

Drainage ditches, biodiversity hotspots for aquatic invertebrates

Defining and assessing the ecological
status of a man-made ecosystem
based on macroinvertebrates

Ralf Verdonschot



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To my parents



Graphoderus bilineatus (Coleoptera: Dytiscidae).

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Samenvatting

Sloten zijn één van de meest voorkomende zoetwaterecosystemen in Nederland. Ondanks dat deze wateren niet uitsluitend in Nederland te vinden zijn – overal in de agrarische gebieden van het noordelijk halfrond zijn sloten aan te treffen – is het Nederlandse polderlandschap met zijn uitgebreide netwerken van sloten uniek op wereldschaal. Desalniettemin is de ongewerveldenfauna van sloten erg slecht bekend in vergelijking met die van de meeste andere stilstaande wateren, zoals plassen en meren. Het geringe aantal studies dat tot nu toe in sloten is uitgevoerd, geeft aan dat sloten een hoge soortenrijkdom kunnen herbergen en kunnen worden beschouwd als belangrijke bronnen van biodiversiteit in het agrarisch gebied. Dit is verrassend voor een kunstmatig, intensief beheerd systeem met als belangrijkste functie hydrologische infrastructuur ter ondersteuning van de landbouw. Tegelijkertijd maakt de positionering in het agrarisch landschap sloten uitermate kwetsbaar voor verstoringen in de nutriënten- en organische stof-huishouding. Deze verstoringen kunnen resulteren in een verandering van een systeem met een gevarieerde flora en fauna naar een hypertroof, polysaproob systeem gedomineerd door algen, cyanobacteriën of kroos.

De effecten van extreme eutrofiëring en organische belasting op de macrofauna in sloten zijn goed bekend. De kennis van de sturende factoren die de samenstelling van de fauna in de ‘standaard poldersloot’ (de eutrofe, vegetatierijke sloot) bepalen, is echter beperkt. Deze kennishiaten, in combinatie met het feit dat er geen goed beeld bestaat van het maximaal ecologisch potentieel van sloten, maakt het moeilijk beheersplannen op te stellen om sloten dusdanig te beheren dat de hydrologische functie van de sloot gecombineerd kan worden met een ecologische functie. In dit proefschrift is beschreven hoe de ruimtelijke configuratie van habitats en de daar heersende milieufactoren op verschillende hiërarchische schaalniveaus binnen een landschap de samenstelling van macrofaunalevensgemeenschappen beïnvloeden. Verder is beschreven hoe deze kennis kan worden geïntegreerd in de monitoring van macrofauna en beoordeling van de ecologische kwaliteit van sloten.

In **hoofdstuk 2** werd aangetoond dat sloten inderdaad kunnen worden beschouwd als bronnen van biodiversiteit voor macrovertebraten in agrarische gebieden. De macrofauna van agrarische sloten in laagveengebieden werd vergeleken met die van semi-natuurlijke petgaten in nabijgelegen natuurgebieden. Ook werden de belangrijkste (a)biotische factoren vergeleken.

De verschillen in deze factoren tussen sloten en petgaten waren groot: sloten bevatten een veel kleiner watervolume, de vegetatie was veel minder gevarieerd, er traden grotere schommelingen in nutriëntenconcentraties op en ze werden regelmatig onderhouden in de vorm van maaien en baggeren. Desondanks was het totaal aantal macrofaunataxa per taxonomische hoofdgroep en het aantal vrij tot zeer zeldzame taxa vergelijkbaar met dat van petgaten. Ook wat betreft functionele eigenschappen van de aanwezige taxa waren de verschillen tussen beide watertypen gering. Verreweg het grootste verschil tussen petgaten en sloten was de grote onderlinge variatie in taxonsamenstelling tussen individuele sloten. De mechanismen die hieraan ten grondslag liggen, kunnen verklaard worden aan de hand van deterministische factoren (milieuomstandigheden, biotische interacties) of de invloed van stochastische mechanismen (processen gerelateerd aan dispersie, kolonisatie-extinctie patronen).

Sloten zijn spatiotemporele heterogene systemen; ze kunnen worden beschouwd als een telkens verschuivend mozaïek van habitats. Een belangrijke driver achter dit patroon is de grote variatie in vegetatiesamenstelling; tussen jaren en soms zelfs tussen seizoenen. Deze heterogeniteit heeft zowel menselijke als natuurlijke oorzaken en is het resultaat van: het zeer snel verlopen van de verlanding, nutriëntenpieken als gevolg van inspoeling vanaf aanliggende landbouwpercelen, het inlaten van gebiedsvreemd water tijdens droogte, de sterke concurrentie tussen plantensoorten onderling en met algen of cyanobacteriën en tenslotte het frequent maaien van de vegetatie en het uitbaggeren van het opgehoopte organische materiaal op de slootbodem. De structuur die de vegetatie die in de sloot tot ontwikkeling komt, kan worden beschouwd als de belangrijkste habitatcomponent voor de slootfauna. Planten vervullen tal van functies voor de macrofauna. Naast het produceren van zuurstof en de rol die ze spelen in de voedselvoorziening via detritus en aangehechte algen, zijn de meeste macrovertebraten afhankelijk van planten om hun levenscyclus te voltooien.

Hoe relevant is nu de plantensoortensamenstelling van de sloot? Zijn het de kenmerken van de vegetatie zelf – de bouw van de plant – die de samenstelling van de macrofauna op microhabitatschaal bepalen, of zijn factoren die op een hoger schaalniveau spelen belangrijker, zoals de nutriëntenhuishouding. In **hoofdstuk 3** is dit onderzocht met behulp van kunstmatige substraten waarmee verschillende groeivormen werden nagebootst. In een aantal in milieuomstandigheden variërende sloten werden series substraten geplaatst, waarna de macrofauna twee maanden de tijd had deze te koloniseren. Zowel de taxonomische samenstelling als de functionele samenstelling van de kolonisten (voedingsgroepen, bewegingsgroepen) werden

onderzocht, omdat verwacht werd dat een niet-taxonomische aggregatie van taxa in functionele categorieën een ander beeld zou geven dan een puur op soorten gerichte benadering. De functionele kenmerken hebben tenslotte een directe relatie met de planten. Het bleek dat de intrinsieke slootfactoren, zoals de fysisch-chemische samenstelling van het slootwater en de samenstelling van de vegetatie rondom de kunstplanten voor een groot deel de taxonomische en de functionele samenstelling van de op de substraten aangetroffen levensgemeenschap bepaalden. De directe rol van de groeivorm van de plant was klein. Toch werkten de op een hogere schaal structurerende factoren door op microhabitatschaal via de samenstelling van het epifyton op de structuren. Er was sprake van een interactie-complex waarbij de wisselwerking tussen voedingsstoffen, waterplanten en algen uiteindelijk invloed uitoefende op de faunasamenstelling.

De voortdurend wisselende milieuomstandigheden en beschikbaarheid van habitat in sloten maakt het noodzakelijk voor de macrofauna om levensstrategieën te hebben waardoor ze in staat zijn om te gaan met veranderingen. Mobiliteit is hierbij een zeer belangrijke eigenschap. Door zich te verplaatsen kunnen de ongewervelden plekken opzoeken die qua (a)biotische omstandigheden geschikt zijn om hun levenscyclus te voltooien. Dit kan op kleine schaal plaatsvinden, maar ook op landschapsschaal: verplaatsingen van honderden kilometers zijn mogelijk. De macrofauna die momenteel in sloten te vinden is, was ooit de fauna van relatief productieve beek- of rivierbegeleidende wateren en moerassen. Als gevolg van verlanding is evolutionair gezien de levensduur van individuele wateren van deze typen zeer kort. In de loop van de evolutie zijn dispersiegerelateerde eigenschappen dan ook sterk ontwikkeld binnen de macrofauna. De verschillen in dispersiecapaciteit tussen soorten kunnen leiden tot een discrepantie tussen de ruimtelijke verdeling van omgevingsfactoren en de aanwezigheid van soorten. De stochastische component van dispersie leidt ertoe dat soorten afwezig zijn op plekken waar ze prima zouden kunnen overleven. De ruimtelijke configuratie van habitats binnen sloten of slootnetwerken is dan ook een cruciaal element wanneer de soortensamenstelling van een sloot wordt onderzocht.

De rol van de ruimtelijke configuratie van habitats komt aan bod in **hoofdstuk 4**. In dit hoofdstuk is de rol die dispersie speelt voor de soortensamenstelling van de levensgemeenschap onderzocht. Variatie in soorteigenschappen, zoals de grootte van de vleugel, kunnen van invloed zijn op de mogelijkheid tot verspreiding en daarmee het koloniseren van geschikte habitats. Er is onderzocht of patronen in soortensamenstelling niet alleen variëren langs milieugradiënten, maar ook of deze een functie zijn van de

geografische afstand tussen monsterlocaties. Als dit laatste het geval is, dan speelt de ruimtelijke configuratie een rol in het structureren van macrofaunalevensgemeenschappen. Dit zou betekenen dat dispersiecapaciteit een belangrijke factor is in het genereren van patronen in soortensamenstelling. Om te testen of het effect van de ruimtelijke configuratie van locaties op de soortensamenstelling gerelateerd was aan het potentiële dispersievermogen, zijn voor aquatische insecten de vleugeloppervlaktes bepaald als een proxy voor dispersiecapaciteit. Deze zijn vervolgens geaggregeerd tot klassen, waarna geanalyseerd of er een relatie was voor deze verschillende klassen tussen dissimilariteit in taxonsamenstelling, milieuomstandigheden en geografische afstand. Het bleek dat zowel de milieu-omstandigheden als afstand een rol speelden, maar het relatieve belang varieerde tussen de vleugelgrootteklassen. Dit geeft aan dat de heterogeniteit tussen individuele sloten niet eenzijdig gegenereerd wordt door de variatie in milieuomstandigheden, met andere woorden door deterministische factoren. Een deel van de variatie is het gevolg van het onvermogen van macrovertebraten potentieel geschikte plekken te (her)koloniseren.

Gezien vanuit een toegepast oogpunt is het vinden van verbanden tussen antropogene verstoringen en veranderingen in de soortensamenstelling en structuur van levensgemeenschappen in spatiotemporeel heterogene systemen lastig. Dit wordt nog eens verder bemoeilijkt door de invloed van stochastische factoren. Het integreren van verschillende aspecten van een macrofaunalevensgemeenschap is een manier om te voorkomen dat een te groot gewicht gegeven wordt aan de specifieke soortensamenstelling of de autoecologische informatie die individuele soorten verstrekken als maat van ecologische kwaliteit van een locatie. Met behulp van deze ‘multimetric’ benadering wordt de nadruk niet alleen gelegd op de specifieke soortensamenstelling, maar ook op meer generieke indicatoren zoals diversiteit, verhoudingen tussen soorten, tolerantie voor bepaalde stressoren en functionele eigenschappen van de levensgemeenschap. In **hoofdstuk 5** is een multimetric index ontwikkeld om de ecologische kwaliteit van de Nederlandse sloten te bepalen. Aan de hand van een grote dataset met slootmonsters van waterbeheerders, welke routinematig de macrofauna van sloten bemonsteren in combinatie met diverse (a)biotische factoren, is een degradatiegradiënt opgesteld. In totaal werden hiervoor 223 monsters gebruikt, die representatief waren voor de invloed van de gecombineerde stressoren eutrofiëring, organische belasting en een verhoging van de saliniteit. Stapsgewijs werd het onderscheidend vermogen van een groot aantal metrics getest met betrekking tot hun relatie met de degradatiegradiënt. Vijf metrics werden uiteindelijk geselecteerd en geïntegreerd in een multimetric index: het aantal

kokerjufferfamilies, het aandeel slakkenfamilies, het aandeel taxa met een voorkeur voor zoet water, de Nederlandse saprobie-index en het aandeel predator-taxa in de levensgemeenschap. In theorie is dit instrument beter in staat om te gaan met de enorme variatie in soortensamenstelling die slootmonsters kenmerkt in vergelijking met bijvoorbeeld het gebruik van alleen indicatorsoorten.

Verspreidingspatronen van macrofaunasoorten kunnen zeer onregelmatig zijn. Dit is bijvoorbeeld het gevolg van kleinschalige, maar frequente veranderingen in milieufactoren en het resultaat van verschillen in dispersiecapaciteit. Wanneer macrofauna bemonsterd wordt voor beoordelingsdoeleinden of het vaststellen van lange-termijn-trends, wordt hiervoor vaak data van één locatie in een polder gebruikt. Het is echter twijfelachtig of monitoringsgegevens die verzameld zijn op één plek wel een goed beeld geven van de aanwezige slootfauna. Eén van de manieren waarop dit probleem aangepakt kan worden, is het opschalen van de bemonstering van een sloot naar de complete polder. Om dit te bereiken – gegeven de beperkte beschikbaarheid van middelen voor routinematige monitoring – moet de gehanteerde methode gemakkelijk en snel toe te passen zijn. In **hoofdstuk 6** worden een efficiënte en kosteneffectieve methode beschreven: het gebruik van macrofaunafuikjes voor de bemonstering van de slootfauna. Dit is een passieve vangtechniek, vergelijkbaar met het gebruik van potvallen om bodembewonende terrestrische ongewervelden te verzamelen. De fuikjes worden in de waterkolom of op de bodem geplaatst met de opening horizontaal of verticaal gericht en daar achtergelaten voor een bepaalde tijdsperiode. Dieren die zich actief door de waterkolom of over de bodem bewegen worden gevangen wanneer ze in de fuik terecht komen. Vanwege hun gebruiksgemak en een hoge mate van standaardisatie zijn de macrofaunafuikjes een waardevol bemonsteringsinstrument. Grootschalige toepassing van deze techniek kan belangrijke inzichten opleveren in de verdeling van organismen binnen een telkens verschuivend mozaïek van verschillende habitats. Dit geeft inzicht in de kwaliteit van de hele polder in plaats van die van één sloot.

Op basis van de inzichten die verkregen zijn in de verschillende onderzoeken, worden in **hoofdstuk 7** de mechanismen beschreven die ten grondslag liggen aan het waargenomen biodiversiteitspatroon in sloten: een hoge soortenrijkdom in sloten in het algemeen, maar met relatief grote verschillen in soortensamenstelling wanneer individuele sloten vergeleken worden. De hoge productiviteit in meso- tot eutrofe sloten leidt voor veel soorten tot de aanwezigheid van voldoende voedsel en andere habitatcomponenten om levensvatbare populaties te kunnen opbouwen en voldoende heterogeniteit waardoor al deze soorten naast elkaar kunnen

voorkomen. Desalniettemin, het regelmatig en onverwacht optreden van verstoringen – met name als gevolg van landbouwactiviteiten en waterbeheer – leidt er ook toe dat de omstandigheden in de sloot frequent wisselen. Een polder kan dan ook het beste gezien worden als een telkens verschuivend mozaïek van verschillende habitats. Wanneer deze verschuivingen als gevolg van verstoringen in balans zijn met de herstelsnelheid van populaties van de soorten waaruit de levensgemeenschap bestaat en/of de kolonisationsnelheid vanuit onverstoorde populaties in balans is met het verdwijnen van verstoorde populaties, kan er een hoge biodiversiteit aanwezig zijn in een polder. Echter, als gevolg van deze processen zijn de individuele soorten vaak sterk verspreid aanwezig over de sloten binnen de polder. Welke soorten precies gevonden kunnen worden, hangt af van de verstoringshistorie van de plek, de eigenschappen die de soorten die aanwezig zijn hebben en de stochasticiteit die samenhangt met dispersie. Er kan dan ook geconcludeerd worden dat naast de in een sloot heersende milieuomstandigheden ook de ruimtelijke configuratie en de veranderingen die in de tijd zijn opgetreden essentieel zijn voor het begrijpen van de mechanismen die ten grondslag liggen aan de soortensamenstelling die je in een sloot aantreft.

Summary

Drainage ditches are one of the most common lentic ecosystems in The Netherlands. Despite drainage ditches are found throughout the agricultural areas of the northern hemisphere, the Dutch ‘polder’ landscape with its vast networks of drainage ditches is unique. Nonetheless, the invertebrate fauna of these man-made waters is poorly known in comparison to that of the semi-natural wetland fragments found in this region. The few studies conducted to date indicate a high biodiversity potential and pinpoint drainage ditches as drivers of biodiversity in agricultural landscapes. This is surprising for a intensively managed man-made system with as main function hydrological infrastructure in support of agriculture. At the same time their positioning in an agricultural landscape makes these systems extremely vulnerable for perturbations, resulting in a shift from a system with a diverse flora and fauna into a hypertrophic, polysaprobic system dominated by floating algae, cyanobacteria or Lemnaceae.

Although the effect of these environmental ‘extremes’ on macroinvertebrates are well known, the drivers structuring the macroinvertebrate assemblages found in eutrophic, vegetation rich drainage ditches – the most common type found in The Netherlands – are not well understood. Gaps in our current understanding of the factors determining drainage ditch assemblage composition, and the inability to assess the ecological status of ditches, hinders the implementation of management practices aimed at combining the hydrological function of drainage ditch networks with the preservation of the aquatic ecosystem. This thesis describes how spatial configuration and environmental factors acting on different hierarchical scales within the landscape influence the structure and composition of drainage ditch macroinvertebrate assemblages, and shows how this knowledge can be integrated into macroinvertebrate monitoring and the assessment of drainage ditch ecological quality.

In **chapter 2** it was shown that drainage ditches can be regarded as biodiversity hotspots for macroinvertebrates in agricultural areas. Macroinvertebrate assemblages of drainage ditches in peatland agricultural areas were compared with the fauna of semi-natural, small peatland lakes in nearby nature reserves, as well as the environmental characteristics influencing the assemblage structure. Despite ditches comprised a much smaller water volume, contained a less diverse vegetation, displayed larger fluctuations in nutrient concentrations and were regularly maintained by man, the total

number of invertebrate taxa recorded per taxonomic group was comparable to small lakes, as was the number of nationally uncommon to very rare taxa. Also similarity in life history characteristics between the two water body types was high. Main difference between small lakes and drainage ditches was the relatively high dissimilarity in taxon composition among the individual drainage ditches. The macroinvertebrate taxa found in the drainage ditches displayed patchy distribution patterns. The mechanisms underlying the observed pattern could be deterministic (environmental factors, biotic interactions) as well as the result of dispersal related stochastic processes (variation in colonization and extinction among locations, dispersal limitation).

Drainage ditches are spatiotemporal heterogeneous environments; they can be regarded as shifting mosaics of habitat patches. This is mainly the result of the large variation in vegetation composition among years and often even among seasons. Patch heterogeneity has both antropogenic and natural causes and results from, amongst others, a fast rate of terrestrialsation, nutrient pulses from the adjacent farmland, inlet of river water during dry periods, competition between plant species and between plants and algae, mowing of the vegetation and dredging to prevent organic matter accumulation. The structure provided by those macrophytes is regarded as the key habitat component for drainage ditch macroinvertebrates. For example, most taxa rely on the presence of vegetation to complete their life cycle. Question is if it are the characteristics of the vegetation itself – the plant architecture – which structure the macroinvertebrate assemblages on patch scale or if the effect of the vegetation is confounded with larger scale environmental factors, such as water chemistry or ditch morphology. In **chapter 3** this was investigated for macroinvertebrates colonizing artificial plants differing in plant architecture in a series of ditches varying in environmental conditions. The colonists were characterized both in terms of taxonomic and functional composition, because it was expected that non-taxonomic aggregation of taxa into functional categories would give a different insight in microhabitat-macroinvertebrate relationships in comparison to approaches based on the taxonomic assemblage composition. Intrinsic ditch factors, such as physicochemical variables and the composition of the vegetation surrounding the artificial plants determined in large part the taxonomical and functional composition of the assemblages recorded. The structuring role of plant architecture was minor. Nonetheless, the processes acting on larger spatial scales were reflected on microhabitat scale, through a mediating role of the epiphyton on the plants.

The constantly changing conditions in drainage ditches, at least on patch scale, demand for strategies to be able to track suited habitats. For many macroinvertebrate taxa, movement is crucial for long term persistence.

Drainage ditch invertebrates are mobile; on patch scale, to track resources or to optimize their position along physicochemical gradients (**chapter 3, 6**), but also on larger spatial scales. The macroinvertebrate fauna found nowadays in drainage ditch networks was once that of oxbow lakes, wetlands and other relatively productive lentic systems found in the floodplains of lowland rivers. On an evolutionary timescale, individual waters of these natural water types can be regarded as relatively unstable and short-lived. This resulted in a high propensity for dispersal in lentic macroinvertebrates. Macroinvertebrates inhabiting a drainage ditch network can be regarded as part of a larger metacommunity. Dispersal related processes could lead to a mismatch between environmental factors and the distribution of macroinvertebrates. Factors like stochasticity and dispersal limitation result in taxa being absent at environmentally suited locations. As a result, spatial configuration of individual ditches and ditch networks becomes a crucial element in understanding the distribution of macroinvertebrates in drainage ditches.

To assess the effects of the spatial arrangement of sites, in **chapter 4** the role of dispersal in structuring the macroinvertebrate assemblages found in drainage ditches was studied. Variation in organismal traits, such as wing size, may affect dispersal rates and thereby the ability to colonize environmentally suited sites. It was examined if patterns in taxon dissimilarity among drainage ditches mirrored not only differences in environmental factors, but also if these patterns were a function of geographic distance, indicating the influence of spatial processes structuring the assemblage composition. To test whether the effect of spatial location in shaping local assemblages was related to dispersal ability, the aquatic insect data was aggregated into wing size classes and the relationship between taxon dissimilarity, environmental variation and spatial configuration was investigated for each wing size class separately. Both environmental filtering and dispersal-related processes were underlying drainage ditch aquatic insect distribution, but its relative importance varied with their dispersal ability. This indicated that the patchiness in macroinvertebrate assemblages observed among ditches was not exclusively generated by deterministic mechanisms. Part of the variation resulted from the inability of macroinvertebrates to reach or recolonize suited vacant locations.

From an applied point of view, establishing causal links between human-induced environmental changes and changes in the composition and structure of macroinvertebrate assemblages can be considered a major challenge in spatiotemporal heterogeneous ecosystems, like drainage ditches. Especially if part of the macroinvertebrates displays distribution patterns related to the spatial configuration of sampling sites and not to the environmental variation present. Integrating different components of the

macroinvertebrate assemblage is one of the ways of avoiding some of the problems associated with relying too much on specific species or the autecological information they provide as the sole indicator of ecological quality. Using this multimetric approach, emphasis is put not only on the specific taxon composition, but also on more general measures, such as overall diversity, assemblage composition, tolerances and functional characteristics of the assemblage. In **chapter 5** such a multimetric index was developed to assess the ecological quality of drainage ditch systems in The Netherlands. Based on a large dataset from regional water district managers, who conduct routine sampling of macroinvertebrates in drainage ditches, a degradation gradient composed of 223 samples was derived, which represented the combined stressors eutrophication, organic pollution and salinity. We used a stepwise process to evaluate the discriminatory efficiency of a variety of metrics for assessing ecological degradation in drainage ditches. Five metrics were selected for the drainage ditch multimetric index: number of Trichoptera families, percentage of Gastropoda families, percentage of taxa preferring fresh water, Dutch Saprobic index, and the percentage of predator taxa. In theory, this tool should be able to cope better with the patchiness of the drainage ditch macroinvertebrate assemblages in comparison to, for example, focusing on indicator species only.

Within the spatiotemporal mosaic of drainage ditch habitat patches, small scale, short-term fluctuations in deterministic factors caused by disturbances and processes related to dispersal could lead to highly scattered distribution patterns of individual species at small spatial scales. When macroinvertebrates are sampled for assessment purposes and especially for trend monitoring it is questionable if the data collected at a single site represents the assemblage present accurately. One of the ways of tackling this problem is to scale up monitoring; the incorporation of whole ditch networks instead of single ditches into macroinvertebrate monitoring schemes. To accomplish this – given the resources available for routine biomonitoring – the method used should be easy and quick. In **chapter 6** an efficient and cost-effective monitoring tool is described: the use of activity traps for capturing drainage ditch macroinvertebrates. Activity trapping is a passive sampling technique, analogous to the common practice of using pitfall traps in terrestrial invertebrate monitoring. Traps are deployed in the water column or on the bottom substrate with their opening facing horizontally or vertically and left in place for a fixed time span. Organisms which move actively through the water column or on the bottom are captured. Because of their relatively low labor requirements and high level of standardization, activity traps appeared to be a valuable tool for lentic biodiversity surveys. Applying such a highly

standardized method on a large scale would give an important insight into the distribution patterns of organisms within the shifting mosaic of habitat patches in drainage ditch networks. The assessment based on such monitoring scheme provides insight in the quality of a ditch network instead of a single ditch.

Based on the insights from this study, in **chapter 7** the mechanisms underlying the observed combination of a high overall species richness in drainage ditches and a considerable divergence in macroinvertebrate assemblage composition when individual ditches are compared is discussed. Because of a high productivity, resulting in a resource abundance exceeding the thresholds to support viable populations as well as sufficient resource heterogeneity to make coexistence of species possible, many macroinvertebrate species could potentially persist in a single vegetated, meso- to eutrophic ditch. Nonetheless, multiple unpredictable disturbances within a drainage ditch network, mainly induced by agricultural and water management practices, result in a shifting mosaic of patches differing in environmental conditions. If these shifts are in balance with the recovery rate of the populations of species of which the assemblage is composed of as well as a situation in which the colonization rate is in balance with the disturbance frequency – resulting in a metapopulation structure which could counterbalance the extinction of local populations – a high species richness is maintained, but only a limited number of species is present at the same time in the individual patches. Which species from the regional species pool are present depends on the disturbance history of the locality, the specific life history traits of the species and stochasticity related to dispersal. In conclusion, the spatiotemporal context is essential for understanding the macroinvertebrate assemblage composition observed at a single locality in a drainage ditch network.

1 General introduction



Drainage ditch in the Gelderse Vallei, Wageningen.

1 General introduction

In the lowlands of Northwestern Europe one of the most prominent – in terms of surface area covered – but also one of the most ecologically degraded landscapes are the agricultural areas. Ongoing intensification of land use practices during the last decennia resulted in a decimation of its species richness (Stoate et al., 2001; Benton et al., 2003; Tschardt et al., 2005). Nowadays, the uncropped margins of farmland, hedgerows, roadside verges and other linear landscape elements are regarded as important refugia for many organisms (Baudry et al., 2000; Marshall & Moonen, 2002; Noordijk, 2009). Whilst the terrestrial fauna received considerable attention, only recently Painter (1999) stressed the importance of drainage ditches as a potential ‘hotspot’ for aquatic macroinvertebrate biodiversity in agricultural areas.

Biodiversity is more and more recognized as a fundamental component of ecosystems, because its functioning shows strong links with species richness and composition (Hooper et al., 2005; Lyons et al., 2005; Isbell et al., 2011). The way biodiversity affects ecosystem functioning depends on, amongst others, species identity, the ecological processes under consideration, scale in space and time and the specific characteristics of the ecosystem (Otto et al., 2008; Gonzalez et al., 2009; Schmid et al., 2009). In freshwater ecosystems such relationships are often not well understood (Strayer & Dudgeon, 2010). This especially holds for small stagnant waters. Traditionally, research and management of lentic aquatic ecosystems have focused on lakes, thereby ignoring the wide array of small aquatic habitat types, under which drainage ditch networks. Consequently, to be able to (i) assess the ecological status of drainage ditch ecosystems as opposed to ‘natural’ aquatic systems, and to (ii) detect ecological degradation and understand the effects of stressors, knowledge on the macroinvertebrates inhabiting drainage ditches and the factors structuring these assemblages is essential.

Environmental characteristics of drainage ditches

Drainage ditches can be found in almost all low lying or wetland areas in the temperate and boreal zones of the Northern Hemisphere (Herzon & Helenius, 2008). One of the most extensive drainage ditch networks in terms of total ditch length and ditch density can be found in The Netherlands. The number of drainage ditches in the Dutch agricultural landscapes lying beneath or just above sea level is impressive (Fig. 1.1). To give an indication, total ditch length

in The Netherlands is estimated around 300,000 km (Higler, 1989). The density of ditches can be as high as 400-1000 m ditch per hectare, especially in peat areas. Other extensive networks can be found in, for example, Great-Brittain (128,000 km; Marshall et al., 1978), Germany (Langheinrich et al., 2004) and the United States (Needelman et al., 2007). This introduction to drainage ditch systems mainly focuses on the Dutch drainage ditch systems, with some examples from other countries or regions.

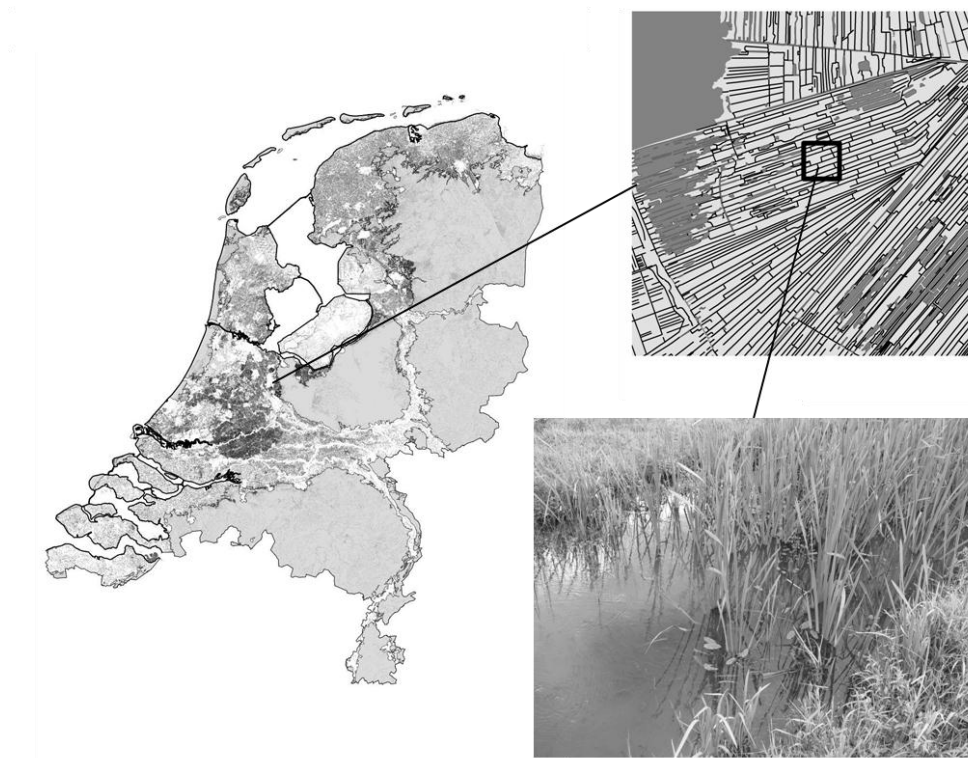


Figure 1.1: Map of the Netherlands showing all waters with a width of ≤ 6 m (indicated with black hairlines). In the low-lying Holocene part of the country (white; clay and peat soils) these lines represent the extensive network of permanent drainage ditches. Lines in the higher parts of the country (gray) mainly represent (channelized) streams. Inset in the top corner shows the Tienhoven drainage ditch network, with numerous small field ditches draining in larger collection ditches, which in turn drain the water in lakes. The photograph gives an impression of one of those field ditches.

Drainage ditches are man-made water bodies, originally dug to reclaim marshes and peatlands. Many drainage ditch networks in The Netherlands are centuries old. For example, in the low-lying peatlands the first ditches were dug already in the eleventh century to drain these hardly accessible areas. In the

fifteenth century extensive drainage networks were constructed to improve land for peat reclamation and agricultural purposes (Hoeksema, 2007). Nowadays, the main function of drainage ditch networks is draining excess rainwater and groundwater seepage from adjacent agricultural lands and vice versa to transport water towards the farmland during dry periods. Additionally, the ditches are used, amongst others, to provide drinking water to cattle, for irrigation purposes, to dispose wastewater, to dilute seepage water with a high salinity and to divide parcels of land.

Several characteristics of drainage ditches make them unique in comparison to other aquatic ecosystems, which is mainly the result of their anthropogenic origin (De Lange, 1972). Ditches are relatively small (approximately 2-8 m wide and up to 1 m deep), and have a strictly regulated, linear shape. Often they are part of an extensive network of small field ditches and larger collection ditches, which drain in canals, rivers or lakes, and thus can be considered as hierarchically structured (Fig. 1.1). The fact that ditches are permanent water bodies distinguishes them from the semi-permanent or intermittent drainage trenches, that generally contain water in winter only. The ditch banks are relatively steep; generally $>30^\circ$, but this depends on soil type and groundwater level. For example, ditches in peat areas often have hollow, irregular banks, with the water level near the ground level, whilst ditches on sand and clay often have steep banks with the water level far beneath the ground level. The ditch bottom is generally covered with a layer of sapropelium of variable thickness.

The small size of ditches leads to a large bottom surface-to-water volume ratio, resulting in a large influence of the processes taking place in the bottom on the physicochemical composition of the overlying water, for example, on nutrient- and oxygen levels. Furthermore, the small water volume leads to a strong influence of diurnal and seasonal changes in temperature (Veening, 1982; Beltman, 1983), and the dominant role of macrophytes in this system. Diel fluctuations in dissolved oxygen concentration are often substantial (Kersting & Kouwenhoven, 1989). Oxygen consumption during the night generally exceeds daily production. This results in a re-occurring period of hypoxia, which is most often observed in the second half of the night and early morning (Fig. 1.2). Furthermore, fluctuations in weather conditions (wind speed, cloud cover, ice formation, temperature) influence the oxygen concentration of the water through water temperature, primary production and wind-induced mixing, which could result in prolonged periods of hypoxia (Welch, 1952; Verdonchot et al., 2010). Finally, excessive growth of floating macrophytes, such as Lemnaceae, periodically halts oxygen production by

altering the underwater light availability and reduce gas exchange between the water and atmosphere.

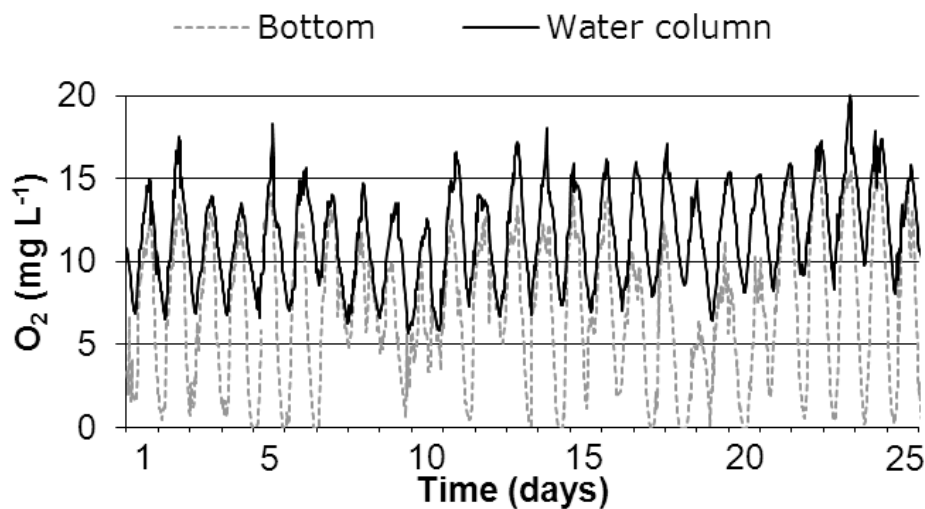


Figure 1.2: Dissolved oxygen concentration in a ditch at the Veenkampen (Wageningen) in 2nd half April- 1st half of May. Submerged vegetation was abundant and consisted of *Elodea nuttallii*, *Potamogeton pusillus* and *Lemna trisulca*. Oxygen was measured between the vegetation in the central part of the ditch, at 10 cm beneath the water surface and 10 cm above the bottom sediment. It shows that hypoxia was a common phenomenon near the bottom of the ditch.

Construction of the drainage ditch networks aimed at manipulating local hydrology in such a way that farming is made as efficient as possible and that the risk of flooding is minimized. With systems of pumps and weirs the water level in the ditch networks is continuously regulated with a high precision (± 10 cm). As a consequence, hydrology of the ditches is completely artificial; it does not follow the natural fluctuations in water level as generated by the seasonal differences in water availability. In many agricultural areas, a fixed water level is retained: low in winter and relatively high in spring and summer. In winter, excess rain water and groundwater seepage is removed rapidly, whilst in summer river water is used to compensate for water shortages (Higler, 1989). Despite water is transported through the network, actual water flow is absent or negligible for most of the time (current velocity 0-5 cm/s). Nevertheless, flow is sometimes present temporarily. Significant water movement is observed, for example, during periods of increase drainage after excessive rainfall or due to the inlet of water from outside the drainage system. Characteristic of these flow events is that the direction of the current is not fixed. Depending on the water level in the ditch opposed to that of the

surrounding area flow can be in both directions. Furthermore, water movement induced by wind could be substantial (Soomers et al., 2010).

To retain the drainage function of ditches, regular maintenance takes place, in the form of mowing of the vegetation and dredging of the bottom sediment. Without maintenance, excessive growth of vegetation results in rapid terrestrialization. Garms (1961) estimated that it takes approximately 7 to 10 years for a eutrophic drainage ditch to transform into a marsh without open water. The impact of these management practices on macroinvertebrates can be considerable. Direct by removing certain species and facilitating others, and indirect by changing the vegetation composition (Beltman, 1987). The machinery and cleaning method used, the rigour of cleaning as well as the frequency and timing of the cleaning events determine the severity of the disturbance caused by ditch management (Twisk et al., 2000) (Table 1.1). Maintenance is also the reason that ditches are never fully shaded by trees or shrubs, because they must be accessible by heavy machinery.

Table 1.1: Overview of ditch management practices in the Netherlands. Depending on the function and dimensions of the ditch, as well as the region, management is carried out by either local farmers or water district managers.

Component	Management type	
	<i>Mowing</i>	<i>Dredging</i>
Conditions	Aquatic vegetation is cut at a height of 0 to 10 cm above the bottom using a ditch-scoop, mowing-basket or mowing-drum.	Organic bottom sediment is removed with a suction-pipe or pullshovel
Timing	Growing season, mainly summer-autumn	Year-round, mainly autumn-winter
Frequency	Generally 1x per y, but up to 3x per y possible	1x per 3-5 y (peat) or 1x per 10-15 y (mineral soils)

Stressors and the main pathway of ecological degradation

In areas with intensive agriculture, ditches often comprise the only non-cropped land. This high edge-ratio makes drainage ditch systems vulnerable for perturbations, especially runoff of nutrients (N + P) and organic matter (Janse & Van Puijenbroek, 1998), but also input of pesticides from surrounding lands (Brock et al., 2010) and trampling of banks by cattle. In certain areas, nutrient enrichment is further enhanced by the common practice of the inlet of river water during summer, which has an important negative side effect because it often leads to a considerable increase in chloride concentrations (Higler, 1989)¹. It should be noted that inlet of water has not always negative consequences for the freshwater ditch ecosystem. In the ditches in low lying

polders in the western part of the country inlet of river water is often necessary to prevent salinization. Furthermore, in some hypertrophic polders, the ditch networks are flushed with river water to actually improve the water quality.

Nutrient enrichment follows a fairly predictable pattern. In most ditches productivity is relatively high. It is likely that even before intensification of agriculture most ditches were in a meso- to eutrophic state. Due to their shallowness and strong vegetation development, nutrient load (eutrophication and accumulation of organic matter) increased rapidly with the advancing succession of the system. Nonetheless, enhanced input of nutrients from agriculture and inlet water disturbed this 'natural' succession towards a terrestrial stage. Whilst the vegetation of mesotrophic drainage ditches in a mid-successional stage is characterized by a species-rich mosaic of submerged, emergent and floating plant species, a slight increase in nutrient load induces the dominance of 'weedy' submerged plant species, such as *Elodea nuttallii* (Portielje & Roijackers, 1995). Excessive growth of these species demands for an increased maintenance frequency to retain the drainage function of the ditch, which negatively influences the less tolerant plant species even further. Ongoing enrichment eventually leads to frequent filamentous and epiphytic algal or cyanobacteria blooms and dominance of Lemnaceae or *Azolla filiculoides*, resulting in decreased light penetration, hindering the development of submerged vegetation (Janse & Van Puijenbroek, 1998) (Fig. 1.3). Currently, a considerable number of drainage ditches in The Netherlands has reached such a hypertrophic and polysaprobic state, sustaining a system dominated by Lemnaceae or cyanobacteria in which terrestrialization is slowed down considerably.

Ecological consequences of an increase in nutrient concentrations and the associated change in vegetation composition are profound. Firstly, the loss of the underwater habitat structure provided by submerged macrophytes results in the impoverishment of the macroinvertebrate assemblages of lentic aquatic systems (Declerck et al., 2005). With the disappearance of the submerged vegetation, a crucial component of the ditch ecosystem is lost. Most lentic invertebrates rely on vegetation to, amongst others, feed, construct tubes and nets, hide from predators, oviposit, pupate and emerge (Downing, 1991). Secondly, increased organic load and the associated increased bottom oxygen demand leads to prolonged periods of hypoxia, and results in the release of toxic compounds (e.g. ammonium, sulphide) (Clare & Edwards, 1983).

1: Although brackish ditches could contain a very specific flora and fauna, comparable to that of other brackish aquatic systems (Nijboer et al., 2003a), an increase in chloride concentration in a freshwater ditch system is regarded as a perturbation here.

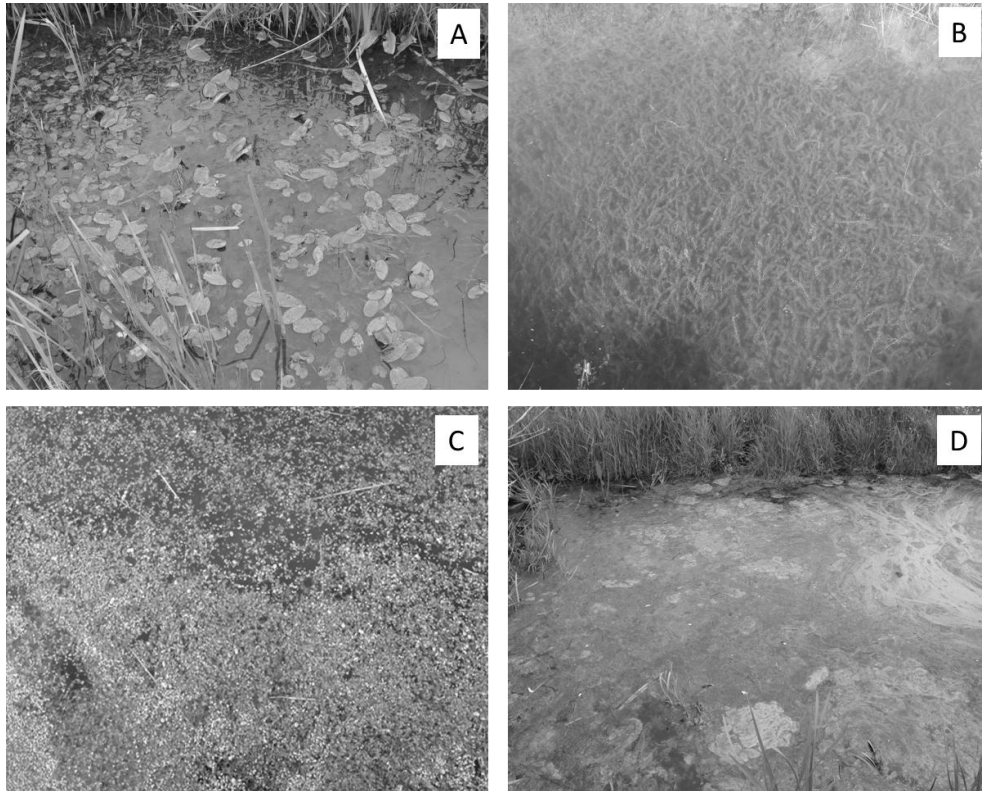


Figure 1.3: Changes in the drainage ditch vegetation with increasing nutrient enrichment. Mesotrophic ditches generally contain a species-rich mosaic of submerged, emergent and floating plant species (A). A slight increase in nutrient load induces the dominance of 'weedy' submerged plant species, such as *Elodea nuttallii* (B). Ongoing enrichment eventually leads to dominance of Lemnaceae (C) or algal/cyanobacteria blooms (D).

Patterns of macroinvertebrate biodiversity in drainage ditches

Recent studies point out the importance of drainage ditches as refuges for the aquatic fauna in the otherwise drained agricultural landscape (Painter, 1999; Armitage et al., 2003; Herzon & Helenius, 2008). Despite the potential threats to ditch biodiversity arising from agricultural practices and ditch management, a relatively high number of macroinvertebrate species is recorded in the Dutch ditch networks. To give an indication, the total number of macroinvertebrate taxa recorded in 279 standard pond net samples collected between 1980-2010 by freshwater ecologists from Alterra (former Rijksinstituut voor Natuurbeheer), only including permanent, mesotrophic to eutrophic drainage ditches and taxa with an abundance of >1 individual, comprised approximately one third of the total Dutch freshwater fauna (Table 1.2). This percentage is

even more impressive given that all samples together represent only $5 \cdot 10^{-4}\%$ of the total ditch length found in The Netherlands.

Table 1.2: Total number of macroinvertebrate taxa recorded in 279 5 m-standard pond net samples collected between 1980-2010 by freshwater ecologists from Alterra (former Rijksinstituut voor Natuurbeheer), only including permanent, meso- tot eutrophic drainage ditches and taxa with an abundance of >1 individual. Number of taxa recorded per taxonomic group is compared to the total number of species ever recorded in inland waters in the Netherlands.

Taxonomic group	No. of species recorded in ditches	Total no. of species recorded in Dutch inland waters	Proportion of total (%)
Tricladia	7	14	50
Gastropoda	35	46 ^a	76
Bivalvia	11	28 ^a	39
Hirudinea	13	27 ^b	48
Oligochaeta	36	158 ^c	23
Araneida	1	1 ^d	100
Hydracarina	84	234 ^e	36
Mysida	1	3 ^f	33
Isopoda	3	4 ^g	75
Amphipoda	3	21(?) ^d	14?
Odonata	23	70 ^h	33
Megaloptera	1	3 ^d	33
Neuroptera	1	5 ^d	20
Ephemeroptera	7	59 ^d	12
Plecoptera	1	27 ⁱ	4
Heteroptera	31	64 ^j	48
Coleoptera	95	353 ^k	27
Diptera: Chironomidae	90	347(?) ^d	26?
Trichoptera	42	181 ^l	23
Lepidoptera	4	7 ^m	57

^a Gittenberger & Janssen, 1998; ^b van Haaren et al., 2004; ^c van Haaren, 2002; ^d Mol, 1984; ^e Smit & van der Hammen, 2000; ^f Kelleher et al., 1999; ^g Huwae & Rappé, 2003; ^h Dijkstra et al., 2002; ⁱ Koese, 2008; ^j Tempelman & van Haaren, 2009; ^k Drost et al., 1992; ^l Higler, 2008; ^m Vallenduik et al., 1997

A number of studies has described the general relationships between drainage ditch macroinvertebrate assemblage composition and environmental variables, emphasizing the importance of macrophyte presence and composition (Scheffer et al., 1984; Higler & Verdonschot, 1989), diel oxygen patterns (Clare & Edwards, 1983), ditch width and depth, nutrient and organic matter loading, acidity and salinity as important environmental factors (Verdonschot & Higler, 1989; Verdonschot, 1992). Nonetheless, the

development of a drainage ditch typology based on a country-wide survey of macroinvertebrates from water district managers was difficult (Nijboer et al., 2003a). The reason for this was that often no clearly delineated communities were found. Only the 'harsh' environments, e.g. extreme in terms of salinity, acidity or organic pollution, were characterized by relatively distinct taxon-poor assemblages. The most common and widespread type, the small, meso- to eutrophic ditch rich in vegetation, comprised a very diverse macroinvertebrate assemblage, but one which was notoriously variable in species composition among sites.

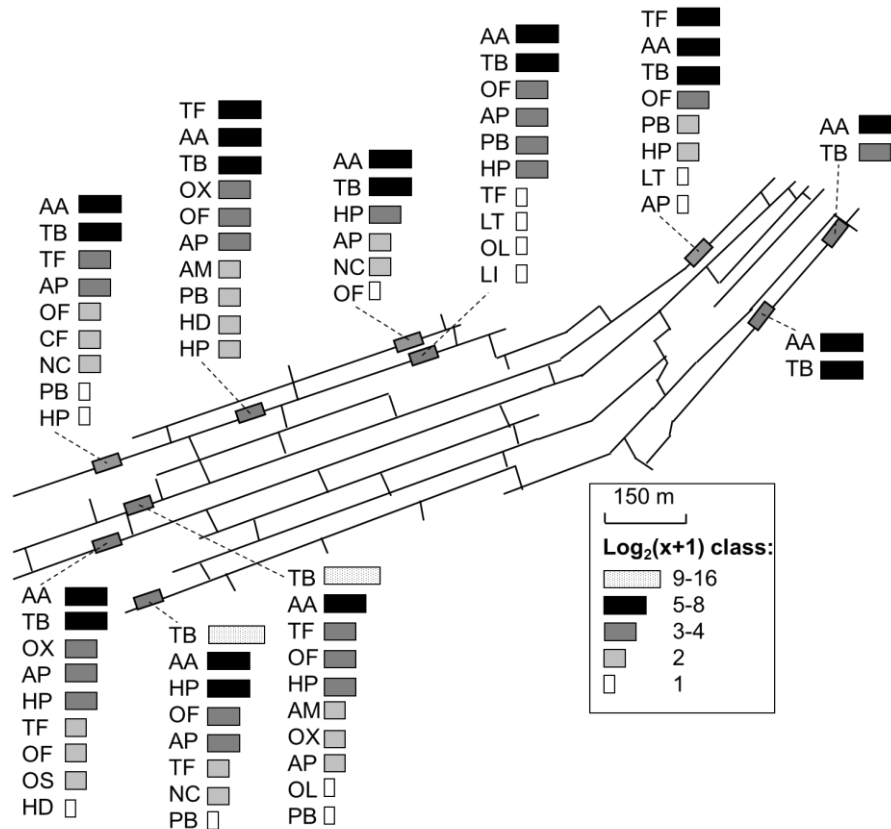


Figure 1.4: Spatial distribution of Trichoptera in a drainage ditch network near Tienhoven (Utrecht) in September 2008. Abundances are expressed in $\log_2(x+1)$ -classes and based on 5 m standard pond net samples of the major habitats present in the ditches. Taxon abbreviations: Agrylea multipunctata (AM), Tricholeiochiton fagesii (TF), Oxyethira sp. (OX), Athripsodes aterrimus (AA), Leptocerus tineiformis (LT), Oecetis furva (OF), Oecetis lacustris (OL), Oecetis strucki (OS), Triaenodes bicolor (TB), Limnephilus sp. early instar (LI), Agrypnia pagetana (AP), Phryganea bipunctata (PB), Cyrnus flavidus (CF), Holocentropus dubius (HD), Holocentropus picicornis (HP), Notidobia ciliaris (NC).

Despite ditch networks are hierarchically structured and drain excess water from large landscape units (e.g. polders), analogous to river networks, these networks do not represent continuous, longitudinal gradients with predictable biological responses (*sensu* the River Continuum Concept; Vannote et al., 1980). Higler (1976) studied a ditch which increased in dimensions along its length and found that there was no such thing as a linear succession of macroinvertebrate assemblages with increasing dimensions. Instead, the ditch contained a mosaic of smaller assemblages with a discontinuous longitudinal distribution. As Higler and Verdonschot (1989) noted more than a decennium later: “Even in one polder ditches show a dazzling variety of habitats and microhabitats, changing from year to year and through the year as well”. This patchiness is reflected in species distributions; an example of the spatial distribution of Trichoptera larvae across a drainage ditch network – which was broadly comparable in terms of environmental characteristics – shows rather erratic patterns in the distribution and abundance of taxa (Fig. 1.4).

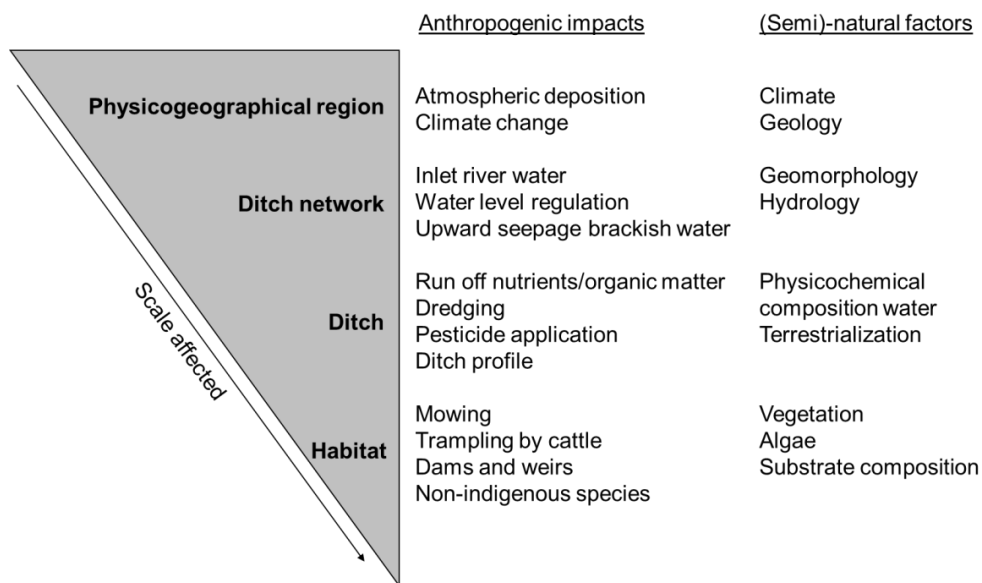


Figure 1.5: *Anthropogenic and natural factors acting on different spatial scales.*

Patchiness of habitats is generated by factors operating on different spatial and temporal scales within a landscape, in a hierarchical context (Wu & Loucks, 1995). A hierarchical structure or nestedness is a property of the system itself, with microhabitats being nested within a habitat patch, which is

part of a drainage ditch, a ditch network and so on (Frissell et al., 1986). Also the main regulatory mechanisms, which have both a natural and an anthropogenic origin, act hierarchically (Fig. 1.5). For example, the inlet of river water influences an entire drainage ditch network, whilst at the same moment cattle trampling of a ditch bank only affects part of the system. The presence of patches within a hierarchy of regulatory factors reflects the action of different variables operating over fluctuating spatiotemporal scales (Thorp et al., 2006). Many of these patterns are inter-linked, enhancing or diminishing effects on patches across scales (Poole, 2002). Generally, with a decrease in scale, the spatiotemporal variability increases, but always depending on the specific characteristics of the patch (Fig. 1.6). In drainage ditches, patch turnover (e.g. changes in macrophyte composition and thus habitat availability) is slower in littoral zone compared to the central water column, mainly as a result of differences in plant species composition and the impact of management.

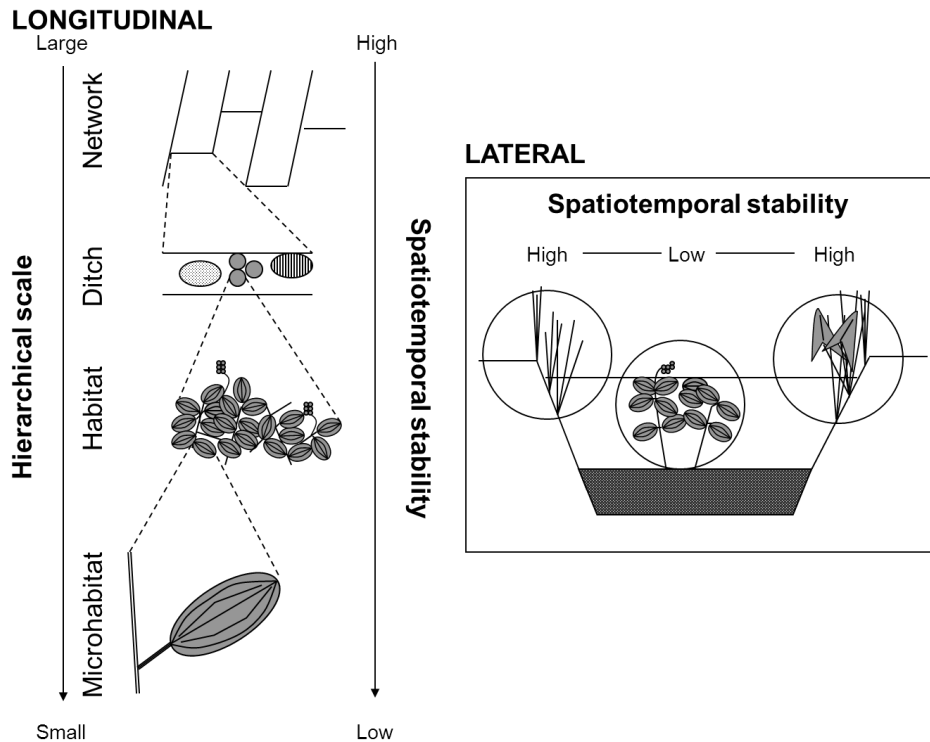


Figure 1.6: Hierarchical organization of a drainage ditch network and its habitat subsystems (modified from Frissell et al., 1986). Lateral variability in spatiotemporal stability differs between the littoral vegetation near the banks and the vegetation in the water column, indicating the influence of patch specific characteristics.

Main habitat patches for most invertebrates inhabiting drainage ditches consist of patches of aquatic vegetation, both in the water column and the littoral zone near the banks (Scheffer et al., 1984; Higler & Verdonshot, 1989). Single macrophyte stands can be viewed as separate patches. On a local scale, these vegetation patches can be very dynamic – both temporally and spatially – varying amongst others in structural complexity, resource availability, and physicochemical conditions (De Lange, 1972; Veeningen, 1982). Several factors could result in large differences in vegetation composition, even between seasons. Firstly, natural vegetation succession, which is delayed or manipulated by mowing and reversed by dredging. Secondly, changes in the physicochemical composition of the water due to, for example, run off of nutrients or inlet of water. Finally, the outcome of competition between plant species and algae or cyanobacteria, for example initiated by weather conditions or nutrient pulses. Predictability of these dynamics for macroinvertebrates can be considered low. On larger scales, such as the whole drainage ditch network, patterns are often more predictable. When certain macrophyte patches are absent in one ditch stretch, it is well possible that it dominates in another ditch within the network during that period, in other words, the aquatic vegetation forms a shifting mosaic. As a result a metastable state can develop at one hierarchical level through incorporation of multiple, non-equilibrium patches from the adjacent lower hierarchical level (Thorp et al., 2006).

A metacommunity perspective on drainage ditch macroinvertebrate assemblages

For macroinvertebrates, persisting and sustaining vital populations in spatiotemporal patchy environments such as drainage ditches can be accomplished in three ways (Bohonak & Jenkins, 2003). Firstly, a species can possess or evolve the physiological and ecological tolerance necessary for survival and reproduction across a broad set of environmental conditions, e.g. being highly generalistic. However, in freshwater invertebrates this is limited to only a small subset of species and only for particular environmental factors due to physical, developmental and genetic constraints (Wellborn et al., 1996). Secondly, a species can rapidly adapt to the environmental change encountered in its habitat, but this is apparently not very common – or an understudied topic – in macroinvertebrates (Petrin et al., 2007). Thirdly, random or directed dispersal could lead to long-term persistence within a spatiotemporal mosaic of habitat patches.

From an evolutionary or historical perspective it is likely that dispersal is relatively common in drainage ditch macroinvertebrates. The invertebrate

fauna found nowadays in drainage ditch networks was once that of oxbow lakes, wetlands and other relatively productive lentic systems found in the floodplains of rivers (Higler & Verdonchot, 1989). On an evolutionary timescale, lentic floodplain water can be regarded as relatively unstable and short-lived. For example, many stagnant floodplain waters go through cycles of rejuvenation during spates, otherwise terrestrialization due to ongoing vegetation succession leads inevitably to their disappearance. At the same time, new waters are created by scouring and the separation of old meanders from the main channel. Thus, under natural conditions, suited habitats for lentic macroinvertebrates are continuously shifting in space and time. As a consequence, one would expect species living in lentic habitats to be characterized by a higher propensity for dispersal than species living in, for example, rivers and large lakes. Ribera et al.(2003) and Hof et al. (2006) showed that this indeed was the case for several insect groups. There is a clear parallel between natural lentic systems and man-made drainage ditches. The fluctuating drainage ditch environment also demands for strategies of coping with a changing patch quality with time.

In the end, moving to other patches is inevitable for many species, and dispersal ability and capacity become important factors for long term persistence of lentic invertebrate populations. Unfortunately, dispersal is one of the least studied – even an enigmatic – element of macroinvertebrate biology (Bilton et al., 2001; Bohonak & Jenkins, 2003). It is known that most macroinvertebrates disperse, but the magnitude and range of dispersal are generally unclear, and often based on a few anecdotic records. When viewed on large geographic scales, small natural lentic habitats are likely to occur in clusters, simply because the terrestrial matrix they are embedded in is suited for their existence in the first place (i.e. floodplains). This means that although single water bodies may become unsuited or eventually disappear, there are always other newly created or rejuvenated waters in a relatively close proximity. For ditches the same appears to hold; although single patches of habitat are relatively short-lived (regular maintenance by mowing and dredging constantly resets natural vegetation succession and thereby prevents terrestrialization, and nutrient pulses from the surrounding agricultural lands could drastically alter conditions within ditch sections) the ditches themselves are part of drainage ditch networks consisting of many ditches (up to 400-1000 m/ha). Often these networks are centuries old. Within such a spatial configuration being capable of dispersing over relatively short distances might be enough to ensure long-term survival of populations.

The importance of dispersal in structuring species assemblages is illustrated in meta-population and metacommunity theory (Levins, 1969;

Wilson, 1992; Hanski, 1999). A metacommunity is defined as a regional set of local assemblages which are spatially distinct but are linked by dispersal of multiple potentially interacting species (Leibold et al., 2004). Although largely theoretical, metacommunity theory placed distribution patterns, population dynamics and interactions between species in a broader landscape context, stressing the importance of different scales in determining the patterns (colonization, extinction, competition) in co-existing invertebrates observed within a single patch. It is likely that freshwater invertebrate populations are part of metacommunities, since they satisfy its main criteria: populations vary in time and space, individuals of different species interact, dispersal influences community dynamics and both stochastic and deterministic local extinctions are observed (Bohonak & Jenkins, 2003; Winemiller et al., 2010).

Leibold et al. (2004) and Holyoak et al. (2005) have distinguished four paradigms for metacommunity theory: patch dynamics, species sorting along environmental gradients, mass-effects through source-sink dynamics, and neutrality. The patch-dynamics paradigm focuses on colonisation-extinction dynamics, with species that have a trade-offs between their biological characteristics (e.g. variation in colonization ability vs. competitive ability). The paradigm assumes that there are multiple identical patches – thereby ignoring the influence of environmental heterogeneity – within a region, in which the populations undergo stochastic extinctions, either for demographic reasons or through environmental disturbances (Leibold 2009). Good dispersers colonize these vacant patches, but are eventually outcompeted by the good competitors; regional coexistence is only possible because of these trade-offs, and if colonization events are on timescales that are similar or slower than these extinctions.

Species sorting assumes that assemblage composition of a heterogeneous mosaic of patches always reflects the variability between individual patches in physicochemical conditions, disturbance rate, and resource availability. Also the outcome of species interactions (e.g. competition, predation) is structured by spatiotemporal fluctuations in the environment. Dispersing individuals can only become successful when reaching an vacant patch if environmental conditions are suitable. According to this theory community assembly is a pure deterministic process in which environmental characteristics exclude the species of the regional species pool which do not possess the set of biological traits matching the environment. Poff (1997) envisaged this process as colonist passing a series of hierarchical environmental filters before successfully colonizing a habitat patch (Fig. 1.7). As a consequence, species sorting leads to predictable assemblages, both spatially (habitats similar in environmental conditions are inhabited by similar

assemblages) and in time (after disturbance, assemblages follow consistent trajectories to return to pre-disturbance conditions) (Lepori & Malmqvist, 2009).

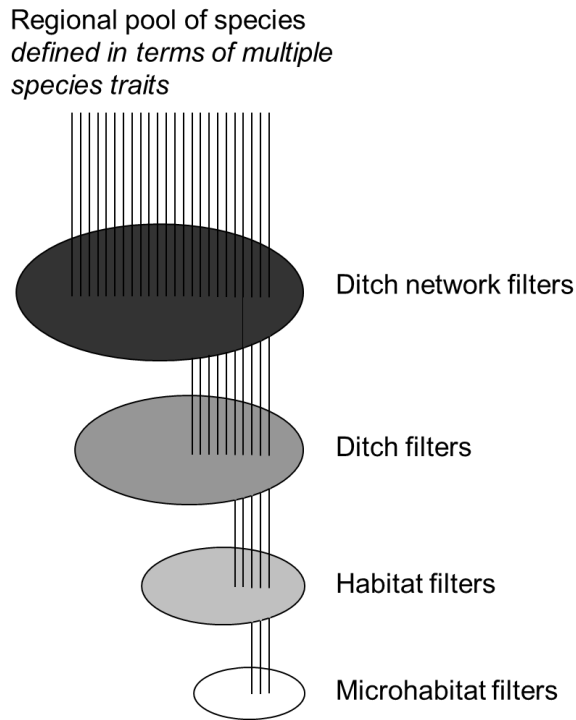


Figure 1.7: Distribution and abundance of species reflects the traits that allow them to pass through multiple habitat filters (abiotic and biotic) at hierarchical spatial scales. Species that lack traits suitable for passing through a large scale filter are limited in abundance at all lower scales (indicated by truncation of vertical lines) (modified from Poff, 1997).

The occurrence of mass effects (Shmida & Wilson, 1985) through source-sink dynamics (Holt, 1985; Pulliam, 1988) could counteract the process of species sorting (Mouquet & Loreau, 2002). When the number of dispersing individuals is very high, it could compensate for the negative effects of superior competitors and adverse environmental variables by constantly supplying new colonists. As a result species will become established in sites in which they cannot sustain viable populations. Consequently, if at a location a heterogeneous mosaic of patches is present, this is not reflected in the macroinvertebrate assemblage composition of these patches.

Neutral theory (Hubbell, 2001) has challenged the species sorting view by suggesting that differences in local species composition and abundance are the result of successive stochastic fluctuations ('ecological drift') in time, as a

result of random patterns in population parameters (e.g. birth, death), colonization and extinction. Theory assumes that macroinvertebrates are competitively equal and show a similar response to local environmental conditions; biological characteristics do not influence the process of community assembly. As a consequence, patch-to-patch variation – despite environmental conditions are similar – can be considerable, but shows spatial dependency as a result of dispersal limitation. Differences between patches can be magnified if the sequence of species colonizing in time can influence the assemblage composition, when priority effects lead to the establishment of multiple stable equilibria (historical contingency; Chase, 2003).

Empirical evidence suggests that macroinvertebrate communities do not necessary completely fit one of the four metacommunity models, but can be regarded as context-dependent mixtures. Thompson and Townsend (2006) showed for stream invertebrate communities that both neutral and niche processes structured these communities, depending on the biological traits of the species studied. Chase (2007) proposed a framework in which deterministic and stochastic processes both influence community composition, but their relative importance depends on the harshness of the environment. He showed that in permanent ponds, representing ‘benign’ environmental conditions where the majority of the regional species pool can potentially persist, stochastic processes prevailed, whereas deterministic processes prevailed in ponds experiencing temporal drought and the ‘harsh’ environmental conditions resulted in niche selection, filtering out species lacking the set of suitable traits. Lepori and Malmqvist (2009) observed in mountain streams disturbed by predictable spring spates the same disturbance driven shifts from stochastic to increasingly deterministic community assembly with an increase in the severity of the disturbance, but showed that this relationship was not monotonic but peaked at an intermediate level of disturbance.

The situation in drainage ditches differs from those described in the examples above, since drainage ditch macroinvertebrates face multiple (un)predictable disturbances. Periodic disturbances of the vegetation and bottom sediment in the form of mowing and dredging, which alone can be regarded as severe disturbances, are complemented by unpredictable disturbances arising from agricultural practices, water management and natural factors such a weather conditions. Ultimately, this results in a situation in which both temporal and spatial patch heterogeneity are very high. Apparently, many macroinvertebrates can cope with this level of heterogeneity, at least temporarily and to a certain degree, given that many macroinvertebrate species are present in drainage ditch networks.

Using macroinvertebrates to define the ecological quality of drainage ditches

Nowadays, the ecological quality of many drainage ditch networks in The Netherlands has been deteriorated due to severe nutrient enrichment. To be able to restore these systems, knowledge is needed to identify the present status of the ecosystem and to predict what changes to expect if the environment changes either due to further degradation or to restoration measures (Nijboer, 2006). Macroinvertebrates are regarded as good biological indicators, which can provide an insight into the current and past conditions of a water body and integrate the effects of multiple stressors (Bonada et al., 2006). Nonetheless, the ecological status of a water body can only be assessed when there is a benchmark, a reference condition, from which can be judged if the measured condition differs from a desired, expected or previous condition (Hawkins et al., 2010). Often this is the condition that is representative of a group of minimally human disturbed or altered sites organized by selected physicochemical and biological characteristics (Reynoldson et al., 1997). In the case of drainage ditches a natural state does not exist. Therefore, the only system state to refer to could be (Higler & Verdonschot, 1992; Stoddard et al., 2006): i.) the best known or remaining condition of the system, e.g. a historical condition or a least disturbed condition, ii.) the potentially optimal condition of the system, derived from the range of environmental variables and other habitat characteristics present or practicable at a site.

In drainage ditches changing environmental conditions due to anthropogenic influences must have resulted in major changes in macroinvertebrate community composition during the last century, but to what extent is unknown. Information on the occurrence of macroinvertebrates in ditches before 1975 is scarce and highly anecdotic (Nijboer et al., 2003b), ranging back to the publication of “In sloot en plas” (Heimans & Thijsse, 1896). With the publication of H.C. Redeke’s ‘Hydrobiologie van Nederland’ some autoecological information on drainage ditch invertebrates is given (Redeke, 1948), as well as in reports of fieldtrips of biologists (e.g. Nieukerken & Van der Velde, 1973). The first ditch macroinvertebrate research, describing assemblage composition in relation to characteristics of the environment, was carried out in the 1970s by L.W.G. Higler and B.G.H.J. Beltman (Higler, 1976; Beltman, 1983). Since environmental change was already apparent at that moment (De Lange, 1972), these observations are not very suitable as a ‘historical’ reference in determining the ecological status of drainage ditch systems. The only potential benchmark left is thus the least disturbed condition currently present in The Netherlands; comprising drainage ditches located in or

near nature reserves without intensive agricultural land use (Nijboer et al., 2003a; Keizer-Vlek & Verdonchot, 2008).

But how to define good ecological quality in a man-made and intensively managed system such as drainage ditches? Basically, there are two views on ecological quality, which are in part interrelated (Nijboer, 2006). In the first view – which is already a century old – quality is based on the abundance of indicators (e.g. species, families, biological traits) (in)tolerant for stressors or changes in habitat structure at the location studied. The first saprobic systems were mainly focused on running waters, and were based on species indicating organic pollution (Kolkwitz & Marsson, 1909). Since species respond to complexes of environmental variables operating on different scales, species can be absent at sites which appear suitable, and species within assemblages interact with each other, the single species approach was soon abandoned and resulted in the development of systems based on combinations of species (e.g. Woodiwiss, 1964; Armitage et al., 1983; Wright et al., 1984), and later a combination of different aspects of the assemblage (diversity, composition, life history traits, habitat preferences) into combined indices, the multimetrics (e.g. Kerans & Karr, 1994; Barbour et al., 1996).

The second view is rooted in nature conservation or conservation of biodiversity and defines a good ecological quality in terms of the presence of rare or threatened species in the water body, or a high species diversity in general. This partly contrasts with the former view, in which quality is often derived from the more frequently occurring or abundant species, but also shows similarities because some of the rare species may be highly indicative for certain typical ecological conditions and biodiversity is often high at reference sites. Species richness of taxonomic groups is often regarded as an indicator of ecological quality, but especially in environmentally ‘harsh’ systems, waters of good ecological quality can be relatively poor in total number of species, indicating the importance of species-identity next to richness alone. Nonetheless, diversity is positively correlated with many measures of ecosystem functioning (Isbell et al., 2011). Abundance distribution of all macroinvertebrate species collected at a location is generally strongly left skewed, with several very abundant species and many rare species, often singletons and doubletons (Preston, 1948). The position of these species within the assemblage is difficult to assess without taking into account the broader geographical context, since rarity is a general term comprising different forms. Rarity can be derived from different combinations of geographical range, habitat specificity and local population size (Gaston, 1994). For assessment purposes, the most interesting species are those that are limited to a narrow range of environmental conditions or have specific habitat requirements.

Measuring and assessing ecological quality of drainage ditches based on macroinvertebrates

Taking into account the shifting mosaic of patches which comprises a drainage ditch network, with organisms displaying a metacommunity structure, not every patch contains all species which potentially could occur there from a deterministic point of view. At least, not at one moment in time. Furthermore, it is an almost impossible task to record all species present in a drainage ditch network. Each macroinvertebrate collection is only a small subsample of the assemblage present. This results in three sources of spatiotemporal variation, one generated by the drainage ditch environment itself, a second referring to the time since last disturbance and a third resulting from the sampling procedure. Especially those species which occur in low abundances within the water body, are highly aggregated, or simply avoid being captured (e.g. in case of pond netting the fast swimmers) are more difficult to record. The subsequent steps of the sample processing generate new sources of variation; organisms with cryptic behavior are harder to detect during sorting of the samples and identification problems arise when species are only reliably identifiable to species level when they have reached the last few instars (e.g. Odonata, Ephemeroptera), resulting in datasets with part of the organisms identified to higher taxonomical levels. As a consequence, ecological quality of drainage ditches can only be determined if these three sources of variation are – at least in part – be accounted for.

Decrease in inter-sample variation can be accomplished by either increasing the number of samples taken within a drainage ditch network in space and/or time, thereby increasing the amount of species-information derived from the network, or by combining different aspects of the assemblage, by incorporating both taxonomical data and biological traits, which makes the derivation of ecological quality less species-dependent, e.g. there is redundancy among the ecological patterns indicated by single species. The former is strongly restricted by logistical and financial constraints, and would only be applicable on large scales with the development of techniques improving sampling and sample processing speed. The latter technique became common practice during the last two decennia, first in the U.S.A. (Rapid Bioassessment Protocols; Barbour et al., 1999) and later also in Europe (AQEM/STAR; Hering et al., 2006) and has resulted in the development of a large number of indices. To date, the number of indices developed for small lentic ecosystems is very low, and none has been constructed for drainage ditches.

Research questions and outline of the thesis

Drainage ditches are one of the most common lentic ecosystems found in The Netherlands but knowledge on the macroinvertebrate assemblages inhabiting these waters is very limited. On a world scale, the Dutch ‘polder’ landscape with its vast networks of drainage ditches is unique, and many macroinvertebrates typical for lentic waters and wetlands nowadays appear to have their main distribution in these anthropogenic habitats (Hof et al., 2008). The few studies conducted to date indicate a high biodiversity potential and pinpoint drainage ditches as important refuges for aquatic biodiversity in agricultural landscapes, which is quite surprising for a intensively managed man-made system with as main function regulation of farmland water quantity. At the same time their positioning in an agricultural landscape matrix makes these systems extremely vulnerable for perturbations, resulting in a shift from a system with a diverse flora and fauna into a hypertrophic polysaprobic system dominated by floating algae, cyanobacteria or Lemnaceae. If biodiversity in ditches declines at the same dramatic rate as observed in the last few decades in the terrestrial agricultural landscape, losses are likely to be substantial.

Although there are clear linkages between changes in macroinvertebrate assemblages and environmental ‘extremes’, such as under hypertrophic and polysaprobic conditions, the drivers structuring the assemblages found in eutrophic, vegetation rich drainage ditches – the most common type found in The Netherlands – are not well understood. As described in the previous paragraphs, drainage ditches are shifting mosaics of patches differing in environmental conditions, with multiple interacting species continuously dispersing between the patches. Environmental factors and (un)predictable disturbances acting at different scales of time and space produce patterns of spatiotemporal heterogeneity to form a dynamic habitat-template to which invertebrates respond (Southwood, 1977; Pringle et al., 1988; Southwood, 1988; Townsend, 1989). It are not only the environmental factors in the ditch which ‘filter’ out species lacking suited traits, but also the role of stochastic mechanisms related to dispersal appear to play an important rol. Gaps in our current understanding of the factors determining the assemblage composition found in ditches makes it very difficult to define, at least on the basis of the macroinvertebrates present, how a ditch system in good ecological state should look like. This inability to assess the ecological status of ditches hinders the implementation of management practices aimed at combining the hydrological function of drainage ditch networks with the preservation of biodiversity.

This thesis describes how spatial configuration and environmental factors acting on different hierarchical scales within the landscape influence the structure and composition of drainage ditch macroinvertebrate assemblages, and shows how this knowledge can be used or integrated into macroinvertebrate monitoring and the assessment of drainage ditch ecological quality. The central objectives of this thesis are:

1. To study the effects of variation in the drainage ditch environment on the taxonomical and functional composition of macroinvertebrate assemblages; from very small scales (microhabitat) to entire drainage ditch networks.
2. To assess the effect of the spatial arrangement of habitats next to environmental factors on macroinvertebrates, incorporating dispersal as a factor structuring macroinvertebrate assemblages
3. To develop tools to assess the ecological quality of drainage ditches based on macroinvertebrates, taking into account the effects of the shifting mosaic of habitat patches and macroinvertebrate assemblages which comprises a drainage ditch network.

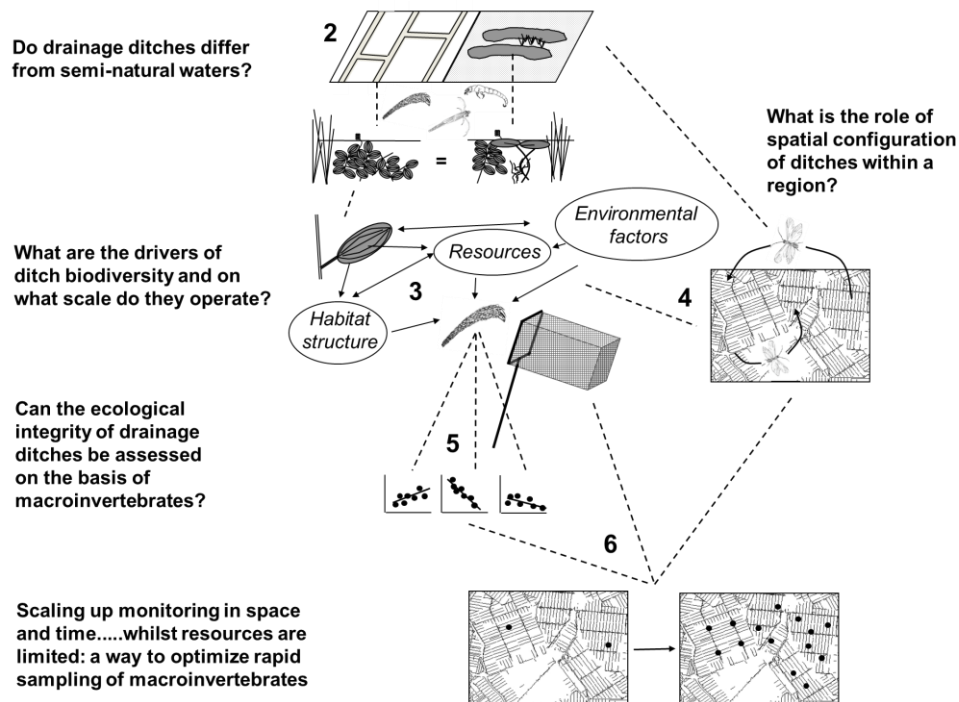


Figure 1.8: Schematic overview of the structure of the thesis and the accompanying chapters.

Figure 1.8 gives a schematic overview of the structure of the thesis and the accompanying chapters. The first two chapters focus on the deterministic factors structuring macroinvertebrate assemblages on relatively small spatial scales; ditch and (micro)habitat. In **chapter 2** differences between agricultural drainage ditches and small semi-natural water bodies, in terms of their biotic assemblages and life history traits, were investigated. Morphological- and physicochemical variables, differences in habitat availability and the presence of fish were incorporated, to identify potential environmental constraints or other structuring mechanisms for drainage ditch macroinvertebrates. By comparing such apparently contrasting aquatic systems, to ecological status of drainage ditch systems could be established. In **chapter 3** the mechanisms underlying drainage ditch macroinvertebrate distribution on microhabitat scale were studied. For vegetation patches, the effect of habitat structure (structural complexity and structure surface area) and resource availability on macroinvertebrates was investigated. Because microscale variables depend on factors operating on a larger spatial scale, for example the nutrient concentrations in the ditch water, these ditch specific factors were studied simultaneously. As a result, the relative importance of patch versus ditch factors for macroinvertebrates could be envisaged.

Whilst in the previous two chapters the focus was primarily on local scale deterministic factors, subsequently the role of stochastic mechanisms was investigated on a larger spatial scale. In **chapter 4** the effect of the spatial distribution of habitats across an entire region was studied. Since drainage ditch networks are comprised of spatiotemporal mosaics of habitat patches, dispersal is an important mechanism for long-term persistence of macroinvertebrate populations. Variation in organismal traits, such as wing size, may affect dispersal rates and thereby the ability to colonize environmentally suited sites. It was examined if patterns in taxon dissimilarity among drainage ditches mirrored not only differences in environmental factors, but also if these patterns were a function of geographic distance, indicating the influence of spatial processes structuring the assemblage composition

Next, the derived results on the role of deterministic and dispersal related processes in structuring drainage ditch macroinvertebrate assemblages were applied to water management practice, by incorporating them into biological monitoring and the assessment of ecological quality of drainage ditch networks. In **chapter 5** a multimetric index based on macroinvertebrates was developed to assess the ecological integrity of drainage ditches, based on a combination of different biological aspects of the assemblages, ranging from diversity indices to tolerance measures. The strength of this approach was that

it avoided putting too much emphasis on the specific species-combination present at a location, thereby keeping in mind the patchiness of the drainage ditch environment. Furthermore, it would be feasible to scale up routine macroinvertebrate monitoring – as currently being carried out by local water district managers – to counteract some of the spatiotemporal variation present in drainage ditch networks. To be able to monitor on large scales, e.g. more sampling points as standardized as possible, without losing realism in terms of sampling and processing time, such a methods must be simple and fast, but informative. In **chapter 6**, the application of an alternative to standard pond netting in drainage ditches is described; the application of activity traps. The use of activity traps is not new: see Brinkman & Duffy (1996) or Turner & Trexler (1997) for a description and comparison with other sampling methods. Therefore, the focus of this chapter was on ways to optimize the technique.

Finally, a synthesis of the preceding chapters is given in **chapter 7**. It describes how the landscape perspective and the metacommunity perspective on patch dynamics apply to drainage ditch networks and their macroinvertebrates and how this knowledge can be used to improve macroinvertebrate monitoring and the assessment of the ecological quality of man-made aquatic systems.

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2 Biodiversity value of agricultural drainage ditches; a comparative analysis of the aquatic invertebrate fauna of ditches and small lakes



Autumn ditch cleaning.

2 Biodiversity value of agricultural drainage ditches; a comparative analysis of the aquatic invertebrate fauna of ditches and small lakes

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Abstract

Drainage ditches are a common aquatic habitat in the lowland agricultural landscape of Northwestern Europe. The invertebrate fauna of these waters is poorly known in comparison to that of the semi-natural wetland fragments found in this region. Whilst most wetlands are designated as nature reserves, drainage ditches are generally viewed purely as hydrological infrastructure in support of agriculture. To assess the conservation value for aquatic invertebrates of these man-made habitats in comparison to that of wetland fragments, the taxonomic composition and life history characteristics of invertebrate assemblages inhabiting 9 small lakes and 9 ditches in peatlands in the Netherlands were compared, as well as the environmental characteristics potentially influencing assemblage structure.

Despite ditches comprised a smaller water volume, contained a less diverse vegetation, displayed larger fluctuations in nutrient concentrations and were regularly maintained by man, the total number of invertebrate taxa recorded per taxonomic group was comparable to small lakes, as was the number of nationally uncommon to very rare taxa. Similarity in life history characteristics between the two water body types was high, except that a higher proportion of atmospheric air breathers was found in ditches, and more plant miners and collector-filterers in small lakes. On a regional scale, a relatively high inter-ditch taxon dissimilarity was observed, resulting in total diversity estimates for ditches exceeding those of small lakes. This study showed that drainage ditches can be a significant habitat type for aquatic invertebrates. In the Netherlands, human-impacted waters in peatland agricultural areas could comprise a diverse invertebrate fauna, similar to that of water bodies in nearby nature reserves.

Keywords: agro-ecosystems, wetlands, life-history traits, macroinvertebrates, peatlands, lentic ecosystems, taxon richness

Introduction

Traditionally, research and management of lentic aquatic ecosystems in lowland areas of north-western Europe have focused on lakes, thereby ignoring small aquatic habitats with an anthropogenic origin, such as drainage ditches. Nevertheless, the latter can be regarded as one of the most extensive aquatic habitats found in agricultural areas. For example, in the Netherlands their combined length is estimated at 300 000 km, and in Great-Britain 128 000 km (Clare & Edwards, 1983). These networks drain excess rainwater or groundwater seepage from surrounding agricultural fields via connected field and collection ditches into rivers and lakes, and vice versa supply water to farmland during dry periods. Thus, ditches can be regarded as the source of water for agricultural drainage systems.

Large-scale drainage in lowland areas, which in north-western Europe started centuries ago and still continues with ongoing agricultural intensification, resulted in the almost complete loss of wetlands. Nowadays, the latter only remain as small fragments surrounded by vast agricultural areas. In agricultural landscapes in the Netherlands, drainage ditch networks are often the only remaining aquatic habitats. These networks have several unique characteristics. First of all, Dutch ditches are linear water bodies of typically several meters wide and up to one meter deep. In combination with negligible water movement, this results in an intensive exchange of matter with the surrounding terrestrial matrix (Herzon & Helenius, 2008). As a consequence, many ditches in the Netherlands are currently in an eu- to hypertrophic state and are degraded due to runoff of nutrients from the neighbouring intensively managed fields (Janse & van Puijenbroek, 1998). Furthermore, to retain their drainage function, management in the form of mowing of the aquatic vegetation and dredging of the accumulated sediment takes place regularly (Beltman, 1984; Twisk et al., 2000). Without management, complete terrestrialization – the infilling of a water body by accumulation of organic material – takes place on a relatively short timescale (Garms, 1961).

Recent studies point out the importance of drainage ditches as reservoirs of invertebrate biodiversity in agricultural areas (Painter, 1999; Armitage et al., 2003; Herzon & Helenius, 2008). General relationships between aquatic invertebrate community composition and environmental variables in drainage ditches have been described, emphasizing the importance of habitat structure generated by the vegetation (Scheffer et al., 1984; Higler & Verdonschot, 1989), diel oxygen patterns (Clare & Edwards, 1983), and ditch dimensions, nutrient/organic loading, and salinity as

important structuring factors (Verdonschot & Higler, 1989; Verdonschot, 1992). Information about the relative biodiversity value of drainage ditches compared to other aquatic ecosystems is scarce. Williams et al. (2004) found that intermittent ditches in Southern England, although supporting fewer species compared to other aquatic ecosystems, contained nationally uncommon species. Painter (1999) suggested that ditches could provide refuges for species characteristic of the formerly extensive (semi)natural lentic ecosystems.

Thus, drainage ditches may have potential to harbour high biodiversity, and may be similar to natural lentic habitats with regard to taxonomic richness, assemblage composition, and functional structure of macroinvertebrate assemblages. Aim of this study was to look at differences between drainage ditches and semi-natural water bodies in terms of their biotic assemblages and life history traits, as explained by morphological- and physicochemical variables, differences in habitat availability and the presence of fish. Semi-natural, small lakes in peatland wetlands in The Netherlands were compared with the drainage ditch networks located in the agricultural lands surrounding these wetlands. In contrast to drainage ditches, these small lakes have, amongst others, a lower edge to water column ratio, a lower rate of terrestrialization and a low level of disturbance (e.g. no sediment dredging). Finally, conservation value of the ditch invertebrate assemblages was addressed by investigating differences in the occurrence of nationally rare species between the water body types.

Materials and methods

Study area

Data were collected from 9 drainage ditches and 9 small lakes in peatland areas across The Netherlands (Fig. 2.1). The small peat lakes, called '*petgaten*', originated from the sixteenth century, when systematic peat dredging produced a typical landscape with many connected, shallow rectangular pits. Due to wind erosion, these pits increased in size (Koster & Favier, 2005). This resulted in the formation of small, shallow lakes with a surface area ranging from $1 \cdot 10^{-4}$ to 0.5 km^2 and a depth of 0.1 to 3 m. These small lakes are now located in nature reserves; the surrounding land use consist mainly of wetland, woodland and shrubs. Drainage ditches are located in the agricultural areas surrounding these wetlands. Farmland consists mainly of meadows used for cattle grazing. Both drainage ditches and small lakes contain water permanently; yearly fluctuations in water level

are minor. Water movement in the drainage ditches is negligible ($0\text{--}5\text{ cm s}^{-1}$); they can be regarded as stagnant waters. Ditch cleaning, in the form of mowing of the aquatic vegetation, occurred in the ditches once a year, in late summer or autumn.

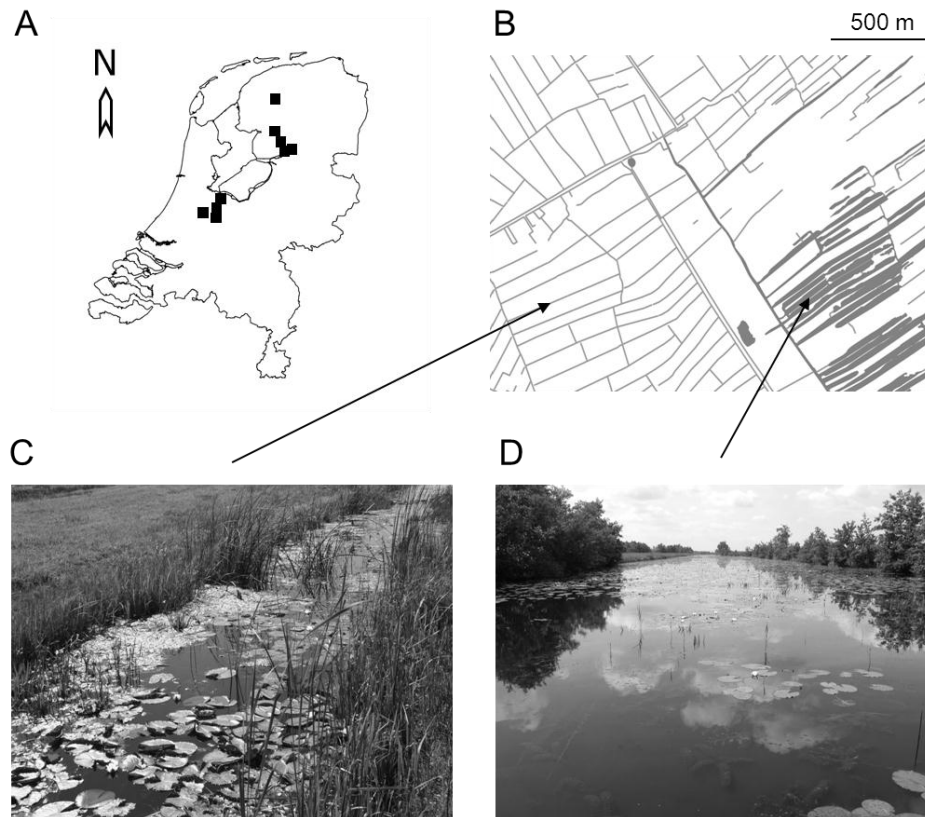


Figure 2.1: A. Location of the study sites within The Netherlands. B. One of the study sites in more detail; hairlines represent drainage ditches, gray areas indicate larger water bodies. Pictures give an impression of a typical drainage ditch (C) and a small, shallow lake; a ‘petgat’ (D).

Data collection

Macroinvertebrates were sampled once in late spring/early summer (2nd half June - 1st half July 2005). This sampling period was chosen to avoid interference of the macroinvertebrate sampling with the moment of ditch cleaning, which generally takes place in autumn. As a consequence, our samples represent only a subset of the total macroinvertebrate diversity present at the sampling locations. Nonetheless, since in macrophyte-rich

lentic systems late spring/early summer is characterized by a relatively high taxon richness (Gerrish & Bristow, 1979), we assume that samples from this season give a good impression of the total taxon richness of the systems sampled.

The sampling method focused on a multihabitat scheme designed for sampling the major habitats in proportion to their presence at a sampling site (AQEM sampling method; Hering et al., 2004). A sampling site was quantified as a section representative for the whole ditch or small lake in terms of morphology and vegetation, 50 m in length and including the entire wetted cross-sectional area over this distance. A sample consisted of 10 sampling units taken from all microhabitat types (e.g. emergent macrophytes, submerged macrophytes, floating algal mats, organic mud) at the sampling site with a coverage of at least 5%. Based on the estimation of total microhabitat coverage the number of sampling units in the individual habitats was determined. A sampling unit is a sampling accomplished by sweeping a 0.5-mm mesh pond net (0.25 x 0.20 m) several times over a length of 0.5 m of the habitat. In total, this procedure results in sampling approximately 1.25 m² water body area.

Material collected was transported to the laboratory, washed over 1 mm and 250 µm sieves, and sorted alive. Because of the large amount of material collected, subsampling turned out to be necessary. Therefore, washed material was homogenized and spread out evenly in a large tray, after which a subsample of 25% of the material was taken. Tricladia were identified immediately after collection. The remaining invertebrates collected were preserved until further processing. Aquatic invertebrates were identified to the lowest taxonomical level practical, mainly species.

Macrophytes, charophytes and aquatic bryophytes were surveyed at the same locations of the macroinvertebrate samples in late spring. All plants present within the boundary of the water body were recorded. Submerged macrophytes were collected by raking over the bottom sediment with a rake at regular intervals. Abundance of plant species was expressed in Tansley cover-classes (Tansley, 1946). According to Den Hartog and Segal (1964), each species was assigned to a growth form category.

Presence of fish in the drainage ditches and small lakes was determined by electric fishing (backpack electrofisher with a single anode using a pulsed direct current). Approximately 75% of the surface area of the small lakes and ditch sections of 100 m were sampled on a single occasion in late summer. Fish were identified to species in the field, measured and returned to the water. Biomass was derived from length-biomass relationships (Klein Breteler & De Laak, 2003).

At each location, physicochemical and morphological features of the water bodies were recorded to characterize both water body types. Average maximum depth and thickness of the layer of particulate organic matter (sapropelium) accumulated on the bottom were measured during macroinvertebrate sampling ($n = 5$ per sampling site). Maximum width of the small lakes was derived from a topographical map, whilst the maximum width of the drainage ditches was measured in the field. A range of physicochemical variables was recorded monthly for a period of one year. Conductivity and pH were directly measured in the field by electrodes (Hach sensION156, Hach Lange GmbH, Düsseldorf, Germany) and 1 L water samples were taken for laboratory analysis of nutrients (NH_4^+ , NO_3^- , total-N, o-P, total-P) and macro-ions (Cl^- , SO_4^{2-}) by Vitens Laboratorium BV accredited according to NEN-EN-ISO/IEC 17025 standard (registration number RvA L 043).

Data processing and analysis

Environmental characterization

Measurements defining the different water body types were those of water body morphology; width, depth and thickness of the sapropelium layer. Since these variables met the assumptions of normality and homogeneity of variances, significant differences ($p < 0.05$) between water body types were determined using independent t-tests. This statistical test and the subsequent tests were conducted in SPSS for Windows (version 15.0; SPSS, Chicago, Illinois).

Linked to the morphology was the difference in habitat- or potential niche availability between drainage ditches and small lakes, determined as the number of growth forms of helo- and hydrophytes found in the water body. Both the mean number of abundant growth forms, defined as Tansley cover-class >2 , and the total number of growth forms were compared, because we assumed that the importance of a growth form as a habitat increased with increasing abundance in the water body. Significance ($p < 0.05$) was determined using non-parametric Mann-Whitney tests, because of deviations from normality and homogeneity of variances.

Fish taxon richness, density and biomass were compared between the water body types. Density and biomass were $\ln(x+1)$ -transformed to meet the assumptions of normality and homogeneity of variances, and significant differences ($p < 0.05$) were determined using independent t-tests.

We were unable to fish in two small lakes. Therefore, these locations were omitted from the comparisons.

Finally, average concentrations of nutrients and macro-ions and seasonal fluctuations in their concentrations were compared, as well as pH and conductivity, to investigate if concentrations were higher and fluctuations were larger in drainage ditches compared to small lakes. Significance ($p < 0.05$) was determined using non-parametric Mann-Whitney tests, because of deviations from normality and homogeneity of variances.

Taxonomic richness and composition

As not all macroinvertebrate specimens collected could be identified to the lowest taxonomic level (for example early instars of insects), an adjustment procedure was applied (e.g. Vlek et al., 2004). This procedure reduced bias in the subsequent analyses due to differences in taxonomic resolution by grouping to a higher taxonomical level (Schmidt-Kloiber & Nijboer, 2004).

Differences in taxonomical richness between ditches and small lakes were calculated for the total invertebrate assemblage as well as for the major individual taxonomical groups. Furthermore, diversity index values, based on the Shannon-Wiener index, were compared. To determine differences in assemblage composition, relative abundance of the taxonomical groups was calculated. Taxon richness and abundance data differed in the extent to which they approached normality and homogeneity of variances. Therefore, differences were tested with independent t-tests for total richness and Shannon-Wiener diversity, whilst richness and abundance of individual taxonomic groups were tested using Mann-Whitney tests.

Homogeneity of the assemblages within one water body type were compared using Jaccard and Bray-Curtis similarity indices, to take both presence-absence and abundance of taxa into account. To show potential differences in taxon density between ditches and small lakes, taxon accumulation curves for the complete assemblages were constructed with the program EstimateS (version 7.5.1; Colwell, 2005). The curves show an increase in taxa collected with every new sample added. When taxon composition of the different samples within a water body type is very dissimilar, a steeper curve is constructed compared to a situation in which the samples are more similar. Curves were smoothed by randomizing the sampling order 50 times, after which means were computed with 95% confidence intervals.

Total invertebrate richness of the water body types could not be derived from the number of samples collected. Therefore, an estimation of

the minimum total richness of drainage ditches and small lakes was made using two approaches: 1.) fitting an asymptotic equation to the taxon accumulation curves, and 2.) using a nonparametric estimator which uses the relative abundances of rare taxa to estimate the number of taxa not captured (Colwell & Coddington, 1994; Colwell, 2005). Following Longino et al. (2002), the Michaelis-Menten equation (MM-means) was used in the former approach. The commonly used Incidence-based Coverage Estimator (ICE) and Chao 2 estimator were chosen as non-parametric estimators. Both estimators showed reliable and consistent estimates at a relatively low sampling effort for littoral pond invertebrates (Foggo et al., 2003). Richness estimators were calculated in EstimateS (version 7.5.1; Colwell, 2005).

Rarity

Rarity of taxa was based on the distribution classification of Dutch macroinvertebrate taxa (Nijboer & Verdonchot, 2004). They distinguished 6 distribution classes based on site occupancy within The Netherlands: very rare (0-0.15%), rare (>0.15%-0.5%), uncommon (>0.5-1.5%), common (>1.5%-4%) , very common (>4-12%), and abundant (>12%). Taxa were assigned to their distribution class. In total, from 79(\pm 4)% of the taxa in the samples a rarity class could be assigned. The remainder comprised a higher taxonomical level or no information about the distribution was available. Average number of taxa per rarity class was compared using Mann-Whitney tests.

Functional- and life history characteristics

Functional- and life history characteristics of the taxa were compared to identify differences in ecosystem functioning or the influence of potential environmental constraints. For each taxon, available functional characteristics were derived from the Dutch lentic macroinvertebrate trait database (available upon request), in which auto-ecological information from a wide variety of literature sources is combined. In total, 9 traits were used, concerning reproduction (development time, voltinism, life span), physiological aspects (respiration mode), dispersal capability (dispersal mode), substrate relationship (habit trait group, oviposition site) and functional role within the ecosystem (functional feeding group, trophic level).

Reproduction traits may give information on the stability of the systems, since instability of habitats could lead to dominance of species with

a short development time, many generations per year, and a short life span. Dispersal may be linked to stability as well. The physiological trait ‘respiration mode’ may give information on the oxygen regime of the water bodies; a high proportion of species which obtain their oxygen from the atmosphere could indicate (unpredictable) periods of hypoxia. Substrate relationship could indicate the role of habitat availability, whilst functional feeding groups and trophic level could give an indication of ditch and small lake ecosystem functioning.

Fuzzy coding was used to describe the relationship between taxa and trait modalities: 0 indicated no affinity, 10 indicated a very high affinity. By assigning points according to the affinity of taxa with several modalities, accuracy of classification was increased (Chevenet et al., 1994). For each sample, the total number of points per trait modality was calculated. Influence of individual taxa was weighed based on their abundance ($\log_2(x+1)$ -transformed). By dividing the weighed score per trait modality by the total trait score, its relative proportion was determined. Differences in proportions of trait modalities were compared using Mann-Whitney tests.

Results

Habitat characterization

Habitat availability

Small lakes were approximately 14 times wider than ditches (lakes 56 ± 53 m, ditches 4 ± 2 m; $Z = -3.578$, $p < 0.0001$), but only slightly deeper, with an average maximum depth of 1.0 ± 0.3 m for small lakes and 0.6 ± 0.4 m for ditches ($t(16) = -2.766$, $p = 0.014$) (Table 2.1). Average thickness of the sapropelium layer was comparable for both water body types (ditches: 0.5 ± 0.4 m, small lakes: 0.4 ± 0.3 m; $t(15) = 0.509$, $p = 0.618$).

Table 2.1: Mean value and range of morphological variables recorded in small lakes and drainage ditches in Dutch peatlands ($n = 9$).

Variable	Small lakes			Ditches		
	mean	min	max	mean	min	max
Maximum width (m)	56	24	190	4.4	0.5	6.4
Maximum depth (m)	1.0	0.7	1.5	0.6	0.1	1.1
Thickness sapropelium layer (m)	0.4	0.1	0.9	0.5	0.1	1.2

Table 2.2: *Vegetation growth forms (Den Hartog & Segal, 1964) recorded in small lakes and drainage ditches in Dutch peatlands.*

Plant type	Growth form	Example taxa
Hydrophyte	Ricciellids	<i>Lemna trisulca</i>
	Ceratophyllids	<i>Ceratophyllum demersum</i> , <i>Utricularia vulgaris</i>
	Myriophyllids	<i>Myriophyllum spicatum</i> , <i>Hottonia palustris</i> , <i>Ranunculus circinatus</i>
	Elodeids	<i>Elodea nuttallii</i> , <i>Fontinalis antipyretica</i>
	Magnopotamids	<i>Potamogeton mucronatus</i> , <i>P. pusillus</i>
	Parvopotamids	<i>Potamogeton lucens</i> , <i>P. crispus</i> , <i>Najas marina</i>
	Characea	<i>Chara globularis</i> , <i>Nitella flexilis</i>
	Stratiotids	<i>Stratiodes aloides</i>
	Lemnids with small leave-like thalli	<i>Lemna minor</i> , <i>Spirodela polyrrhiza</i>
	Magnonymphaeids	<i>Nuphar lutea</i> , <i>Nymphaea alba</i>
	Parvonymphaeids	<i>Hydrocharis morsus-ranae</i> , <i>Potamogeton natans</i> , <i>Persicaria amphibia</i>
Helophyte	Helophytes with blade-like leaves	<i>Sparganium erectum</i> , <i>Typha angustifolia</i> , <i>Iris pseudacorus</i> , <i>Carex pseudocyperus</i> , <i>Butomus umbellatus</i> , <i>Acorus calamus</i>
	Helophytes with leafless stems, small diameter	<i>Eleocharis palustris</i> , <i>Equisetum fluviale</i> , <i>Juncus effusus</i>
	Helophytes with leafless stems, large diameter	<i>Phragmites australis</i> , <i>Schoenoplectus lacustris</i>
	Pleusthelophytes with leaves mainly above the water surface	<i>Calla palustris</i> , <i>Menyanthes trifoliata</i> , <i>Potentilla palustris</i> , <i>Berula erecta</i> , <i>Myosotis scorpioides</i> , <i>Mentha aquatica</i>
	Pseudohydrophytes with broad leaves above the water surface, often also under-water leaves present	<i>Alisma plantago-aquatica</i> , <i>Sagittaria sagittifolia</i> , <i>Rumex hydrolapathum</i>

Vegetation was present in all water bodies sampled. Average taxon richness of hydrophytes was higher in small lakes (15 ± 2) compared to ditches (9 ± 3) ($t(16) = -4.708$, $p = 0.000$), whilst the number of helophytes recorded in both water body types was comparable (both 14 ± 5 ; $t(16) = -0.228$, $p = 0.822$). In total, 5 helophyte growth forms and 11 hydrophyte growth forms could be distinguished (Table 2.2). The number of hydrophyte growth forms present in small lakes was significantly higher compared to ditches, both for all growth forms ($Z = -2.375$, $p = 0.019$) and

with only the relatively abundant growth forms included ($Z = -3.013$, $p = 0.002$) (Fig. 2.2A). For helophytes, there was a significant difference between ditches and small lakes when only the abundant growth forms were taken into account ($Z = -2.672$, $p = 0.014$), but this effect disappeared when also the relatively rare growth forms were included ($Z = -0.922$, $p = 0.637$) (Fig. 2.2B).

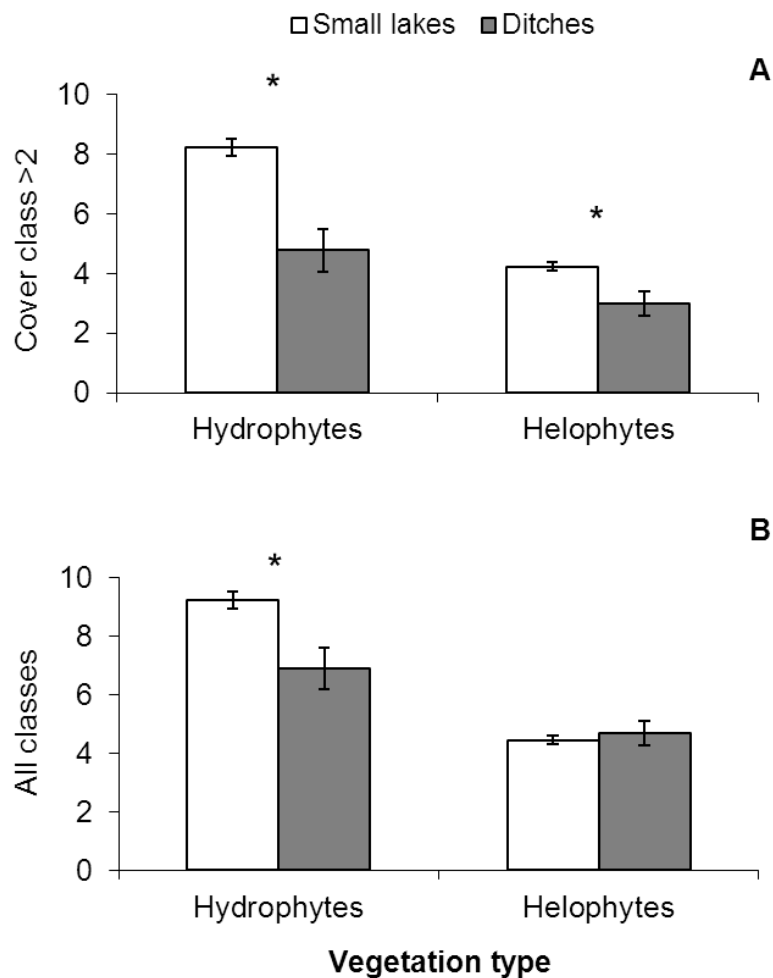


Figure 2.2: Comparison of the mean number of vegetation growth forms ($\pm 1SE$) recorded in small lakes and drainage ditches in Dutch peatlands ($n = 9$), based on relatively abundant plant species, defined as Tansley cover-class >2 (A), and with rare plant species included (B). Significant differences (Mann-Whitney tests, $p < 0.05$) are indicated with an asterisk.

Physical-chemical stability

Physicochemical conditions were rather similar in ditches and small lakes, except that small lakes had a higher seasonal average pH, nitrate- and sulphate concentration, whilst the average concentration of orthophosphate was higher in ditches (Table 2.3). Coefficients of variation of ammonium, orthophosphate and total-P were high in ditches compared to small lakes, indicating that for these nutrients, variation between individual ditches was relatively high. Based on the seasonal range recorded for the physicochemical variables, it became clear that fluctuations in pH and orthophosphate were significantly higher in ditches compared to small lakes, whilst in small lakes larger fluctuations in nitrate were found (Table 2.3).

Table 2.3: Mean value and range of physicochemical variables measured monthly during one year in small lakes (SL) and drainage ditches (DI) in Dutch peatlands ($n = 9$). Values were compared using Mann-Whitney tests; significant differences ($p < 0.05$) are indicated with an asterisk. Coefficient of variation (CV) indicated the variation between sampling locations within one water body type.

	Variable	Mean (± 1 SD)		CV		Z	P
		SL	DI	SL	DI		
Mean	pH	7.6 \pm 0.3	7.1 \pm 0.2	0.03	0.03	-3.49	**
	Conductivity ($\mu\text{S cm}^{-1}$)	369 \pm 82	358 \pm 116	0.22	0.33	-0.22	*
	Cl ⁻ (mg L ⁻¹)	36 \pm 19	37 \pm 15	0.52	0.40	-0.75	ns
	NH ₄ ⁺ (mg N L ⁻¹)	0.10 \pm 0.02	0.19 \pm 0.23	0.17	1.19	-0.40	ns
	NO ₃ ⁻ (mg N L ⁻¹)	0.21 \pm 0.07	0.11 \pm 0.04	0.33	0.36	-3.14	**
	o-P (mg P L ⁻¹)	0.01 \pm 0.00	0.07 \pm 0.11	0.46	1.62	-2.00	*
	SO ₄ ²⁻ (mg L ⁻¹)	23 \pm 10	15 \pm 6	0.44	0.43	-2.25	*
	total-N (mg N L ⁻¹)	1.4 \pm 0.2	2.1 \pm 0.9	0.15	0.42	-1.72	ns
	total-P (mg P L ⁻¹)	0.06 \pm 0.02	0.14 \pm 0.13	0.29	0.98	-1.37	ns
Range	pH	0.8 \pm 0.3	1.4 \pm 0.4	0.31	0.28	-2.88	*
	Conductivity ($\mu\text{S cm}^{-1}$)	169 \pm 114	226 \pm 174	0.68	0.77	-0.57	ns
	Cl ⁻ (mg L ⁻¹)	24 \pm 15	41 \pm 28	0.64	0.68	-1.46	ns
	NH ₄ ⁺ (mg N L ⁻¹)	0.09 \pm 0.08	0.39 \pm 0.56	0.82	1.43	-1.02	ns
	NO ₃ ⁻ (mg N L ⁻¹)	0.65 \pm 0.43	0.20 \pm 0.21	0.67	1.00	-2.49	*
	o-P (mg P L ⁻¹)	0.01 \pm 0.02	0.16 \pm 0.26	1.83	1.63	-2.35	*
	SO ₄ ²⁻ (mg L ⁻¹)	11 \pm 7	17 \pm 19	0.64	1.08	-0.58	ns
	total-N (mg N L ⁻¹)	1.6 \pm 0.9	2.5 \pm 1.9	0.56	0.75	-1.37	ns
	total-P (mg P L ⁻¹)	0.07 \pm 0.06	0.25 \pm 0.27	0.85	1.09	-1.81	ns

* $p < 0.05$, ** $p < 0.001$, *** $p < 0.0001$

Presence of fish

Fish were absent in one ditch, while all other water bodies contained one or more individuals. The number of fish species recorded in small lakes (7.9 ± 1.8) was higher compared to ditches (3.3 ± 2.5) ($t(14) = 3.99$, $p = 0.001$). In terms of abundance, both expressed as number of individuals per ha ($t(14) = 1.168$, $p = 0.262$) and biomass per ha ($t(14) = 1.876$, $p = 0.082$), no significant differences were observed between the habitat types. Between sampling locations within both water body types, differences in biomass and abundance were considerable (Fig. 2.3A,B).

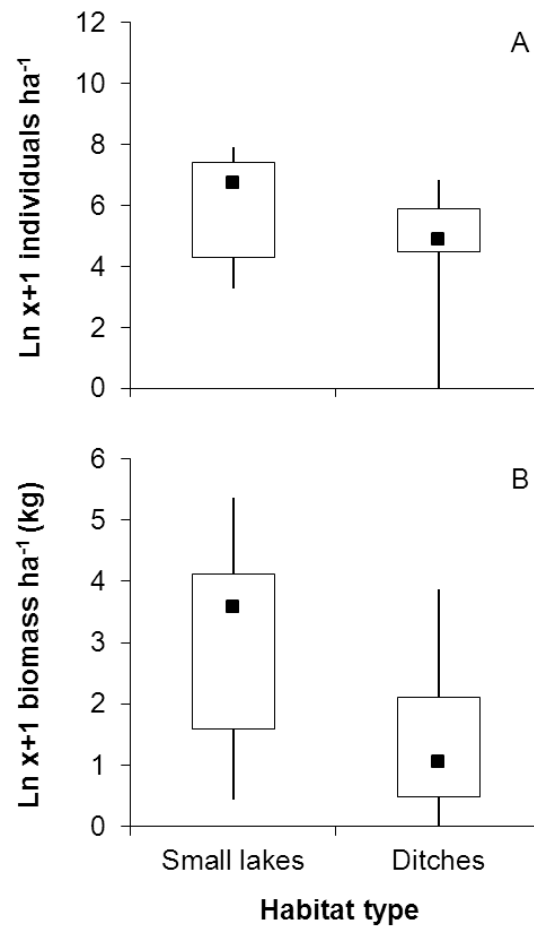


Figure 2.3: Boxplots of fish abundance per ha, expressed in number of individuals (A) and total biomass (B). Range bars show maximum and minimum values. Boxes are interquartile ranges (25th percentile to 75th percentile); squares represent medians.

Table 2.4: Summary table of macroinvertebrate families recorded. The total number of taxa, total abundance and frequency of occurrence per water body type ($n = 9$) is given. The number within parentheses indicates the total number of taxa recorded per family across small lakes and ditches.

Tax. group	Family	Small lakes			Ditches		
		taxa	abun	freq	taxa	abun	freq
Tricladia	Dugesidae (2)	2	10	5	1	5	4
Tricladia	Planariidae (1)	1	5	5	1	8	3
Tricladia	Dendrocoelidae (2)	2	4	3	1	2	2
Gastropoda	Valvatidae (2)	2	28	6	2	18	5
Gastropoda	Viviparidae (1)	1	1	1	1	1	1
Gastropoda	Bithyniidae (2)	2	144	9	2	48	7
Gastropoda	Hydrobiidae (2)	2	23	4	0	0	0
Gastropoda	Ancylidae (1)	1	1	1	0	0	0
Gastropoda	Lymnaeidae (6)	5	50	9	4	128	8
Gastropoda	Acroloxidae (1)	1	8	4	0	0	0
Gastropoda	Physidae (1)	1	13	6	1	67	8
Gastropoda	Planorbidae (9)	7	174	9	9	340	9
Bivalvia	Sphaeriidae (3)	2	182	9	3	294	8
Hirudinea	Glossiphoniidae (7)	5	28	8	6	28	7
Hirudinea	Piscicolidae (1)	1	1	1	1	1	1
Hirudinea	Erpobdellidae (3)	3	47	8	2	65	8
Oligochaeta	Naididae (8)	6	205	9	7	206	9
Oligochaeta	Tubificidae (2)	2	112	9	2	245	9
Oligochaeta	Lumbriculidae (1)	1	3	1	1	16	4
Araneae	Argyronetidae (1)	1	4	3	1	86	3
Hydracarina	Hydrachnidae (2)	2	5	3	2	6	4
Hydracarina	Limnocharidae (1)	1	10	3	1	3	3
Hydracarina	Eylaidae (2)	1	3	3	2	5	5
Hydracarina	Hydryphantidae (2)	0	0	0	2	2	2
Hydracarina	Hydrodromidae (1)	1	113	9	1	40	8
Hydracarina	Oxidae (4)	4	28	7	1	19	5
Hydracarina	Limnesiidae (5)	5	103	8	4	41	6
Hydracarina	Hygrobatidae (2)	1	1	1	1	1	1
Hydracarina	Unionicolidae (6)	5	77	8	5	74	5
Hydracarina	Pionidae (14)	10	77	9	11	70	7

Tax. group (continued)	Family	Small lakes			Ditches		
		<i>taxa</i>	<i>abun</i>	<i>freq</i>	<i>taxa</i>	<i>abun</i>	<i>freq</i>
Hydracarina	Aturidae (1)	1	5	3	1	3	1
Hydracarina	Mideidae (2)	2	31	7	2	11	3
Hydracarina	Arrenuridae (20)	10	177	9	19	173	9
Maxillopoda	Argulidae (1)	0	0	0	1	1	1
Mysida	Mysidae (1)	1	6	3	0	0	0
Isopoda	Asellidae (3)	3	168	9	3	376	9
Amphipoda	Gammaridae (3)	2	109	7	2	276	8
Decapoda	Cambaridae (1)	1	1	1	0	0	0
Odonata	Lestidae (2)	0	0	0	2	4	2
Odonata	Coenagrionidae (4)	3	73	9	3	32	8
Odonata	Aeshnidae (2)	2	7	6	1	7	3
Odonata	Libellulidae (1)	1	2	2	1	5	3
Ephemeroptera	Baetidae (2)	2	34	6	1	60	5
Ephemeroptera	Caenidae (3)	3	348	9	3	235	9
Heteroptera	Corixidae (4)	3	16	4	4	47	8
Heteroptera	Naucoridae (1)	1	29	9	1	58	8
Heteroptera	Nepidae (2)	1	5	2	1	1	1
Heteroptera	Pleidae (1)	1	30	8	1	156	9
Heteroptera	Notonectidae (1)	1	7	3	1	4	3
Heteroptera	Mesoveliidae (1)	1	6	4	1	2	1
Heteroptera	Hydrometridae (1)	0	0	0	1	2	2
Heteroptera	Veliidae (2)	1	1	1	1	1	1
Heteroptera	Gerridae (1)	1	2	2	1	3	3
Megaloptera	Sialidae (1)	1	33	3	1	53	7
Coleoptera	Haliplidae (1)	1	5	2	1	6	4
Coleoptera	Noteridae (2)	2	2	2	2	7	3
Coleoptera	Dytiscidae (13)	5	16	7	11	24	7
Coleoptera	Gyrinidae (1)	1	6	5	1	17	4
Coleoptera	Hydrophilidae (7)	3	4	4	5	32	7
Coleoptera	Dryopidae (2)	0	0	0	2	2	2
Coleoptera	Elmidae (1)	0	0	0	1	3	1
Coleoptera	Scirtidae (3)	2	5	1	2	78	5

Tax. group (continued)	Family	Small lakes			Ditches		
		<i>taxa</i>	<i>abun</i>	<i>freq</i>	<i>taxa</i>	<i>abun</i>	<i>freq</i>
Coleoptera	Chrysomelidae (1)	0	0	0	1	1	1
Coleoptera	Curculionidae (1)	1	2	2	1	4	1
Diptera	Limoniidae (1)	1	5	4	1	6	3
Diptera	Chaoboridae (2)	1	9	5	2	10	2
Diptera	Dixidae (1)	1	3	2	0	0	0
Diptera	Ceratopogonidae (1)	1	62	9	1	128	8
Diptera	Chironomidae (54)	42	1021	9	43	638	9
Diptera	Stratiomyidae (2)	1	2	1	2	11	4
Diptera	Sciomyzidae (1)	0	0	0	1	1	1
Trichoptera	Hydroptilidae (5)	3	81	7	4	66	7
Trichoptera	Leptoceridae (8)	7	108	9	5	117	9
Trichoptera	Limnephilidae (3)	1	2	2	3	5	2
Trichoptera	Molannidae (1)	0	0	0	1	1	1
Trichoptera	Phryganeidae (2)	2	15	5	2	24	6
Trichoptera	Polycentropodidae (5)	5	89	9	4	80	6
Lepidoptera	Pyralidae (3)	1	9	4	3	8	4

Assemblage richness and composition

Taxonomical richness and composition

The total number of invertebrate taxa recorded in drainage ditches was 226 (4598 individuals), the number recorded in small lakes was lower (201 taxa, 3996 individuals) (Table 2.4). In total, ditches and small lakes shared 150 taxa. The average number of taxa in ditches (75 ± 15) was comparable to the taxon richness of small lakes (81 ± 8) ($t(16) = -1.081$, $p = 0.296$). Also, Shannon-Wiener index values (ditches 3.49 ± 0.03 , small lakes 3.63 ± 0.02 ; $t(16) = -1.208$, $p = 0.245$) did not differ between the two water body types. When analyzed individually, most taxonomic groups displayed the same pattern as total richness, except for Ephemeroptera, for which richness was significantly higher in small lakes (Table 2.5). Differences in relative abundances were found in several taxonomic groups. Heteroptera and Coleoptera accounted for a significantly larger proportion of the assemblage in drainage ditches, whilst Odonata and Chironomidae were relatively more abundant in small lakes (Table 2.5).

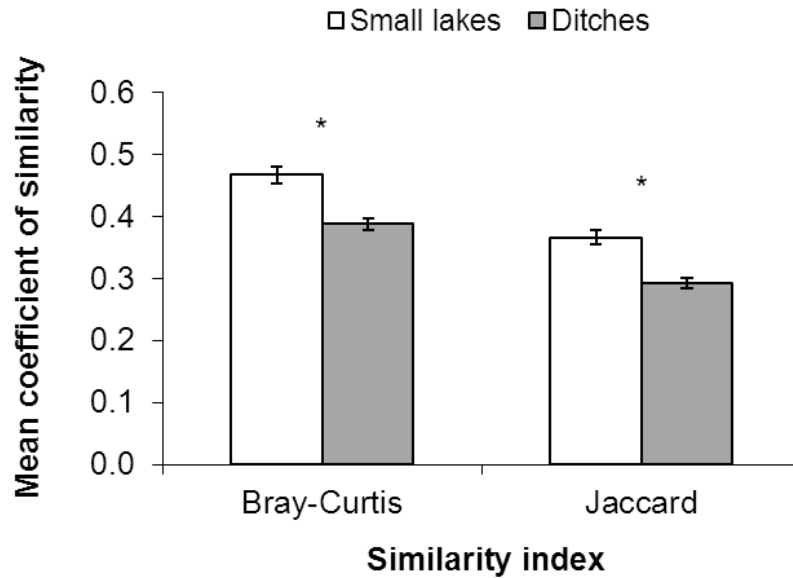


Figure 2.4: Comparison of the coefficients of similarity ($\pm 1SE$) of small lake and drainage ditch macroinvertebrate assemblages, based on the means of all possible sample combinations ($n = 36$) within a water body type. Similarity indices based on taxon presence (Jaccard) as well as taxon abundance (Bray-Curtis) are given. Significant differences (Mann-Whitney tests, $p < 0.05$) are indicated with an asterisk.

Table 2.5: Comparison of average macroinvertebrate taxon richness and relative abundance of major taxonomic groups ($\pm 1SE$) found in small lakes (SL) and drainage ditches (DI) in Dutch peatlands ($n = 9$). Significance ($p < 0.05$) is determined by Mann-Whitney tests.

Tax. group	Mean # taxa		Z	P	Mean % abundance			
	SL	DI			SL	DI	Z	P
Gastropoda	10.6±1	8.7±1	-1.47	ns	11±1	12±3	-0.31	ns
Bivalvia	1.8±0.1	1.4±0.3	-1.09	ns	4±2	5±2	-0.13	ns
Hirudinea	3.1±0.5	2.9±0.6	-0.41	ns	2±0.3	3±0.9	-0.18	ns
Oligochaeta	3.8±0.5	4.6±0.4	-1.23	ns	8±3	10±4	-0.13	ns
Hydracarina	17.1±1	14.1±1.9	-1.38	ns	17±2	12±3	-1.46	ns
Crustacea	3.2±0.4	2.7±0.3	-1.31	ns	6±2	13±3	-1.99	ns
Odonata	2.7±0.3	2.1±0.3	-1.26	ns	2±0.2	1±0.2	-2.52	*
Ephemeroptera	3.1±0.2	1.9±0.3	-2.86	*	9±2	8±3	-1.28	ns
Heteroptera	3.9±0.5	4.8±0.6	-1.25	ns	2±0.4	6±1	-2.61	*
Coleoptera	3.1±0.9	5.9±1.1	-1.88	ns	1±0.3	4±1	-3.05	**
Chironomidae	16.3±1	15.4±1.1	-0.63	ns	26±4	15±3	-2.16	*
Trichoptera	6.9±0.8	5.4±0.9	-1.16	ns	8±1	6±2	-1.81	ns

* $p < 0.05$, ** $p < 0.001$, *** $p < 0.0001$

The average similarity in taxon composition between all possible ditch-small lake pairs was 0.28 ± 0.05 based on the presence/absence of taxa (Jaccard coefficient of similarity) and 0.37 ± 0.05 based on the abundance of taxa (Bray-Curtis coefficient of similarity). Invertebrate assemblages found in small lakes were more uniform compared to ditches, both when based on the presence ($Z = -4.64$, $p < 0.0001$) and abundance ($Z = -4.25$, $p < 0.0001$) of the taxa recorded (Fig. 2.4). Taxon accumulation curves did not reach the asymptote with 9 samples per water body type, which indicated that in both ditches and small lakes more taxa could be collected with an increasing sampling effort (Fig. 2.5). Although no asymptote was reached, there appeared to be a difference in the shape of the curves. Drainage ditch accumulation curve showed a trend towards a continuous steep increase, whilst the curve of small lakes appeared to slowly level off with an increasing number of samples added.

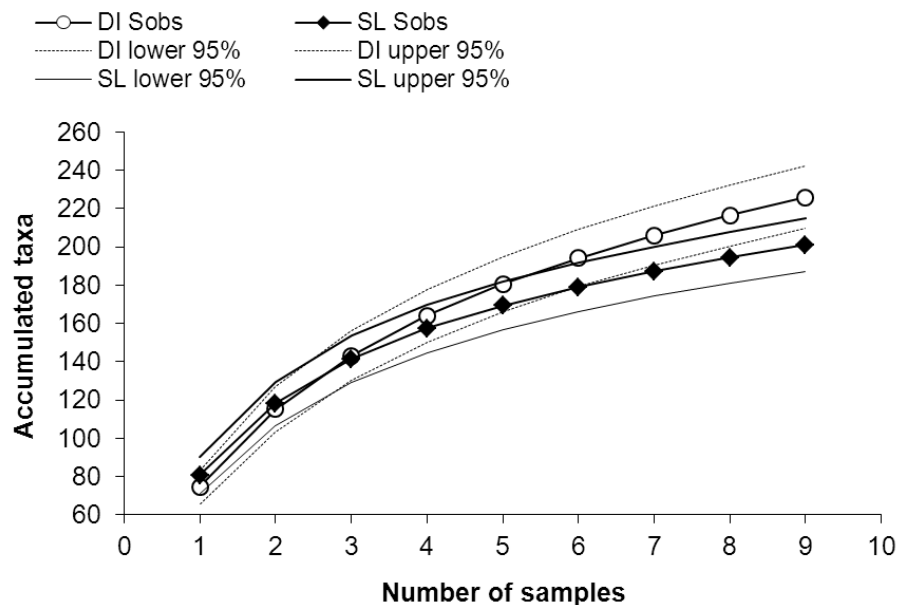


Figure 2.5: Sample-based macroinvertebrate taxon accumulation curves with 95% confidence intervals of drainage ditch (DI) and small lake (SL) samples. Sample order was randomized 50 times to obtain means (S_{obs}).

As predicted by the shape of the accumulation curves minimum 'true' richness estimations for drainage ditches were higher compared to small lakes, independent of the type of estimator used (Fig. 2.6). The

asymptote generated by the Michaelis-Menten means was relatively stable with new samples added, predicting a total richness of 296 taxa for ditches and 242 taxa for small lakes based on 9 samples. ICE, and especially Chao 2, both predicted an even higher taxon richness, and showed a continuous increase in number of taxa at 9 samples.

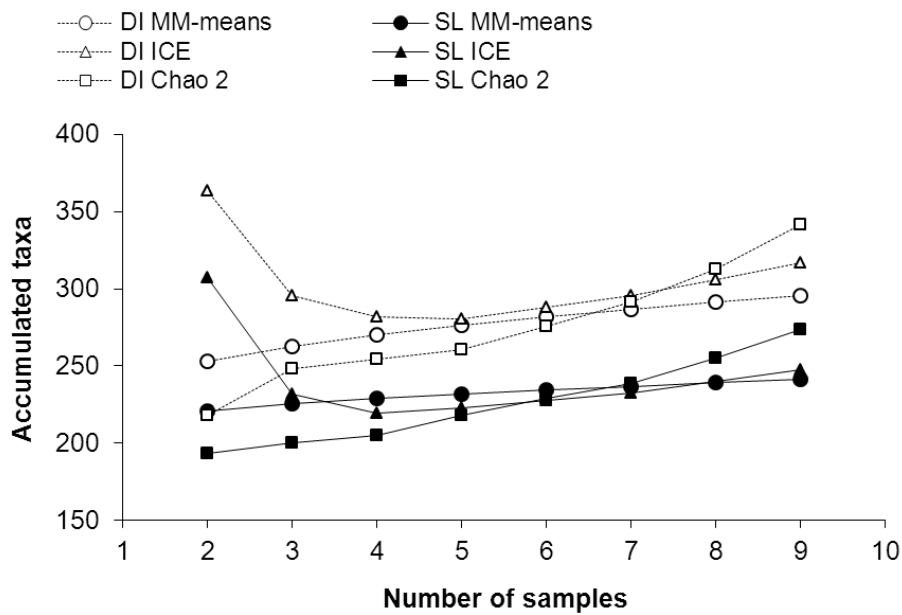


Figure 2.6: Estimated minimum total macroinvertebrate richness of drainage ditches and small lakes, derived from fitting the Michaelis-Menten equation (MM-means) to the taxon accumulation curves, and based on the nonparametric Incidence-based Coverage Estimator (ICE) and the Chao 2 estimator.

Table 2.6: Number of uncommon, rare and very rare macroinvertebrate taxa recorded in drainage ditches and small lakes in Dutch peatlands ($n = 9$). Rarity is based on the distribution classification of Dutch macroinvertebrate taxa (Nijboer & Verdonchot 2004).

Habitat type		Rarity class			Total richness
		Uncommon	Rare	Very rare	
Small lakes	Total	17	7	2	201
	Unique	8	5	2	51
Ditches	Total	15	10	6	226
	Unique	6	8	6	76
Shared		9	2	0	150

Table 2.7: Comparison of relative proportions of trait modalities ($\pm 1SD$) based on the macroinvertebrate assemblages found in small lakes (SL) and drainage ditches (DI) in Dutch peatlands ($n = 9$). Significance ($p < 0.05$) is determined by Mann-Whitney tests.

Trait	Modality	Mean%±1SD			
		SL	DI	Z	p
Reproduction					
Voltinism	Univoltine + semivoltine	32±7	39±9	-1.55	ns
Development time	>1 year	3±1	3±1	-1.37	ns
Life span	>1 year	12±3	10±4	-1.63	ns
Physiology					
Respiration mode	Atmospheric air	11±2	18±5	-3.13	**
Dispersal					
Dispersal mode	Aerial active	35±7	34±8	-0.22	ns
	Aerial passive	24±5	21±4	-1.37	ns
	Aquatic active	33±5	36±8	-1.28	ns
	Aquatic passive	8±4	8±3	-0.13	ns
Substrate relation					
Habit trait group	Sediment burrower	7±3	9±5	-0.22	ns
	Clinger	7±2	7±3	-0.04	ns
	Climber	19±1	22±5	-1.81	ns
	Plant miner	7±4	3±2	-2.43	*
	Sprawler	21±3	21±3	-0.04	ns
	Swimmer/diver	26±3	28±5	-0.49	ns
	Temporary attached	8±2	8±3	-0.40	ns
	Water surface	2±1	1±1	-1.63	ns
	Attached to host	2±0	2±1	-0.31	ns
Oviposition site	Eggs attached to substrate	52±7	48±8	-0.93	ns
	Eggs in plant tissue	9±3	11±4	-0.66	ns
	Eggs free in/on water	16±6	17±4	-0.04	ns
	Eggs carried by organism ^A	20±9	23±8	-0.84	ns
Functional role					
FFG ^B	Collector-gatherer	29±5	30±7	-0.22	ns
	Collector-filterer	18±4	12±3	-2.60	*
	Piercer of plant/algal cells	3±2	2±2	-1.41	ns
	Parasite	2±1	2±1	-0.22	ns
	Predator (engulfer/piercer)	29±6	32±4	-1.19	ns
	Scraper/grazer	12±4	12±4	-0.22	ns
	Shredder	7±2	10±3	-1.72	ns
Trophic level	Detritivore	34±5	35±6	-0.40	ns
	Herbivore	30±5	26±4	-1.37	ns
	Carnivore	34±6	36±6	-0.66	ns
	Parasite	2±1	2±2	-0.04	ns

* $p < 0.05$, ** $p < 0.001$, *** $p < 0.0001$, ^A or ovoviviparous, ^B functional feeding group

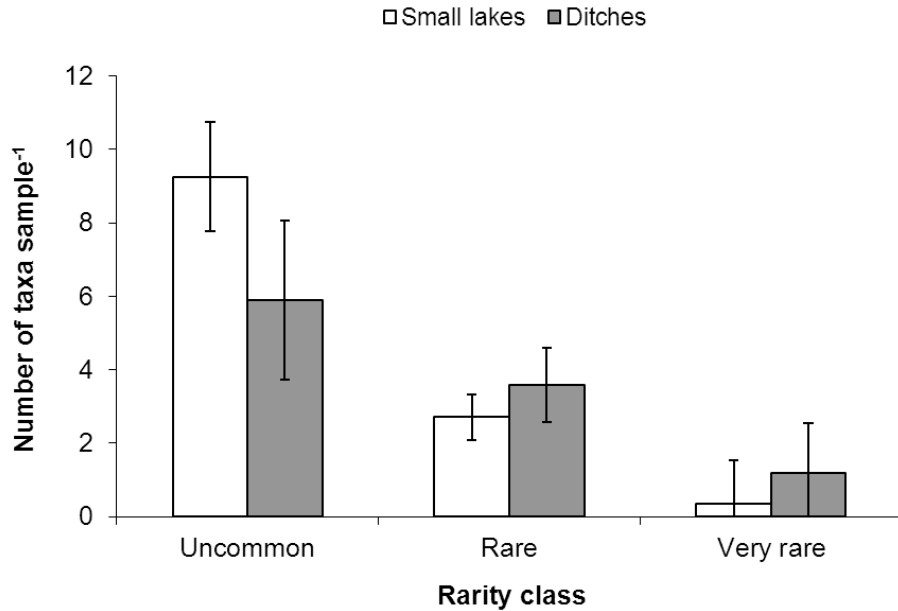


Figure 2.7: Comparison of the mean number of uncommon to very rare macroinvertebrate taxa (± 1 SE) recorded in small lakes and drainage ditches ($n = 9$), divided by the total number of taxa collected to correct for differences in richness. Rarity classification was based on the distribution classification of Dutch macroinvertebrate taxa (Nijboer & Verdonschot, 2004).

Rarity

In total, drainage ditches contained 31 uncommon to very rare taxa, whilst in small lakes 26 taxa were recorded. In ditches, the total number of rare and very rare taxa was higher compared to small lakes, but the total number of taxa collected was also higher, which potentially biases the results (Table 2.6). The mean number of uncommon-very rare taxa per sample, when corrected for the total number of taxa collected, did not differ significantly between water body types: uncommon taxa ($Z = -1.72$, $p = 0.094$), rare taxa ($Z = -0.97$, $p = 0.351$), and very rare taxa ($Z = -1.40$, $p = 0.241$) (Fig. 2.7).

Functional- and life history characteristics

Reproduction traits did not give an indication of the occurrence of frequent disturbances in drainage ditches – e.g. dredging and mowing – compared to small lakes that are not maintained by man. Long-lived taxa with a relatively long development time and slow reproduction were present in similar

proportions in both water body types (Table 2.7). Nevertheless, there was a highly significant difference in the proportion of taxa which used atmospheric air for respiration, which was higher in drainage ditches ($Z = -3.13$, $p = 0.001$). Dispersal mode did not differ between water body types; the proportion of the assemblage dispersing passively and actively, and by wind or water were similar. Relationship with substrate, both in terms of habit traits and oviposition behavior, was also similar between ditches and small lakes, except for plant miners, which were better represented in small lakes ($Z = -2.43$, $p = 0.014$). Functional role of the taxa collected differed with regard to the proportion of collector-filterers in the assemblage, which was higher in small lakes ($Z = -2.60$, $p = 0.008$). Proportion of other functional feeding groups, as well as the distribution over trophic levels was similar between water body types (Table 2.7).

Discussion

This study showed that drainage ditches can be a significant habitat type for aquatic invertebrates. Taxon richness of permanent agricultural drainage ditches and semi-natural, small lakes in peatlands in the Netherlands was comparable. Furthermore, both water body types supported a similar number of nationally uncommon, rare and very rare taxa. On a regional scale, drainage ditch invertebrate taxon composition was more varied compared to that of small lakes, indicating a relatively high beta-richness. Finally, total diversity estimates for ditches were far higher.

A limitation of our study is the small sample size. To strengthen the results, as based on 9 sites per water body type, extending the number of samples and ditch types sampled (e.g. different agricultural land use types) is recommended. Nevertheless, the results obtained here are in line with several recent studies describing and explaining the relatively high richness recorded in small lentic ecosystems, such as ponds and drainage ditches (Williams et al., 2004; De Meester et al., 2005; Scheffer et al., 2006; Davies et al., 2008a).

Variability in environmental characteristics

The high invertebrate beta-richness recorded in drainage ditches may reflect specific, localized conditions acting on a micro- or ditch stretch scale, e.g. habitat structure, nutrient concentrations, or diel oxygen patterns (De Meester et al., 2005; Scheffer et al., 2006). Here, habitat structure in terms of number and abundance of vegetation growth forms appeared to be less

important in differentiating the invertebrate assemblages, since small lakes were considerably richer in growth forms, but did not contain more invertebrate taxa. This contrasts the findings of Brown et al. (1988), who suggested that there is a positive relationship between vegetation heterogeneity and taxon richness. Furthermore, distributions by habitat trait groups and ovipositioning mode generally did not differ between the water body types, indicating that habitat use by invertebrates in ditches and small lakes was comparable despite the difference in growth form availability. Presumably, presence of aquatic vegetation per se, or the availability of certain key structures or habitat configuration is more important than simply the number of growth forms (Jeffries, 1993; Taniguchi et al., 2003; McAbendroth et al., 2005; Thomaz et al., 2008). The latter could explain the difference observed in plant miners, which is directly related to the plant species composition (Dvořák & Best, 1982).

Large fluctuations were observed among and within ditches in orthophosphate, total-P, and ammonium. This variability is characteristic of small lentic water bodies in agricultural areas (Søndergaard et al., 2005; Davies et al., 2008a). Being embedded in an agricultural landscape, in combination with having a high aquatic-terrestrial contact zone, results in a strong control of the surrounding land use on the functioning of the aquatic ecosystem (De Meester et al., 2005). Associations of lentic macroinvertebrates with physicochemical characteristics often act via indirect pathways. For example, nutrient enrichment does not influence invertebrates in ditches directly, but through changes in food availability (epiphyton, phytoplankton, and detritus), habitat structure through changes in plant species composition or vegetation density, and accumulation of organic matter and subsequently oxygen depletion (Clare & Edwards, 1983; Blumenshine et al., 1997). Surprisingly, observed differences in nutrient concentrations were not reflected in the functional composition of the invertebrate assemblages of ditches and small lakes. Trophic structure was comparable, as was the ratio between functional feeding groups, with a relatively higher proportion of collector-filterers recorded in small lakes as the only exception.

In contrast, oxygen concentration might possibly have exerted a strong influence on the invertebrate assemblages of drainage ditches, given the large difference in the proportion of atmospheric air breathers recorded between ditches and small lakes. This could be an indication of temporal oxygen stress in ditches (Clare & Edwards, 1983; Coimbra et al., 1996). In this study oxygen concentrations at the moment of sampling were relatively high (pers. obs.), but since the oxygen concentration in small water bodies

fluctuates strongly (Kersting & Kouwenhoven, 1989), both temporarily and spatially, this does not give an indication of the oxygen regime of the sampling sites and hinders the establishment of a link between macroinvertebrate occurrence and oxygen concentrations in the field. Another explanation for the preponderance of air breathers in ditches is its high bottom surface to water volume ratio. There is often a strong link between the presence of atmospheric air breathing macroinvertebrates and water body edges in freshwater habitats because a short distance to the air-water surface is necessary for siphon breathing and eases replenishing air stores (P. Williams, pers. comm.).

Scheffer et al. (2006) emphasized the role of ecological interactions with fish – through predation and hindering macrophyte development – in explaining the high biodiversity of small lentic systems, in which fish are often scarce or even absent. Although we found a higher fish taxon richness in small lakes compared to ditches, biomass and abundance were extremely variable in both water body types. Furthermore, macrophytes were abundant in all water bodies. Therefore, we regarded the influence of fish on the invertebrate assemblages of minor importance in explaining the differences between water body types.

We did not include contamination of drainage ditches with residues of pesticides from the adjacent agricultural land as a potential structuring factor. Since in the ditches under study the water volume was small and flow was negligible, residues of pesticides entering these water bodies can persist for longer periods and thus pose a potential risk to a range of macroinvertebrates (van den Brink et al., 1996; Brown et al., 2006). To what extent this was the case here is unknown, but since land use adjacent to the study ditches was primarily pasture, concentrations are likely to be low. Nonetheless, it cannot be ruled out that pesticide residues were present and part of the differences in taxon composition and beta-richness between drainage ditches and small lakes may thus be explained by the variability in toxic compound concentrations among ditches.

Importance of stochastic events in community assembly

Hydrosere succession, in combination with the ‘resetting’ of the ecosystem through dredging and mowing of the vegetation could potentially generate a wide array of habitats, both temporarily and spatially (Caspers & Heckman, 1982). In the ditches studied, regular ditch management does not seem to affect the long-lived invertebrates or taxa with slow developing juveniles. This indicates that deleterious effects of ditch management, if any, on the

assemblage composition are minor, which is in line with Beltman (1984), who found only short-term effects of ditch cleaning on ditch invertebrate abundance. On the other hand, too frequent or too rigorous cleaning could have more profound effects on the invertebrate assemblages (Twisk et al., 2000). Thus, the constantly changing ditch environment offers opportunities for many species, but also requires for strategies of coping with the temporal variability in environmental conditions of the drainage ditch habitat.

Since individual small lentic ecosystems are on an evolutionary timescale relatively short-lived habitats, this resulted in the development of a wide array of adaptations to living in a continuously changing environment, often with life history traits linked to dispersal (Ribera et al., 2003; Hof et al. 2008). In this study, a comparison of invertebrates that differed in dispersal mode did not show any differences between the two water body types; both active and passive invertebrate dispersers, regardless of dispersal took place by air or water, comprised comparable proportions of the assemblages of ditches and small lakes. The apparent stability of small lakes, and their large surface area, did not result in overrepresentation of one of the categories, which contrasts the findings of Rundle et al. (2002), who demonstrated that taxonomic groups with different dispersal mechanisms showed different distribution patterns across habitat gradients. Possibly, the high degree of physical habitat connectivity in drainage ditches in comparison to small lakes counteracts the effects of their relative instability and small individual size.

Yet dispersal may not be important in structuring the invertebrate assemblages and generating differences among sites, since dispersal capacity does not imply actual successful dispersal (Bohonak & Jenkins, 2003). Unfortunately, little is known about the actual dispersal capacity and dispersal rate of aquatic invertebrates (Bilton et al., 2001). Independent of the mode of dispersal, dispersal capability differs between species, which ultimately results in dispersal limitation. Furthermore, the order of arrival and identity of colonists could have profound consequences for the development of the invertebrate assemblage through priority effects (Jenkins & Buikema, 1998). If vacant habitats occur regularly, for example, through ditch cleaning, stochastic events associated with dispersal may result in the occurrence of different assemblages at environmentally similar sites, at least temporarily (Leibold et al., 2004; Scheffer et al., 2006). Possibly, these differences disappear with ongoing community assembly if the water body or habitat exists long enough. The result may be a more

uniform assemblage as found here in the more permanent small lakes in comparison to ditches.

Implications for conservation

Several studies have pinpointed drainage ditches as a surrogate habitat for lentic aquatic invertebrates, which natural habitats have been decimated due to land cultivation (Painter, 1999; Watson & Ormerod, 2004). It is assumed that these species comprised the invertebrate fauna of the waters in floodplains, marshes and bogs once found in lowland Europe. On the other hand, the opposite pattern may also hold; proximity of ditches to other, more natural, water bodies may be crucial to maintain their diversity. Regardless of whether populations of invertebrates found in drainage ditches are relicts from past wetlands or result from mass-effects of other habitats, the fact that human-impacted waters in peatland agricultural areas in the Netherlands could comprise a diverse invertebrate fauna similar to that of water bodies in nearby nature reserves is an important finding.

The patchy distribution of the ditch invertebrate fauna, either resulting from specific, localized conditions acting on a ditch stretch scale, or stochastic events related to dispersal, leads to a high drainage ditch beta-richness at a regional scale. Our results indicate that even the smallest water bodies within a peatland drainage system are potentially important as carriers of biodiversity, and not only the large waters (as for Europe described in the EC Water Framework Directive 2000/06/EC), or those found in nature conservation areas, which are often not designated to specifically protect its aquatic biodiversity. It remains unclear if drainage ditches comprise a distinctive faunal assemblage type, as drainage ditches both shared taxa with small lakes and sustained unique taxa.

Because of the commonness of drainage ditches in many lowland agricultural areas, these waters offer potential habitat for aquatic invertebrates. Unfortunately, many drainage ditches have been severely degraded due to eutrophication, organic pollution and the use of pesticides, and contain impoverished invertebrate assemblages. Nevertheless, because of their relative small catchment size in comparison to, for example, rivers changes in agricultural management could significantly enhance biodiversity (Davies et al., 2008b). For example, a decrease of fertilizer use or pesticide application, a switch from conventional to organic farming, and a widening of field margins, could be beneficial not only for the terrestrial biota, but also for the aquatic fauna (Herzon & Helenius, 2008).

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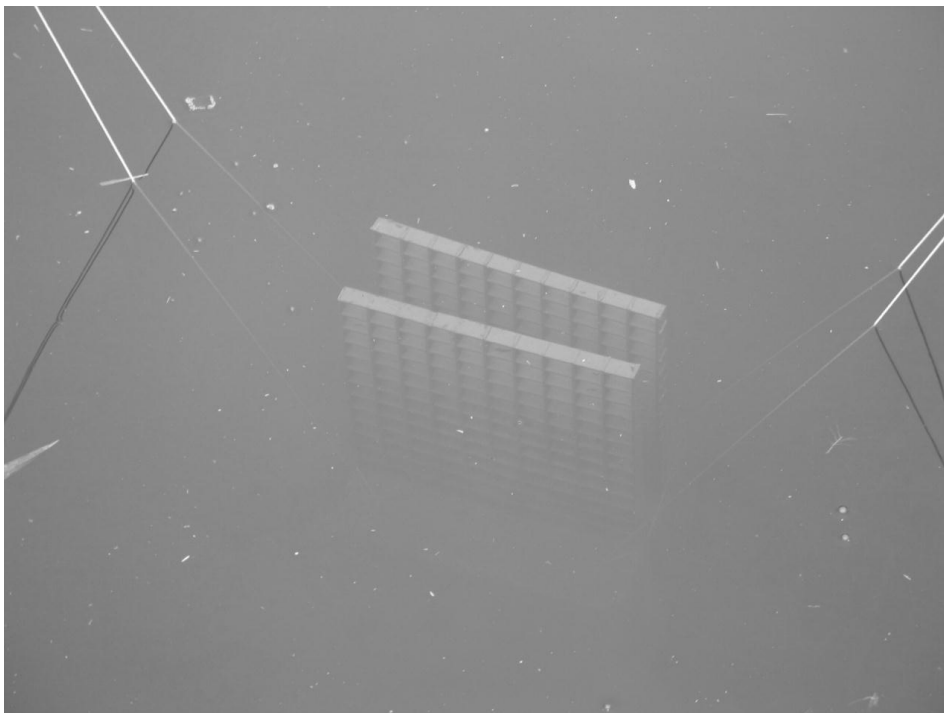
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3 Importance of habitat structure as a determinant of the taxonomic and functional composition of lentic macroinvertebrate assemblages



Submerged artificial structure.

3 Importance of habitat structure as a determinant of the taxonomic and functional composition of lentic macroinvertebrate assemblages

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Abstract

Variation in habitat structure provided by macrophytes is regarded as one of the determinants of macroinvertebrate species composition in lentic ecosystems, but mechanisms underlying this relationship appear to be confounded with site-specific factors, such as physicochemical factors, epiphyton and composition of the vegetation. To better understand the relationship between structural complexity of a macrophyte stand and its macroinvertebrate assemblage composition, it is essential to determine the ecological role of different components of habitat structure for the phytomacrofauna. Using artificial structures as macrophyte mimics, representing three growth forms (stems, broad-leaved, finely dissected) and three structure surface areas (0.1, 0.2, 0.3 m²), a full factorial field experiment was conducted in a series of drainage ditches. We investigated if macroinvertebrate assemblages colonizing the structures were affected by an increase in macrophyte structure surface area, structural complexity, or by a combination of both, and if the observed patterns were consistent among sites differing in physicochemical and habitat characteristics. Assemblages were characterized both in terms of taxonomic and functional composition, because we expected that non-taxonomic aggregation of species into functional categories would give a different insight in habitat complexity-macroinvertebrate relationships in comparison to approaches based on the taxonomic assemblage composition. Ditch intrinsic factors, in part reflected in the periphyton on the structures, explained the major proportion of the variance in both the taxonomical macroinvertebrate assemblages and functional groups among structures. Contrary to our expectation, patterns in the taxon-based and functional dataset resembled each other. Only a minor contribution of growth form to the explained variance was observed in the taxonomical dataset, whilst differences in functional composition were unrelated to habitat structure. In conclusion,

processes operating on larger spatial scales overrode the micro-scale effects of habitat structural complexity and surface area on macroinvertebrates.

Keywords: habitat complexity, functional groups, phytomacrofauna, drainage ditches

Introduction

Habitat structure is a key factor determining the occurrence and distribution of macroinvertebrates in freshwater ecosystems (Downing, 1991). In the littoral zone of lentic waters, macrophytes are often the most distinct habitat components. On a microhabitat scale, the habitat complexity provided by the architecture of these plants, together with plant identity and structure surface area, account for differences in species richness and abundance of epiphytic macroinvertebrates (Jeffries, 1993; Taniguchi et al., 2003; Thomaz et al., 2008). In general, macrophytes with finely dissected leaves harbour a higher macroinvertebrate species richness and larger numbers of individuals compared to plants with a simple architecture, like stems (e.g. Cheruvil et al., 2002; Warfe & Barmuta, 2006). The mechanisms underlying this relationship are difficult to separate, because the different aspects of habitat structure – structural complexity and structure surface area – have independent as well as joint effects (Johnson et al., 2003).

A number of explanations have been put forward to explain the observed differences in species richness between structurally simple and complex habitats (Lawton, 1983). The higher surface area per volume occupied by complex plants is likely to be colonized by a larger number of macroinvertebrates, representing a larger proportion of the local species pool. This results in a higher species richness, purely as the result of a passive sampling effect (Connor & McCoy, 1979). Also, the larger the structure surface area provided by a macrophyte, the more individuals can be supported, allowing species to maintain larger populations that have a reduced extinction risk (McArthur & Wilson, 1967). Furthermore, increased habitat complexity results in an increased species diversity by providing more microhabitats or potential niches for colonization by different species. Increased resource availability can be the result of a large surface area per se, which increases the chance of including different resources (Williams, 1943). It can also be a direct effect of plant architecture, when an increase in complexity leads to an increased range of feeding, resting, and hiding places. For example, predator-prey interactions are mediated directly by the structure of the vegetation, resulting in reduced macroinvertebrate

predation by fish in more complex habitats (Crowder & Cooper, 1982; Warfe & Barmuta, 2006). Furthermore, detritus trapping ability increases with plant complexity, thereby positively affecting detritivore richness (Rooke, 1984; Taniguchi et al., 2003).

Whilst species richness generally responds positively to an increase in habitat structural complexity, the relationship between densities of single species and habitat structure is often variable (O'Connor, 1991; Beck, 2000; Taniguchi & Tokeshi, 2004). Which components of habitat structure are important depends in large part upon the specific life-history characteristics of the organisms in question (Kershner & Lodge, 1990; Anderson, 1998). On a microhabitat scale, habitat structure can be regarded as one of the environmental variables which may 'filter' species with suitable traits from the local species pool to coexist on a macrophyte, which may result in a close correspondence between habitat structure and the functional composition of macroinvertebrate assemblages (Poff, 1997; Heino, 2005, 2008). For example, the architecture of a structure determines if a macroinvertebrate is able to efficiently move around within the habitat and utilize the resources provided, which is reflected in the habit, feeding mode and food types used by macroinvertebrates present on a structure.

To better understand the relationship between the structural complexity of a macrophyte stand and its macroinvertebrate assemblage composition, it is essential to determine the ecological role of different components of habitat structure for the phytomacrofauna. These ecological relationships with different aspects of habitat structure could well be derived from the functional structure of the macroinvertebrate assemblage recorded on a structure. In this study, we investigated if non-taxonomic aggregation of species into functional categories gave a different insight in habitat complexity-macroinvertebrate relationships in comparison to approaches based on the taxonomic assemblage composition. Since micro-scale patterns are inherently related to patterns and processes acting on larger spatial scales (Frissell et al., 1986; Poff, 1997), it was examined if the relationship between macroinvertebrates and habitat structure was consistent over multiple localities.

We carried out a field experiment in a series of drainage ditches, to study if macroinvertebrate assemblages colonizing structures were affected by an increase in macrophyte structure surface area, structural complexity, or by a combination of both. In this experiment we used artificial substrates differing in structural complexity and structure surface area as macrophyte analogs. Macroinvertebrate assemblages were characterized in terms of taxon richness, taxonomic assemblage structure, and functional

composition. Since all three measures comprise different aspects of a biological community, it was a question how they individually respond to habitat complexity. We also studied if the patterns observed, either taxonomic or functional, were consistent over sites, although we expected that differences between ditches, e.g. in terms of nutrient concentrations or vegetation, could lead to variation in available resources (periphyton, detritus) on the structures or differences in the pool of potential colonizers.

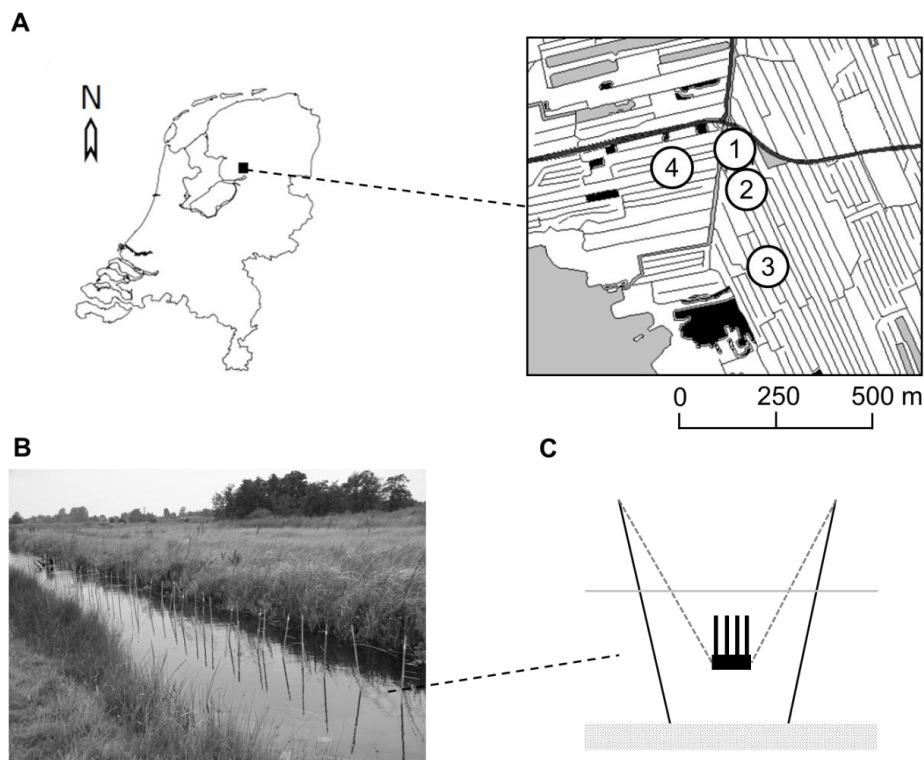


Figure 3.1: A: Map of the study area. The drainage ditch network is displayed as black hairlines. The experiment took place in the ditches marked with 1-4. B: Transect in ditch 3. C: Experimental unit, consisting of an artificial structure positioned 10 cm beneath the water surface in the centre of the ditch by ropes attached to two bamboo poles.

Materials and methods

Study site

The study was carried out in 4 adjacent drainage ditches located in an agricultural area northeast of lake Bovenwilde near the village of Giethoorn,

The Netherlands (Fig. 3.1A). Drainage ditches are small, permanent, line-shaped, stagnant water bodies, originally dug to drain excess water from surrounding agricultural fields. They are a prominent feature of the landscape in the lowlands of north-western Europe. In The Netherlands alone, total ditch length is approximately 300,000 km. Despite intensive perturbations through maintenance, by mowing and dredging of the aquatic vegetation, ditches can harbour a high diversity of macroinvertebrates, that closely resembles communities found in natural ponds, marshes, and shallow lakes (Higler & Verdonschot, 1989; Verdonschot, 1992).

Experimental design and sampling

To standardize macrophyte surface area and structural complexity, and to prevent decay and senescence, artificial structures were used instead of natural vegetation. Microhabitat structural complexity was represented by 3 types of artificial structures, mimicking commonly encountered growth forms in lentic ecosystems (Fig. 3.2). Of each artificial analog, structures with 3 different surface areas (0.1 m², 0.2 m², and 0.3 m²) were constructed. Each treatment was replicated once in each of the 4 ditches. This resulted in 2x9 treatments, which were applied in a full-factorial experimental design.

The most simple growth form resembled stems of emergent vegetation (e.g. *Phragmites australis*). This structure was characterized by only vertical surface area and relatively large interstitial spaces. Stems were mimicked using rigid plastic tubes (PVC, ø 10 mm, length 23.6 cm, closed on top), which were placed vertically, and evenly spaced (1 cm apart) in combinations of 12, 24, and 36 tubes. The second type of growth form represented submerged macrophytes with relatively broad leaves (e.g. *Potamogeton lucens*). This structure comprised both horizontal and vertical surface areas, with relatively large interstitial spaces. Broad-leaved plants were mimicked using perforated sheets made out of PVC (0.2 cm thick). Each artificial structure consisted of two vertically placed parallel sheets, spaced 4 cm apart, with inner dimensions of each square opening of 1.7 x 1.7 cm, and a width of 1.2 cm. Three sheet dimensions were used (width x height): 20 x 8 cm (0.1 m²), 20 x 17 cm (0.2 m²), 20 x 26 cm (0.3 m²). The third growth form mimicked submerged macrophytes with many small or finely dissected leaves, growing in dense beds (e.g. *Myriophyllum spicatum*, *Ceratophyllum demersum*). These structures were characterized by a surface area consisting of numerous whorled strands orientated in all directions, with many small interstitial spaces. Structures were made of Black Matala filter sheets (Matala Water Technology Company, Taiwan), consisting of

fused strands of thermo-polypropylene compounds (ϕ 1.5 mm) with a surface area of $190 \text{ m}^2/\text{m}^3$. Sheet dimensions were (width x height): 6.4 x 20.5 cm (0.1 m^2), 12.8 x 20.5 cm (0.2 m^2), 19.2 x 20.5 cm (0.3 m^2).

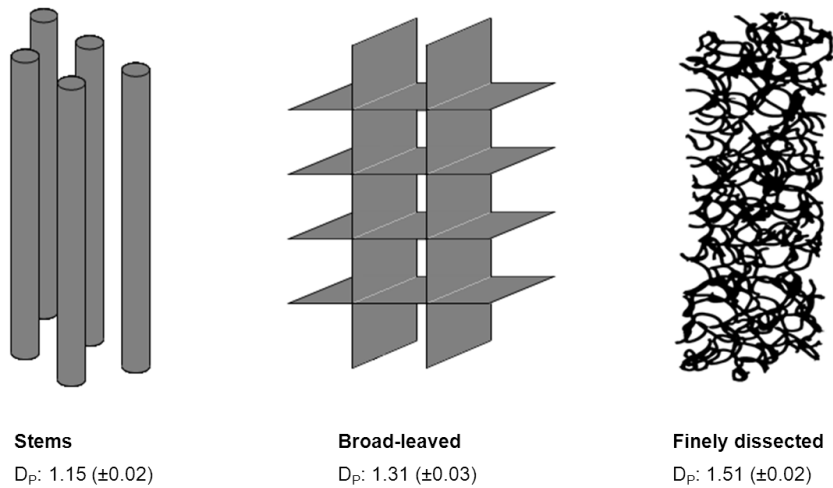


Figure 3.2: Artificial structures used in the experiment, representing different growth forms of macrophytes. Complexity of the growth forms is derived from its fractal dimension and is expressed as mean edge complexity (D_p) $\pm 1SE$.

To get an indication of the degree of complexity of the structures, fractal dimension of each of the growth forms was calculated based on its edge complexity (D_p), which gives an indication of the degree of dissection of the structures (McAbendroth et al., 2005) (Fig. 3.2). From the stems and broad-leaved structures, 4 quadrats of 3 x 3 cm were randomly selected, magnified 4 times and processed into a digital black-and white image of 450 x 450 pixels (1 pixel width = 0.066 mm). To derive the fractal dimension of the finely dissected structure, 4 quadrats of 3 x 3 cm, 1 cm deep, were photographed and the resulting pictures (magnification 4 times, resulting in a digital image of 450 x 450 pixels) were converted to binary images. ImageJ software (version 1.38, Rasband, 1997-2005) was then used to analyse the fractal structure of each image. ImageJ uses a box count algorithm to quantify the fractal dimension of the perimeter of the structures. A series of grid sizes ranging from 2 to 256 pixel widths (box sizes 0.133 mm to 17.0 mm) were used to estimate the perimeter covered by the structures at different measurement scales. Fractal dimension was estimated from the slope of the perimeter estimate plotted against the grid size (both $\log_{10}(x)$ -transformed).

Table 3.1: Main environmental characteristics of the 4 experimental ditches in September. Relative macrophyte cover is expressed as Tansley cover classes: absent (0), rare (r), frequent (f), abundant (a), co-dominant or dominant (cd).

Parameter	Ditch			
	1	2	3	4
<i>Habitat characteristics</i>				
Ricciellids (cover class)	r	a	0	f
Myriophyllids (cover class)	r	0	0	a
Elodeids (cover class)	0	f	0	cd
Parvopotamids (cover class)	0	cd	0	0
Characea (cover class)	r	0	0	0
Stratiotids (cover class)	cd	cd	cd	cd
Lemnids (cover class)	0	r	r	r
Magnonymphaeids (cover class)	f	r	r	r
Parvonymphaeids (cover class)	f	f	f	f
Floating clusters of algae (cover class)	f	a	cd	f
Helophytes with blade-like leaves (cover class)	cd	f	cd	f
Helophytes with leafless stems (cover class)	cd	f	r	cd
Pleustohelophytes (cover class)	f	f	f	f
Pseudohydrophytes (cover class)	r	r	r	r
Thickness sapropelium layer (m)	0.5	0.4	0.5	0.4
Depth (m)	0.6	0.7	0.5	0.5
Width (m)	5	5	4	4
<i>Physicochemical variables</i>				
pH	7.3	8.1	6.8	7.2
Conductivity ($\mu\text{S cm}^{-1}$)	258	283	311	401
Dissolved oxygen saturation (%)	86	112	73	76
Dissolved oxygen ($\text{mg O}_2 \text{ L}^{-1}$)	8.7	10.8	8.8	7.4
Ammonium ($\text{mg NH}_4^+ \text{ L}^{-1}$)	0.05	0.05	0.05	<0.03
Nitrate ($\text{mg NO}_3^- \text{ L}^{-1}$)	<1	<1	<1	<1
Nitrite ($\text{mg NO}_2^- \text{ L}^{-1}$)	<0.01	<0.01	<0.01	<0.01
Kjeldahl Nitrogen (mg N L^{-1})	1.7	1.6	1.5	1.5
Total-phosphorus (mg P L^{-1})	0.04	0.03	0.04	0.05
Ortho-phosphate ($\text{mg PO}_4^{3-} \text{ L}^{-1}$)	0.05	<0.03	<0.03	<0.03
Sulphate ($\text{mg SO}_4^{2-} \text{ L}^{-1}$)	15	11	24	<2
Chloride (mg L^{-1})	39	38	39	35
Iron (mg L^{-1})	0.05	0.04	0.03	0.06
Sodium (mg L^{-1})	21	21	23	21
Calcium (mg L^{-1})	22	23	28	32
Magnesium (mg L^{-1})	4.7	4.0	5.7	6.0
Kalium (mg L^{-1})	0.7	0.3	4.4	1.0

In the field, all structures were fixed in horizontal concrete plates (length 21 cm, width 16 cm, height 2 cm) to hold them in place. They were positioned in the centre of the ditches, with the top end at a depth of 10 cm beneath the water surface (Fig. 3.1B, C). Each structure was connected with ropes in-between two bamboo poles, to reduce movement due to wind or waterfowl activity. Structures were positioned randomly along a transect, with an inter-structure distance of 2 m. Floating (except Lemnids) and submerged macrophytes present in the upper layer of the water column were removed along the transects within a zone of 1 m to prevent interference with the artificial structures. During the last week of July 2007 the artificial structures were put into place and they were retrieved during the first week of October 2007. Colonization time was based on De Pauw et al. (1994), who stated that colonization of artificial substrates by the majority of the macroinvertebrate assemblage present in a water body took less than 2 months. Structures were retrieved using a modified pond net (mesh size 500 μm) with a specially designed opening to facilitate retrieval (opening tapering to the top, smallest width 35 cm, broadens to 45 cm over a length of 50 cm). Structures and contents of the pond net were put into buckets and transported to the laboratory. During the experiment, one stem structure with a surface area of 0.1 m^2 was lost from ditch 4 and could not be recovered.

To get an indication of the differences between the 4 ditches on a scale exceeding that of the microhabitat introduced in the form of the artificial structures, ditch morphology, physicochemical variables and composition of the vegetation were recorded in September (Table 3.1). Physicochemical parameters were measured once per ditch; dissolved oxygen concentration, pH and conductivity were measured directly, whilst concentrations of nutrients and macro-ions were determined in the laboratory. Proportional cover of vegetation growth forms, as classified by Den Hartog and Segal (1964) and expressed in Tansley-classes (Tansley, 1946; transformed to proportional cover classes), was estimated for 50 m ditch stretches, as were ditch dimensions (width, depth) and thickness of the sapropelium layer covering the ditch bottom.

Periphyton methods

To determine chlorophyll-a content, biomass and composition of the periphyton, material was removed from the artificial structures with a brush from 6 randomly selected tubes for the simple structures, 18 randomly selected squares for the broad-leaved structures, and 40 cm^2 of the outside

of the Matala sheets for the finely dissected structures. Half of the material collected was used to determine chlorophyll-a content. The periphyton collected from the structures was rinsed with distilled water and the suspension was subsequently concentrated on Whatman glass fibre filters (GF/C). Filters were stored at -80°C until further analysis. Pigments were extracted in the dark with 95% ethanol and analyzed photospectrometrically. To determine the relative proportion of algal groups and detritus in the periphyton, the rest of the sample was homogenized and subsampled by taking 1 ml with a pipette. The subsample was put on a slide, and placed under the microscope. The relative proportion of each of the dominant algal groups and detritus particles in the subsample was estimated based on areas covered in the slide. The majority of the material collected from the structures comprised of filamentous green algae and detritus. Proportions of individual cells or colonies of green algae, blue-green algae, diatoms and desmids were negligible ($\leq 1\%$), and therefore excluded from the analyses. The remaining material was concentrated and dried to a constant weight at 70°C , to obtain an estimate of the periphyton and associated material biomass.

Macroinvertebrate methods

In the laboratory, the artificial structures were rinsed and the periphyton was carefully removed with a brush to collect macroinvertebrates which clinged to the structure or were present in the periphyton layer. Collected material was sieved over a $250\text{ }\mu\text{m}$ mesh. Tricladia were identified immediately after collection. The remaining material was preserved in 96% ethanol until further processing. Using a dissecting microscope, invertebrates were separated from the detritus and algae. Both Oligochaeta and Chironomidae were very numerous on the artificial structures and identification of these groups is a time-consuming process. Therefore, for Oligochaeta a maximum of 150 individuals per sample was identified, and for Chironomidae a maximum of 500 individuals. The remaining individuals were counted. Oligochaeta were mounted on slides in polyvinyl-lactophenol for identification. Except for Chironomidae, invertebrates were identified to the lowest taxonomic level possible. Because of a rather large number of taxonomic inconsistencies in early instars, chironomids were identified to genus-level only. As not all specimens could be identified to the lowest taxonomic level, e.g. early instars, damaged specimens, an adjustment procedure was applied. By grouping to a higher taxonomic level

this procedure reduced bias due to differences in taxonomic resolution (Schmidt-Kloiber & Nijboer, 2004).

Table 3.2: Description of lentic macroinvertebrate functional feeding groups and habit trait groups. Modified from Merritt and Cummins (1984) and Heino (2008).

Trait	Characteristics
<i>Functional feeding group</i>	
Gatherer	Feed on trapped FPOM.
Filterer	Filter suspended FPOM from the water column, actively or passively (water is filtered through tubes by undulating movements). Often build nets/tubes for capturing food.
Piercer	Feed on algae growing on the structures by piercing and sucking cells.
Predator	Attack other organisms and ingest whole animals or parts or suck body fluids.
Scraper	Scrape periphyton and associated material from structure surface.
Shredder	Feed on trapped CPOM, both living and decomposing material.
Parasite	Live parasitically of other animals.
<i>Habit trait group</i>	
Burrower	Inhabit fine sediments, some construct tubes extending above the surface of the substrate or may ingest their way through sediments.
Climber	Adapted for living on structures, with modifications for moving vertically on stems.
Clinger	Construct fixed retreats, e.g. tubes, attached to surface of structures.
Swimmer	Adapted for swimming between structures or swimming by rowing with specially adapted hind legs, cling or crawl on structures for short periods.
Sprawler	Inhabit the surfaces of structures and sediments, usually with modifications to stay on top of the sediment.

Characterisation of functional groups

Feeding habits and habit traits of lentic macroinvertebrate taxa were combined into functional groups, because these traits could give insight into the role of habitat structure for macroinvertebrates: functional feeding groups provide information on the feeding modes of macroinvertebrates and the food types used, and habit trait groups include information on the mobility of organisms and where their food is obtained (Heino, 2005, 2008) (Table 3.2). Taxa were assigned to a functional feeding group and to a habit trait group according to Merritt and Cummins (1984), Monakov (2003), Moog (1995) and Tachet et al. (2000). Additional information on

Chironomidae and Oligochaeta was added based on Brinkhurst and Jamieson (1971), Chekanovskaya (1981), and Moller Pillot (2009) (Table 3.3). In some cases there were inconsistencies in the functional classification of taxa between literature sources. In case a taxon could be assigned to more than one category, either within a classification or between different classifications, the most frequently encountered dominant category (based on fuzzy coding; highest score represents highest affinity) was assigned. None of the taxa had no highest score when multiple classifications were compared.

Table 3.3: Frequency of occurrence and total abundance of functional groups on structures. A frequency of occurrence of 100% means that the taxon is found in all samples ($n = 71$). The functional group is a combination of functional feeding group and habit traits. Common representatives of each group are given.

Functional group	Freq.	Abun.	Example taxa
Burrower-filterer	34	91	<i>Pisidium</i> sp.
Burrower-gatherer	55	301	<i>Chironomus</i> sp., <i>Cladopelma</i> sp.
Burrower-predator	1	1	<i>Cryptochironomus</i> sp.
Climber-filterer	45	440	<i>Bithynia tentaculata</i> , <i>B. leachii</i>
Climber-gatherer	56	210	<i>Slavina appendiculata</i> , <i>Pristina longiseta</i>
Climber-parasite	34	33	<i>Alboglossiphonia hyalina</i> , <i>Hemiclepsis marginata</i>
Climber-piercer	79	328	<i>Oxyethira</i> sp., <i>Tricholeiochiton fagesii</i> , <i>Agraylea sexmaculata</i>
Climber-predator	100	532	Coenagrionidae, <i>Alboglossiphonia heteroclita</i> , <i>Dugesia lugubris/polychroa</i> , <i>Helobdella stagnalis</i>
Climber-scraper	99	1296	<i>Gyraulus albus</i> , <i>G. crista</i> , <i>Anisus vorticulus</i> , Lymnaeidae
Climber-shredder	31	27	<i>Agrypnia pagetana</i> , <i>Catachysta lemnata</i> , <i>Elophila nymphaeata</i>
Clinger-filterer	100	8223	<i>Tanytarsus</i> sp., <i>Dicrotendipes</i> sp., <i>Glyptotendipes</i> sp.
Clinger-gatherer	97	4023	<i>Dero digitata</i> , <i>D. obtusa</i> , <i>Cricotopus</i> sp., <i>Microtendipes</i> sp.
Clinger-predator	99	612	<i>Cyrrhus flavidus</i> , <i>Holocentropus picicornis</i> , <i>H. dubius</i>
Sprawler-gatherer	100	3453	<i>Caenis</i> sp., <i>Paratanytarsus</i> sp., <i>Psectrocladius</i> sp., <i>Acrivotopus</i> sp.
Sprawler-predator	100	4532	Pentaneurini, <i>Procladius</i> sp., <i>Tanytus</i> sp.
Sprawler-shredder	70	683	<i>Asellus aquaticus</i> , <i>Proasellus meridianus</i>
Swimmer-gatherer	100	10298	<i>Nais variabilis</i> , <i>N. simplex</i> , <i>Stylaria lacustris</i> , <i>Cloeon</i> sp.
Swimmer-predator	100	3100	Ceratopogonidae, <i>Unionicola crassipes</i> , <i>Erpobdella nigricollis</i> , <i>Brachypoda versicolor</i>
Swimmer-shredder	68	107	<i>Gammarus</i> sp., <i>Triaenodes bicolor</i>

Statistical analyses

General patterns in macroinvertebrate taxonomical and functional richness were explored using univariate statistical techniques. Since the number of macroinvertebrates counted and identified in each sample differed considerably, rarefaction was applied to control for the effects of macroinvertebrate abundance on taxon richness and functional richness (Gotelli & Colwell, 2001). Rarefaction was performed on each sample to generate an expected number of taxa or functional groups in that sample for a fixed number of individuals. From each sample, a random number of individuals was chosen, which corresponded to the smallest observed number of individuals across structures (73 individuals). Taxon or functional richness used in the subsequent analyses was the number of taxa or functional groups within this subsample (Downes et al., 2000).

Taxon richness was analysed with a 3-factor analysis of variance (ANOVA). Fixed factors in the analysis were growth form (stems, broad-leaved, complex), surface area (0.1, 0.2 and 0.3 m²), and site (ditch 1 to 4). To meet assumptions of normality and homogeneity of variances, data were $\sqrt[4]{x}$ -transformed. Post hoc testing was performed using Tukey HSD tests, with $\alpha = 0.05$. Statistical analysis analogous to taxonomic richness was not possible for rarefied functional richness due to major deviations from normality and heterogeneity of variances. Therefore, factors were analysed separately using Kruskal-Wallis ANOVAs, followed by Mann-Whitney U tests as a post hoc procedure (Bonferroni corrected for the number of pair-wise comparisons).

Since periphyton growing on the structures could be important in structuring macroinvertebrate assemblages and functional group composition, relationships between periphyton, habitat complexity and site were investigated. To show if there were any significant differences among growth forms and ditches in periphyton and associated detritus on the structures, amount of chlorophyll-a and periphyton and associated detritus biomass were compared using two-way ANOVAs with ditch and growth form as fixed factors. To meet assumptions of normality and homogeneity of variances, data were $\log_{10}(x+1)$ transformed for chlorophyll-a and \sqrt{x} -transformed for biomass. Furthermore, it was investigated if there was variation among ditches and growth forms in the proportions of filamentous green algae and detritus particles in subsamples of the periphyton. Factors were analysed separately using Kruskal-Wallis ANOVAs, followed by Mann-Whitney U tests as a post hoc procedure (Bonferroni corrected for the number of pair-wise comparisons). All

statistical analyses were performed in SPSS for Windows (version 15.0, SPSS Inc.).

Multivariate ordination techniques, performed with CANOCO (version 4.5; Ter Braak & Šmilauer, 2002) and PcOrd for Windows (version 4.25; McCune & Mefford, 1999), were used to identify relationships between the macroinvertebrate assemblages or functional groups found on the structures, microhabitat variables and intrinsic ditch factors. Microhabitat variables were divided into two separate groups; microhabitat structural characteristics and periphyton. Microhabitat structural characteristics included in the analyses were plant identity (growth forms, recorded as 3 dummy variables) and structure surface area. The measure of fractal dimension (D_p), indicating the increasing complexity of the structures, was not included as a separate factor in the analyses, since it was multicollinear with plant identity. Variables describing periphyton were chlorophyll-a content, periphyton and associated detritus biomass and the relative proportion of filamentous green algae in the periphyton.

Intrinsic ditch factors contributing to inter-ditch variability in the macroinvertebrate assemblages or functional groups found on the structures included, amongst others, nutrient and macro-ions concentrations, vegetation structure and composition and ditch dimensions. These variables were subdivided into two categories; physicochemical variables and habitat characteristics (Table 3.1). Since each category comprised many variables, principal components analysis (PCA) was used to extract composite descriptors of ditch physicochemical and habitat heterogeneity. Only those principal components that explained a significant non-random part of the variation were retained (broken-stick model; Jackson, 1993). PCAs of physicochemical variables and habitat characteristics both extracted three significant components from these extended sets of variables. Loadings (Pearson correlation coefficients) of each variable on the individual components were calculated to derive the main descriptors of each component (Table 3.4). Sample scores of the sites (ditch 1-4) on the significant principal components were used as new quantitative variables for the subsequent ordinations (physicochemical variables: P1-P3, habitat characteristics H1-H3).

Prior to the multivariate analyses, rarefied taxon abundances and abundances per functional group were $\log_2(x+1)$ transformed to minimize the effect of high macroinvertebrate densities. Detrended Correspondence Analysis (DCA), with detrending by segments and down-weighting of rare taxa, was used to determine the gradient length of the taxonomic and functional dataset. Maximum gradient length was 1.99 for the taxonomic

dataset and 1.17 for the functional dataset, which indicated that a linear response model would best fit the data (Ter Braak & Šmilauer, 2002). Therefore, PCAs were used in order to explore the variability in taxonomic and functional composition of the macroinvertebrate assemblages collected from the structures, unconstrained by the chosen environmental variables. To aid interpretation of the gradients derived from the analyses, the explanatory variables (microhabitat- and intrinsic ditch variables) were added as supplementary variables.

Table 3.4: Intrinsic ditch factors (see Table 3.1) were divided into two categories; physicochemical variables (A.) and habitat characteristics (B.). Principal components analyses (PCAs) were used to extract composite descriptors of these groups. Based on the loadings of each variable on the significant principal components (PC), expressed as Pearson correlation coefficients, its main descriptors ($r > 0.80$; in bold) were determined.

A. Physicochemical variables

Variable	Pearson correlation coefficient (r)		
	PC-1	PC-2	PC-3
Ammonium (mg NH ₄ ⁺ L ⁻¹)	-0.86	0.51	0.01
Calcium (mg L ⁻¹)	0.97	0.06	-0.24
Chloride (mg L ⁻¹)	-0.74	0.65	0.18
Total-phosphorus (mg P L ⁻¹)	0.92	-0.04	0.39
Ortho-phosphate (mg PO ₄ ³⁻ L ⁻¹)	-0.38	-0.02	0.93
Iron (mg L ⁻¹)	0.36	-0.77	0.53
Kalium (mg L ⁻¹)	0.41	0.90	-0.12
Magnesium (mg L ⁻¹)	0.91	0.38	0.15
Natrium (mg L ⁻¹)	0.12	0.99	0.00
Kjeldahl Nitrogen (mg N L ⁻¹)	-0.74	-0.25	0.63
Sulphate (mg SO ₄ ²⁻ L ⁻¹)	-0.64	0.77	0.05
pH	-0.57	-0.73	-0.37
Conductivity (μS cm ⁻¹)	0.92	-0.22	-0.31
Dissolved oxygen saturation (%)	-0.80	-0.51	-0.32
Dissolved oxygen (mg O ₂ L ⁻¹)	-0.89	-0.01	-0.46
Eigenvalue	0.466	0.278	0.138
Broken-stick eigenvalue	0.202	0.144	0.114
% of total variance explained	46.64	27.76	13.84

B. Habitat characteristics

Variable	Pearson correlation coefficient (r)		
	PC-1	PC-2	PC-3
Thickness sapropelium layer (m)	-0.86	-0.15	-0.49
Ditch cross-sectional area (m ²)	-0.03	0.19	0.98
Characea (% cover)	-0.76	-0.48	0.43
Elodeids (% cover)	0.84	-0.51	-0.22
Helophytes with blade-like leaves (% cover)	-0.97	0.16	-0.20
Helophytes with leafless stems (% cover)	-0.08	-0.99	0.11
Lemnids (% cover)	0.76	0.48	-0.43
Magnonymphaeids (% cover)	-0.76	-0.48	0.43
Myriophyllids (% cover)	0.29	-0.90	-0.33
Parvopotamids (% cover)	0.54	0.46	0.70
Ricciellids (% cover)	0.75	-0.21	0.63
Stratiotids (% cover)	-0.58	0.66	0.48
Floating clusters of filamentous algae (% cover)	-0.21	0.84	-0.5
Eigenvalue	0.341	0.265	0.207
Broken-stick eigenvalue	0.211	0.149	0.118
% of total variance explained	34.10	26.45	20.73

Table 3.5: Three-factor analysis of variance (ANOVA) of the effects of growth form (stems, broad-leaved, dissected), structure surface area (0.1, 0.2, 0.3 m²) and site (ditch 1-4) on the expected number of taxa per structure as generated by rarefaction.

Effect	df	MS	F	P
Ditch	3	0.09	19.3	0.000
Growth form	2	0.01	2.25	0.121
Surface area	2	0.01	1.46	0.245
Ditch * growth form	6	0.02	5.26	0.001
Ditch * surface area	6	0.01	1.00	0.439
Growth form * surface area	4	0.01	2.20	0.089
Ditch * growth form * surface area	12	0.01	1.78	0.092
Error	35	0.01		

Redundancy analysis (RDA) was used as subsequent analysis, to estimate the total variation in the macroinvertebrate data that could be explained by the explanatory variables directly. RDA is the constraint form of the PCA, in which the components (ordination axes) are constrained by linear combinations of environmental variables. Since we had a hierarchically structured set of explanatory variables, we used hierarchical canonical variance partitioning to decompose the explained variance in macroinvertebrate assemblage composition and functional group

composition among those sets of explanatory variables (Borcard et al., 1992; Cushman & McGarigal, 2002). By partialling out the effects of separate factors across hierarchical scales, independent and confounded proportions of the explained variance by different factors can be quantified. Only variables that explained a significant proportion of the total variance in the macroinvertebrate data, based on a Monte Carlo permutation test with 499 permutations ($p < 0.05$), were included in the analysis.

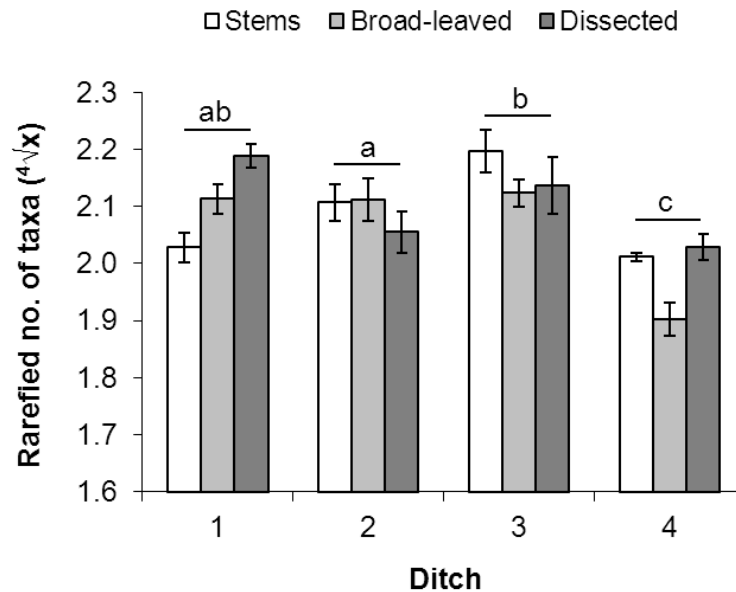


Figure 3.3: Mean ($\pm 1SE$) expected number of taxa per ditch per growth form as generated by rarefaction ($4\sqrt{x}$ transformed). Ditches indicated with different letters are significantly different (Tukey post hoc comparisons, $p < 0.05$). There is a significant interaction between ditch and growth form, as shown by the divergent richness patterns between ditches when different growth forms are compared.

Results

Taxonomic and functional richness

A total of 38,288 individuals were recorded on the structures, consisting of 151 taxa. Dominant taxonomic groups were Chironomidae (41.8% of the total number of individuals, 25 taxa) and Oligochaeta (25.8%, 18 taxa). Taxa were assigned into 19 functional groups (Table 3.1). Dominant functional groups were swimmer-gatherers (26.9% of the total number of individuals) and clinger-filterers (21.5%). Rarefied taxon richness differed significantly among ditches (Table 3.5, Fig. 3.3). Both structure surface area and growth

form did not affect rarefied taxon richness, although a significant interaction between ditch and growth form indicated that the observed macroinvertebrate response to habitat structure differed among ditches (Table 3.5, Fig. 3.3). Non-parametric analyses of rarefied functional richness on the structures showed that there was neither an effect of structure surface area ($H(2) = 1.33$, $p = 0.514$), nor of growth form ($H(2) = 1.695$, $p = 0.429$). Nonetheless, there was a significant difference between ditches ($H(3) = 36.22$, $p = 0.000$). Variation in functional richness among ditches resembled that of taxonomic richness (Fig. 3.4).

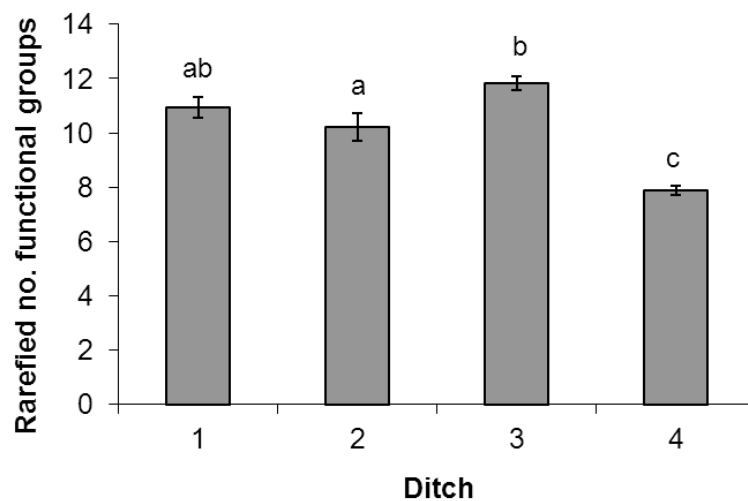


Figure 3.4: Mean ($\pm 1SE$) expected number of functional groups per ditch as generated by rarefaction. Ditches indicated with different letters are significantly different (Mann-Whitney U non-parametric post hoc comparisons, Bonferroni corrected $p < 0.0083$).

Periphyton and associated detritus

Accumulated periphyton and associated detritus biomass on the structures was comparable across growth forms, but differed significantly among ditches (Table 3.6, Fig. 3.5A). Chlorophyll-a content of the periphyton on the structures was affected by growth form (Table 3.6); concentration on the stems was significantly higher compared to dissected structures (Tukey post hoc comparisons, $p < 0.05$), and broad-leaved structures took an intermediate position, with a comparable mean chlorophyll-a content to both stems and dissected growth forms. Furthermore, there was an effect of ditch, as well as a significant interaction between ditch and growth form,

indicating that the chlorophyll-a content of the periphyton on the different growth forms varied among ditches (Table 3.6, Fig. 3.5B).

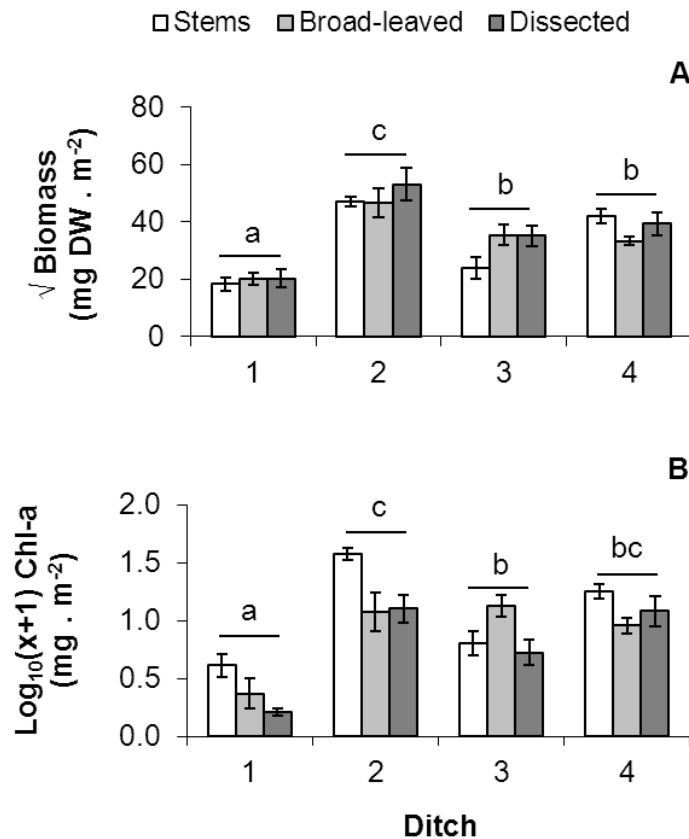


Figure 3.5: Mean ($\pm 1SE$) A: periphyton and associated detritus biomass and B: chlorophyll-a content of the periphyton per growth form per ditch. Ditches indicated with different letters are significantly different (Tukey post hoc comparisons, $p < 0.05$). In chlorophyll-a content, there was a significant interaction between ditch and growth form, as shown by the divergent patterns between ditches when different growth forms are compared.

Estimation of the relative proportion of filamentous green algae and detritus particles in subsamples of the periphyton showed that there was variation in the proportions of the two components among ditches and growth forms, which completely resembled each other (Fig. 3.6). When growth forms were compared among ditches, a significant difference was observed in ditch 2 ($H(2) = 13.8$, $p = 0.001$); the proportion of filamentous algae was higher on stems in comparison to broad-leaved and dissected

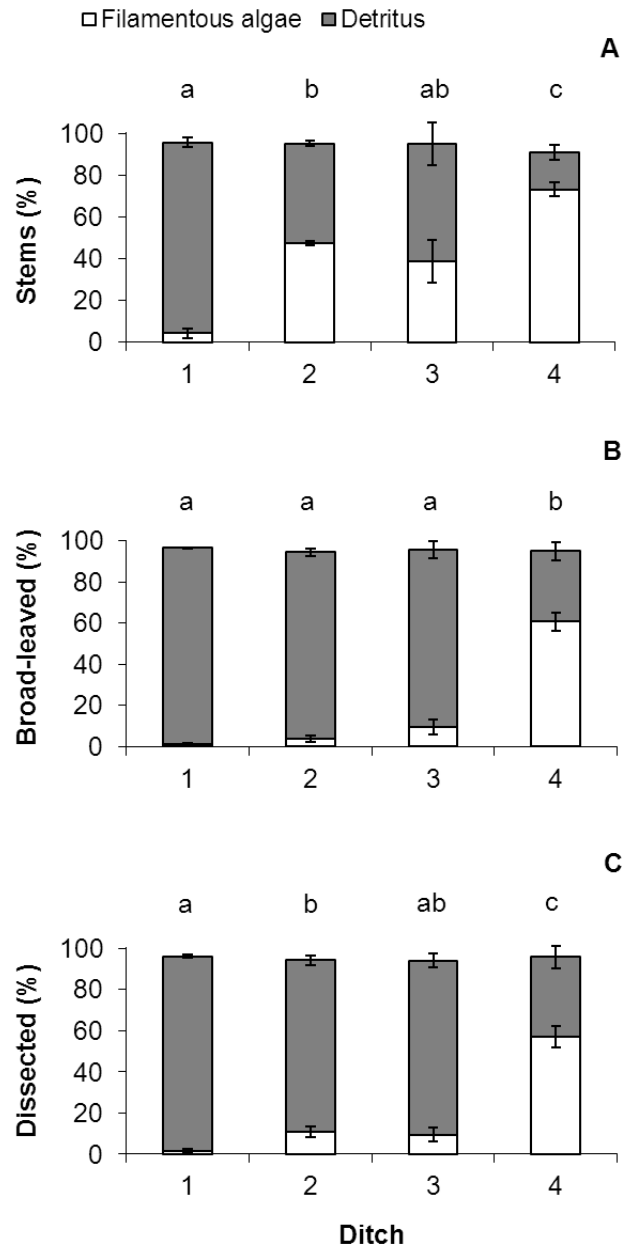


Figure 3.6: Mean ($\pm 1SE$) relative proportion of filamentous green algae and detritus particles in a subsample of the periphyton collected from the structures, displayed as stacked columns per ditch. Panels represent different growth forms; A: stems; B: broad-leaved; C: dissected. Ditches indicated with different letters are significantly different (Mann-Whitney U non parametric post hoc comparisons, Bonferroni corrected $p < 0.0083$).

structures (Mann-Whitney U non-parametric post hoc comparisons, Bonferroni corrected $p < 0.023$). No differences between growth forms were observed in the other ditches. Comparison of each of the 3 growth forms across ditches revealed differences for stems ($H(3) = 17.2$, $p = 0.001$), broad-leaved ($H(3) = 17.5$, $p = 0.001$), and dissected ($H(3) = 18.9$, $p = 0.000$) structures. Although there was variation in response among growth forms, the relative proportion of filamentous green algae was always higher in ditch 4 compared to the other ditches (Mann-Whitney U non-parametric post hoc comparisons, Bonferroni corrected $p < 0.0083$) (Fig. 3.6A-C).

Taxonomic and functional assemblage structure

Unconstrained analyses showed that 53.8% of the variation in the rarefied taxonomic dataset was explained by the first 4 PCA-axes (eigenvalues PCA-axes 1-4: 0.231, 0.144, 0.103, 0.060; all significant) (Table 3.7). Total variation explained in the rarefied functional group dataset was slightly higher compared to the taxonomic classification (57.1%), despite that only the variation explained by first three axes (eigenvalues PCA-axes 1-3: 0.238, 0.204, 0.128) differed significantly from random (Table 3.7). Along PCA-axes 1 and 2 a clear separation of samples derived from different ditches was visible (Fig. 3.7A). This pattern was not apparent along PCA-axes 3 and 4 (Fig. 3.7B). For the functional group dataset, only ditch 4 was clearly separated along PCA-axis 1 (Fig. 3.7C, D).

In the rarefied taxonomic as well as the functional dataset all components of both groups of intrinsic ditch factors (physicochemical and habitat) correlated strongly to moderately to one or multiple PCA-axes (Table 3.7). Furthermore, on microhabitat scale periphyton variables (biomass, chlorophyll-a, proportion of filamentous algae) displayed moderate correlations with most PCA-axes. Contrastingly, microhabitat structural characteristics were relatively unimportant in explaining the variation in macroinvertebrate assemblage composition. Only stems showed a moderate correlation with PCA-axis 4 in the taxonomic dataset (Fig. 3.7B, Table 3.7). Contribution of structure surface area in explaining the derived patterns appeared to be negligible.

Table 3.7: Results of PCA-analyses performed on the rarefied taxonomic macroinvertebrate assemblages and functional groups found on the structures. For each environmental variable, inter-set correlations are given with the PCA-axes ($r > 0.7$ good correlation, bold; $r > 0.4$ moderate correlation, italic). Actual eigenvalues in combination with expected eigenvalues, as determined with the broken-stick method, are given to determine the significance of the axes (ns: not significant).

Variable	Taxonomical composition (PC)				Functional groups (PC)			
	1	2	3	4	1	2	3	4 ^{ns}
<i>Intrinsic ditch factors</i>								
Physicochemical PC1	0.70	-0.28	-0.54	0.13	0.78	-0.24	-0.32	0.04
Physicochemical PC2	-0.53	-0.77	-0.18	0.07	-0.40	-0.68	-0.15	0.08
Physicochemical PC3	0.41	-0.45	0.65	-0.30	0.27	-0.31	0.72	0.03
Habitat PC1	-0.23	-0.73	0.51	-0.21	-0.28	-0.59	0.52	0.06
Habitat PC2	0.89	0.03	0.31	-0.19	0.75	0.09	0.45	-0.01
Habitat PC3	-0.29	0.59	0.62	-0.18	-0.44	0.52	0.43	-0.07
<i>Microhabitat characteristics</i>								
Stems	0.02	0.01	0.16	0.43	0.02	-0.08	0.01	-0.42
Broad-leaved	0.03	-0.04	-0.16	-0.08	0.00	0.07	-0.12	0.17
Dissected	-0.05	0.03	0.01	-0.35	-0.02	0.01	0.10	0.25
Structure surface area	0.03	0.00	-0.01	-0.15	0.00	-0.02	-0.06	0.06
Biomass	-0.16	0.59	-0.34	0.24	-0.08	0.49	-0.44	0.02
Chlorophyll-a	-0.07	0.50	-0.40	0.45	0.08	0.39	-0.46	-0.10
Prop. filamentous algae	0.37	0.28	-0.50	0.37	0.48	0.17	-0.42	-0.07
Eigenvalue	0.231	0.144	0.103	0.060	0.238	0.204	0.128	0.080
Broken-stick eigenvalue	0.047	0.038	0.033	0.031	0.194	0.139	0.111	0.092
Variance explained (%)	23.1	14.4	10.3	6.0	23.8	20.4	12.8	8.0

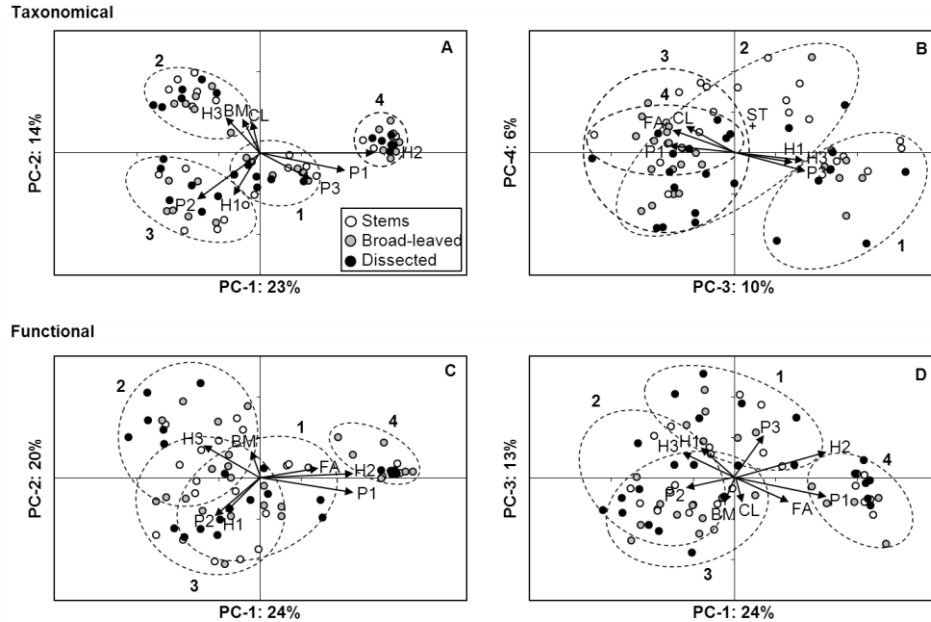


Figure 3.7: Biplots of PCA-axes 1-4 for rarefied taxonomic macroinvertebrate assemblages (A, B) and 1-3 for functional groups (C, D) found on the structures. Individual structures are represented by circles with growth forms indicated by different colours. To aid interpretation of the diagram, microhabitat characteristics (ST: stems; BM: periphyton biomass; CL: chlorophyll-a; FA: proportion of filamentous algae) and intrinsic ditch factors (H1-3: principal components 1-3 of habitat characteristics; P1-3: principal components 1-3 of physicochemical variables) were displayed as supplementary environmental variables, and as such did not influence the ordinations. Envelopes are drawn around samples derived from one ditch, which are indicated with 1-4. For clarity, only environmental variables with an inter-set correlation of $r > 0.4$ are shown. Nominal variable ST is indicated with +, continuous variables are indicated with arrows.

The sum of all constrained eigenvalues using all explanatory variables and no covariables was 0.499 for the taxonomic and 0.486 for the functional dataset. As expected from the patterns derived from the unconstrained ordination, variance partitioning in redundancy analyses showed that occupancy of structures by macroinvertebrate taxa and functional groups was best explained by intrinsic ditch factors (Fig. 3.8). Major proportion of the total explained variance in the taxonomic assemblage structure comprised of the independent effect of ditch (28%), whilst 14.9% was shared with the microhabitat characteristics. The independent effect of microhabitat contributed another 7.1% to the explained variance. From the second tier partitioning it became clear that the small – but significant – independent effect of microhabitat comprised fully of habitat structural characteristics. The unique contribution of habitat

structure to the variance explanation, after accounting for intrinsic ditch factors and periphyton, was fully comprised of growth forms (stems $\lambda_A = 0.02$, $F = 2.05$, $p = 0.002$; broad-leaved $\lambda_A = 0.01$, $F = 1.46$, $p = 0.03$). Structure surface area was not a significant determinant of taxonomic assemblage composition ($\lambda_A = 0.01$, $F = 1.06$, $p = 0.360$). Although the contribution of periphyton on the structures to the total explained variance was considerable, its effect was completely confounded with ditch. Second tier partitioning of intrinsic ditch factors into habitat characteristics and physicochemical variables was not possible, because the remaining variance was negligible after accounting for one of the two datasets, indicating a similar structure.

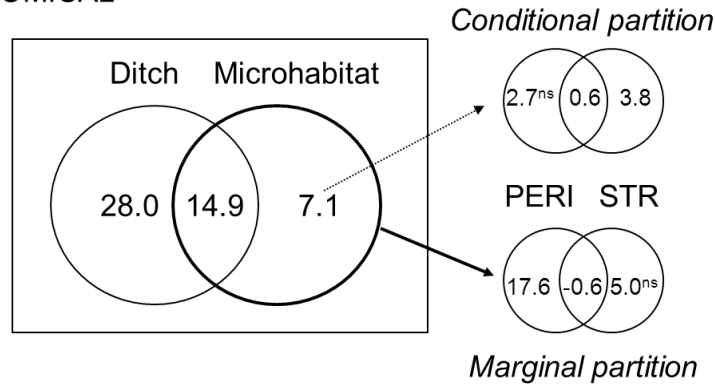
Intrinsic ditch factors were even more important in explaining functional group structure (Fig. 3.8). The independent effect of ditch was 26.5%, and another 16% was confounded with microhabitat characteristics. Contrasting to the taxonomical assemblage, there was no independent effect of microhabitat. Percentage of variance in the functional group data explained by the periphyton present on the structures was completely confounded with the effects of ditch, as shown by the second tier marginal partition. Again, partitioning of intrinsic ditch factors into habitat characteristics and physicochemical variables was not possible.

Discussion

Microhabitat structural complexity

An increase in microhabitat structural complexity did not result in an increase in either rarefied taxonomic or functional group richness. This contrasts the findings in several previous studies, in which a positive relationship was observed between richness and structural complexity (Jeffries, 1993; Taniguchi et al., 2003; Warfe & Barmuta, 2006). Nonetheless, finding a lack of response is not unique (Cyr & Downing, 1988a; McAbendroth et al., 2005). Possibly, variation in response among studies is generated by the way habitat structure has been quantified, which could have a profound influence on the shape of the species richness-habitat complexity relationship (McAbendroth et al., 2005; Thomaz et al., 2008; Warfe et al., 2008). Besides a methodological cause, it could also be an effect of macroinvertebrate colonization patterns or habitat use. For example, mass-colonization from the surrounding environment due to high recruitment could obscure any significant effects, as does preferential use of only parts of the structures (Anderson, 1998).

TAXONOMICAL



FUNCTIONAL

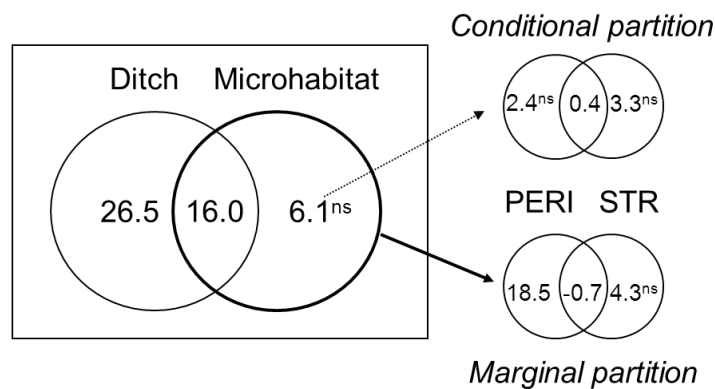


Figure 3.8: Results of first- and second tier variance partitioning of the influence of microhabitat characteristics and intrinsic ditch factors on macroinvertebrate assemblage taxonomical and functional group structure. Each circle represents a group of variables, overlapping portions indicate joint effects. Total variance explained by microhabitat characteristics can be partitioned into the effects of periphyton (PERI) and habitat structure (STR). Second tier conditional partitioning shows only the independent effects of microhabitat characteristics, whilst marginal partitioning comprises the total variance explained by this group. Surface area of circles is not on scale. Partitions which were not significant (Monte Carlo permutation test, $p > 0.05$) are indicated with ns.

Despite an effect on taxon richness was lacking, structural complexity did affect the composition of the assemblages colonizing the structures. A small fraction of the total variance in the macroinvertebrate dataset was uniquely explained by structural complexity of the growth forms, indicating that each growth form harboured a slightly different macroinvertebrate assemblage. Other studies (Dvořák & Best, 1982; Rooke,

1984; Higler & Verdonchot, 1989) described the same phenomenon: despite varying strongly in structural complexity, emergent-, floating- and submerged macrophytes had many macroinvertebrates in common, with only a small proportion of the species showing a clear preference for certain vegetation types. The presence of vegetation per se is probably more important than the plant architecture (Barnes, 1983; Downing, 1991).

Functional group composition was unrelated to structural complexity. This was surprising, since one would expect that grouping macroinvertebrates according to their functional relationship with habitat structure may give a better insight in habitat complexity-diversity associations in comparison to a taxon-based approach. Maybe other traits related to habitat structure were more important, which were not incorporated into our functional classification. For example, several studies have shown that body size displayed a clear relationship with structural complexity (Taniguchi & Tokeshi, 2004; McAbendroth et al., 2005). Since we did not measure body size, it is unknown if this was a relevant trait in our experiment. Related to this, suitability of a habitat is scale dependent; a small organism in proportion to the structure it lives on perceives the complexity of a habitat differently compared to a larger organism (Bartholomew & Shine, 2008; Warfe et al., 2008).

Structure surface area

Structure surface area did not affect microhabitat taxonomic or functional richness and composition, contradicting the often observed positive species-area relationship (Preston, 1962; Rosenzweig, 1995). Since rarefied assemblages were used for the analyses, the data was modified for an increase in species richness purely as a result from an increase in the number of individuals colonizing the structure. As shown by Thomaz et al. (2008) and Heino and Korsu (2008), the latter could play an important role in generating species richness in epiphytic and epilithic macroinvertebrate assemblages. By correcting for this sampling effect, only the role of structure surface area per se is measured. This indicated that even the largest structures used in the experiment did not appear to provide new or more resources, offering niche opportunities for species which could not persist on the smaller structures, or resulted in lower extinction rates of established immigrants, two commonly used explanations for a positive species richness-area relationship (Williams, 1943; McArthur & Wilson, 1967). Possibly, the difference in surface area provided for colonization was simply too small to generate strong species-area effects (Turner & Tjørve, 2005).

Intrinsic ditch factors

Intrinsic ditch factors, comprising physicochemical variables and habitat characteristics operating on ditch scale, were clearly more important in determining macroinvertebrate taxon composition and functional structure than the experimentally introduced microhabitat structural complexity. Nonetheless, the large-scale effect of ditch was in part reflected on micro-scale, in the form of differences in periphyton composition and abundance on the structures. Studies describing such an overriding effect of site conditions are scarce (but see Cyr & Downing, 1988a,b; Suren & Winterbourn, 1992; Cheruvilil et al., 2002). This is surprising, since it is well known that trophic status influences assemblage composition through resource quality and quantity (e.g. Townsend et al., 1998; Yanoviak, 2001; Wojdak, 2005) and that environmental factors operating on larger spatial scales influence the composition of macroinvertebrate assemblages on micro-scale (Poff, 1997; Richards et al., 1997).

A strong overriding effect of ditch as opposed to the effects of structural complexity and surface area could have resulted from differences in the species composition of epiphytic invertebrates living among the macrophytes surrounding the experimental ditch area. Biotic mechanisms such as predation, competitive exclusion, and selective ovipositioning influence the assemblage composition found in the ditches, resulting in differences in the species pool of potential colonists before the start of the experiment (Higler & Verdonchot, 1989; Orr & Resh, 1992; Wellborn et al., 1996; Tolonen et al., 2003). Therefore, the assemblage recorded on the structures may simply reflect the epiphytic species composition of the nearby natural vegetation, which constantly migrate onto the structures introduced in the ditches. Since the ditches differed in terms of physicochemical variables and natural macrophyte composition, this could already have acted as an environmental filter operating on a larger spatial scale than that of microhabitat.

The shared variance of periphyton on the structures and the intrinsic ditch factors in explaining macroinvertebrate composition indicated that part of the ditch environmental variability was reflected in the periphyton on the structures. This was supported by the univariate analyses of the periphyton, which showed that ditch strongly affected the patterns in periphyton and associated detritus biomass, amount of chlorophyll-a and the relative proportion of filamentous green algae present on the structures. Amongst others, this could be a direct result from nutrient concentrations in the water (e.g. total-P and orthophosphate concentration) or of the

presence of the natural vegetation in the ditch, which both potentially influence periphyton development (e.g. *Stratiotes aloides*; Mulderij et al., 2006). Larger spatial scale ditch effects thus appeared to override the patterns and processes occurring on micro-scale, in this case on the scale of individual structures.

Because both sets of explanatory variables were confounded, it was not possible to deduct if the observed patterns in macroinvertebrate assemblages resulted directly from the periphyton composition or were generated indirectly through the ditch factors. If periphyton composition affected macroinvertebrate composition directly, it could have acted via two pathways. Firstly, periphyton on the structures, as well as the detritus particles trapped between the algae, serves as a food source for colonizing macroinvertebrates (Rooke, 1984). Secondly, periphyton forms microstructures and creates habitat heterogeneity by inducing patchiness for macroinvertebrates inhabiting the macrostructure, adding to the complexity of the habitat (Allan, 1995). In turn, macroinvertebrates present on the structures affect this resource base and microstructure continuously, e.g. by grazing and tube construction (Feminella & Hawkins, 1995; Hillebrand & Kahlert, 2001; Harrison & Hildrew, 2001).

In the drainage ditches studied, environmental filtering (*sensu* Poff, 1997) of macroinvertebrate species with suitable traits from the local lentic species pool appeared to act primarily on scales exceeding that of microhabitats. The amount of variance explained by intrinsic ditch factors was comparable between the taxon-based assemblage and the functional groups found on the structures, indicating that both functional and taxonomic approaches described the same patterns in community composition, a phenomenon which is also observed in other macroinvertebrate studies (Finn & Poff, 2005; Heino et al., 2007). This opposed our expectation that ecological relationships with different aspects of a microhabitat, in this case the epiphytic macroinvertebrate-macrophyte relationship, could well be derived from the functional structure of the macroinvertebrate assemblage found on a structure, because this is less biased by, for example, the role of stochasticity in determining the taxon composition of localities. Resemblance between the patterns derived from taxonomic and non-taxonomic aggregation of species into functional categories can in part be explained by the interrelationships between traits and the phylogeny of the macroinvertebrates possessing them (Resh et al., 1994; Poff et al., 2006). Another cause of the observed pattern could simply be the underlying macroinvertebrate abundance distribution; dominant

macroinvertebrates on the structure in terms of abundance automatically comprise the dominant functional groups.

Concluding remarks

With only a minor contribution of habitat structural complexity in structuring macroinvertebrate assemblages and no effects on its functional composition, whilst intrinsic ditch factors, such as physicochemical variables and the composition of the vegetation surrounding the experimental structures determined in large part the taxonomical and functional composition of the assemblages recorded, one could question the role of plant architecture in generating drainage ditch macroinvertebrate distribution patterns. Nonetheless, as shown in this experiment, processes acting on larger spatial scales are reflected on microhabitat scale, partly through a mediating role of the periphyton. Patterns in macroinvertebrate assemblage composition and functional groups derived from habitat structures within a water body, such as the epiphytic fauna of macrophytes, thus give insight into larger scale patterns and processes acting within the ecosystem.

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4 **Does wing size play a role in shaping lentic insect assemblages?**



Oligotrichia striata (Trichoptera: Phryganeidae) adult.

4 Does wing size play a role in shaping lentic insect assemblages?

Ralf C.M. Verdonschot, Piet F.M. Verdonschot

Abstract

Drainage ditch networks are comprised of spatiotemporal mosaics of habitat patches. For aquatic insects inhabiting these waters dispersal is an important mechanism for long-term persistence. Variation in organismal traits, such as wing size, may affect dispersal rates and thereby the ability to colonize environmentally suited sites. We examined if patterns in taxon dissimilarity among drainage ditches mirrored not only differences in environmental factors, but also if these patterns were a function of geographic distance, indicating the influence of spatial processes structuring the assemblage composition. To test if the effect of spatial location in shaping local assemblages was related to dispersal ability, the aquatic insect data was aggregated into wing size classes and the relationship between taxon dissimilarity, environmental variation and spatial configuration was investigated for each wing size class separately. Our analyses showed that taxon dissimilarity in large winged insects did not correlate to spatial location of the sampling sites, but was related to environmental heterogeneity among sites. Insects with the smallest wings did not show an effect of inter-site distance either. Also in this group taxon dissimilarity was correlated with environmental variation only. In the intermediate wing size classes a distance effect was observed, although in the second largest wing size class spatial configuration was autocorrelated to the environmental variation among sampling sites. It appears that both environmental filtering and dispersal-related processes are underlying drainage ditch aquatic insect distribution, but its relative importance varies with dispersal ability.

Keywords: drainage ditches, environmental filtering, macroinvertebrates, species turnover, colonization

Introduction

Patterns in local species richness and turnover of species composition across small lentic freshwater ecosystems within a region are a function of variation in environmental factors, immigration and extinction (Loreau, 2000; Hillebrand & Blenchner, 2002). Environmental factors act as filters by

putting constraints on the distribution of aquatic organisms (Poff, 1997), and result in species sorting along environmental gradients (Leibold et al., 2004). The structuring role of environmental factors is especially important when habitats tend to be more extreme and unpredictable (Resh et al., 1988; Poff & Ward, 1989). Environmental conditions in meso- to eutrophic small water bodies (e.g. ponds, oxbow lakes, drainage ditches) can be regarded as relatively unstable. On a timescale of several years to decades major shifts in environmental conditions take place, both predictable and unpredictable. Eventually, advancing terrestrialization leads to the complete disappearance of water bodies, in small eutrophic systems already within a decade (Garms, 1962).

The ephemeral nature of individual water bodies and the specific microhabitats they contain resulted in the development of multiple life history traits related to overland dispersal capacity or ability in lentic invertebrates (Ribera et al., 2003; Marten et al., 2006; Hof et al., 2008). A wide array of adaptations has evolved in species belonging to different taxonomic groups, within the constraints of their basic morphology, to be able to disperse between water bodies (Bilton et al., 2001). Dispersal connects local communities; each local macroinvertebrate assemblage can be regarded as part of a larger regional metacommunity, with dispersal of species between the individual water bodies as an important process maintaining its structure (Bohonak & Jenkins, 2003). Environmental change, stochastic events or biotic interactions may lead to local extinction of populations, counterbalanced by a constant flux of individuals actively or passively immigrating from other water bodies.

When dispersal is not limiting, turnover in environmental conditions between water bodies is always reflected by predictable changes in the macroinvertebrate assemblages present, resulting in the same sets of species being abundant at environmentally similar sites (niche-based species sorting; Leibold et al., 2004). Differences in dispersal ability due to, for example, life history characteristics or landscape properties (degree of connectivity, presence of dispersal barriers) could lead to species being temporarily absent from apparently suitable locations. If dispersal ability is the key explanatory factor in structuring lentic invertebrate assemblages, dissimilarity in species composition is positively related to geographic distance between sites, irrespective of the presence of environmentally suited habitats (Nekola & White, 1999; Tuomisto et al., 2003). Niche-based species sorting underlying aquatic insect distribution patterns received most empirical support, but its relative importance as opposed to dispersal-based distribution patterns differed considerably between taxonomic groups,

habitat types and spatial scale studied (Cottenie, 2005; Thompson & Townsend, 2006; Soininen et al., 2007a).

However, direct estimates of dispersal capacity or distance are absent for most aquatic insect species (Bilton et al., 2001). Therefore, exploring spatial patterns related to dispersal and the mechanisms underlying the observed patterns relies on the use of biological or morphological proxies. Since such approaches do not give information on the actual dispersal rate, they must be seen as a simplification to investigate broad scale patterns in insect distribution. Wing size is directly or indirectly, through the often suggested wing size - body size relationship (Svensson, 1975; McLachlan, 1986; Briegel, 1990; Kovats et al., 1996) related to dispersal in aquatic insects. It has been suggested that insects with a large body size and/or large wings are good colonizers, occupying large geographic ranges because they are capable of dispersing over large distances and are able to actively select suitable habitats for reproduction (Malmqvist, 2000; Jenkins et al., 2007; Rundle et al., 2007a). Contrastingly, most invertebrates with small wings are weak fliers. Therefore, in these organisms long distance dispersal mainly takes place passively, as aerial plankton driven by the wind (Rundle et al., 2007b). Passive dispersal leads to the introduction of a highly stochastic component, a lottery effect, decreasing the chance of successful colonization of environmentally suitable habitats when dispersing over long distances (Bilton et al., 2001; Fonseca & Hart, 2001).

As a result, the probability of good dispersers being absent from environmentally suited sites should be small, at least on a regional scale, in comparison to the weak fliers, which should display a much higher turnover between sites with distance, because their appearance in a water body has a large stochastic component. In this study, this presumption was tested by comparing aquatic insect assemblage dissimilarity across different wing size classes in a series of peatland drainage ditches within the Netherlands. It was examined if at regional scale: 1.) the observed taxon dissimilarity among ditches mirrored not only differences in environmental factors, but also if these patterns were a function of geographic distance, indicating the influence of spatial processes structuring the assemblage composition 2.) if an effect of geographic distance could be linked to variation in adult wing size as a measure of dispersal ability.

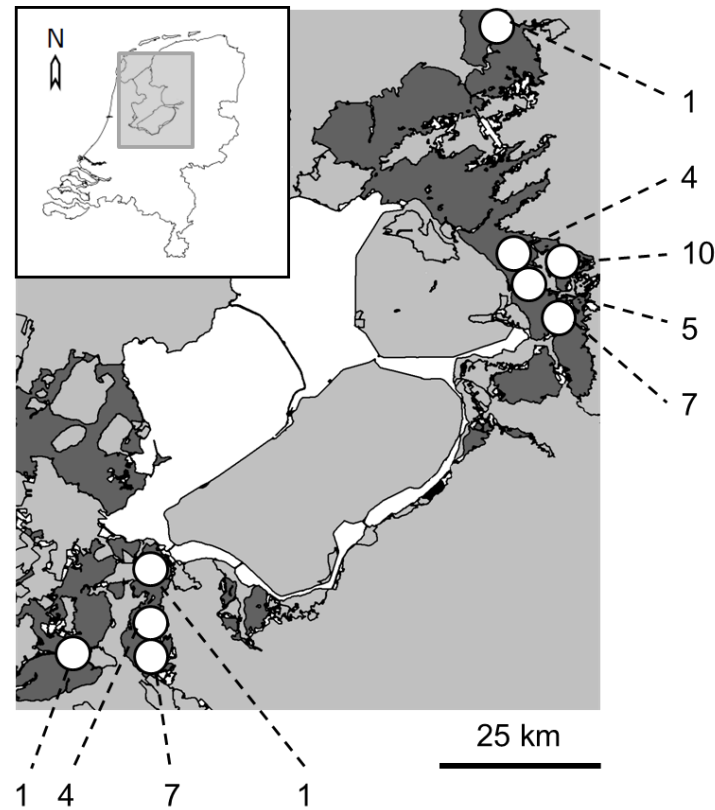


Figure 4.1: Map of the study area and its positioning within The Netherlands. Dark areas are peatlands, with circles representing the sampling areas. Numbers indicate the number of drainage ditches sampled within the different sampling areas.

Methods

Study area

The study was conducted in the peatland district of the Netherlands (Fig. 4.1). In this area extensive networks of drainage ditches were dug to be able to regulate the water regime for agricultural purposes. These series of interconnected small, shallow drainage ditches (up to 8 m wide and 1 m deep) often represent the only non-cropped landscape elements, forming a discrete, but connected habitat matrix with a high geographical replication of sites (Herzon & Helenius, 2008). Actual water movement is negligible ($0-5 \text{ cm.s}^{-1}$), therefore the ditch networks can be regarded as stagnant systems. Intensive farming on the fields adjacent to the ditches results in high ditch nutrient levels. As a consequence, excessive growth of macrophytes in the

ditches is common. Therefore, to retain its drainage function, regular management takes place, in the form of mowing of the vegetation and dredging of the accumulated bottom sediment.

Despite their artificialness and high nutrient levels, ditch networks often harbour a rich macroinvertebrate community (Verdonschot & Higler, 1989; Verdonschot, 1992). A number of studies described the relationships between macroinvertebrate community composition and environmental variables in drainage ditches, pointing out the importance of habitat structure generated by the vegetation, oxygen level, dimensions, nutrient/organic loads, and chloride concentration (due to the inlet of river water or groundwater seepage with a high chloride concentration) as environmental filters (Clare & Edwards, 1983; Scheffer et al., 1984; Verdonschot & Higler, 1989; Verdonschot, 1992). Terrestrialization, management practices and other anthropogenic impacts lead to a constantly changing ditch environment in space and time, in terms of vegetation structure and composition, water volume and physical-chemical characteristics. Therefore, ditch networks can be regarded as shifting mosaics of habitat patches, which makes them a suitable model system for investigating distribution patterns in aquatic invertebrates.

Table 4.1: *Number of site pairs per distance class. Distance classes are based on the shortest distance between two sampling sites. In total, 40 sites were sampled, resulting in 780 possible site pair combinations.*

Distance class (km)	No. of site pairs
0-0.5	50
0.5-1	26
1-2	27
2-4	72
4-8	178
8-16	38
16-32	12
32-64	26
64-128	350
128-256	1

Sampling methodology

Based on field studies and population genetic analyses it has been suggested that the majority of dispersal events took place over relatively short

distances, with only a small proportion of the population dispersing over longer distances (Kovats et al., 1996; Bunn & Hughes, 1997; Delettre & Morvan, 2000; Berendonk & Bonsall, 2002). Therefore, in this study distance between sampling sites was varied to represent the variation in dispersal range encountered by actively dispersing insects. Randomly chosen ditch stretches (length 50 m) were sampled once in various ditch networks in summer-autumn ($n = 40$). This resulted in 780 possible ditch sampling site pairs, with an inter-ditch distance ranging from 0.02 to 133 km (Table 4.1).

Given that the distribution of the aquatic insect species inhabiting the peatland drainage ditches exceeds the scale of our study, every environmentally suited site should be within reach of all taxa, given enough time to colonize. Therefore, drainage ditches were chosen as study sites because environmental change in these water bodies is rapid, e.g. changes in environmental conditions take place on a relatively short time scale (years to one decade). This increased the chance that our one-time sampling captured a situation in which sites which were potentially environmentally suited were not yet (re)colonized. We do not know where the actual connectedness of different drainage ditches truly starts and ends for aquatic insects. Here we defined our metacommunity as the individual ditches containing the local populations and the entire peatland area as the region in which long distance dispersal takes place. However, studies on the success rate of dispersal events are lacking in most aquatic insects, so we can only assume that the geographic scale used here is the appropriate one.

A pond net (width 25 cm, mesh size 0.5 mm) was used to sample vegetation and associated bottom material over a total length of approximately 2.5 m. The sample was divided over the dominant vegetation growth forms present by pooling separate sweeps of 0.5 m. Material collected was transported to the laboratory, washed over 1 mm and 250 μm sieves, and sorted alive. Aquatic insects were identified to the lowest taxonomical level practical, mostly species. Diptera: Nematocera and Neuroptera were identified to genus only because of a high number of taxonomic inconsistencies within these orders. In Heteroptera and Coleoptera, only adults were identified.

At the time of macroinvertebrate sampling, a range of environmental factors was recorded. Water chemistry was measured by taking a water sample from each site, which was analysed for nutrients and macro-ions in the laboratory. Percentage cover of growth forms of the vegetation (emergent-, submerged-, and floating vegetation) were estimated along the 50 m ditch stretches, as well as the land use adjacent to the ditch

stretch. Depth and width measurements were taken to determine the dimensions of the ditches.

Wing size estimation

Wing size was chosen as a proxy of dispersal ability, which was expressed as the wing surface area (mm^2). Other variables, such as wing loading and wing beat frequency as well as flight muscle size and available energy sources also affect flight ability (Malmqvist, 2000), but such data were very difficult to obtain for all species recorded. Therefore, we chose a proxy which could be derived for all taxa collected in the study. Wing surface area was crudely estimated by multiplying (fore)wing length and (fore)wing width (Carron, 2007). Since a very broad range of taxa was present in the drainage ditches, spanning several orders of magnitude in wing size, we assume that these crude wing surface area estimations still give reliable results. Nonetheless, we are aware that calculation of the exact wing surface areas, e.g. by digital photo analysis, would make the results stronger.

Wing size data was compiled from the literature for Ephemeroptera (forewings; Bauernfeind & Humpesch, 2001), Nematocera (Cranston et al., 1989a,b; Murray & Fittkau, 1989; Nilsson, 1997; Disney, 1999; Sæther & Wagner, 2002), Trichoptera (forewings; Malicky, 2004; Mosely, 1939; Tobias & Tobias, 1981), Megaloptera and Neuroptera (forewings; Elliott, 1996), Lepidoptera (forewings; Agassiz, 1996). No data was available for several Trichoptera species (forewings) and all Coleoptera, Heteroptera and Odonata (forewings) sampled. Therefore, wing lengths and widths of collection material, collected at a wide range of locations across The Netherlands (Alterra reference collection) were measured to get an approximation of the size ranges. Because wing size parameters were rather variable within species (e.g. between sexes, populations, seasons; Delettre, 1988), the mean of the minimum and maximum values per species was used, in case of genera the mean of the data provided for the smallest and largest species within a genus.

Statistical analyses

To investigate if dissimilarity in aquatic insect composition between sites mirrored dissimilarities in environmental conditions, environmental data were summarized using Principal Components Analysis (PCA). Overall environmental ‘summary’ scores (groups of correlated environmental parameters) were generated to display the environmental variation of among

sites. PCA was conducted in CANOCO for Windows 4.5 (ter Braak & Šmilauer, 2002), with environmental variables ($\log_{10}(x+1)$ transformed) centred and standardized. Inter-site geographic distances were calculated by measuring the shortest distances between all site pairs from a topographical map using GIS-software.

For most aquatic insect groups there was as much variation in wing size within as between taxonomic groups. As a result, wing size could not be used as a direct proxy for dispersal ability of individual taxonomic groups. Therefore, the aquatic insect assemblages recorded at the sampling sites were grouped according to wing size instead of their taxonomic relationship. For each taxon, the wing surface area estimations were $\log_2(x+1)$ transformed. These transformed estimations were grouped into 4 wing size classes: <2 (wing surface area estimation: <3 mm²), 2-4 (3-15 mm²), 4-6 (15-63 mm²) and >6 (>63 mm²). For each wing size group, abundance data was $\log_2(x+1)$ transformed and expressed as pairwise dissimilarities, based on Sørensen (Bray-Curtis) distances. Based on the PCA environmental scores and the geographic distances, matrices were constructed containing pairwise Euclidean dissimilarities between sites. Bray-Curtis dissimilarities and Euclidean distances were calculated using PcOrd 4.25 for Windows (McCune & Mefford, 1999).

Mantel tests (Manly, 1997) were used to investigate to what degree the assemblage dissimilarities per wing size class between sites correlated with geographic distances, indicating the structuring role of spatial configuration, and dissimilarity in environmental conditions, identifying species sorting as the key process shaping the aquatic insect distribution pattern. Before assemblage dissimilarities were correlated, it was tested if spatially neighbouring sites were more environmentally similar than distant sites (e.g. if the environmental and geographical matrices displayed autocorrelation; Legendre, 1993), to determine if it was necessary to use partial Mantel tests. In a partial Mantel test the correlation between two matrices was tested while controlling for the effect of a third matrix. The statistical significance of each correlation, expressed as the Pearson correlation coefficient (r_M), was determined using a randomization test (10,000 iterations). Mantel tests were performed with the program *zt* (Bonnet & van de Peer, 2002). Since multiple wing size classes derived from the same samples were compared, statistical significance was Bonferroni corrected for multiple testing ($p = 0.05/4; 0.0125$).

Besides a relationship with wing size as a proxy of dispersal ability, there are other attributes that could influence the patterns observed for the different wing size classes. Three potentially important taxon attributes are

taxon identity, overall abundance and distributional range. The role of taxon identity was explored by comparing the relative proportions of different taxonomic groups per wing size class. Differences and trends in abundance and site occupancy across wing size classes were investigated using non-parametric tests (Kruskal-Wallis test, Jonckheere-Terpstra test). Tests were conducted in SPSS for Windows (version 15.0; SPSS Inc., Chicago, Illinois, USA).

Table 4.2: Characteristics of the peatland drainage ditches studied ($n = 40$), measured once in summer or autumn along 50 m ditch stretches. Median and range (between parentheses) are given for each variable, as well as the Pearson's correlations (r) with PCA-axes 1 and 2 ($r > 0.7$ good correlation, bold; $r > 0.4$ moderate correlation, italic).

Environmental variable	Value	Pearson correlation coefficient (r)	
		PCA-1	PCA-2
<i>Ditch dimensions</i>			
Width (m)	3.7 (1.4-7.5)	0.27	0.68
Maximum depth (m)	0.5 (0.2-1.1)	0.08	0.72
<i>Adjacent land use</i>			
Cropland (%)	0 (0-100)	-0.76	-0.27
Grassland (%)	95 (0-100)	0.12	-0.45
Marshland (%)	0 (0-100)	0.19	0.60
Woodland (%)	0 (0-25)	0.01	0.30
<i>Ditch vegetation</i>			
Submerged vegetation cover (%)	38 (0-95)	0.25	0.01
Emergent vegetation cover (%)	15 (5-80)	0.42	-0.34
Floating vegetation cover (%)	5 (0-90)	0.50	0.19
<i>Macro-ions</i>			
Calcium (mg L ⁻¹)	34.8 (10.3-52.0)	-0.25	-0.37
Chloride (mg L ⁻¹)	29.4 (11.9-148)	-0.36	0.81
Kalium (mg L ⁻¹)	3.8 (0.1-19)	-0.74	-0.10
Total iron (mg L ⁻¹)	0.04 (0.01-0.82)	-0.83	-0.28
Magnesium (mg L ⁻¹)	4.5 (2.8-15)	-0.65	0.41
Natrium (mg L ⁻¹)	16 (7.5-97)	-0.38	0.80
Sulphate (mg L ⁻¹)	11 (1.0-67)	-0.63	0.66
<i>Nutrients</i>			
Kjeldahl-Nitrogen (mg N L ⁻¹)	1.4 (0.2-6.9)	-0.73	-0.17
Ammonium (mg N L ⁻¹)	0.04 (<0.03-3.44)	-0.84	-0.26
Nitrite (mg N L ⁻¹)	<0.002(<0.002-0.019)	-0.64	-0.04
Nitrate (mg N L ⁻¹)	<0.1(<0.1-0.2)	-0.34	-0.02
Ortho-phosphate (mg P L ⁻¹)	<0.005 (<0.005-0.229)	-0.25	0.10
Total phosphorus (mg P L ⁻¹)	<0.02 (<0.02-0.305)	-0.15	0.26

Results

Dissimilarity in environmental conditions between sites

Based on the eigenvalues of the ordination axes of the PCA, the environmental variables recorded (eigenvalue PCA axis 1: 0.240, 2: 0.184) were summarized into two main sets of environmental summary variables. PCA axis 1 (eigenvalue 0.240, 24.0% explained) mainly comprised of variation in organic loading, whilst PCA axis 2 (eigenvalue 0.184, 18.4% explained) corresponded to differences in dimensions of the ditches sampled and the concentrations of Na^+ and Cl^- , indicating the periodic inlet of river water with a relatively high salinity (Table 4.2, Figure 4.2). From this point on, the environmental summary variable represented by PCA axis 1 will be referred to as E1 and the variable represented by PCA axis 2 as E2. PCA-axes 3-5 still explained a significant proportion of the total variance in the dataset (Broken-stick eigenvalue < actual eigenvalue; eigenvalue PCA axis 3: 0.112, axis 4: 0.090, axis 5: 0.080) but were not used in the subsequent analyses because they contributed considerably less to the total explained variance in comparison to the first two PCA-axes.

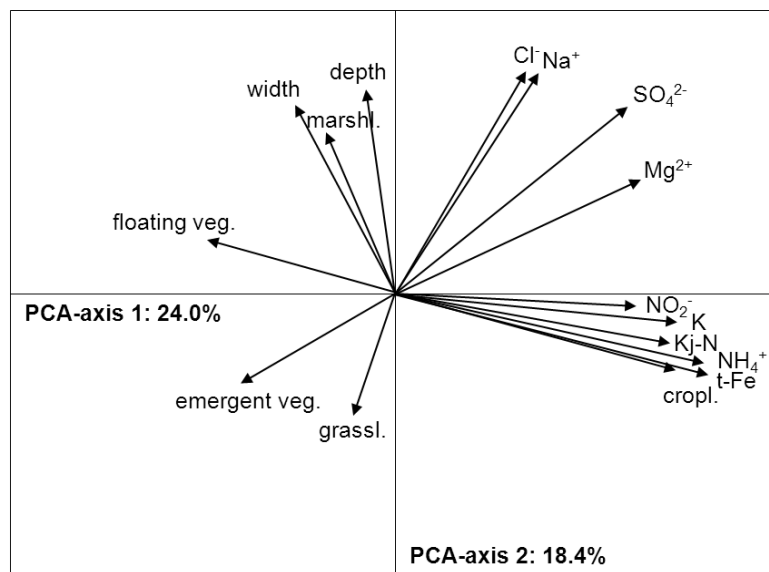


Figure 4.2: Biplot of the first two Principal Components Analysis (PCA) axes, based on the environmental variables recorded at the drainage ditch sampling sites ($n = 40$). Percentage of total variance explained is given for each axis. Arrows indicate the direction of increase of the environmental variables. Length of an arrow indicates its explanatory value. The angle between an arrow and an axis indicates the strength of the correlation with that axis.

Taxon composition of wing size classes

In total, 20131 individuals were collected in the drainage ditches, consisting of 199 aquatic insect taxa. There were large differences between the taxonomic groups in terms of taxon richness and abundance (Table 4.3). The largest number of taxa collected (76) belonged to $\log_2(x+1)$ wing size class 2-4, followed by the wing size classes <2 and 4-6 (both 45) and finally wing size class >6 (33). Taxon distribution over the wing size classes differed considerably between taxonomic groups (Figure 4.3). Nematocera and Coleoptera dominated the two smallest wing size classes, whilst Odonata represented the most important group in the largest wing size class. Besides differences in taxonomic composition, the wing size classes differed in terms of average per taxon abundance ($H(3) = 11.985$, $p = 0.007$) (Figure 4.4A). There was a significant trend towards a lower average abundance with increasing wing size class ($J = 5777.0$, $z = -3.148$, $p = 0.002$). Site occupancy did not differ among wing size classes ($H(3) = 3.611$, $p = 0.307$) (Figure 4.4B).

Table 4.3: Overview of the total number of taxa and total number of individuals collected per taxonomic group in the 40 drainage ditches, as well as the mean number of taxa and individuals ($\pm 1SD$) per sample.

Taxonomic group	Total # taxa	Total # ind.	Mean # taxa sample ⁻¹	Mean # ind. sample ⁻¹
Odonata	17	1329	4 \pm 1	33 \pm 36
Ephemeroptera	5	3677	3 \pm 1	92 \pm 64
Heteroptera	25	1380	6 \pm 3	35 \pm 29
Coleoptera	59	524	6 \pm 3	13 \pm 12
Diptera: Nematocera*	54	8222	17 \pm 5	206 \pm 113
Trichoptera	34	4335	7 \pm 3	108 \pm 125
Megaloptera	1	245	0.6 \pm 0.5	6.1 \pm 8.6
Neuroptera*	1	3	0.1 \pm 0.2	0.1 \pm 0.3
Lepidoptera	3	416	1.1 \pm 0.7	3.5 \pm 6.5

*based on genera

Spatial autocorrelation of environmental variation and geographic distance

Before the taxon dissimilarity per wing size class among sites was correlated with E1 and E2 it was tested if these environmental summary variables displayed spatial autocorrelation. Dissimilarity in E1 was not correlated to the distance matrix ($r_M = 0.086$, $p = 0.133$). Contrastingly, dissimilarity in E2 did display spatial autocorrelation ($r_M = 0.350$, $p = 0.0001$), indicating that

dissimilarity in this environmental summary variable increased with increasing distance between drainage ditches sampled. To identify the independent effects of distance and E2, it was necessary to test correlations between dissimilarities in taxon composition and one of these variables while controlling for the effect of the other variable.

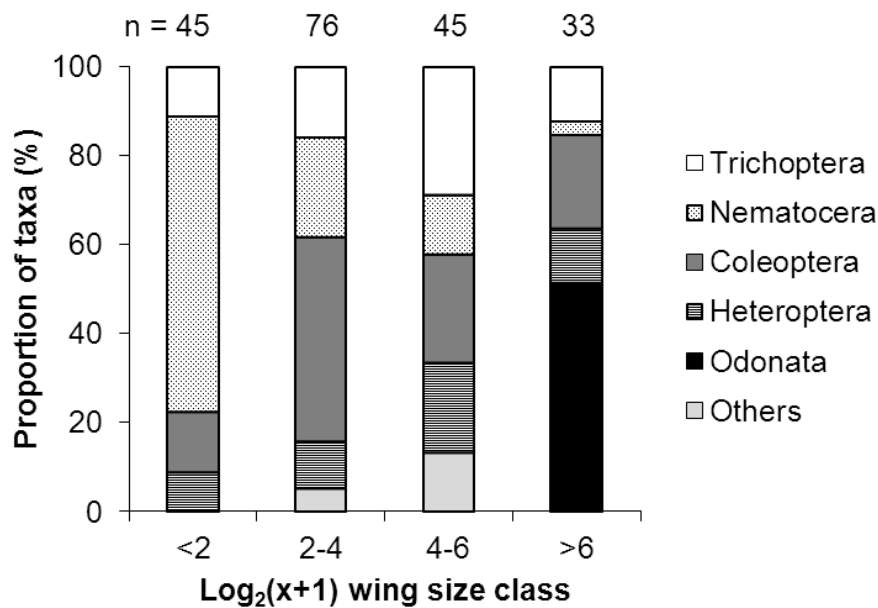


Figure 4.3: Relative proportion of taxa per taxonomic group for the $\log_2(x+1)$ wing size classes. The number above the bars is the total number of taxa per wing size class. Group 'others' is a combination of several minor taxonomic groups: Megaloptera (1 taxon), Neuroptera (1), Lepidoptera (3) and Ephemeroptera (5).

Correlations between taxon dissimilarity, environmental variation and geographic distance

Dissimilarity in taxa with the smallest wing size (wing size class < 2) between drainage ditches sampled did not correlate with geographic distance, but was correlated to dissimilarities in environmental conditions (Table 4.4). There was a significant correlation with dissimilarity in E1 and E2, although in the latter a significant correlation was obtained only after controlling for the effect of geographic distance. Dissimilarity in taxa belonging to wing size class 2-4 correlated to geographic distance between sampling sites. Despite displaying a significant correlation in the simple Mantel test for E2, partial Mantel tests showed that only the correlations

between geographic distance and assemblage dissimilarity were significant. This indicated that – due to spatial autocorrelation – it was not possible to distinguish an effect of E2 from the effect of distance, because the effect of E2 was completely confounded with distance. In wing size class 4-6 the opposite pattern was observed; partial Mantel tests showed that there was a significant correlation with E2 after controlling for the effect of distance, while vice versa there was no significant correlation with distance after controlling for E2. This indicated that in wing size class 4-6 any effect of distance was fully confounded with E2. Finally, assemblage dissimilarity of the taxa with the largest wing size (wing size class >6) displayed a significant correlation with E2 only.

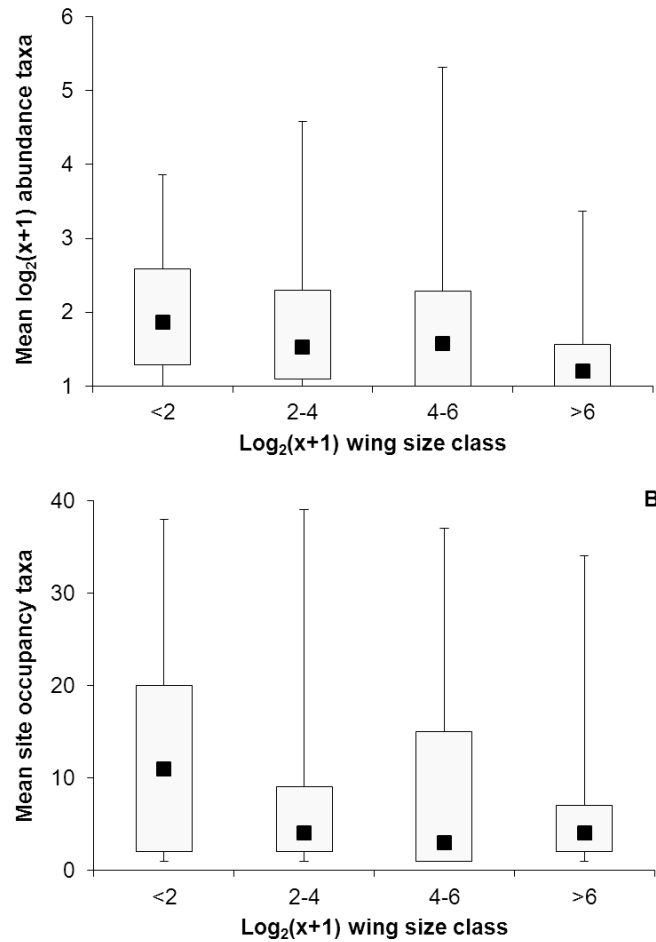


Figure 4.4. Boxplots of the (A.) mean abundance of individual taxa and (B.) mean site occupancy of individual taxa per $\log_2(x+1)$ wing size class. Range bars show maximum and minimum values. Boxes are interquartile ranges (25th percentile to 75th percentile); squares represent medians.

Table 4.4: Correlation coefficients (r_M) derived from simple and partial Mantel tests for 50 m ditch stretches ($n=40$) based on Bray-Curtis dissimilarities among ditches. Taxon dissimilarity (S) per wing size class was correlated to the geographic distance between ditches (D) and dissimilarity in environmental variables (E). $E1$ = nutrient loading (PCA1), $E2$: dimensions/salinity (PCA2). In the partial Mantel tests, the correlation between matrix S and E or D was tested while controlling for a third matrix (E or D). Significant correlations are shown in bold.

Log ₂ (x+1) wing size class	Simple Mantel test r_M			Partial Mantel test r_M			
	S.D	S.E1	S.E2	S.E1 D	S.D E1	S.E2 D	S.D E2
< 2	0.001	0.293*	0.163	0.294*	-0.025	0.174*	-0.061
2 - 4	0.226**	0.077	0.208*	0.059	0.221*	0.141	0.167*
4 - 6	0.224**	0.090	0.376**	0.073	0.218**	0.326**	0.106
> 6	0.146	0.103	0.286**	0.091	0.139	0.253*	0.052

Significance (Bonferonni-corrected) * $p < 0.0125$, ** $p < 0.001$

Discussion

We predicted that in drainage ditches the distribution of large-winged species should be mainly environmentally structured, as a result of their ability to actively chose their preferred habitats over relatively large spatial scales. Small-winged species on the other hand should display a strong distance effect, because they rely on passive means of dispersal. In this group reaching vacant suited habitat patches becomes a matter of chance. Indeed, our results showed that taxon dissimilarity in large winged insects did not correlate to spatial location of the sampling sites, but was related to environmental heterogeneity among sites. Contrary to our hypothesis, we found that the insects with the smallest wing surface area did not show an effect of inter-ditch distance either. Also in this group taxon dissimilarity was correlated with environmental variation only. Surprisingly, in the intermediate wing size classes a distance effect was observed, although in the second largest wing size class spatial autocorrelation made it impossible to separate the independent effects of distance and environmental heterogeneity.

The finding that large winged insects are not strongly spatially restricted is in line with other studies (Thompson & Townsend, 2006; Jenkins et al., 2007; Chaput-Bardy et al., 2008). In this study, Odonata were the main representatives of the largest wing size class, together with several large taxa belonging to the Coleoptera, Heteroptera and Trichoptera. Particularly these insects are able to 1.) time the start of dispersal or manoeuvre into air currents, 2.) survive long enough to reach distant

patches (e.g. in terms of life span, energy reserves, desiccation resistance), 3.) quickly move around to find environmentally suited sites to reproduce or to oviposit (Csabai et al., 2006; Rundle et al., 2007b). All these factors contribute to successful long distance dispersal and (re)colonisation of vacant habitat patches, resulting in a close linkage between large winged insect assemblages and environmental gradients. The structuring role of environmental factors in the largest wing size class is an indication of niche-based species sorting being the main mechanism underlying the distribution patterns of these aquatic insects.

But what about the smallest wing size class? The insects belonging to this group, which in this study was mainly composed of Nematocera (e.g. small Chironomidae, Ceratopogonidae), are not capable of actively flying long distances. In these organisms dispersal takes place passively – mainly by wind – introducing a stochastic component to dispersal (Bilton et al., 2001; Rundle et al., 2007b). As a result, small winged insects do not have control over their dispersal events in terms of direction or duration. Our analyses suggest that small-winged insects inhabiting drainage ditches are capable of counteracting the adverse effects associated with passive dispersal. It is likely that they employ a different strategy to disperse effectively, as suggested by Shurin et al. (2009) when explaining similar distance-dissimilarity patterns in diatoms, zooplankton and macroinvertebrates. According to Soininen et al. (2007a,b) passive dispersal is even more effective than active dispersal.

The relatively high taxon abundance recorded within this wing size class could be part of the explanation for the pattern observed (Gaston & Lawton, 1988; Fenchel, 1993). A large population size, due to a high reproduction rate in small organisms or the fact that more individuals can inhabit a unit of habitat space, results a large pool of potential colonists, thereby increasing the chance of successfully colonizing environmentally suited vacant sites and counteracting the stochasticity introduced by dispersing passively. Given that there were no differences in taxon occurrence across sites, dispersing passively does not lead to ubiquitous distributions, which suggests that species sorting along environmental gradients is the main mechanism underlying taxon distribution in the smallest wing size class, just as it was in the largest wing size class.

Contrastingly to the environmentally structured smallest and largest wing size groups, aquatic insects with intermediate wing sizes did show a distance effect. This suggests that dispersal processes play an important role in the distribution of these taxa in drainage ditches. A possible explanation for spatial configuration being important for insects in this wing size range

is that they are not abundant enough for effective long distance passive dispersal and too small for active long distance dispersal. As a result, the taxa comprising this intermediate size range have local, 'clumped' distributions. Since these 'clumps' were in part unrelated to environmental variation among sites, at least in $\log_2(x+1)$ wing size class 2-4, is it well possible that the observed distribution is generated by a 'rescue effect', in which immigration from a vital population can act as a source to maintain 'sink' populations in adjacent environmentally marginal habitat, that would otherwise go extinct (Holt, 1985; Pulliam, 1988; Gotelli, 1991). Another explanation for the observed pattern is given by Rundle et al. (2002): they found that Coleoptera – here comprising a relatively large proportion of the second smallest wing size class – may perform numerous small-scale movements between water bodies during a season, exploiting several habitats for short periods of time without reproducing there. Nonetheless, this explanation only holds for taxonomic groups with an aquatic adult life stage.

In his hypothetical model for microbial eukaryotes, Finlay (2002) predicted that there is a transition point in the body size range where the effects of a high abundance and its associated mass dispersal on organisms distributions disappear and that organisms become more geographically restricted. Soininen et al. (2007b) predicted an unimodal relationship between assemblage dissimilarity among sites and organism body size in organisms that can disperse actively, with the smallest organisms being passively transported over large spatial scales and the largest organisms having extensive range sizes. Our results support these predictions and can be incorporated into a conceptual framework of the relative importance of different dispersal modes in relation to the distribution of drainage ditch aquatic insects across environmental gradients and spatial scales (Fig. 4.5).

The fact that part of the environmental heterogeneity was correlated to the spatial location of the sampling sites did obscure the pattern in the intermediate wing size classes, especially in the second largest wing size class, since both spatial configuration and environmental variation displayed a similar pattern. This hindered the interpretation of the data derived for these wing size classes. Furthermore, the environmental summary variable derived from the PCA displaying spatial autocorrelation comprised the strongly correlated variables ditch dimensions and salinity. Finding such correlation is not surprising given the hierarchical design of Dutch peatland drainage ditch systems. Larger ditches are generally influenced more by the inlet of river water with a high concentration of NaCl than the smaller field ditches, since the former serve as a supplier of water to the latter (Higler,

1989). This raises the question if drainage ditch size has any relationship with the patterns found or that it is salinity that acts as the environmental filter. Available area of suited habitat is regarded as an important factor in explaining aquatic insect distribution patterns in relation to colonisation and extinction dynamics (Rundle et al., 2002). Unfortunately, with the data collected in this study it is not possible to address this potential effect of habitat size.

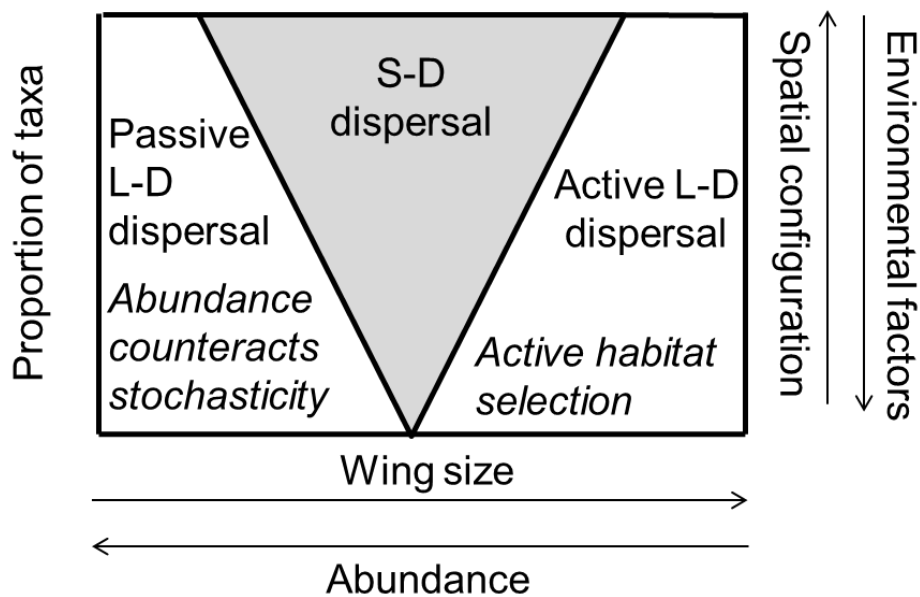


Figure 4.5. Conceptual framework of the relative importance of different dispersal modes in relation to the distribution of drainage ditch aquatic insects across environmental gradients and spatial scales. Environmental filtering applies in small winged highly abundant taxa, despite they rely on passive dispersal. Stochasticity associated with being dispersed by, for example, the wind is counteracted by the high number of dispersing individuals. Large winged taxa are able to actively choose sites with suited environmental conditions on a large spatial scale. Taxa with an intermediate wing size are not abundant enough for effective long distance passive dispersal and too small for effective long distance active dispersal. These taxa mainly disperse locally. As a consequence the distribution of these insects relates primarily to the spatial configuration of water bodies. L-D: long distance, S-D: short distance; direction of arrows indicates an increase in absolute value or in relative importance.

Based on this study it can be concluded that besides local environmental variables, also the spatial distribution of sampling sites across a region plays an important role in structuring local assemblages, resulting in taxa being absent at apparently suitable locations. With the increasing fragmentation of aquatic habitats due to anthropogenic activities, dispersal

ability becomes more and more important as a life history characteristic determining the composition of local species assemblages. Furthermore, it could have important consequences for the application of aquatic insects as indicators of impairment of aquatic ecosystems (Brown et al., 2011). Strong spatial effects on assemblage structure could have profound consequences for macroinvertebrate-based bioassessment, in which it is generally assumed that niche-based species sorting is the mechanism underlying assemblage composition. Therefore, further expanding the autoecological knowledge of aquatic insect species, with special emphasis on their dispersal ability, is crucial to identify the mechanisms behind diversity patterns observed in lentic ecosystems.

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**5 Development of a multimetric index based on
macroinvertebrates for drainage ditch networks in
agricultural areas**



Heterogenous vegetation in a drainage ditch near Tienhoven.

5 Development of a multimetric index based on macroinvertebrates for drainage ditch networks in agricultural areas

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Abstract

Drainage ditches are a prominent feature of many intensively managed agricultural areas. These small, shallow, line-shaped waterbodies could harbor a rich macroinvertebrate community, resembling that of natural small lentic ecosystems. Despite their high biodiversity potential, many ditch ecosystems are degraded due to nutrient enrichment, resulting in a shift from a mesotrophic system characterized by a diverse vegetation of emergent-, submerged-, and floating macrophytes to a hypertrophic state dominated by Lemnaceae or phytoplankton. Tools to assess the ecological quality of drainage ditches are currently lacking. Therefore, a multimetric index based on macroinvertebrates was developed to assess the ecological quality of drainage ditch systems in The Netherlands. Based on a large dataset from regional water district managers, who conduct routine sampling of macroinvertebrates in drainage ditches, a degradation gradient composed of 223 samples was derived, which represented the combined stressors eutrophication, organic pollution and salinity. We used a stepwise process to evaluate the discriminatory efficiency of a variety of diversity, abundance/composition, tolerance/sensitivity, and functional metrics for assessing ecological degradation in drainage ditches. After evaluating metric range, strength of correlation to the stressor gradient, degree of redundancy, and sample- and seasonal repeatability, five metrics were selected for the drainage ditch multimetric index: number of Trichoptera families, percentage of Gastropoda families, percentage of taxa preferring fresh water ($Cl^- < 300 \text{ mg.L}^{-1}$), Dutch Saprobic index, and the percentage of predator taxa. The relationship of these single metrics with the stressor gradient is discussed.

Keywords: index of biotic integrity, bioassessment, lentic ecosystems, agroecosystems, eutrophication, bioindicators

Introduction

Drainage ditches are small, stagnant, line-shaped water bodies, dug to improve rainwater run off and regulate the groundwater level of surrounding agricultural areas. They are a prominent feature in the landscape of the lowlands of northwestern Europe; in The Netherlands alone, total ditch length is approximately 300,000 km. To retain the drainage function of ditches, dredging and mowing of vegetation takes place regularly. Despite intensive maintenance by man, ditches can harbor a high species diversity, which closely resembles natural communities found in marshlands, oxbows, and the littoral zone of shallow lakes (Verdonschot & Higler, 1989; Verdonschot, 1992).

Recent studies point out the importance of drainage ditches as drivers of biodiversity in agricultural areas (Painter, 1999; Armitage et al., 2003; Herzon & Helenius, 2008). Drainage ditches have a high potential in terms of biodiversity, as described in historical records and which is still observed in some extensively managed areas (e.g. Higler & Verdonschot, 1989; Armitage et al., 2003). In the Netherlands most ditches do not reach this potential because they are severely degraded due to runoff of nutrients and organic matter from the neighboring, intensively managed meadows and croplands (Janse & van Puijenbroek, 1998). Apart from this, nutrient concentrations are further increased by the common practice of the inlet of river water during summer. This is done to retain a constant water level to make farming as efficient as possible. The inlet of river water also results in increased chloride concentrations (Higler, 1989). Overall, a considerable number of drainage ditches in the Netherlands has reached a hypertrophic and polysaprobic state, sustaining a system dominated by Lemnaceae or bluegreen algae.

Ecological consequences of an increase in nutrient concentrations are profound. The vegetation of mesotrophic drainage ditches is characterized by a species-rich mosaic of submerged, emergent and floating plant species. A slight increase in nutrient load induces the dominance of 'weedy' submerged plant species, such as *Elodea nuttallii* (Portielje & Roijackers, 1995). Ongoing enrichment eventually leads to frequent filamentous and epiphytic algal blooms and dominance of Lemnaceae or *Azolla filiculoides*, resulting in decreased light penetration, hindering the development of submerged vegetation (Janse & van Puijenbroek, 1998). Furthermore, it results in the impoverishment of the macroinvertebrate fauna (Clare & Edwards, 1983).

In The Netherlands, regional water district managers conduct routine surveys of the flora and fauna inhabiting drainage ditch networks. Assessment of the ecological quality of these sampling locations is mainly based on national assessment and Water Framework Directive criteria. We refer to good ecological quality as a state of ecological integrity, in which all appropriate (a)biotic elements are present in the ecosystem and processes occur at appropriate rates (Angermeier & Karr, 1994), reflecting the conditions under which human influence is limited to periodic ditch cleaning. Although sites with a good ecological quality as well as heavily degraded systems are easily discerned, both in terms of vegetation and macroinvertebrate assemblage composition, recognition of the patterns of loss of ecological integrity proved to be difficult. One of the reasons why detecting ecological degradation of drainage ditch ecosystems is problematic results from an only basic understanding of the relationships between the structure and functioning of ditch ecosystems and the impact of anthropogenic activities. This lack of knowledge of ditch ecology is not restricted to The Netherlands alone, but appeared to apply across Europe and North America (Herzon & Helenius, 2008).

To assess the ecological quality of a water body, a combination of components reflecting the structure and functioning of the ecosystem should be used (Karr & Chu, 1999; Barbour et al., 1999). By combining parameters providing information on different ecosystem features into a multimetric index, the ecological quality of a water body can be derived. In case of drainage ditches, both macroinvertebrates and macrophytes can potentially be used to develop such an index. Nevertheless, most ditches in agricultural areas are poor in macrophyte species, whilst harboring a diverse macroinvertebrate assemblage. Therefore, in this study we chose to focus on macroinvertebrates. Assessment of ecological quality based on macroinvertebrates has a long history, mainly in streams, rivers and lakes. Only recently, several indices for small lentic ecosystems have been developed (e.g. Burton et al., 1999; Solimini et al., 2008; Trigal et al., 2009).

In this study, we investigated if it was possible to assess the ecological quality of drainage ditches, analogous to the multimetric indices developed for other aquatic systems. Aim of this study was to 1.) select macroinvertebrate-based ecological indicators suited to confirm the best available status and to detect degradation in drainage ditches, and 2.) combine these indicators into a multi-metric index to assess the ecological quality of drainage ditch systems. A large dataset collected by regional water district managers was used to evaluate a wide variety of taxonomic, compositional, tolerance, and functional characteristics of the

macroinvertebrate assemblages. Based on their discriminatory efficiency with increasing degradation and their repeatability across samples and seasons, best performing metrics were combined into a drainage ditch multimetric index.

Methods

Data collection

In the Netherlands, drainage ditches are included in the surface water monitoring network of water district managers, and are sampled following a standardized sampling procedure: a stretch representative of the whole ditch (approximately 50 m) is chosen, of which the distribution of habitat types (e.g. bottom substrate type, emergent and submerged vegetation) is estimated. Subsequently, 10 ditch sections of 0.5 m in length are selected in proportion to the surface area covered by each of the major habitat types and sampled using a pond net (mesh-size 500 μm , width 30 cm), up to a total length of 4 m of vegetational habitats and 1 m bottom substrate habitats. Samples are transported to the laboratory, where they are sieved through 1.0 mm and 500 μm sieves. Macroinvertebrates are sorted alive and identified to the lowest taxonomical level practical.

Data used were collected in 1980-2008, and included a wide variety of locations. Sampling sites ranged from ditches in nature conservation areas, considered as minimally impacted and of good ecological quality, to ditches located in intensively used agricultural areas. In total, the dataset contained 290 sites, sampled in spring, summer or autumn. Furthermore, 2 datasets collected as part of other studies, but according to the same sampling protocol, were used to test metrics for variability regarding repeated sampling of the same location (8 minimally impacted sites within one drainage ditch network) and seasonality (18 sites sampled in both spring and autumn within the same year). Only sites where environmental variables were recorded during macroinvertebrate sampling were selected. Land use adjacent to the 50 m ditch stretches was recorded, as well as the soil type. Bank slope was estimated visually for both banks using three classes: level ($<30^\circ$), intermediate ($30\text{--}60^\circ$) or steep ($>60^\circ$). Channel width and maximum water depth were measured at 5 randomly selected points along the ditch stretch. Data on ditch hydrology, in terms of influence of groundwater seepage and the inlet of river water during dry periods was derived directly from the water managers. Percentage cover of floating, submerged and emergent vegetation and floating algal mats was estimated visually for the

ditch stretch. Measurements of pH, conductivity and dissolved oxygen were carried out in the field directly, whilst water samples were taken and analyzed in the laboratory for ammonium, nitrate, total nitrogen, total phosphate and chloride concentrations.

Table 5.1: Physical-chemical parameters and site characteristics based on land use, hydromorphology, water chemistry and vegetation, used to derive environmental gradients in drainage ditches ($n = 223$). For land use and hydromorphology data multiple categories of one parameter could be present at a site, resulting in total proportions exceeding 100%.

Parameter	Median value	10%-90% percentiles	Proportion of sites (%)
<i>Land use</i>			
Nature reserve (0/1)			25
Extensive grassland/marshland (0/1)			25
Cropland (0/1)			22
Urban area (0/1)			9
Horticulture (0/1)			12
Pasture (0/1)			63
<i>Hydromorphology</i>			
Bottom substrate peat (0/1)			30
Bottom substrate sand (0/1)			35
Bottom substrate clay (0/1)			38
Channel width (m)	3.5	1.0-8.9	
Channel depth (m)	0.5	0.2-1.0	
Bank slope <30° (0/1)			25
Bank slope 30-60° (0/1)			50
Bank slope >60° (0/1)			30
Groundwater seepage (0/1)			33
Inlet of river water in dry periods (0/1)			48
<i>Water chemistry</i>			
pH	7.6	6.8-8.4	
Conductivity (mS m ⁻¹)	44	18-122	
Oxygen (mg L ⁻¹)	6.2	2.3-9.6	
Ammonium (mg N L ⁻¹)	0.4	0.07-1.6	
Nitrate (mg N L ⁻¹)	0.4	0.03-3.7	
Total nitrogen (mg N L ⁻¹)	4.0	1.7-7.5	
Total phosphate (mg P L ⁻¹)	0.3	0.09-1.7	
Chloride (mg L ⁻¹)	101	29-382	
<i>Vegetation</i>			
Floating vegetation cover (%)	5	0-75	
Emergent vegetation cover (%)	5	1-60	
Submersed vegetation cover (%)	10	0-74	
Floating algal mat cover (%)	0	0-25	

Data preparation

The macroinvertebrate datasets of different water district managers were combined into a single database. Inconsistencies in data formats and scientific nomenclature were resolved. The resulting taxon list showed considerable taxonomic overlap, mainly as a result of difficulties identifying early instar specimens. Since it was unknown if a specimen identified to, for example, genus level in one sample was actually an early instar of a species recorded in another sample a taxonomic adjustment procedure was necessary to avoid multiplication of the same information during analysis (Nijboer & Verdonschot, 2000; Schmidt-Kloiber & Nijboer, 2004; Vlek et al., 2004). When specimens were identified to species (lowest taxonomic level), apart from a few exceptions, which were only identified to genus or family (higher taxonomic levels), the higher taxonomic levels were omitted and the lowest taxonomic level was kept. When specimens identified to genus or family level were abundant compared to the specimens identified to species level (frequency of occurrence >20% of all the species belonging to this genus or family), the lower taxonomic level(s) were aggregated to the higher taxonomic level.

Definition of stressor gradient

Since drainage ditches are artificial water bodies, located in agricultural areas and maintained by dredging and mowing of the vegetation, 'natural' or reference sites do not exist. Therefore, we could not evaluate the discriminatory ability of the metrics by comparing the distribution of each metric to a set of pre-classified reference sites (e.g. Barbour et al., 1999), but included a gradient of sites covering the whole range of degradation (Hering et al., 2006a). Since the macroinvertebrate assemblage composition of sites varies with natural gradients, we first assured that no natural gradients were included in the degradation gradient, to prevent selecting metrics that appear to respond to the degradation gradient but are in fact correlated with the natural gradient (Stoddard et al., 2008). Earlier clustering and ordination-based analyses of the macroinvertebrates of drainage ditches indicated that besides anthropogenic factors such as eutrophication and organic pollution the occurrence of characteristic macroinvertebrate assemblages was related to acidity, drought, and shading (Verdonschot & Higler, 1989; Verdonschot, 1992; Verdonschot & Nijboer, 2000). To diminish the influence of these natural factors, intermittent, shaded (>50% of at least one bank), and acid (pH <6) sites were excluded from the

analysis. This resulted in a dataset of 223 sites (Fig. 5.1, Table 5.1). It should be noted that eutrophication and organic pollution can be natural factors in small lentic ecosystems during the process of terrestrialization. Nonetheless, since drainage ditches are cleaned at least yearly, an increase of nutrient richness or organic load can be regarded to have an anthropogenic basis. The same holds for the chloride concentration: naturally brackish waters are not included in the dataset, high chloride concentrations result from the inlet of river water during dry periods or groundwater seepage with a high salinity.

To describe the major patterns in environmental conditions across the ditches and to determine the position of samples along the main stressor gradients, environmental data was analyzed using Principal Components Analysis (PCA), after centering and standardization of the variables (Hering et al., 2006a,b). PCA reduces the large number of variables to fewer uncorrelated axes of environmental variation, which represent the main environmental gradients. Ditch dimensions, physicochemical and vegetation parameters were $\log_{10}(x+1)$ transformed before analysis. PCA was conducted in CANOCO for Windows 4.5 (ter Braak & Šmilauer, 2002).



Figure 5.1: Map of The Netherlands showing drainage ditch sampling locations used for MMI development ($n = 223$, black dots), seasonal repeatability test ($n = 18$, open square), and sample repeatability test ($n = 8$, open circle).

Metrics

In total, 244 metrics were calculated from the macroinvertebrate data, representing 4 categories (Hering et al., 2006a): diversity/richness metrics, composition/abundance metrics, functional and habitat preference metrics, and tolerance/sensitivity metrics (Appendix 5.1). Metrics were derived from the autoecological information collected for the AQEM assessment program (Hering et al., 2004), and environment and habitat preferences of Dutch macroinvertebrates (salinity preference and Dutch Saprobic index; Verberk et al., *in press*). A database of functional and life history characteristics of drainage ditch macroinvertebrates was compiled of autoecological information collected from a variety of data and literature sources (list available upon request).

Diversity/richness metrics ($n = 74$) consisted of the number of species/genera/families of various taxonomic groups, total number of species/genera/families, total number of individuals ($\ln(x)$ -transformed), number of EPT taxa/genera/families, Shannon diversity Index, Simpson diversity Index, Simpsons' evenness, Margalef index, and the number of non-indigenous species. Composition/abundance metrics ($n = 94$) consisted of the percentage of 1, 2 and 5 most dominant taxa, non-insects, non-indigenous taxa, EPT, and the various taxonomic groups at different taxonomic levels. Functional characteristics and habitat preference metrics ($n = 62$) comprised functional feeding group, habit trait group, trophic level, mode of respiration, life span, development time, number of generations per year, and microhabitat preference. Finally, tolerance/sensitivity metrics ($n = 14$) consisted of indices based on taxa and individuals indicating the tolerance for saprobity and the percentage taxa/individuals preferring fresh water (salinity). Tolerance for salinity was based on individual classes as well as the different classes summarized in an index, because the response to salinity displayed a clear threshold between freshwater taxa and the other classes. All metrics within the functional and habitat preference category and tolerance/sensitivity category were based on fuzzy-coded data (10 points distributed per taxon over the relevant classes).

Metric selection

Four criteria were used to test each metric (Fig. 5.2). Firstly, the range of each metric was examined, to ensure that it was able to discern between different system states (Stoddard et al., 2008; Purcell et al., 2009). To be included, the range of metrics must be >5 in case of counts or $>10\%$ in

case of relative proportions, and the number of samples with value 0 should not exceed 33.33%. Secondly, metrics should be significantly ($p < 0.01$) correlated with the environmental gradient derived from the PCA, using the Spearman rank correlation test (Hering et al., 2006a); these metrics are hereafter called candidate metrics. By using rank correlation analyses, we specifically targeted metrics responding in a linear way to stressors. There are also metrics displaying a non-linear response (e.g. unimodal, threshold; Vlek et al., 2004), but to improve applicability, we focused on metrics responding linearly to disturbance (Bonada et al., 2006). Thirdly, metrics that showed strong inter-correlations (Spearman's $\rho \geq 0.7$) were defined as redundant (Hering et al., 2006a). Metrics were evaluated for redundancy among and between categories. Within each group of redundant metrics, the metric that showed the strongest correlation to the stressor gradient was kept. Spearman rank correlation tests were conducted in SPSS for Windows 15.0 (SPSS Inc., 2006). Fourthly, the remaining metrics were tested for repeatability (Klemm et al., 2002). Metric scores should remain similar when sampling is repeated at the same location across seasons within a year. Metrics were calculated for samples taken in spring (April-June) and autumn (October-November) at the same site ($n = 18$ sites) to determine this within-year variability. For each metric, the average coefficient of variation (CV) among sites was calculated. Metrics were regarded stable across seasons when the average deviation was $< 20\%$. Furthermore, metric scores should remain stable when a series of samples is taken at the same location. This between-sample variability was determined based on a series of 8 samples collected in the same drainage ditch network within a period of two weeks. Metrics were calculated for each sample, and the CV was determined. A deviation of $< 5\%$ across samples was regarded acceptable. Only metrics with both an acceptable within-year variability as well as a between-sample variability were kept. These metrics are called hereafter core metrics.

Multimetric index development and calculation

We iteratively tested combinations of core metrics to develop the final multimetric index (MMI). For each combination, the index was calculated as the mean of all metrics included. To calculate the final MMI, metrics were standardized to a score ranging from 0 (worst quality) to 1 (best quality). For each metric, the minimum and maximum scores of 0 and 1 were set as the 2.5% and 97.5% percentiles of all individual metric values, to minimize the effect of potential outliers in the dataset (Blocksom et al. 2002). Scores outside the range were rounded to 0 or 1. Combinations of metrics were

selected in a stepwise fashion, starting with the best performing metric from each category, e.g. the metric showing the strongest correlation with the stressor gradient, to ensure that the MMI reflected different - non-redundant - ecological characteristics of the ecosystem (Karr & Chu, 1999; Hering et al., 2006a). Additional metrics were added as long as they increased the coefficient of determination of the index, e.g. its overall efficiency.

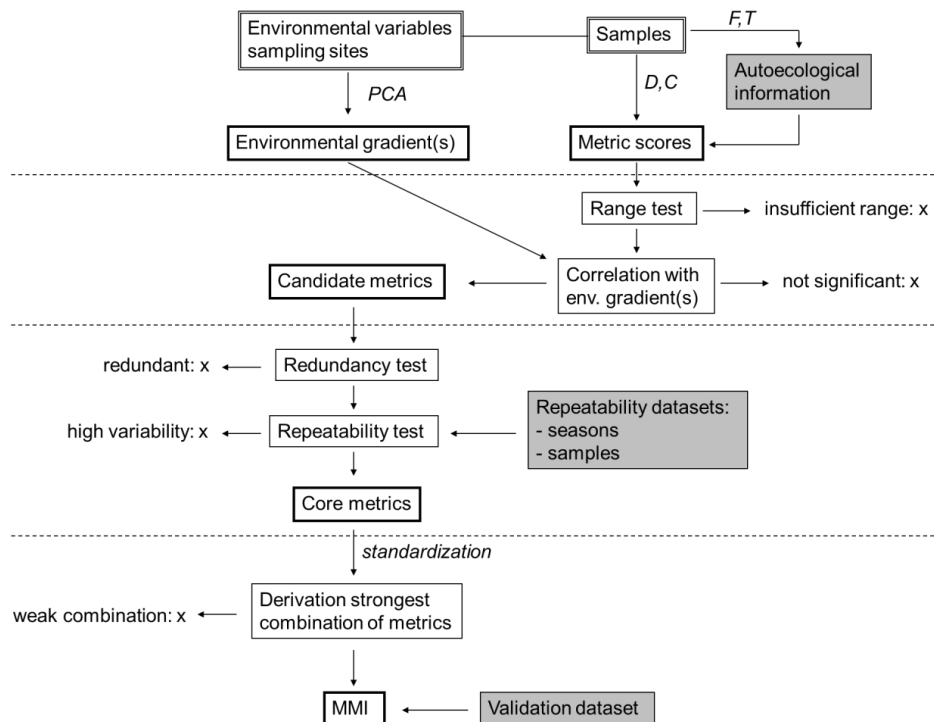


Figure 5.2: Flowchart describing the steps used to evaluate metrics and integrate metrics into a MMI. Abbreviations of metric categories: R, diversity/richness; C, composition/abundance; F, functional and habitat preference; T, tolerance/sensitivity; x, excluded.

Validation of MMI

No new data for the validation of the MMI was available. Therefore, an existing dataset was used, consisting of 53 sites belonging to a variety of drainage ditch types. Intentionally, this dataset was used for clustering and ordination-based analyses of the macroinvertebrates of drainage ditches, and forms the basis of the Dutch cenotypology (Verdonschot & Nijboer,

2000). A cenotypology describes different water types and their stages of degradation. A group of samples with a similar macroinvertebrate assemblage composition and environmental conditions is defined as a cenotype. Environmental variables characterizing a cenotype can refer to a reference situation (in this case best available condition) or a certain stage of degradation. All cenotypes are mutually related in terms of key (a)biotic factors, which represent the major ecological processes. Changes in these factors (anthropogenic or natural) could lead to a transition from one cenotype to another. To determine the degradation stage of each cenotype, the macroinvertebrate community composition in combination with the values for environmental variables along key environmental gradients were used for interpretation with expert-judgement (Verdonschot, 1992; Vlek et al., 2004). For all 53 samples, the assigned quality class based on the cenotypology was compared to the score derived from the MMI, to investigate if the ecological quality of the sampling sites was assessed equally by both approaches.

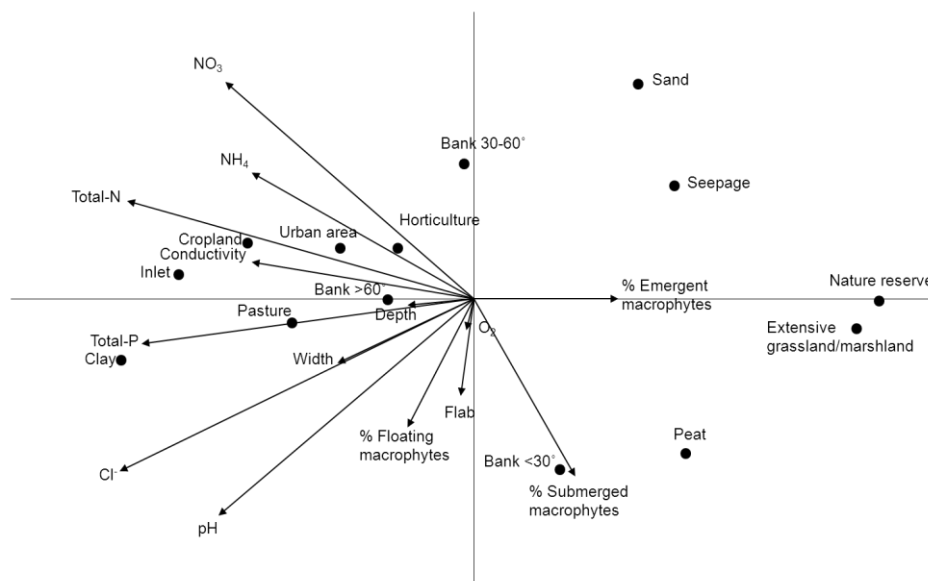


Figure 5.3: Biplot of the first two axes of the PCA of environmental variables, representing the associations between the environmental variables on the sampling locations. Arrows represent continuous variables and point in the expected direction of the steepest increase in value. Its relative length compared to other arrows is an indication of the correlation strength of the variable. Angle between two arrows indicate its correlation. Black dots represent the centroids of nominal variables.

Results

Stressor gradient

The first PCA-axis explained 15% (eigenvalue 0.15) of the variation in the environmental data, and represented a combined gradient of nutrient enrichment and increased salinity (Fig. 5.3). Amongst others, it showed an increase in total P and total N, chloride and conductivity, with on the right side in the diagram relatively nutrient poor ditches influenced by groundwater seepage, located in nature reserves and rich in emergent vegetation, and on the left side hypertrophic ditches in areas with intensive agriculture. The second PCA-axis (eigenvalue: 0.10) explained another 10% of the variation. It mainly described differences in bank slope, bottom sediment and vegetation cover between ditches on sandy soils and ditches on peat soils, and can be regarded as a descriptor of habitat structure instead of indicating a stressor gradient. The amount of variation explained decreased with each subsequent axis: eigenvalue axis 3: 0.07, and eigenvalue axis 4: 0.06. PCA-axis 1 was used as the stressor gradient for multimetric index development.

Metric selection

Variation in metric values across samples was too small in 98 metrics, which were omitted. This first step in metric selection mainly affected the diversity/richness (53% of all metrics within this category omitted), composition/abundance (46%), and tolerance/sensitivity (50%; brackish and saline classes of the salinity metric) categories, and to a much lesser extent the functional/habitat preference category (15%).

The remaining metrics were correlated with the eutrophication gradient, which resulted in 65 candidate metrics showing a positive or negative significant correlation ($p < 0.01$). Many non-significant metrics were found in the functional/habitat preference category (63%), whilst the proportion of significantly correlating metrics was much larger in the diversity/richness (27%), composition/abundance (24%), and tolerance/sensitivity (43%) categories.

The redundancy test eliminated another 40 metrics, which comprised between 10-21 % of the metrics within the categories. Functional/habitat preference metrics displayed some redundancy across categories; metrics comprising percentage Gastropoda abundance, genera, and taxa were correlated to percentage clinger individuals, as well as with

scaper taxa and individuals. Percentage Isopoda and Crustacea abundance was correlated to percentage shedder individuals. Cross-category redundancy was common between the diversity and composition/abundance category, especially in Trichoptera, EPT, Hydracarina and Chironomidae related metrics. Within the tolerance/sensitivity category, redundancy was observed within the category only.

The remaining 23 candidate metrics were screened for repeatability (Table 5.2). Large variation between spring and autumn samples was recorded in 12 metrics, and sample repeatability was regarded too small in 13 metrics. Metrics which were considered to show much seasonal variation, also displayed too much variation between samples taken at the same location. The only exception was the number of Heteroptera genera, which only displayed too much between-sample variation. Repeatability test eliminated almost all metrics based on percentage individuals in the assemblages.

MMI development

In total, 10 core metrics were potentially suited for inclusion in the MMI. The number of metrics per category was variable, as well as the strength of the relationship between the stressor gradient and each single metric (Table 5.2). Diversity/richness metrics and composition/abundance metrics showed the poorest performance, only two diversity/richness and two composition/abundance metrics passed the screening procedure (3% and 2% of all metrics considered in these categories). The other two categories were better represented; 6% of the functional/habitat preference category metrics and 14% of the tolerance/sensitivity metrics.

Iteratively testing combinations of standardized metrics resulted in an optimal MMI consisting of 5 core metrics (Table 5.3). Integration of these metrics into an index resulted in a fit of 37% with the eutrophication gradient ($R^2 = 0.366$; Fig. 5.4). Diversity category was represented by the number of Trichoptera families. Percentage of the total assemblage comprised of Gastropoda families represented the abundance/composition category. Functional feeding group percentage predator taxa was selected from the functional/habitat preference metrics. Both tolerance/sensitivity metrics were included in the final index, which was not surprising, since the strength of the association of individual metrics with the stressor gradient was relatively high in the sensitivity/tolerance metrics compared to the

other categories. Salinity tolerance was included as the percentage of the assemblage comprised of freshwater taxa, and the influence of saprobity was included in the form of an taxon-based index.

Table 5.2: Metrics from 4 categories (D, diversity/richness; C, composition/abundance; F, functional/habitat preferences; T, tolerance/sensitivity) showing a significant correlation with the eutrophication gradient (PCA 1) and their response to increased nutrient loading: <, decrease; >, increase. Results from the seasonal and sample repeatability tests are shown, with a mean coefficient of variation of <20% for seasonal repeatability and <5% for sample repeatability as threshold values (metrics showing acceptable variation in bold).

Metric	Metric category	Spearman's ρ correlation	Observed response	Seasonal repeatability mean CV (%)	Sample repeatability CV (%)
# Trichoptera families	D	0.31	<	16	4.2
# Hydracarina genera	D	0.26	<	33	7.7
# Heteroptera genera	D	0.23	<	17	10
# Oligochaeta genera	D	0.22	<	38	11
# Chironomidae genera	D	0.17	<	16	2.9
% Non-insect ind.	C	0.24	>	17	3.1
% Gastropoda ind.	C	0.27	>	37	21
% Isopoda ind.	C	0.28	<	39	17
% Diptera (excluding Chironomidae) ind.	C	0.19	<	40	23
% Ephemeroptera + Plecoptera + Trichoptera ind.	C	0.26	<	43	5.6
% Gastropoda families	C	0.39	>	11	3.7
% Hirudinea genera	C	0.29	>	39	15
Salinity tolerance: % taxa preferring fresh water	T	0.61	<	0.38	0.13
Salinity tolerance: % ind. preferring oligohaline conditions	T	0.48	>	25	16
Saprobic index (taxon-based)	T	0.42	>	0.94	0.53
Habit trait group: % ind. habit burrower	F	0.22	<	35	21
Habit trait group: % ind. habit sprawler	F	0.18	<	21	6.8
Functional feeding group: % taxa predator	F	0.22	<	6.0	3.6
Respiration type: % taxa air breather	F	0.18	>	8.9	4.4
Microhabitat preference: % taxa preferring silt	F	0.21	>	6.6	2.2
Microhabitat preference: % ind. preferring CPOM	F	0.20	>	25	11
Microhabitat preference: % ind. preferring mineral substrate	F	0.23	<	22	7.6
Microhabitat preference: % ind. preferring silt	F	0.36	>	19	3.0

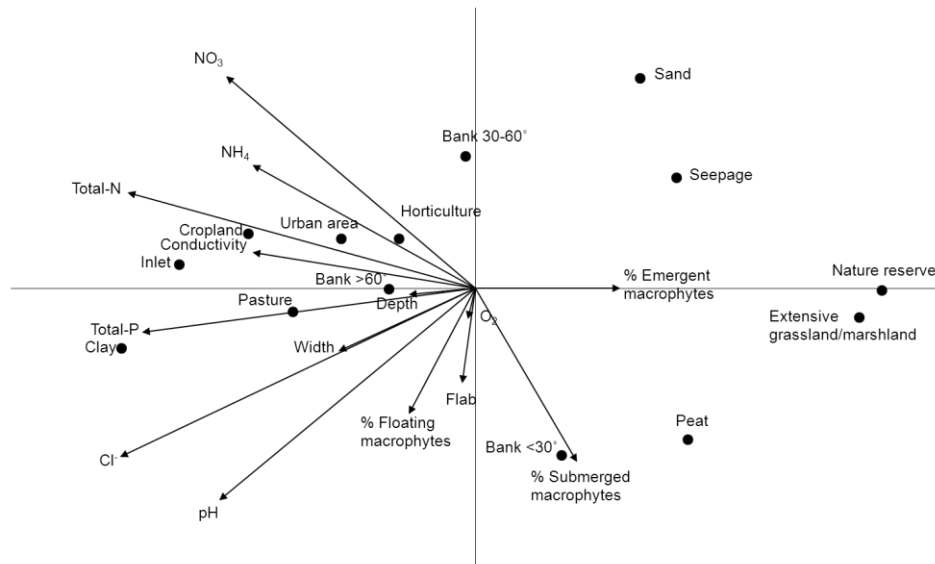


Figure 5.3: Biplot of the first two axes of the PCA of environmental variables, representing the associations between the environmental variables on the sampling locations. Arrows represent continuous variables and point in the expected direction of the steepest increase in value. Its relative length compared to other arrows is an indication of the correlation strength of the variable. Angle between two arrows indicate its correlation. Black dots represent the centroids of nominal variables.

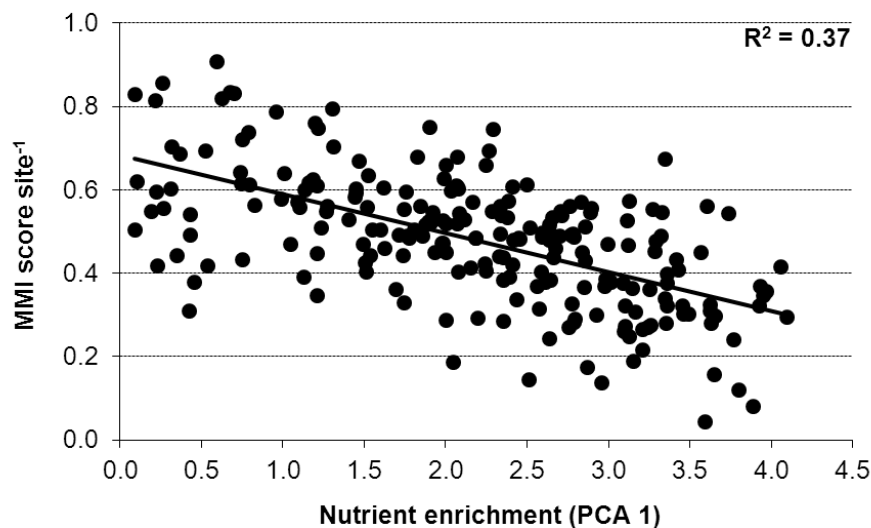


Figure 5.4: Relationship between the MMI score per sampling site (0: worst ecological condition; 1: best condition) and an increase in nutrient enrichment, expressed as the sample scores derived from PCA-axis 1.

Table 5.3: Candidate metrics per category, with their lower- and upper anchors used to standardize the metrics to a scale ranging from 0 to 1. Their response to increased nutrient loading is given: <, decrease; >, increase. Candidate metrics indicated with an asterisk were integrated into the final MMI.

Candidate metric	Response	Lower anchor (2.5% percentile)	Upper anchor (97.5% percentile)
<i>Diversity/ richness</i>			
# Trichoptera families*	<	0.0	5.0
# Chironomidae genera	<	1.0	17
<i>Abundance/ composition</i>			
% Non-insect individuals	>	29	93
% Gastropoda families*	>	6.1	33
<i>Tolerance/ sensitivity</i>			
% Freshwater taxa*	<	91	97
Saprobic index (taxon-based)*	>	2.0	2.4
<i>Functional/ habitat preferences</i>			
% Predator taxa*	<	18	41
% Air breathers	>	13	56
% Taxa preferring silt	>	20	41
% Individuals preferring silt	>	12	59

Index validation

Comparison of the MMI scores with the ecological quality classes derived from the cenotypology of Verdonschot and Nijboer (2000) showed a gradual transition in MMI scores mirroring the cenotypology quality classes (Table 5.4). This indicated that the variation in the scores of the newly developed MMI was generally congruent with the ecological quality classes of the cenotypology.

Table 5.4: Comparison of the MMI scores (0: worst ecological condition; 1: best condition; divided into classes of 0.1) with the ecological quality classes (bad-good) derived from the cenotypology of Verdonschot and Nijboer (2000) for the validation dataset ($n = 53$). Number of samples is given per combination of quality class and MMI score.

Cenotype quality class	Multimetric index score class									
	0.0- 0.1	0.1- 0.2	0.2- 0.3	0.3- 0.4	0.4- 0.5	0.5- 0.6	0.6- 0.7	0.7- 0.8	0.8- 0.9	0.9- 1.0
Bad			1							
Poor				2	2					
Moderate				2	6	16	15			
Good						1	5	2	1	

Discussion

The cascade of deleterious effects resulting from eutrophication in drainage ditches should – at least in theory - be readily detectable in the composition of macroinvertebrate assemblages, given the shifts in physicochemical variables and vegetation structure observed with ongoing eutrophication (Portielje & Roijackers, 1995; Janse & van Puijenbroek, 1998). During the process of metric selection it became clear that this was not always the case. Diversity/richness and composition/abundance metrics often did not encompass a large enough range across all available data, taxa showed rather erratic patterns of occurrence, and metrics based on taxon abundance often showed large between-sample and seasonal variation.

There are several factors which could explain these patterns. First of all, despite a high total macroinvertebrate species richness recorded in drainage ditches (Higler & Verdonshot, 1989; Verdonshot, 1992; Armitage et al., 2003), the distribution of species and individuals is often patchy, both within- and between ditches. This could be the result of variation in microhabitat characteristics, resource availability, biotic interactions, and stochastic events (de Meester et al., 2005; Scheffer et al., 2006). The relationship between environmental variables and macroinvertebrate taxon composition is not always strong, especially because eutrophication has many indirect effects on the fauna. Furthermore, the dataset is comprised of macroinvertebrate samples collected over decades by many workers at a wide variety of locations. Therefore, it is inevitable that - despite a standardized sampling protocol – a certain degree of sampling variability due to inter-operator pond netting differences and sorting of collected material is introduced. Vice versa, the construction of a degradation gradient by using PCA also introduces variation, since it results in a gradient of a combination of environmental variables. Not every taxon responds to the same environmental variables, and especially not always in a linear way (Vlek et al., 2004).

Despite these problems, the strength of the multimetric approach was that via the metric selection procedure, the influence of these sources of variation was minimized as much as possible. Still, the resulting fit of the final MMI with the degradation gradient of 37% indicated that considerable variation remained. Since drainage ditches are artificial water bodies, calibration against a near natural reference state is not possible, which makes it difficult to assess the strength of the MMI. Nonetheless, the percentage fit with the degradation gradient found in this study is comparable to the response of individual macroinvertebrate metrics to a

PCA-gradient composed of increased nutrient loading and agricultural land use in lowland streams, which R^2 was on average 0.26 ($n = 10$, 0.09-0.37) (Johnson et al., 2006). Furthermore, the similarity between the MMI scores and the independent ecological quality classification of the external ditch dataset indicated that the combination of metrics used in the MMI, which represent different components of the macroinvertebrate assemblage, mirrored the overall change in macroinvertebrate assemblage composition observed along the degradation gradient as derived from the ditch cenotypology.

Only one metric from the diversity/richness category and one from the composition/abundance category was included in the final MMI; the number of Trichoptera families and the proportion of Gastropoda families within the assemblage. Trichoptera are commonly used as water quality indicators, often incorporated in the sum of Ephemeroptera, Plecoptera, and Trichoptera taxa (Wallace et al., 1996; Norris & Thoms, 1999). This EPT-index was less suitable for application in drainage ditches, since Plecoptera were very rare and Ephemeroptera were represented by a few abundant species, which are regarded relatively insensitive to eutrophication and organic pollution (Menetrey et al., 2008). An increase in Gastropoda densities and richness with increased nutrient loading is common in lentic systems and mainly results from an increase in food availability with eutrophication (Osenberg, 1989; Thomas & Daldorph, 1994; Costil & Clement, 1996).

Grouping macroinvertebrates based on their functional characteristics and habitat preferences, or tolerance/sensitivity to stressors should be less sensitive to the taxon variation often observed in diversity and composition metrics, because different taxa can display the same preference or response, or possess equal functional characteristics (Bady et al., 2005). Tolerance/sensitivity metrics can be seen as surrogates for different aspects of macroinvertebrate physiology, life history and behavior. Still, a relatively high number of tolerance metrics did not pass the range test, mainly because taxa indicative for some of the tolerance classes were lacking and many functional/habitat preference metrics did not correlate to the stressor gradient.

An important tolerance/sensitivity indicator of degradation in drainage ditch ecosystems was the increase in relative abundance of macroinvertebrates which are able to tolerate oligo- to mesohaline conditions. Although chloride was one of the main components of the stressor gradient derived from the PCA, high nutrient levels always coincided with relatively high chloride concentrations. Therefore, it is not

known if the pattern observed is solely the result of an increase in chloride concentration or of a combination of factors. Nonetheless, the chloride concentration alone could have a structuring effect on the macroinvertebrate assemblage composition of freshwater ecosystems (Muñoz & Prat, 1994; Williams et al., 1997; Triest et al., 2001; Piscart et al., 2005; Morgan II et al., 2007). Also, the taxon-based saprobic index contributed significantly to the drainage ditch MMI. Amongst others, increased organic load results in decreased oxygen availability, alters the suitability of the substrate and leads to changes in food availability (Wood & Armitage, 1997; Lake et al., 2000). Since organic loading affects macroinvertebrates in many ways, it is not surprising that a measure of saprobity is incorporated in the index, as it is in many assessment systems (e.g. Hering et al., 2004).

The functional characteristics and habitat preference category was represented by a negative response of the percentage predators in the assemblage. A similar decrease was observed by King and Richardson (2003), who recorded a reduction of the proportion of predators in wetland macroinvertebrate assemblages with an increase in total-phosphorous. Reduction of the proportion of predators in the assemblage could indicate two different pathways of degradation, which are not mutually exclusive. Firstly, it could reflect a reduced abundance and/or diversity in types of invertebrate prey (Royer et al., 2001). Secondly, it could be an indication of loss of habitat structure due to changes in ditch macrophyte composition (Jeffries, 1993; Taniguchi et al., 2003; Tolonen et al., 2003; Warfe & Barmuta, 2006). In the PCA, shifts in vegetation composition – and thus habitat structure – corresponding to stages of degradation were not clearly delineated, in contrast to the increase in nutrients. This is probably the result of the method used in regular monitoring programs; to note vegetation only as percentage cover of growth forms. No distinction was made between individual species, representing different levels of habitat complexity, resulting in a ditch dominated by one species of submerged vegetation being classified equally in comparison to a species rich submerged vegetation covering the same surface area.

Conclusions

The multimetric index developed in this study is the first attempt to assess the ecological quality of drainage ditches using macroinvertebrates, and is one of the few indices to date developed for small lentic ecosystems. It can be concluded that integrating different ecological components of

macroinvertebrate communities inhabiting drainage ditches into one index proved to be a fruitful approach for assessing the quality of this type of man-made aquatic ecosystems, in which no clear natural- or reference states can be distinguished and degradation is caused by a cascade of indirect effects resulting from nutrient enrichment due to agricultural activities. Furthermore, single metrics point out some of the direct effects of eutrophication in drainage ditches, such as changes in resource availability and loss of vegetation structure, thereby envisaging the components of the drainage ditch ecosystem responsible for the high biodiversity observed in relatively undisturbed drainage ditch systems.

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Appendix 5.1: Metrics used in the study.

Metric	Classes	Defined for:
<i>Functional category</i>		
Functional feeding groups	shredder scraper/grazer collector/gatherer filterer herbivore piercer predator piercer/shredder/engulfer parasite	% taxa/ind.
Habit trait groups	swimmer/diver skater burrower/interstitial miner sprawler climber clinger temporary attached to substrate permanently attached to substrate attached to host	% taxa/ind.
Trophic level	Detritivore Herbivore Carnivore Parasite	% taxa/ind.
Source of oxygen	water air	% taxa/ind.
Life span	1. <0.6 year 2. 0.6-1 year 3. >1 year	index taxa/ind.
Voltinism	1. semivoltine 2. univoltine 3. bivoltine 4. multivoltine	index taxa/ind.
Development time	1. <0.6 year 2. 0.6-1 year 3. >1 year	index taxa/ind.
Microhabitat preference	Mineral sediment (clay-sand-fine gravel) Coarse gravel, stones Organic sediment (mud-silt) Coarse particulate organic matter Wood Macrophytes	% taxa/ind.

Metric (continued)	Classes	Defined for
<i>Tolerance category</i>		
Salinity	1. <300 mg Cl.L ⁻¹ 2. 300-1000 mg Cl.L ⁻¹ 3. 1000-3000 mg Cl.L ⁻¹ 4. 3-10 g Cl.L ⁻¹ 5. >10 g Cl.L ⁻¹	% taxa/ind./index
Saprobity	1. oligosaprobic (<0.1 mg NH ₄ .L ⁻¹ / >8 mg O ₂ .L ⁻¹ / <1 mg BOD.L ⁻¹) 2. beta-mesosaprobic (0.1-0.5 mg NH ₄ .L ⁻¹ / 6-8 mg O ₂ .L ⁻¹ / 1-5 mg BOD.L ⁻¹) 3. alfa-mesosaprobic (0.5-4.0 mg NH ₄ .L ⁻¹ / 2-6 mg O ₂ .L ⁻¹ / 5-13 mg BOD.L ⁻¹) 4. polysaprobic (>4.0 mg NH ₄ .L ⁻¹ / <2 mg O ₂ .L ⁻¹ / >13 mg BOD.L ⁻¹)	index taxa/ind.
<i>Diversity category</i>		
Total assemblage	Total richness Total abundance (ln x)	# taxa/gen./fam. # ind.
Single taxonomic groups	Hydracarina Mysida Amphipoda Isopoda Aranea Bivalvia Chironomidae Coleoptera Diptera (excluding Chironomidae) Ephemeroptera Gastropoda Heteroptera Hirudinea Lepidoptera Megaloptera Odonata Oligochaeta Plecoptera Trichoptera Tricladia Crustacea EPT non-indigenous	# taxa/gen./fam.

Development of a drainage ditch multimetric index

Metric (continued)	Classes	Defined for
Diversity indices	Shannon's diversity Simpson's diversity Simpson's evenness Margalef's index	index
<i>Composition category</i>		
Dominance	dominant 2 most dominant 5 most dominant	% taxa
Single taxonomic groups	Hydracarina Mysida Amphipoda Isopoda Aranea Bivalvia Chironomidae Coleoptera Diptera (excluding Chironomidae) Ephemeroptera Gastropoda Heteroptera Hirudinea Lepidoptera Megaloptera Odonata Oligochaeta Plecoptera Trichoptera Tricladia Crustacea EPT non-indigenous non-insect	% ind./taxa/gen./fam.

6 Optimizing the use of activity traps for aquatic biodiversity studies



Activity trap catch.

6 Optimizing the use of activity traps for aquatic biodiversity studies

R.C.M. Verdonshot

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Abstract

I investigated the effectiveness of activity traps for macroinvertebrate monitoring in shallow, heavily vegetated drainage ditches and explored 2 ways to optimize the use of activity traps for monitoring purposes. I tested the effects of trapping duration (48, 96, and 168 h) and use of attractants (bait and preconditioned leaves). The number of taxa and individuals captured increased with trapping duration. Based on the taxon accumulation curves, deployment times of 48 h and 96 h were equally efficient in capturing new taxa, but a trapping duration of 168 h was much more efficient and resulted in a larger number of taxa collected with every new sample added. Of the attractants offered in the traps, only bait caused differences in the macroinvertebrate assemblage recorded. After 48 h, more predators were captured in traps with bait than in control traps and traps with preconditioned leaves. This effect disappeared with longer trapping duration. Because of their relatively low labor requirements and high level of standardization, activity traps appear to be a valuable tool in lentic biodiversity surveys, especially when deployed for a longer period than has usually been reported. The use of bait is advisable only if capture of specific taxa is required and not for standard monitoring purposes.

Keywords: sampling method, monitoring, passive sampling, macroinvertebrates, activity-density, mobility, attractants, drainage ditches.

Introduction

In small lentic ecosystems like ponds and ditches standardized monitoring of macroinvertebrates is hindered by the development of dense stands of emergent and submerged vegetation during the growing season. Pond netting, the sampling technique most commonly applied in the bioassessment of shallow lentic water bodies (e.g. method EN 27828; BSI, 1994), cannot be

considered quantitative when submerged structures obstruct sweeps, which decreases the speed of sweeps, increased the chance of macroinvertebrate escape, and enhances interoperator sampling differences (Furse et al., 1981; O'Connor et al., 2004). Variability in the quantity of submerged material (with their associated macroinvertebrates) collected by uprooting and breaking plant parts during the sweeps also influences the number of organisms captured. Thus, comparing abundances of individual species between samples can be problematic.

Box samplers can be used to obtain a standardized quantitative estimation of biodiversity and to overcome the problems associated with pond netting (Gates et al., 1987; Higler & Verdonschot, 1989; O'Connor et al., 2004). However, sample processing is time consuming and costly because large amounts of material are collected, and many samples are needed to compensate for the patchy distribution of taxa and aggregations of individuals (Downing, 1984). This drawback makes box sampling less useful for large-scale application because bioassessment methods are expected to yield a large amount of information about the community in a cost-effective way (Karr & Chu, 1999).

An alternative is to sample lentic macroinvertebrate assemblages with a combination of complementary techniques, a strategy that is advised in many studies in which sampling devices were compared (Whiteside & Lindegaard, 1980; Higler & Verdonschot, 1989; Turner & Trexler, 1997), but this practice is not common in aquatic biodiversity surveys. Among the various devices that are available, the activity or funnel trap is considered effective for capturing mobile macroinvertebrates (Murkin et al., 1983; Hilsenhoff, 1987; Brinkman & Duffy, 1996; Turner & Trexler, 1997; Becerra Jurado et al., 2008). Activity trapping is a passive sampling technique. Activity traps generally are deployed in the water column or on the bottom substrate with their funnel opening facing horizontally or vertically and left in place for a fixed time span (e.g. Elmberg et al., 1992; Muscha et al., 2001). Interoperator effects on the sampling procedure are minimized, and because sampling at night is possible, invertebrates with diel differences in activity can be captured (Hampton & Friedenbergs, 2001). After retrieval, samples can be preserved immediately. No macrophytes or detritus are collected, so sorting is not required, and this source of variation is excluded (Haase et al., 2006).

How many organisms are collected with activity traps depends on the density of the population being sampled, the mobility and activity of the organisms, and their susceptibility to capture (Greenslade, 1964). Therefore, the traps actually record the activity-density of the fauna (*sensu* Thiele, 1977), a measure potentially under the influence of many environmental and biotic

factors that are sources of sampling variation, especially when trapping duration is short. That preservatives cannot be used complicates the use of activity traps to capture macroinvertebrates in freshwater habitats. Trapped macroinvertebrates are confined in a very small volume of water, and this confinement inevitably results in mortality and strong biotic interactions within the trap.

Despite the fact that trapping duration appears to be a key factor determining the successful use of traps in inventories of aquatic ecosystems, I found no studies that specifically explained the choice of a particular deployment time. Increasing trapping duration could optimize the efficiency of activity traps by increasing the number times organisms encounter the traps, thereby decreasing variation among samples. On the other hand, longer trapping durations increase the risk of mortality and could bias results toward certain groups (e.g., large predators).

Another way to optimize trapping success is to use attractants, such as bait or decaying plant material, in the traps. Low-molecular-weight metabolites released by decaying organisms attract a wide array of predators and omnivores that use these chemical cues to identify and locate food sources (Brönmark & Hansson, 2000; Burks & Lodge, 2002). Bacteria, fungi, and epiphyton on decaying plant material also release chemical cues that can attract detritivores (de Lange et al., 2005). Attractants often are used for species that are difficult to survey, but general application might be possible if many aquatic organisms could be lured to the traps.

I studied the effectiveness of activity traps in shallow, heavily vegetated drainage ditches and explored 2 ways to optimize the use of activity traps for monitoring purposes: 1.) increased trapping duration and 2.) use of bait and preconditioned leaves as attractants. I investigated the effects of these approaches on total taxonomic richness and abundance and richness and abundance of taxa categorized by trophic level and mode of locomotion.

Methods

Study area

The study was conducted in the first ½ of September 2008 in a series of drainage ditches in Polder Achteraf, Utrecht, The Netherlands (Fig. 6.1A). Polder Achteraf is an extensive agricultural area drained by numerous linear drainage ditches that are fed mainly by groundwater seepage from nearby sandy ridges (Fig. 6.1B). The amount of seepage is enough to maintain a more

or less constant water level throughout the year but too low to generate substantial unidirectional water movement.

I selected 4 adjacent, interconnected drainage ditches for study based on similarity in dimensions (width 3.5 ± 0.1 m, depth 0.4 ± 0.1 m; average ± 1 SD, $n = 4$), bottom sediment (mixture of peat and sandy patches), trophic state (total P = 0.021 ± 0.001 mg P/L, total N = 1.68 ± 0.41 mg N/L), and aquatic vegetation. Emergent vegetation cover in the 4 ditches was $75 \pm 11\%$ and was dominated by *Phragmites*, *Sparganium*, *Sagittaria*, and *Alisma*. Submerged vegetation cover was $19 \pm 12\%$ and consisted of *Elodea* and *Potamogeton*. Floating vegetation covered $6 \pm 3\%$ of the water surface of the ditches and was dominated by *Potamogeton*, *Nymphaea*, and *Hydrocharis*.

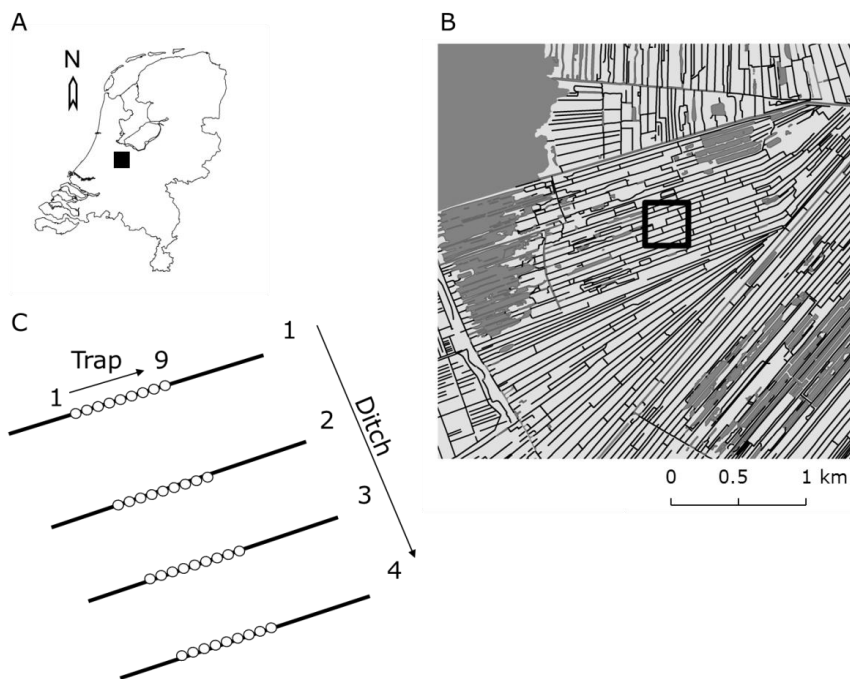


Figure 6.1: A.—Location of the study site within The Netherlands. B.—Study site in more detail; black hairlines represent drainage ditches, gray areas indicate larger water bodies. C.—Sampling grid of activity traps established at the study site. The grid consisted of 4 ditches, each containing 9 activity traps, with an intertrap spacing of 0.5 m and a between-ditch spacing of ~ 50 m.

Study design

I established a sampling grid of 36 horizontal activity traps in the drainage ditches. The grid consisted of 4 rows of traps, 9 traps/row, with 0.5 m between traps. The rows corresponded with the 4 adjacent drainage ditches spaced ~ 50

m apart (Fig. 6.1C). I used 2 attractant treatments and a control (no attractant added). Attractants consisted of 20 g cat food (= bait; Felix duck and poultry in jelly; Purina®) or 5 g of fresh *Alnus glutinosa* leaves, dried to a constant mass at 70°C and preconditioned for 48 h in pond water at room temperature before application. I replicated each treatment 12 times, and randomized treatments over the sampling grid.

To investigate the effect of trapping duration, I sampled in 3 consecutive rounds in which I applied the same treatments (control, leaves, bait), but changed trapping duration from 48 h (1st round) to 96 h (2nd round) to 168 h (3rd round). I retrieved all 36 traps after each round. I cleaned the traps, renewed their contents, and redistributed treatments randomly over the sampling grid.

Sampling and sample processing

Traps consisted of a 2-L glass jar with a polyethylene funnel (outer diameter = 9.5 cm, inner diameter = 2.1 cm) over the opening. The trap was connected to the outer end of a 0.5-m stainless steel rod pushed into the sediment to keep the trap in place. I placed each trap in a horizontal position against the bank of the ditch with the funnel facing toward the middle of the ditch and the top of the funnel at a depth of 5 cm beneath the water surface.

During deployment, I lowered traps into the water column with their openings covered with 250-µm mesh to prevent entry of macroinvertebrates when the traps filled with water. For trap retrieval, I lifted traps carefully to the water surface, turned them upright, and removed them from the water. I poured the contents through a sieve (250-µm mesh) and washed them into a bottle with 70% ethanol. I removed macroinvertebrates attached to the inside of the jar and included them in the sample, but discarded organisms in the funnel.

In the laboratory, I identified macroinvertebrates to the lowest practical taxonomic level. Preserving the samples in the field resulted in identification problems in Tricladida. Therefore, I identified this group to genus. Identifying early-instar invertebrates to species level often was not possible, so mixed taxonomic levels (family, genus, and species) were used in some groups of invertebrates. Therefore, I applied an adjustment procedure to the data set to reduce bias caused by differences in taxonomic resolution (Schmidt-Kloiber & Nijboer, 2004). I took a conservative approach because I did not know whether the specimens identified to family level were actually early instars of species that already were recorded or were different species. I grouped these species to a higher taxonomic level.

Analysis of trapping duration

All statistical tests were conducted in SPSS for Windows (version 15.0; SPSS, Chicago, Illinois). Because the same 4 ditch stretches were sampled 3 times within a period of 2 wk, I used repeated-measures analyses of variance to test whether differences in number of individuals and number of taxa caught per trap were related to trapping duration. I use type of attractant (control, leaves, bait) as the between-subjects factor (with 12 replicates for each treatment) and the 3 trapping durations (48 h, 96 h, 168 h) as the within-subjects factor. I $\log_{10}(x)$ -transformed the number of taxa and number of individuals before statistical analysis to meet assumptions for normality and homogeneity of variances. I used Bonferroni-corrected pairwise comparisons based on the estimated marginal means as a post hoc procedure for trapping duration.

I also investigated the effect of longer trapping duration on the relative number of individuals and taxa captured by comparing the average catch/trap standardized to the number of taxa/individuals captured per hour for each trapping duration. Increased or decreased abundance could indicate sudden changes in the activity-density of macroinvertebrates caused by the environment (abiotic factors) or the trap itself (mortality). Therefore, I quantified the effect of trapping duration on the total number of individuals and taxa and on various taxonomic groups separately. I used nonparametric Jonckheere–Terpstra tests to detect trends. I used only untreated traps to avoid interference of the treatments applied to the traps. I used Bonferroni-corrected levels of significance for the number of taxonomic groups tested ($0.05/10$, $\alpha = 0.005$). I used only taxonomic groups with an average abundance of >1 individual/trap.

I also compared taxon accumulation curves for each trapping duration. I smoothed curves by randomizing the sampling order 50 times and computed means with 95% confidence intervals with the program EstimateS (version 7.5.1; Colwell, 2005). I calculated both sample- and individual-based curves. Sample-based curves describe taxon density and show an increase in taxa collected with every new sample added. The number of individuals captured can confound the observed differences between the trapping durations. Thus, because macroinvertebrate abundance is likely to increase with increasing trapping duration, I also computed individual-based accumulation curves, which give the number of taxa captured when a similar number of individuals is collected (comparison of taxon richness). Accumulation curves reach asymptotes. I considered curves asymptotic if the last 2 values were within 1% of each other and the last 20% of the values of the curve were within 2% of the final value.

Attractants

To test for the effects of attractants on the trophic rank of the macroinvertebrate taxa caught, I used multivariate analyses of variance with 2 dependent variables: number of predator taxa and number of detritiherbivore taxa. I based classification of taxa to trophic rank on Merritt and Cummins (1984), Moog (1995), and Tachet et al. (2000). In the case of omnivores, I classified taxa according to their primary food source. I excluded parasites from the analyses.

Differences in trapping duration could cause changes in the chemical cues released by the attractants and, consequently, differences in taxonomic composition of the catches. Therefore, I conducted separate analyses for the different trapping durations. I $\log_{10}(x + 1)$ -transformed data to meet the assumptions of normality and homogeneity of variances. These criteria were met for all variables except the leaves treatment for predator taxa at $t = 168$ h (Kolmogorov–Smirnov test, $p = 0.008$; Levene's test, $p = 0.001$). I compared means with Tukey's Honestly Significant Difference (HSD) multiple comparisons ($\alpha = 0.05$).

I used indicator value analysis (IndVal; Dufrêne & Legendre, 1997) to detect characteristic taxa for each of the attractants. The IndVal test combines measurements of the degree of specificity of a taxon to certain treatments and its fidelity (frequency of occurrence) within that treatment. The maximum value (100%) is attained when all specimens of a taxon are found in traps with the same treatment and when the taxon occurs in all samples of that treatment. I considered taxa with an IndVal $> 55\%$ characteristic for a treatment (symmetrical indicator, *sensu* Dufrêne & Legendre, 1997). I evaluated significance ($p < 0.05$) of each taxon IndVal with a Monte Carlo test (99999 permutations). I calculated indicator values with PcOrd for Windows (version 4.25; McCune & Mefford, 1999).

Because the mode of locomotion of invertebrates could influence the number of taxa caught in the traps, I further classified predators and detritiherbivores according to their mode of locomotion (taxa capable of swimming vs. taxa that cannot swim; Merritt & Cummins, 1984; Moog, 1995; Tachet et al., 2000). This classification yielded 4 trait groups: swimming predators, nonswimming predators, swimming detritiherbivores, and nonswimming detritiherbivores. For each trait group, I compared the number of taxa caught per trapping duration among the attractant treatments. Data were not distributed normally, even after transformation. Therefore, I used Kruskal–Wallis tests, followed by Mann–Whitney U tests as a post hoc procedure (Bonferroni corrected: $0.05/3$; $\alpha = 0.017$) to compare the 4 groups.

Results

A total of 3361 individuals belonging to 90 taxa were caught in the 108 activity traps. The 5 most dominant taxa collected were *Triaenodes bicolor* (Trichoptera) with 47% of the total macroinvertebrate abundance, *Gammarus* sp. (Amphipoda; 12%), *Cloeon* sp. (Ephemeroptera; 3%), *Stylaria lacustris* (Oligochaeta; 3%), and *Dugesia* (Tricladida; 2%).

Table 6.1: Effect of an increase in trapping duration on the relative number of individuals captured per trap for various taxonomic groups. Catch for the different trapping durations was standardized to number of individuals captured per hour and tested for trends in abundance with Jonckheere–Terpstra tests. Only untreated traps were used in the analysis ($n = 12$ /trapping duration). The level of significance was Bonferroni corrected for the number of taxonomic groups analyzed. ns = not significant, * = significant (1-tailed) $p < 0.005$ (Bonferroni corrected).

Taxonomic group	J	z	p
Platyhelminthes	230	0.435	0.342 ^{ns}
Oligochaeta	316.5	3.125	0.001*
Hydracarina	265.5	1.445	0.075 ^{ns}
Amphipoda	199	-0.495	0.309 ^{ns}
Ephemeroptera	204.5	-0.345	0.372 ^{ns}
Heteroptera	258	1.310	0.093 ^{ns}
Coleoptera	250	1.015	0.153 ^{ns}
Diptera:Chironomidae	243	0.894	0.187 ^{ns}
Diptera:non-Chironomidae	251.5	1.176	0.127 ^{ns}
Trichoptera	281.5	1.911	0.026 ^{ns}

Trapping duration

Across all treatments, 476 individuals belonging to 59 taxa were caught when trapping duration was 48 h. An increase in trapping duration to 96 h resulted in a total catch of 922 individuals and 65 taxa, and a trapping duration of 168 h yielded 1963 individuals and 82 taxa. Across all treatments, the mean number of taxa ($F_{2,66} = 44.0$, $p = 0.000$) and number of individuals ($F_{2,66} = 69.1$, $p = 0.000$) per trap increased with trapping duration (Fig. 6.2A, B).

The pattern differed when data were standardized to an equal trapping duration (individuals/taxa captured $\text{h}^{-1} \text{ trap}^{-1}$). Total number of individuals captured per h remained constant with increasing trapping duration (mean ± 1 SE; $t = 48$ h: 0.63 ± 0.11 individuals $\text{h}^{-1} \text{ trap}^{-1}$, $t = 96$ h: 0.83 ± 0.19 individuals $\text{h}^{-1} \text{ trap}^{-1}$, $t = 168$ h: 0.85 ± 0.13 individuals $\text{h}^{-1} \text{ trap}^{-1}$; $J = 31.0$, $z = 1.03$, $p = 0.176$), whereas the number of taxa captured per h decreased as trapping duration increased ($t = 48$ h: 0.27 ± 0.03 taxa $\text{h}^{-1} \text{ trap}^{-1}$, $t = 96$ h: 0.20 ± 0.01 taxa $\text{h}^{-1} \text{ trap}^{-1}$, $t = 168$ h: 0.15 ± 0.01 taxa $\text{h}^{-1} \text{ trap}^{-1}$; $J = 2.00$, $z = -3.24$, $p =$

0.000). When data for each taxonomic group were analyzed separately, the number of individuals caught per h was comparable for all 3 trapping durations (Table 6.1). Oligochaeta were the only exception, and showed a significant positive trend in abundance with increasing trapping duration ($J = 316.5$, $\chi = 3.125$, $p = 0.001$).

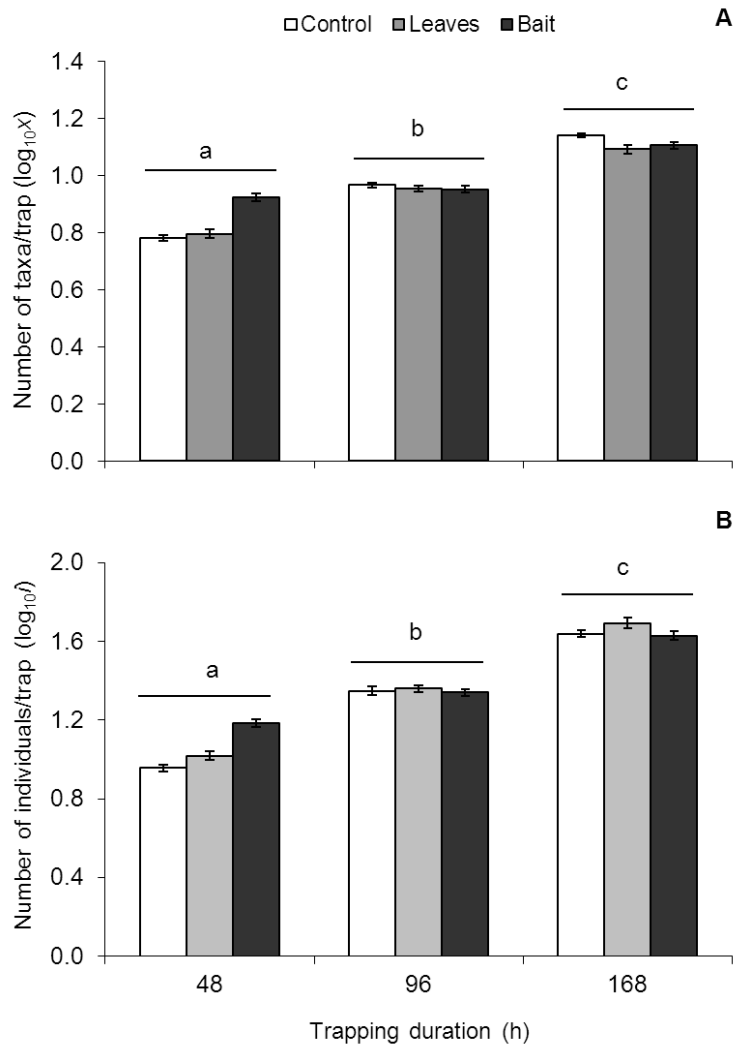


Figure 6.2: $\log_{10}(x)$ -transformed mean (± 1 SE) total number of taxa/trap (A) and total number of individuals/trap (B) for attractant treatments and trapping durations. Bars with the same letters are not significantly different.

The rate of taxon accumulation per sample did not differ significantly between trapping durations of 48 and 96 h. The overlapping 95% confidence

intervals indicated that the number of taxa added per sample was similar for $t = 48$ and $t = 96$ (Fig. 6.3A). A trapping duration of 168 h appeared to be more efficient for collecting taxa. The rarefaction curve was steeper, and more taxa were caught. At >5 samples, 95% confidence intervals for $t = 168$ h did not overlap with the 95% confidence intervals for 48 h and $t = 96$ h (Fig. 6.3A). None of the 3 curves reached an asymptote, a result indicating that only part of the macroinvertebrate assemblage was captured.

When accumulation curves were expressed as number of taxa accumulated per individual, 95% confidence intervals for all 3 curves overlapped, at least for the smallest number of individuals comparable for all trapping durations (Fig. 6.3B). This outcome indicated that, for a fixed number of individuals caught, a similar number of taxa was collected and the seemingly greater efficiency at $t = 168$ h could have been partly an effect of collecting more individuals.

Attractants

Attractants had no effect on the total number of individuals ($F_{2,33} = 0.48$, $p = 0.621$) or total number of taxa ($F_{2,33} = 0.68$, $p = 0.515$) captured regardless of trapping duration, and attractant treatment and sampling duration did not interact significantly, a result indicating that the patterns observed for the different treatments were comparable across sampling durations (Fig. 6.2A, B). In contrast, the trophic rank of the taxa caught appeared to affect the response to the attractant treatments in traps (Pillai's Trace, $p = 0.022$). When trapping duration was 48 h, attractants influenced trapping results for predators ($F_{2,36} = 6.02$, $p = 0.006$) but not for detritiherbivore taxa ($F_{2,36} = 0.95$, $p = 0.397$) (Fig. 6.4A). More predator taxa were caught with baited traps than with control traps and traps containing leaves. Attractants did not influence predators or detritiherbivores caught when trapping duration was increased to 96 h (Pillai's Trace, $p = 0.289$; predator taxa: $F_{2,36} = 1.24$, $p = 0.303$; detritiherbivore taxa: $F_{2,36} = 2.07$, $p = 0.143$; Fig. 6.4B) or to 168 h (Pillai's Trace, $p = 0.131$; predator taxa: $F_{2,36} = 1.787$, $p = 0.183$; detritiherbivore taxa: $F_{2,36} = 1.983$, $p = 0.154$; Fig. 6.4C).

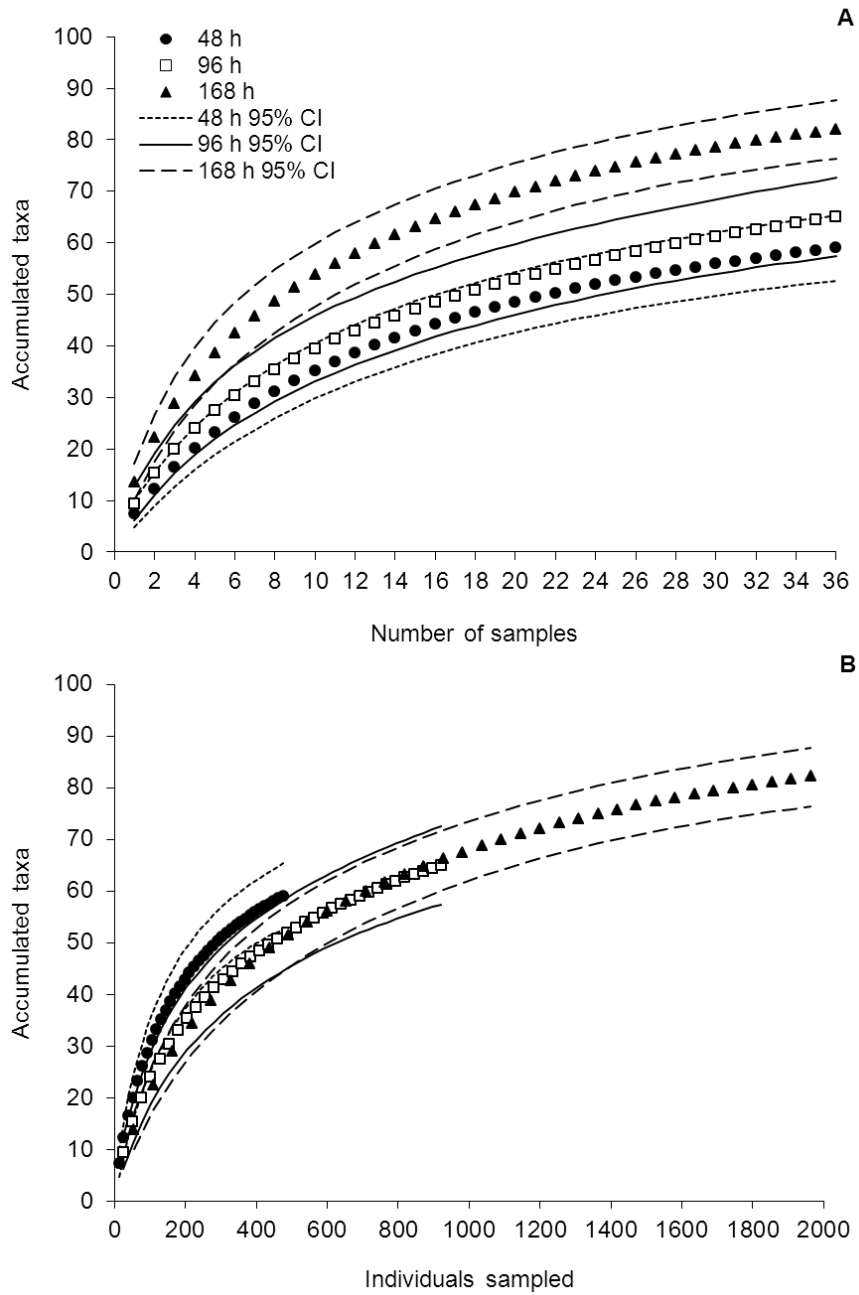


Figure 6.3: Sample-based (A) and individual-based (B) taxon accumulation curves with 95% confidence intervals (CI) of activity trap catches for different trapping durations: $t = 48, 96$, or 168 h. Sample order was randomized 50 times to obtain means.

The triclad *Dugesia* sp. (IndVal score 69%, $p = 0.000$) could be considered characteristic for the baited traps, but only when trapping duration was 48 h. The specificity of this taxon for baited traps disappeared with longer trapping duration because its frequency and abundance decreased in baited traps and increased in the other treatments. The beetles *Cybister lateralmarginalis* (IndVal score 33%, $p = 0.025$) and *Graphoderus cinereus* (IndVal score 33%, $p = 0.025$) occurred in higher numbers than expected by chance in the baited traps when trapping duration was 48 h. When trapping duration was 168 h, the chironomid *Orthocladus bolsatus* (IndVal score 43%, $p = 0.020$) occurred in higher numbers than expected by chance in the traps containing leaves, and nymphs of Naucoridae (IndVal score 35%, $p = 0.047$) occurred in higher numbers than expected by chance in control traps. IndVal scores for these taxa were <55% because of their occurrence in low numbers in the traps. These taxa were considered asymmetrical indicators, and their potential indicator value could be separated from the possibility that their presence was accidental or anecdotal.

Mode of locomotion affected trapping results. For control traps, the number of swimming predator ($H[2] = 18.327$, $p = 0.000$), swimming detritiherbivore ($H[2] = 9.615$, $p = 0.005$), and nonswimming detritiherbivore ($H[2] = 7.126$, $p = 0.025$) taxa differed significantly among trapping durations (Fig. 6.5A). The number of swimming predator taxa was greater at $t = 96$ h than at $t = 48$ h ($U = 20.5$, $p = 0.002$, $r = -0.62$), but did not differ significantly between $t = 96$ and $t = 168$ h ($U = 38.5$, $p = 0.049$, $r = -0.40$). The number of swimming detritiherbivore taxa did not differ between $t = 48$ h and $t = 96$ h ($U = 47.0$, $p = 0.184$, $r = -0.31$) or between $t = 96$ h and $t = 168$ h ($U = 37.5$, $p = 0.036$, $r = -0.43$), but did differ significantly between $t = 48$ h and $t = 168$ h ($U = 25.5$, $p = 0.005$, $r = -0.56$). The number of nonswimming detritiherbivore taxa did not differ significantly among trapping durations (post hoc Mann–Whitney U test), indicating that differences between trapping durations were small (Fig. 6.5A). For baited traps, only the number of nonswimming detritiherbivore taxa differed significantly among trapping durations ($H[2] = 9.591$, $p = 0.003$).

The number of nonswimming detritiherbivore taxa was higher at $t = 168$ h than at $t = 96$ h ($U = 25.5$, $p = 0.004$, $r = -0.57$), but did not differ significantly between $t = 48$ h and $t = 96$ h ($U = 55.0$, $p = 0.367$, $r = -0.21$) or between $t = 48$ h and $t = 168$ h ($U = 33.5$, $p = 0.022$, $r = -0.48$) (Fig. 6.5B). For traps containing leaves, the number of swimming predator ($H[2] = 9.019$, $p = 0.008$) and nonswimming herbivore ($H[2] = 12.562$, $p = 0.002$) taxa differed significantly among trapping durations. The number of swimming predator taxa was higher when $t = 96$ h than when $t = 48$ h ($U = 28.5$, $p =$

0.01, $r = -0.53$) and was comparable between $t = 96$ h and $t = 168$ h ($U = 51.0$, $p = 0.229$, $r = -0.25$). The number of nonswimming detritiherbivore taxa did not differ significantly between $t = 48$ h and $t = 96$ h ($U = 46.0$, $p = 0.127$, $r = -0.33$) or between $t = 96$ h and $t = 168$ h ($U = 34.5$, $p = 0.030$, $r = -0.45$), but was significantly higher when $t = 168$ h than when $t = 48$ h ($U = 15.5$, $p = 0.001$, $r = -0.68$) (Fig. 6.5C).

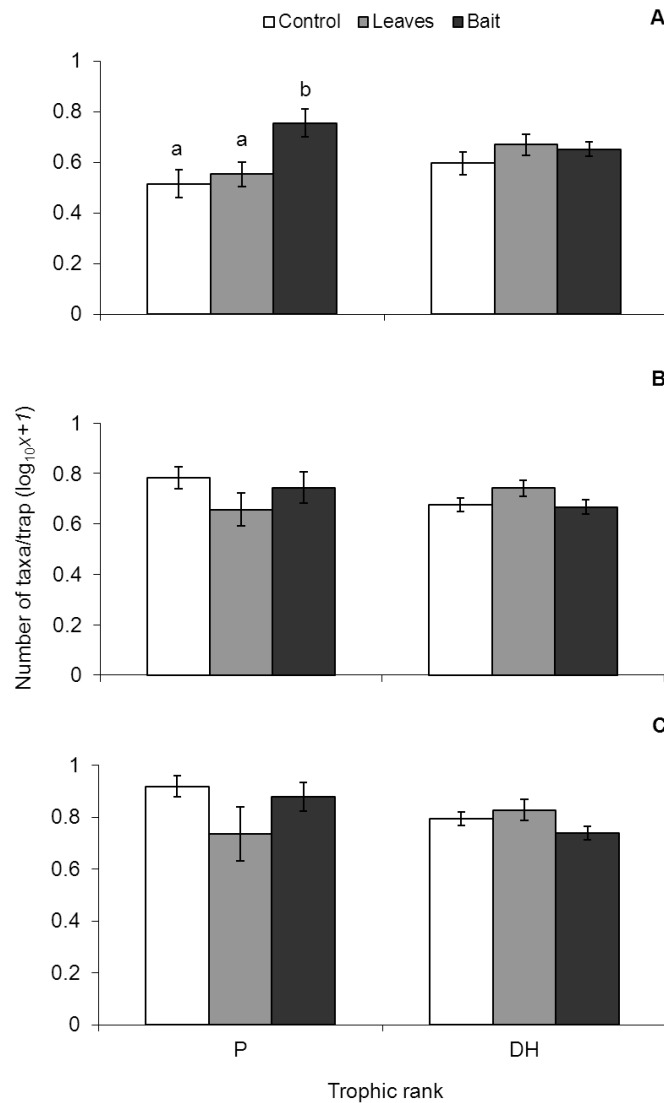


Figure 6.4: Mean (± 1 SE) number of predator (P) and detritiherbivore (DH) taxa/ trap for trapping durations: $t = 48$ (A), 96 (B), or 168 h (C). Bars with different letters are significantly ($p < 0.05$) different. Within groups, bars without letters are not different.

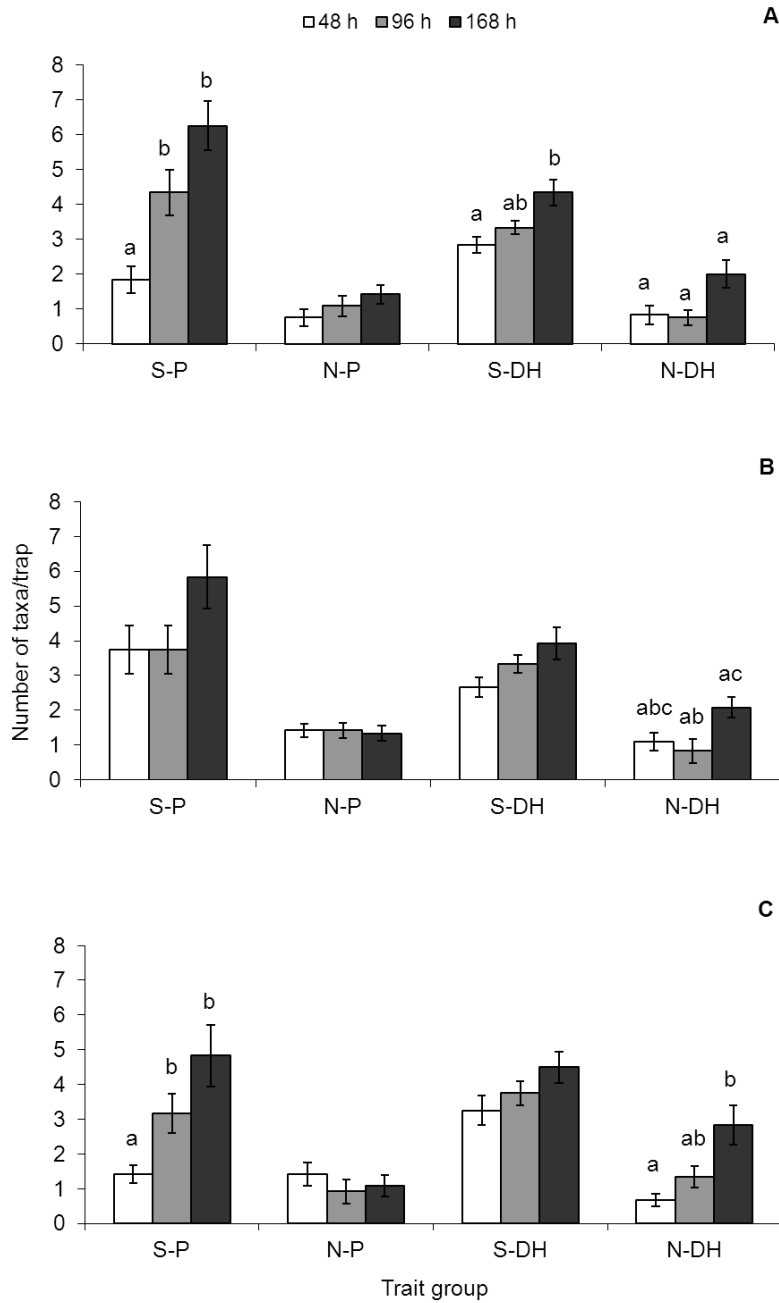


Figure 6.5: Mean (± 1 SE) number of taxa/trap for predators (P) and detriti-herbivores (DH) with different modes of locomotion (swimmers [S], nonswimmers [N]) for attractants: control (A), bait (B), or leaves (C). Bars with different letters are significantly ($p < 0.05$) different. Within groups, bars without letters are not different.

Discussion

Trapping duration

Most investigators who have used activity traps to catch macroinvertebrates have used trapping durations of 24 to 48 h (e.g. Murkin et al., 1983; Brinkman & Duffy, 1996; Turner & Trexler, 1997; Hyvönen & Nummi, 2000; Becerra Jurado et al., 2008). Our results indicate that this duration is too short, at least when the goal of a study is to describe the macroinvertebrate assemblage present in a water body. Extending the trapping duration to 96 h or 168 h resulted in a considerable increase in the number of macroinvertebrate taxa and individuals recorded. Trapping efficiency, in terms of adding new taxa with every new sample collected, increased markedly, especially for a trapping duration of 168 h. Because deployment and retrieval time remain equal regardless of trapping duration, this increase in efficiency offers the possibility of gaining more information with the same labor in the field. Extra effort is required only for counting and identification of the larger number of individuals and taxa collected per trap.

The goals of a study dictate how long traps should be deployed. The absolute increase in total number of taxa collected with increasing trapping duration should be weighed against the decrease in relative number of taxa caught/h when trap deployment times are standardized to an equal trapping duration. A short trapping duration probably captures mostly invertebrates with high activity-density (abundant, very mobile, or both), whereas a longer trapping duration increases the chance of including uncommon or less-mobile taxa. Abundant taxa could be interesting from a functional point of view (for example, foodweb studies, ecosystem functioning) but often are generalist species that are both locally common and widely distributed on a larger geographical scale. Specialists or sensitive species usually have a more limited distribution and tend to be locally uncommon, at least in human-affected ecosystems (Brown, 1984; Hanski & Gyllenberg, 1997). Specialists or sensitive species could more informative as indicators of, for example, environmental change (Cao et al., 1998). Therefore, the need for longer trapping durations seems to be greater when activity traps are used for bioassessment or biodiversity studies than when the main interest is the relative abundance and composition of the abundant taxa.

However, rarity is a relative concept. Many of the taxa I caught in low abundance would have been quite common had another sampling technique been used. An example is Gastropoda, a bias that Brinkman and Duffy (1996) also noted. The macroinvertebrate assemblage collected depends on the

activity and mobility of macroinvertebrates, so mode of locomotion is an important factor determining movement potential and, thus, the trapping rate of organisms (Turner & Trexler, 1997). Swimming invertebrates were well represented in the traps, a result that is not surprising because their active movement through the water column increases their likelihood of encountering the funnel opening. Taxa that cannot swim have a much lower probability of encountering the trap opening because they have to reach the trap actively by climbing the structure or by passive transport toward the trap, as might happen, for example, when they are dislodged by wind-induced water movement. As expected, nonswimming taxa were trapped in lower numbers than swimming taxa. However, mode of locomotion can not always be determined based on morphology alone and can vary with life stage or instar. For example, early instars of Chironomidae occasionally disperse passively through the water column, whereas late instars live in tubes attached to the substrate (Davies, 1976).

A problem associated with defining the role of locomotion of the macroinvertebrates collected is that the actual trapping range of the activity traps is unknown. Little is known about the home range of macroinvertebrate species in lentic freshwater ecosystems (van de Meutter et al., 2006), so the exact origin of the organisms collected is difficult to derive. I do not know whether the home ranges of the taxa collected overlapped a series of proximate traps or just one trap, but any overlap probably varied over different scales for different species. Nevertheless, as trapping duration increased, the rate at which invertebrates encountered control traps was relatively constant. This outcome indicates that the traps did not deplete macroinvertebrate populations in their immediate surroundings. Had depletion occurred, the capture rate would have been high immediately after traps were deployed, followed by a decline with increasing trapping duration. However, the opposite scenario also was not the case, i.e., traps did not become more attractive over time for certain groups of invertebrates. An increase in capture rate with trapping duration would have indicated active colonization of the traps.

Using more traps with a shorter trapping duration does not provide the same trapping efficiency as using fewer traps with a longer trapping duration, at least not for a trapping duration of 168 h. I see 2 possible explanations for the increase in efficiency with a longer trapping duration. First, the increase could have been a sampling effect if the chance of including new taxa became higher because the number of individuals increased rapidly with increased trapping duration (Douglas & Lake, 1994). This explanation is supported by the fact that the higher efficiency of the longest trapping duration disappeared when the number of new taxa added was standardized per individual captured.

Second, a trapping lag linked to mode of locomotion or activity pattern might exist for certain taxa. Whether a deployment time of >168 h would yield an even higher trapping efficiency by including additional taxa is not known. This lack of clarity makes it difficult to predict the sampling effort needed to describe adequately the macroinvertebrates present in the study system. On the other hand, further increasing trapping duration has several potential problems. First, the longer the traps are deployed, the greater the chance of trap disturbance by weather conditions, water level fluctuations, or animals and fish. Second, longer duration could increase mortality of macroinvertebrates and lead to loss of individuals or hinder identification.

Physicochemical factors, habitat structure, and biotic interactions all influence invertebrate activity-density patterns. For example, fluctuations in water temperature, O₂ concentration, daylight intensity, resource availability, and predator activity can suddenly induce or reduce the activity of organisms (Murkin et al., 1983; Wellborn et al., 1996; Schloss, 2002; Tolonen et al., 2003). Oligochaeta was the only taxonomic group for which I observed a change in activity pattern with increasing trapping duration. The taxa caught (mainly *Chaetogaster* sp. and *Stylaria lacustris*) were relatively good swimmers, so mode of locomotion probably was not the main factor explaining this increased abundance. A possible explanation could be an Oligochaeta bloom. Population doubling time for the dominant taxa observed is ~4 to 5 d at 20°C (Löhlein, 1999). The question then is what could have triggered such a bloom. My study took place in a relatively short time period with no large weather fluctuations, so I infer that no major changes in conditions that could have resulted in large deviations in activity-density occurred during the sampling period. Populations of vertebrate predators (fish, frogs, newts) in the ditches and the density of the submerged vegetation structure also did not change during the study (pers. obs.). Therefore, I speculate that resource availability arising from epiphyton growth on the inside of the trap or an algal bloom in the ditch might have changed and could have induced an increase in population size and in capture rate.

Another important issue is the influence of predators in the traps on the total number of individuals and taxa recorded. Elmberg et al. (1992) found that invertebrate predators affected neither the abundance nor the taxonomic diversity of activity-trap catches. I was unable to investigate this idea because predators were present in every trap. Nevertheless, both the number of predators and the number of detritiherbivores increased with trapping duration, results indicating that accumulation of predators in the traps did not cause a depletion of the number of detritiherbivores. Predators might feed mainly on zooplankton (which I did not take into account), or perhaps their

feeding rate was very low. A low feeding rate of predators could be the consequence of a low O₂ concentration in the traps. The presence of dead organisms in the traps leads to a rapid O₂ depletion (pers. obs.) because of increased bacterial respiration. Low O₂ concentrations occur frequently in drainage ditches (Kersting & Kouwenhoven, 1989) and most macroinvertebrates there can survive short-term O₂ stress. Thus, low O₂ concentrations lead to reduced activity instead of direct mortality (Kolar & Rahel, 1993). Thus, low O₂ concentrations decrease the rate of interaction among captured fauna. If this is the case, including air in the traps (e.g., by filling the traps to 75% with water) might lead to a higher rate of biotic interactions in the traps. Regardless, the actual extent of intratrap predation is unknown and is an unstudied but important question in activity-trap methodology.

Attractants

The use of attractants to improve trapping efficiency gave mixed results. Bait increased the number of predatory macroinvertebrate taxa relative to in controls when $t = 48$ h, and comparable numbers of predators were reached in the 2 treatments only when trapping duration was ≥ 96 h. This finding indicates that chemical cues from inside the trap were released into the water column and attracted macroinvertebrates. Cat food was an especially strong attractant for *Dugesia* flatworms. *Dugesia* have well developed chemoreceptors for detecting chemical cues of potential food sources and actively search for food, which enhances their trapping rate (Seaby et al., 1995). Baited traps also tended to attract large Dytiscidae, but these beetles were trapped in densities that were too low for statistical analysis.

The size and shape of the plume of infochemicals generated by the bait is not known, but its effects were of short duration. Baited traps increased captures only for a trapping duration of 48 h. Seaby et al. (1995) found that predatory responses of Hirudinea and Tricladida to decaying prey declined dramatically after 24 h, and none were feeding at 48 h. I did not find Hirudinea in higher numbers in baited than in control traps, despite considerable trophic overlap with Tricladida. Leeches and Tricladida might partition food resources in the ditches such that leeches use more living prey (Seaby et al., 1996).

Chemical cues also are generated by trapped macroinvertebrates (Brönmark & Hansson, 2000; Burks & Lodge, 2002). The strength of these macroinvertebrate cues in the traps is unknown, as is whether these chemical signals were stronger than the cues generated by the bait. If this latter possibility is the case, the accumulation of organisms in the trap, both alive and

dead, could have interfered with the chemicals released from the bait. Moreover, the presence of live invertebrates in the traps could have affected the behavior of the organisms in the surrounding water column. Predator avoidance based on chemical cues is common among freshwater organisms (Brönmark & Hansson, 2000; Burks & Lodge, 2002), and the presence of certain predators in the trap might deter prey from approaching the trap. Predators were captured in every trap, so certain species might simply have avoided the traps completely because of their presence. On the other hand, one individual of a species could have attracted other members of their species into the trap, e.g., for reproduction (Hilsenhoff, 1987).

Another type of cue could have arisen from macroinvertebrates that died or decayed in the traps as a result of predation or adverse conditions. When traps were recovered, most contained several dead invertebrates. In particular, plastron breathers drowned rapidly in the traps because they could not replenish their air supply. Chemical cues from dead or wounded organisms in the trap can deter species that respond to the chemical cues released by dead conspecifics and could result in trap avoidance (Burks & Lodge, 2002). Alternatively, decaying macroinvertebrates might be analogous to the bait I added to the traps and generate a strong chemical cue for invertebrate scavengers.

Addition of leaves to the traps did not result in differences in taxonomic composition or abundances compared to other treatments. I see 2 explanations for this outcome. First, decaying organic material is available in high quantities in densely vegetated ditches, so detritivores had a large array of alternative food sources. Second, invertebrates are attracted to the bacteria, fungi, and epiphyton associated with the dead organic matter instead of to the leaf material itself (de Lange et al., 2005). Therefore, despite preconditioning of the leaves in the laboratory, the level of conditioning of the leaf material might have been too low to release a chemical cue strong enough to attract macroinvertebrates.

Despite their apparent short-term effectiveness for certain taxa, use of attractants in traps is not common in freshwater macroinvertebrate studies, except those of crayfish (e.g., Somers & Stechey, 1986). A major problem with chemical attractants is that their effects are species specific and ecosystem dependent. For example, *Gammarus pulex* was readily attracted to bait in streams (Allan & Malmqvist, 1989), but in the ditches in my study, their capture rate did not differ between baited and unbaited traps. This specificity makes standardization of baited traps very difficult and reduces their usefulness for large-scale application.

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7 Synthesis



Drainage ditch in winter.

7 Synthesis

In Dutch water management and policy making drainage ditches are generally viewed purely as hydrological infrastructure in support of agriculture. The fact that drainage ditches comprise a functioning aquatic ecosystem, harbouring a wide array of organisms and biological processes, has largely been overlooked. Also the amount of scientific research devoted to drainage ditches is negligible in comparison to rivers and lakes. This is remarkable, because with a total length of approximately 300,000 kilometers and with a density of up to 400-1000 m ditch per hectare, the extensive ditch networks found throughout the The Netherlands can be regarded as one of the major aquatic systems in the country. The anthropogenic origin and intensive management regime of drainage ditches is likely the underlying cause of being almost completely neglected as a potential carrier of aquatic biodiversity.

That this line of reasoning is not justified is shown in chapter 2. A comparison of macrophyte-rich, eutrophic peatland drainage ditches and semi-natural small shallow lakes showed that both types of lentic ecosystems, despite differing in terms of nutrient dynamics and habitat availability, harbored taxon rich macroinvertebrate assemblages. Ditches did not contain only common taxa, also the number of nationally rare species did not differ between the two water body types. Actually, there was much overlap in taxonomic composition between the agricultural drainage ditches and semi-natural small lakes. Similar patterns were found in other agricultural landscapes (with very different types of ditches, P. Williams pers. comm.) across Europe (Williams et al., 2003; Davies et al., 2008).

An important difference between drainage ditches and small lakes was the relatively high site-to-site variation in taxon composition between ditches (Chapter 2). Mechanisms that cause this variability in taxon composition can be classified as purely deterministic, when habitat heterogeneity (the shifting mosaic of habitat patches differing in environmental conditions; Chapter 1) results in conditions suited for some species, but adverse for others, and stochastic mechanisms, related to differential colonization/extinction dynamics after disturbance (Chase, 2010). In this thesis the influence of both deterministic and stochastic mechanisms on the structure and composition of drainage ditch macroinvertebrate assemblages is studied.

The relative importance of both mechanisms in shaping macroinvertebrate assemblages is crucial for successful biomonitoring and assessment. Water district managers in The Netherlands conduct routine surveys of the fauna in their waters, under which drainage ditches, which they use for assessment purposes. Most assessment techniques assume a deterministic distribution of organisms. Dispersal related processes interfere with this presumed match between species and its environment. Here, knowledge on the mechanisms underlying drainage ditch macroinvertebrate assemblage distribution was applied for optimizing the monitoring of drainage ditch macroinvertebrates and the bioassessment of drainage ditch ecological quality.

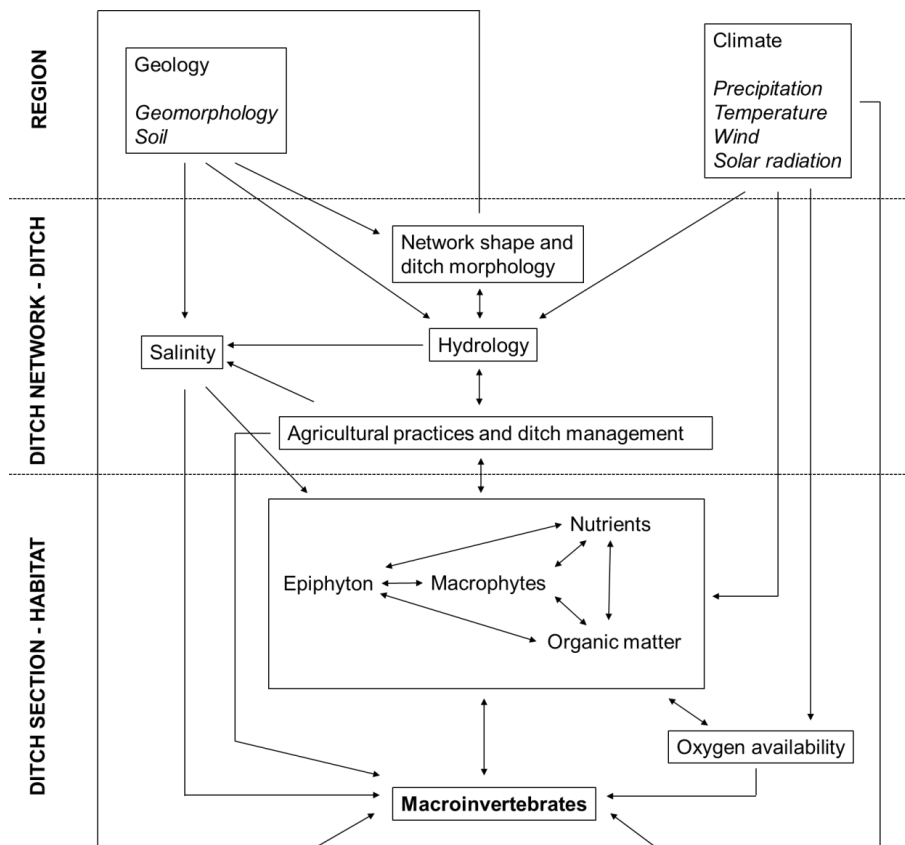


Figure 7.1: Factors influencing drainage ditch macroinvertebrate assemblages.

Spatiotemporal heterogeneity in drainage ditch networks forms a dynamic habitat-template to which macroinvertebrates respond

Variation in macroinvertebrate assemblage structure and composition among localities could arise from purely deterministic mechanisms, such as differences in local physicochemical conditions (Chapter 3, 4, 5). The environmental conditions present at a locality act as ‘filters’ (Poff, 1997); they influence the probability that specific species are able to persist because they possess the right attributes suited to the constraints acting at that locality. These filters, which could have both a natural and an anthropogenic origin, work on different spatial and temporal scales. They produce patterns of spatiotemporal heterogeneity – a shifting mosaic of patches differing in environmental conditions – to form a dynamic habitat-template to which invertebrates respond (Southwood, 1977, 1988). In this thesis, several environmental filters were identified, operating on different spatiotemporal scales (Fig. 7.1).

Salinity

Viewed at a large spatial scale, for example, entire ditch networks or regions within The Netherlands, the ionic content of the ditch water can be regarded as the most important environmental filter for macroinvertebrates in meso- to eutrophic drainage ditches (Chapter 4, 5). The locally elevated salinity of the ditch water due to the inlet of chloride-rich river water, agricultural practices or brackish groundwater seepage leads to considerable changes in the structure of the macroinvertebrate assemblage. Also on smaller scales, differences in the concentration of solutes between ditches, such as the dissociated cations Na^+ , K^+ , Ca^+ and Mg^+ , display correlations with differences in macroinvertebrate assemblage composition (Chapter 3). As shown in chapter 5, an increase in chloride concentration correlates strongly with a decrease in aquatic insect richness and abundance. In ditches, especially Trichoptera seem to be sensitive. Physiological constraints can result in the absence of insect species in waters with a high salinity (Williams & Feltmate, 1992), but it is likely that other factors are also involved, since insects are common in many saline inland wetlands (Mendelssohn & Batzer, 2006). According to Daly et al. (1998) competition with non-insects (e.g. Crustacea) could be one of the underlying mechanisms. Another reason for the impoverished fauna of ditches with a high chloride concentration could be the result of waters with a high salinity being generally poor in submerged macrophytes, which makes these ditches

less suited for phytomacrofauna. Nonetheless, these waters generally have a littoral vegetation composed of *Phragmites australis* (Nijboer et al., 2003), which – at least in part – compensates for the lack of vegetation in the water column.

The macrophyte, epiphyton, nutrients and organic loading interaction complex

Being situated in an agricultural matrix results in a relatively high nutrient- and organic matter input into the drainage ditch system. Often these nutrient pulses are local, impacting only parts of drainage ditch networks or occurring in certain periods of the year. Furthermore, the readily available nutrients cause a rapid vegetation development in the ditches that results in a fast accumulation of organic material on the ditch bottom. As a result vegetation succession toward a terrestrial stage is accelerated. Major difference in comparison to salinity, which acts as a direct environmental filter and operates on large spatial scales, is that these pulses of nutrients and organic matter have mainly indirect and local effects on the macroinvertebrate assemblages. They act primarily through the macrophytes and the algae (mainly epiphyton) present in the ditch (Chapter 2, 3, 4, 5).

Macrophytes play a central role in the drainage ditch ecosystem; they can be regarded as keystone structures (*sensu* Tews et al., 2004). On ditch scale, trophic status displays a clear link with macrophyte abundance and composition (Bloemendaal & Roelofs, 1988; Portielje & Roijackers, 1995). By influencing the vegetation, it indirectly affects the habitat availability for macroinvertebrates. The presence of underwater vegetation structure – in the form of submerged vegetation or the submerged parts of emergent or floating plants – is essential for macroinvertebrates (Higler & Verdonschot, 1989). Most macroinvertebrates partly or completely depend on the presence of macrophytes to persist in the ecosystem during their life cycle. Amongst others, vegetation serves as or offers attachment sites for the main food sources for detritivores and herbivores, acts as a refuge to predation or facilitates the capturing of prey, can be used to position themselves along an oxygen gradient, and is necessary for a diverse array of biological functions of organisms (e.g. oviposition sites, attachment sites for tubes and nets) (Crowder & Cooper, 1982; Rooke, 1984; Kolar & Rahel, 1993; Dvořák, 1996; Taniguchi et al., 2003; Warfe & Barmuta, 2006).

As shown in chapter 3, the habitat structural characteristics of macrophyte patches were relatively unimportant. Only a minor proportion of the macroinvertebrates responded to the type of growth form present in

the ditches studied. Contrastingly, the availability of resources on the vegetation – epiphyton, trapped detritus and their associated microorganisms – explained a considerable proportion of the variance in phytomacrofaunal assemblage composition at patch scale. In turn, these resources were influenced by the physicochemical properties of the environment. Such linkages between nutrient concentrations of the water, resource availability and macroinvertebrate community composition are well known from lotic ecosystems (Feminella & Hawkins, 1995; Hillebrand, 2002). The biotic components of aquatic systems are inherently linked to the productivity of the ecosystem. A linkage between primary producers and the resources they supply to organisms as a basis of species richness is not uncommon in ecosystems across the world. One of the primary hypotheses put forward to explain these biodiversity patterns is the species-energy theory (Wright, 1983; Rosenzweig, 1995; Honkanen et al., 2010; Hurlbert & Jetz, 2010). The shape of the relationship of productivity to species richness is generally unimodal at small spatial scales, but at larger spatial scales often positive monotonic relationships are observed across ecosystems (Waide et al., 1999; Mittelbach, 2010).

Several hypotheses have been proposed to explain the shape of the relationship between productivity and species richness, with special emphasis on the positive and negative slopes. A potentially high species richness in meso- to eutrophic ditches can be explained with the ‘More individuals hypothesis’ (Srivastava & Lawton, 1998), which suggests that a high resource availability within an area could support more individuals, and that communities with more individuals include more species, because a higher species abundance decreases the probability of local extinctions. It should be noted that another way in which this pattern could be generated is purely through passive sampling; more productive areas support more individuals and will thereby contain more species if individuals are randomly selected from the regional species pool (Evans et al., 2005; Chapter 3). A higher productivity can also cause an increase in the availability of ‘rare’ resources, exceeding the thresholds at which they can support viable populations of those species which rely on these resources. According to this “Niche position hypothesis” species utilizing these resources are only able to persist under these conditions, resulting in a higher species richness (Abrams, 1995; Evans et al., 2005). Finally, a high productivity could also lead to an increase in species richness by mitigating biotic interactions. More energy may result in longer food chains and greater numbers of predators (Chapter 5). As a result prey densities are lowered, reducing interspecific

competition and thereby promoting coexistence (Evans et al., 2005; Honkanen et al., 2010).

The decrease in species richness under very high levels of productivity (see also the composite environmental gradient in chapter 5) is most commonly explained by the 'Dominance Hypothesis' which suggests that when productivity is very high, a few species are able to dominate and competitively exclude other species (Huston, 1994; Rosenzweig, 1995). In drainage ditches this effect can be illustrated with the effect of mass development of certain species of filamentous algae in the epiphyton under hypertrophic conditions. This results a lower resource diversity for the higher trophic levels and only macroinvertebrates able to utilize the resources provided under these conditions are able to flourish. These species often occur in high abundances, which is possible because of the high productivity (e.g. Gastropoda dominance; Chapter 5). Nevertheless, negative side effects of hypertrophy and/or polysaprobity, such as hypoxia due to increased respiration, could exert an even larger effect on the macroinvertebrate assemblage and further decrease the number of species found.

Dissolved oxygen availability

The interaction between macrophytes, epiphyton, nutrients and organic load is not only crucial in determining the resources available for macroinvertebrates; the balance between primary production and decomposition of organic material is the main determinant of the waters oxygen regime. The occurrence of periods of hypoxia, either predictable or unpredictable, plays an important structuring role for macroinvertebrates (Clare & Edwards, 1983; Williams, 1996; Wellborn et al., 1996; Verberk et al., 2011). Here, evidence of the role of dissolved oxygen concentration in structuring the macroinvertebrate assemblage of drainage ditches was indirect; finding a relatively high proportion of macroinvertebrates with adaptations to oxygen deficits in ditches (Chapter 2, 5) and through differences in saprobic valences (which are directly related to oxygen availability; Bonada et al. 2006) among the fauna of ditches differing in nutrient loading and saprobity (Chapter 5).

Since hypoxic conditions and the fluctuations in chemical compounds associated with it are inherent to living in drainage ditches or other wetland environments, it is not surprising that many strategies have evolved to cope with low oxygen availability (Sharitz & Batzer, 1999). Some species avoid hypoxic situations by moving to the oxygenated zone of the

water body (Moore & Burn, 1968; Kolar & Rahel, 1993). Others have evolved physiological or behavioral mechanisms to resist hypoxia, through respiratory pigments, anaerobic metabolism, using atmospheric air for respiration or improving the oxygen uptake rate, e.g. by increasing oxygen availability by generating water flow along their body (Chapter 2, 5; Eriksen et al., 1984; Hoback & Stanley, 2001). For these species – which comprises many lentic macroinvertebrates, given the high species richness in drainage ditches – a short period of hypoxia does not put direct constraints to their distribution.

This does not mean that the fluctuations in dissolved oxygen concentration in ditches have no effect on macroinvertebrate performance at all. Given the highly impoverished assemblages found in hypertrophic polysaprobic ditches, which are generally dominated by a small number of highly abundant tolerant species, a prolonged period of anoxia is deleterious for most of the macroinvertebrate assemblage (Verdonschot, 1992; Nijboer et al., 2003). This is not only the result of the lack of oxygen, but also of the release of various for macroinvertebrates toxic components into the water under anoxic conditions (Maltby, 1995). Furthermore, even when conditions are less severe, all extra energy spend to obtain oxygen from the water, reposition themselves against the oxygen gradient present in the water, or inhibition of movement because of a lack of oxygen costs energy, which cannot be allocated to other functions, such as growth and development (Davies et al., 1992; Bjelke, 2005).

Multiple unpredictable disturbances result in highly divergent macroinvertebrate assemblages

Theoretically, many macroinvertebrate species could persist in a single ditch if i) strong environmental constraints are absent (e.g. high salinity or extensive periods of anoxia as environmental filters) ii) sufficient productivity results in a resource abundance exceeding the thresholds to support viable populations, and iii) coexistence of species is made possible through sufficient resource heterogeneity. Nonetheless, the variation in species composition among individual ditches or even ditch stretches is generally relatively high (Chapter 2). This divergence in assemblage composition can be explained by the way macroinvertebrate populations are affected by the instable nature of the drainage ditch environment. Macroinvertebrates in drainage ditches face a series of disturbances. Here, a disturbance is defined as any relative discrete event in time that removes macroinvertebrates and opens up habitat space which can be colonized by

individuals of the same or different species (Townsend, 1989). For example, a sudden increase in nutrient concentrations due to nutrient runoff of adjacent fields often leads to the development of extensive floating algal beds or Lemnaceae dominance. This completely alters the environmental conditions in the ditch stretch (e.g. prolonged periods of anoxia, poor underwater light conditions), at least temporarily. Also, too frequent or too rigorous ditch maintenance can be regarded as a severe disturbance with deleterious effects on the assemblages present (Beltman, 1987; Twisk et al., 2000). The predictability of these disturbances is low and depends on many variables, ranging from management decisions and regional policy making to weather conditions. As a result, a drainage ditch can be an extremely variable and unpredictable environment: the timing of the shifts in the mosaic is unpredictable, as well as the rate and magnitude of the changes.

For macroinvertebrates, persisting and sustaining vital populations in the unpredictable drainage ditch environment is only possible if they can i) remain present in the patch and avoid or tolerate periods of adverse conditions, or ii) track the 'windows of opportunity' provided within the drainage ditch network by moving from patch to patch. Given the extremely variable and unpredictable conditions in drainage ditches, a third strategy, synchronizing development with the spatiotemporal variability of the environment, does not seem to be a common strategy in drainage ditch systems, if it is present at all. After conditions in the ditch stretch have changed, three responses could be observed: the population is not affected by the disturbance, the population size is decreased, or the population goes (eventually) extinct. If the population is decreased due to environmental change, recovery of the population is possible through the remaining individuals (e.g. after mowing of the vegetation, individuals that survived in refugia such as the ditch bank or between uncut plant roots). If the population went extinct, recolonization from metapopulations in other patches or ditches – which are, for example, in a different successional stage – could take place, resulting in a new 'post-disturbance' population of the same species. Due to the differences in timing, rate and magnitude of disturbances among ditches, the relative importance of these responses in contributing to macroinvertebrate assemblage structure differs from ditch to ditch.

The role of dispersal in shaping drainage ditch macroinvertebrate assemblages

In the end, moving to other patches is inevitable for most species since the chance of extinction is high due to the unpredictable nature of the drainage ditch environment. As a result, dispersal ability and capacity become important factors for long term persistence of lentic invertebrate populations. Environmental changes are relatively rapid on small spatial scales, but when viewed on scales exceeding that of the patch, overall variability is much smaller. Thus, habitat predictability or stability in time is relatively low on patch scale, but on larger spatial scales the drainage ditch habitat is more predictable. Since the drainage ditch density in the Netherlands is very high (up to 400-1000 m ditch/ha), being capable of dispersing over relatively short distances might be enough to ensure long-term survival of populations.

Minimizing the need for dispersal appears to be – at least from an evolutionary point of view – beneficial, since in invertebrates a wide array of trade-offs with dispersal capacity or ability has evolved (Harrison & Dobson, 2008). Well known are the trade-offs between dispersal capacity and fecundity, of which many examples come from wing-dimorphic insects, for example in aquatic Heteroptera and Coleoptera (Roff, 1986; Zera & Denno, 1997). Even if fecundity is not directly affected, dispersal could have negative consequences for reproduction. For example, increased metabolic rate in dispersing Lepidoptera decreased their life span considerably. Since life span was positively related to the number of mating and oviposition opportunities, its reproduction success was affected (Hanski et al., 2006). Investments in dispersal may also result in reduced resource allocation to other traits that are not directly associated with reproduction, but related to acquiring resources, avoiding predators and environmental tolerance, e.g. improving regional coexistence but lowering local – within patch – coexistence of species. An example is the trade-off between the effectiveness of resource exploitation and dispersal capacity observed in Homoptera, in which one group of species has the ability of compensatory feeding on plants which deteriorate in nutritional value with time, whilst another group is capable of rapidly moving to new plants, resulting in niche partitioning (Huberty & Denno, 2006). Another trade-off is the colonization-competition trade-off (Levins & Culver, 1971; Hastings, 1980; Yu & Wilson, 2001; Calcagno et al., 2006). It makes coexistence possible under non-equilibrium conditions because due to dispersal limitation, superior competitors cannot exploit all available resources within a shifting

mosaic of habitat patches, offering opportunities for inferior competitors, which due to their good dispersal abilities can reach unoccupied patches before the superior competitor does. Finally, other trade-offs with dispersal include tolerance to extremes or fluctuations in certain physicochemical variables, and susceptibility to predation (Wellborn et al., 1996).

As a result of these trade-offs, there is considerable variation in dispersal capacity among macroinvertebrates. When dispersal is restricted in many macroinvertebrate species, the relative importance of stochasticity in structuring the assemblage is high as opposed to deterministic factors (Leibold et al., 2004; Lepori & Malqvist, 2009; Chase, 2010). As a consequence of dispersal limitation, macroinvertebrates can be absent at environmentally suited localities, simply because they were not able to reach these localities or because they went extinct there and were not yet able to colonize the localities again. This was illustrated by investigating the distribution of aquatic insects in drainage ditch networks on a regional scale (Chapter 4). Relatively poor dispersers have strongly clustered distributions, especially when viewed on large spatial scales, simply because they were not able to expand their distribution from these clusters (yet) and not because the surrounding habitat was not suited to complete their life cycle. Nevertheless, despite the poor dispersal capacity of species in this group long distance dispersal events (purely by chance or mediated by man, e.g. unintentional introduction with mowing machinery) can still lead to successful colonization of distant empty patches of habitat. For good dispersers, deterministic mechanisms are more important in comparison to dispersal related processes. Their distribution tracks abiotic and biotic changes in the environment, resulting in spatiotemporal variation in site occupancy and abundance. Good active dispersers are able to choose suited patches of habitat within a spatiotemporal mosaic and are able to avoid situations with, for example, many competitors or a high predation pressure. Passive dispersers with large numbers of colonists accomplish the same (in this case the small taxa), simply because the high number of dispersing individuals counteracts the negative consequences of the stochasticity associated with dispersing passively.

Post-disturbance community assembly in drainage ditches

After disturbance, population recovery of relict populations depends on the life history traits of the species and the quality of the patch, amongst others, abundance of resources, presence of competitors and conditions for reproduction (Siepel, 1996). At the same time, there is a constant supply of

colonists. Which species colonize the patch depends on the species dispersal ability and capacity as well as the size and distance to the nearest populations (Chapter 4). All colonists which pass the environmental filters present can potentially establish new populations, although sometimes local resident assemblages put restrictions on the species that could colonize next. Assemblage structure, especially the population sizes of different species, could diverge among localities as a result of stochastic variation in the sequence of species arrivals, even under identical environmental conditions and an identical regional species pool; e.g. there is a prominent role for priority effects (de Meester et al., 2005). This results in historical contingent community assembly (Fukami, 2009). Influence of the latter is supported by a number of recent studies (e.g. Irving et al., 2007; Vanschoenwinkel et al., 2007; Chase, 2010).

Nonetheless, when a species becomes established, it is not likely that it will be completely eliminated by the other species present or arriving subsequently from other localities, as shown in colonization studies of ponds (Barnes, 1983; Friday, 1987). Despite the large body of evidence describing the structuring role of competition and predation in freshwater ecosystems (e.g. Holomuzki et al., 2010), true competitive exclusion or complete consumption of populations appears to be very rare in macroinvertebrate assemblages (Vinson & Hawkins, 1998; Heino, 2005). There are different mechanisms which could explain the absence of severe competition among macroinvertebrates in freshwaters. Firstly, it is well established that many organisms differ in their niche positions along the multiple dimensions of the Hutchinsonian n -dimensional niche space (Hutchinson, 1957; Whittaker et al., 1973; Fox, 1981; Holt, 2009). In aquatic systems, such a pattern is demonstrated in, amongst others, stream macroinvertebrates and lentic mollusks (Soininen et al., 2011). Although these species interact, for example, by sharing the same habitat, they do not compete for resources because of niche differences. Secondly, even if macroinvertebrate species have identical niches the fact that they are not sedentary organisms makes that they cannot outcompete each other (Siepel, 1994).

Furthermore, if there is some form of competition among some of the species in the ditch, the spatiotemporal heterogeneity of the environment could mitigate the interactions between these competing species, thereby promoting species coexistence in a heterogeneous environment (Amarasekare, 2003; Davies et al., 2009; Holomuzki et al., 2010; White et al., 2010). For example, availability of macroinvertebrate food fluctuates continuously, on timescales much smaller than the

development time of the invertebrates consuming these resources; detritus quality changes in weeks, epiphyton in days, bacterial colonies in hours, whilst completing all larval stages of many detriti-herbivore insects generally takes months. Given the relatively opportunistic food preferences of many invertebrate species (Merritt & Cummins, 1984; Moog, 1995; Monakov, 2003) and a high productivity food limitation in drainage ditches is unlikely. Nonetheless, acquiring these resources as efficient as possible demands for strategies of coping with the spatiotemporal variation encountered, e.g. moving around within the habitat to optimize feeding efficiency (Chapter 6). At the same time, environmental factors change (e.g. dissolved oxygen concentration, presence of habitat due to ditch maintenance), offering advantages or disadvantages to certain species. For example, although lethal oxygen thresholds are not exceeded, the need to ventilate to obtain oxygen from the water cost energy. This energy cannot be allocated to other functions, such as growth, or the organisms are forced to leave their preferred food patch to position themselves at the in that situation most optimal locality against the oxygen gradient. To complicate things even further, predation removes organisms directly or alters prey behavior, thereby offering new opportunities for the remaining set of individuals.

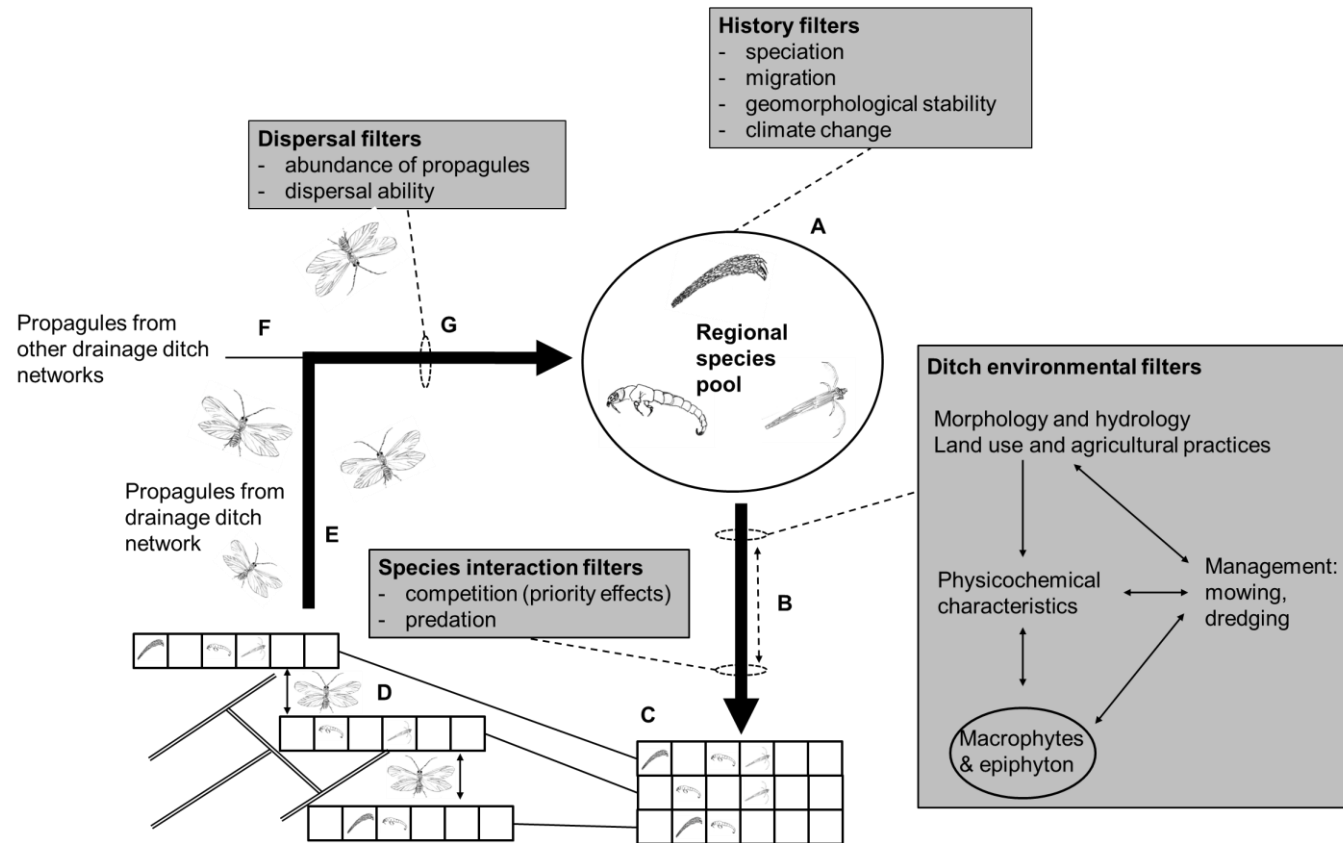
A conceptual model explaining the divergence in drainage ditch macroinvertebrate assemblages within ditch networks

Vegetated meso- to eutrophic ditches with a low salinity have a high biodiversity potential (Chapter 2, 5). Theoretically, most species from the regional lentic species pool should be able to occur in these systems. Nonetheless, processes occurring simultaneously and at multiple spatial scales within a region influence the macroinvertebrate assemblage found at a single location within a drainage ditch network (Chapter 3, 4, 5), resulting in highly divergent assemblages when individual ditches are compared. Firstly, deterministic mechanisms (e.g. shifts in patch quality due to anthropogenic or natural disturbances) are underlying these dynamic patterns. Especially the high frequency and unpredictability of disturbances in the ditch environment limits the number of species that could occur together within a single patch at a certain moment in time. This results in a patchy macroinvertebrate assemblage structure within a drainage ditch network, a mosaic of assemblages all differing to a greater or lesser degree in species composition. In time, the species composition of the patches changes, driven by the changes in environmental conditions as well as due to colonization by species dispersing from other patches. Thus,

metapopulation dynamics of species are the second important factor underlying the divergence in assemblage composition among ditches within a ditch network (Figure 7.2).

Depending on the shifts in patch environmental conditions which take place within the drainage ditch network, populations of some species flourish, whilst others remain marginal. Species which are unaffected by most disturbances, resulting in large populations, or species which are able to establish large populations before the patch is disturbed again have clear advantages for long-term persistence: a decreased risk of extinction and a higher chance of propagules having established populations in other patches within the mosaic (Hanski, 1982; Gotelli, 1991; Rosenzweig, 1995; Gaston et al., 2000; Verberk et al., 2010). Even if habitats are not completely suited, highly abundant species can still be present due to mass effects from core-populations (Shmida & Wilson, 1985; Magurran, 2007). Nonetheless, given the patchiness in species distributions among drainage ditches, this does not seem to apply to most species (Chapter 2). Actually, the opposite appears to be the case: only several species are present almost everywhere, whilst most others occur in low densities only and are often absent when individual ditches are compared. With common species occupying most habitats, and the scarce to rare species displaying increasingly scattered distributions, aquatic systems display a certain degree of nestedness, with species-poor localities containing subsets of the assemblages found in species-rich localities (McAbendroth et al., 2005; see also Trichoptera distribution pattern in Chapter 1).

Figure 7.2 (next page): Schematic representation of the interactions between local (environmental conditions and biotic interactions) and regional factors (dispersal and colonization-extinction patterns) in determining local assemblage composition in drainage ditch networks. A. The regional species pool represents the species available to colonize a location. Exact composition of this pool depends on the history of the region and its macroinvertebrate assemblages. B. Species from the regional species pool arriving at a location are filtered based on their tolerances to environmental factors and preferences for specific habitat components. Besides environmental filters, also biotic interactions play an important role for species to establish a population. Both sets of filters are not independent; there are many inter-relationships. C. An macroinvertebrate assemblage at a locality is composed of species inhabiting the different microhabitats available. Generally these are the macrophytes and its associated epiphyton. D. Availability and quality of the microhabitat patches changes constantly, resulting in a shifting mosaic of suited patches. Species track this heterogeneity, either by moving around during their aquatic life stage or as an adult by ovipositioning in, for example, an adjacent ditch. E. Part of the individuals of the species present disperses from the drainage ditch network and becomes part of the regional species pool. F. Species from other drainage ditch networks (or other lentic systems) can potentially contribute to the regional species pool. G. The process of dispersal filters the propagules. Modified from Hillebrand and Blenckner (2002) and Brown et al. (2011).



This situation can be explained by unpredictable shifts in the balance between the frequency of disturbance (F_D), the recovery rate of relict populations (R_R) and the recolonization rate (R_C) (Siepel, 1996) (Fig. 7.3). Resident populations of disturbance-sensitive-species are removed when the frequency of disturbance is much higher compared to the recovery rate of the population. If the disturbance regime remains unaltered in time, it is simply not possible for those species to establish a population. When the frequency of disturbance is lower than the recovery rate of the population, or the population is not affected by the disturbance at all, it could expand until all habitat space and resources are used, eventually resulting in a small group of species dominating the patch (Connell, 1978; Huston, 1979). If the recovery rate of the populations is more or less equal to the frequency of disturbance, extinction is minimized whilst dominance is suppressed, resulting in a highly diverse mixture of species with relatively small population sizes. Since in ditches the type of disturbance and its frequency are rather unpredictable, all three scenarios could apply in time for all species present. As a consequence, changes in assemblage composition in the past also affect the present composition. Patch history is essential in understanding the assemblage composition today (Ricklefs, 1987).

Given the metacommunity structure of drainage ditch assemblages, the process of extinction and decimation of local populations as a result of disturbances is counteracted by colonization (Fig. 7.3). If the colonization rate of species is lower than the frequency of disturbance, many patches remain uncolonized. If the colonization rate is higher than the frequency of disturbance, the species return rapidly after disturbance, leading to homogenization of the mosaic of habitat patches in terms of species composition. If colonization rate and disturbance frequency are balanced, species are absent for shorter or longer periods, but could eventually return to every patch within the mosaic. Especially the latter scenario promotes divergence in assemblage composition among patches. At the same time, this divergence makes drainage ditch assemblages extremely vulnerable for homogenization of environmental conditions on larger scales, for example, as a result of a sudden increase in salinity at network scale. This disrupts the metacommunity structure of the drainage ditch assemblages, resulting in a decrease in the number of colonists arriving from un- or less impacted patches.

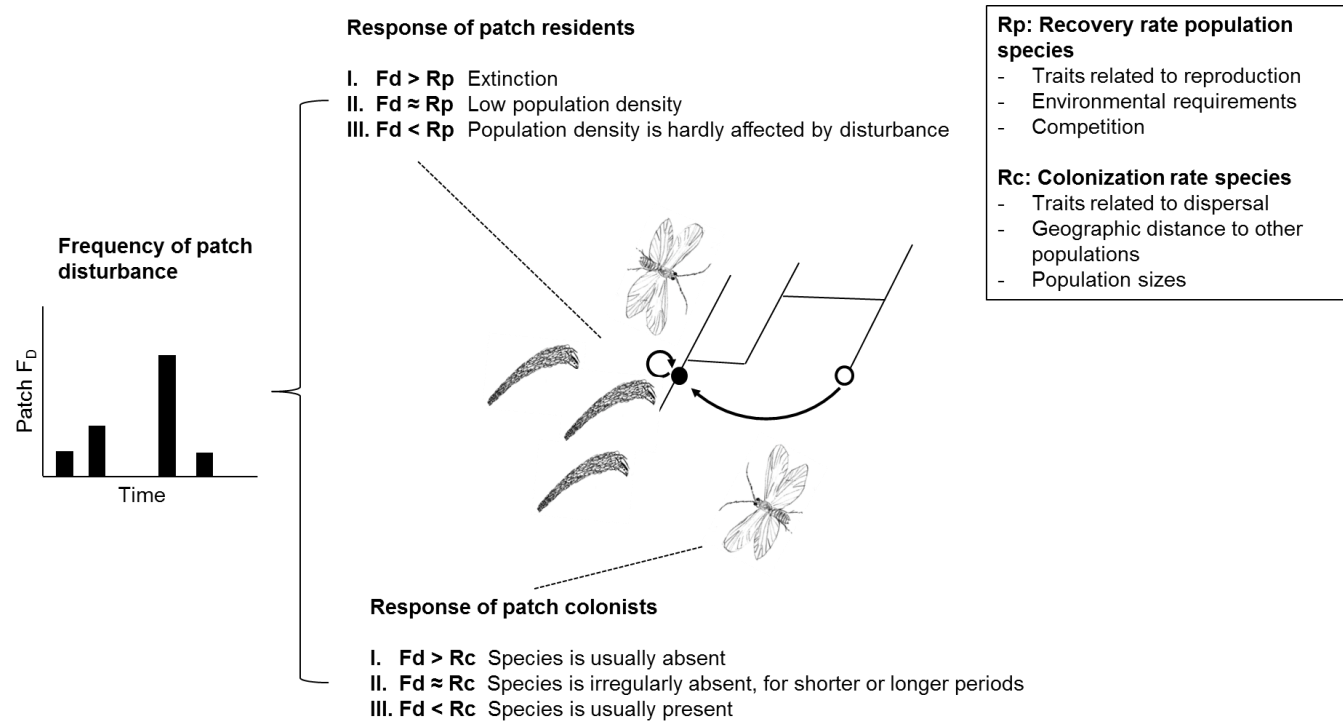


Fig. 7.3: Shifts in the balance between the frequency of disturbance (F_D), the recovery rate of relict populations (R_R) and the recolonization rate (R_C) (Siepel, 1996) because of frequent, unpredictable disturbances in drainage ditch networks result in highly divergent assemblages when viewed on patch scale. Depending on the species specific response to the disturbance, situation I to III can be observed within a patch.

Under which disturbance regime biodiversity is maximized ultimately depends on the life history traits of the species; a mixture of population (number of propagules, reproduction mode, voltinism) and dispersal parameters (wing size, body size, dispersal mode) in combination with the degree of spatiotemporal variation within the drainage ditch network, the availability of a variety of refuges. This does not have to be at an intermediate level of disturbance, *sensu* the intermediate disturbance hypothesis, in which infrequent disturbances offer opportunities for a wide array of species to occur together (Connell, 1978). It is the response of the macroinvertebrate assemblages to the shifting mosaic of habitat patches which determines the effect. Even if disturbances are highly frequent, but macroinvertebrates can keep track of the changes by dispersing among the patches, species diversity can be maintained at a high level ('mobility controlled' assemblages; Townsend, 1989). On the other hand, one extreme disturbance which exceeds the tolerance of many species and has an impact on a large spatial scale could exert strong and persistent effects on the assemblage structure.

Implications for the biomonitoring and assessment of drainage ditch ecological quality based on macroinvertebrates

As shown in the previous paragraphs, it is very hard to predict the exact species combination that could be found in a meso- to eutrophic macrophyte-rich ditch at a certain moment in time. There is no such thing as a typical meso- to eutrophic drainage ditch community, represented by a static set of species, at least not on small spatial and temporal scales. Therefore, the potential drainage ditch macroinvertebrate fauna can best be viewed on a larger scale, as all species occurring in lentic and very slowly flowing lotic systems. These species comprise the regional species pool. Since little is known about the true dispersal rate of macroinvertebrates, it is unknown what should be considered as the complete 'region'; depending on the species this could range from less than a kilometer to hundreds of kilometers (Chapter 4). Given the distribution of many lentic macroinvertebrate species within Europe, maybe regional could even be read as when viewed on the scale of macroinvertebrate biogeographical regions (Ecoregion 13 or 14; Illies, 1978). Combinations of all the members of the regional species pool can potentially make up a single drainage ditch assemblage at a certain point in time when these species were able to pass the different filters applicable.

From an applied point of view establishing causal links between environmental changes and changes in the composition and structure of macroinvertebrate assemblages can be considered a major challenge. As described in the previous paragraphs a sample of the macroinvertebrate assemblage of a drainage ditch, such as the standard 5-m pond net sample as collected by Dutch water managers, is only a snapshot of the diversity of a ditch in space and time, a subsample of the total number of species present in the drainage ditch network. The locally abundant species, in terms of patch occupancy or number of individuals, are relatively easy to record. Determining the presence of less common species is more difficult and recording all species within a water body will require an immense sampling effort. Within the spatiotemporal mosaic of drainage ditch habitat patches, small scale short-term fluctuations in deterministic factors and processes related to dispersal could lead to highly scattered distribution patterns of these species at small spatial scales. Considering the macroinvertebrate fauna of drainage ditch networks within a metacommunity framework, a continuous exchange of individuals between ditches within the drainage ditch network or neighboring aquatic systems leads to a situation in which turnover in taxon composition within single patches can be high.

When using 5 m standard pond net samples to determine the assemblage composition of ditches, as used in routine biomonitoring in The Netherlands, the scale of sampling is restricted to 10 sections of 0.5 m along a 50 m ditch stretch. This technique gives a representation of the macroinvertebrate assemblage present in that section, but it is doubtful if this gives enough information to extrapolate this to larger spatial scales (representative of different ditches within a drainage ditch network) or when viewed over longer timescales (e.g. when sampling is repeated for several years). As a consequence, when macroinvertebrates are sampled for assessment purposes and especially for trend monitoring it is questionable if the data collected represents the assemblage present at the location well enough. One option to tackle this problem is to scale up monitoring within the drainage ditch network. Despite variability in species composition is high on a small spatial scale, e.g. when sampling single patches of vegetation, when viewed on scales exceeding that of the patch, overall variability is likely to be much smaller. This is especially true when whole ditch networks are incorporated into randomized monitoring schemes. To accomplish this, in terms of resources available for biomonitoring, the method used should be easy and quick. Activity traps proved to be useful for capturing drainage ditch macroinvertebrates (Chapter 6). Because of

their relatively low labor requirements and high level of standardization, activity traps appear to be a valuable tool in large scale lentic biodiversity surveys. Learning more about the spatiotemporal patterns in macroinvertebrate species distributions on a scale exceeding that of a single patch is necessary to better understand the functioning of species assemblages on larger spatial scales, e.g. in a metacommunity context. In the end, dispersal of species among the individual patches within the drainage ditch network is crucial for long term persistence in the frequently disturbed unpredictable drainage ditch environment.

Environmental heterogeneity and the shifting mosaic of habitat patches especially affect the uncommon species in the assemblage, which comprise the majority of the assemblage. As a result, identifying change in macroinvertebrate assemblages resulting from negative anthropogenic influences is difficult to separate from the natural variation in the assemblage. Of course, the homogenizing force of severe degradation (strong environmental filters), e.g. under high levels of organic pollution or the inlet of chloride-rich water, resulting in the persistence of a few species which occur in very high densities, is readily detectable (Chapter 5; Verdonschot, 1992; Nijboer et al., 2003). The challenge lies in identifying and explaining the onset and early phases of degradation. With the ongoing loss of natural resources it has become an urgent task to identify 'early warning signals' in aquatic ecosystems, before the system collapses into a self-sustaining degraded state (e.g. clear and turbid shallow lakes; Scheffer, 1998), in this case drainage ditches permanently dominated by Lemnaceae or algae.

Distinguishing these 'early warning signals' or 'silent indicators' of a degradation of ecological quality from the natural variation at a site is a major challenge in spatiotemporal heterogeneous environments such as drainage ditches. Three commonly mentioned indicators of ecological quality of water bodies are: i.) species richness of a locality, e.g. all species present in the ditch, ii.) presence of some set of characteristic or indicator species, common or rare, iii.) diversity of ecosystem functions performed by the species present. In fact, all three definitions comprise potential important components indicative of the quality of the ecosystem. Species richness represents the reservoir of species available to track the spatiotemporal variation in the drainage ditch environment. Changing conditions could result in the common species becoming rare and vice versa. Indicator species illustrate the specific conditions at a certain moment in time, mostly environmental factors or habitat characteristics. By matching species tolerances to environmental conditions the status of the system can

be assessed. Finally, the ecosystem functions performed by different species (e.g. mediating decomposition by transforming organic matter, grazing of algae) are important for the functioning of the entire ecosystem. Loss of functions leads inevitably to the degradation of the ecosystem. These three components are not independent; there are many inter-relationships, for example, a high species richness could result in the presence of many different species able to perform the same ecosystem function. This functional redundancy could be useful for overall ecosystem functioning if one species goes extinct at a location and is replaced by a functional equivalent species (Covich et al., 2004).

Actual incorporation of the three components was done by defining biological integrity of water bodies as the benchmark of ecological quality (Karr & Dudley, 1981): ‘the capability of supporting and maintaining a balanced, integrated, adaptive community of organisms having a species composition, diversity, and functional organization comparable to that of natural habitat of the region (here best available situation because of anthropogenic origin; Stoddard et al., 2006)’. In case of drainage ditches this can be interpreted as a situation in which disturbance frequency – either anthropogenic or natural – is in balance with the recovery rate of the populations of species of which the assemblage is composed of as well as a situation in which the colonization rate is in balance with the disturbance frequency, resulting in a metapopulation structure which could counterbalance the extinction of local populations. As a consequence, in a drainage ditch network with a high level of biological integrity species richness is high, but individual species are distributed over different patches within the network. Shifts in environmental conditions as a result of disturbances can be tracked by the species, either from relict populations or by dispersing individuals and overall ecosystem functioning is maintained.

Integrating different components of the macroinvertebrate assemblage – the multimetric approach – is one of the ways of avoiding some of the problems associated with using specific species or the autoecological information they provide as indicators of ecological quality. This is useful in drainage ditches, since the exact species composition of individual ditches is hard to predict. Using the multimetric approach, emphasis is put not only on the specific taxon composition, but also on more general measures, such as diversity, assemblage composition, tolerances and functional characteristics. Therefore, it should be able to cope better with the patchiness of the drainage ditch macroinvertebrate assemblages in comparison to, for example, focusing on indicator species only (Chapter 5). Still, it does not cope with shifting baselines due to natural

or anthropogenic variation on longer timescales. Focusing on the life history traits of macroinvertebrates and combining them into life history strategies or tactics (Verberk et al., 2008) would be a fruitful approach to get a better insight into the consequences of environmental change on macroinvertebrate assemblages. Unfortunately, this requires extensive knowledge on the autecology of the species involved, information which is currently insufficient known or highly anecdotal for most macroinvertebrate species.

Future research questions

This thesis shed some light on the drivers underlying the drainage ditch macroinvertebrate diversity patterns observed in the Dutch drainage ditch systems and its consequences for biomonitoring and assessment. Still, many questions remain unanswered and can be interesting starting points for future studies:

- Why does an increase in salinity result in such a significant impoverishment of the ditch insect fauna (Chapter 5)? Given the abundance of insects in freshwaters, surprisingly few species have evolved adaptations to tolerate brackish conditions. Is this the result of physiological constraints, competition with non-insects or changes in habitat structure?
- It is unknown which relationship exists between ditch density per unit of land surface area and species richness of its individual patches; if ditch density is low, it could decrease the chance of recolonization of patches after disturbance, simply because the number of potential colonists is low. As a consequence, disturbances could lead to the extinction of populations of relatively poor dispersers more quickly compared to networks with a high ditch density, leading to a lower overall biodiversity. In other words, hypothetically ditch macroinvertebrate resilience to disturbance is higher in areas with a high ditch density because of a higher recolonization rate.
- Related to the former question: could homogenization of the fauna of drainage ditch networks due to a sudden, strong increase in salinity, trophy or saprobity (exceeding the tolerance limits of many species) result in a loss of its metacommunity structure and with that its resilience to future disturbances. Furthermore, how much patch heterogeneity is needed to sustain this balance within a

drainage ditch network, is this a linear relationship or is there a threshold value?

- Is the ‘relevant scale of study’ similar for all macroinvertebrates, or should each order or size class be viewed on separate scales (e.g. the size difference between a small-bodied Chironomidae vs. a large-bodied Odonata spans more than an order of magnitude). Depending on the landscape scale relevant to the organisms, different processes are likely to be important in structuring its abundance and distribution.

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Carlijn, het feit dat ik de laatste delen van dit proefschrift naast je ziekenhuisbed heb geschreven, spreekt boekdelen. Het is onvoorstelbaar hoe bizar dingen in het leven kunnen lopen en het huisje-boompje-beestje gevoel ineens wreed verstoord kan worden. Gelukkig ben je de sterkste en strijdvaardigste vrouw die ik ken en weet ik zeker dat je dit tot een goed einde gaat brengen, hoe lang de weg ook zal zijn. Tenslotte natuurlijk nog de boefjes, Isa en Mats: het is fijn dat jullie er zijn! Isa, je mooie waterbeestjes-tekeningen hebben een prominent plekje gekregen op de kaft van het boekje.

Curriculum vitae

Ralf Carsten Marijn Verdonschot werd op 17 juni 1981 geboren in Kampen. Zijn jeugd bracht hij door in Leersum. Van kleins af aan was hij met natuur bezig en was hij te vinden bij de vennen op de Utrechtse Heuvelrug of in de uiterwaarden van de Nederrijn. Als klein jongetje ging hij regelmatig mee tijdens veldwerk van het toenmalige Rijksinstituut voor Natuurbeheer en maakte kennis met de zoetwaterecologie. Tijdens zijn middelbareschooltijd werd hij lid van de Jeugdbond voor Natuur en Milieustudie en bracht veel tijd door in de natuur. Hij werd toen een steeds fanatiekere vogelaar. Na afronding van het VWO aan het Revis Lyceum in Doorn begon hij in 2000 aan de studie Biologie aan de Wageningen Universiteit. Hier was de keuze voor de ecologie snel gemaakt. Tijdens de afstudeervakken werden de eerste wetenschappelijke stappen gezet bij de vakgroep Natuurbeheer en Plantenecologie. In de uiterwaarden van de Waal, bestudeerde hij de relatie tussen vegetatietypen en het voorkomen van loopkevers. Hier werd zijn interesse gewekt voor de entomologie. Vervolgens werd het terrestrische werkveld toch ingeruild voor de aquatische ecologie, misschien voor veel mensen niet geheel onverwachts (met de paplepel ingegoten?). Bij de vakgroep Aquatische Ecologie en Waterkwaliteitsbeheer en bij de Vlinderstichting deed hij onderzoek naar libellen: enerzijds naar de relatie tussen het voorkomen van libellensoorten bij vennen en de milieuomstandigheden die daar heersten en anderzijds aan de hand van een labexperiment waarin de preferentie van larven voor bepaalde habitatstructuren werd bestudeerd. Tijdens zijn stage vertrok hij in 2006 voor een half jaar naar Canada, om bij de Surface and Groundwater Ecology Group van de University of Toronto de fauna van met water gevulde boomholtes te bestuderen. Na terugkomst uit Canada studeerde hij af en kon tijdelijk als uitzendkracht aan de slag bij Alterra. Daarna werkte hij een jaar als junior onderzoeker bij Stichting Bargerveen in Nijmegen, waar hij onderzoek deed naar de ongewerveldenfauna in de kustduinen. Een mogelijkheid om terug te keren naar Alterra deed zich voor en daar ging hij in 2008 aan de slag als junior onderzoeker bij het team zoetwaterecologie. De eerste jaren werd gewerkt aan het PLONS-project, waarvan het eindresultaat dit proefschrift is geworden. Momenteel werkt hij binnen diverse projecten, waaronder onderzoek aan de ongewerveldenfauna van beekbegeleidende broekbossen en zeggenmoerassen en de habitat- en systeemgeschiktheid van beken en stroomgebieden voor beekvissen.

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