Lotic dispersal of lentic macroinvertebrates

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Little is known on dispersal of lentic macroinvertebrates. We quantified dispersal of lentic macroinvertebrates through pond connections in a highly connected pond system, and investigated how dispersal rates were affected by connection properties and time of the day (day, night). Furthermore, by comparing the composition of assemblages of dispersing macroinvertebrates with the macroinvertebrate assemblages of source ponds, we tested whether dispersal was neutral or a taxon-specific process. We found that many taxa dispersed through the pond connections. Taxa richness of the dispersing macroinvertebrate assemblage was proportional to taxa richness in the source ponds. The number of individuals that dispersed, however, was not related to source pond densities, possibly because of the highly patchy distribution of lentic macroinvertebrates within ponds. Elevated dispersal rates were recorded for Baetidae, Chironomidae and Physidae, indicating a taxon-specific use of pond connections as dispersal pathway. None of the physical properties of the connections affected dispersal. Macroinvertebrates dispersed more during the night than during daytime. Of seven tested families, Chaoboridae and Chironomidae showed higher dispersal during the night, probably resulting from diel vertical migration, since pond connections mainly transported near-surface water. Flying and non-flying invertebrates dispersed equally frequent through pond connections. For non-flying invertebrates that disperse infrequently over land, dispersal through pond connections may provide an important additional means of dispersal.

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Understanding spatial and temporal dispersal patterns has become an important issue in landscape management and conservation biology. Dispersal of individuals among habitats may affect the dynamics, persistence and genetic structure of local populations (Slatkin 1987, Peckarsky et al. 2000, Malmqvist 2002). At a higher level, the same process may generate changes in community structure in both source and sink habitats (Bilton et al. 2001, Bohonak and Jenkins 2003). Despite its importance, in many organisms the nature and extent of dispersal remain poorly known, mainly due to methodological problems such as the vague delineation of habitats and populations (e.g. many marine and terrestrial systems) or the numerous difficulties involved with detecting or quantifying dispersing organisms (many insects and freshwater organisms) (Bilton et al. 2001, De Meester et al. 2002).

Freshwater invertebrates occur in habitats that represent discrete sites surrounded by an inhospitable terrestrial landscape. Dispersal between habitats is achieved using a variety of mechanisms such as active flight in adult insects and passive dispersal by animal vectors (phoretic dispersal), or wind (Brown et al. 1997, reviewed in Bilton et al. 2001). Dispersal in freshwater invertebrates is notoriously difficult to obtain directly, and the extent and modes of dispersal remain poorly understood (Bilton et al. 2001, Hoffsten 2004). As a result, a large number of studies rely on indirect
estimation of dispersal from colonization events (Brown et al. 1997, Rundle et al. 2002, Anderson and Smith 2004), or the use of markers like stable isotopes (Caudill 2003) and genetic markers (Meyran et al. 1997, Hughes et al. 1999, Kelly et al. 2001). Colonization events may provide a relatively good view on the rate and extent of dispersal, but, generally, information about the origin of the organisms and the mechanism of dispersal is lacking. Stable isotope labeling may enable one to track the origin of dispersing animals, but its applicability is largely restricted to systems with a set of well-known and clearly defined source habitats. Notwithstanding its undisputable merits, inference of dispersal using genetic markers is not yet an exact science and several methodological problems remain (Bossart and Prowell 1998).

Several surveys have concluded the existence of some agreement between genetic and demographic methods (e.g. Berry et al. 2004), but many have indicated discrepancies in specific cases (Rousset 2001 and references therein). More specifically, only a fraction of dispersal may translate into effective gene flow when establishment success is low due to local interactions (De Meester et al. 2002). Clearly, indirect approaches are not sufficient to understand dispersal patterns, making direct estimates essential (Bossart and Prowell 1998).

A significant number of ponds and reservoirs worldwide were created or strongly modified by human activities. Often, multiple ponds were created close to each other, and connected by canals, small streams or overflows (e.g. ponds designed for fish-farming). In connected systems, these aquatic connective elements may constitute an important pathway for dispersal of aquatic invertebrates that is additional to dispersal over land. Compared to the latter, dispersal through connective elements is well delineated and therefore relatively easy to quantify. Moreover, pond connections can be very important dispersal pathways, as has been shown for zooplankton, both in terms of numbers (high dispersal rates reported by Michels et al. 2001a, Walks and Cyr 2004), as well as in terms of its prominent effects on the composition of the local communities (Cottenie et al. 2003), and the structure and genetic composition of local populations (Michels et al. 2001b). For lentic macroinvertebrates, however, no quantitative studies exist that investigated the potential of pond connections for dispersal.

This study aims to directly quantifying dispersal patterns of lentic macroinvertebrates through pond connections in a highly connected pond system. More specifically, we will consider three aspects of dispersal that have important ecological ramifications and are largely unknown for aquatic insects. First, we will evaluate whether the dispersal tendencies through pond connections are taxon-specific. Additionally, we will test whether dispersal via pond connections differs between macroinvertebrates with a different overland dispersal mode. As dispersal over land occurs with a higher frequency in active dispersers (flying insects) compared to passive dispersers (dispersal by wind or phoretic dispersal) (Brown et al. 1997, Hoffsten 2004), we will specifically evaluate whether passive overland dispersers compensate for this by increased lotic dispersal. This knowledge is of crucial importance, for example in modeling dispersal in a metacommunity context. Second, the nature of connecting structures is a critical point that has received much attention for dispersal over land (Goodwin and Fahrig 2002, Wratten et al. 2003), but has largely been neglected in dispersal through water. The pond connections in our study system vary considerably in connection type (piped, open rivulet), discharge rate, flow rate and length, which allows us to investigate the effect of these physical connection properties on macroinvertebrate dispersal rates. Third, dispersal patterns may strongly differ between day and night. In lotic systems, for example, it is well known that dispersal by drift is more frequent at night when animals suffer less predation risk by fish (Cowell and Carew 1976, McIntosh et al. 2002). In lentic systems, the documented differences between day and night in activity and vertical distribution of macroinvertebrates (Marklund et al. 2001, Berendonk et al. 2003) may change the actual subset of the macroinvertebrate community that is prone to dispersal, since overflows only transport water from a subset of the water column. To test for a diurnal pattern in dispersal, we sampled a subset of the pond connections during both day- and nighttime.

**Material and Methods**

**Study area**

The study area is the Nature Reserve “De Maten”, a protected heath land of ca 300 ha situated near Genk in the northeastern part of Belgium. The reserve comprises 34 small, shallow and eutrophic ponds, connected to each other by a complex network of rivulets and overflows (Michels et al. 2001b, Cottenie et al. 2003, Fig. 1). The ponds in the complex are in an approximately linear setting, with a 15 m drop between the most upstream and the most downstream ponds, causing a unidirectional water flow through the system. The ponds vary in size from 0.07 to 9.53 ha and have an average depth of 55 cm. Macrophytes are present in all ponds, but the area covered strongly varies among different ponds (1–40%). In spite of the high level of connectivity, the composition of the macroinvertebrate communities differs considerably among the ponds (Van de Meutter et al. 2005).
Sampling dispersal through pond connections

As is common in fish ponds, the water of pond connections (both piped and open) in “De Maten” enters and leaves the lakes through cylindrical tubes (20 cm diameter) that are incorporated in the dykes. This allows for easy quantitative sampling of dispersal from pond to pond through these connections. Therefore, we used a 20 cm long PVC tube (diameter 20 cm) with a conical net (45 cm long, mesh size 500 μm) attached to its end, which was mounted on the end of the inlet of the receiving pond. Inlets were usually situated halfway down in the water column of the receiving pond; outlets were all situated near the water surface of the source pond.

In total, 28 pond connections were sampled once during daytime for a period of 6 h during 23–26 September 2003. To test for day/night differences in dispersal rates of macroinvertebrates through the pond connections, we sampled 20 out of these 28 pond connections in an identical way during nighttime (starting 2 h after sunset) on 28 and 29 September 2003. Climatic conditions during the entire sampling period were relatively constant with frequent showers and rain causing high flow rates. Dispersal samples were fixed in 4% formaldehyde in the field and all macroinvertebrates were sorted in the laboratory. Identification of macroinvertebrates was achieved to family level, except for Actinida, Hirudinea and Oligochaeta, which were not further identified. For convenience, we will use the term “families” when referring to any of these taxa.

Physical properties of pond connections

We determined four physical properties of the pond connections that could possibly influence macroinvertebrate dispersal rates: length of the connection, flow rate, discharge volume and type of connection. Length refers to the total distance traveled by the water through the connection from one pond to the other, and was measured in the field (short connections) with a tape measure or calculated from topographical maps to the nearest 5 m (connections >30 m long). Flow rate was defined as the difference in time between adding salt to the water at the inflow of a connection and the resulting peak in conductivity measured at the outflow or at 20 m from the inflow (long connections), divided by the distance between both. We calculated discharge volumes (l/s) as the product of the surface area of a cross-section of the water flow and the flow rate. Finally, we categorized pond connections in two groups: completely piped connections and small open rivulets with a small pipe at their inlet and outlet. The physical properties of all sampled connections are summarized in Appendix 1.

Pond sampling

To be able to relate the species composition in samples of dispersing macroinvertebrates through connections to the macroinvertebrate composition of the source pond, we sampled the macroinvertebrate community of 15 source ponds (see Appendix 2) once during daytime between 18 and 22 September 2003. Samples were taken
by wading the ponds and sampling with a net (24 × 24 cm, mesh size 500 μm). Samples were standardized in both time (10 min) and length (sampling along a littoral trajectory of 75 m). Sampling trajectories represented all major littoral microhabitats in their proportion present in a pond. The sampling error of this method was tested by comparing replicate samples of three ponds in De Maten, and was shown to be low and negligible compared to inter-pond differences of invertebrate community structure (see Appendix 3). The sampling procedure includes epiphytic and free-swimming littoral macroinvertebrates, but excludes typical benthic species. Pond samples were treated identically as the samples of dispersing macroinvertebrates.

Statistics

To investigate the relationship between the number of dispersing macroinvertebrates and the number of macroinvertebrates in source pond samples, and between the number of dispersing families and the number of families in source pond samples, we applied regression analysis. Since only daytime samples were available for all ponds, nighttime data of dispersal were not used in these analyses (N = 14). To test whether dispersal tendencies through the pond connections were family-specific (i.e. whether some families were over-represented in the dispersal samples based on their relative abundance in the source pond), we performed an ANCOVA. We included Family as the categorical variable, with family-specific dispersal abundances per sample as the dependent variable (N = 15/family) and with the respective number of individuals of each family in the source ponds as the covariate. Significant effects of Family indicate that families have different corrected dispersal rates, and interactions between Family and the covariate indicate that the relation between the source density and dispersal rate differs between families. Significant effects of Family were further explored with post-hoc Fisher LSD tests. Because prevalence and density of many macroinvertebrate families in the source ponds were too low to do reliable statistical testing, we selected the ten macroinvertebrate families with the highest median numbers in the source ponds: Acroloxidae, Baetidae, Chironomidae, Coenagrionidae, Corixidae, Culicidae, Dixidae, Limoniidae, Physidae and Pyralidae. To test whether lotic dispersal in active overland dispersers (taxa with flying adults; Baetidae, Chironomidae, Coenagrionidae, Corixidae, Culicidae, Dixidae, Limoniidae and Pyralidae) differs from that in passive overland dispersers (taxa that cannot fly; Acroloxidae, Physidae), we repeated the ANCOVA, but with Dispersal mode and Family nested in Dispersal mode as the categorical predictors. Possible effects of connection type, connection length, discharge volume, and flow rate on the number of dispersing macroinvertebrates and macroinvertebrate families, were evaluated using an ANCOVA with the number of dispersing macroinvertebrates or macroinvertebrate families as the dependent variable, connection type as the categorical predictor, and connection length, discharge volume, and flow rate as the covariates. To test whether dispersal rates of macroinvertebrate families were differentially affected by the connection characteristics, we performed an ANCOVA with the numbers of dispersing individuals for seven macroinvertebrate families as the dependent variable (N = 28/family), with Family and connection type as categorical predictors and with connection length, discharge volume and flow rate as the covariates. Since the effect of the connection characteristics on dispersal can only be evaluated for macroinvertebrates that frequently disperse, only seven families that occurred in five or more daytime dispersal samples were used in this analysis: Chironomidae, Coenagrionidae, Corixidae, Lymnaeidae, Oligochaeta, Physidae and Pyralidae.

Differences between daytime and nighttime dispersal rates for the number of macroinvertebrates and the number of macroinvertebrate families were analyzed using repeated measures ANOVA (rmANOVA), with the respective rates of daytime and nighttime dispersal as the repeats. To test whether families showed a different pattern in daytime versus nighttime dispersal, we performed a rmANOVA with Family as the categorical variable and the number of dispersing individuals of the families during daytime and during nighttime as the repeats. The following five families that were present in at least five samples (day- or nighttime) were included in the latter analysis: Baetidae (N = 11), Chaoboridae (N = 5), Chironomidae (N = 19), Oligochaeta (N = 6) and Physidae (N = 10). Samples of connections where no individuals of a particular family were obtained during both daytime and nighttime sampling were excluded from the analysis for that family.

The numbers of macroinvertebrates in ponds and dispersal samples were Log(X + 1)-transformed for all analyses to meet ANOVA and regression assumptions. Connection lengths were Log(X)-transformed. All analyses were performed using STATISTICA 6.0 (Anon. 2001). Means are given ±1 standard error.

Results

On average, 29.2±10.9 macroinvertebrates and 3.3±0.4 families of macroinvertebrates were found dispersing through the pond connections within a 6 h time interval. In total, 29 families of macroinvertebrates were observed to disperse through the pond connections, while 45 families were present in the pond samples (see Appendix 2). Six families were found dispersing through the connections, while they were not observed in the ponds:
Argyronetidae, Chaoboridae, Gammaridae, Gyrinidae, Hydropsychidae and Simuliidae. Nepidae were observed in both, but were represented by *Ranatra* in ponds and by *Nepa* in the connections. Of these families, Argyronetidae, Gammaridae and Gyrinidae were only found once in the samples. Finally, Hydropsychidae and Simuliidae are typical rheophylic families (Schmedje and Colling 1996) and have never been found before in the ponds of De Maten, despite the seasonal monitoring of all ponds over three consecutive years (Van de Meutter unpubl.). The latter two taxa likely originated from the pond connections themselves instead of from the source ponds, and they were excluded from all further analyses.

**Is the extent of dispersal through pond connections family-specific?**

The number of dispersing macroinvertebrate families was positively related to the number of macroinvertebrate families in the source ponds ($F_{1,13} = 8.59$, $p = 0.012$, adjusted $R^2 = 0.35$, Fig. 2a), but the total number of dispersing individuals did not depend on macroinvertebrate abundance in the source pond ($F_{1,13} = 2.23$, $p = 0.16$, adjusted $R^2 = 0.08$, Fig. 2b). Using the finer genus-level identifications (see Appendix 2) available for 66% of families did not change patterns found in our family-level analysis of relationships between source and dispersal taxa ($F_{1,13} = 5.29$, $p = 0.040$, adjusted $R^2 = 0.25$). After correction for differences in family abundance in the source ponds, significant differences were detected in dispersal rates among the ten selected macroinvertebrate families (ANCOVA, Family: $F_{9,200} = 3.02$, $p = 0.002$, Fig. 3). Baetidae, Chironomidae and Physidae were more likely to disperse than Acroloxidae, Coenagrionidae, Corixidae, Culicidae, Dixidae, Limoniidae and Pyralidae (Fisher LSD: all $p < 0.05$), and Chironomidae were more likely to disperse than Baetidae and Physidae (Fisher LSD: both $p < 0.001$).

**Do the physical properties of the connections affect dispersal?**

Neither the number of dispersing individuals nor the number of dispersing families was influenced by connection length, connection type, discharge volume or flow rate (individuals: all $p > 0.16$, families: all $p > 0.36$) or any of their interactions (individuals: all $p > 0.53$, families: all $p > 0.37$). The comparison of seven

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**Fig. 3.** Adjusted mean ($\pm 1$ standard error) dispersal rate (6 h) for ten macroinvertebrate families with the highest median occurrences in the ponds. Adjustment was done taking the number of individuals in the source population into account using an ANCOVA (Kerlinger and Pedhazur 1973). Family means that differ based on a LSD test are indicated with a different letter. Scaling of the y-axis is on a log-scale.

The comparison of active and passive overland dispersers yielded no significant difference in dispersal rate through pond outlets between both (Dispersal mode: $F_{1,7.79} = 0.44$, $p = 0.53$; Dispersal mode × Abundance source pond: $F_{1,3.38} = 0.034$, $p = 0.86$).

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**Fig. 2.** The number of dispersing macroinvertebrate families (A) and the number of dispersing individuals (B) through the outgoing pond connections over a period of 6 h relative to their numbers in the respective source ponds. Note that data of (B) are presented on a log-scale.
frequently dispersing families revealed no family-specific differences in their relation with the physical properties of the connections (all interactions with family: \( p > 0.35 \)).

**Does dispersal differ between day and night?**

The number of dispersing families did not differ between day and night (families: \( F_{1,13} = 1.87, p = 0.19 \)), but the number of dispersing individuals was higher during the night than during the day (individuals: \( F_{1,13} = 6.10, p = 0.028 \)). A restricted analysis only including the five most abundant families (Baetidae, Chaoboridae, Chironomidae, Oligochaeta and Physidae) showed a higher number of dispersing individuals during the night (day/night: \( F_{1,36} = 4.91, p = 0.049 \); Fig. 4), which applied to all five families (family \( \times \) day/night: \( F_{4,36} = 1.30, p = 0.29 \)). Dispersal, however, was only significantly higher during nighttime than during daytime for Chaoboridae and Chironomidae (Fisher LSD, Chaoboridae: \( p = 0.040 \); Chironomidae: \( p = 0.048 \)). No significant differences between daytime and nighttime dispersal samples were observed for the other families (all \( p > 0.64 \)).

**Discussion**

Lentic macroinvertebrates occur in isolated, island-like habitats, separated by inhospitable terrestrial landscape. Dispersal between habitats may be achieved by active flight or passive dispersal over land or, in connected systems, via aquatic connections between ponds (Bilton et al. 2001). Although dispersal is a main driver of both local and regional dynamics of species, knowledge about the patterns and means of dispersal often is poor (Bohonak and Jenkins 2003). Our results show the potential of pond connections for lentic macroinvertebrate dispersal and describe characteristics of the dispersal patterns. Dispersal via pond connections was specific with regard to taxon, not influenced by the physical properties of the connections and, at least for some families, showed a diurnal pattern. We stress that, because we used family level resolution, different patterns that exist at lower taxonomic levels (genus, species) may have been obscured. Our observations also only give a snapshot of lotic dispersal, temporal differences in dispersal rate may exist.

**Is the extent of dispersal taxon-specific?**

Family richness of lotic dispersers correlated positively with family richness of source ponds communities. Dispersal tendencies were family specific, and were higher for Baetidae, Chironomidae and Physidae compared to other families. Assuming lotic dispersal of lentic invertebrates occurs mainly as the passive transport of free-floating or swimming organisms, dispersal may be more frequent in organisms that frequently swim or float. High dispersal rates of Baetidae and Chironomidae may be due to frequent swimming in these groups, but this mechanism cannot explain high dispersal in the non-swimming Physidae. Non-swimming taxa probably disperse through the connections traveling on floating fragments of macrophytes, which may explain high dispersal rates of Physidae. Unfortunately, we do not have behavioural data to confirm this. Alternatively, different dispersal rates among families may also occur by drifting rheophilic species ending up in samples of the pond connections. Indeed, in an accompanying study we found that representatives of several families were found in connecting streams but, however, not in the physically similar incoming streams (streams originating outside the reserve, not connected to an upstream pond), suggesting many of them actually originated from the upstream ponds (see Appendix 4). Also, pipes were found not to harbour any of the families found in the ponds. As we did not find differences in dispersal between natural connecting streams and pipes (see further), clearly the majority of invertebrates found dispersing must have originated from the upstream ponds. Finally, note that our sampling method did not include macroinvertebrates living in the mud and not in the vegetation. As lotic dispersal probably occurs mainly in floating and swimming organisms, and as pond outlets were situated near the water surface, we expect lotic dispersal of larvae of mud-inhabiting species to be negligible in our study system.

Contrary to our expectations, the number of dispersing macroinvertebrates was not related to abundances in the source ponds. We suggest that this may reflect the highly patchy distribution of both freshwater microhabitats (e.g. macrophyte beds, patches of floating debris, ...) and macroinvertebrates within
these microhabitats (Diehl and Kornijów 1998, Benoît et al. 1998). Our pond sampling technique integrates macroinvertebrates over all littoral habitats and over a large volume of water. However, the macroinvertebrate community that may be actually prone to transport through the pond connections is probably spatially confined to the direct proximity of the pond outlet, and may, by chance, deviate in terms of relative abundances of families from the integrated pond samples.

Dispersal over land by lentic macroinvertebrates can be achieved actively by flight or by passive transport. Based on colonization events in new habitats and on the distribution of species across the landscape, several studies have indicated flightless organisms to exhibit lower dispersal abilities than active fliers (Brown et al. 1997, Hoffsten 2004, Van de Meutter unpubl., but see Rundle et al. 2002). In the present study, dispersal via the pond connections was relatively frequent and did not differ significantly among actively and passively overland dispersers. In actively flying macroinvertebrates, the contribution of dispersal via the pond connections to total dispersal may be negligible. However, in passively overland dispersers that only infrequently disperse, pond connections may serve as an important extra pathway for dispersal, which can shape temporal and spatial patterns in populations and communities.

Is dispersal affected by the physical properties of the connections?

Flow rate and discharge volume of pond outlets did not affect dispersal rate or taxa richness of the dispersing macroinvertebrate assemblage. This is somewhat counterintuitive, since one would expect the transported water volume to be related to the total number of macroinvertebrates transported. Again, we suggest that this may result from the highly patchy distribution of both macrophytes and lentic macroinvertebrates within the ponds, generating high variability in dispersal among pond connections. Also, the range of discharge volumes in the present study is relatively small, and dispersal rates may differ among pond connections with more diverging discharge volumes. Open rivulets and piped connections showed a similar potency for transmitting dispersing invertebrates, and supported a similar dispersal rate and dispersing macroinvertebrate assemblage.

Does dispersal differ between day and night?

Lentic macroinvertebrates dispersed more frequently during the night than during the day. As high dispersal rates probably mainly result from a high number of invertebrates in the upper water layers near the pond outlets, high dispersal rates during the night may indicate diel vertical migration of macroinvertebrates to the pond surface at night. Of seven frequently dispersing families, increased nighttime dispersal could be shown for Chaoboridae and Chironomidae. Both Chaoboridae and Chironomidae are known to perform diel vertical migrations from the sediment during daytime to the pond surface at night (Marklund et al. 2001, Berendonk et al. 2003), which is in agreement with the idea that increased dispersal results from nighttime vertical migrations towards the pond surface.

Conclusions

Knowledge about dispersal of lentic macroinvertebrates is still very scarce. This study expands the existing knowledge by showing that overflows and rivulets in connected pond systems constitute an important potential dispersal pathway for lentic macroinvertebrates, as was previously shown for cladocerans (Michels et al. 2001a) and helophytes (Kirchner et al. 2003). By impacting dispersal, pond connections may function as key regulators of metapopulation and metacommunity dynamics (Van de Meutter et al. in press). As such, connecting or disconnecting ponds can be a powerful tool in landscape management for both pest control and species conservation. For some families, lotic dispersal occurred mainly at night, probably because of diel vertical migration. Finally, dispersal via pond connections was equally frequent in active fliers and passively overland dispersers. Future research should focus on the relative effect of lotic dispersal on both genetic and community level patterns of diversity in lentic invertebrates. Assuming overland dispersal is much more frequent in active fliers, especially comparing these patterns between actively flying dispersers and passive dispersers may yield valuable insight into the relationship between dispersal rate, metacommunity structure and spatial community dynamics (Leibold et al. 2004).

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