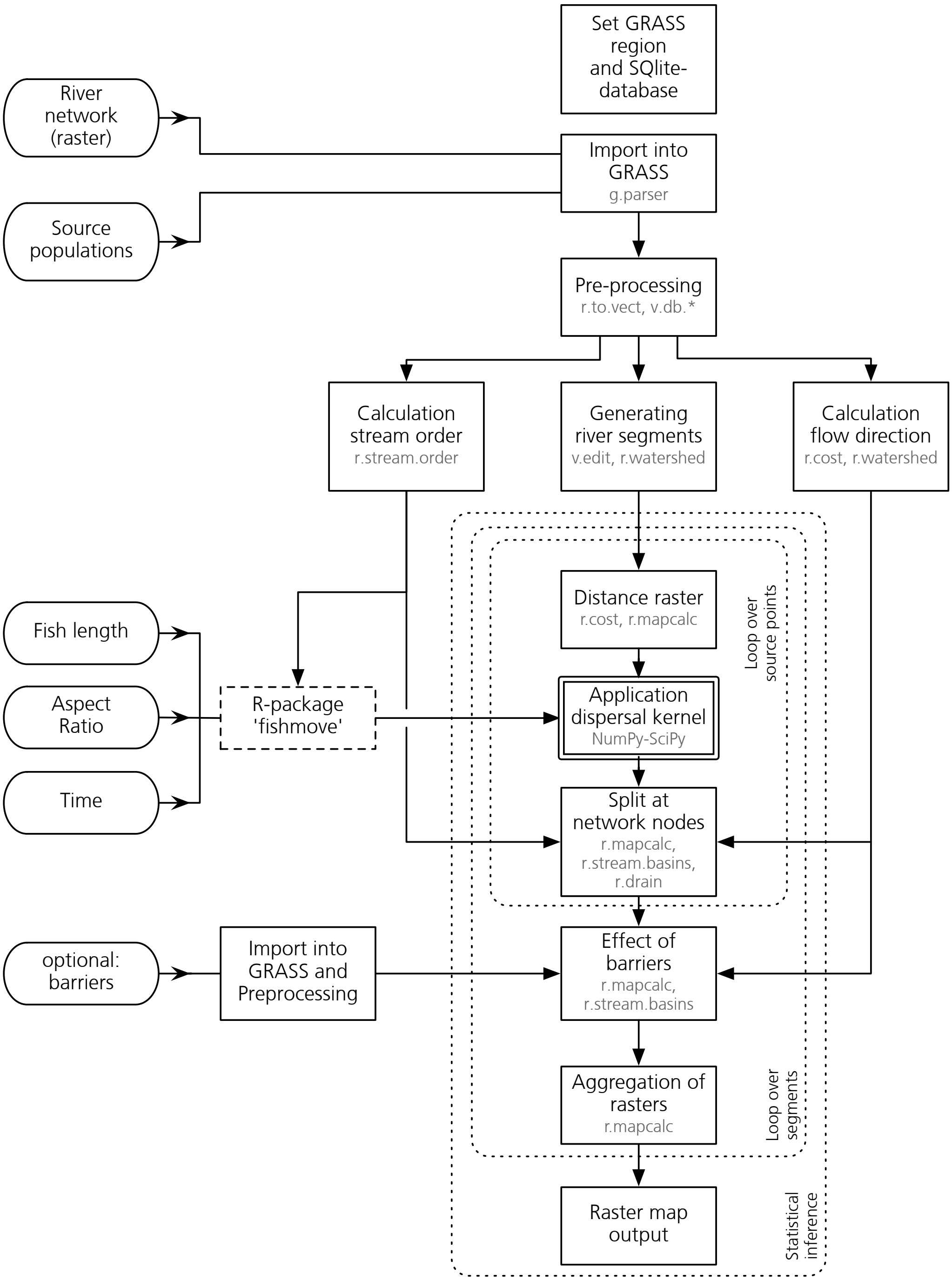


Figure 2.2: Flow chart of main computational steps of FIDIMO.

in which the stream segment number provides the category value for the output raster map.

Due to the importance of distinguishing up- and downstream positions of cells within the stream network (e.g. to determine if a barrier is up- or downstream of a particular source population), r.watershed (`http://grass.osgeo.org/grass65/manuals/r.watershed.html`) is applied, a built-in watershed basin analysis tool in GRASS that generates a set of raster maps indicating e.g. flow accumulation, drainage direction and the location of streams. In FIDIMO, the flow direction is calculated using so-called pseudo-elevation maps created by r.cost (`http://grass.osgeo.org/grass65/manuals/r.cost.html`). This command generates a raster map showing the cumulative cost of moving between different geographic locations on an input raster map whose cell category values represent costs. Applying r.cost specifically on a raster where the costs per cell refer to the actual spatial resolution and starting from the outflow point creates a map with increasing values (distance) while proceeding upstream in the network. Hence, the resulting raster map shows higher values in the headwaters and lower values in the downstream part of the river network indicating also flow direction.

In addition, the output of the GRASS tool r.watershed is used for calculating Strahler stream order (Strahler 1957) and Shreve stream order (Shreve 1966) using the GRASS add-on r.stream.order (Jasiewicz and Metz 2011). The stream order maps are prerequisites for the calculation of actual movement distances and for the split of populations in upstream movement at network nodes (Fig. 2.3).

During the pre-processing, the raster map of source populations or the map with randomly set source populations, respectively, are converted to a source population point file. In a later stage each point will act as a source for dispersal with a starting probability that is either derived from the input raster cell value or is set to “1” in case of random input. Extracting information of the particular stream order and stream segment number and adding it to a new “Segment” and “Strahler” column complements the source point’s attribute table.

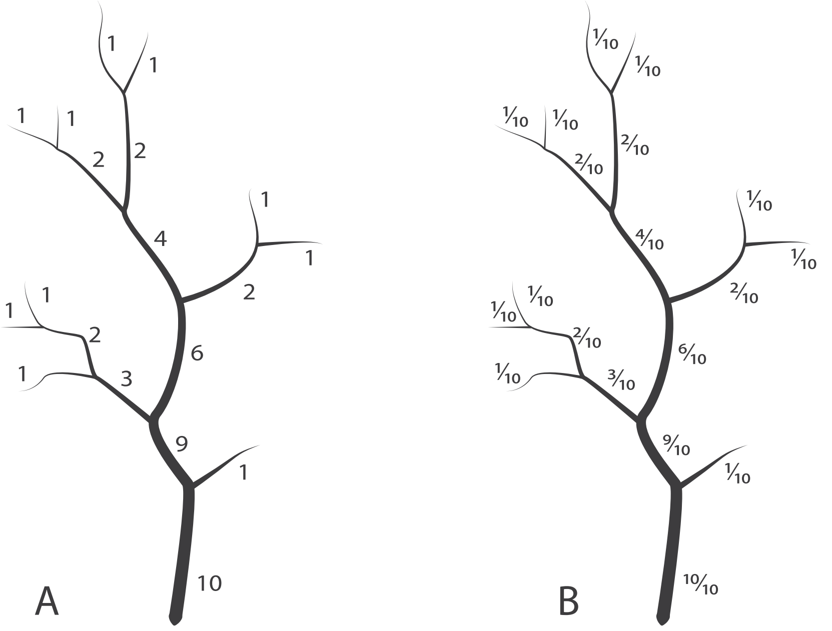


Figure 2.3: (A) original concept of Shreve stream order (Shreve, 1966) and (B) relative Shreve stream order used as weighting factor for upstream dispersal.

Core model

The FIDIMO main part builds on nested loops over each source point in each stream segment. This segment-wise approach allows for a combined computation of source points that share common upstream barriers and thus reduces computational time. The dispersal kernel and its underlying parameters (σ_{stat}, σ_{mob}, p) are calculated using the R package 'FISHMOVE' based on the user-supplied input and the Strahler stream order of each source point. To reduce computational time, dispersal kernels for a broad range of stream orders are calculated and stored in a Python object in advance and recalled at the particular computation step.

As next step a raster map containing distances from each source point are calculated (GRASS command r.cost) providing the basic map for the application of the dispersal kernel. This distance map and the dispersal kernel are truncated at a maximum distance where the truncation criterion (user supplied percentage of area under dispersal kernel, default = 99%) is achieved.

The previously generated distance raster map only describes the distance of each raster cell centre to the source. Thus r.mapcalc, an arithmetic GRASS tool for raster map layers calculates real distances of the lower (x_{lower}) and upper boundary (x_{upper}) of each cell based on the spatial resolution of the raster and considering how the flow passes each cell (orthogonal or diagonal). Both distance maps are exported to NumPy arrays (via the GRASS command grass.script.array) and act as the lower and upper limits for the integration of the fish dispersal kernel and thus for its discretisation in definite space:

$$\int_{x_{lower}}^{x_{upper}} f(x)dx = \left\{ \begin{array}{c} \text{fraction of the} \\ \text{population/probability for the interval} \\ [x_{lower}, x_{upper}] \end{array} \right\} \tag{2.2}$$

FIDIMO uses the SciPy tool for cumulative density functions (stats.norm.cdf()) for calculating the cell discrete probabilities based on:

$$cdf(x_{lower}) = \int_{-\infty}^{x_{lower}} f(x)dx \tag{2.3}$$

$$cdf(x_{upper}) = \int_{-\infty}^{x_{upper}} f(x)dx \tag{2.4}$$

$$\int_{x_{lower}}^{x_{upper}} f(x)dx \triangleq cdf(x_{upper}) - cdf(x_{upper}) \tag{2.5}$$

The map derived must be corrected because some of the fish moving upstream enter the tributaries. Hence, the probability of the occurrence of a fish species must be split at river junctions. In FIDIMO, the fish moving upstream are apportioned to the main stem and tributary based on stream order since local stream size is positively related to fish dispersal (Hitt and Angermeier 2008). A raster map of the relative stream order is created (Shreve's (1966) stream order divided by the maximum upstream stream order) and is used as a multiplication factor for upstream movement (see Fig. 2.3B). Shreve's stream order is used instead of the Strahler order since it is considered a better approximation of stream size (Knighton 1998). In Shreve's method, a magnitude of one is assigned for all exterior branches. Consequently, confluent tributaries are added up so that the confluence of two first order streams result in a second order stream. Each additional confluent tributary increases the resulting stream order by its magnitude. The approach to portion the probability of occurrence based on stream order is a reasonable but gross approximation. We are aware that the choice of a dispersal route in a dendritic network is strongly species dependent (Hitt and Angermeier 2008) as well as related to physical and chemical properties of the confluent streams (e.g. Banks 1969; Neeson et al. 2011; Rakowitz et al. 2008; Thorstad et al. 2008). Downstream movement was restricted to the main stem only (using the GRASS command r.drain) disregarding any change in movement direction during one dispersal step.

If information on migration barriers are provided, only those that are located upstream of the processed stream segment are selected and ordered according to their distance from the segment. Subsequently, starting with the most downstream barrier, the part upstream of each barrier is multiplied by the barrier specific passability rate. The part of the population that is hindered in further upstream movement is relocated downstream each barrier, linearly decreasing to a distance of in maximum 200 m below. This approach accounts for the typical accumulation effect of fish downstream of barriers (Jurajda et al. 1998).

Finally, all generated maps are aggregated in a raster output map representing the probability density based on the dispersal kernel of 'FISHMOVE'.

2.3 Technical implementation and software

FIDIMO has been written in the Python programming language (version 2.6.6, `http://www.python.org`) as an add-on for GRASS GIS (GRASS command r.fidimo; GRASS version 6.4.2 or newer). GRASS (Neteler and Mitasova 2007) is a Free and Open Source Software (FOSS) for geospatial analysis supplying high vector and raster GIS functionality that is fully accessible via the GRASS Python scripting library and supports SQLite (`http://www.sqlite.org`) as database backend. Thus, it provided the necessary tools for automatising all steps of the analysis in the presented Python script.

In addition to GRASS GIS, running FIDIMO requires the following five software tools or packages: (i) r.stream.* add-on is a toolkit used for Hortonian analysis of rasterised stream networks (Jasiewicz and Metz 2011); (ii) R (version 3.0.0, R Development Core Team 2013) and the R-package 'FISHMOVE' (version 0.1-1, Radinger and Wolter 2013) provide statistical values of fish movement distances used for model parameterisation; (iii) RPy2 (`http://rpy.sourceforge.net`) provides the interface between R and Python; (iv) NumPy (version 1.6.0, Oliphant 2006), the Python extension for numerical calculations on large matrices, and (v) SciPy (version 0.9.0, Jones et al. 2001), a library of algorithms and mathematical tools for Python used to apply the continuous dispersal kernel on a spatially discrete raster grid.

FIDIMO can be launched as a script inside a running GRASS GIS session or installed as an add-on to GRASS GIS using g.extension. Like other GRASS modules, it can be launched from the command line (GRASS command r.fidimo.py); however, it also provides the auto-generated GRASS graphical user interface (GUI) implemented with g.parser (Fig. 2.1).

3 Sample Application

3.1 Dataset for sample application

For presenting and testing FIDIMO a raster stream network has been generated from the 3 arc-seconds void-filled digital elevation models (HydroSheds, `http://hydrosheds.cr.usgs.gov`, Lehner et al. 2008) for the Northern Limestone Alps in Lower Austria (Austria) (2 tiles: 45N-10E and 45N-15E). The r.stream.* toolkit was used to extract a smaller part of the stream network (River Erlauf upstream the town Wieselburg, 580 km2 catchment area, 47.75-48.15 N, 14.85-15.40 E, WGS84, Fig. 2.4). The script to generate and reproduce the sample dataset is provided in the Supplementary Material. After transformation the sample application has been computed in the projected coordinate system ETRS89 / UTM zone 33N (EPSG code: 25833) with a spatial raster resolution of 150 m.

All final descriptive and inferential analyses of the created raster output maps were conducted in R (version 3.0.0, R Development Core Team 2013) using the packages ‘raster’ (version 2.1-25, Hijmans and Etten 2013) for accessing raster maps and ‘ggplot2’ (version 0.9.3, Wickham 2009) for illustrations.

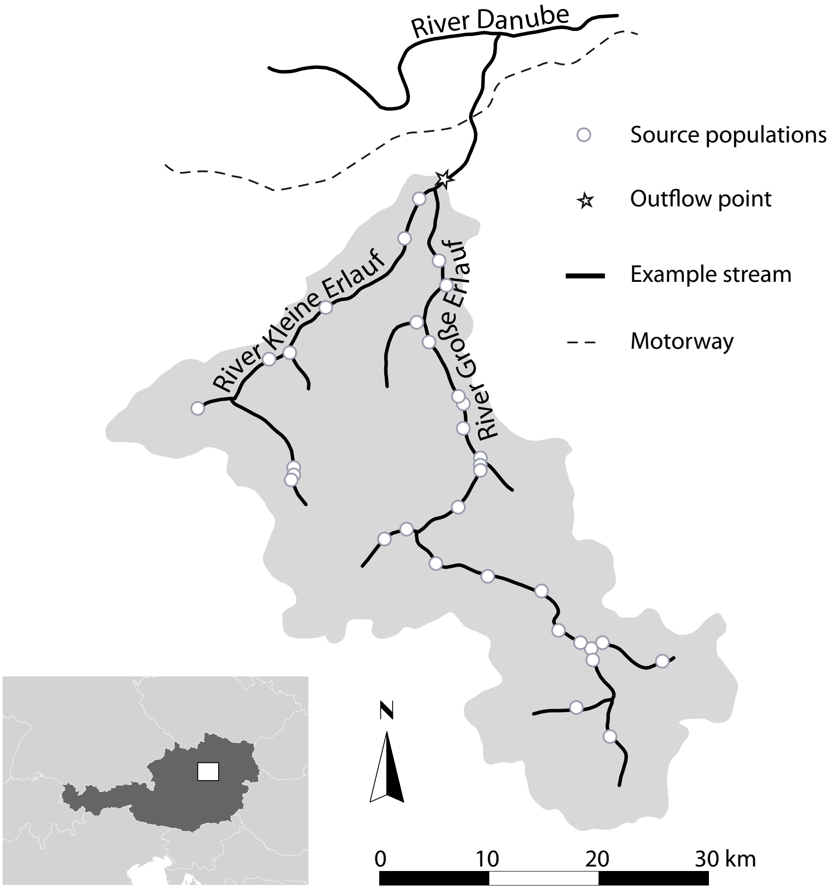


Figure 2.4: Map of the sample catchment showing River Erlauf (Austria) and the location of the randomly selected source populations.

3.2 Application of FIDIMO

The fish dispersal model FIDIMO has been tested for two native fish species: bullhead *Cottus gobio* (length = 100 mm, aspect ratio of caudal fin = 1.03) and brown trout *Salmo trutta* (length = 200 mm, aspect ratio of caudal fin = 1.25) with random source populations (5% of all cells, n = 32 cells). The species-specific values for fish length and the aspect ratio of the caudal fin (Froese and Pauly, 2011) were derived automatically by FIDIMO from the R-package 'FISHMOVE'. Both fish species dominated in the modelled upper reaches of River Erlauf.

In total three model runs have been performed representing three consecutive time steps of 365 days each. The output raster map per time step was used as input for the subsequent time step. The statistical configuration was set to “confidence interval” to compute output maps for the fitted mean as well as for the upper and lower confidence level of the fish dispersal parameters (see R-package ‘FISHMOVE’). All other options of the model were set to default.

The river network consisted of 652 raster cells (spatial resolution: 150 m) in total. Although started with the same number of source populations, *C. gobio* and *S. trutta* spread to 151 and 308 (fitted mean value) cells, respectively, in the first modelled time step (Fig. 2.5). The numbers of occupied cells of the associated lower and upper statistical intervals (confidence interval, CI) were 117-206 and 231-403, respectively. The number of occupied cells for the two fish species steadily increased to 253 ($\mathrm{CI} = 220$-295) and 462 ($\mathrm{CI} = 427$-516) cells in the second time step and to 333 ($\mathrm{CI} = 307$-373) and 551 ($\mathrm{CI} = 525$-591) cells in the third time step. Accordingly, from the first to the last time step, the mean probability per cell decreased from 0.218 ($\mathrm{CI} = 0.160$-0.284) to 0.099 ($\mathrm{CI} = 0.088$-0.108) for *C. gobio* and from 0.107 ($\mathrm{CI} = 0.082$-0.142) to 0.060 ($\mathrm{CI} = 0.056$-0.063) for *S. trutta*.

The comparison of the raster map values distribution revealed significantly distinct dispersal patterns between both fish species and all time steps (two-sample Kolmogorov-Smirnov test, all $p\text{-values} < 0.05$) except for one pairwise comparison (*Cottus gobio*, Step 1, upper interval $\sim$ *Salmo trutta*, Step 1, lower interval).

4 Discussion and conclusion

The fish dispersal model FIDIMO (GRASS command r.fidimo) for the first time provides a tool for modelling, predicting and simulating spatial patterns of fish dispersal in river networks with a real integration of GIS. Most existing dispersal models and analysis frameworks ascribe a key role to geographical information (Euclidian distances, real dispersal pathways along streams), e.g. in the description of dispersal kernels. However, fish dispersal along river networks has never been implemented in geographical information systems as a real modelling tool so far.

This software has been developed to apply the characteristics of leptokurtic fish movement on a rasterised river network. Fish dispersal is viewed as a process at population level with stationary and mobile components and is modelled as a lep-

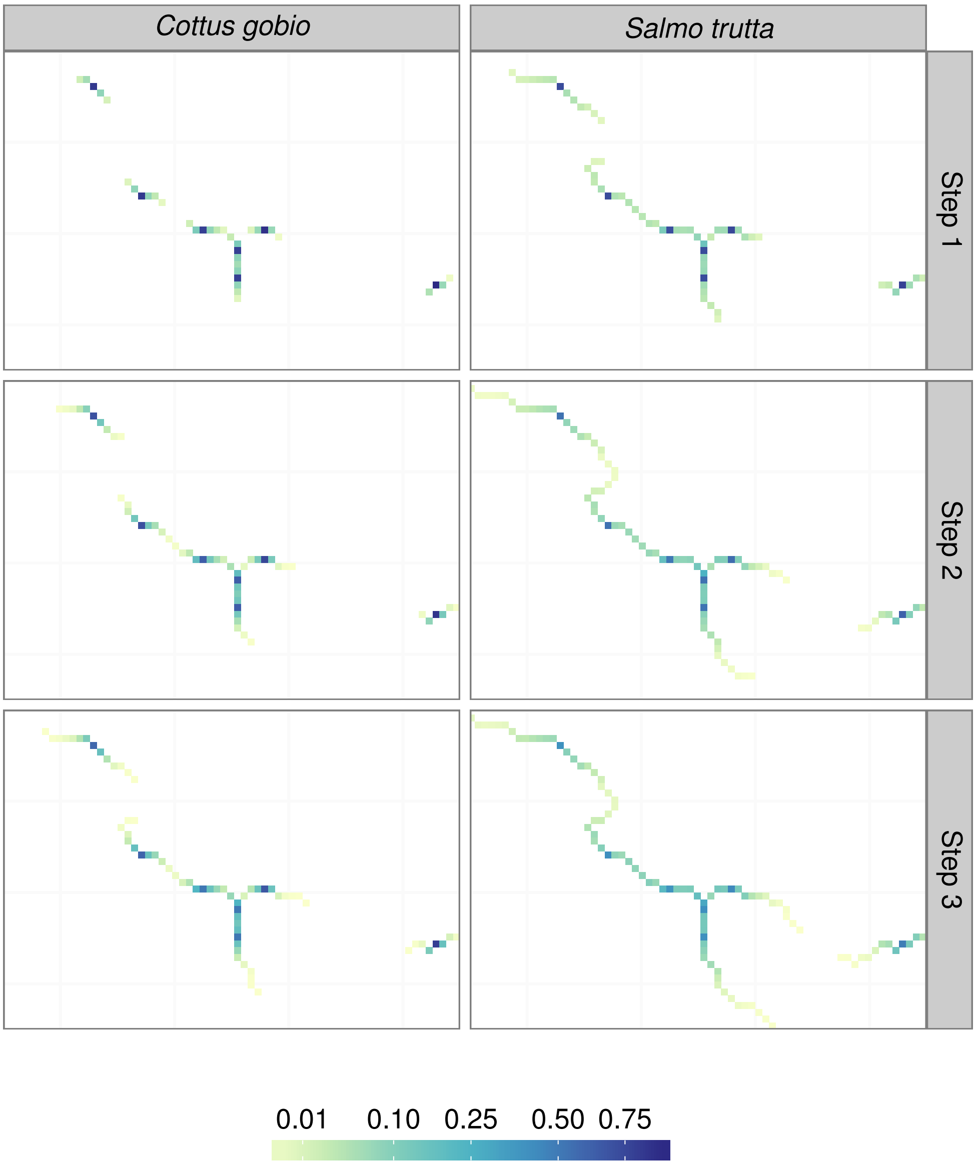


Figure 2.5: Output of a sample application of FIDIMO for a subset of the River Erlauf (resolution = 150x150 m). Model runs for three consecutive time steps (each 365 days) for two fish species (*Cottus gobio*, L = 100 mm; *Salmo trutta*, L = 200 mm) and 32 (5%) source populations. Raster cell values show probabilities of occurrence of a fish after each modelling step.

tokurtic diffusion process spreading from spatially predefined source populations. FIDIMO yields probabilities of occurrence of a fish in a river raster cell based on empirically derived dispersal kernels after the modelled time step. In the formulation of FIDIMO the leptokurtic probability function is similarly declining to both sides of the origin. Thus, the current model does not account for asymmetric dispersal, a feature potentially considered for future improvement.

The results of the model's sample application yielded different dispersal distances and probabilities related to fish species and time, where the larger *Salmo trutta* (length = 200 mm) reaches more cells in the river network than the small bodied *Cottus gobio* (100 mm) in the same time period. Larger body length is paramount and positively related to swimming performance (Wolter and Arlinghaus 2003) and a lower aspect ratio indicates a swimming mode of lower endurance (Webb 1994). Both factors are higher in salmonids than in cottids, directly related to differences in their swimming performance (e.g. Tudorache et al. 2008) and well explain the observed differences in raster cell occupation after all time steps. Former studies have shown that fish may recolonize newly available habitats in very short time (Detenbeck et al. 1992). Niemi et al. (1990) documented faster recovery times in salmonids than cottids (0.17 years vs. 2 years until first appearance). Correspondingly, in the sample application *Salmo trutta* could reach over 75% of all cells in the catchment, while the smaller *Cottus gobio* spread to only 50% of the cells in the same period of three years (Fig. 2.6).

A large contrast between the high peak of the stationary component and relatively fat tails of the mobile component characterises a leptokurtic dispersal kernel. This was well reflected in the observed abrupt step in the frequency distribution of the raster cell probabilities (Fig. 2.6) due to the absence of cells with probabilities between 0.1 and 0.8. The stepwise modelling approach also revealed that this step-like feature diminishes with the number of modelling steps.

A further contribution of our model is the consideration of the upper and lower statistical bounds of dispersal kernels to account for the uncertainty in empirically observed dispersal patterns. The application results did not detect large differences within the output maps displaying the statistical bounds (lower and upper confidence level of the calculated fish dispersal parameters from 'FISHMOVE', Radinger and Wolter (2013)).

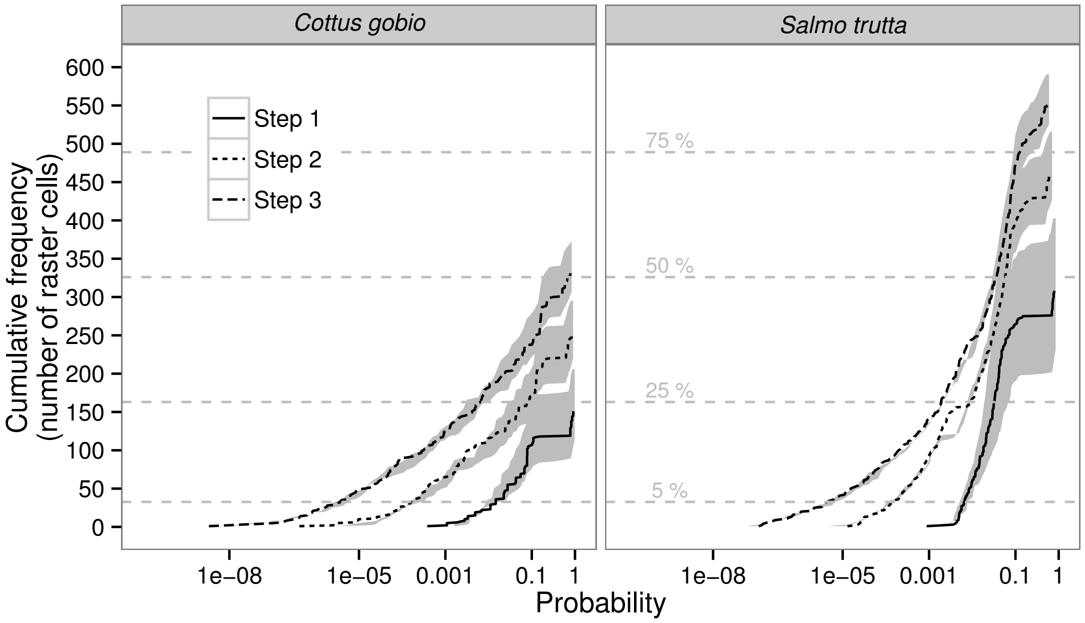


Figure 2.6: Cumulative frequency distribution of raster cell probability values of the sample application output; results for the fitted mean (black lines) and the associated statistical bounds (grey areas) representing three time steps (each 365 days) for two fish species species (*Cottus gobio*, L = 100 mm; *Salmo trutta*, L = 200 mm). The dashed grey lines indicate percent coverage of the total river network.

Moreover, it has been demonstrated that running FIDIMO in a loop enables analysing fish dispersal over several time steps. This provides further opportunities to compute various other population processes such as establishment of a species, fish reproduction and mortality for each cell in intermediate steps. Furthermore, this allows coupling FIDIMO to habitat- and spatially explicit population dynamic models and thus extends the existing model to a complex, powerful and promising ecological tool in a geographical information system.

Despite these potential future applications FIDIMO also has some limitations at its actual stage of development: As the model's parameters are based on empirical studies that cover a broad range of species, fish lengths, time scales and stream sizes, FIDIMO only allows modelling a broad estimation of fish dispersal. This also includes that the model might be applied only to average flow conditions or long-term ecological questions of more than a year as the model does not consider hydrological or in-stream hydraulic information. Furthermore the model includes fish specific information only by its length and aspect ratio of the caudal fin, the latter as proxy for swimming mode. This allows the application of model to a broad range of species, but it conversely neither directly distinguishes species-specific locomotion types nor considers physiologically determined swimming speeds (Webb 1994). Although the application of FIDIMO is possible for large river systems the most appropriate application of FIDIMO with the lowest uncertainty is for smaller river systems of stream orders less than 7 or discharge up to 15 m^3s^{-1} as these limits also demarcate the scale of the majority of the underlying empirical data of the R-package 'FISHMOVE' (Radinger and Wolter 2013) which is implemented in FIDIMO. Furthermore, FIDIMO does not model fish movement on individual basis and therefore, does not consider any environmental cues such as temperature, hydrological changes, and physico-chemical stimuli that might trigger and influence individual fish's movement (Albanese et al. 2004).

Migration barriers such as weirs, dams and culverts often prevent fish from moving upstream and lead to the fragmentation of fish populations (Blanchet et al. 2010). The implementation of the EU Water Framework Directive (WFD, European Parliament and Council of the European Union 2000) aims in achieving good ecological status of surface waters. Among others migration facilities are frequently planned to improve the longitudinal connectivity of rivers for fish. This remains tremendous work, not only because of several thousand existing barriers without any migration facility (Fehér et al. 2012). Already existing fish migration facilities are often limited in their efficiency and passability by fish. A recent review of existing fish passage facilities by Noonan et al. (2012) revealed a mean upstream passability rate of only 41.7% with great differences between species and types of barriers. This study further revealed a restricted mean downstream passage efficiency of only 68.5% (Noonan et al. 2012). In FIDIMO, movement interruptions in river networks are considered as barriers with species-specific passability rates. Accordingly, only a part of the population can pass and disperse upstream barriers, while the remaining fish accumulate downstream the obstacle, a pattern often observed but rarely measured (Jurajda et al. 1998). Similarly, Pépino et al. (2012) mathematically described a model of heterogeneous fish movement with distinct passability rates of structural barriers and showed its effect on the shape of dispersal kernels for salmonids. Consequently, our approach needs prior knowledge on the species-specific passability rates of each barrier in the network. Meixler et al. (2009) modelled fish swimming abilities and barrier height as main factors correlated with successful fish passage. In this context, Kemp and O'Hanley (2010) reviewed different methods for assessing fish passage abilities and considered GIS a useful tool for e.g. prioritizing barrier removal. Furthermore, model runs simulating different barrier passability settings for certain fish species might allow assessing the effects of barrier removal or provision of fish migration facilities or deriving threshold values for minimum fish passage efficiency to achieve ecological improvements according to the WFD. Currently FIDIMO considers only upstream passability rates of barriers. Thus, an updated version of the model should also improve this feature and also allow considering downstream passability rates.

The aim of the model development was to create a first working GIS based dispersal model for fish rather than optimising the computation performance. Hence, the computation time strongly depends on the amount of input source population cells and the performance of the underlying GRASS GIS processes. In this context it is recommended to carefully balance the calculation time needed for a model run and the geographic resolution for ecologically meaningful outcomes. Parallelising parts of the model code could contribute to significantly faster computation times and would allow for analysing large river networks with a large number of source populations.

The use of the open source programme GRASS GIS and Python as main modelling tools allows free access to the code and facilitates easy modifications, adoptions and improvements of the model. Hence, the model source code is open and publicly available and a continuously updated version of the Python script can be downloaded and installed as GRASS GIS add-on (including a documentation file) from `https://svn.osgeo.org/grass/grass-addons/grass6/raster/r.fidimo/`. It is released under the terms of the GNU General Public License and the copyright of the model belongs to the GRASS development team and J. Radinger.

In conclusion, the newly developed fish dispersal model FIDIMO (GRASS command r.fidimo) described here provides the missing link between conceptual considerations on dispersal modelling (McMahon and Matter 2006), empirically observed patterns of fish movement (Radinger and Wolter 2013; Rodríguez 2002) and the strengths of geographically explicit modelling in FOSS GIS (Steiniger and Hay 2009). The model can be used for various different species and any river network meeting the input requirements. Thus, despite the limitations discussed above, FIDIMO is very open to manifold use for future applications. For instance, it might serve to assess the species-specific spatio-temporal recolonization potential of a restored river habitat from adjacent river sections. Thus, it might help in both, to reconstruct recolonization patterns observed in empirical studies in the past (Detenbeck et al. 1992) and to predict future probabilities of fish that might reach a restored habitat within an engineering timeframe. The model might also contribute to understand, reconstruct and predict the spread of invasive species. Furthermore, studies analysing dispersal and population dynamics based on genetic exchange processes could benefit from a complementation and extension by a GIS-based dispersal model.

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Chapter 3

Disentangling the effects of habitat suitability, dispersal and fragmentation on the distribution of river fishes

Disentangling the effects of habitat suitability, dispersal and fragmentation on the distribution of river fishes

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submitted

Habitat suitability, dispersal potential, and fragmentation influence the distribution of stream fishes. However, the relative influence of these factors and their interacting effects on species distributions are poorly understood, thereby, inducing uncertainty about approaches for riverine rehabilitation and conservation. Using data describing 17 common stream fishes, we combine species habitat suitability models (MaxEnt) with a species dispersal model (FIDIMO), as well as a worst-case scenario of the influence of river fragmentation on dispersal. We then use a framework involving generalized linear mixed models to determine factors structuring species occurrences within a river network.

The results showed significantly positive main as well interacting effects of both, local-scale habitat quality and species-specific dispersal ability on fish species distribution. Interestingly, no significant effects of migration barriers on the distribution of the modelled fish species could be detected. Further, within the rather short time frames of less than ten years modelled, dispersal and consequently accessibility of habitats performed superior over habitat suitability in explaining species' presence. The importance of dispersal decreased in time, as more habitats became approached over longer time periods, resulting in habitat suitability becoming increasingly relevant in determining species' presence.

Concluding, as fish are mobile organisms with well-developed dispersal abilities they are able to utilise local habitat patches within a wider river network. Hence, besides restoring essential habitats also their accessibility and thus the distance to the nearest source populations and species-specific dispersal performance are key prerequisite for successful river rehabilitation. Both also determine the time lag for successfully (re)colonising a rehabilitation measure. Based on these findings, we emphasise thoroughly considering the spatial arrangement of source populations, their position relative to barriers and the fish's dispersal ability in prioritisation of connectivity measures. In the long run, providing (access to) new suitable, essential habitat patches is key for successful river rehabilitation.

Keywords: discontinuous distribution; habitat suitability modelling; dispersal of river fishes; river network; river restoration success; movement barriers; network connectivity

1 Introduction

The single and interacting impacts of habitat suitability, migration barriers and dispersal abilities of species on the distribution of river fishes have been neither disentangled nor quantified. This study provides a modeling approach for quantifying the single factor contributions aiming to improve not only our scientific understanding of principal drivers of the assemblage structure of fishes in rivers, but also to derive management advice for successful river rehabilitation and improving diversity of fishes.

The hierarchical nature and dendritic structure of river systems has been widely recognised (Altermatt 2013; Grant et al. 2007). It reflects the longitudinal functional integrity within larger catchment areas and comprises reach-scale (e.g. habitat suitability) as well as network-scale processes (e.g. migration). The hierarchical river structure and their longitudinal hydro-physical (e.g. sediment transport, Strahler 1957) and biological patterns (e.g. river continuum, Vannote et al. 1980) have been well described, while the underlying biological processes gathered much lesser attention at the river network scale (Fagan 2002; Lowe 2003; Radinger et al. 2013).

Distribution of fishes in river networks is typically discontinuous with alternating patches of species' absence and presence generated by environmental fluctuations, habitat complexity and suitability, dispersal of species, and biotic interactions (Angermeier et al. 2002). Especially habitat requirements (e.g. Crisp 1996; Mann 1996), Habitat shifts and linkages (e.g. Fullerton et al. 2010) and the impact of migration barriers (Reidy Liermann et al. 2012) are relatively well studied. Numerous sophisticated fish habitat models provide quantitative habitat suitabilities for single (e.g. PHABSIM, Milhous and Waddle 2012, [) and multiple reaches within catchments (e.g. Species distribution models, Guisan and Thuiller 2005), while the connectivity between habitats along river networks is typically discussed separately from their quality. Recently, studies jointly examined dispersal and habitat quality in regard to spatial autocorrelation (e.g. Diebel et al. 2010) and similarity among stream fish assemblages (e.g. Stoll et al. 2013).

In addition to habitat quantity, the spatial arrangement and accessibility of suitable habitat influences the distribution of species, so these factors are important during rehabilitation and river conservation. Restored habitats might not become accessible if they are too distant, out of dispersal range or disconnected by migration barriers. Therefore, both reach scale habitat improvements and dispersal govern colonisation processes and accordingly the success of ecological restoration (Diebel et al. 2010).

Despite being emphasised as interacting factors, dispersal constraints and migration barriers have not yet been explicitly addressed by fish habitat suitability models. Therefore, this study combines models of habitat suitability and fish dispersal to disentangle and quantify the single and joint effects of (i) habitat suitability, (ii) dispersal ability and (iii) migration barriers on the distribution of river fishes.

Recently developed methods provide parameters to quantitatively describe the heterogeneous patterns of fish dispersal (Radinger and Wolter 2013; Rodríguez 2002) and account for barrier effects on dispersal kernels (Pépino et al. 2012), which allows modelling dispersal of fishes in river networks by explicitly considering stationary and mobile components of a fish population as well as the location and passability of barriers (Radinger et al. 2013). The established method MaxEnt (Elith et al. 2011) was used to estimate species-specific habitat suitability and the novel GIS model FIDIMO (Radinger et al. 2013) was applied to quantify heterogeneous fish dispersal of 17 fish species in a medium-sized lowland river network.

It was hypothesised that i) the probability of being present is highest at sites with higher habitat suitability, improved accessibility and no impacts of migration barriers; ii) the interaction between habitat and dispersal governs the spatially discontinuous distribution of fishes in river networks; and iii) the importance of dispersal decreases in time, because dispersal is a function of time with more habitats being approached over longer time periods resulting in habitat suitability becoming more relevant in determining species' presence.

2 Methods

2.1 Study river catchment and species data

The analysis was carried out for the north German River Treene (N: $54°46'19''N$, S: $54°21'36''N$, W: $9°04'50''E$, E: $9°44'01''E$), a typical lowland sand bed river (length = 77 km, catchment = 760 km^2) which is fragmented by 52 barriers (e.g. weirs, bottom sills, dams). The State Agency for Agriculture, Environment and Rural Areas (LLUR), Schleswig Holstein, kindly provided data on the river network, habitat characteristics, migration barriers and fish sampled at 81 sites between 2004 and 2011 (Fig. 3.1). Fish were sampled by electric fishing along river segments of 400 m average length (160-1100 m) following standard sampling protocols (Dußling et al. 2004). Abundance data have been standardised by the length fished (CPUE - catch per unit effort) to fish per 100 m and occurrence data transformed to presence-absence. The 17 most frequent species with at least 10 presences were selected for the modelling (Table 3.1).

2.2 Model framework

The overall framework to model the presence/absence of each species consisted of three sub models: (1) a habitat suitability model (MaxEnt, Phillips et al. 2006; Phillips and Dudík 2008) based on instream-habitat and topological river network

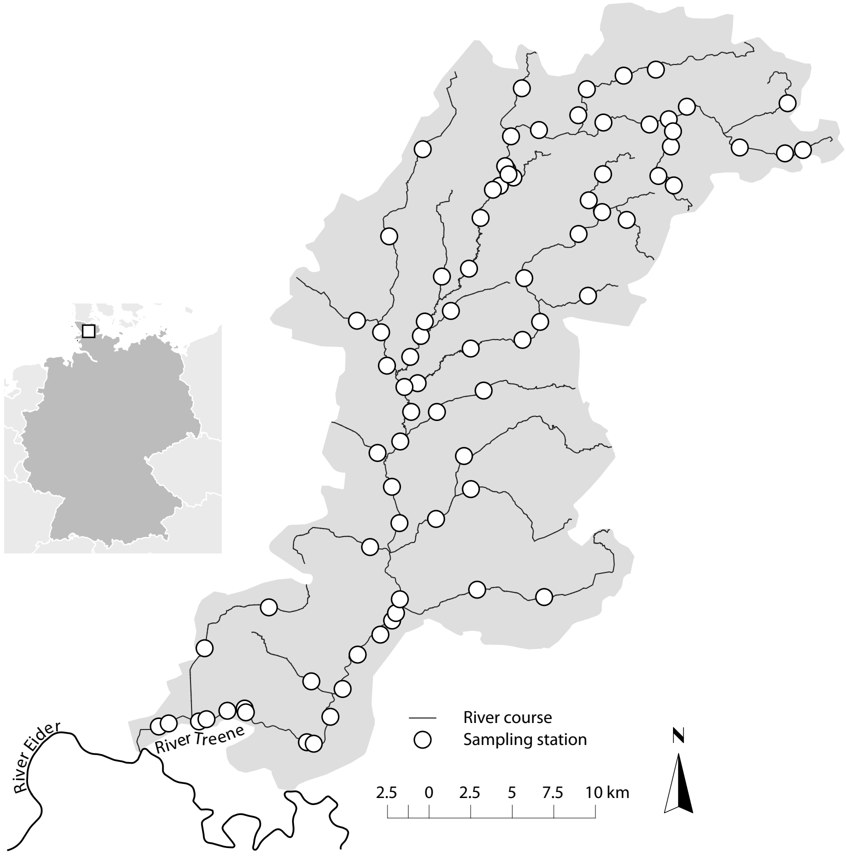

Figure 3.1: Location of the 81 sampling sites in the River Treene catchment, Germany.

characteristics at sites where the species was present, (2) the fish dispersal model FIDIMO (Radinger et al. 2013) to calculate a probabilistic distance-based estimate of heterogeneous dispersal based on species-specific dispersal abilities and (3) a second FIDIMO including barriers to quantify their impact on movements of fishes.

Habitat suitability (HS)

The species-specific suitability of habitats available within the river network was assessed using the maximum entropy model MaxEnt (Elith et al. 2011; Phillips et al. 2006). This predictive niche model examines the relation between the occurrence of a species and the site's environmental conditions (presence-habitat

Table 3.1: Number of presences / absences and frequency of fish species analysed at 81 sampling sites.

Code	Common name	Scientific name	Presence/Absence	Frequency
Anguilla	European eel	*Anguilla anguilla*	63/18	0.78
Blicrkna	White bream	*Blicca bjoerkna*	24/57	0.3
Cobienia	Spined loach	*Cobitis taenia*	29/52	0.36
Esoxcius	Northern pike	*Esox lucius*	56/25	0.69
Gastatus	Three-spined stickleback	*Gasterosteus aculeatus*	61/20	0.75
Gobiobio	Gudgeon	*Gobio gobio*	54/27	0.67
Gymnrnua	Ruffe	*Gymnocephalus cernua*	19/62	0.23
Lampilis	River lamprey	*Lampetra fluviatilis*	23/58	0.28
Lampneri	European brook lamprey	*Lampetra planeri*	15/66	0.19
Leucatus	Sunbleak	*Leucaspius delineatus*	16/65	0.2
Leucscus	Common dace	*Leuciscus leuciscus*	29/52	0.36
Percilis	European perch	*Perca fluviatilis*	52/29	0.64
Phoxinus	Eurasian minnow	*Phoxinus phoxinus*	30/51	0.37
Pungtius	Ninespine stickleback	*Pungitius pungitius*	50/31	0.62
Rutiilus	Roach	*Rutilus rutilus*	48/33	0.59
Salmario	Brown trout	*Salmo trutta fario*	49/32	0.6
Tincinca	Tench	*Tinca tinca*	18/63	0.22

relationship, Franklin 2009). Predictions using MaxEnt are solely inferred from presence points, while absence might be caused by other influences than habitat characters. Therefore, MaxEnt seemed a well appropriate method which is commonly used to model fish habitat suitability (Elith et al. 2011) and provides generally good, consistently well performing models (Elith et al. 2006) especially for small sample sizes (Pearson et al. 2007).

MaxEnt models were calculated for 17 fish species (Table 3.1) based on 38 environmental predictors (see Appendix, Table A.3). The environmental predictor dataset originates from a state-wide assessment of the hydromorphological status of rivers using the LAWA on-site standard procedure (Kamp et al. 2007). Further, three topological variables have been added: Strahler (1957) stream order, Shreve

(1966) stream order and distance from mouth (distance to the junction with River Eider). Variables without variation within the catchment were dropped and those describing similar features meaningfully merged. Subsequently, count variables were standardised by the length of the river segment and vector data transformed into raster format (resolution 50 x 50 m). Predictors were aggregated over 200 m up- and downstream (or less up to the next barrier) to average focal mean and median values for continuous and ordinal variables, respectively, to account for the length of sampling sites and within-home range movements (Guisan and Thuiller 2005).

Habitat models were calculated for each species in three steps to achieve the most parsimonious one: Firstly, a global model was built including all variables. Secondly, all variables $< 3\%$ contribution or permutation importance were dropped (Young et al. 2013). Thirdly, the final model was trained using the reduced variable dataset. MaxEnt's default settings were used for all model calculations (Elith et al. 2011) and the replicates option was set to 10-fold cross-validation to obtain estimates of model performance (AUC, Area under the curve). Phillips et al. (2006), Phillips and Dudík (2008) and Elith et al. (2011) provide further details on MaxEnt.

The final, trained model was projected to the entire catchment to create a map quantifying the logistic probability of species-specific habitat suitability (HS) with continuous values from 0 (low) to 1 (high suitability).

Species dispersal (DI)

The novel open source GRASS GIS (Neteler and Mitasova 2007) fish dispersal model FIDIMO (Radinger et al. 2013) was applied to assess species dispersal from each sampling site. FIDIMO calculates species- and size class-specific fish dispersal as a leptokurtic diffusion process from predefined sources (Radinger et al. 2013). Typically, the modelled dispersal probabilities are highest close to source (high abundance at starting point) and decline with distance based on empirically derived leptokurtic dispersal kernels (reviewed by Radinger and Wolter 2013; Rodríguez 2002).

FIDIMO was calculated using the presence sites as starting points for dispersal and the species-specific CPUE at each site as weighing factor for the non-truncated dispersal kernel. All models were calculated with a generalised and rasterised river network (resolution 50 x 50 m) and run for nine time intervals (1-9 years) to assess temporal effects. As FIDIMO simultaneously calculates dispersal from all starting points, the output map shows overlapping dispersal probabilities of both moving mobile and non-moving stationary fish at the sources. Thus, the model output had to be corrected by the probabilities remaining at the initial starting cells to exclude any auto-influence of the starting point.

Finally, the catchment-wide output map quantified the effect of dispersal from nearby sources (DI) based on species-specific and CPUE-weighted dispersal kernels.

Barrier effects (BE)

To determine the potential effect of migration barriers on the presence of a species, a second FIDIMO was run including the 52 barriers situated in the catchment. In FIDIMO barriers are handled by blocking a certain ratio (up to 100% depending on the type of barrier) of the upstream moving fish. Consequently, the probability of reaching upstream areas was reduced by this barrier-specific passage rate. In the River Treene catchment all barriers were modelled fully impassable to determine the probability of presence/absence expected with dispersal in the most extreme scenario of river fragmentation. As for the FIDIMO runs without barriers, all models were calculated for nine time intervals with a fixed random seed for exactly reproducible results.

Subtracting the FIDIMO probability maps without from those with barriers yielded output maps of spatially distributed differences between both analyses. More negative values indicated areas more strongly affected by barriers. Consequently, these output maps provide a quantitative estimate of the barrier effects (BE) for each species.

Statistical analysis

Parameter values for habitat suitability (HS), species dispersal (DI) and the effect of barriers (BE) were extracted from the modelled raster maps for each sampling site, fish species and time step, assembled in an analysis matrix and averaged over all time steps.

Generalised linear mixed models (GLMM, Bolker et al. 2009) were used to explore relationships between the presence/absence of species (binomial model, logit-link) and the three predictors HS, DI and BE as fixed effects. The models were fitted with species-specific random intercepts or full random model structure (intercepts and slopes). Additionally, each model was calculated including two-way interactions between the fixed effects. The most complex GLMM included interaction terms and the full random model structure:

$$\begin{aligned} logit(Y_i) = \alpha + \beta_{HS}HS + \beta_{DI}DI + \beta_{BE}BE + \\ \beta_{HS:DI}HSDI + \beta_{HS:BE}HSBE + \beta_{DI:BE}DIBE + \\ a_i + b_{iHS}HS + b_{iDI}DI + b_{iBE}BE + \epsilon_i \end{aligned} \tag{3.1}$$

where Y_i = the presence/absence of species i; α = intercept, β_k = odds ratio for HS, DI, BE; a_i = random intercept; b_{ik} = random slopes for HS, DI, BE; ϵ_i = residual term.

All input variables were centred around their median to improve the interpretability of the predictor's model coefficients and interactions (Schielzeth 2010). Confidence intervals (95% CI) were calculated for all coefficients based on 500 parametric bootstrap simulations (percentile method, Carpenter and Bithell 2000). As relative measures of model quality Akaike's (AIC) and the Bayesian information criterion (BIC) were computed and R^2_{COR} (Cameron and Windmeijer 1996) as measure of the linear correlation between fitted and observed values. For a visual analysis of the full random GLMM and its interactions, 10000 posterior simulations of the model coefficients were calculated and displayed with one varying parameter (HS or DI), one parameter dichotomously fixed to low and high values (HS or BE) and the remaining parameter fixed to its median.

To evaluate how the relative importance of HS, DI and BE developed over time, GLMMs with random slopes for species were fitted for all nine time steps. Because the predictor variables differed in their variances, they were standardised to units of phenotypic standard deviations (SD over all time steps) and centred before comparing relative importance and effect sizes (Schielzeth 2010).

All spatial analyses were carried out in GRASS GIS version 6.5 (GRASS Development Team 2010) using r.fidimo (Radinger et al. 2013) for modelling fish dispersal and r.rdfilter for calculating focal predictor variables. The statistical analyses were carried out in R (version 3.0.1, R Development Core Team 2013) using the packages 'DISMO' (version 0.8-11, Hijmans et al. 2013) combined with MaxEnt (version 3.3.3k, Phillips et al. 2006) for habitat suitability, 'SPGRASS6' (version 0.8-1, Bivand 2013) and 'RASTER' (version 2.1-25, Hijmans and Etten 2013) for the interaction with GRASS, 'LME4' (version 1.1-1, Bates et al. 2013) for fitting GLMMs, and 'ARM' (function sim(), version 1.6-09, Gelman and Yu-Sung 2013) for posterior simulation of GLMM effect sizes.

3 Results

The mean overall number of presence and absence records for all 17 species modelled was 37 (Standard Deviation, SD = 17) and 44 (SD = 15), respectively. The frequency of occurrence ranged from 0.19 (relatively rare, *Lampetra planeri* (Bloch, 1784), 15 records) to 0.75 (common, *Gasterosteus aculeatus* Linnaeus, 1758, 61 records) (Table 3.1).

The habitat suitability models performed generally well (mean cross-validated AUC = 0.74) with best results for *Lampetra fluviatilis* (Linnaeus, 1758) (AUC = 0.917, SD = 0.038) and weakest for *Pungitius pungitius* (Linnaeus, 1758) (AUC = 0.601, SD = 0.083). The habitat suitability over all species was significantly higher at sites with presences (n = 512, mean = 0.57, SD = 0.18) than with absences (n = 576, mean = 0.2, SD = 0.20) (Wilcoxon rank sum test, one-tailed, W = 28437, Z = -23.01, $P < 0.0001$; Fig. 3.2a).

Visual inspection of the modelled maps for HS and DI revealed that both predicted habitat suitability and modelled dispersal probability match the observed presence/absence patterns and vary among species (Fig. 3.3).

FIDIMO provided consistent maps. Larger, frequently occurring species reached more cells (e.g. *Anguilla anguilla* (Linnaeus, 1758), 4889 cells, 90% of the catchment within one year) than smaller, rare species (e.g. *Leucaspius delineates* (Heckel,

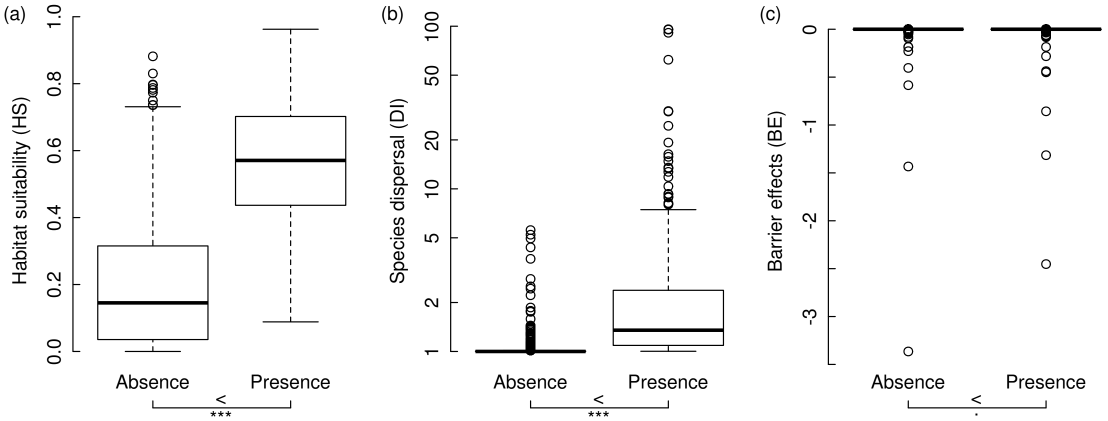

Figure 3.2: Differences in (a) habitat suitability, (b) species dispersal probability and (c) barrier effects between all absences (n = 576) and presences (n = 512). Significance levels (*** < 0.0001, . < 0.05) based on one-tailed Wilcoxon rank sum test.

1843), 1335 cells, 25% of the catchment). Accordingly, the number of cells was positively correlated with fish length (Spearman rank correlation, rho = 0.84, $P < 0.0001$) and correspondingly, also the share of inaccessible catchment due to barriers (Spearman rank correlation, rho = 0.87, $P < 0.0001$) ranging between 0% (*Cobitis taenia* Linnaeus, 1758) and 19% (*Esox lucius* Linnaeus, 1758). Dispersal probability (DI, Fig. 3.2b) and effect of barriers (BE, Fig. 3.2c) over all species were significantly higher for sites with presence (DI: n = 512, mean = 2.01, SD = 8.15; BE: n = 512, mean = -0.013, SD = 0.14) than absence (DI: n = 576, mean = 0.068, SD = 0.39; BE: n = 576, mean = -0.012, SD = 0.16) indicated by Wilcoxon rank sum tests (one-tailed, W = 16496, Z = -25.35, $P < 0.0001$ resp. W = 139683.5, Z = -1.89, P = 0.029). Detailed information on HS, DI and BE for all modelled species is summarised in Table 3.2.

The single GLMMs between presence/absence and HS, DI and BE (with and without random slopes) revealed significant effects (log odds-ratios) for HS ($\beta_{HS} = 9.52$, CI = 8.28 to 11.17 resp. $\beta_{HS} = 9.31$, CI = 8.26 to 10.42) and DI ($\beta_{DI} = 37.09$, CI = 22.58 to 66.07 resp. $\beta_{DI} = 2.91$, CI = 2.40 to 3.59) while the effects for BE ($\beta_{BE} = 3.38$, CI = -42.78 to 46.06 resp. $\beta_{BE} = -0.04$, CI = -1.77 to 1.48) were not significant. All three single models yielded consistently better results when ran-

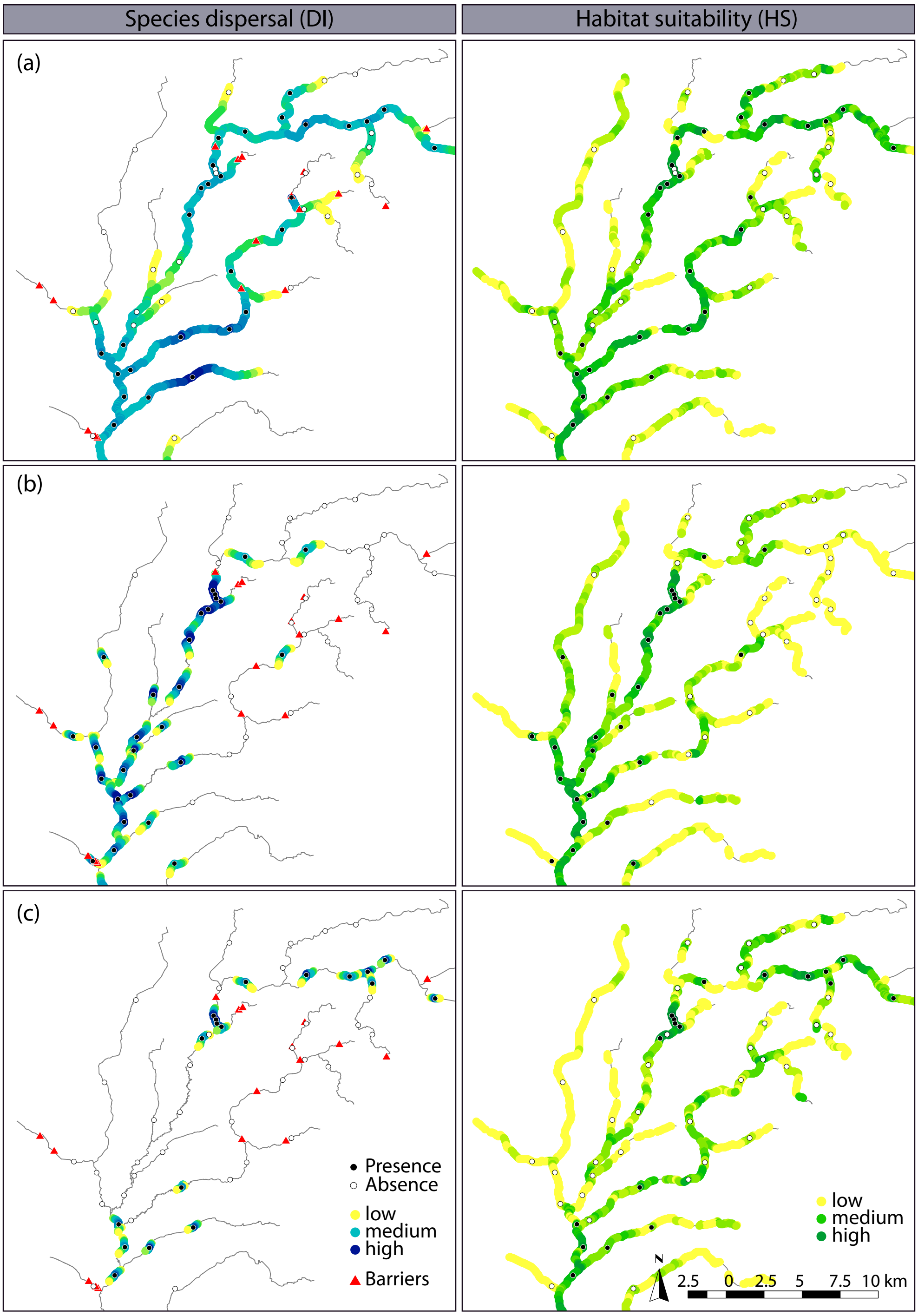

Figure 3.3: Discontinuous patterns of species dispersal and habitat suitability for three selected species: (a) *Rutilus rutilus*, (b) *Phoxinus phoxinus* and (c) *Cobitis taenia*. Dispersal maps (bright to dark = low to high dispersal probability) based on CPUE-weighted leptokurtic dispersal kernels calculated with FIDIMO considering impassable barriers (triangles). Habitat suitability maps (bright to dark = low to high suitability) predicted using MaxEnt.

Table 3.2: Mean values (and standard deviation) of habitat suitability (HS), CPUE-weighted dispersal probability (DI) and barrier effects (BE) contrasting absence and presence sites for 17 modelled species.

	Habitat suitability (HS)		Species dispersal (DI)		Barrier effects (BE)	
	absence	presence	absence	presence	absence	presence
Anguilla	0.29 (0.14)	0.54 (0.18)	0.032 (0.042)	0.50 (0.65)	-0.00086 (0.0031)	-0.017 (0.072)
Blicrkna	0.21 (0.21)	0.63 (0.20)	0.12 (0.44)	0.98 (1.84)	-0.014 (0.065)	-0.0011 (0.0043)
Cobienia	0.20 (0.20)	0.63 (0.20)	0.00045 (0.004)	0.86 (1.25)	-4.9e-12 (9.2e-11)	0
Esoxcius	0.30 (0.24)	0.55 (0.15)	0.066 (0.11)	0.091 (0.10)	-0.003 (0.0085)	-0.0025 (0.0063)
Gastatus	0.27 (0.20)	0.55 (0.18)	9e-06 (6.2e-05)	1.43 (2.00)	0	-6.9e-06 (0.00011)
Gobiobio	0.14 (0.13)	0.54 (0.17)	0.025 (0.13)	2.88 (4.58)	-5.8e-05 (0.00034)	-0.029 (0.24)
Gymnrnua	0.20 (0.20)	0.60 (0.18)	0.043 (0.25)	0.58 (0.63)	-0.00043 (0.0047)	0
Lampilis	0.066 (0.13)	0.58 (0.23)	0.22 (0.79)	6.11 (8.99)	-0.11 (0.53)	0
Lampneri	0.15 (0.17)	0.64 (0.14)	0.0058 (0.051)	2.42 (7.25)	-1.8e-06 (1.9e-05)	-6.8e-06 (5.4e-05)
Leucatus	0.26 (0.23)	0.66 (0.18)	0.24 (0.89)	0.45 (0.86)	-0.012 (0.097)	-6.3e-08 (5.9e-07)
Leucscus	0.23 (0.21)	0.59 (0.16)	0.063 (0.18)	0.59 (0.69)	-7.5e-05 (0.00075)	-0.0015 (0.008)
Percilis	0.14 (0.14)	0.57 (0.20)	0.032 (0.073)	0.91 (1.23)	-0.002 (0.0081)	-0.036 (0.15)
Phoxinus	0.075 (0.088)	0.59 (0.21)	0.0023 (0.025)	14.22 (29.34)	-0.0023 (0.025)	-3.5e-10 (5.3e-09)
Pungtius	0.37 (0.16)	0.55 (0.17)	0.0065 (0.028)	1.22 (1.85)	-1e-05 (8.6e-05)	-1.1e-16 (2.3e-15)
Rutiilus	0.22 (0.21)	0.56 (0.17)	0.063 (0.16)	0.74 (1.47)	-0.0037 (0.013)	-0.0069 (0.023)
Salmario	0.2 (0.099)	0.55 (0.19)	0.04 (0.10)	1.34 (2.07)	-0.00082 (0.0048)	-0.061 (0.38)
Tincinca	0.26 (0.19)	0.60 (0.14)	0.0011 (0.0039)	0.038 (0.038)	-1.4e-06 (1.1e-05)	-2.2e-18 (1.6e-17)
mean	0.20 (0.20)	0.57 (0.18)	0.068 (0.39)	2.01 (8.15)	-0.012 (0.16)	-0.013 (0.14)

Table 3.3: Results of the single GLMMs. Parameter coefficients (α intercept, β log-odds-ratios) for median-centred fixed effects: habitat suitability (HS), dispersal probability (DI) and barrier effects (BE) and species-specific random intercepts a_i (and slopes b_i); in parentheses: parametric bootstrapped 95% confidence intervals, in bold: significant effects.

	logit(Y$_i$) $\sim$	random slope and intercept $\alpha + \beta_X X + a_i + b_{iX} X + \epsilon_i$			random intercept $\alpha + \beta_X X + a_i + \epsilon_i$		
		HS	DI	BE	HS	DI	BE
Fixed effects	α	-0.21 (-0.75-0.37)	**-0.69** **(-1.15–0.11)**	-0.15 (-0.62-0.38)	-0.31 (-0.92-0.24)	**-0.83** **(-1.29–0.32)**	-0.14 (-0.62-0.40)
	β_{HS}	**9.52** **(8.28-11.17)**			**9.31** **(8.26-10.42)**		
	β_{DI}		**37.09** **(22.58-66.07)**			**2.91** **(2.40-3.59)**	
	β_{BE}			3.38 (-42.78-46.06)			-0.04 (-1.77-1.48)
SD Random effects	a_i	1.11 (0.58-1.49)	1.01 (0.51-1.51)	0.97 (0.54-1.35)	1.15 (0.64-1.57)	0.98 (0.59-1.32)	1.01 (0.58-1.49)
	b_{iHS}	1.39 (0.13-2.67)					
	b_{iDI}		45.35 (25.97-58.26)				
	b_{iBE}			57.52 (22.10-140.83)			
	AIC	754.5	818.74	1317.51	754.68	1045.05	1328.95
	BIC	779.46	843.7	1342.47	769.66	1060.03	1343.93
	deviance	744.5	808.74	1307.51	748.68	1039.05	1322.95
	R$^2_{COR}$	0.61	0.61	0.22	0.6	0.45	0.21

dom slopes were included. Especially the DI model substantially improved from AIC = 1045.05 to AIC = 818.74 when including the random slope for DI which widely varied between species (SD b_i DI = 45.35, CI = 25.97 to 58.26). Overall, the full random structure models for HS and DI provided the two best single models with slightly higher performance of HS (AIC = 754.5). The single GLMM coefficients and model performances are given in Table 3.3.

As for the single GLMMs, also the multiple GLMMs including all predictors performed better with random slopes included (AIC = 604.12 to 611.54 vs. AIC = 645.70 to 710.98) (Table 3.4). The multiple, full random structure model without interactions revealed significant coefficients for HS (β_{HS} = 7.38, CI = 6.16 to 9.14) and DI (β_{DI} = 26.42, CI = 11.38 to 50.41), while the odds-ratio for BE (β_{BE} = 12.12, CI = -3.17 to 27.38) did not significantly differ from zero. Moreover, the odds of presence while holding all predictors at their median levels (HS = 0.37, DI = 0.03, BE = 0) were $exp(-0.70) = 0.50$, which equals 0.33 probability of presence. Random slopes for DI were highly variable among species (SD b_{iDI} = 34.07, CI = 27.10 to 44.93). The conditional modes for b_{iDI} ranged from -30.43 (*E. lucius*) to 60.31 (*C. taenia*) and were slightly inversely correlated with fish length (Spearman rank correlation, rho = -0.45, P = 0.07).

No substantial improvements could be achieved by including two-way interactions between HS, DI and BE. However, simulation models and visual analysis of interaction terms (Fig. 3.4) revealed differences in the effect of DI on the probability of presence when interacting with low and high HS ($\beta_{HS:DI}$ = -3.98, CI = -18.63 to 10.59; Table 3.4, Fig. 3.4b). In contrast, the pronounced interaction term of HS:BE ($\beta_{HS:BE}$ = -272.97, CI = -628.24 to -151.00, Table 3.4), did not result in significantly different probabilities of presence at high or low BE when interacting with HS (Fig. 3.4a). No significant patterns were detected for the interaction of DI:BE ($\beta_{DI:BE}$ = -18.57, CI = -205.27 to 20.88; Table 3.4, Fig. 3.4c). In general, lower values of BE (high barrier effects) caused higher uncertainty as indicated by the simulated confidence intervals.

The temporal analysis of the relative effect sizes of HS, DI and BE over nine years revealed DI as most important predictor, at least double that of HS and BE together (Fig. 3.5). While the importance of DI had high uncertainty and declined over time from approximately 9 to 7, HS remained stable around 2 with

Table 3.4: Results of the multiple GLMMs. Parameter coefficients (α intercept, β log-odds-ratios) for median-centred fixed effects: habitat suitability (HS), dispersal probability (DI) and barrier effects (BE) plus their two-way interactions as well as species-specific random intercepts a_i (and slopes b_i); in parentheses: parametric bootstrapped 95% confidence intervals, in bold: significant effects and interactions.

		random slope + intercept		random intercept	
	logit(Y$_i$) $\sim$	$\alpha + \beta_{HS}HS + \beta_{DI}DI + \beta_{BE}BE+$ $a_i + b_{iHS}HS + b_{iDI}DI + b_{iBE}BE + \epsilon_i$		$\alpha + b_{HS}HS + \beta_{DI}DI + \beta_{BE}BE$ $+a_i + \epsilon_i$	
		+ interactions $+\beta_{HS:DI}HSDI$ $+\beta_{HS:BE}HSBE$ $+\beta_{DI:BE}DIBE$		+ interactions $+\beta_{HS:DI}HSDI$ $+\beta_{HS:BE}HSBE$ $+\beta_{DI:BE}DIBE$	
Fixed effects	α	**-0.77** **(-1.20–0.25)**	**-0.7** **(-1.21–0.14)**	**-0.86** **(-1.31–0.34)**	**-0.63** **(-1.17–0.11)**
	β_{HS}	**7.18** **(5.67-9.24)**	**7.38** **(6.16-9.14)**	**8.1** **(6.82-9.11)**	**8.2** **(7.20-9.54)**
	β_{DI}	**26.88** **(12.93-52.50)**	**26.42** **(11.38-50.41)**	**4.12** **(3.23-5.54)**	**1.29** **(0.88-1.89)**
	β_{BE}	-33.24 (-83.67-9.54)	12.12 (-3.17-27.38)	**-37.03** **(-78.09–3.08)**	0.88 (-0.66-3.00)
	$\beta_{HS:DI}$	-3.98 (-18.63-10.59)		**-8.22** **(-10.76–4.55)**	
	$\beta_{HS:BE}$	**-272.97** **(-628.24–151.00)**		**-244.2** **(-535.80–99.80)**	
	$\beta_{DI:BE}$	-18.57 (-205.27-20.88)		-13.72 (-45.70-43.60)	
SD Random effects	a_i	0.76 (0.19-1.16)	0.72 (0.10-1.17)	0.87 (0.40-1.22)	1 (0.53-1.42)
	b_{iHS}	1.08 (0.37-3.31)	0.97 (0.38-3.30)		
	b_{iDI}	33.6 (29.06-36.93)	34.07 (27.10-44.93)		
	b_{iBE}	3.82 (1.39-8.28)	15.17 (10.27-22.87)		
	AIC	604.12	611.54	645.7	710.98
	BIC	688.98	681.43	685.64	735.94
	deviance	570.12	583.54	629.7	700.98
	R$^2_{COR}$	0.74	0.74	0.68	0.65

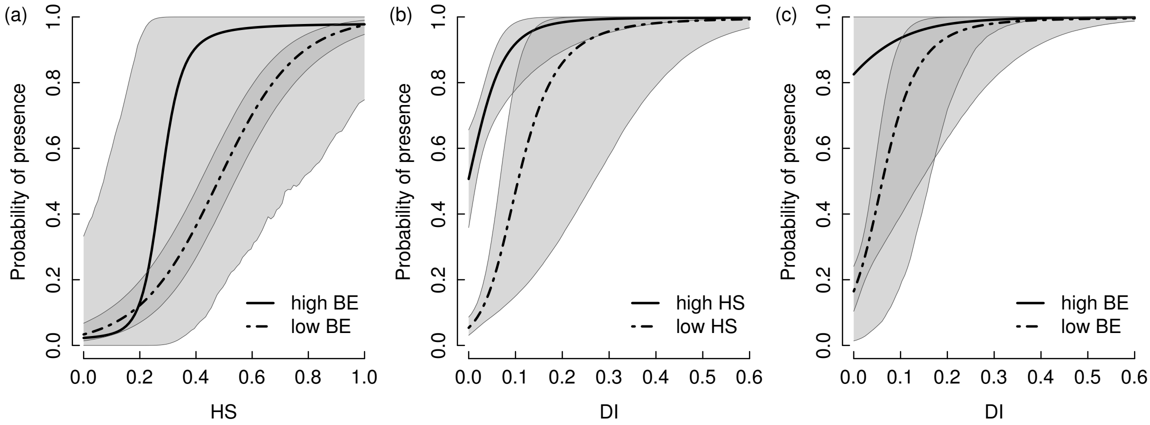

Figure 3.4: Relationship between the probability of presence and the two significant parameters (a) habitat suitability (HS) and (b, c) CPUE-weighed dispersal probability (DI) and their interaction with the dichotomously fixed barrier effects (BE, high = -0.19, low = 0) and HS (high = 0.6, low = 0.2). Results based on best multiple GLMM including interaction terms and full random structure. 95% confidence intervals indicated in grey based on 10000 posterior simulations of model coefficients.

low variation. BE was consistently close to 0 with slightly higher values in the first year (Fig. 3.5).

4 Discussion

Presence and absence of all 17 fish species with frequencies of occurrence $\geq$10 could be accurately modelled. As expected, both local-scale habitat quality and species-specific dispersal ability contributed to the typically discontinuous distribution of fishes in river networks (Angermeier et al. 2002).

This study clearly demonstrated the significant influence of habitat suitability and dispersal ability on the fish species distribution both confirming the first hypotheses widely and the second fully. HS was the best still not exclusive predictor for the absence or presence of a species. As hypothesised, the probability of presence was significantly higher at sites with good species-specific habitat quality. An increase of 0.1 HS more than doubled ($exp(\beta_{HS} * 0.1) = exp(0.738) = 2.09$) the

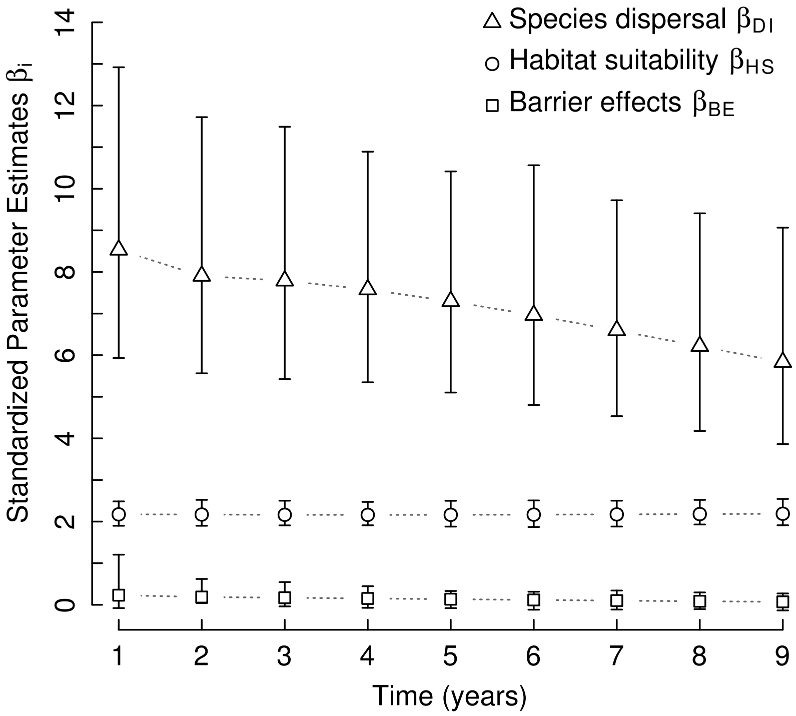

Figure 3.5: Importance (standardised effect sizes) of species dispersal, habitat suitability and barrier effects over time. Results are based on multiple GLMM (no interactions) with species as random factor and scaled and median-centred fixed effects. Error bars are based on parametric bootstrapped confidence intervals (95%).

odds of presence which emphasises the importance of recent attempts to improve in-stream fish habitats (e.g. Lorenz et al. 2013; Wolter 2010).

As expected, the hypothesised importance of dispersal ability for colonising suitable habitat patches was clearly supported. DI as weighted measure of probability that a certain target habitat becomes approached from nearby source populations was significantly positively related to the probability of presence. An increase of 0.1 DI yielded a 14-fold increase ($exp(\beta DI * 0.1) = exp(2.642) = 14.01$) of the odds of presence. With fixed average habitat suitability (HS = 0.37) and no fragmentation by barriers (BE = 0) an increase in DI from 0 to 0.1 increases the overall probability of a presence record from 0.17 to 0.75 ($plogis(-0.70 + ((0.1 + (-0.03245)) * 26.42)))$). DI must reach at least 0.06 (with HS and BE fixed at their median) to exceed the threshold of 0.5 probability of presence. This corresponds for example to the dispersal probability of a 150 mm sized species reaching a 5300 m distant target reach from a source population with 100 individuals after 3 years (Radinger and Wolter 2013). More abundant source populations and larger and thus wider dispersing species will both increase the dispersal probability. The results are consistent with findings of spatial autocorrelation of fish populations along river networks (e.g. Grenouillet et al. 2008); however, they go well beyond pairwise, distance-related comparisons of fish species assemblage similarity by integrating species-specific leptokurtic dispersal, size of source populations, the dendritic structure of river networks and simultaneous dispersal from all potential sources. This study has explicitly separated species dispersal from the spatial distribution and thus potential autocorrelation of habitat features (Legendre 1993). Hence, the findings presented here are not only in accordance with, but might even provide the mechanistic explanation of reported structuring of local assemblages of fishes influenced from connected streams close by (Hitt and Angermeier 2008) or by a regional species pool within about 5 km (Stoll et al. 2013).

The third hypothesis regarding the importance of dispersal through time was also supported by the data. In the initial phase dispersal became especially important with DI being four times more important than HS when considering short time steps. Over longer periods the importance of HS relative to DI increases, because larger parts of the catchment are already colonised, dispersal kernels typically flatten and species become less dispersal limited (Radinger and Wolter 2013). Then HS increasingly determines the successful colonisation of a site.

Rather surprisingly, the first hypothesis was partially rejected as no significant effects of migration barriers on the distribution of the 17 modelled non-diadromous fish species could be observed. There was a trend of higher probability of presence associated with improved connectivity as a decrease of 0.1 BE tripled the odds of presence ($exp(\beta_{BE} * 0.1) = exp(1.212) = 3.36$). However, this trend was not significant. Correspondingly, Van Looy et al. (2014) and Branco et al. (2012) detected only minor respectively not any effects of dam density and connectivity on fish-based metrics and the distribution of river fishes, respectively.

There are two main reasons for the inability of this study to detect significant barrier effects: First, diadromous fish species were not considered. In contrast to most other fishes, these species migrate from the sea to headwaters and thus depend on unrestricted longitudinal connectivity of the whole network. Secondly, the models were run for the most frequent species only, with at least ten occurrences, i.e. numerous presences in the catchment and upstream and in between barriers. Therefore, even river stretches upstream of barriers contained founder populations serving as origin for dispersal and flawing the potential barrier effects. This observation of fishes present even in heavily fragmented river sections is typical and often explained by downstream drift dispersal (e.g. Pavlov 1994) as well as the highly variable and species-specific passage rates of barriers (Bourne et al. 2011; Kemp and O'Hanley 2010). Especially over long time periods barriers might temporarily or accidentally allow for fish passage depending on species, fish size and especially on hydrological conditions (Bourne et al. 2011). Accordingly, the findings presented here indicate also the importance of the spatial arrangement of source populations and their relative position in relation to the barriers within the river network.

This study does not at all ignore or question the extensively demonstrated impact of barriers and habitat fragmentation on river ecosystems and aquatic biodiversity (e.g. Dynesius and Nilsson 1994; Fullerton et al. 2010; Reidy Liermann et al. 2012). However, especially in regard to river rehabilitation, plain metrics of fragmentation like the number of barriers per river kilometre or the number/size of disconnected patches (e.g. Dynesius and Nilsson 1994; Van Looy et al. 2014) might not be meaningful as summary statistics of barriers fail to account for the context between the spatial arrangement of habitat patches, directional dispersal potential and non-uniform influence of barriers. The use of more sophisticated GIS-based dispersal models (e.g. FIDIMO, Radinger et al. 2013) could improve analyses of barrier impacts but in particular allow for deriving and prioritising river rehabilitation measures.

Corresponding to the limited ability in detecting barrier effects, restored longitudinal connectivity might not result in quantifiable biotic improvement, if e.g. the segments up- and downstream of a barrier already contain the target species, if no new or essential habitats become available for the species or if connectivity measures are not accompanied by habitat enhancements (Kail and Wolter 2011). The overall importance of accessible habitats was underlined by the results of the mixed models indicating that habitat suitability and the dispersal from proximal highly abundant source populations govern the spatial distribution of freshwater fishes. Accordingly, reported failures of local habitat improvements might simply result from the lack or distance of source populations (Haase et al. 2012; Lepori et al. 2005) respectively from a general ignorance of dispersal processes in river restoration planning (Altermatt 2013). This study fully substantiated the conclusions by Diebel et al. (2010) that stream restoration will be most effective when it builds on the existing spatial arrangement of habitat characteristics and incorporates the location of source populations and the dispersal abilities of fishes.

In sum, the results presented have several practical implications for river restoration: First of all the well-known fact that habitat is key. Restoring essential habitats is a key prerequisite for successful river rehabilitation, even at the local scale. Secondly, fish are mobile organisms with well-developed dispersal abilities and are thus, able to utilise local habitat patches within a wider river network. However, depending on the distance to the nearest founder population and species-specific dispersal performance this might take time, which has to be also considered in any evaluation of restoration measures. Even if barriers might not directly affect, they still interfere with habitat rehabilitation and increase the uncertainty of restoration success. Thirdly, the model framework provided here combines species habitat suitability models based on catchment-wide physical habitat features with newly developed mechanistic fish dispersal models in river networks to account for the species-specific dispersal abilities and movement constraints.

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General Discussion

Rivers are subject to multiple pressures and the commonly discontinuous pattern of fish colonisation in rivers is jointly controlled by abiotic factors such as local habitat conditions in addition to biotic factors such as dispersal (Jackson et al. 2001). However, knowledge on fish dispersal patterns and its interaction with habitat conditions is thus far limited and the tools for modelling fish dispersal in dendritic river networks have been missing so far.

Overall, this thesis could fully reach its initial aims and can provide results and methods to develop, parameterise and apply a fish dispersal model for freshwater fish species. With three consecutive papers, it contributes to a better mechanistic understanding of the typical heterogeneous dispersal patterns of river fish **(first paper, Part 1)**, provide tools (FIDIMO) to model fish dispersal in river networks using a GIS software **(second paper, Part 2)** and shows how dispersal interacts with local habitat conditions in the colonisation of river reaches **(third paper, Part 3)**.

5 How and how far are fish dispersing?

The *first paper of this thesis* (**Part 1**) provides the first comprehensive compilation and quantitative analysis of freshwater fish movement. This emphasises the importance of considering fish populations as heterogeneous entities where individual specimens exhibit varying levels of mobility. The principle objectives of the first study were reviewing and determining movement distances of stationary and dispersal relevant mobile components of fish populations and identifying determining factors for dispersal distances. For the review, 160 empirical datasets from 71 studies on movement of 62 riverine fish species were evaluated, completed and analysed in a standardised way based on refitted leptokurtic dispersal kernels.

Similarly to earlier studies by e.g. Gowan and Fausch (1996) these results disproved fish populations as being restricted in their movement, they rather form populations consisting mainly (appr. 2/3) of stationary individuals but also include highly mobile dispersal relevant individuals (appr. 1/3). So, this study goes beyond findings that considered fish movement as homogeneous, independent from temporal scales and restricted to a 'home range' (Minns 1995; Woolnough et al. 2009) and stresses the importance of considering fish dispersal as heterogeneous (Crook 2004; Gowan and Fausch 1996). Furthermore, it extends existing knowledge of heterogeneous fish dispersal in salmonids (Gowan et al. 1994; Rodríguez 2002) and provides generalised information on heterogeneous dispersal parameters for a broader group of many other species (12 families) which display differing traits such as sculpins (Hudy and Shiflet 2009) and cyprinids (Stott 1961). Thus, it enables more general conclusions on fish dispersal which might be extrapolated even to other species and thus depict valuable information especially on rare and endangered species which are of high interest in restoration ecology, but are typically less studied especially in regard to their dispersal abilities.

Generally, species-specific dispersal kernels (probability-density function of movement away from an initial source population) provide a commonly used tool for all kinds of population and individual based modelling (e.g. Kot et al. 1996). Thus, quantitative and empirically derived information to parameterise dispersal kernels is a decisive for a meaningful application in dispersal models (see **Part 2**). For the dispersal kernels of the analysed empirical studies, three quantitative movement parameters could be extracted: the movement distance of a stationary (σ_{stat}) and a mobile component (σ_{mob}) as well as the share of the stationary component (p).

A share of one third and two thirds emerged as a general pattern of the mobile and stationary component of a fish population (p), respectively, which is slightly lower than reported for salmonids (81% stationary, Rodríguez 2002). However, no ecological predictor for the share of the stationary/mobile individuals could be found. Other studies suggest, that the number of mobile individuals of a population might be related to the habitat and its connectivity (e.g. Hanski et al. 2004), to phenotypic attributes (e.g. size and growth, Skalski and Gilliam 2000) and to individual behavioural differences in heterogeneous populations (e.g. boldness, Fraser et al. 2001). Moreover, it can be assumed that an improved and more complex habitat with a higher availability of resources (per capita) and enhanced structural variability (e.g. to hide from predators) results in decreased movement and thus a higher share of the stationary component (e.g. Albanese 2001). Einum and Nislow (2005) and Einum et al. (2006) examined the effects of density-dependence on dispersal of juvenile Salmon and found that the likelihood to emigrate from a site increases in with population density. However, the dependency of the degree of mobility (in the sense of mobile and stationary components of a population) on population density and/or resource availability in river ecosystems remains unclear. Thus environmental (e.g. habitat dependence, physico-chemical stimuli), fish internal (physiological and behavioural) and population induced factors (e.g. population density, collective group behaviour) that potentially determine the actual share of the stationary/mobile component of a source population clearly need further empirical examination. This is especially important for future applications of dispersal models in restoration ecology as any long-term survival of populations strongly depends on a sufficiently large number of individuals that move to and potentially colonise newly available habitats (Kokko and Lopez-Sepulcre 2006). Consequently, the success of a restoration measure might not only be dependent on the habitat in the receiving reach but also on the quality of the source habitat.

Four variables were considered to be primary controllers of dispersal distances: fish length, swimming type, river size and time. Hence, the mean movement distance of the stationary component (σ_{stat}) and of the mobile component (σ_{stat}) increased with the size of a fish, its aspect ratio (which is a proxy for its swimming and metabolism level, Pauly 1989), the size of the river measured as stream order (Strahler 1957) and with time. Considering solely these four significant factors (combined in a multiple regression model), approximately 65% and 77% of the variation in the movement distance (σ_{stat} and σ_{mob} respectively) among all analysed studies could be determined. Of all predictors, fish size was the most important explaining 46% and 44% of the variation respectively. These results are in accordance with other findings that related the movement or home range of fish size to its body size (e.g. Minns 1995; Peters 1983), the size of the water body (e.g. Woolnough et al. 2009) and time (e.g. Skalski and Gilliam 2000; Thompson 1933). In contrast to other studies, this review related the predictors to standardised movement parameters, which can be also used to describe a dispersal kernel. Thus, this study enables to directly infer the shape of the dispersal kernel from a set of four simple and easily obtainable environmental and fish internal factors (see R-package FISHMOVE, `http://cran.r-project.org/web/packages/fishmove/fishmove.pdf`) and consequently highly facilitates its application in a fish dispersal model (e.g. FIDIMO, **Part 2**).

6 FIDIMO: How to model fish dispersal with GIS-tools?

The *second paper of this thesis* (**Part 2**) aimed to provide the novel FIsh DIspersal MOdel FIDIMO, which is the first tool for predicting and simulating spatio-temporal patterns of fish dispersal in river networks considering movement barriers with a real integration of GIS.

FIDIMO provides the missing link between conceptual considerations on dispersal modelling (McMahon and Matter 2006) with empirically observed leptokurtic fish movement patterns (Rodríguez 2002, **Part 1**) and the strengths of geographically explicit modelling in Free and Open Source GIS (Steiniger and Hay 2009). Therefore, it uses empirically derived movement distances for a stationary (σ_{stat}) and mobile (σ_{mob}) component which can be predicted from fish length, river size, aspect ratio of the fish's caudal fin and time (see first paper of this thesis, **Part 1**). Together with the share of the stationary component, which was approximately 2/3 in average, these factors and a multiple regression model (provided by the R-package FISHMOVE) depict the main input parameters to mathematically describe the typical leptokurtic pattern of fish dispersal. The model computes dispersal along the river network as a probability of moving away from a spatially given source population based on so-called dispersal kernels, the mathematical description of the probability to disperse (probability-density functions, Eq. 2.1).

Consequently FIDIMO follows earlier approaches to model dispersal as spatially explicit process within GIS environments and to apply dispersal kernels as a key model descriptor. Accordingly, the successful use of GIS systems for modelling dispersal by applying dispersal kernels has already been shown for the spread of terrestrial plants (Fox et al. 2007; Pitt et al. 2011) and insects (e.g. Modular Dispersal in GIS, MDiG Pitt 2008; Pitt et al. 2009), but also the drift spread of marine fish larvae (Fischer et al. 2011). However, FIDIMO goes beyond such (mostly terrestrial) models and extends the approach for fish by modelling dispersal along a rasterised river network and by explicitly incorporating the typical leptokurtic spread of river fish as well as by optionally considering differently permeable movement barriers that lower the probability to approach upstream habitats. The size of the river is included in the model as one of the predictors determining the dispersal distance (**Part 1**). Moreover, the river size is also used to portion the share of individuals to the main stem and the tributary at network nodes during upstream migration, so that most fish remain in the main stem and only a smaller part moves into the tributary dependent on its size.

FIDIMO was programmed for the GRASS GIS (Neteler and Mitasova 2007), and can be executed as an add-on to GRASS using its internal graphical user interface. The single required input parameters are explained in detail in **Part 2** and generally include the (i) rasterised river network, (ii) the geographical location of source populations, (iii) values for the parameterisation of the dispersal kernel functions and (iv) optionally the locations and characteristics (passability rates) of migration barriers.

FIDIMO can be considered a hybrid model (combining multiple approaches: empirical data, regression, diffusion, GIS etc., Parrott 2011) and is part of the rapidly evolving field of ecoinformatics which supports the discovering, managing, analysing, visualising and preserving of ecological information (Michener and Jones 2012). Furthermore, FIDIMO has entirely been programmed as free (in the sense of 'freedom', Stallman 1985) and open source software (FOSS) and thus provides an active contribution to 'open science' in applied ecology. Similarly to Rocchini and Neteler (2012), we emphasise the importance of FOSS in ecology to avoid black box calculations and to make computationally derived results reliable and understandable to others, so that the scientific community as well as river managers maximally benefit from the software. Consequently, like other FOSS, FIDIMO also provides the freedom to: i) to run the code for any purpose, ii) to study the code and adapt it, iii) to redistribute the code and iv) to improve and release the code to the public (Rocchini and Neteler 2012; Stallman 1985).

Of course, as with any other computer model applied as a decision support tool in 'real'-world ecology, FIDIMO also needs to be used with caution as it is still a simplified representation of a complex ecological process which will never fulfil all three claims for generality, reality and precision at the same time (see Fig. 0.2, Levins 1966). With increasing computational capabilities and the open code, it is tempting to incorporate many other potentially determining factors and to vary them on a wider scale. Unfortunately, increasing the number of model factors and their ranges of variation will result in increasingly larger interactions and a higher probability of increased overall uncertainty (Saltelli et al. 2001). Consequently, the inherent uncertainty of such models that represent complex ecological systems makes it difficult to judge the plausibility of modelled outcomes (Parrott 2011). Here, novel genetic approaches to analyse fish dispersal in fragmented river networks (Baguette et al. 2013; Paz-Vinas et al. 2013) might be useful for validation reasons and for comparison with a mechanistic process-based model like FIDIMO (Radinger et al. *in prep.*).

Despite its novelty and its potential future application as a decision support tool in restoration and river ecology, FIDIMO is still a 'young' code and has some limitations that need to be discussed in future improvements of the software. In particular, knowledge on processes that control the typical leptokurtic shape of the dispersal kernel, as well as the complex interactions between dispersal probability, environmental and inter- and intraspecific processes clearly needs further examination to be incorporated in mechanistic dispersal models for riverine fish species. FIDIMO is under continuous development (`http://grasswiki.osgeo.org/wiki/AddOns/GRASS7/raster#r.fidimo`) and has already been greatly expanded over its initial published version which is highly facilitated by its FOSS nature. The most recent improvements (see Biodiversa-project FISHCON, BMBF grant number 01LC1205) already allow: i) transforming modelled dispersal probabilities into counts of arriving fish, ii) modelling dispersal with spatially varying shares of the mobile component (e.g. density-habitat dependency), iii) considering habitat-dependent dispersal (e.g. attractiveness of a 'sink'-habitat) and iv) combining the dispersal model with spatial explicit models of population growth.

Overall, the model FIDIMO, and its on-going further development contributes to a comprehensive understanding of fish dispersal, allows the prediction of spatio-temporal colonisation patterns, the estimation of time lags in fish response to river management (e.g. rehabilitation) and the temporal patterns of fish distribution.

7 Habitat vs. dispersal: What is shaping the distribution of river fish?

While the first two parts covered empirically derived dispersal patterns and development of an appropriate dispersal model, the *third paper of this thesis* (**Part 3**) aimed to disentangle and quantify the single contributions of habitat suitability, dispersal constraints and network fragmentation on the distribution patterns of riverine fish. Therefore, information of heterogeneous fish dispersal (**Part 1**) as included in the novel Fish Dispersal Model FIDIMO (**Part 2**) was applied in combination with species habitat/distribution models (MaxEnt) in a modelling framework to predict the discontinuous distribution of 17 fish species in the German River Treene.

Generally, environmental heterogeneity, habitat suitability, dispersal ability of species and fragmentation are factors shaping the discontinuous distribution of fish in rivers (Angermeier et al. 2002). Although being decisive for the recolonisation of newly available habitats and thus for the success of rehabilitation and conservation measures in river networks, the spatial dynamics of fish populations and their governing factors is virtually ignored by resource managers (Jackson et al. 2001).

The presented results contribute to a mechanistic understanding of colonisation patterns as they showed significant positive and interacting effects of both, local-scale habitat quality and species-specific dispersal ability on the distribution of fish species, whereas no significant effect could be found for barriers. We could find that already minor improvements of the accessibility of a (e.g. newly available) habitat had remarkably large effects on the probability of being colonised. This spatial influence of connected and adjacent habitats has generally been discussed around the term ‘spatial autocorrelation’ (Legendre 1993). Accordingly, also Hitt and Angermeier (2008) and Stoll et al. (2013) showed that fish assemblages are highly determined by the accessibility from connected adjacent species pools in the immediate environment. Similarly, Nakagawa (2014) explained through statistical analysis that the spatial variation in species assemblages at the medium scale is largely determined by distance-constrained dispersal. The results and mechanistic modelling framework strongly support these findings. The importance of species-specific dispersal processes from multiple source populations with varying distances, constrained by barriers, could be quantified for the first time. Moreover, it could be demonstrated that novel, spatially explicit software tools (FIDIMO, described in **Part 2**) that consider the leptokurtic movement patterns of fish (**Part 1**), which can be combined with other models (e.g. suitability and/or distribution models) are extremely helpful to disentangle multiple potential constraints/pressures in spatially highly variable river ecosystems. The further development of such spatially explicit and applied GIS models, in combination with rapidly advancing methods in genetic dispersal modelling, suggests a promising path for the future management of rivers on catchment scale as well as prioritising and predicting the success of river restoration measures (habitat improvements, barrier removal etc.).

Furthermore, the results showed that the importance of dispersal decreased over longer time periods in favour of habitat suitability which becomes increasingly relevant in determining species' presence. This outcome is closely related to the characteristic of dispersal kernels that typically flatten over time and more habitats can be approached at longer time frames (**Part 1**). Consequently, local-scale restoration and improvements of river habitats are highly recommended for (re-)establishing natural river-type specific biotic species communities. However, fish are typically mobile and undertake various movements in their immediate environment (**Part 1**) and thus, their occurrence is also determined by the physical habitat conditions at larger spatial scales (Radinger et al. *in prep.*, Nakagawa 2014).

Rather surprisingly, no significant effect of barriers on the spatial distribution and colonisation of the 17 modelled fish species in the Treene river could be detected. This outcome is in concordance with recent findings by Van Looy et al. (2014) and Branco et al. (2012) that found only minor or no effect of barriers on the distribution of fish in river networks. However, the study does not question the impact of barriers at all (e.g. Dynesius and Nilsson 1994; Fullerton et al. 2010; Reidy Liermann et al. 2012) as it i) does not include diadromous species that depend on unrestricted long-distance dispersal in the entire network and ii) covers only the most frequent species present in the modelled catchment. The results can be explained as most species were already present in many reaches of the network including upstream parts. Thus barriers might be passed in downstream direction (e.g. larval drift, Pavlov 1994) and the barriers passability rates might be higher than initially considered e.g. under specific hydrologic conditions (Bourne et al. 2011; Kemp and O'Hanley 2010). Consequently, it is extremely important for the assessment of river fragmentation to consider the effects of barriers always in relation to the spatial arrangement of source populations and their relative position within the river network.

Overall, the results are in accordance with earlier findings that fish distribution patterns are governed by a highly complex system of environmental and spatial factors (dispersal, fragmentation, habitat suitability, etc) and multiple spatial and temporal scales (e.g. Angermeier and Winston 1998; Nakagawa 2014; Taylor et al. 2006). It could be shown that the application of spatio-ecological model frameworks (as described in **Part 3**) and spatially explicit dispersal models (e.g. FIDIMO, **Part 2**) can be extremely useful to disentangle the single biotic, environmental and spatial effects and their respective scales, especially also in catchments effected by multiple pressures.

In conclusion, based on the findings, it can be emphasised that the prioritisation of connectivity measures (e.g. opening new, suitable habitat patches) and the restoration of stream reaches might be most efficient if the spatial arrangement of source populations, their relative position in relation to barriers and the fish's dispersal ability are considered.

8 Major findings

In conclusion, the major findings of the thesis are:

- ✓ Fish dispersal is typically **leptokurtic** consisting of **stationary** σ_{stat} **and mobile components** σ_{mob}
- ✓ We calculated quantitative dispersal parameters based on **fish length, swimming performance, stream size and time**
- ✓ FIDIMO allows for the **prediction and simulation of spatio-temporal patterns of fish dispersal** (e.g. time lags in fish response, minimum size of founder populations)
- ✓ Besides the **restoration of essential habitats** their **accessibility** (spatial arrangement of source populations, position relative to barriers, the fish's dispersal ability) is highly decisive

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Appendix

Table A.1: Characteristics of original datasets (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). Fitted movement parameters (see Methods): σ_{stat} = Movement distance of stationary component, σ_{mob} = Movement distance of mobile component, p = share of the stationary component.

		Fish		Stream size				Movement parameters				
Scientific name	Waterbody	L (mm)	AR^a	SO	W (m)	D (m^3s^{-1})	T (d)	σ_{stat} (m)	σ_{mob} (m)	p	Study type	Source
Catostomidae												
Catostomus commersoni	Grand River (CA)	404	1.59	6^b	45^o	46.6	7	19.81	170.17	0.49	T	Brown et al. (2001)
Moxostoma duquesnii	Missouri rivers (US)	285^a	2.29		1.3		148	1037.82	31388.31	0.67	M	Funk (1957)
Moxostoma erythrurum	Missouri rivers (US)	288^a	1.17				174	1525.71	108077.28	0.66	M	Funk (1957)
Centrarchidae												
Ambloplites rupestris	Massie Creek (US)	159	1.05	4^c	11.6	1.08	824	221.94	4999.44	0.74	M	Brown (1961)
Ambloplites rupestris	Missouri rivers (US)	194	1.05				209	1179.37	16073.55	0.75	M	Funk (1957)
Ambloplites rupestris	East Fork Poplar Creek (US)	154^a	1.05	3^c	5	1.51^q	1095	68.65	266.34	0.86	M	Gatz and Adams (1994)
Lepomis auritus	Ichawaynochaway Creek (US)	49	1.87	5	34	26.23^q	383	4.17	89.65	0.9	Tr	Freeman (1995)
Lepomis auritus	East Fork Poplar Creek (US)	108^a	1.87	3^c	5	1.51^q	31	78.09	385.06	0.84	M	Gatz and Adams (1994)
Lepomis auritus	East Fork Poplar Creek (US)	108^a	1.87	3^c	5	1.51^q	92	49.21	301.1	0.47	M	Gatz and Adams (1994)
Lepomis auritus	East Fork Poplar Creek (US)	108^a	1.87	3^c	5	1.51^q	1095	92.61	1047.14	0.54	M	Gatz and Adams (1994)
Lepomis auritus	Durant Creek (US)	130	1.87	2^c	2.5	0.02^q	153	4.36	131.05	0.55	M	Skalski and Gilliam (2000)
Lepomis cyanellus	Missouri rivers (US)	200^a	1.59				136	983.63	15538.81	0.85	M	Funk (1957)

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		Fish		Stream size				Movement parameters				
Scientific name	Waterbody	L (mm)	AR^{a}	SO	W (m)	D (m^3s^{-1})	T (d)	σ_{stat} (m)	σ_{mob} (m)	p	Study type	Source
Lepomis cyanellus/megalotis	Little Glazypeau Creek (US)	69		2^{c}	4.9^{p}	0.18^{p}	730	21.23	375.85	0.95	M	Smithson and Johnston (1999)
Lepomis macrochirus	Brushy Fork (US)	191^{a}	1.39	3	5	0.6^{q}	1095	89.6	1216.38	0.89	M	Gatz and Adams (1994)
Lepomis macrochirus	East Fork Poplar Creek (US)	191^{a}	1.39	3^{c}	5	1.51^{q}	1095	168.42	2570.89	0.63	M	Gatz and Adams (1994)
Lepomis macrochirus	East Fork Poplar Creek (US)	191^{a}	1.39	3^{c}	5	1.51^{q}	1095	109.08	1920.69	0.87	M	Gatz and Adams (1994)
Lepomis megalotis	Missouri rivers (US)	115^{a}	0.86				228	1168.72	31253.05	0.83	M	Funk (1957)
Micropterus dolomieui	Massie Creek (US)	219	1.43	4^{c}	11.6	1.08	1007	283.64	6404.42	0.57	M	Brown (1961)
Micropterus dolomieui	Missouri rivers (US)	280	1.43				234	965.69	13211.48	0.66	M	Funk (1957)
Micropterus dolomieui	Middle Snake River (US)	301	1.43	8^{c}	65^{o}	1.46	547	98.41	2757.04	0.87	M	Munther (1970)
Micropterus punctulatus	Missouri rivers (US)	300^{a}	1.64				180	122.81	24745.95	0.91	M	Funk (1957)
Micropterus salmoides	Missouri rivers (US)	400^{a}	1.22				291	1726.27	36209.92	0.72	M	Funk (1957)
Micropterus salmoides	East Fork Poplar Creek (US)	400^{a}	1.22	3^{c}		1.51^{q}	1095	167.94	2754.58	0.69	M	Gatz and Adams (1994)
Micropterus salmoides	St. Johns River (US)	240	1.22	6^{c}	200^{o}	140.17^{q}	1647	1326.31	27547.82	0.26	M	Moody (1960)
Micropterus salmoides	Savannah River (US)	343	1.22	7^{c}	95^{o}	250.04^{q}	14	64.01	1185.18	0.68	T	Paller et al. (2005)
Micropterus salmoides	Upper Steel Creek (US)	343	1.22	3^{c}		1	14	30.09	192.88	0.65	T	Paller et al. (2005)
Micropterus salmoides	Lower Steel Creek (US)	343	1.22	3^{c}		3.01^{q}	14	91.6	1004.22	0.59	T	Paller et al. (2005)
Pomoxis annularis	Missouri rivers (US)	250^{a}	1.62				91	111.44	50357.36	0.24	M	Funk (1957)
Cottidae												
Cottus bairdii	Seven Mile Creek (US)	69	1.18	2	5.8	0.19^{e}	53	0.5	7.33	0.6	T	Breen et al. (2009)
Cottus bairdii	Seven Mile Creek (US)	69	1.18	2	5.8	0.19^{e}	43	0.61	8.78	0.82	T	Breen et al. (2009)
Cottus bairdii	Cowan Creek (US)	57	1.18	1^{c}	3.7^{o}	0.23^{q}	14	0.17	3.08	0.54	M	Brown and Downhower (1982)
Cottus bairdii	Gibson Creek (US)	57	1.18	1^{c}	5^{o}	0.23^{q}	14	0.01	2.22	0.39	M	Brown and Downhower (1982)
Cottus bairdii	Nantahala River (US)	84^{a}	1.18	3	5.7	5.75^{q}	730	6.58	55.59	0.51	M	Lamphere (2005)

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		Fish		Stream size				Movement parameters				
Scientific name	Waterbody	L (mm)	AR^a	SO	W (m)	D (m^3s^{-1})	T (d)	σ_{stat} (m)	σ_{mob} (m)	p	Study type	Source
Cottus bairdii	Trout Creek (US)	84^a	1.18	3^c	3.8	0.37	60	12.94	70.84	0.62	M	McCleave (1964)
Cottus bairdii	Shope Fork (US)	57	1.18	4	5.5^e	0.24	45	1.37	21.37	0.8	M	Petty and Grossman (2004)
Cottus bairdii	Shope Fork (US)	84^a	1.18	4	5.5^e	0.24	45	1.67	8.14	0.85	M	Petty and Grossman (2004)
Cottus girardi	Smith Greek (US)	78^a		3	7.1	0.23	75	1.69	65.47	0.59	M	Hudy and Shiflet (2009)
Cottus girardi	Smith Greek (US)	78^a		3	7.1	0.23	367	14.12	231.06	0.76	M	Hudy and Shiflet (2009)
Cottus gobio	Laarse Beek (BE)	76	1.03	2^d	4		119	0.16	152.94	0.22	M	Knaepkens et al. (2004)
Cottus gobio	Steenputbeek (BE)	76	1.03		1		119	3.86	21.47	0.77	M	Knaepkens et al. (2004)
Cottus gobio	Steenputbeek (BE)	76	1.03		1		241	5.19	35.56	0.55	M	Knaepkens et al. (2004)
Cottus gobio	Steenputbeek (BE)	73	1.03	2^d	4^e		121	6.3	36.15	0.68	M	Knaepkens et al. (2005)
Cottus gobio	Steenputbeek (BE)	73	1.03	2^d	4^e		180	7.47	78.2	0.66	M	Knaepkens et al. (2005)
Cottus gobio	Steenputbeek (BE)	73	1.03	2^d	4^e		272	7.15	62.11	0.76	M	Knaepkens et al. (2005)
Cottus pollux	Inabe River (JP)	74^a	1.5	2^e	8.05	1.34	322	26.97	104.24	0.93	M	Natsumeda (1999)
Cottus pollux	Inabe River (JP)	74^a	1.5	2^e	8.05	1.34	119	24.43	139.94	0.86	M	Natsumeda (1999)
Cottus pollux	Fujii River (JP)	76	1.5	2	1.8	0.26	365	2.51	64.99	0.71	M	Natsumeda (2007)
Cottus pollux	Fujii River (JP)	64	1.5	2	1.8	0.16	365	2.99	41.64	0.76	M	Natsumeda (2007)
Cottus rhenanus	Falogne brook (FR)	95		2^e	3.7	0.6	393	8.67	90.89	0.64	M	Ovidio et al. (2009)
Cyprinidae												
Abramis brama	Grand Canal (IE)	380	1.74		17.5		4	30.63	1046.6	0.49	T	Donnelly et al. (1998)
Barbus barbus	River Ourthe (BE)	395	1.85	4^f	25^o	32^f	112	1940.55	19231.04	0.66	T	Baras (1998)
Barbus barbus	Middle Severn (GB)	366	1.85	7^g	40^o	59.83^g	610	509.2	6344.55	0.78	M	Hunt and Jones (1974)
Barbus barbus	Nidd (GB)	523	1.85	5^g	12	8	486	1404.93	7469.8	0.5	T	Lucas and Batley (1996)
Barbus haasi	Vallvidrera Creek (ES)	155		1	1.6	0.03	153	7.18	71.34	0.67	M	Aparicio and Sostoa (1999)
Barbus haasi	Vallvidrera Creek (ES)	155		1	1.6	0.03	244	9.69	86.84	0.58	M	Aparicio and Sostoa (1999)
Barbus haasi	Vallvidrera Creek (ES)	155		1	1.6	0.03	365	6.59	86.95	0.57	M	Aparicio and Sostoa (1999)

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		Fish		Stream size				Movement parameters				
Scientific name	Waterbody	L (mm)	AR[a]	SO	W (m)	D (m^3s^{-1})	T (d)	σ_{stat} (m)	σ_{mob} (m)	p	Study type	Source
Clinostomus funduloides	Durant Creek (US)	60	1.95	2^c	2.5	0.02^q	153	7.23	132.47	0.32	M	Skalski and Gilliam (2000)
Cyprinus carpio carpio	Grand River (CA)	572	1.89	6^b	45^o	46.6	7	7.07	57.61	0.45	T	Brown et al. (2001)
Cyprinus carpio carpio	Missouri rivers (US)	399	1.89				395	1468	47684	0.69	M	Funk (1957)
Gobio gobio	Mole (GB)	114	1.37	5^g	6.9	1.4	67	195	1494	0.66	M	Stott (1967)
Gobio gobio	Mole (GB)	114	1.37	5^g	6.9	1.4	315	58	931	0.69	M	Stott (1967)
Leuciscus idus	Elbe (CZ)	378	1.75	9^h	125	293	14	3429.39	3713.5	0.7	T	Kuliková et al. (2009)
Leuciscus idus	River Elbe (DE)	461	1.75	9^h	350	517.5	1064	18616.93	166438.17	0.76	T	Winter and Fredrich (2003)
Leuciscus idus	River Vecht (NL)	433	1.75	4^i	45	32	1064	39762.58	78713.18	0.7	T	Winter and Fredrich (2003)
Mylopharodon conocephalus	Pine Creek (US)	233	1.79	2^c	6.4	0.235	444	10.8	421.83	0.27	M	Grant and Maslin (1999)
Nocomis leptocephalus	Durant Creek (US)	80	1.47	2^c	2.5	0.02^q	153	7.33	79.65	0.52	M	Skalski and Gilliam (2000)
Ptychocheilus grandis	Pine Creek (US)	400^a	0.77	2^c	6.4	0.24	417	57.63	360.95	0.5	M	Grant and Maslin (1999)
Rutilus rutilus	River Roding (GB)	153	1.48	4^g	6.5	0.61	145	169.25	1283.74	0.7	M	Bolland et al. (2009)
Rutilus rutilus	Grote Nete (BE)	234	1.48	5^e	8^e	5.17^e	7	40.91	268.21	0.27	T	Geeraerts et al. (2007)
Rutilus rutilus	Kleine Nete (BE)	239	1.48	5^e	12^e	6.74^e	7	57.21	1159.38	0.5	T	Geeraerts et al. (2007)
Rutilus rutilus	River Vesdre (BE)	232	1.48	6^j	40^e	11.4^e	7	5.99	222.79	0.38	T	Geeraerts et al. (2007)
Rutilus rutilus	Rivers Thames/Mole (GB)	250^a	1.48				67	106.27	621.95	0.8	M	Stott (1961)
Rutilus rutilus	River Mole (GB)	131	1.48	5^g	6.9	1.4	67	55	593	0.7	M	Stott (1967)
Rutilus rutilus	River Mole (GB)	131	1.48	5^g	6.9	1.4	315	84	1027	0.61	M	Stott (1967)
Rutilus rutilus	River Thames (GB)	250^a	1.48	6^g	60	38.9^g	49	28.09	1865.13	0.83	M	Williams (1965)
Semotilus atromaculatus	Durant Creek (US)	90	1.11	2^c	2.5	0.02^q	153	10.76	49.18	0.42	M	Skalski and Gilliam (2000)
Snyderichthys copei	Salina Creek (US)	145		3	6.44^e	4.9	1095	71.94	451.59	0.84	M	Rasmussen (2010)
Squalius cephalus	River Roding (GB)	246	1.42	4^g	6.5	0.61	145	85.96	1219.4	0.72	M	Bolland et al. (2009)

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		Fish		Stream size				Movement parameters				
Scientific name	Waterbody	L (mm)	AR^a	SO	W (m)	D (m^3s^{-1})	T (d)	σ_{stat} (m)	σ_{mob} (m)	p	Study type	Source
Squalius cephalus	River Spree (DE)	300^a	1.42	6^e	25	15	77	1619.11	26424.25	0.72	T	Fredrich et al. (2003)
Tinca tinca	Grand Canal (IE)	390	1.45		17.5		4	95.86	3209.46	0.46	T	Donnelly et al. (1998)
Esocidae												
Esox lucius	Grand Canal (IE)	810	1.39		17.5		4	56.76	1881.73	0.43	T	Donnelly et al. (1998)
Esox lucius	River Gudenå (DK)	787	1.39	5^k	70	40	3	54.46	757.94	0.92	T	Koed et al. (2006)
Esox lucius	River Frome (GB)	365	1.39	4^g	11^e	6.04^g	365	85.74	438.81	0.74	M	Mann (1980)
Fundulidae												
Fundulus heteroclitus heteroclitus	Canary Creek (US)	89^a	0.9	1^c	11.5^o		52	1	9.64	0.14	Tr	Lotrich (1975)
Fundulus notatus	Cahokia Creek (US)	43	0.83	4	8.2	4.23^q	1	2.7	21.44	0.7	M	Alldredge et al. (2011)
Fundulus notatus	Cahokia Creek (US)	44	0.83	4	8.2	4.23^q	1	5.9	42.36	0.62	M	Alldredge et al. (2011)
Fundulus olivaceus	Big Creek (US)	52	0.8	3	6.4	0.12^q	1	0.62	2.68	0.75	M	Alldredge et al. (2011)
Ictaluridae												
Ameiurus natalis	Missouri rivers (US)	225^a	0.87				76	196.65	10352.34	0.77	M	Funk (1957)
Ictalurus punctatus	Missouri rivers (US)	406	1.7				309	1404.94	38811.62	0.47	M	Funk (1957)
Pylodictis olivaris	Missouri rivers (US)	760	1.19				341	1476.88	37477.34	0.66	M	Funk (1957)
Moronidae												
Morone americana	Patuxent River (US)	180	1.78	5^c	2000^o	10.2^r	365	635.73	42367.8	0.38	M	Mansueti (1961)
Percidae												
Etheostoma flabellare	Harkers run (US)	52^a	0.51	2^c	4.5^o	0.22^q	32	2.76	69.08	0.8	M	Mundahl and Ingersoll (1983)
Etheostoma flabellare	Roanoke River (US)	62	0.51	5^e	11.5	4.98^e	120	3.26	172.61	0.92	M	Roberts and Angermeier (2007)
Etheostoma nigrum	Harkers run (US)	39^a	0.63	2^c	4.5^o	0.22^q	32	0.45	56.45	0.95	M	Mundahl and Ingersoll (1983)
Etheostoma podostemone	Roanoke River (US)	58		5^e	11.5	4.98^e	120	3.76	163.62	0.91	M	Roberts and Angermeier (2007)

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		Fish		Stream size				Movement parameters				
Scientific name	Waterbody	L (mm)	AR^a	SO	W (m)	D (m^3s^{-1})	T (d)	σ_{stat} (m)	σ_{mob} (m)	p	Study type	Source
Perca fluviatilis	Kleine Nete (BE)	139	1.4	3	7	6.74^s	545	60.41	864.06	0.48	M	Bruylants et al. (1986)
Percina nigrofasciata	Ichawaynochaway Creek (US)	60	1.3	5	34	26.23^q	487	3.06	136.56	0.85	Tr	Freeman (1995)
Percina roanoka	Roanoke River (US)	55		5^e	11.5	4.98^e	120	3.88	188.81	0.94	M	Roberts and Angermeier (2007)
Percina roanoka	Roanoke River (US)	43^a		6	23	9.97^e	1807	15.05	2706.34	0.87	M	Roberts et al. (2008)
Sander lucioperca	Middle Level (GB)	500^a	1.39	6^g	35^o	1.36^g	365	66.02	7737.58	0.69	M	Fickling and Lee (1985)
Sander lucioperca	Relief Channel (GB)	500^a	1.39	6^g	72^o	13.50^g	365	60.1	4736.72	0.44	M	Fickling and Lee (1985)
Sander lucioperca	River Gudenå (DK)	584	1.39	5^k	34	40	3	152.63	774.29	0.5	T	Koed et al. (2000)
Rivulidae												
Rivulus hartii	Guanapo River (TT)	47		4	10^e	0.06^e	60	1.48	9.16	0.44	M	Gilliam and Fraser (2001)
Salmonidae												
Oncorhynchus clarkii clarkii	Middle Fork of Salmon River (US)	343^a	2.14	6^c	20^o	42	1309	1602.91	38422.11	0.33	M	Bjornn and Mallet (1964)
Oncorhynchus clarkii clarkii	Hobo Creek (US)	75	2.14	2	1.5	0.1	183	34.18	227.32	0.67	Tr	Bryant et al. (2009)
Oncorhynchus clarkii clarkii	Beaver Creek (US)	244	2.14	1	3^o	0.47^q	365	205.56	2445.06	0.68	M	Hilderbrand and Kershner (2000)
Oncorhynchus clarkii clarkii	Chamberlain Creek (US)	107	2.14	2^e	1.75	0.1	24	69.89	258.25	0.73	Tr	Schmetterling (2004)
Oncorhynchus clarkii pleuriticus	North Fork Little Snake River (US)	214					92	146.51	1127.69	0.59	T	Young (1996)
Oncorhynchus clarkii utah	Thomas fork (US)	313					48	11.84	161.99	0.37	T	Schrank and Rahel (2006)
Oncorhynchus gilae	Main Diamond (US)	209	1.65	1^e	2.5^e	0.04	244	14.37	97.83	0.89	M	Rinne (1982)
Oncorhynchus gilae	McKnight (US)	134	1.65	2^e	2.5^e	0.04	244	14.87	203.16	0.41	M	Rinne (1982)
Oncorhynchus gilae	McKnight (US)	173	1.65	2^e	2.5^e	0.04	92	29.26	97.11	0.7	M	Rinne (1982)
Oncorhynchus gilae	South Diamond (US)	156	1.65	1^e	2.5^e	0.04	244	17.36	414.1	0.6	M	Rinne (1982)

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		Fish		Stream size				Movement parameters				
Scientific name	Waterbody	L (mm)	AR^a	SO	W (m)	D (m^3s^{-1})	T (d)	σ_{stat} (m)	σ_{mob} (m)	p	Study type	Source
Oncorhynchus mykiss	Middle fork of Salmon River (US)	600^a	1.67	6^c	20^o	42	1309	1415.56	37018.14	0.66	M	Bjornn and Mallet (1964)
Oncorhynchus rhodurus	Higashimata Stream (JP)	159		2	3		365	14.89	72.37	0.87	M	Nakano et al. (1990)
Oncorhynchus rhodurus	Higashimata Stream (JP)	159		2	3		365	15.53	179.89	0.63	M	Nakano et al. (1990)
Salmo salar	Tverrelva River (NO)	60	2.05	2^e	3.5	0.63^m	33	9.16	80.38	0.91	M	Hesthagen (1988)
Salmo salar	Tverrelva River (NO)	60	2.05	2^e	3.5	0.63^m	57	9.34	69.45	0.96	M	Hesthagen (1988)
Salmo salar	Tverrelva River (NO)	60	2.05	2^e	3.5	0.63^m	82	10.6	110.59	0.73	M	Hesthagen (1988)
Salmo salar	Tverrelva River (NO)	60	2.05	2^e	3.5	0.63^m	77	0.82	25.86	0.48	M	Hesthagen (1990)
Salmo trutta	Grand River (CA)	455	1.25	6^b	45^o	46.6	7	18.73	133.65	0.52	T	Brown et al. (2001)
Salmo trutta	Doyleston Drain (NZ)	270	1.25	1^e	2.7^e		365	71.86	457.45	0.78	M	Burnet (1969)
Salmo trutta	South Branch (NZ)	270	1.25	3^l	18.3^l	4^l	2190	39.1	362.47	0.74	M	Burnet (1969)
Salmo trutta	Au Sable River South Branch (US)	522	1.25	3^c	20	6.5	2	32.65	457.89	0.85	T	Clapp et al. (1990)
Salmo trutta	Au Sable River South Branch (US)	522	1.25	3^c	20	6.5	14	36.35	4230.72	0.33	T	Clapp et al. (1990)
Salmo trutta	River Gwyddon (GB)	200^a	1.25	3^g	3.6	0.2	14	4.02	34.66	0.58	M	Harcup et al. (1984)
Salmo trutta	River Gwyddon (GB)	200^a	1.25	3^g	3.6	0.2	21	4.78	28.39	0.47	M	Harcup et al. (1984)
Salmo trutta	River Gwyddon (GB)	80^a	1.25	3^g	3.6	0.2	14	6.5	34.04	0.74	M	Harcup et al. (1984)
Salmo trutta	River Måna (NO)	213	1.25	4^m	15^o	12.7	0.25	9.23	72.05	0.88	T	Heggenes et al. (2007)
Salmo trutta	Tverrelva River (NO)	130	1.25	2^e	3.5	0.63^m	33	2.76	116.63	0.86	M	Hesthagen (1988)
Salmo trutta	Tverrelva River (NO)	130	1.25	2^e	3.5	0.63^m	57	10.6	135.04	0.86	M	Hesthagen (1988)
Salmo trutta	Tverrelva River (NO)	130	1.25	2^e	3.5	0.63^m	82	2.01	114.82	0.81	M	Hesthagen (1988)
Salmo trutta	Tverrelva River (NO)	125	1.25	2^e	3.5	0.63^m	77	0.11	32.54	0.57	M	Hesthagen (1990)
Salmo trutta	Au Sable River North Branch (US)	277	1.25	3^c	17^o	4.05	1825	992.83	12108.63	0.76	M	Shetter (1968)
Salmo trutta	Au Sable River South Branch (US)	290	1.25	3^c	20^o	3.8	1825	1327.31	12914.37	0.5	M	Shetter (1968)
Salmo trutta	Main Au Sable River (US)	256	1.25	3^c	27^o	3.85	1825	213.52	10345.78	0.84	M	Shetter (1968)

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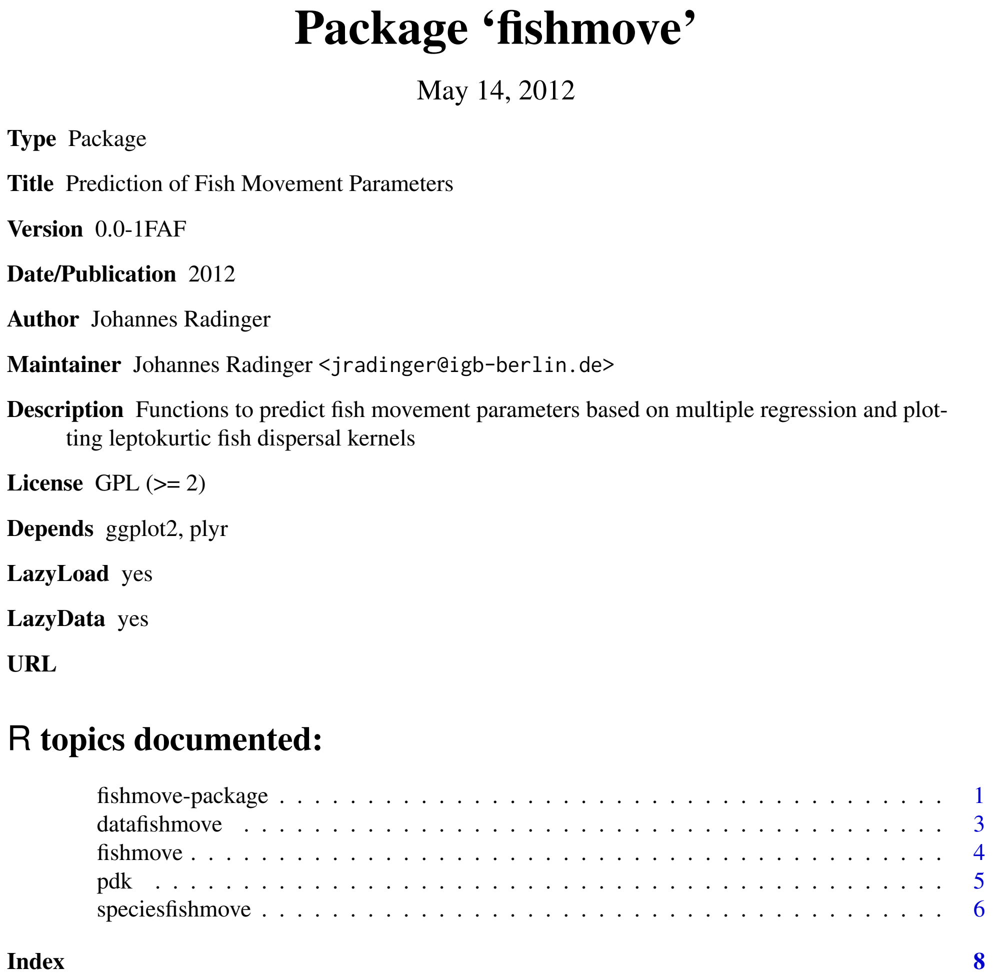
		Fish		Stream size				Movement parameters				
Scientific name	Waterbody	L (mm)	AR^a	SO	W (m)	D (m^3s^{-1})	T (d)	σ_{stat} (m)	σ_{mob} (m)	p	Study type	Source
Salmo trutta	Candover Brook (GB)	200^a	1.25	2^g	5	0.561^g	92	40.85	296.94	0.77	M	Solomon and Templeton (1976)
Salmo trutta	Candover Brook (GB)	200^a	1.25	2^g	5	0.561^g	458	39.89	552.45	0.71	M	Solomon and Templeton (1976)
Salmo trutta	Motupiko River (NZ)	547	1.25	5^e	12	5.2	336	266.2	11005.79	0.61	T	Young et al. (2010)
Salmo trutta	Credit River (CA)	416	1.25	5^e	19.5	3.4^e	439	163.75	17651.07	0.54	T	Zimmer et al. (2010)
Salvelinus fontinalis	Jack Creek (US)	150	1.54	1^e	4.65	0.1	85	33.84	389.85	0.5	Tr,M	Gowan and Fausch (1996)
Salvelinus fontinalis	North Fork Cache la Poudre River (US)	150	1.54	2^e	4.65	0.1	104	6.29	216.81	0.23	Tr,M	Gowan and Fausch (1996)
Salvelinus fontinalis	Jack Creek (US)	150	1.54	1^e	4.05	0.1	85	22.32	299.46	0.61	Tr,M	Riley et al. (1992)
Salvelinus fontinalis	North Fork Cache la Poudre River (US)	150	1.54	2^e	3.7	0.1	104	7.54	220.83	0.13	Tr,M	Riley et al. (1992)
Salvelinus fontinalis	Au Sable Rivers and Hunt Creek (US)	217	1.54				1825	975.9	7468.79	0.98	M	Shetter (1968)
Salvelinus leucomaenis leucomaenis	Jadani Stream (JP)	199	1.99	2^e	9.5^e		64	36.27	325.48	0.78	M	Nakamura et al. (2002)
Salvelinus leucomaenis leucomaenis	Jadani Stream (JP)	199	1.99	2^e	7^e		64	36.66	381.73	0.54	M	Nakamura et al. (2002)
Salvelinus leucomaenis leucomaenis	Jadani Stream (JP)	199	1.99	2^e	9.5^e		108	25.42	228.61	0.78	M	Nakamura et al. (2002)
Salvelinus leucomaenis leucomaenis	Jadani Stream (JP)	199	1.99	2^e	7^e		108	37.39	297.37	0.48	M	Nakamura et al. (2002)
Salvelinus leucomaenis leucomaenis	Jadani Stream (JP)	199	1.99	2^e	9.5^e		220	33.36	1014.92	0.77	M	Nakamura et al. (2002)
Salvelinus leucomaenis leucomaenis	Jadani Stream (JP)	199	1.99	2^e	7^e		220	36.43	333.98	0.62	M	Nakamura et al. (2002)
Salvelinus malma malma	Middle fork of Salmon River (US)	375^a	1.87	6^c	20^o	42	1309	1473.65	37807.62	0.36	M	Bjornn and Mallet (1964)

Continued on next page

		Fish		Stream size				Movement parameters				
Scientific name	Waterbody	L (mm)	AR[a]	SO	W (m)	D (m^3s^{-1})	T (d)	σ_{stat} (m)	σ_{mob} (m)	p	Study type	Source
Salvelinus malma malma	Hobo Creek (US)	78	1.87	2	1.5	0.1	183	34.46	231.03	0.54	Tr	Bryant et al. (2009)
Thymallus thymallus	Glomma G2 (NO)	320	1.96	8[m]	85[o]	250	3285	463.31	35334.28	0.5	M	Heggenes et al. (2006)
Thymallus thymallus	Glomma G3 (NO)	320	1.96	8[m]	150[o]	250	3285	70.95	22276.38	0.5	M	Heggenes et al. (2006)
Thymallus thymallus	Trysilelva River lower part (NO)	320	1.96	6[m]	75[o]	77	1825	421.53	20779.46	0.58	M	Heggenes et al. (2006)
Thymallus thymallus	Trysilelva River upper part (NO)	320	1.96	6[m]	60[o]	77	1825	294.95	5589.49	0.66	M	Heggenes et al. (2006)
Thymallus thymallus	Kemijoki River (FI)	325	1.96	4[n]	200[o]	338[t]	1	21.85	230.72	0.84	T	Nykänen et al. (2001)
Thymallus thymallus	Kemijoki River (FI)	324	1.96	4[n]	200[o]	338[t]	1	13.52	317.2	0.61	T	Nykänen et al. (2001)
Sciaenidae												
Aplodinotus grunniens	Missouri rivers (US)	450[a]	1.03				351	1213.51	118618.15	0.44	M	Funk (1957)

a	Fishbase.org (Froese & Pauly, 2011)
b	Grand River Information Network (Grand River Conservation Authority, 2011)
c	NHDPlus, National Hydrography Dataset (http://www.horizon-systems.com/nhdplus)
d	A. Kobler, personal communication
e	Additional Information from the original author
f	M. Ovidio, personal communication
g	National River Flow Archive (Centre for Ecology and Hydrology, 2011)
h	Hydroecological Information System VUV (T. G. Masaryk Water Research Institute, 2011)
i	B. Makaske, personal communication
j	A. Demoulin, personal communication
k	N. Friberg, personal communication
l	S. McMurtrie and J. Walter, personal communication
m	National River Network Database ELVIS (Norges vassdrags- og energidirektorat NVE, 2011)
n	J. Huhtala, personal communcation
o	Google Earth, version 6.0.1.2032 (beta)
p	(Taylor et al., 2006)
q	USGS StreamStats (U.S. Geological Survey, 2011)
r	T. Miller, personal communication
s	C. Geerearts, personal communication
t	Hydrological Information Finland (Finnish Environment Insitute (SYKE), 2011)
M	Mark-Recapture
T	Telemetry
Tr	Traps



Package ‘fishmove’

May 14, 2012

Type Package

Title Prediction of Fish Movement Parameters

Version 0.0-1FAF

Date/Publication 2012

Author Johannes Radinger

Maintainer Johannes Radinger `<jradinger@igb-berlin.de>`

Description Functions to predict fish movement parameters based on multiple regression and plotting leptokurtic fish dispersal kernels

License GPL (>= 2)

Depends ggplot2, plyr

LazyLoad yes

LazyData yes

URL

R topics documented:

Figure A.2: R Package ‘FISHMOVE’ reference manual. Version 0.0-1FAF. The most recent and up-to-date version of ‘FISHMOVE’ can be downloaded from: `http://cran.r-project.org/web/packages/fishmove/fishmove.pdf`

Table A.3: Range of environmental variables (based on Ahrens 2007) used in the analysis.

Code	Variable	mean (min, max)
DisM	Distance from mouth (m)	51181.13 (5100, 87700)
SOSh	Stream order Shreve	2.55 (1, 19)
SOSt	Stream order Strahler	1.38 (1, 3)
ChDe	Channel depth (m)	0.45 (0.01, 1.8)
ChWi	Channel width (m)	3.98 (0.2, 100)
ChWV	Channel width variability categories of 1: no, 2: low, 3: medium, 4: high, 5: very high	1.73 (1, 4)
CSFo	Cross-section form categories of 1: natural, 2: near natural, 3: erosive cross-section - varying, 4: failed embankment, 5: erosive cross-section - deep, 6: trapezoid, 7: V-shaped, 8: rectangular	5.12 (1, 8)
FlVe	Flow velocity categories of 1: no ($< 5\,cms^{-2}$), 2: low ($5 - 20\,cms^{-2}$), 3: medium ($20 - 40\,cms^{-2}$), 4: high ($40 - 80\,cms^{-2}$), 5: very high ($> 80\,cms^{-2}$)	2.81 (1, 5)
BAEr	Bed alteration - erosion (n/100 m)	0.11 (0, 7.72)
BAOt	Bed alteration - others (n/100 m)	0.09 (0, 11.17)
BAWa	Bed alteration - waste deposition (n/100 m)	0.12 (0, 18.42)
CBFO	Channel bed features - others (n/100 m)	0.06 (0, 17.4)
CBFR	Channel bed features - riffle pool (n/100 m)	0.06 (0, 8.41)
InVe	Instream vegetation categories of 1: nFo, 2: submerged, 3: floating leaved, 4: emerged macrophytes	1.82 (1, 4)
SMaS	Submerged macrophyte species (n)	0.74 (0, 4)
SuDi	Substrate diversity categories of 1: no, 2: low, 3: medium, 4: high, 5: very high	0.85 (0, 1.84)
SuHa	Substrate - hard gravel stones (%)	14.68 (0, 100)
SuMa	Substrate - macrophytes (%)	4.17 (0, 100)
SuSa	Substrate - sand (%)	57.74 (0, 100)
SuSo	Substrate - soft mud clay silt (%)	21.29 (0, 100)
SuWo	Substrate - wood (%)	2.12 (0, 80)
BFLW	Bank features - large wood (n/100 m)	0.06 (0, 5.49)
BFOt	Bank features - others (n/100 m)	0.04 (0, 4.4)
BPGr	Bank protection - green categories of 0: no, 1: one bank, 2: both banks	0.02 (0, 2)
BPWa	Bank protection - walls categories of 0: no, 1: one bank, 2: both banks	0.01 (0, 2)
BPno	no Bank protection categories of 0: no, 1: one bank, 2: both banks	1.45 (0, 2)
BPRi	Bank protection - riprap categories of 0: no, 1: one bank, 2: both banks	0.03 (0, 2)

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Code	Variable	mean (min, max)
BPWo	Bank protection - wood categories of 0: no, 1: one bank, 2: both banks	0.44 (0, 2)
RVRe	Riparian vegetation - reeds categories of 0: no, 1: one bank, 2: both banks	0.03 (0, 2)
RVSp	Riparian vegetation - sparse categories of 0: no, 1: one bank, 2: both banks	1.73 (0, 2)
RVTF	Riparian vegetation - trees, forest categories of 0: no, 1: one bank, 2: both banks	0.24 (0, 2)
CFIB	Channel features - islands braiding (n/100 m)	0.02 (0, 4.38)
CFLW	Channel features - large wood (n/100 m)	0.02 (0, 12.27)
CFNa	Channel features - narrowing (n/100 m)	0.09 (0, 12.27)
CFWi	Channel features - widening (n/100 m)	0.09 (0, 18.42)
ChDV	Channel depth variability categories of 1: no, 2: low, 3: medium, 4: high, 5: very high	1.61 (1, 5)
FlDi	Flow diversity categories of 1: no, 2: low, 3: medium, 4: high, 5: very high	1.77 (1, 4)
Plan	Planform categories of 1: meandering, 2: wormed, 3: strongly sinuous, 4: sinuous, 5: slightly sinuous, 6: straight, 7: channelized	5.65 (1, 7)

Ahrens, U. 2007. Gewässerstruktur: Kartierung und Bewertung der Fließgewässer in Schleswig-Holstein. Jahresbericht Landesamt für Natur und Umwelt des Landes Schleswig-Holstein 2006/07. 115–126. Landesamt für Natur und Umwelt des Landes Schleswig-Holstein, Flintbek.