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Biological processes of connectivity and metapopulation dynamics in aquatic ecosystem restoration

Biological processes of connectivity and metapopulation dynamics in aquatic ecosystem restoration

Didderen K.
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Alterra-report

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ABSTRACT

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In this review a literature study and results from EURO-LIMPACS are used to define relevant biological processes of connectivity and metapopulation dynamics as parts of the development of cause-effect and recovery chains. The review focuses on the over-arching biological processes of connectivity and metapopulation dynamics for freshwaters (lakes, rivers and marine ecosystems).
The report starts with general definitions, concepts and ecological theory behind connectivity and metapopulation dynamics in relation to restoration. Some of the methods to describe and quantify dispersal behaviour, metapopulation dynamics, connectivity and colonization events are reviewed. Specific case studies are described that show the role of connectivity and metapopulation dynamics in restoration success.
Restoration success is dependent on the possibility of populations to colonize the new and restored habitat. Due to knowledge gaps and scale discrepancies, both habitat and dispersal constraints still restrict restoration outcome in many programmes. Determining the right scale for species, the extent of the required (different) habitats, the scale a which processes like dispersal and connectivity occur in the context of restoration and even the scale at which large-scale processes that eventually influence habitat quality is an important aspect of successful restoration. However the spatial scales that are most important often remain poorly understood. Finally, our main aim was to construct a driver – pressure – state – impact – recovery chain for the biological processes of metacommunity dynamics and connectivity:

Keywords: freshwater, river, lake, wetland, metapopulation, connectivity, macroinvertebrate, macrophyte, fish, restoration, colonization, dispersal

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Preface

The WFD explicitly recognises that a catchment perspective is a requisite for sustainable land use management and mitigation measures. Incorporating knowledge from WPs 6.1-3 and from Module 5 on future scenarios of how climate change will affect future land use, WP6.4 will focus on comparing the cause-effect-recovery chains for lakes, rivers and marine ecosystems, taking into account processes and functional features in different ecosystems and over-arching biological processes of connectivity and metapopulation dynamics. Special focus will be placed on the use of species traits and functional information in cross-water category comparisons.

In Task 6.4.3 'Linking catchment scale processes and global change to cause-effect and recovery-chains' a literature study was done to define relevant biological processes of connectivity and metapopulation dynamics to be used to construct the cause-effect and recovery chains

Summary

In this review a literature study and results from EURO-LIMPACS are used to define relevant biological processes of connectivity and metapopulation dynamics as parts of the development of cause-effect and recovery chains. The review focuses on the over-arching biological processes of connectivity and metapopulation dynamics for freshwaters (lakes, rivers and marine ecosystems).

The report starts with general definitions, concepts and ecological theory behind connectivity and metapopulation dynamics in relation to restoration. Metapopulation theory is important to restoration ecology since it deals with the factors that determine the likelihood of local extinctions and subsequent recolonisation. Metapopulations rely upon dispersal in order to exist. Without dispersal local populations are not part of a metapopulation. Dispersal constraints limit the capacity to colonise new suitable habitats or former habitats where extinction has occurred. Colonisation success depends on habitat suitability and connectivity. Connectivity in freshwater ecosystems is scale dependent. So, after restoration the re-occuring species should overcome both dispersal and environmental constraints; the latter both of the habitat to be colonised as well as the environment in between source and destination.

Some of the methods to describe and quantify dispersal behaviour, metapopulation dynamics, connectivity and colonization events are reviewed. As with all research the quantitative outcome largely depends on the selected methods, the underlying assumptions and the scale used and therefore different research questions are in need of different research methods. Empirical estimates of dispersal are either direct or indirect. Direct methods involve trapping and mark-release-recapture techniques. Indirect methods involve genetic markers and spatial techniques, like spatial mapping.

The aspects of patch suitability, connectivity and dispersal, are dealt with in more detail. One of the key factors in restoration is the restoration of the physical habitat. This restoration will result in a restoration of ecosystem functioning and increase of the availability of empty habitat patches suitable for recolonisation. The habitat suitability is amongst others dependent on the refugia present during environmental extremes. Refugia to overcome extremes of droughts, spates and temperature decide on the resilience of ecoystems. In order to create suitable habitat for some species other species, that affect the focal species' habitat, need to be involved in restoration efforts and planning. In this way metapopulation dynamics and connectivity for non-focal species can become important in the restoration process. Apart from the biological interactions, temporal aspects of connectivity and dispersal between essential habitats is another important aspect to take care of in restoration. Connectivity at the longitudinal, lateral, vertical and temporal axis is important for the recovery of both ecosystem structure and function. In restoration all four pathways should be considered. Along each path distance and the presence of barriers, like dams and weirs, between the source population and the restored habitat are crucial. Finally, each organism groups has its own dispersal behaviour. In many

lentic ecosystems, restoration efforts are focussed on restoring macrophyte communities, assuming they have a central role as moderators of the (a)biotic habitat of many other species. In invertebrates it is shown that the role of dispersal and recruitment limitation may be critical in shaping community structure of newly created habitat. On the other hand, for fish even where local populations remain during restoration, dispersal can still be important to sustain or increase the current population size.

Specific case studies are described that show the role of connectivity and metapopulation dynamics in restoration success.

Restoration success is dependent on the possibility of populations to colonize the new and restored habitat. Due to knowledge gaps and scale discrepancies, both habitat and dispersal constraints still restrict restoration outcome in many programmes. Apart from hard barriers also unrecognised physical barriers can be of importance. Re-colonisation can also be disturbed by the arrival of non-native species outcompeting the targeted newcomers.

Determining the right scale for species, the extent of the required (different) habitats, the scale a which processes like dispersal and connectivity occur in the context of restoration and even the scale at which large-scale processes that eventually influence habitat quality is an important aspect of successful restoration. However the spatial scales that are most important often remain poorly understood.

Finally, our main aim was to construct a driver – pressure – state – impact – recovery chain for the biological processes of metacommunity dynamics and connectivity:

1 Introduction

1.1 Freshwater ecosystem restoration

Freshwater ecosystems provide important services, like clean drinking water, fisheries, hydropower, recreation and agriculture production (Palmer 2009). Consciousness that these services are threatened and might not be sustained in the future has led to major restoration efforts in streams and rivers (Bernhardt et al., 2005, Roni et al 2008, Miller et al. 2010) wetlands (Mitsch, 1998, Zedler 2000), fens (Lamers et al. 2002) and lakes (Jeppesen et al. 2007). As a consequence, freshwater ecosystem restoration is still rapidly growing in terms of numbers of projects and amount of money spent (Jansson et al 2007) and restoration ecology is an increasingly important field (Omerod 2003). However, restoration effort does not always provide restoration success (Bond & Lake 2003).

According to the WFD, all European countries should implement management measures by 2012 to restore degraded water bodies back to good ecological status by 2015 or to prevent deterioration of water bodies in high and good status. Central to many restoration efforts is the assumption that rehabilitation of physical habitat structure and diversity (Palmer, 1997) and reduction of pressures to reference levels will lead to the restoration of biological communities. For long freshwater restoration efforts have been targeted at the reestablishment of physical structure (Bond & Lake 2003, Halle & Fattorini 2004, Miller et al. 2010). This type of restoration relies on the often mentioned 'Field of Dreams Hypothesis', i.e. 'if we build it, they will come', referring to the assumption that if physical habitats are restored, species will recolonise them (Palmer et al. 1997). However, evidence is accumulating, that physical structure enhancement and pressure reduction are not sufficient to restore ecosystem processes and no guarantee for the recovery of good ecological status (Smokorowski et al. 1998, Larson et al. 2001, Beschta 1994), and biological factors need to be included (e.g. Mackay 1992, Hughes, 2007 , Wim, 2009 , Roni et al. 2008, Bond & Lake 2003)

For example, ecological processes such as dispersal and recruitment might limit biotic responses to physically restored ecosystems (Bond & Lake, 2003). Re-colonisation potential further affects the extent and trajectory of recovery: depending on the presence or absence and depletion of source populations, recovery time may vary from a few years to several decades. Accordingly, the ability of a species to recolonise a restored site will depend not only on the appropriate habitat being present, but among other things on the ability to get there (Hughes 2007) or the propagule bank available as a source population.
An increasing number of studies approve of the importance of biological processes, like dispersal, connectivity and metapopulation dynamics, in influencing restoration success and predicting restoration outcome (Fig. 1).

Knowledge of these factors, likely to explain or improve results of restoration measures in freshwater habitats is scarce and existing knowledge is hardly ever incorporated in restoration planning (Bond & Lake 2003, Palmer 2009).

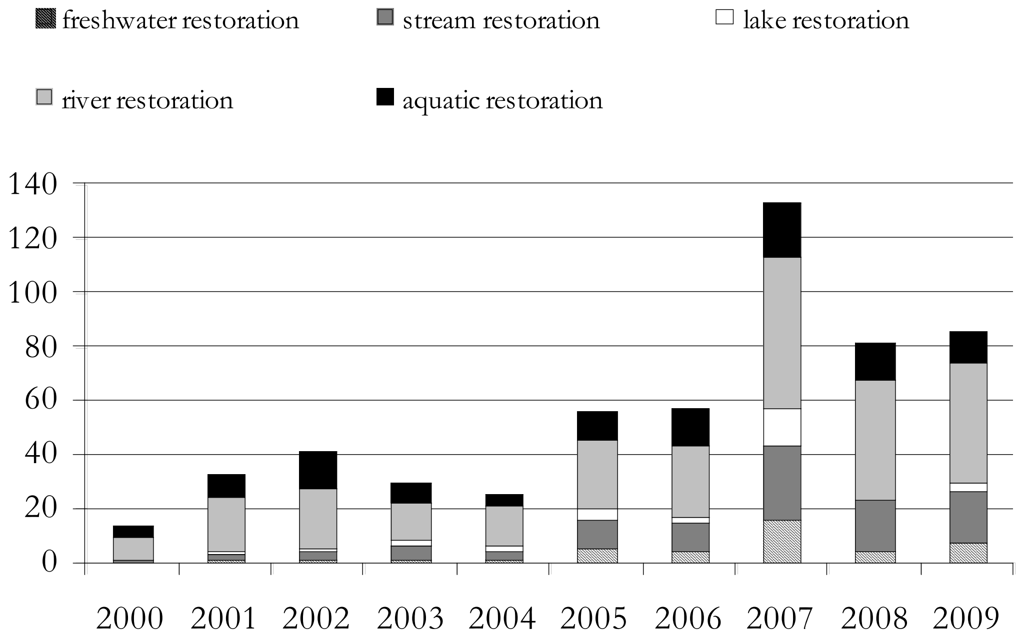


Figure 1. Number of papers resulting from a literature search (ISI Web of Schience) over 2000-2009, specifying 'dispersal' or 'connectivity' or 'metapopulation dynamics' in combination with the terms specified in the legend.

In this review a literature study and results from EURO-LIMPACS are used to define relevant biological processes of connectivity and metapopulation dynamics as parts of the development of cause-effect and recovery chains. The review focuses on the over-arching biological processes of connectivity and metapopulation dynamics for freshwaters (lakes, rivers and marine ecosystems).

The overview starts with general definitions, concepts and ecological theory behind connectivity and metapopulation dynamics. The third chapter will give an outline on methods used to study and quantify connectivity and metapopulation dynamics. Chapter 4, 5 and 6 will concentrate on subsequently on patch suitability, connectivity and dispersal. In chapter 7 specific case studies will outline the role of connectivity and metapopulation dynamics for restoration success.

2 Ecological theory

Ecological restoration of freshwater ecosystems includes altering a degraded ecosystem in a way as to re-establish the system's structure and function, usually aiming to bring it back to its original (pre-disturbance) state or to a less degraded, more desirable state (Palmer 2009).
The field of restoration ecology is relatively young, therefore many general ecological theories are applied in this field. When ecological theory is not sufficient, or when scientists are not involved in the process, adaptive ecology is applied.

In this chapter a short outline of some theoretical frameworks with regard to ecosystem processes that are important for freshwater restoration are given. For general information see reviews on metapopulation ecology (Hanski 1999, Hanski & Gaggiotti, 2004), metacommunities (Holyoak et al., 2005), dispersal (Woiwod et al. 2001), genetics and evolution of dispersal (Clobert et al. 2001), dispersal ecology (Bullock et al. 2001), seed dispersal (Levin et al. 2003), dispersal in freshwater invertebrates (Bilton et al. 2001), and connectivity (Bennett 1998, Crooks & Sanjayan 2006).

2.1 Metapopulation dynamics

2.1.1 The metapopulation perspective

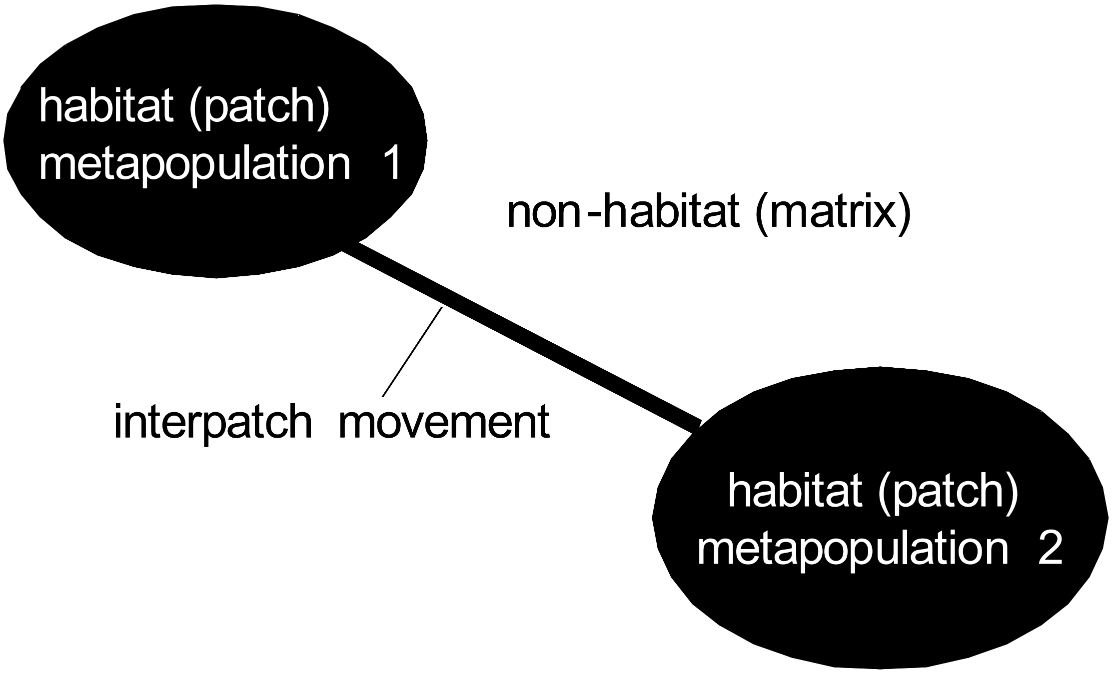


Figure 2. Simple patch-corridor-matrix model (Rorman 1995).

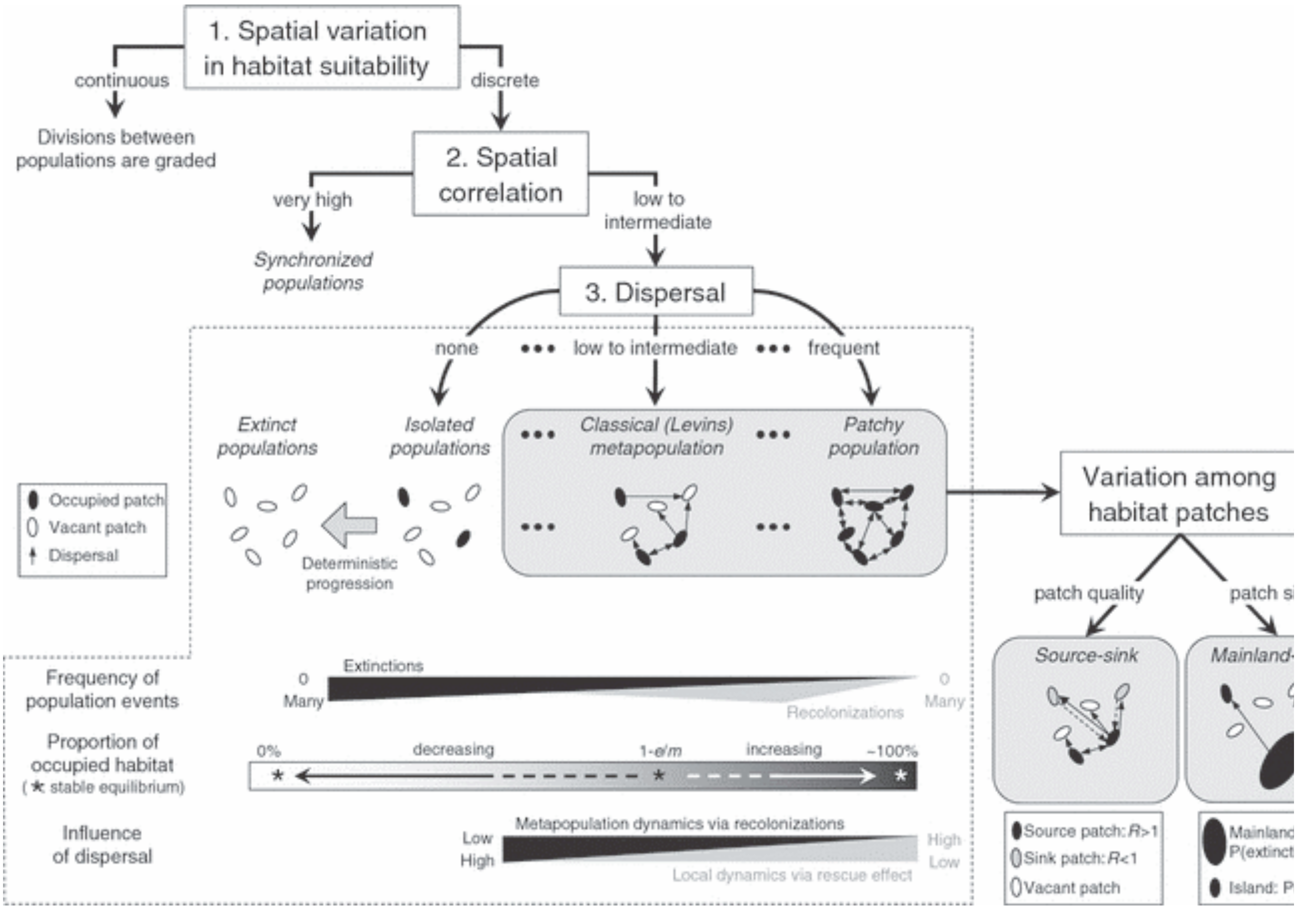
Metapopulation theory is important to restoration ecology since it deals with the factors that determine the likelihood of local extinctions and subsequent recolonisation (Bennet 2001). Metapopulations are defined as a group of spatially delimited conspecific populations existing in a balance between extinction and recolonisaton (Levin 1970), and spatially linked by dispersal (Hastings and Harrison 1994). To distinguish metapopulations from local population, three basic conditions must be met: 1 the local populations inhabit discrete habitat patches, separated from other suitable habitat by non-habitat (matrix); 2. the dynamics of different local populations are asynchronous, making simultaneous stochastic extinction very unlikely; 3. at least some of the habitat patches are interconnected by dispersal.

The traditional approach to population ecology assumes that habitats are available as homogeneous continuous patches. However, due to habitat loss and fragmentation increasing numbers of species have a spatial population structure that resembles a metapopulation structure, with environments consisting of discrete patches of suitable habitat surrounded by uniformly unsuitable habitat (matrix, Fig. 2) (Hanski 1999) with corridors linking (some) habitat patches (Forman 1995) .

Within metapopulation theory landscapes are viewed as networks of suitable habitat patches inhabited by local populations that are relatively discrete entities in space together making op assemblages of metapopulations (Hanski 1999) that interact via migration and gene flow. Both heterogeneity of habitat suitability and dispersal rates vary across temporal and spatial scales, species and landscapes (Rieman & Dunham 2000), making up different types of metapopulation models (Harrison & Taylor (1996), Schlosser & Angermeier 1995, Schtickzelle & Quinn 2007). At one extreme, frequent dispersal leads to high levels of recolonisation and patch occupancy, yielding a “patchy” population structure, that in fact act as a single population, rather then a metapopulation. In contrast if rates of dispersal and/or recolonisation are very low, a ‘non-equilibrium metapopulation’ structure, referring to a progressive pattern of local extinctions without sufficient recolonisation, such that patch occupancy ultimately declines to zero. At intermediate levels of dispersal a classic (Levin’s) metapopulation with similar sized populations, existing in a balance between extinction and recolonisation occurs.

The mainland-island and source-sink metapopulation models differ from the classic model in that some populations have a greater potential for providing emigrants. In mainland-island this difference is due to larger patch size of the mainland, whilst in source sink a higher habitat quality in sources, make them more suitable for reproduction and survival, making them primary origins of colonisers for adjacent island/sink populations.

Applying these models to populations of lotic fishes showed that their population structure supports a hybrid model. At small spatial scales the populations resembles a patchy population, whilst at a larger scale mainland-island and source-sink interactions become apparent (Schlosser & Angermeier 1995). However a study on 5 salmonid species, where patterns potentially reflect metapopulation structuring, indicated that given the present limited understanding of salmonid metapopulations (e.g. the understanding of processes that actually link local populations), application of and generalisations from unrealistic models is not favoured for salmonid conservation or restoration (Rieman & Dunham 2000).



Dispersal

Metapopulations rely upon dispersal in order to exist. Without dispersal local populations are not part of a metapopulation. Spatial isolation of species in fragmented landscapes are due to restrictions of dispersal. Dispersal constraints limit the capacity to colonise new suitable habitats, former habitats where extinction has occurred or to supplement declining populations (Macdonald et al. 2002).

Dispersal is affected by local scale and metapopulation-level factors. It is favoured by high population density (resource competition), low population density (risk of extinction) and used to avoid inbreeding, competition with sibs and extinction (Hanski 1999).

2.1.2 Patch quality

The suitability of habitat patch characteristics might vary in area, degree of isolation and quality (Hanski 1999). In general, populations inhabiting small isolated patches are considered more likely to go extinct, while populations that inhabit large, well connected patches are more likely to be recolonised.

Habitat or patch suitability, at the same time defining unsuitable habitat, is dependent on many (a)biotic factors and may vary as a continuous variable to distinguish between ‘rich’ (high quality) and ‘poor’ (low quality) habitats (Hanski 1999). However, the availability of so-called ‘key habitats’ is not scaled to this axis, since key habitats are important at a certain period (i.e. spawning grounds for fish), but not synonymous to high quality habitats.

Apart from spatial variation habitat suitability may also vary over time as different stadia of single species might require different resources, with corresponding biotic and abiotic conditions. Additional temporal variation of habitat suitability is dependent on resource patches being ephemeral, suitable for a limited period each year or temporally connected (Hanski 1999). Furthermore habitat patches, their suitability and their connection to other patches can be defined on multiple spatial scales (Schooley & Branch 199, Wiens 2002). For example, in riverine landscapes, habitats can be classified at different levels of a nested hierarchy, starting from the level of the microhabitat, through to pool/riffle, reach, segment and eventually the level of the stream and catchment (Frissell e tal. 1986).

Habitat patches of freshwater organisms are embedded in a medium, water, that exerts a determinative and variable physical force on the system, influencing hydrology and through that food-resource availability, flood pulses, or simply the physical force (Wiens 2002). Varying water flow makes the patch structure of riverine landscapes quite dynamic, when patches move and change shape and composition. Floodplain landscapes shift between terrestrial and aquatic phases. Lakes habitat patches may vary due to e.g. wave action or mixing.

Another special feature to aquatic metapopulations is the matrix, land, surrounding freshwater habitat patches and being uninhabitable (as opposed to less habitable) for most species.

In wetland restoration recently a new approach is used, combining patch suitability with the characteristics of connections. The so-called Operational Landscape Units (OLUs) consist of combinations landscape patches with their hydrogeological and biotic connections (Verhoeven et al., 2008).

2.1.3 Extinction and colonization

The response of population to habitat degradation includes reductions of population size, patch occupancy and eventually isolation and extinction. In early stages of habitat destruction, while the remaining habitat is still well connected, populations are primarily affected by habitat loss. The population size is reduced in proportion to the remaining total area of the habitat. With increasing habitat destruction the degree of connectivity between the remaining fragments is reduced and habitat fragmentation begins to amplify the impact of habitat loss, leading to a high non-linear response of species to diminishing amounts of habitat (Hanski 1999 and Bascompte & Sole 1996). This means that when reversing degradation, i.e. during restoration, restoring only a small portion of suitable habitat does not automatically result in a proportional occupancy of high quality habitat patches with the necessary connectivity. When this fragmented stage is reach only major efforts will lead to a structural improvement of metapopulation persistence.

The distinction between habitat loss and fragmentation is important to establish restoration goals. For some species restoration of individual habitat patch size or quality might be sufficient, while for others the spatial arrangement between the habitats is more limiting and a substantial effort to increase both percentage of suitable habitat and connectivity between patches is essential.

In fragmented landscapes species assemblage of metapopulations can occupy suitable habitat patches in varying proportions. The decline of a species, with consequent reduction in population size and range, can result in a decrease in the percentage of patch occupancy. In such conditions, the species can be absent even from habitat patches offering suitable environmental situations. On the other hand, recovery of a species, will lead to the colonization of new habitat patches and increased patch occupancy. Patch occupancy depends on patch area and isolation, with small and isolated patches being most likely to be empty (Hanski 1999).

Apart from a decrease in patch occupancy fragmentation can lead to isolation of sub-populations. Populations that may have originally been part of a metapopulation may become isolated.

Metapopulation viability largely depends on extinction and recolonisation potential, depending on patch size, patch quality and the degree of patch connectivity. If colonization is larger then extinction a population will persist.

Extinction-area relationships, based on the assumption that populations size increases with area (species-area relationship) assumes that the probability of extinction decreases with increasing area. Another prediction stats that the lifetime of a population increases with size, in other words time to extinction decreases with population size.

Recolonisation of patches that have suffered local extinction is a central issue in restoration ecology (Hobbs 2002). The probability of successful colonization of an empty habitat patch is predicted by the number of immigrants arriving, the propagule size, the mode of reproduction, the reproductive value of the colonizing individual and the niche width. Colonization of numerous and large propagules, with high reproductive value, niche width and asexual reproduction is predicted to be most successful (Hanski 1999). It is hypothesised that there is a negative correlation between dispersal ability and competitive ability. Species most prone to extinction and less prone to colonise new habitat may often be abundant, superior competitors, which may have traded greater competitive ability for lower recolonisation rates (Mc Donald et al 2002).

Different methods are used to asses minimum requirements of patch or populations sizes e.g. population viability analysis (PVA)

In order to predict the minimum number of individuals that has a good likelihood of long term survival the concept of 'minimum viable population' (MVP) in metacommunity theory is translated to an analogous concept of 'minimum viable metapopulation' (MVM) defined as the minimum number of interacting local populations needed to ensure long term persistence. This can then be used to estimate the 'minimum amount of suitable habitat' (MASH), defined as the minimum density (or number) of suitable habitat patches necessary for metapopulation persistence (Hanski et al. 1996), that is important for restoration planning. Minimum patch size for a viable local population can be estimated in several ways. One method is to use records of presence–absence in a suite of patches in conjunction with an estimation algorithm; for example, minimum patch size = habitat required for a 50% probability of presence. Another example is the density–area method, that estimates minimum patch size as the smallest area in which no new individuals are encountered.

Since metapopulation persistence depends on both extinction and colonization, conservation efforts could be aiming to reduce extinction risk (e.g. by improving habitat quality and enlarging habitat patches) and enhancing colonization rate (e.g. by translocation) and patch connectivity of metapopulations.

Connectivity in a landscape depends on the relative isolation of habitat patches from one another and the extent to which the unsuitable habitat (matrix) represents a barrier to movement of organisms. Recovery of local population that are expected to depend on metapopulation dynamics depend on regional rather then local efforts. Since local populations, especially if small, are susceptible to extinction, local restorations measures will at best lead to temporary success. Restoration should therefore be planned at the regional (metapopulation) scale (Hanski 1999). However empirical evidence metapopulation-level restoration success is anecdotal.

2.1.4 Metacommunities

Metapopulation theory was until recently focused on the dynamics of single species, but more and more multi-species approaches are known from literature. For example extensions are known to impede pairs of interacting species (Hanski, 1999), such as competitors or predator and prey.
With these extensions the colonization and extinction rates of the focal species become functions not only of habitat characteristics, but also of the presence of the other species (Leibold & Miller 2004) More recently even more complex systems are addressed, but work on these so-called ‘metacommunities’ (Leibold et al. 2004) with a much higher level of complexity is still sparse. As opposed to metapopulation research where the persistence of a metapopulations in a system of connected habitat patches is the central issue, at this more complex level (metacommunities) the central issue is what is regulating coexistence of multiple species in a system.
Metapopulation and metacommunity dynamics are theoretical frameworks that are used to describe key-factors in population and community ecology. However modelling habitat suitability and degrees of connectivity of metacommunities is a complicated task since multiple spatial and temporal levels should be incorporated depending on the species involved.

2.2 Dispersal

The term dispersal can refer to all movement of individuals (Watkinson & Gill 2002) (or other dispersing agents such as gametes or seeds) between discrete habitat patches (Bilton et al 2001, Wiens 2001). Other definitions often incorporate *effective* or generational dispersal (Bullock et al., 2002), ie. successful establishment of reproductive individuals, which indicates the movement will eventually lead to gene flow (Louette & de Meester 2005, Havel & Madley 2006), regardless of the dispersing agent considered. For propagules the dispersal parameter estimated may or may not refer to effective dispersal, depending on the study design. In mobile animal species, effective dispersal requires establishment of the species, i.e. dispersers have to reproduce in the population where they settle. Similarly, gamete dispersal is termed effective if it results in successful transmission of genes. Effective dispersal includes colonization of the new site, which implicates the new site must have all the necessary abiotic and biotic conditions needed for survival. Furthermore, the disperser must secure enough resources to support future growth and reproductive efforts. Eventually, some definitions of dispersal incorporate the ability of reaching a distant suitable habitat patch and establishing a new population (Ribero 2008). Differences in dispersal ability relate not only to species specific mobility but also to the ability to establish new populations.

Dispersal results in (re-)colonization of extinct or new sites or in gene flow, which reduces the probabilities of extinction inbreeding depression and loss of genetic material in local populations (Soons 2006). Studies of dispersal are fundamental to understand and predict processes in metapopulation dynamics, ecological genetics, landscape ecology, life-history and restoration ecology (Bullock et al. 2001). The implications of dispersal are numerous, influencing the spatial distribution of alleles, individuals, and species in populations and communities and it plays a central role in population genetics, population dynamics, and community ecology (Broquet & Petit 2009). Dispersal allows populations to cope with environmental changes (Kokko & L´opez-Sepulcre 2006), and suitable habitat to be colonized.
In restoration ecology a special interest in dispersal is related to its central role in affecting the number of individuals present in source and target populations and the dispersal limitation relating to the dispersal capacity of target organisms and their ability to colonize empty habitat patches. Animals with good potential for dispersal are more likely to be able to disperse to newly restored sites (Hughes, 2007 #5).

2.3 Community assembly

The concepts of community assembly arise from the observation that only certain species are able to establish and survive in any given area and that species tend to occur in recognizable and repeatable combinations or temporal sequences (Hobbs et al 2007). The set of rules that might be identified to describe the processes underlying predict the way communities assemble are termed assembly rules. Most concepts in assembly theory originate from community ecology, yet they are recently also mentioned a central theme in restoration ecology that needs attention (Lockwood 1997, Temperton et al 2004, Hobbs et al. 2007), since it helps to identify what factors explain community membership and at the same time what factors constrain community membership. Temperton et al. (2004) recently evaluated the broad field of community assembly in relation to restoration. Local community membership of species from a regional species pool includes overcoming dispersal and environmental constrains (Fig. 3). The regional species pool is ‘filtered’ for species with appropriate dispersal capabilities and abilities to establish, i.e. to deal with the environmental conditions (overcome habitat constraints) as well as the other (overcome biotic constrains) (Poff 1997, Lake et al. 2007, Belyea & Lancaster 1999, Hobbs et al 2004). Alteration of the filter mesh could help to allow for certain species to establish, in this way governing restoration efforts.

Due to dispersal and environmental constraints, this colonisation process from an intact regional pool, which involves dispersal and environmental filters (Fig. 3a) , may apply in many situations (Lake et al. 2007). However, in heavily impacted systems the regional species pool may be depleted, and only consist of resistant species (Fig. 3b). If regional species pools are depleted, e.g. in degraded landscapes, restoration to any target may be unpredictable without knowledge of the remaining species in the regional pool (Lake et al. 2007) and the way filters act upon these species.

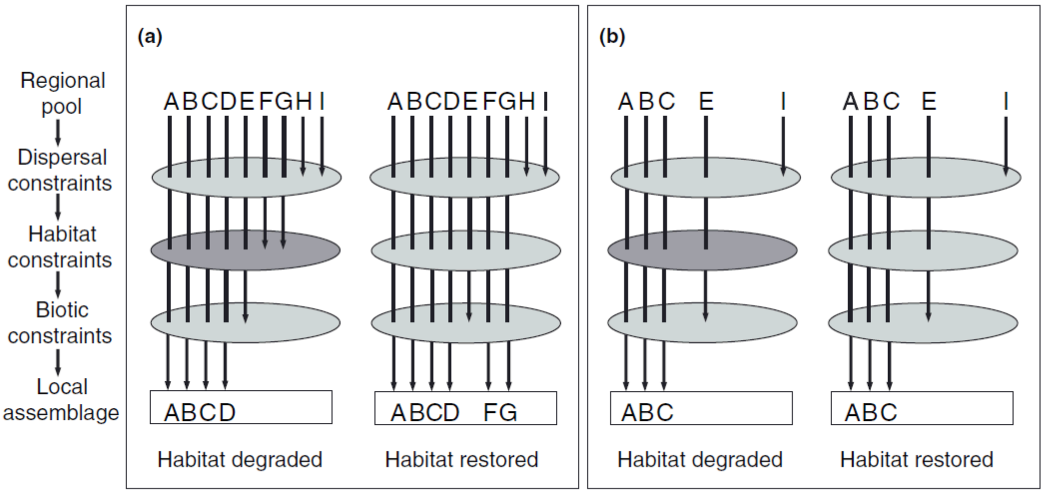


Figure 3. Colonisation process from an intact regional pool, where dispersal and environmental constraints act as filters (Lake et al. 2007).

2.4 Connectivity

Connectivity from a landscape perspective can be defined as the flow of energy, matter and organisms between landscape components (Ward et al., 2002) and depends on the relative isolation of habitat elements from one another and the extent to which the so called 'matrix' (Fig. 2) represents a barrier to movement of organisms (Hobbs, 2002). In a community or population perspective a more narrow definition of connectivity 'the degree of movement of organisms' (sensu Crooks 2006), where less movement is indicating a smaller degree of connectivity, is also used.

Connectivity is dependent on several factors which can be largely grouped in two main components 1): structural connectivity: the spatial arrangement of habitats, barriers, connections and other elements in the landscape, also referred to as patterns 2): functional connectivity: the connectivity of individual species or ecological processes depending on e.g. dispersal behaviour, recruitment, life history traits and availability of dispersal vectors, also referred to as processes (Wiens 2002)
As a structurally connected landscape may be functionally connected for some species and not for others (Crooks, 2006 #38) and functionally connected habitats are not necessarily structurally connected, it is important to differentiate between these two components when cause-effect-recovery chains of freshwater ecosystems are regarded. However cross-linkage of the two factors, is often observed since patterns and processes tend to influence each other.

1. Structural connectivity

The landscape physical structure that are most important to predict the degree of structural connectivity are distance, connection type suitability and presence of barriers. Shorter distances between suitable habitat patches relate to a more structurally connected landscape. Most features are often indirectly a measure of distance, for example elevation, elevation difference and current velocity, with higher current velocities decreasing downstream distances, but increasing upstream distances. Other factors may include suitability and quality of interpatch structures, for example the availability of dead water zones. The presence of barriers will lead to less connectivity.

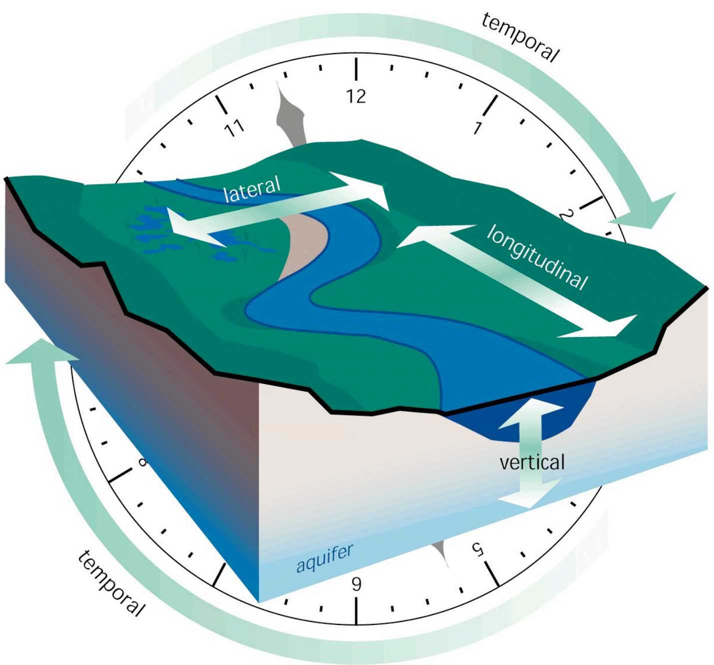
2. Functional connectivity.

Functional connectivity depends on the mobility and the habitat specificity of individuals species (Hobbs 2002).

A further division differentiates two types of information on functional connectivity that exist in scientific literature, 1) potential connectivity, usually based on indirect measurements (e.g. genetic markers), traits or theory and 2) actual connectivity, a direct estimate of the movement of individual organisms, i.e. direct estimate of the transfer of individual species.

2.4.1 Connectivity of aquatic ecosystem

For freshwater ecosystems connectivity at various hierarchical landscape levels is important: between subcatchments, between catchments and between regions (with several catchments), as well as between catchments and marine environments (Pringle, 2001). On a local scale (habitat) connectivity is multidirectional. For example in stream ecology streams are regarded to consist of groups of interacting habitat patches in four dimensions. Three spatial dimensions are distinguished: connections along the stream (longitudinal), between the stream and riparian and upland areas (lateral), and between the channel and the hyporheic zone (vertical), and temporal variation is the fourth dimension (Ward, 1989; Fig. 4).



Dimensions of the stream corridor. A four-dimensional framework serves as a good starting point for examining stream corridors..
In Stream Corridor Restoration: Principles, Processes, and Practices, 10/98.
Interagency Stream Restoration Working Group (FISRWG)(15 Federal agencies of the US).

Figure 4. Connectivity of stream ecosystems in four dimensions (Interagency Stream Restoration Working Group FISRWG) 1998).

Another aspect that is unique to aquatic ecosystems is the directional flow of water (Wiens 2002), enhancing unidirectional connectivity. Except for isolated standing waters and more recently human created or influenced lakes, water moves in a single direction. The unidirectional nature of the main dispersal agent, water, causes downstream dispersal to be more likely then upstream dispersal. The condition by which matter, energy and/or organisms are linked via water flow is termed hydrologic connectivity (Pringle 2001). In rivers and streams, but also many natural lakes wetlands and estuaries, connectivity is then provided by the medium of the landscape more than by the structural configuration of the mosaic itself. Well connected metapopulations in riverine ecosystems are characterized by the linear arrangement of the meta-populations along the river. On land, (multi)directional flow is only observed for aerial or wind-borne organisms or materials. In aquatic ecosystems hydrologic connectivity is one of the main factors explaining connectivity of freshwater organisms.

Hydrologic connectivity can be periodical, for example when flooding temporarily connects the fragmented floodplains with the main stream channel. In this way habitats are expanded and nutrients, sediment, organic matter and organisms are transported. The temporal dimension of connectivity is crucial. Apart from the connections being temporal, the spatial specifity and timing of the connections and subsequent ecological processes have to be considered. If a target species is dependent on the accessibility of e.g. spawning grounds at a specific period each year, restoration efforts should be aiming to restore connectivity at this specific period as the restoration of water flow alone is not sufficient to restore the ecosystem.

Lost linkages or disconnections of stream-side channels are intended to occur over time. Therefore, the target endpoint of restoration effort is also likely to be temporally dynamic (Palmer et al. 2005). Temporal connectivity is not incorporated within early static models of riverine ecosystems, e.g., the river continuum concept (Vannote et al. 1980). However the four dimensions of Ward (1989), do include this temporarily variable dimension of connectivity.

3 Measuring dispersal, colonization and connectivity

This chapter will describe some of the methods when dispersal behaviour, metapopulation dynamics, connectivity and colonization events are studied in freshwater ecosystems. As with all research the quantitative outcome largely depends on the selected methods, the underlying assumptions and the scale used and therefore different research questions are in need of different research methods.

Methodologies associated with measurements of dispersal and their difficulties are subject to many studies (Bullock et al. 2001). Empirical estimates of dispersal are either direct or indirect. Direct methods involve mark-release-recapture, originally deployed to estimate population sizes (Rundle et al. 2007). These methods provide information on actual dispersal, but at the same time measure all dispersal, including dispersal that is non effective.

Furthermore direct estimates have been proven to be difficult to obtain (Bilton et al. 2001, Rundle et al. 2007, Hughes 2007). Dispersal events are unpredictable and vary widely both spatial and temporal and methods often include population biases. Furthermore some propagules do not lend themselves for direct studies (e.g. small propagules, Rundle et al. 2007). Indirect methods rely on successful gene flow, providing estimates of effective dispersal, connectivity and colonization rates on the basis of genetic material. In this way indirect techniques provide information on feasibility of dispersal, rather then explaining the frequency of occurrence, extent of dispersal events or the mechanisms therein.

3.1 Direct methods

3.1.1 Trapping

Trapping is used to measure direct movement of a variety of organisms. For example seed traps are used to measure long distance wind dispersal by plants (Green & Calogeropoulos), hydrochory distance (Middleton 1995), dispersal period (Boedeltje et al. 2004), or macrophyte propagules retention (Engstrom et al 2009)

Furthermore in order to directly study freshwater insect flight in streams a number of devices is known to be used, where dispersal rate, distance and direction can be measured directly. A first method includes the 'sticky trap' using a layer of sticky adhesive substance on transparent material. When used in Danish streams the sheets were set up transversely over the stream, with one sticky side facing upstream and the other downstream (Madsen et al. 1973). Another device frequently used is the window trap (Chapman and Kinghorn 1955) or flight interception trap, consisting of a vertical stretch of glass, transparent plastic or fine netting, in this way intercepting flying insects which will then fall and are subsequently collected in a trough with water and detergent ((Sutherland, 2006). A third method is the use of catches in Malaise traps of the bilateral type (Malaise 1937) were a tent shaped trap made of fine netting will lead flying insects to the collection chamber on the top of the roof. Furthermore light traps, or combinations of methods are used (Bilton, 2001 #52).

Trapping of flying insects is often referred to as 'qualitative' or seems to provide anecdotal information (Bilton, 2001 #49) and therefore this method is often used in combination with other techniques. Actively moving aquatic invertebrates can be trapped by activity traps (Murkin et al 1983) and bait traps, while insect emergence traps are used to trap emerging adults of flies, mayflies, stoneflies and caddisflies (Sutherland 2006).

Trapping has been used in fish migration research (Henderson 2003) for example to catch downstream migrating fish (Cresswell 1977,) or to establish the efficiency of fish ladders (Zitek et al. 2008). However more recent techniques include direct trapping of "images' or counts rather then the specimen, by using either underwater videography (Meynecke et al 2008), hydroacoustics and automated fish counting (Lucas & Baras 2000)

3.1.2 Mark – recapture techniques

Mark – recapture techniques, or mark-release-recapture (MRR) studies are frequently used in several groups of organisms and a huge and expanding literature on the subject exist (Williams 2002). Originally the technique was mainly used to estimate population sizes, whereby the number of caught and released animals (n1) in relation the estimate of the total population size (N) is similar to the number of recaptured animals (m2) compared to the number of animals caught in a second session (n2). This technique is used to estimate parameters dispersal, recruitment, survival etc.

$$N = n1\ n2 / m2$$

N = population size (or number of dispersing, incoming
n1= number of animals caught in the first capture session
n2 = number of animals caught in the second capture session
m2 = number of animals caught in both sessions (recaptures)

External marking may consist of physical marking, i.e. dyes, stains or pigments applied as discrete markings or marking an entire animal and has been applied for decades (Costello 1959). Examples may list the use of colored beads in Trichoptera or (Bilton et al. 2001), combinations of a number written on the forewing (with indelible pen) and a dot of paint on the thorax of Odonata species (Purse et al. 2003) adipose clips, branding or laser marking and subcutaneous tags or fluorescent elastomeres in fish (Skalski et al 2009).

Internal marking techniques using stable isotopes have been used to investigate dispersal distances in freshwater insects (Bilton et al. 2001, Macneale et al. 2005). More recently more advanced techniques using transponder tags are developed and widely used (Bilton et al 2001, Nathan et al 2003). Telemetry studies use a range of methods, including passive integrated transponder (PIT), radio frequency identification (RFID), acoustic and satellite telemetry, depending on study aims and the performance of equipment in different habitats (Cooke and Wagner 2004, Holland et al. 2006, Ebner 2009).Similarly, various tagging techniques are required for telemetry studies of the diverse fauna occupying freshwater ecosystems (Ebner 2009). These transponder techniques have expanded the knowledge on dispersal distance and behaviour based on a signal transmitted between an electronic device, such as a tag or transponder and a reading device, such as a scanner or transceiver.

Potential problems with marking techniques include unknown effects of the markings on welfare and performance of species. The impossibility to capture sufficient numbers of animals or a within-population difference in the likelihood of specimen to be caught or recaught can lead to biased population samples. Furthermore, the timescale between two sampling moments should be sufficiently small in order to decrease the risk of population fluctuations or the loss of markings during the sampling period. MRR studies are known to be biased due to the finity of the study area, where the extent of the bias varies with the dispersal distance relative to the size of the study area (Koening et al. 1996). The probability of detecting dispersal events declines directly and dramatically with dispersal distance.

In the context of restoration MRR methods might be insufficient to detect colonisation or restored habitat patches due to the unpredictability, lengthiness and often rarity (Hughes, 2007) of dispersal events.

3.1.3 Direct techniques in new habitats

When entirely new habitats are created, the origin of colonizing species is often largely unknown. Although aquatic habitats can be described as discrete patches, colonizing species may use vectors like wind, mammals, birds or land. In order to predict the colonization potential of newly created habitats, dispersal behaviour of neighbouring source populations could be estimated. Since colonization of new habitats occurs through a diversity of vectors predicting the location of the source pool for colonization, let alone measuring the dispersal potential beforehand, is difficult.

3.2 Indirect methods

3.2.1 Genetic markers

Genetic methods are often and increasingly used to obtain indirect measures of dispersal (as reviewed by Broquet & Petit 2009) or connectivity. These methods rely on the idea that if dispersal is common, genetic composition of populations will be homogeneous. On the other hand if dispersal is limited among populations, genetic composition will diverge as a result of random genetic drift and/or natural selection. As a result connected populations will share alleles and alleles will occur in similar frequencies, while limited dispersal will lead to different alleles or alleles differing in relative frequencies (Slatkin 1985).

Quantitative estimates of genetic differentiation among populations are expressed as F statistics, which varies between 0 (all populations have the same alleles in the same frequencies) and 1 (each population is fixed for a different allele) (Hughes, 2007).

Several advantages over direct techniques are mentioned in literature. For example, rare dispersal events that would be missed in short term ecological study using direct techniques are implicitly averaged into gene flow estimates. Furthermore, genetic assays can be applied to nearly all life history stages, including dormant eggs or embryos (e.g. Go´mez et al. 2000). Additionally movement is not altered due to the technique chosen (for example by marking or following an organism).

However, disadvantages of indirect techniques are often described in literature as well. First of all, patterns of genetic variation are the result of five main processes: nonrandom mating, natural selection, mutation, random drift (a function of effective population size) and gene flow. In both theoretical and empirical studies, the role of one or several of these processes are inferred by making simplifying assumptions about the others. Therefore, models that underlie traditional gene flow estimates should be critically assessed (Bohonak 1999, Bohonak & Jenkins, 2003). Furthermore genetic similarities among populations provide a long-term 'average' of gene flow and caution should accompany the use of gene flow estimates for making inferences about dispersal (Bohonak & Jenkins, 2003).

In restoration of freshwater ecosystems the use of genetic markers is for example used to explain dispersal patterns and colonization sequences or predict restoration outcome for mammals (Marcelli et al. 2009), fish (Raeymackers et al. 2009), macroinvertebrates (Hughes 2007), amphibians (Semlitsch 2000), zooplankton (Louette & de Meester 2005) and macrophytes (Uesugi et al 2007).

The range of DNA markers that can be used are reviewed by Osborne et al. 2001

3.2.2 Spatial distribution

Spatial issues, such as the extent to which species can disperse, are also important in ecosystem restoration. Communities frequently show positive spatial autocorrelation, where sites close together have more similar species composition than those further apart. The spatial distribution of species or populations can be used as an indirect approach to gain insight in dispersal, connectivity and metapopulation dynamics and eventually used to predict or evaluate restoration success. This approach typically requires a complete regional survey of occupied and vacant habitat patches.

Examples of these studies include the use of measures of community similarity and positive spatial autocorrelation (SA) as an indirect measure of dispersal and dispersal constraints in ponds, lakes and rivers (Shurin et al. 2009, Briers & Biggs 2005). Species that are dispersal limited show a greater SA then more effective dispersers (Shurin et al. 2009). However one should carefully incorporate environmental factors as well, since species distribution could also be driven by spatial cohesion of environmental conditions among sites, thus referring to environmental differences rather then dispersal constrains (Briers & Biggs 2005).

An assessment of the spatial distribution of *Dreissena polymorpha* was used to determine processes that produced observed patterns of invasion (invasion history) of the species in two lake-rich areas (Belarus and Midwestern United States) (Kraft et al 2002). Dispersal distances were inferred from a nearest neighbour analysis, a method that might be suited to produce information in patterns of restoration as well.

More recently spatial patterning of organisms has also been shown be relevant for evaluating restoration success. For example, in a study by Pottier et al (2009) spatially explicit methods were used to evaluate a restoration project on the river bank of the River Rhone. Spatial analysis of plant traits were used to analyse how initial restoration treatments and spontaneous ecological processes act together to produce spatial heterogeneity of plant species.

3.3 Restrictions

As for all ecological methods, there are biases and (dis)advantages to each technique. Studies that try to combine several techniques often conclude that a specific technique is opposing a second one.

For example, the suitability of interception traps to estimate flight direction were questioned when simultaneously performed mark recapture techniques showed upstream flight direction, while the opposite pattern was found with trapping (Macneale et al. 2004). In this light a technique should be selected depending on the research questions and restrictions of each technique should be incorporated in the design and when interpreting the results. Furthermore using a combination of techniques at the same time will improve the understanding of underlying processes.

4 Habitat patch suitability

One of the key factors in restoration ecology is the restoration of physical habitat, leading to an increase in the availability of suitable habitat patches. This will lead to restoration of ecosystem functioning and increase the availability of empty habitat patches ready for recolonisation. Since the literature on physical habitat properties of individual species and consecutive biotic responses are numerous, available for a diversity of freshwater ecosystems and a multitude of species (e.g. Kottelat & Freyhof, 2007, Haslam & Wolesly 1987), these are not further discussed.

In this chapter we will outline general patterns and processes that influence physical habitat properties and subsequent habitat suitability and patch quality, that have recently been shown to be of importance in freshwater restoration.

4.1 Extremes and refugia

Most restoration projects incorporate the restoration of abiotic conditions to a fixed end-point, i.e. an ideal average condition. However, communities tend to be shaped by abiotic extremes.

For example, most streams are restored to function optimally during average flows, whereas communities often are controlled by ecological processes that act during extreme flow events. When restoration success of channel complexity enhancement was studied, it was shown to vary with flow rates (Engstrom et al 2009). In this study, surrogate propagules were used to test the effect of flow rate on propagule retention and deposition. Discharge affected not only the number of artificial propagules trapped but also their stranding patterns. At low flows, more artificial propagules were retained compared to high flows. This study indicates that stream restoration should be designed for optimal function during flow rates of interest, i.e. those discharges under which the ecological processes in question are most important, which in this case is, during high flow.

Thus, restoration output can largely vary with the frequency of extreme events and therefore, restoration planning should be shaped according to the tolerance range (the maximum and minimum extent of habitat characteristics) of target species. Furthermore, re-colonisation of a species is only likely when the entire scope, i.e. the maximum and minimum spatial extent and temporal duration of habitat use (Schneider, 1994) is restored.

In addition to shaping communities, extreme events will amplify the importance of the presence of refugia. One way by which organisms survive natural disturbances is by the use of refugia: accessible (often suboptimal) microhabitats or regions within a stream reach or watershed where adequate conditions for organism survival are maintained during extreme circumstances that threaten survival, (e.g. drought, flood, temperature extremes, increased chemical stressors, habitat disturbance). Proposed local flow refugia include lateral stream margins, dead water zones, dead wood (Borchart 1993) and the hyporheic zone (Matthaei et al. 2004).

Refugia from drought and temperature stress include waterholes (Rayner et al 2009) for fish, or cold-water refuges generated by groundwater entering the channel (Ebersole et al. 2003)..
In many situations refugia might have been lost during degradation. For example, channelization increases the severity of floods directly, but also reduces the availability of flow refugia, leading to a reduced capacity of biota to recover from floods (Negishi, Inoue & Nunokawa, 2002). Examples from the literature in which refugia from disturbance have been actively targeted in restoration of freshwater ecosystems are still rare. Along with habitat enhancement, restoring refugia, in this way enhancing the resistance and resilience to both natural and anthropogenic disturbances, may therefore be critical to survival of target populations (Lake et al 2007).

4.2 Biological interactions

If, due to restoration efforts the abiotic environment is changed enough to enable biota to re-establish, the changes might be insufficient to restore ecosystem functions. Especially, when these processes involve coupled biotic–abiotic processes (e.g. biogeochemistry, succession of plant communities or community assembly). Therefore, changing the interaction between abiotic and biotic states is often a necessary first step for successful system recovery. In streams and river communities, biotic interactions such as competition, grazing, or predation have been shown to be very important in determining ecosystem functioning (Matthaei et al 2004). The 'harsh-benign-concept' (Peckarsky, 1983) hypothesis variability of the relative importance of abiotic and biotic interactions in ecosystems of differing stability. For example, Townsend (1989) and Poff & Ward (1989) hypothesize that the importance of biotic interactions, although important in stable streams, decreases with increasing frequency of hydrologic disturbances (peak discharge), indicating that abiotics control the community build up in 'harsh' systems and increasing importance of biotic interactions when the system is more 'benign'.
Subject to many studies is the he importance of biological interactions in determining ecosystem structure and function (Matthaei et al. 2004), which illustrates the importance of including these factors in restoration planning. This includes accounting for a lengthily restoration period that may be needed to restore ecosystem function. Timescales over which outcomes from restoration are typically sought (< 10 years), might be insufficient to detect the abiotic-biotic community and ecosystem responses (Bond & Lake 2003).

4.2.1 Ecosystem engineering

Ecosystem engineers are species that modify the abiotic environment, thereby directly or indirectly modulating the availability of resources to other species. They affect other organisms by creating, modifying, maintaining or destroying habitats (Jones et al. 1994). Despite widespread recognition of these often important effects, the ecosystem engineering concept has yet to be widely used in restoration ecology.
examples of ecosystem engineering in freshwater ecosystems are dam building by beavers (Whright 2002), the creation of weed beds by aquatic macrophytes

(Carpenter & Lodge 1986), filtering and reef building by *Dreissena* species (Zaiko et al. 2009), burrowing of macro invertebrates, digging of nestholes of fishes (Moore 2006)), stabilization of fine gravels by net-spinning Hydropsychidae caddisfly larvae (Johnson et al. 2008), the effect of crayfish and fish as bioturbators of stream sediments (Stazner et al. 2000, Stazner et al. 2003, Stazner & Sagnes 2008) and shell production by molluscs (Guterrieze et al. 2002).
In order to create suitable habitat for some species other species, that affect the focal species' habitat, need to be involved in restoration efforts and planning. In this way metapopulation dynamics and connectivity for non-focal species can become important in the restoration process.

4.3 Long term and large scale processes

There is a general consensus that conditions today are not the same as they were a century ago and are continuing to change. Predictions that climate change will result in high levels of warming, as well as altered precipitation, combined with continuing land use change is likely to impact abiotic as well as biotic processes.
This continuing change is and will influence recovery potential in several ways and implications of climate and land use change must therefore be considered for the broader practice of ecological restoration (Harris et al. 2006). In particular, the likelihood of restoring historical or reference conditions is questioned as biophysical conditions will continue to change. For example, a 25 year study on the recovery of streams after acidification showed that climate affected recovery patterns either through effects on organisms or effects on acid-based status (Ness et al. 2004; Evans 2005; Eimers et al. 2007). Restoration goals should therefore depend on current conditions and changing conditions of the future (Harris et al. 2006, Hobbs et al. 2007.)

Adaptation strategies will be of importance tot cope with changing conditions. This advocates genetic diversity among and within species as a key attribute of ecosystems required to ensure resilience and adaptability (Harris et al. 2006). Most recent restoration projects focus on restoring abiotic conditions, enabling spontaneous colonisations of restored sites from local populations. Colonisation from local sources and translocation with the exclusive use of local material is often predicted to be more likely to result in better restoration outcomes because local species/populations are better adapted to the local environment, maintain the genetic integrity of the site, provide better habitat, and prevent any potential pollution of the local gene pool.
However, little genetic variation leaves little space for adaptation that may be needed to cope with the changed circumstances due to climate change and extinction rates might be increased. Therefore, it is suggested that space for evolutionary development must be incorporated into conservation and restoration programs (Harris et al 2006, Rice and Emery 2003). Rice and Emery (2003) emphasise that when considering source populations for restoration a balance between an acceptable level of genetic load and the capacity for further adaptive shifts must be sought, in this way adjusting the balance between existing adaptation and potential adaptation. An example in plant restoration is the creation of regional seed mixes that are

delineated by climate zones but also contain genotypes collected from a variety of microenvironments within each zone (Rice & Emery 2003). Another approach would be to collect planting material from the edges of a species range (Rice & Emery 2003).

Broadhurst et al (2008) suggest that seed sourcing should concentrate less on local collection and more on capturing high quality and genetically diverse seed to maximize the adaptive potential of restoration efforts to current and future environmental change.

4.4 Land-water interface

Organisms often need different habitats during different life stages, leading to a temporal variation of habitat suitability. Numerous species require both aquatic and terrestrial environments for reproduction and survival, e.g. amphibians such as frogs and salamanders and aquatic insects such as Odonata, Trichoptera (Hoffman 2000) and Plecoptera. Restoration of solely part of the habitat will therefore not provide all necessary resources for the species and re-colonisation of a species is only likely when the entire scope of habitat use (Schneider, 1994) is restored.

The availability of the different high quality habitats, the availability of land habitat and even more important the connection between habitat types is often overlooked when restoring certain freshwater habitats. Additionally, some species only inhabit the very specific habitat that occurs where terrestrial and aquatic ecosystems meet: the riparian or littoral zone. The riparian and littoral zone, although limited in overall extent, provide important connections between habitats. Furthermore the so called ‘edge-effect’ is hypothesised to cause higher biological diversity at the land/water interface than in adjacent patches (Naiman & Decamps 1990). The riparian zone connects upstream and downstream areas, for example in streams or canals and laterally it is an important connection as it connects water and land habitats. The stream corridor revealed as the main 'highway' for adult dispersal (Petersen et al. 2004), includes the riparian strip extending 10-20 m on either side of the channel. Since the riparian strip is the main habitat for adult aquatic insects, serves as a refuge, acts as a buffer to certain abiotic extremes and influences hydrologic patterns and are important to species that are restricted to the conditions in this unique habitat (Bennet 2001) its management may affect the biodiversity of aquatic communities.

In order to restore freshwater ecosystems, adjacent important habitats for target species, including riparian zones, connections and land habitats should be included in the restoration efforts.

4.5 Temporal quality

The temporal character of habitats is important when considering habitat quality and might partially explain restoration successes or failures (Bond & Lake 2003). Patches might be ephemeral or suitable for a limited period each year and single target species might require different habitats at different life stages (Hanski 1999). Hence, restoring an ecosystem depends not only on the restoration of high quality habitats, but more importantly the restoration of high quality habitats being present at the right time.

For example, the maintenance of amphibian communities (Semlitsch 2000, Snodgrass 2000) or the structure of macro invertebrate communities (Wilcox 2001) are strongly influenced by the hydroperiod of wetland or pond habitats. Since larvae may be killed if the site dries before metamorphosis can occur, restoration success depends on synchrony between the annual availability of water (i.e., time of filling, hydroperiod length) and the timing of reproduction. On the other hand, pools with longer hydroperiods attract more predator species (Semlitsch 2000) and predators may cause local extinctions of prey species. These studies indicate that for some species hydroperiod should be incorporated as a primary criterion for wetland or pond restoration. The hydroperiod, but also levels and timing of flood pulsing (Junk et al. 1989) and tidal pulsing (Middleton 2002) are important temporal aspects of the habitat, contributing to total habitat quality. Restoration efforts should be directed towards restoring natural levels and timing of these aspects.

Since habitat restoration efforts are generally aimed at restoring a habitat for a particular life-stage, lack of habitat for all stages might not result in establishment of target species. For example, local abundances of aquatic insects may depend more on factors affecting the adults, such as the availability of suitable oviposition sites (Peckarsky et al. 2000, Blakely et al. 2006) than on the specific characteristics of juvenile or adult habitat. Other utilize distinct habitats as juveniles and adults (Hoffman 2000), in which case concurrent restoration of spatially isolated habitats might be required (Bond & Lake 2003).

Apart from the temporal character of single habitat patch suitability, temporal aspects of connectivity and dispersal between essential habitats is another important aspect.

5 Connectivity

Longitudinal connectivity refers to a directional within system (catchment) connectedness, e.g. upstream-downstream or river-estuary connections. Longitudinal connectivity is de major determinant of the movement of water, energy and matter and critical to many processes and dispersal (Wiens 2002). Movement along the longitudinal gradient induces a gradual shift in abiotic an biotic characteristics along (Vanote 1980, Ward 1989), making up among other things, the zonation of streams (Huet 1959). Today, longitudinal connectivity is often obstructed by structures like dams (Dynesius & Nilsso 1994), weirs, resulting in alternating lotic and lentic habitats, as conceptualised by the 'serial discontinuity concept' (SDC, Ward & Stanford 1983)

Lateral connectivity refers to a connection that provides the movement of material and organisms from one distinct system to the next, like channel-floodplain connections in streams, or connections between different wetland systems or estuaries in lentic systems. The importance of interactive pathways, of biota and abiota, along the lateral (transverse) dimension between the river channel and riparian zones, including surface floodplain dynamics has been recognised and conceptualised (Pautou and Decamps 1985, 'Flood Pulse concept' Junk et al. 1989, Ward 1989). Nowadays, river regulation, in the form of dams, levees or bank facing, restricts both the lateral connectivity between the river and the floodplain and the temporal and spatial variance in connectivity in the main stem of the river (Wiens 2002).

Vertical connectivity comprises of connectivity of surface water and the structures beneath soil, groundwater) and above (air) the water.
The most obvious example of vertical connectivity is the link between surface waters and the hyporheic zone, i.e. the saturated zone below and alongside the channel that contains water derived from the stream (Stanford & Ward 1988, Boulton 2007). Vertical connectivity in streams is conceptualized in the 'Hyporheic corridor concept' (Stanford & Ward 1993). Vertical connections comprise of patterns of upwelling, downwelling, and groundwater movement and are driven by interactions between geomorphology (permeability of the sediment) and flow regime. Humans have disrupted the exchange between streams and their hyporheic zones by changing patterns of sediment redistribution (siltation and the clogging of pore spaces) and water flow (Hancock, 2002). Strategies used to restore vertical connectivity include flushing out sediments that have contributed to clogging of interstitial space (colmation), and placing logs in the stream to increase water exchange between channel and sediment (Jansson et al. 2007).

According to Ward & Stanford's (1995) "extended serial discontinuity concept (ESDC)", along a three-reach river model, the relative strength of the longitudinal pathways is highest in the constrained headwaters, vertical interactions reach their

maximum in the braided middle course and lateral connectivity plays the major role in alluvial floodplain rivers (Jungwirth et al. 2000).
Connectivity at any of these axes may be important for the recovery of both ecosystem structure and function and should be considered in restoration of aquatic ecosystems.

Temporal connectivity, as a fourth dimension, refers to the periodical character of linkages, for example when flooding temporarily connects the fragmented floodplains with the main stream channel. Therefore, the target endpoint of restoration effort is also likely to be temporally dynamic (Palmer et al. 2005).If a target species is dependent on the accessibility of key habitat (e.g. spawning grounds) at a specific period each year, restoration efforts should be aiming to restore connectivity at this specific period as the restoration of water flow alone is not sufficient to restore the ecosystem.

5.1 Distance and scale

Distance is known to limit species and populations boundaries and therefore connectivity is decreasing at increasing distance (Junk & Wantzen 2006). For example during a study in seven small, upland streams draining catchments, malaise traps were set out in transects perpendicular to each stream. Results showed that the vast majority of insects were taken either directly over, or very close to, the stream channel and regardless of land use, the flight of mayflies and caddisflies was concentrated along the stream, rather than perpendicular to it (Petersen et al 2004). In general rates of colonisation will depend on the distance between the restored area and the source populations (Kareiva 1990). The isolation of restored habitat is, apart from ‘hard barriers’ like dams and weirs, associated with the presences of ‘soft barriers’. These barriers include large distances, that cannot be overcome by dispersal (dispersal constraints) or because conditions at intervening habitat is not suitable to provide connectivity of the restored freshwater system (Bond & lake 2003).
The degree of isolation of floodplain lakes, is also related to distance, as is conceptualized by the four phases of lotic-lentic hydrological connectivity (Drago et al 2008), who distinguishes 4 phases depending on the degree of isolation: 1) channeled water phase, 2) overbank phase, 3) drainage phase, and 4) isolation phase.

Most studies that describe examples of re-colonisation after restoration refer to connectivity at very small spatial scales. In these studies re-colonising species are mostly originating from source populations within catchments, e.g. in- stream colonisation of invertebrates using drift (Mackay 1992). The importance of choosing the right spatial scale of observation is also reflected by the fact that the strength of connectivity is likely to vary across spatial scales (Jenkins & Boulton 2003). For example in the Darling River, Australia ecological connectivity was greater at small spatial scales (patches within lakes 100–1000 m, among lakes 10^4–10^5 m) than at larger spatial scales (reaches 10^5–10^6 m) as was shown by the microinvertebrate colonization sequences in the Darling River floodplain during flooding.

5.2 Physical structures

In streams several physical structures are hypothesized to enhance longitudinal connectivity in streams (Wiens 2002). The riparian zones, (paragraph 4.4, Johansson et al 1996) acts as corridors for dispersal, enhancing longitudinal connectivity. Previous work in streams, has suggested longitudinal connectivity could also be related to the presence of dead water zones (Wiens 2002). Dead water zones (DWZ) are places such as backwaters, pools or behind large obstacles, where the water is out of the main flow and is stored temporarily.
As a study by Bond et al. (2000) suggest, dispersal distances and connectivity of drifting organisms might not only be related by the overall proportion of DWZ in a stream, but also be influenced by the spatial organization of DWZ within a reach.
Similarly, the occurrences of areas of low flow and physical obstacles that work as retention agents are shown to be of importance to plants (Johansson et al. 1996) These zones work as retention agents for hydrochorous plants in streams (Riis 2008).
Not only the structure of habitat, but also the arrangement of non-habitat influence the degree of connectivity. There is, for example, a number of studies demonstrating that the (intervening) movements of pool-dwelling fish are enhanced when intervening habitats are shorter (Lonzarich et al. 2000), deeper (Gilliam & Fraser 2001), or have lower velocities (Schaefer 2001). The physical characteristics of corridors that enhance connectivity and that could be incorporated in the design are reviewed by Heslenfeld (2003, coastal and marine areas).

5.3 Elevation and slope

Altitude and position in the catchment is important in defining the degree of movement (Wiens, 2002), or connectivity. Apart from the different habitat characteristics (e.g. stream order) elevation and slope also bring about physical barriers, influencing connectivity. For example, because the energy required for upstream dispersal is positively related to elevation difference or slope, in a study of Lowe (2006) it was predicted that gene flow of a salamander population was negatively related to change in elevation between sampling sites. Molecular techniques showed that genetic distances between downstream and upstream sites were positively related to change in elevation over standardized 1-km distances, indicating that connectivity is shaped by patterns of isolation by slope. However a second study (Lowe et al 2008) showed that the influence of slope on dispersal and gene flow is related to species specific behaviour. Movements of two salamander species showed contrasting directional biases. Consistent with predictions of how movement biases interact with slope to affect dispersal and gene flow, genetic distance increased with slope for a upstream biased moving species, contrasting to a and decrease with slope in a species with a downstream bias.
In a study of Hughes (2007) it was hypothesized that for flying adults of aquatic invertebrates sites in lowland streams with limited altitudinal differences between sites may be easier to reach than upstream sites. This is because upstream sites are connected to one another via lowland streams that have different characteristics and

therefore may be difficult for animals to traverse. However there was no evidence since dispersal seemed to occur usually within a stream, rather then across.

5.4 Human induced connectivity and fragmentation

Historically, biogeographic barriers to the movement of aquatic organisms existed at multiple spatial scales and contributed to the development of unique regional faunas. At the same time, without human induced barriers (dams, weirs, lack of hydrologic connectivity in regulated systems) freshwater systems were historically well connected, to both other parts of the catchment, as well as the landscape.

Connectivity and colonization routes created by human activities can largely enhance dispersal of freshwater organisms. Humans have provided a variety of pathways by which aquatic species can circumvent historical biogeographic barriers. These include both authorised and unauthorised stocking, construction of canals and water conveyance systems, transport in ship ballast water, fishing and angling gear (including boats) transferred among water bodies and intentional release of ornamental and other captive species (Rahel 2005). This causes native species to be replaced by cosmopolitan species, leading to freshwater homogenization.

At the same time, due to a lack of connectivity, habitats become largely fragmented, leading to decreasing dispersal rates, inbreeding and increased risk of extinction. Furthermore habitat fragmentation will alter the physical environment of the remnant habitat, leading to an even larger risk of extinction (Saunders et al. 1991). In this way fragmentation, poses a threat to the existence of locally adapted or native species.

Freshwater restoration can influence homogenization of aquatic biota through two major mechanisms: by removing barriers to movement and by restoring natural habitat conditions (Rahel 2005). Removal of movement barriers may facilitate the spread of non-native species and thus contribute to biotic homogenization. Conversely, populations of native (target) species may rely on increased connectivity in order to colonize a restored habitat patch. Restoration of natural flow regimes and habitat conditions may reduce biotic homogenization by favouring regional native species over cosmopolitan, non-native species (Rahel 2005).

6 Dispersal behaviour

6.1 Macrophytes

Recently, the ecology of plant dispersal in relation to restoration success has become an increasingly important research subject. Restoration of plants can be the restoration target, but the structuring role of plants creating habitat for target fauna is another frequently re-emerging topic. Since life history traits of plants are well studied, many recent studies use this knowledge in order to explain declining patterns or outcomes of restoration measures.

6.1.1 Dispersal types

Dispersal in freshwater plants is diverse and depending on the propagule-type. Three types of propagules are used: seeds, vegetative parts and fruits. Dispersal may be aided by abiotic vectors water (hydrochory) and wind (anemochory), while biotic vectors may include dispersal inside (endozoochory) or on (epizoochory) animals and dispersal by humans (Table 1).

Propagule dispersal by water is most common and assumed to be effective for aquatic plants, because water transports seeds selectively to other wet places (Soons 2006), while wind is more likely to disperse propagules to terrestrial than to aquatic sites (Cook, 1987). However, water can only transport seeds to areas that are connected by surface water flows and downstream of seed source areas. Water borne dispersal ways can consist of rivers (Johansson et al 1996) flooding of wetlands (Cellot et al., 1998) or tidal currents (Bakker et al. 1996). Unlike water, wind can transport propagules in all directions and is therefore important for dispersal to upstream water bodies and to water bodies not connected by surface water flows. Wind dispersal transports propagules to a wider range of sites than water, and therefore reaches more sites but with lower seed densities (Soons, 2006).

Dispersal of macrophytes by waterfowl is another relatively well studied (Clausen et al. 2002, Figuerola & Green, 2002) way of dispersal. Furthermore dispersal by mammals (Barrat-Segretain, 1996) and fish (Chick et al. 2003, Pollux et al 2006) have been recorded as well. Since human dispersal of plant seeds is known to be important for long distance dispersal (Wichman et al 2009), human mediated dispersal (HMD), often referred to as ‘secondary dispersal’, is likely to be of importance to freshwater of riparian plant dispersal as well.

In general, aquatic macrophytes are regarded as good dispersers, caused by a combination of long-distance dispersal of sexual propagules and high local dispersal of asexual clones (Santamaria 2002), that result in broad distributional ranges of most species. However, recent changes in aquatic environments, especially changes in hydrologic regimes, has been disrupting natural dispersal routes. For example, damming and diversions of streams has lead to degradation of aquatic and riparian communities in many river systems (Nilsson and Berggren 2000, Rood et al. 2003).

Table 1. Dispersal aided by different (a)biotic vectors.

abiotic vector	1	hydrochory	water
		anemochory	wind
biotic vector		endozoochory	birds
			mammals
			fishes
		epizoochory	mammals
			birds
		human-assisted	

6.1.2 Life histories

There is a large difference in life history traits related to dispersal. For example, in wetlands most species possess seeds that float for a long period accompanied by long dispersal distances, whereas in other species the diaspores sink immediately upon release (e.g. *Zannichelia*, Johansson et al. 1996). Although water-aided dispersal is generally considered the most important vector of macrophyte dispersal in wetlands, few important species, e.g. *Phragmites* and *Typha*, depend on anemochory. Furthermore, wind can aid the distribution of other propagules, i.e. by blowing water-dispersed propagules over large distances (Weisner & Strand 2002).

Another distinction is that between plant species that are restricted to wet habitat and species that occur in riparian zones. A study by Dalhgren and Ehrlen (2005) showed that the distributions of emergent species were less affected by hydrologic connectivity than those of submerged and floating-leafed types. This pattern reflects that emergent plants can occur in habitat patches surrounding the lakes and are not restricted to hydrological connected habitats, indicating water-assisted dispersal is more important to submerged and floating leaved species.

For species of ephemeral wetland types (for instance, successional stages in the terrestrialisation process) successful dispersal is crucial, because the habitat patches that these species occupy have a short life span (Soons 2006) and dispersal might not only be constrained in space, but also in time.

Seeds from both emergent and submerged (macrophytes are known to occur in seed banks. In seed banks the abundance of annuals is often higher then of perennials, possibly explained by the high fraction of perennial submerged macrophytes that rely on vegetative propagation for dispersal (Weisner & Strand 2002).

6.1.3 Macrophyte dispersal and restoration

In many wetlands and lakes, restoration efforts are focussed on restoring macrophyte communities, assuming they have a central role as moderators of the (a) biotic habitat of many other species. Restoration requires that propagules are present at restored sites. If abiotic conditions are suitable, colonisations from available seed banks or dispersing plant propagules seems often sufficient in order to achieve restoration success (Weisner & Strand 2002). After activation of the seed bank, the development of a restored area depends on further dispersal from plant propagules (Bakker et al 1996), illustrating the additional importance of dispersal for second phase restoration.

Efforts aimed at restoring macrophytes communities can entail increasing light availability in lakes (Weisner & Strand 2002), e.g. by lowering the water table or by biomanipulation (i.e. removing zooplanktivorous fish biomass) thereby activating available seed banks.
Although dispersal is often shown to be not limiting few examples exist showing that a lack of hydrologic connectivity might result in a decrease in hydrochorous dispersal. For example, a study by Merrit and Wohl (2005) showed dispersal is significantly decreased downstream of dams, where the number of hydrochoric seeds in the water column is diminished by nearly 95%. Hydrological measures that include restoring natural hydrologic regimes, increasing flood regimes, a more frequent lateral connection of rivers and their floodplains (Merrit et al. 2002) or removal of dams (Merrit & Wolh 2005) will increase hydrochoric dispersal. For example Rood et al. (2003) showed that restoration focussed on restoring more naturalized instream flow patterns allowed for dramatic partial recovery of riparian vegetation along a severely degraded desert river through natural recruitment and growth processes.

If a seed bank is absent or depleted and other propagules sources are lacking, often human assisted dispersal is needed. Examples are the use of donor seed banks, by pumping sediment of neighbouring water bodies to a receiving new or extinct water body. Additionally, submerged macrophytes have been dispersed by spreading of plant fragments over the water surface (Weisner & Strand 2002) or active planting (Cronck & Fennessy 2001).

Plant dispersal in rivers is mostly continuous and can be distant, with rivers and their riparian zones serving as corridors for dispersal (Merrit 2002) Literature suggests that the availability of propagules may not be limiting to effective dispersal, especially for species using hydrochory in well connected streams. For example, when plant dispersal and colonization was studied by Riis (2008), results showed that the number of drifting shoots and seeds per day during the growing season were numerous, and caused no constraint to colonisation. It appears that primary colonization (germination) is the main constraint to regaining vegetation in lowland streams in general and in vegetation-free rehabilitated streams in particular. It is therefore suggested that, if plant colonisation is a target for stream rehabilitation, it is important to enhance retention and colonisation of propagules by creating areas of low flow and by providing physical obstacles to work as retention agents in the stream.

An important factor influencing establishment success of macrophytes in restored ecosystems is competition. Macrophyte development is largely affected by light availability which can be influenced by the presence of algae, periphyton or other macrophytes. On the other hand grazing can have direct effects on macrophyte development (Weisner & Strand 2002). An important aspect is the competitive availability of good colonisers, many invasive species tend be good colonists (Zedler 2000), which might be related to differences in dispersal constraints and propagules longevity compared to native or target species.

6.2 Invertebrates

Freshwater invertebrate dispersal, with many definitions e.g. 'movement between discrete habitat patches' or 'movement of organisms away from their natal habitat' (Macneale 2005, Purse et al 2003) can be classified in either active of passive dispersal (Fig. 5). Freshwater invertebrates are able to reach and colonize bare habitat patches through different dispersal mechanisms using wind, water, land or animals (mammals, birds, amphibians, reptiles or other insects (reviewed by Bilton et al 2001)) by drifting, crawling, swimming and flying (Mackay 1992). The establishment of propagules banks promoting temporal dispersal is known to occur in crustaceans and bryozoans that disperse passively through the transport of desiccation resistant propagules (Bilton et al, 2001). Some dispersal pathways and mechanisms of freshwater invertebrates are reviewed by Bilton et al. 2001, Charalambidou & Santamaria 2002, Green & Figuerola 2005, Lancaster & Briens 2009, Downes & Reich 2008).

6.2.1 Active dispersal

Adult flight is an important dispersal mechanisms for a majority of aquatic insects allowing dispersal over a wide area and readily colonize new, ephemeral or frequently disturbed systems (Schmidt et al. 1995, Bilton et al. 2001, Winterbourn & Crowe 2001, Rundle et al. 2007). Most insect species have a relatively long larval life spent in the water, accompanied by a short stage as a winged adult (Hughes et al. 2008). Duration of the adult stage can range from a few hours to a few weeks depending on the species (Bilton et al., 2001). Flight can be used for either longitudinal or by lateral migration. Dispersal distances related to active flight are known to cover few to several thousands of kilometres. For example the cosmopolitan species *Pantala flavescens* or 'globe skimmer' is known to disperse thousands of kilometres, even reaching ephemeral habitat patches on remote islands in the Pacific (Buden 2010). Range size, a variable derived from dispersal distances, is known to be related to body architecture: The range of *Enallagama* damselflies from North-America showed to be positively related to wing length (Rundle et al. 2007).

Since many stream insects drift downstream in their larval stage, it is often hypothesized and tested that adult flight is necessarily directed upstream to compensate for this net larval displacement downstream, known as the 'colonization cycle' (Muller, 1982), or '(stream) drift paradox'. This colonization cycle has been tested for both stretches of mountainous rivers and between a coastal stream and its estuaries ((Muller, 1982 #39). Results indicate significantly higher rates of upstream movement for ranges of mayflies, stoneflies, salamanders and freshwater shrimp (Hughes 2007) and Trichoptera. Other studies indicate, the colonisation cycle is nonexistent and that random flight may be sufficient to explain movement patterns of stream invertebrates (Anholt, 1995).

Lateral dispersal of flying adults is less often studied therefore its role and magnitude in aquatic insect dispersion has been often underestimated. Although many studies indicate lateral dispersal may be negligible (Hughes 2007, Griffith et al 1998) recent studies reveal the importance of inter-stream or inter-catchment dispersal (Smith et al 1995, Petersen et al. 2004, Briers et al. 2004, Masters et al. 2007). In such context, *Baetis* ovipositing adults emerging from nearby less affected systems most likely served as the main source of colonization of acidified streams via flying compared to within stream drift (Masters et al 2007). Examples of studies where different directions of dispersal are simultaneously studied for individual species or groups are anecdotal. Furthermore multidirectional or multiscale studies often include an indirect estimate of the dispersal mechanisms (Monaghan et al. 2002).

6.2.2 Passive dispersal

Drift, or downstream displacement is a common way of passive transport for many stream invertebrates (Waters 1972), and known to promote large scale population displacements within streams. Other mechanisms of passive dispersal include hitchhiking or phoresy, including attachment to mobile animal vectors or resting stages in the guts of animals (Bohonak 1999, Green & Figuerola, 2002, Figuerola & Green 2005, Bilton et al 2001, Vandeschoenewinkel et al, 2008a en b). In recent year expanding knowledge on diaposing eggs have shown the importance of passive dispersal of small propagules for aquatic invertebrates (reviewed by Bilton et al. 2001) and the existence of dormant propagule banks that are hypothesised to promote dispersal in time (Bilton et al. 2001, Bohonak & Jenkins 2003). The dispersal biology of invertebrates whose small cryptic propagules resemble seeds, is often similar to dispersal mechanisms in plants (Rundle et al. 2007).

6.2.3 Life histories

Life history characteristics related to invertebrate dispersal include the mode of dispersal (passive vs. active), dispersal vectors used (wind, water, animals), production of dispersive stages (resting eggs), timing of reproduction, flight efficiency (Rundle et al 2007). Passive dispersers tend to be smaller then actively dispersing organisms (Fig. 5)
Aquatic invertebrates with a mobile adult stage (e.g. flying insects) often show widespread patterns of dispersal, e.g. across areas of continuous forested habitat (Hughes et al. 2000) or around the world (Buden 2010). In contrast, many fully aquatic invertebrates, such as snails, mussels, shrimp and crayfish, show marked differences in genetic structure across sub-catchments, suggesting restricted dispersal on a small spatial scale (Hughes et al. 1996). These data suggest that many aquatic organisms will have a limited ability to recolonise disturbed areas, even after they have been restored.

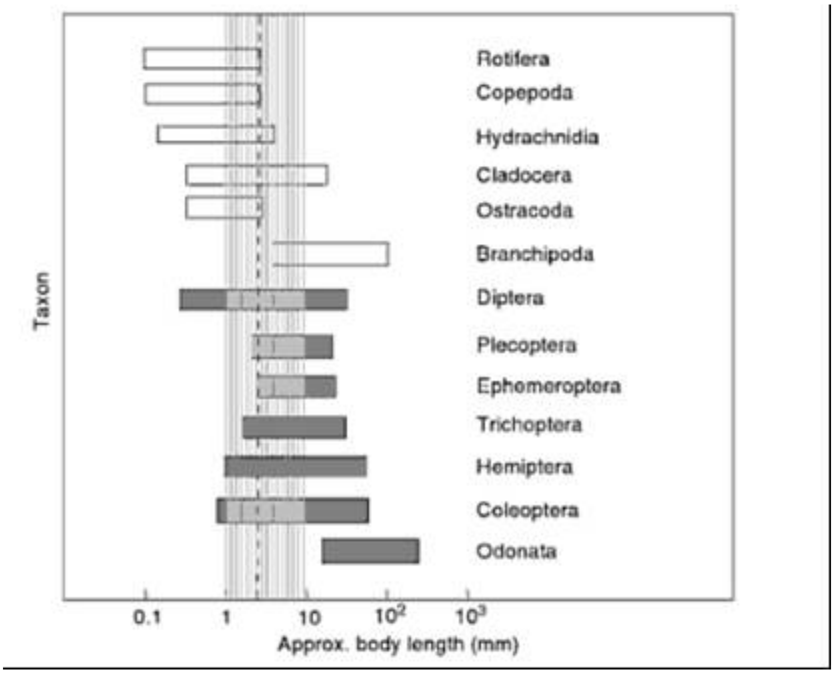


Figure 5. Approximate size ranges of adults in selected groups of freshwater invertebrates, divided into active and passive dispersers. Passive dispersers (open bars) generally have smaller modal body sizes than active dispersers (shaded bars). The shaded area indicates the size range in which the transition to cosmopolitanism has been predicted to occur (Finlay 2002), whilst the dotted line indicates the size below which flying insects are frequent members of the aerial plankton (Rundle et al. 2007).

In an attempt to establish the major dispersal mechanism in aquatic insects, the importance of stream drift and adult flight were compared and results are suggesting that adult flight is the major mechanism of dispersal for these insects (Hughes et al. 2008) .

Dispersal pathways of invertebrate species may vary in time, depending on seasonal cues and different life stages (eggs vs. larvae vs. adult stage) leading to different scenarios of dispersal extent (Figure 6.).
Even within a single life stage often a combination of pathways is explaining dispersal patterns. For example Vandeschoenewinkel et al (2008) showed that for a rock pool metacommunity the combination of short distance wind dispersal and hdyrochory during rainfall were important, while amphibian mediated dispersal was less important. Furthermore outcome of dispersal studies may vary depending on the dispersal scale of the species subject to the study (Monaghan et al 2002), where within stream, across stream and across drainage dispersal can vary widely within communities. The simultaneous study of multiple species, including multiple life stages at multiple spatial scales and multiple dispersal vectors helps determine the relative importance of each. However using this information to predict restoration outcome is a rather complex task. Therefore more general principals of dispersal constraints in relation to restoration should be incorporated in restoration planning. It is important to determine which species or life stages are most constrained, most

sensitive to inappropriate habitat quality or size and, therefore, require most attention during restoration.

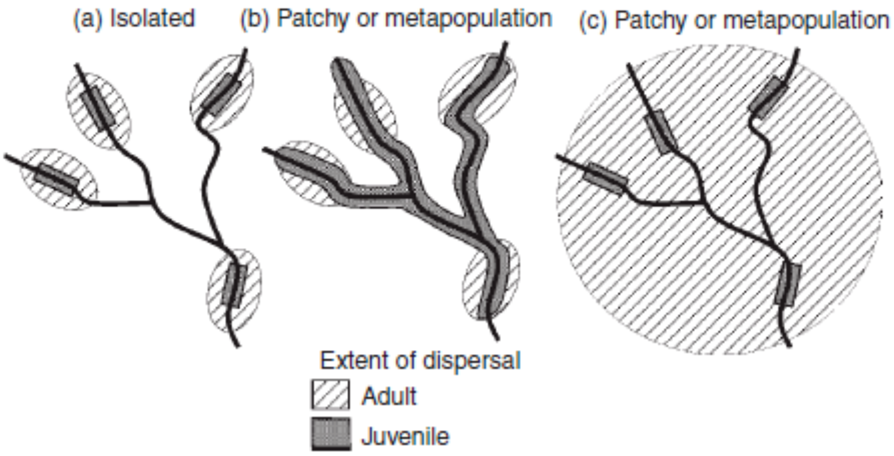


Figure 6. Scenarios of dispersal extent by adult and juvenile stages in a catchment.(a) Both adults and juveniles have very limited dispersal ability, leading to a series of isolated populations on different channels or locations along channels. (b,c) These illustrate situations where there are markedly different dispersal abilities by different life-history stages, which may result in patchy populations or metapopulations depending on the exact dispersal frequencies at different life-history stages (after Downs and Reich 2008) .

6.2.4 Invertebrate dispersal and restoration

Dispersal ability and the presence of natural barriers can pose a major constraint to the recovery of disturbed ecosystems (Madsen et al. 2006). Research that provides knowledge on dispersal ability of target species can be helpful in restoration planning and predicting restoration outcome. Colonisation potential is dependent on dispersal mechanisms of invertebrates. However, successful dispersal will not always account for long term establishment and persistence of a species. For example, when the effects of isolation and connectivity on the structure of both adult and larval dragonfly (Odonata: Anisoptera) communities formed at physically identical artificial ponds were studied, dispersal and recruitment limitation showed to act as filters on the richness of communities (McCauly 2006). Furthermore, the richness of larval recruits in artificial ponds was lower than the richness of adult dispersers observed at ponds. Results from this study highlight the importance behaviourally limited dispersal may have in taxa morphologically capable of broad dispersal and suggest that the role of dispersal and recruitment limitation may be critical in shaping community structure of newly created habitats.

Dispersal distances and constraints can help to predict the time to restoration or propose restoration strategies. A study by Fuchs & Stazner (1990) in Germany showed that in a 400m restored reach that was connected to almost completely intact communities upstream and downstream of a 400 m restored reach, sufficient recovery of benthic macroinvertebrate fauna could be achieved in relatively short periods. However, in a rather isolated stream reach with a high diversity of physical habitats after restoration and with the closest intact lotic ecosystems of a comparable type 20-25 km away, sufficient recovery of benthic macroinvertebrate fauna was not achieved within five years after restoration.

Similarly, Purse et al (2003) advocate that management efforts towards restoring populations of a rare damselfly should incorporate restoration of suitable habitat in the vicinity of existing populations. By studying the dispersal ability of the species *Coenagrion mercuriale,* average movement within continuous areas (< 25 m) of habitat and colonization distances (maximum 1 km), were established. This quantitative information was used to recommend that management effort should be directed towards maximizing the likelihood of *C. mercuriale* recolonising sites naturally within 1-3 km of other populations (particularly within large clusters). Strengthening of the existing metapopulation, by enhancing the empty site occupancy, is preferred over restoring small isolated sites or clusters of sites that would leave local populations prone to extinction.

6.3 Fish

6.3.1 Dispersal types

Contrary to macrophytes and macroinvertebrates, fish are largely obligate active dispersers with only watercourses as relevant dispersal pathways. As such, they may be highly influenced by hydrologic connectivity patterns. In general, fish are regarded as strong swimmers, relating this life history characteristic to long dispersal distances. On the other hand, for fish, since they are dependent on hydrologic connectivity, they are less likely to disperse than species with life histories that include different ways of dispersal (e.g. aquatic insects both swimming as larvae and actively dispersing overland as adults). Evidence that the movement of salmonids is restricted (to typically <50 m Rodriguez 2002) has been described in many studies that test the 'restricted movement paradigm'.

Species and age specific dispersal distances in fish are related to swimming performance. On the other hand structural connectivity is largely explaining functional connectivity of fish population. For example, populations of fish species that live in a stream with many waterfalls or wires are less connected than similar populations inhabiting a low-gradient river without obstructions (Hughes 2007). Almost any area with a vertical spill of water; high water velocities, shallow depth or lacking in light can prevent or delay fish movement. This may lead to increased predation, loss of breeding opportunities and in some cases the local extinction of fish species (O'Brien 1999). Furthermore, negative consequences of noise, physical harm by pumping stations and can are responsible for decreasing dispersal distances.

Apart from swimming a major pathway of establishment of fishes is introduction by humans. A review on the mechanisms by which non-native species are intended introduced lists a long history of motives that have been leading to fish introduction by men (Copp et al. 2005). The primary motivations to introduce fish are ornamental (garden and aquarium) purposes, stocking (extensive fish culture, sport fishing), intensive aquaculture, bio-control and cultural.). The earliest recording of a freshwater fish introduction in most European countries is that of the common carp, recorded to be introduced 6000 to 7000 BC (Lintermans 2004, Copp et al. 2005). More recently due to increasing transportation and large-scale morphological changes in waterways, the list of pathways of introductions has been extended by unintended introduction, for example via ballast water of ships or the recent expansion of Ponto-Caspian gobies in Europe (Copp et al. 2005) aided by the construction of the Main-Donau Canal.

6.3.2 Life histories

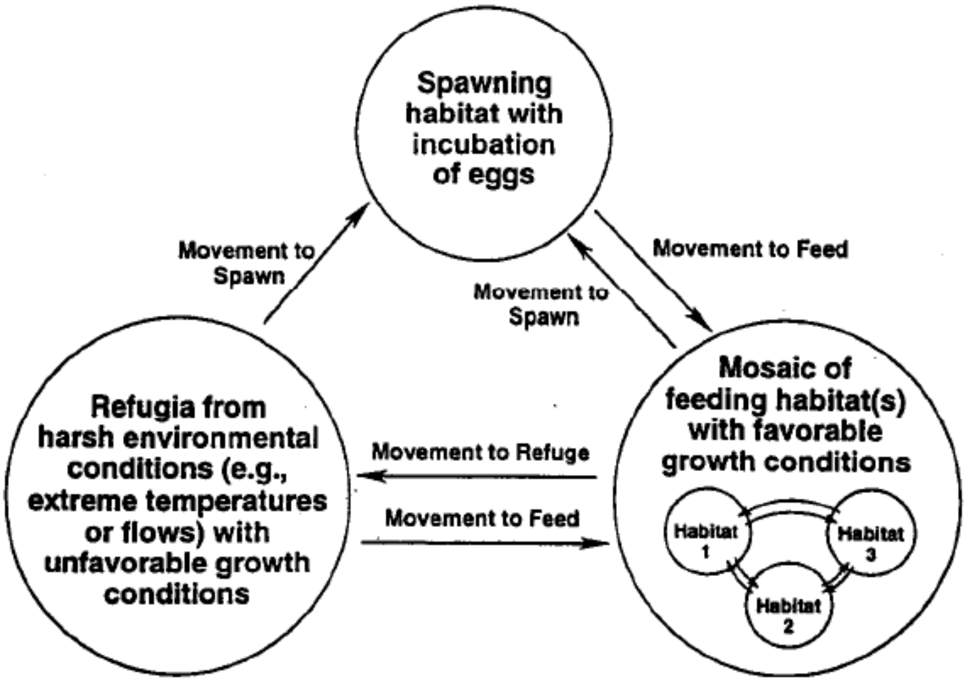


Figure 7. Habitat use and movement of stream fish (after Schlosser and Angermeier 1995) throughout their life.

Since most fish species use a diversity of habitats throughout their lives (Milner 1984, Schlosser & Angermeier 1995; Fig. 7), connectivity between the different patches is essential for persistence of the species. Life history characteristics vary widely and dispersal or migration between different habitat patches is important starting from the microscale (feeding migration), within catchment migration of residential populations (e.g. refuge and spawning migration) through to large scale migratory movement of diadromous fishes that migrate between salt and freshwater in order to reproduce.

Migratory life histories of fishes are largely divided in four categories: 1. residential species, 2. potamodromous species who migrate locally or regionally within freshwater systems, 3. diadromous species that migrate between salt and freshwater and 4. oceanodromous species who migrate within saltwater ecosystems. Homing is an exceptional migratory life history that includes the migration of species back to their natal habitats, as is well known to occur in salmonids (Fig. 8).

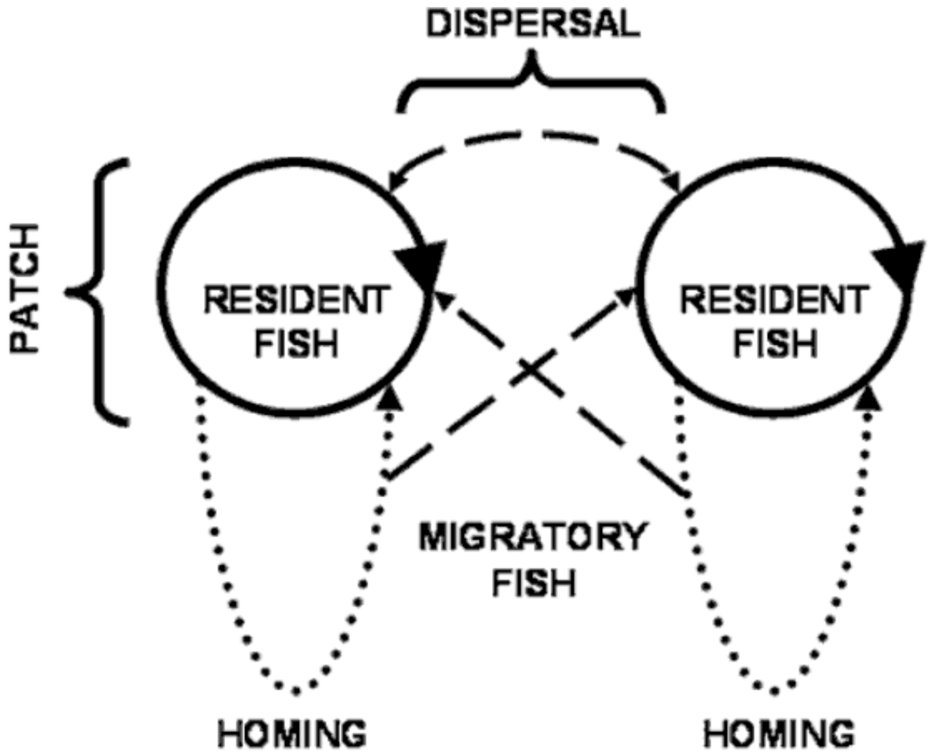


Figure 8. Generalised life history of salmonid fishes, depicting spatial structuring, migratory life histories, and dispersal pathways (from Dunham et al. 20020. Resident fish are classified as non-migratory, while migratory individuals perform homing behaviour to reproduce in their natal habitats (dotted lines). Dispersal can occur from both resident and homing populations to new habitat patches (dashed lines).

Apart from differing migratory life histories of adults a segregation of habitat patch characteristics for each life stage, egg, larvae, adult(stages) can be observed. Since the diversity of habitats that are used within a species are often much more variable compared to macrophytes and invertebrate species, additionally the scope of the scale at which connectivity and dispersal between habitat patches is important is much wider.

6.3.3 Fish dispersal and restoration

Dispersal of fishes from nearby source populations is of uttermost importance for the colonization of restored habitat, in the absence of active introductions. Even where local populations remain during restoration, dispersal can still be important. For example, Riley and Fausch (1995) found that 2 years after habitat restoration of a stream, even though all species were initially present at restored sites, dispersal was responsible for increases in abundance of three species of salmonid, rather than survival or recruitment of the remaining population.

7 Case studies

7.1 Colonization of new habitats

Ways in which invertebrates colonize lotic habitats are reviewed by Mackay (1992), relating patterns in behaviour, trophic ecology, and life history to colonization potential. Recolonisation of streams depends on four main sources: drift, upstream migration within the water, migration from within the substrate, and aerial sources, e.g., oviposition (Williams 1976). Macroinvertebrate propagules for colonization are made increasingly available by asynchronous and aseasonal life cycles, long oviposition periods, and refuges or propagules banks in the streambed or neighbouring waterbodies. Furthermore substrate texture and associated food supplies, competition, and predation shape the colonisation sequence (Mackay 1992). In the colonisation sequence, first, epilithon-browsers and filter feeders can use the resources of smooth stones; gatherers colonize as fine detritus accumulates; grazers increase as periphyton becomes established. Shredders and predators tend to be late arrivals. Recurring ecological patterns among early colonizers suggest that knowledge of the hydrologic regime, food resources, and dominant taxa can be used to predict the overall resilience of a stream community and the time to restoration.

Examples of colonisation sequences after restoration (Tikkanen et al 1994, Lorenz et al 2009) show that new taxa in restored reaches, have a high dispersal potential and are thus often the first colonizing species. For example Lorenz et al (2009) show that in two restored German lowland stream reaches he majority of the new species belong to the orders Coleoptera (e.g., Orectochilus villosus, Nebrioporus canaliculatus and Laccobius minutus) and Trichoptera (e.g., Oecetis ochracea and Anabolia nervosa), with adult flight stages and high dispersal potential as a characteristic for the colonising species. Other insect orders and particularly rare species are underrepresented indicating a long time to restoration for species less prone to dispersal.

The presence of near-natural and undisturbed sites is essential for re-colonization (Spa¨nhoff and Arle 2007). These sites should exist within flight distance of the insects or within range of the dispersal capacity of other invertebrate species. Brooks and others (2002), Muotka and others (2002), and Parkyn and others (2003) observed is therefore restoration may fail without the presence of source populations. A study by Lepori et al. 2005 shows that after the initial recolonisation, the diversity of macroinvertebrates did not increase markedly in the restored section, possibly due to lack of source populations

Apart from colonisation sequences of stream patches, extinction and colonisation sequences after (natural) disturbances have been described. For example, the sequential local extinction of stream insects during drought is largely a function of their resistance to changing abiotic and biotic conditions (Boulton & Lake 2008), and this can be paralleled to processes in restoration. For example, the sequential local extinction of stream insects during drought, shows that the first aquatic insects to be impacted are those requiring cool, well-oxygenated, fast flowing water. Loss of these conditions soon eliminates torrenticoles such as blephariceríd dipteran larvae and several families of mayflies, stoneflies and caddisflies. Furthermore, these highly specialised species take a long time to recolonise (Williams, 2006). In degraded ecosystems, occurring at the end of the disturbance gradient, species have often long been exposed to the disturbance and only resistant species remain. Species that are well adapted to natural regimes tend to have disappeared and are least likely to return In addition, source populations, for example in a different catchment, often have simultaneous gone extinct by the same mechanism (eg reduced water quality or connectivity). Restoration measures may fail if there are no stream reaches in the vicinity that can act as sources of fauna (Lorenz et al. 2009).

In general, rates of colonisation will depend on the distance between the restored area and the source populations (Kareiva 1990) and additionally the dispersal abilities of the relevant species. Restoration success is dependent on the possibility of source populations to colonize the new and restored habitat. Since most dispersal is known to occur over short distances (Bond & Lake 2003) populations in the vicinity of a restored site are most likely to act as source populations and restoration efforts are preferably focussed on habitat patches in the vicinity of these populations (Purse et al. 2003).
Conceptualised by Spanhoff and Arle (2007) colonisation in streams occurs rapidly from refuges in the restored stream section, but a much longer time is needed for the colonisation of new species from other stream systems (Fig. 9).

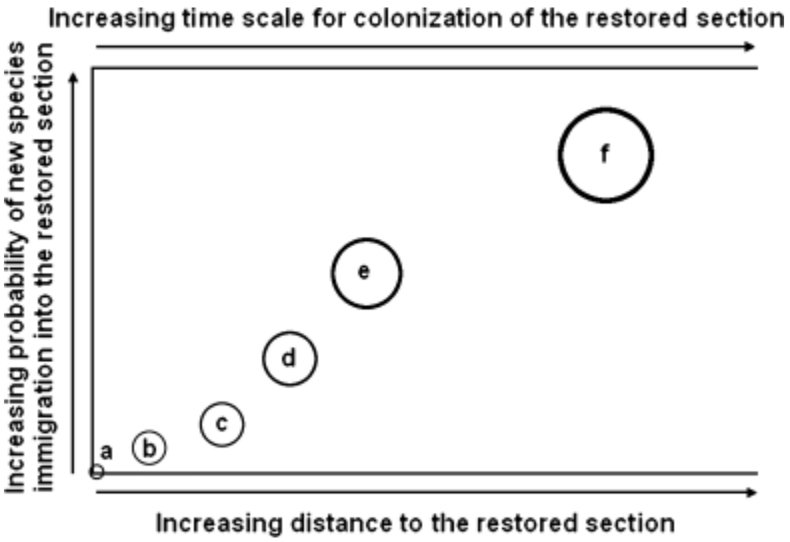


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Figure 9. Locations from which aquatic organisms can colonize restored sections in the upstream reach of a stream. The size of the circles represents the species pool of the particular location relative to the species pool of the stream section after restoration. a, Refuges in the restored stream section (e.g., hyporheic zone); b, upstream reaches; c, downstream reaches; d, tributaries; e, neighboring streams; and f, other stream systems. Immigration from a to d can be facilitated by downstream drift or upstream movement, whereas immigration from e and f can be facilitated

by flight (winged insects) or phoretic dispersal only (larvae of various aquatic invertebrates, e.g., water mites or mussels). The distances of b, c, and d depend on the location of the restored section within the stream system.

Post-restoration recovery rates of macroinvertebrates are highly variable and have been described ranging from within 1 year (Biggs et al. 1998; Laasonen 1998; Brooks et al. 2002; Moerke et al. 2004) and others failing to detect recovery even after several years (Fuchs & Statzner 1990; Friberg et al. 1998).

Despite some examples of taxa that are occasionally known to disperse over large distances (e.g. dragonflies, Wikelski et al. 2006 of Golden perch Bond & lake 2003), most direct studies that include colonization of restored ecosystems refer to very small spatial scales (Mackay 1992). Studies that include information on colonisation, incorporating source populations at a larger scale are often based on genetic patterns (Hughes et al., 1998; Wilcock et al., 2001; Monaghan et al., 2002; Schultheis and Hughes, 2005) or isotopic markers (Briers et al., 2004; MacNeale et al., 2005).
Cross-catchment dispersal has been rarely described, but few studies show that dispersal, especially of insects with flying adults, is occurring across catchments (Masters et al 2007). For example, a study encompassing the ecological recovery of streams from acidification, provides direct evidence for inter-catchment dispersal. Eight species from the orders of Ephemeroptera, Plecoptera and Trichoptera were caught as adults alongside acid streams where larvae never occurred in 21 years of benthic sampling. In this example it is rather the unsuitability of the habitat, rather than the dispersal capability of species that limits recovery of the stream ecosystem. Insect dispersal between catchments, although still sparsely studied, has wider relevance to the recovery and restoration of river ecosystems following basin-scale impacts. Especially when source populations have simultaneously died out, restoration can only be achieve through long distance dispersal or by actively introducing source material.

When source populations are locally of regionally conserved, colonisation might originate from neighbouring sources. As shown by Hughes (2007) dispersal of freshwater taxa across catchments is subsidiary. She used genetic data from a range of freshwater species to assess the importance of life cycle and position in the landscape (i.e. upland versus lowland streams) on connectivity patterns (and thus recolonisation potential) among populations.
The research showed that in general, except for aquatic insects with an adult flight stage, contemporary dispersal across catchment boundaries is negligible. Dispersal among streams within catchments appeared to be more limited than was predicted from knowledge on life histories, except for fish in lowland rivers and streams. In conclusion, this study indicates that with the exception of some flying insects, and fishes in lowland rivers, natural recolonisation of restored sites is only likely from sites within the same stream. If a species has disappeared from the whole stream, then restoration of habitat alone may not be sufficient for its re-establishment (Hughes, 2007).

Since some studies indicate that dispersal capability does not limit recovery of freshwater ecosystems (Masters et al. 2007), other factors are hypothesized to affect

colonization and colonisation time. These factors include: mating or oviposition behaviour, the presence of obstacles, 'propagule pressure' and the availability of oviposition substrata and of different connected habitats related to different life stages (Blakely et al 2006).
A study of Blakely et al. (2006) focused on the causes of the lack of macroinvertebrate community response to restoration works in 4 different urban streams in New-Zealand. They showed that adding boulders as oviposition substrata for caddisfly species enhances the number of deposited egg masses in some locations. Furthermore, road culverts showed to impede upstream flight. Both the availability of oviposition substrata as barriers to upstream flight seem to cause a lack of recruitment in upstream reaches of urban streams, thereby slowing down the colonization speed of these restored streams.

A study by Jahning & Lorenz (2008) investigated the effect of substrate availability on macroinvertebrate diversity following stream restoration. In Germany stream restoration measures often included re-establishing multiple channels (from single-channel streams) to increase habitat heterogeneity. It was hypothesized that increased habitat heterogeneity will lead to different macroinvertebrate communities on similar substrates. When comparing differences in macroinvertebrate assemblages in single- and multiple-channel stream it showed that different substrates host different assemblages, however assemblages on similar substrates in single- and multiple-channel sections showed only minor differences. The results indicate that stream restoration projects that incorporate a diversity of substrates, including high quality habitats (e.g. large wood), will create stepping stone habitats for re-colonisation of a diverse macroinvertebrate assemblage. The availability of different substrata in this case influences colonization potential of the macroinvertebrate community.

A study by Brederveld et al (2006) compared species compositions in seven restored sections to those of seven nearby unrestored sections within the 3-5 year period after restoration. They attempted to link differences in species’ colonization success to the species presence in the regional species pool, and to the species’ dispersal abilities. The results showed that colonization success is highly dependent on abundance in local and regional species pool for both plants and macroinvertebrates. For plants dispersal strategies have an additional influence on colonization success, with short living plants with high production of small, well dispersed seeds colonizing best. Macroinvertebrates were probably limited by the lack of connectivity on larger spatial scales, but the existence of dispersal constraints for macroinvertebrates could not be confirmed. Effects of increased plant diversity might improve habitat suitability for macroinvertebrates, hence improving colonization success on a larger time scale.

7.2 Retention and colonisation potential of hydrochorous plants

The hydrologic regime is considered to be one of the most important factor influencing transport and deposition of propagules along rivers (Engstrom et al 2009) governing survival and colonisation of hydrochorous plants.
In wetlands, water level fluctuations engender temporal variability in drift and aerial colonisation of

In a Swedish stream formerly channelized for timber floating, restoration measures resulted in a more natural flow regime and more complex morphology of the stream. It was hypothesized that these restoration measures would enhance the retention of propagules. The study demonstrated that restoration of channel complexity through replacement of both boulders and large wood indeed enhanced retention of plant propagules. However, retention after restoration was only larger with high flow rates, while at low flow rates water borne propagules were less likely to reach riparian areas suitable for establishment (Engstrom et al 2009).

Other research suggests (Riina 2008) both retention and colonization are of importance to hydrochorous plants. Survival of dispersed propagules (shoots and seeds), were studied in a 300-m stream reach in a macrophyte-rich lowland stream during one growing season The number of drifting shoots and seeds per day during the growing season caused no constraint to colonisation. The main bottleneck for plant colonisation in macrophyte-rich lowland streams turned out to be the primary colonisation (development of attached roots in the sediment from vegetative propagules or seedlings) of retained shoots and seeds, due in part to low retention success and to unsuccessful colonisation of retained. Therefore it is important to enhance retention and colonisation of propagules by creating areas of low flow and by providing physical obstacles to work as retention agents in the stream.

A study by Yallop & O'Connol (2000) followed the first two years of the colonisation three newly created lagoons in 1995 and inundated between 1996 and 1997. After a period of 2 years the flora was dominated by filamentous algae. Macrophytes *Zannichellia palustris* L., *Chara spp*. And *Myriophyllum spicatum* developed in relatively clear shallow waters. Since one of the lagoons is predicted to receive most propagules, but at the same time is the most sheltered lagoon with reduced turbidity, inter-lagoon difference could not be appointed to a single factor.

7.3 Using population genetics to select and evaluate restoration measures

A case study in Belgium by Raeymaekers et al. (2009), reconciling the restoration of the native fish fauna with the preservation of historical water mills, showed that population genetic structure of fish can be used to assess the genetic connectivity and additionally the impact of fragmentation on a local catchment scale. In this study the population genetic structure of *Gasterosteus aculeatus*, was used to assess connectivity in the Zwalm sub-basin. Dispersal was lower in above- than in below-mill populations, and water mills provoked genetic differentiation and loss of genetic variation. The impact of individual mills strongly increased with upstream distance and water mill height. One mill caused significant genetic differentiation, despite the presence of a fish passage. This detailed picture of the genetic connectivity in stickleback is indicative for the basin's fauna, since many species share the same migratory pathways and barriers to dispersal.

Based on the detailed genetic structure of the stickleback restoration measures were proposed, i.e. building a fish passage. Furthermore reassessment of stickleback genetic structure after a decade was suggested to reveal whether restoration measures have been effective.

The study showed that population genetic studies may be particularly useful during the selection of river restoration measures. Secondly the alterations in the genetic structure after restoration can be used to assess restoration output.

In replanting schemes for macrophytes in wetland restoration often two option are discussed 1) the use of local clones or propagules, assumingly locally adapted 2) a diversity of clones or propagules, with a maximum genetic diversity promoting adaptation based on the conditions at the (to be) restored site. Evidence that genetic differences within species can affect restoration outcomes is anecdotal.
In a tidal wetland restoration site in Delaware Seliskar (1996 & 2000) planted cordgrass (*Spartina alterniflora*) from Georgia, Delaware and Massachusetts and *Distichlis spicata* from California, Utah, Delaware, and Georgia. The genotypes from different locations differed in stem density and height, belowground biomass and depth distribution, decomposition rate, and carbohydrate allocation.
Both experiments show that local clones do not automatically provide the best option for the recreation of wetlands. For example for *Distichlis spicata* plants from the regenerated line exhibited both highest shoot biomass and a high decomposition rate (Selikar & Gallagher 2000) indicating that the introduction of alternative strains of plants might improve restoration success.
A study by Winfield and Hughes (2001) was carried out to determine the importance of choice of black poplar clones in river restoration schemes. Cuttings were collected from black poplars from a wide geographical range in Britain. Although total genetic diversity of the source trees used in this study was low, there were still significant differences in growth response and morphometric characteristics (mean leaf area, mean branch angle) among the plants derived from different source trees. The results suggest that, in restoration schemes, choice of clone affects the balance of sex ratios, viable genetic diversity and survival of plantings on varied sites.
Based on these, and other results it is recommended that restoration should be designed to ensure adequate genetic diversity for the avoidance of inbreeding and the ability to adapt to subsequent environmental disturbances (Travis et al. 2004, Koppitz & Kühl. 2000, Harris et al. 2006, Broadhurst et al 2008).
On the other hand some species consist of very restricted genetic provenances, so that planting stock should be restricted to that from the site (Adam 2009) or from the region (Rice & Emery 2003). Introductions of non-native genotypes are considered dangerous because they are hypothesised to cause disruption of natural patterns of geographic variation in genotype frequencies and introduce genes which are poorly adapted to local conditions. Intraspecific hybridisation of local and non-local genotypes may have a negative impact on the genetic structure of local which may seriously endanger both the native populations and the entire community in which the species lives (Hufford & Mazer 2003, Van der Mijnsbrugge et al. 2009).

To allow restorationists to make informed choices about whether genetic diversity should be manipulated or strictly maintained based on material of local provenance first of all the source of material should be determined for each species well in advance of restoration. Collection of source material for restoration may include stocks that have a local or even a regional extent and in some circumstances it may not be necessary to set restrictive criteria for collection (Wilkinson 2001). Since most scientific evidence of replanting success is based on terrestrial or saltmarsh ecosystems, the introductions of local or alternative genotypes of plants and animals to freshwater restoration sites deserves further attention.

In recent times it is even suggested that restoration efforts could help to anticipate on global warming e.g. by deliberately using source material from warmer sites (Rice & Emery 2003, Adam 2009). Since restored sites under global change conditions might not identical to reference of neighbouring sights use of source material that is variable enabling local adaptation might be advisable in freshwater restoration.

7.4 Assisted colonisation

Assisted colonisation (also referred to as managed relocation, assisted migration, or assisted translocation) is an attempt to establish a species or community by moving it from one part of its range to another (Macdonald et al 2002). Assisted colonisation has emerged as a potential restoration measure (Cronk & Fennesy 2001) and in the light of global change as an intervention strategy to conserve species at their outer limits (Hoegh-Guldberg 2008).

For restorationist assisted colonisation is a last-alternative option, and colonisation of restored habitat preferably depends on natural dispersal and the self- organisation capacity of ecosystems (self-design approach). Only if the propagules bank (e.g. wetland seed bank) is depleted and dispersal is highly limited, assisted colonisation is considered (design-approach). Transplantations have often been used for the conservation and reintroduction of sensitive species as mitigation for environmental impacts, which has been shown to result in typically low success rates (Griffith et al. 1989, Falk et al 1996). Several guidelines are available for the restoration of rare species, communities or ecoystems (IUCN 1998; SERI 2002) and replanting in wetlands (Cronk & Fennesy 2001). When choosing this option, some considerations must be observed:

A first consideration is, whether the establishment of species at the target location is technically feasible, and whether the abiotic characteristics of the new location match the needs of the species (Cronk & Fennesy 2001, Hoegh-Guldberg et al.2008).

Secondly, it is necessary to determine if an introduced population would be self-sustainable. Determining the minimal viable population size, the life history characteristics of the species (especially growth and reproduction characteristics), and the availability of sufficient genetic diversity help to predict the success rate (Cronk & Fennesy 2001, Broadhurst et al. 2008)

Another consideration is if the species can become a nuisance or enhance the introduction of other nuisance species (Cronk & Fennesy 2001, Hoegh-Guldberg et al.2008). Introduced plants or other organisms can have a weedy character (Cronk & Fennesy 2001) and in addition, they can carry diseases and parasites. Another factor (paragraph x and y) is that the introduction of non-local genotypes can alter the genetic structure and breeding systems of local populations. Apart from ecological risks, socioeconomic concerns must be considered (e.g. toxic plants might be undesirable in areas that are used for grazing livestock)

The impact of harvesting on the source population needs to be considered as well (Broadhurst et al. 2008).

Previous research on assisted colonisation in freshwater ecosystem, hardly ever provide a framework that can act as a guideline for risk assessment, management framework and how to proceed. Such frameworks could assist in distinguishing between circumstances that require moderate action, such as habitat enhancement (conventional restoration measures), or those that require more extreme action, such as assisted colonization.

8 Restoration constraints

8.1 Barriers to colonization and establishment

Restoration success is dependent on the possibility of populations to colonize the new and restored habitat. Due to knowledge gaps and scale discrepancies, both habitat and dispersal constraints still restrict restoration outcome in many programmes (Lake et al. 2007).

For example, since most dispersal is known to occur over short distances and linearly in streams, instream barriers can largely constrain the possibilities of colonization (Bond & Lake 2003). A study by Blakely et al. (2006) revealed formerly unrecognized physical barriers to aquatic insect colonization in urban streams. Road culverts showed to act as partial barriers to upstream flight with 2.5 x more individuals occurring downstream of road culverts than upstream.

Apart from 'hard barriers', like dams and weirs, soft barriers are associated with the isolation of restored habitat. This isolation might be related purely to distance of the restored site to the source population, to unfavourable intervening habitat or to dispersal constraints of the target species of interest, resulting in unlikely colonisation of the restored habitat (Bond & Lake 2003).

Even without dispersal constraints, colonization that leads to actual establishment might be restricted due to insufficient habitat quality (habitat limitation or establishment limitation) (e.g. minimal habitat size, lack of oviposition sites) (Blakely et al. 2006).

8.2 Introduction of non-native species

Freshwater systems are suggested to be particularly prone to invasions by alien species, as they are utilised intensively by people in ways that maximise opportunities for spread and establishment of invaders (Schreiber et al 2002). Invasion of exotic species after restoration may play a role in the restoration process in the different ways. Due to their life history characterization as being both good colonizers after disturbance and persistent community members, exotic species may respond rapidly to habitat restoration and are likely to return after removal (D'Antonio & Meyerson 2002), thereby outcompeting native biota (Bond & Lake 2003). Additionally, although native species often become demographically vulnerable as a result of habitat fragmentation, invasive or otherwise undesirable species are often well established in degraded lands. These species can thereby establish a dominant position in degraded systems and, thus, management efforts can have the unintended effect of facilitating the spread of these species (Suring et al 1994). Furthermore, formerly isolated ecosystems could become connected due to restoration measures that enhance connectivity leading to introductions exotic species. Often these exotic species are the first species to arrive, possibly indicating a life history advantage.

Once introduced invading species can largely alter the (a)biotics of a restored site. Invading species have been shown to compete for resources (food and space) with native species. Furthermore, they can change the recipient environment by acting as an ecosystem engineer, or even by providing habitat for native species (Schreiber et al. 2002).

Examples of connectivity restoration leading to unintended spread of invasive species are numerous (Kondolf et al. 2006). For example, Paillex et al. (2009) focused on the macroinvertebrate response related to the increases in lateral connectivity of secondary channels. The effects of an increase in the hydrologic connectivity on the biological characteristics of macroinvertebrate assemblages were assessed with a model indicating gradient maximum colonization potential in the most connected channels. Nevertheless, the post-restoration sampling showed a large proportion of colonizers were favoured by the restoration operations and non-native species occurred in the restored channels. In their recommendations the scientists state that in restoration projects a diversification of the hydrologic connectivity of channels is to be preferred over maximum hydrologic connectivity (Paillex, 2009).
Another example describes the invasion of zebra mussel *Dreissena polymorpha* to formerly isolated basins that were connected via canals in North American Great Lakes. Zebra mussel initially invaded via ballast water, and subsequently invaded through canals and lakes, as did some species of fish (Mills et al. 1993). Additionally intercatchment connections in Australia caused formerly isolated fish species to become introduced to new watersheds, thereby threatening local species' existence (Lintermans 2004).

In some recent cases, naturally connected systems are being intentionally fragmented to prevent or hamper introduction of undesirable invasive fish species. For example, the use of dams to prevent sea lampreys from reaching spawning grounds in Great Lake tributary streams (Porto et al. 1999). Another example is the availability of only small scour pools for native fish, too small to support larger-bodied exotic invaders (Bond & Lake 2003).

Although most effects of invading species are classified as negative and unwanted, some studies indicate that invading species might positively influence native species (Rodriguez 2006). For example, in a study by Schreiber et al. (2002) experiments were carried out in which the densities of the invading aquatic snail *P. antipodarum*: were experimentally manipulated. Results showed that there were no negative effects and even a positive relationship between *P. antipodarum* densities and native fauna abundance and densities was observed. Mechanisms that lead to include habitat modification, trophic subsidy, pollination, competitive release, and predatory release (Rodriguez 2006).

In the context of restoration both negative and facilitating effects of invading species should be integrated, either to minimise invasions and their impacts or to modify the expected outcome of restoration (Jannsson et al. 2007). Furthermore, connectivity is not always good, nor always bad since like all changes, connectivity is likely to benefit some organisms at the expense of others (Kondolf et al 2006)

8.3 Considerations of scale in restoration projects

As restoration effort usually occur on a small scale (i.e. habitats), tailored to the important scale for target species, and ecological processes subject to restoration on a large scale, there is a discrepancy between the two (Bult et al 1998; Jansson et al. 2007, Lake et al. 2007). This so called scoping problem can lead to a mismatch between the requirements of individual species and the scale at which habitat or connections are restored. Many scientists therefore stress the need of large scale restoration efforts (Bond & Lake 2003, Lake et al. 2007, Palmer 2009), advocating whole watershed and whole estuary restoration efforts. At the same time often socioeconomic constraints (resources and conflicts of interest) will limit projects on a large scale.

Processes related to metapopulation dynamics, dispersal and connectivity play a role on different scales and the observed scale of importance is depending on scope of the study. For example frequency of dispersal of invertebrates among lakes, depends upon perspective and spatial scale (Havel & Medley 2006): When two adjacent lakes are observed, dispersal might seem limited, since a single species is occurring in one lake, whilst being absent in another. On the other hand when genetic markers are used to study a global set of lakes, this same species is rapidly invading reservoirs in new regions indicating nearly unlimited dispersal capability.

A second example is the scale at which dispersal and colonization processes in stream ecosystems are important for restoration. Within stream colonization of aquatic invertebrates through drift is a well studied phenomenon (Townsend en Hildrew 1976). On a larger scale, i.e. catchment or even across catchments, other processes (e.g. insect flight) become important and these are less frequently studied.

Freshwater ecosystems are typically embedded in a heterogeneous landscape and restoration sites are not only influenced by activities in the target area, but also by processes around it (Wiens 2002). Connectivity among the different components, that usually differ largely in scale is important for targeting habitat at a specific habitat.

Apart from ecological processes the right scale of habitat is important as well. For many species habitat size is of central importance and largely predicts the viability of the metapopulation (Bond & Lake 2003). Therefore even if correct types of habitat are restored, but at the wrong scale, still restoration may not be effective.

In restoration ecology another scaling issue occurs, when knowledge is to be extrapolated to a different scale. It might not be possible to extrapolate knowledge on abiotic factors known to work on a specific scale to a different scale since assumptions and generalizations are scale specific. Therefore it is difficult to incorporate all the required information at the right scale that is needed to predict the processes by which restored ecosystems develop.

Determining the right scale for species, the extent of the required (different) habitats, the scale a which processes like dispersal and connectivity occur in the context of restoration and even the scale at which large-scale processes that eventually influence habitat quality is an important aspect of successful restoration. However the spatial scales that are most important often remain poorly understood.

8.4 Accumulation effects

As outlined restoration projects often deal with more then one factor important for restoration outcome. In many systems both the lack of landscape connectivity and sufficient local propagule sources severely limit the regeneration of native species in degraded communities. Causes of declines of source populations of native species can be habitat destruction and fragmentation, which will limit the effectiveness of regional pools as a source of propagules for recolonisation. This, combined with the absence of native species in the degraded site and the loss of a native propagule bank, limit the regenerative ability of many native species in restoration projects (Surin et al 1994).

So in order to encourage re-establishment, not only local factors should be restored, but measures to improve the quality of source populations or enhance connectivity should be incorporated in restoration effort as well.

8.5 Goals and monitoring

Although a multitude of studies provide theoretical frameworks, guidelines, research needs and issues that are important for freshwater restoration, only few studies provide evidence of how this ecological knowledge might enhance restoration success. Goals of restoration projects typically encompass a multitude of objectives (species groups, ecological, cultural and landscape values) and a multitude of measures. Thus, evaluation of the response of a single factor to a single measure tends to be difficult (Roni et al. 2008).

A second major bottleneck is the lack of sufficient monitoring (Rodi et al. 2008. Palmer et al 2005), allowing for insufficient learning from both successful and unsuccessful restorations (Jansson et al 2007, Palmer 2009). This holds especially true for dispersal, connectivity and metapopulation dynamics. As discussed in chapter 3, dispersal is extraordinarily difficult to study (Macdonald et al. 2002) and methods to study dispersal have many restrictions even when a combination of techniques (direct and indirect) is used. In addition these techniques are mostly used to study dispersal and connectivity in existing ecosystems and are hardly ever used in restoration projects.

Furthermore, conclusions from studies on the effects of dispersal constraints and connectivity constraints are almost never firm and hard to extrapolate to the restoration practice, since results are confounded by the effects of environmental constraints, which can not be excluded. However, the frequently occurring general recommendation in proposed guidelines for restoration projects (Palmer et al 2005, Perrow & Davy 2002), including appropriate monitoring and publishing of the results, will help to gain insight into the processes important to successful restoration and are.

9 Synthesis

Restoring appropriate habitat is still the main component of aquatic ecosystem restoration efforts. Although the importance of establishing the suitable abiotics is stressed by a multitude of studies, the awareness that other factors should be considered as well is apparent in recent recommendations on freshwater restoration (Bond & Lake 2003, Jansson et al 2007).

There are several, more ore less connected issues that are repeatedly stressed in a multitude of studies:

1) Incorporating the spatial and temporal scope (i.e. maximum and minimum) of the habitat and the connectivity between the various habitat patches, including both abiotic and biotic components;

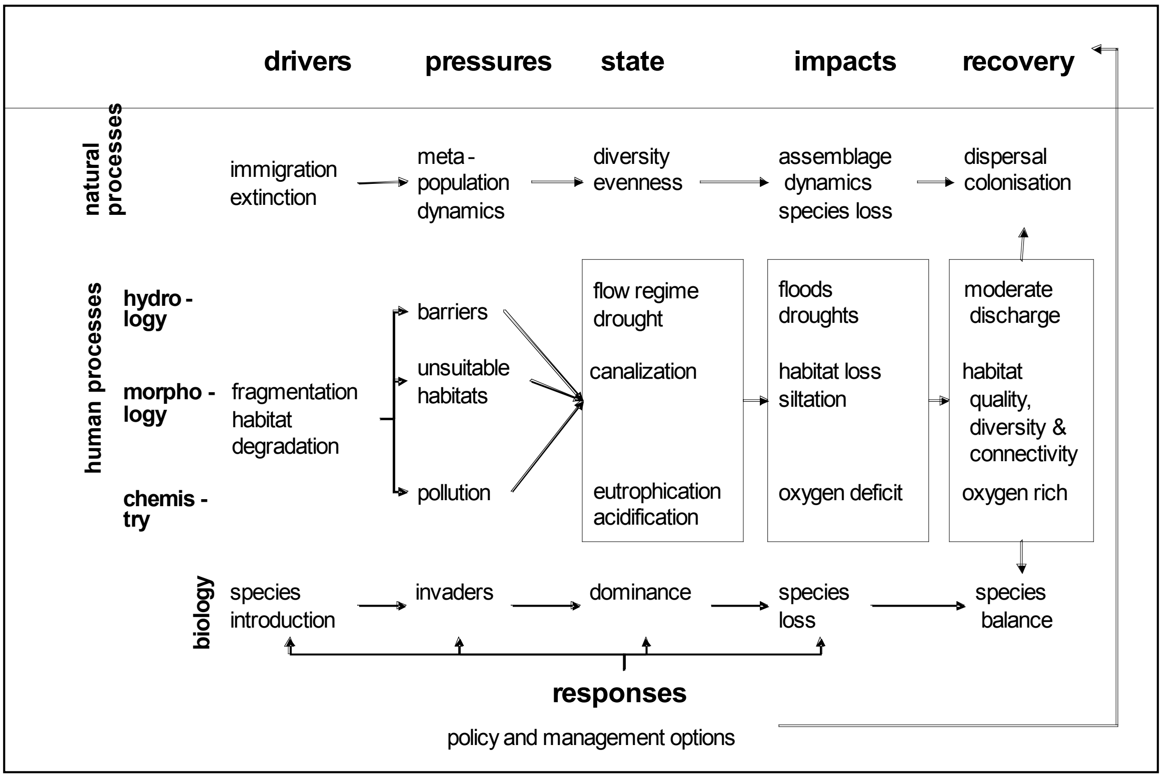
2) Incorporating the knowledge of source populations and dispersal ability or constraints in predicting restoration outcome.

However few studies attempt to match this ecological background with empirical data.

Most restoration projects incorporate the restoration of abiotic conditions to a fixed end-point, i.e. an ideal average condition. However, communities tend to be shaped by abiotic extremes and restoration planning should be shaped according to these extremes. Re-colonisation of a species is only likely when the entire scope, i.e. the maximum and minimum spatial extent and temporal duration of habitat use is restored. Furthermore, extreme events will amplify the importance of the presence of refugia. Along with habitat enhancement, restoring refugia, in this way enhancing the resistance and resilience to both natural and anthropogenic disturbances, may be critical to survival and colonisation of target populations.

Subject to many studies is the he importance of biological factors in determining ecosystem structure and function, providing both habit structure and biological interactions that shape community build up. In order to create suitable habitat for some species other species, that affect the focal species' habitat, need to be involved in restoration efforts and planning. Furthermore the restoration target often includes community build up, indicating the importance of incorporating the role of biological interactions in restoration planning. This includes accounting for a long restoration period that may be needed to restore ecosystem function, including biotic factors.

Finally, our main aim was to construct a driver – pressure – state – impact – recovery chain for the biological processes of metacommunity dynamics and connectivity: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morpho-logy
chemis-try
fragmentation habitat degradation
barriers
unsuitable habitats
pollution
flow regime drought
canalization
eutrophication acidification
floods droughts
habitat loss siltation
oxygen deficit
moderate discharge
habitat quality, diversity & connectivity
oxygen rich
biology
species introduction
invaders
dominance
species loss
species balance
responses
policy and management options

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Appendix 1