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The incidence and turnover of temporary pond macroinvertebrate metacommunities over ten years.

Michael James Jeffries,

Division of Environmental Management,
School of Applied Sciences,
Ellison Building,
Northumbria University,
Newcastle upon Tyne,
NE1 8St
UK

Correspondence author: michael.jeffries@unn.ac.uk

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"This paper has not been submitted elsewhere in identical or similar form, nor will it be during the first three months after its submission to Hydrobiology"

Abstract.

Ponds support a rich biodiversity. This diversity arises in part because of the number and heterogeneity of ponds over the landscape. Studies of ponds suggest that distinct metacommunities develop within individual ponds but most examples are based on short-term one, perhaps two, year surveys. This study reports the development and turnover of the early summer macroinvertebrate metacommunities in thirty small, adjacent temporary ponds from their creation in 1994 over ten years to 2004. Invertebrate metacommunities were defined by multivariate classification and the incidence of these communities modelled using hydrology and plant communities as predictor variables. Distinct metacommunities established in the first year of the ponds' creation, the first two years dominated by a pioneer fauna associated with long summer dry phases. A permanent water fauna established during the following two years which lacked dry-phases, followed by a return of summer dry phases resulting in a loss of some permanent water taxa and re-colonisation by some temporary water species creating new metacommunities. Models of the incidence of these metacommunities proved effective supporting the hypothesis that the turnover of metacommunities can be treated similarly to that of individual species. The metacommunities were not a linear successional sequence; the communities that re-assembled following resumption of dry phases reflected the contingent history of each pond. Species-sorting dominated the establishment and turnover of these metacommunities, along with the storage effect primarily via egg banks. Mass-effects, operating through the provision of taxa from the local landscape species-pool, also played a role throughout the ten years.

Introduction.

The last twenty years has seen a remarkable renaissance in the study of pond ecology (Oertli et al., 2009). A wealth of studies have demonstrated the importance of ponds for their disproportionately rich biodiversity, e.g. Williams et al. (2003), Biggs et al. (2005), and ponds have provided a very effective practical arena for exploring fundamental ecological processes (Wilbur, 1997; Oertli et al., 2009). Ponds are important for the richness of their wildlife and number of rare species, (e.g. Collinson et al., 1995), their role in geochemical cycles (e.g. carbon capture, Downing et al., 2008) and have an iconic status in many societies (e.g. significance of ponds in Welsh culture, Rees 1998). The number, ubiquity and scatter of ponds across many landscapes has also resulted in them providing useful arenas in which to investigate fundamental ecology. Ponds and their wildlife have provided data for studies from the genetic scale, e.g. comparing measures of effective distance in studies of genetic differentiation of *Daphnia* populations, Michels et al. (2001), up to large scale landscape and temporal studies, e.g. regional diversity of water beetles across the palearctic influences diversity within individual ponds, Kholin and Nilsson, (1998). Ponds have long played a role in studies of community ecology, especially the interplay of local conditions and interactions within ponds versus the role of dispersal, colonisation and allied processes operating beyond the habitat itself, e.g. Darwin's experiments dunking a duck's feet into aquaria to test their role as potential vectors of juvenile molluscs, (Darwin, 1859).

Studies of pond communities include long-standing traditions of both extensive survey (e.g. the distribution of Mollusca amongst English ponds, Boycott 1936) and intensive experiment (e.g. manipulation of invertebrate food webs, Wilbur 1997). The majority of studies on pond wildlife show that the biodiversity within any individual pond varies in response to many influences, from the specific local conditions within a pond to regional landscape characteristics. Whilst most studies of pond communities have focused on spatial diversity, which can be assessed from short-term, perhaps one year, surveys, a smaller number of studies incorporating data from more than one or two years suggest that the characteristic diversity of pond communities is temporal as well as spatial (invertebrates; Jeffries, 1994; Chase, 2007; Florencio et al., 2009; Ripley & Simovich, 2009; invertebrates and plants, Williams et al., 2008; plants Jeffries, 2008; Rhazi et al., 2009; amphibians Rannap et al., 2009). The sheer diversity of communities that results from these multiple influences is a particular feature of ponds, Williams et al. (2003); however it is hard to generalise patterns, sometimes suggesting that pond communities may be dominated by random (or stochastic) assembly processes (Talling, 1951; Nabout et al., 2009).

Because of this spatial and temporal variation, ponds have proven instructive habitats to test different models of metacommunity assembly (e.g. invertebrates Cottenie et al., 2001; Urban 2004; Cottenie & De Meester, 2004; Ng et al., 2009; phytoplankton Vanormelingen et al., 2008; plants Jeffries, 2008). Existing studies support the species-sorting hypothesis as the predominant model for pond invertebrate metacommunities (Cottenie et al., 2001; Cottenie & De Meester, 2004; Urban 2004; Ripley & Simovich, 2009), which emphasises the variability of conditions between patches, resulting in varied metacommunities because different species have differing needs and tolerances. Mass-effect processes, which emphasise the importance of immigration and establishment across the landscape (Holyoak et al., 2005) may also have a role. The same studies which have demonstrated the role of species-sorting have also shown mass-effects; e,g, dispersal is important for providing the taxa upon which species-sorting acts, Cottenie & De Meester, (2004, 2005), whilst Howeth & Liebold (2008) showed dispersal of phytoplankton dampened outcomes of trophic interactions and Vanormelingen et al. (2008), reported phytoplankton in adjacent, connected ponds showed similarities suggesting dispersal mass effects although local species-sorting dominated. Dispersal through time is also important for temporary ponds, particularly the role of egg banks or other dormant stages, the so-called storage effect, as a means of coping with environmental variation (Chesson, 1985; Shea et al., 2004). The re-appearence of taxa emerging from eggs or other drought resisting life stages is a process which integrates community variation across time (Vandekerkhove et al., 2005) , essentially "dispersal from the past" (Bohonak

and Jenkins, 2003). Studies of pond communities have not supported either the patch dynamic models, in which habitat patches are assumed to be similar and metacommunities undergo asynchronous colonization and extinction thereby creating variety at the landscape scale or the neutral model, which assumes species do not differ in either dispersability or niche requirements (Holyoak et al., 2005).

The invertebrate communities of temporary ponds have proved instructive for studying metacommunities; temporary ponds are often small, numerous and prone to changes driven by hydrological variation, making them effective habitats for studying longer term change. Temporary ponds are also a globally important habitat, their significance now recognised after many years of neglect (Collinson et al*.,* 1995; Williams et al*.,* 2001. See Brown, 1951 for early appreciation of these once neglected habitats). Their metacommunities are determined primarily by the hydrological regime, Williams (2006), but can also show marked biotic interactions (e.g. the impact of the temporary pool specialist tadpole shrimp *Triops newberryi* (Packard) reducing populations of other invertebrates in pools, Walton, 2001). Although studies of temporary ponds are dominated by short-term surveys confined to one year, longer-term investigations suggest temporal change is significant, e.g. Jeffries (1994) described community turnover in small ponds responding to hydrological variation over six years, Bauder (2005) demonstrated the importance of precipitation for controlling pond hydrology over twenty years and Chase (2007) explored the role of drought as a factor homogenizing invertebrate communities over the course of four years. These studies suggest that the metacommunities of temporary ponds may come and go in a way analogous to the extinction and colonisation of individual species.

Characterisations of pond invertebrate communities have been dominated by the use of multivariate classification and ordination to summarise and describe metacommunities and their relationships to environmental variables. Whilst turnover between years in some longer term studies has been represented using such strategies (e.g. Jeffries 1994) the actual incidence and turnover of metacommunities has not been modelled.

This study specifically aimed to characterise and model the incidence and turnover of temporary pond invertebrate metacommunities over a long term (ten year) period. The study ponds were dug in 1994 and sampled regularly until 2004, and the incidence of the communities modelled in the same way as the turnover of individual species can be investigated. This required the following objectives, (1) describing and tracking changes to invertebrate communities over several years, (2) identification of distinct and ecologically meaningful metacommunities and (3) modelling the incidence of metacommunities.

Methods.

The site.

Thirty small ponds (each pond 1 m^2, 30 cm deep with a 40 cm deep central area) were dug in a seasonally flooded field at Hauxley Nature Reserve, Northumberland, UK, in the Autumn of 1994. Ponds were arrayed across a roughly triangular area of the field dominated by National Vegetation Classification S19 *Eleocharis palustris* (L.) swamp (Rodwell, 1995). All ponds filled with water within a day of being dug. The Hauxley Nature Reserve supports many temporary and permanent ponds, and is part of an extensive set of wetland reserves running southward from Hauxley for 10 km along Druridge Bay providing ample sources for colonisation.

The ponds are very small but comparable in size to habitats such as pools (De Bie et al., 2008), rock pools (Vanschoenwinkel et a., 2009) and microcosms (e.g. Fernandez et al., 2009) used in studies of invertebrate communities. Small pools were widespread throughout Druridge Bay but generalising results to larger pond, permanent ponds may be problematic given the evidence that small pools have lower species richness (De Bie et al., 2008). The ponds were close together, arrayed over an area approximately 30m east-west and 25m

north-south, much closer together than recognised spatial constraints on the dispersal of freshwater invertebrates (Shurin et al., 2000; Bilton, Freeland & Okamura 2001; Lundkvis et al., 2002; Urban, 2004). As with their small size this may constrain extending insights to larger, more dispersed ponds, although the proximity of each pond is again typical of small, temporary pond systems which can show marked differences between communities at such scales (Jeffries, 1989; Ripley & Simovich, 2009). The first animals, the Corixidae *Corixa punctata* (Illiger) and the Dytisidae *Agabus bipustulatus* (L.), were observed in the ponds within days, and, by January 1995, all ponds supported some invertebrates, e.g. the Cladoceran *Daphnia obtusa* Kurz in twenty ponds with an additional 17 taxa recorded.

Sampling.

Animals. Animals were sampled in early summer (late May through to early July), the precise time varying as water levels fell towards the summer dry phase. In addition samples were taken some years in autumn when ponds had refilled and in late January; these data are not used for the primary analyses reported but here they provide useful insights into re-establishment of taxa from eggs banks or recolonisation. Each sample consisted of a presence/absence list of taxa in the pond. This list was obtained by firstly sweeping a small fine mesh (0.5mm) net through the pond, the contents of which emptied into a white tray from which smaller animals (e.g. Copepoda) were picked out. This was followed by a larger dip net (mesh 1mm), swept though the ponds, again the contents tipped out into a tray and examined, until no new taxa could be found, or at least five sweeps even if no more had been added by previous sweeps. The smallest animals recorded were Harpacticoida and *Chydorus* sp. whilst the largest were adult Salamandridae; smaller taxa e.g. Rotifera and protistans were not included. Once sampling was complete the animals were the returned to their pond. Pilot studies estimated that five sweeps captured a mean of 89% of taxa with in the size ranges.

Although the majority of taxa were identified in the field examples of small (e.g. Ostracoda, Copepoda) or taxonomically difficult groups (e.g. *Hydroporus* beetles, Chironomidae) were kept for laboratory identification. Identification was to species level for most taxa, except for Chironomidae and Copepoda (genus) or Harpactocioida, and Ceratopogonidae recorded as family. In addition juvenile stages of many taxa were recorded separately and are kept so in the analyses. For example the water-boatman *Notonecta glauca* L. was as an adult and juvenile; the analyses included adults and juvenile instars as two separate taxa. A few species have been combined together in analyses because determining their presence could not be done reliably without killing substantial numbers, perhaps every individual, for detailed examination, which would defeat the purpose of the sampling regime which was intended; *Hydroporus striola* (Gyllenhal) and *H. Pubescens* (Gyllenhal) combined as *Hydroporus* spp., *Helophorus brevipalpis* Bedel and *H. obscurus* combined as *Helophorus* spp. and *Dixella* midges.

The use of presence/absence data alone is simplistic, ignoring the likely importance of relative abundance. However the presence/absence data allowed most individuals to be put back into their ponds alive, minimising losses which could have had an important impact on these small habitats given the long term sampling strategy of the study. Presence/absence data has proved effective for characterising macroinvertebrate communities of similar ponds (Jeffries, 1989, 1994). The effect of infrequent taxa on subsequent analyses was explored by comparing classifications using all the taxa with data from which species occurring in only <=1% or <= 5% of samples had been excluded.

In autumn 1996 and January 1997 twenty-two species of invertebrate which had previously been absent or infrequent in the ponds were added to some ponds as part of an experimental manipulation predator-prey ratios (16 herbivores to ten ponds, 6 predators to another ten. For full details see Jeffries, 2002). The majority established and colonised adjacent ponds naturally and are included in the data and analyses.

Hydrology. Ponds were visited regularly throughout the years of the study and each pond was recorded in one of three conditions (1) dry (no open water, exposed substrate), (2) wet (open water over the substrate) or (3) inundated and connected to adjacent ponds. Dry and inundated dates were recorded from the inclusive date at which the pond was first recorded in that condition to the date at which it was recorded as having changed state. Visits were more frequent during periods of drying and refilling, so that in most cases the dates are accurate to within 3 days. So for each pond there is an individual record of its hydrological condition throughout every year.

Macrophyte vegetation. The plants within each pond were recorded to characterise the individual ponds' habitats. The plant communities in the ponds were sampled immediately before sampling the animals. Plants were recorded using a $1m^2$ quadrat with cross-wires at 10 cm intervals, giving 81 intersections inside the pond area, the intersections used as point samples (full details in Jeffries 2008). Distinct plant communities showed a deterministic pattern of succession linked to the age of the pond and the local hydrology, the latter contingent on the spatial position of the pond. So, the plants provide a characterisation of the local habitat within each pond, reflecting a range of wider environmental influences. (for full details of the plant communities see Jeffries, 2008). The plant communities were used in this study as categorical predictor variables in the models of animal metacommunities (Table 1).

Analyses.

The primary objectives of this study were to (1) describe how communties developed and changed over several years, (2) identify distinct metacommunities in the early summer ponds and (3) model the incidence of different macroinvertebrate metacommunities.

Note that the analyses used to describe and define the metacommunities (steps (1) and (2)) were carried out on data sets containing all taxa and also data sets from which taxa occurring in <=1% or <=5% of samples had been removed, to examine the effects of infrequent taxa on outcomes. Both data sets with rarer taxa removed gave similar outcomes, with 18 of the samples classified differently to the full data set and slightly more ecologically coherent metacommunities, so all final classifications and models presented here refer to the data set with taxa of <=5% frequency removed.

(1) Describing the communities and summarising relationships to hydrological variables. The samples from individual ponds from each sampling occasion were firstly described and summarised by Redundancy Analysis (RDA) to explore relationships with hydrological variables and year. Previous studies of individual species over shorter time periods suggested that dry and flood phases during the preceding twelve months along with plant communities within ponds were important influences on species incidence (e.g. Jeffries, 2005), so these were now used to describe variation between metacommunities. RDA was chosen for the data summary following exploratory analysis, Lepš & Šmilauer, (2003). RDA was run on CANOCO 4.5.

(2) Identifying and defining metacommunities. To identifiy metacommunities the invertebrate samples from the ponds were classified into groups using TWINSPAN (Hill, 1979). TWINSPAN classification divides samples into progressively smaller groups, the groups being characterised by indicator species. In this study the samples were the individual ponds from each summer sampling occasion (e.g. pond 1 in 1997, pond 2 in 2003) and the data used to classify the metacommunities were the taxa presence/absence lists for each sample. In most years data were available for all thirty ponds though in some years one or two ponds had become too dry to sample and in 2004 only fourteen ponds were sampled before sudden, rapid drying. The analyses included the taxa added during in Autumn 1996 and January 1997 as part of the predator:prey manipulation. Whilst this intervention by itself was likely to affect, perhaps even create, the metacommunities there was no evidence of community adjustments due to interactions and the majority of species established widely beyond the ten

ponds to which they were added, many persisting throughout the subsequent years of the study (Jeffries, 2002). TWINSPAN was run on Community Analysis Package (CAP) 3.1.

TWINSPAN classification was run through three rounds of division. After two rounds TWINSPAN had distinguished four groups of samples which corresponded with distinct changes to metacommunities over the ten years. A third round of divisions created eight end groups, two of which were very small. So the following models and analyses used the four groups created by two rounds of TWINSPAN divisions. Differences between groups were tested using Analysis of Similarity (ANOSIM) and the average similarity of samples within groups and relative contributions of individual taxa to these measures were described by SIMPER (ANOSIM and SIMPER both run on CAP 3.1).

(3) Modelling the incidence and turnover of metacommunities, 1996-2004. The four metacommunities identified by TWINSPAN were multinomial data. Because the same ponds were sampled each year the data have a repeat-measures structure which undermines the use of basic multinomial regression or generalized linear modelling (GLM), and the multinomial count data are also likely to violate assumptions of multivariate normal distributions required for linear mixed model. Instead generalized estimating equations (GEE), an extension of GLM which specifically allow for data with some form of correlation or clustering and do not require normalized distributions, were used (Zeger & Liang, 1986; Hedeker & Gibbons, 2006; Norusis, 2008). GEE models require the specification of a correlation matrix to describe the within-subject dependency, although GEE is robust even if the most appropriate correlation matrix is not selected (Hedeker & Gibbons, 2006).

GEE equations use the same broad strategy as GLM, specifying a data type and a link-function which are then modelled and can incorporate factorial and scale predictor variables. There are disadvantages with GEE models; they are not fully parametric (Lipsitz & Fitzmaurice, 2009). Familiar Akaike Information Criterion (AIC) measures of goodness of fit cannot be used because the GEE does not use maximum-likelihood estimation although a substitute quasi-likelihood under independence criterion (QIC) has been proposed (Pan, 2001) and incorporated in statistical packages (e.g. Norusis, 2008). However QIC statistics cannot be derived for multinomial data such as the set of metacommunities in this study. The effectiveness of incidence models has often been tested by comparing observed results against the predicted frequencies but prediction success and simple tests such as Chi-square give an exaggerated confidence in results, not least because such measures do not account for variations in prevalence in the data (Manel et al., 2001). A suggested alternative measure, Cohen's Kappa which makes allowance for prevalence in the data has been widely used in ecology, because Kappa adjusts for prevalence and, perhaps, because the scale (0, no agreement, to 1.0, a perfect match) is intuitive (Manel et al., 2001), although Kappa may not be the most effective measure either (Liu et al., 2005). GEE models remain comparatively untested; in this study the model outcomes are tested using Kappa and the results from a standard multinomial model are included for comparison to demonstrate the importance of the repeat-measures adjustments in the GEE model.

The GEE model was run with the TWINSPAN final group membership (i.e. metacommunity type) for each pond sampled on each occasion as the dependent variable. The model therefore consisted of multinomial regression with a cumulative logit link function. The chosen correlation matrix was AR(1) first-order autoregressive, which requires equal time intervals between samples (early summer to early summer in this study) and assumes that data from one sample occasion are correlated with the results from the previous occasion; this seems the most intuitively likely form of correlation for these data. Other possible matrices were tested and did not give markedly different results. The predictor variables were the length of previous year's summer dry phase, length of previous winter flooding, length of spring dry phase, distance of individual ponds measured as x and y co-ordinates across the array of ponds and plant communities, the latter a factorial variable using the eight plant metacommunities identified by Jeffries (2008) as individual factors. Previous studies of the Hauxley

ponds showed that hydrology and plant communities were effective predictor variables in models of species' incidence (Jeffries 2005) and the initial RDA (Figure 2a) confirmed their likely value as predictors of metacommunities. There is some collinearity between variables. Long winter inundations were associated with shorter summer dry phases, but previous tests of species' incidence suggested that different species may be correlated with conditions at different phases of the hydrological cycle so the three distinct, seasonal hydrological predictors were retained in the GEE. Also the variation between plant communities appeared to be due to hydrological variation which is ultimately determined by spatial position (Jeffries 2008), but many of the animals appeared to be associated with the vegetation types themselves, rather than the ultimate, underlying hydrological determinants of the plant communities, so plants communities were also retained in the model. GEE models were run on PSAW 17.0.

Results.

Hydrology. Between autumn 1994 and summer 2004 the site showed marked hydrological variations (full details in Jeffries, 2008). From autumn 1994 to the end of 1996 the site underwent winter inundations linking most ponds followed by a summer dry phase with all ponds drying out for between 67 and 133 days. From December 1996 to June 1999 a sustained period of flooding occurred, with no ponds drying out and most linked together driven by unusually heavy rain in June 1997 (a 1:1250 event, Wheeler, 1999), referred to hereafter as the 97-99 wet-phase. In July 1999 summer dry phases resumed, most ponds drying out for variable periods in summer between 199-2004.

(1) Overview of colonisation patterns and development of invertebrate communities. A total of 139 taxa were recorded from the summer samples between 1995-2004, nine of which were juvenile stages for which adults were also present (e.g. *N. glauca*), whilst several taxa represent multiple species which could not be separated in the field (e.g. Dixidae). Figure 1 shows the total number of taxa recorded in each year, which ranges from 49 in 1995 to 85 in 2000, and mean numbers of taxa in the ponds from 1995 to 2004.. The introduction of taxa in Autumn 1996 and January 1997 is not associated with a sudden increase in taxa per pond, although by summer 1998 (i.e. 18 months after the last introductions) many had become widespread naturally across all ponds. This spread coincided with the 97-99 wet-phase, so, although the additions were affecting the character of the metacommunties but the majority of permanent pond taxa established naturally e.g. the ephemeropteran *Cloeon dipterum* (Linnaeus), suggesting that this period was characterised by the assembly of distinct permanent pond metacommunities and not solely an artefact of the additions.

Distinct patterns of incidence occur amongst the individual taxa (Figure 3). Some taxa occurred every year although frequency varied, e.g. *Daphnia obtusa* (Cladocera). Other taxa, e.g. the ostracod *Heterocypris incongruens* (Ramdohr) were found in the first few years, but were absent or very infrequent in 1998 and 1999 following the 97-99 wet-phase then reappeared following resumption of summer dry phases. An opposite pattern was shown by taxa which colonised during the 97-99 wet-phase but were either entirely lost in subsequent years, e.g. *Chaoborus crystallinus* (DeGeer). A fourth group of taxa appear to be slower colonists, establishing only later in the survey period e.g. the leech *Erpobdella octoculata* (L.). The majority of taxa were recorded less frequently, their distributions resembling less coherent versions of the four frequency distributions shown by the more frequent species.

The RDA (Figure 2) summarises the relationships between individual pond communities and hydrological and plant community variables between 1996 and 2004; The RDA in Figure 2a summarises the distribution of 248 individual pond samples by showing the average ordination positions for each year set, (e.g. mean for all ponds in 1996). The RDA showed metacommunities were strongly related to pond hydrology, in accordance with the wealth of examples documenting similar patterns in temporary ponds from around the world (Williams, 2006). The variance of species data explained by axes 1 and 2 was low, 8.6% and 5.7% respectively, whilst the species-environment variance was 38.8% and 25.7%, (Monte Carlo permutation tests of axes'

significance, P<0.001 for both axes). The most important trend is the shift from pioneer communities associated with sparse vegetation and summer dry phases in 1996 and 1997, to the metacommunities of 1998 and 1999 when ponds remained wet, then, once summer dry phases began again from 1999 onwards a retrenchment combining some taxa which established during the wet years along with re-establishment of some species associated with summer dry phases (Figure 2a).

(2) Defining the animal metacommunities. The four groups of samples distinguished by two rounds of TWINSPAN were significantly different to one another (Table 2. ANOSIM, dissimilarities between groups A-D range from 57.6% – 75.3%, P<0.001 for all pair-wise comparisons). There is a striking separation between the metacommunities of groups A and B which were found during the prolonged inundation of the 97-99 wet-phase versus the metacommunities of groups C and D which occurred in years affected by summer dry phases, both before (group D) or after (group C) the 97-99 wet-phase (Figure 2b). Figure 2b presents the RDA by plotting mean ordination position for the ponds in each of the four metacommunities A-D. The metacommunities of groups A and B were dominated by taxa associated with more permanent ponds, e.g. various Corixidae. Group C consisted of samples predominantly from 2001-2004 during which summer dry phases re-established and the group is characteristised taxa by a combination of surviving species from the 97-99 wet-phase, e.g. *Crangonyx pseudogracilis* along with re-established temporary pond taxa, e.g. *Helophorus* spp. beetles. The metacommunities of group D were predominantly 1996 and 1997 samples along with some ponds from 2001-2004 which had longer summer dry phases.. This group is characterised by pioneer taxa which were widespread in the first two years, e.g. the ostracod *Eucypris virens* (Jurine), as well as the absence of permanent water taxa which were lost once prolonged summer dry-phases resumed.

Figure 3 shows the frequency of selected taxa across the 30 ponds for each year 1995-2004; taxa have been chosen to represent distinct patterns, e.g. taxa found throughout the study or taxa which established during the 97-99 wet-phase but were lost when summer dry-phases resumed.

Only four groups is a rather coarse level of separation but the metacommunities of the four groups accorded well with the broad hydrological changes over the years of the study.

(3) Modelling the incidence of the metacommunties. Results from the GEE model are given in Table 3. The predicted categorisation of individual ponds versus the observed metacommunities is summarised in Table 4, along with predicted versus observed results from a standard multinomial model to demonstrate the effect of using the GEE model to adjust for repeated measures effects. The GEE model effects were highly significant for all predictor variables. The model parameters were significant for all three hydrological variables, and some of the plant community factors (Table 3). Kappa for the GEE model = 0.660, within the "substantial agreement" range (0.6-0.8). Results for the straight-forward multinomial regression model show much better prediction of metacommunity group, the Kappa measure = 0.877. The GEE model provided a working correlation matrix for the first order autoregression structure which gave correlations between one year and the next of 0.164, one year to two years later of 0.055 and one year to three years later of 0.018. Whilst GEE models are not primarily designed to focus on the precise repeat-measures structure these results show some correlation of metacommunities across years.

All three hydrological variables are significant, with both summer and spring dry phases positive meaning that the longer the ponds were dry the more likely they were to contain the metacommunities C or D, whilst winter inundation gave a negative parameter, so the longer the inundation lasted the more likely it is that metacommunities A or B will occur. Plant communities 9 and 12 both gave significant and positive parameter estimates (Table 3), suggesting that metacommunities C and D were associated with these plants. Plant communities 9 and 12 were both found primarily in 1996 and 1997, the sparse *Leptodictyum riparium* (Hedw.)

Warnst. or *Ranunculus aquatilis* of these ponds providing no cover when pond dried, leaving exposed, baked substrate. The easterly and northerly distance measures were also significant with a positive GEE parameter; ponds to the east and south of the array tended to dry first and for longest hence the association with metacommunities C and D.

Discussion.

Over 100 species were recorded from the ponds over the ten years. The total species list across all the ponds was always considerably higher than the mean number per pond, e.g. 1995 highest total in a pond 25 taxa, total across all ponds 49; 2000 highest total in a pond 34 taxa, total across all ponds 85. Therefore the overall richness supports previous evidence for the ecological value of temporary ponds (Collinson et al., 1995) and of the value of pond clusters to increase local diversity (Williams et al., 2008).

The objectives of this study were to describe the establishment and re-assembly of metacommunities over several years and test if the incidence and turnover of discrete metacommunities could be modelled effectively. The core outcomes are that distinct metacommunities were identified and that the GEE model provided moderately effective prediction of metacommunity turnover. Whilst the models used hydrological and macrophyte habitat variables as predictors the role of hydrology is not the primary focus of this study; the relationship between hydrology and communities is not in itself surprising (reviewed Williams, 2006). The more important outcome is the evidence for turnover of metacommunities identified in these ponds which supports the idea of metacommunities coming and going over the years, so that the disproportionately high biodiversity of pond systems is partly temporal as well as spatial.

The distribution of metacommunities never absolutely tracked hydrology and in part this may arise because of the correlations between years suggested by the autoregressive correlation incorporated in the repeat-measures structure of the GEE model; thus even if hydrology changed markedly from one year to the next there is a hangover from the metacommunity of the previous year, primarily the result of the storage effect (Chesson, 1994). Whilst the GEE model is partly a statistical necessity to adjust results for the impact of the repeat-measures sampling the results highlighted this ecologically significant phenomenon, suggesting that the characteristics of an individual pond or perhaps the presence of a metacommunity in a previous year have an effect across years. The metacommunities were at least partly contingent on the precise patch and what was there before, most likely because of the storage effect (Chesson, 1985; Shea et al., 2007). Evidence from years in which autumn samples were taken one to two weeks after ponds refilled and before any re-connecting floods occurred, showed temporary pond crustacean, e.g. *Daphnia obtusa* and *Eucypris virens*, present, suggesting re-establishment from eggs banks. Some species lacking specific drought tolerant life stages, e.g. *Asellus aquaticus*, would also re-appear rapidly, suggesting some storage effect survival amongst plant debris and substrate. Other taxa associated with permanent water, e.g. *Simocephalus vetulus,* did not re-appear. The results show the importance of time and habitat history in the development of the metacommunities. The earliest metacommunities of 1995 and 1996 and those of 2001 onwards developed after dry-phases the previous summer. However the 2001+ metacommunities retained some permanent water species; without knowing that a 26 month wet-phase had occurred in the intervening years allowing the permanent taxa to establish the substantial differences between early and later years post-summer dry-phase metacommunities would be hard to explain. Overall the ten year time span reveals the development of and changes to a distinct number of metacommunities; the changes appeared to be driven by the different responses of species to the changing habitat.

The pioneer fauna was lost from most ponds during the 97-99 wet-phase when no ponds dried out for at least 26 months and many permanent pond taxa established, in part due to the experimental additions of Autumn 1996/January 1997, but also due to extensive natural colonisation e.g. the turbellarian *Dugesia lugubris*. So, the metacommunities of the 97-99 wet-phase are not simply the pioneer fauna plus other species

accumulated over time; they are also defined by the loss of the pioneers. None of the pioneer species were wholly lost from the site over the ten years, many re-appearing in later years ponds when summer dry-phases were re-established from 1999 onwards, although they were often absent from ponds which were by then dominated by *Leptodictyum riparium* swards. Some species only arrived later in the survey, e.g. *Erpobdella octoculata*, or, in some cases were associated with plant communities which had only developed by this later stage, e.g. the ostracod *Cypricercus fuscatus* (Jurine) in ponds with dense *Leptodictyum riparium* swards. Jeffries (2005) showed that extinction and colonisation by several species widespread across the Hauxley ponds showed very particular and species-specific associations with differing plant communities. So the metacommunities established and changed in response to the taxas' varying abilities to colonise, differential responses to variations in the length or dry and wet-phases between the years and changing plant communities which were probably also altering the physicochemical environments in the ponds, supporting the species-sorting model of metacommunity assembly for these ponds. By 2003 -2004 a mosaic of metacommunities was present, comprising some from group C representing combinations of permanent and temporary water taxa, and a re-establishment of some group D metacommunities dominated by a temporary pond/pioneer fauna which was also characteristic of most ponds in 1995 and 1996. So, the changes are not simply a linear succession but suggest that taxa were moving back and forth across the landscape, suffering local extinction in response to changing hydrology but re-assembling later as summer dry-phases resumed

The turnover of metacommunties at the local scale at Hauxley results from individual species responding to local conditions in the ponds. This fits the species-sorting model of assembly which has been demonstrated for other pond systems (Cottenie et al*.,* 2001; Cottenie & De Meester 2004, 2005; Urban 2004). Hydrological variation between ponds was marked and well known to drive species-sorting during metacommunity assembly (e.g. Urban, 2004). The plant communities are also likely to create variation within ponds. Plant communities 9 and 12, characterised by sparse *Letptodictyum riparium* or *Ranunculus aquatilis* respectively and, if they dried out, left exposed substrate, were significant in the GEE model and associated with the temporary pond metacommunities. Whilst this may be an incidental correlation (both the animal and plant metacommunities independently responding to the hydrology) it is also likely that the plants create distinct conditions within each pond, both when the pond is wet but also during the dry-phase, e.g. thick moss swards stopped the substrate drying out. The rapid arrival of taxa into the new ponds, the establishment of many permanent water species between 97-99 wet-phase and the return of temporary water taxa from 2000 onwards also show the importance of the wider landscape and the role of mass-effect processes; the taxa have to come from somewhere and the arrival of dispersers creates a re-supply of species which are then winnowed each year by species-sorting within the ponds, similarly to the processes demonstrated for larger, interconnected permanent ponds by Cottenie & De Meester (2004). Dispersal of pond invertebrates is itself complex and can be influenced by conditions within a pond or by the surrounding landscape. For example Yee et al. (2009) demonstrated that dispersal cues for adult Dysticidae included density of plants and numbers of conspecifics within a pond, whilst Brinkley and Resetarits (2009) showed that vegetation canopy in the landscape around ponds acted as a filter affecting aquatic beetle community composition.

The Hauxley ponds benefit from being part of an extensive sequence of wetland nature reserves. The nearest other wetlands are within 5 and 50 metres of the study ponds, although these were shallow, *L. riparium* dominated wetlands and many of the taxa establishing at Hauxley have not been found in these adjacent sites so were coming from much further afield; for example the nearest temporary ponds supporting the *Ranunculus aquatilis*/*Chara vulgaris* plant communities and drying out to leave exposed mud were 285 metres distant.

Hydrology dominates the ecology of temporary ponds (Williams, 2006); the development and turnover of the Hauxley pond invertebrate metacommunities is no exception. The drying and flooding at Hauxley followed a broad seasonal pattern with finer-grained variation superimposed in response to unusual quantities and timing

of rainfall (Jeffries , in press). Rainfall patterns in Northumberland are predicted to alter in response to wider climate change, with a 10% decrease in total annual rainfall, increased seasonality and localised extreme precipitation, combined with a rise in summer temperatures of up to 2°C (North East Climate Change Adaptation Project, 2008). The results of this study show that the Hauxley metacommunties and their counterparts across the region are likely to show significant changes if these climatic predictions become reality. The invertebrates in these thirty, small ponds cannot be shielded from such changes, but the results suggest that they could survive in the wider landscape if there are sufficient numbers and diversity of ponds and the landscape allows dispersal. The metacommunities could re-assemble at other sites, so long as these are available and the animals can disperse to them. Conservation of temporary pond species in the face of climate change will require adaptation at the landscape scale to allow metacommunities to move, establish, retreat and re-assemble as they did at Hauxley.

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Table 1. Predictor variables used in the Generalized Estimating Equations models and Redundancy Analysis

Variable	Description
Previous summer's dry phase (days). ("SU" in Figure 2)	Length of dry phase during the previous summer. In most years ponds dried out sometime between June through to October. The precise length, start and end dates varied. Incorporated in the GEE model as a scale variable
Previous winter inundation (days). ("W" in Figure 2)	In some winters ponds filled to overflowing and linked up with some or all other ponds. Incorporated in the GEE model as a scale variable
Spring dry phase (days).("SP" in Figure 2)	In a few years some ponds dried out during March-April then refilled before the summer sampling period. Incorporated in the GEE model as a scale variable
Plant communities (eight communities, entered into model as factors)	The plants in the ponds showed marked spatial and temporal changes throughout the study period. Eight substantive communities were identified correlated with the spatial variations of hydrology across the site and years, full details in Jeffries, (2008). The main differentiation was between ponds with thick swards of the moss *Leptodictyum riparium* covering the kept substrate which was kept moist when ponds dried out, versus ponds dominated by annuals such as *Ranunculus aquatilis* and *Chara vulgaris*, which died away leaving exposed, baked substrate when ponds dried. The communities are numbered Groups 8-15, matching numbering in Jeffries (2008) for easier reference . The eight groups were incorporated in the GEE model as eight levels within a factor. The following is a brief summary of key features of each group. Group 8, scattered *R. aquatilis, few other plants*; Group 9, extensive but thin *L. riparium*; Group 10, Thick *L. riparium* sward with extensive *Glyceria fluitans*; Group 11, thick *L. riparium* with extensive *Eleocharis palustris*; Group 12, limited, mixed plant cover primarily *R. aquatilis*; Group 13, dominated by thick mats of *Spirogyra sp.* with grasses and some *C. vulgaris*; Group 14 *C. vulgaris* most abundant plant with grasses and rushes; Group 15, Thick mats of *Spirogyra* sp., very few other plants.
Distance X & Y, (m) (="X" and "Y" in Figure 2)	Although the ponds are all close together so that distance alone is unlikely to limit dispersal some spatial effects are possible. The position of each pond within a rectangular area encompassing all the ponds was recorded as x (north-south) and y (east-west) co-ordinates. These were incorporated into the model as a simple record of spatial position.

Table 2. The four metacommunity groups A-D defined by TWINSPAN classification along with their hydrological characteristics and plant communities associated with each group. Hydrological measures are given as group mean, days ± 1 standard deviation. The frequency with which each plant community type occurs in each set is given; the eight plant communities are numbered **8** to **15** in bold, their characteristics outlined in Table 1, e.g. **15** 20 means that plant community type **15** occurred in 20 of the samples in that group. Hydrological differences between groups were tested with one-way ANOVA (ANOVA results. Previous summer dry-phase F=86.6, df 3, 244, P<0.001. Previous winter inundation F=144.68, df 3, 244, P<0.001. Preceding spring dry-phase F=19.2, df 3, 244, P<0.001. Post-hoc Gabriel's test due to unequal numbers of samples, Field, 2009), used to identify differences between groups. Dry phases and inundations that are not significantly different at P<0.05 were indicated by the same superscript a, b, c, d).

Group ID. Within group % similarity.	Group A, N=61, Av. Sim. 52.2%.	Group B, N=28 . Av. sim. 56.9%.	Group C, N=82, Av. sim. = 44.9%	Group D, N=77. Av. sim. = 42.0%.
Frequency of samples from years in group	**1998** 30, **1999** 30, **1997** 1	**2000** 25, **2001** 3	**2001** 25, **2002** 23, **2003** 18, **2004** 11, **2000** 5	**1996** 28, **1997** 29, **2003** 11, **2002** 6, **2004** 3,
Summer dry phase	1.3 ± 9.9 [a]	22.8 ± 6.0 [b]	32.4 ± 30.0 [b]	76.4 ± 38.3 [c]
Winter inundation	161.4 ± 70.7 [a]	17.9 ± 18.5 [b,c]	38.4 ± 37.1 [b]	13.6 ± 31.0 [c]
Spring dry phase	0.0 [a]	0.2 ± 0.8 [a]	11.1 ± 10.7 [b]	6.4 ± 13.2 [c]
Plant community.	**15** 20, **13** 19, **10** 11, **11** 5, **14** 5, **12** 1.	**14** 13, **10** 7, **11** 3, **15** 2, **8** 1, **12** 1, **13** 1,	**10** 33, **11** 23, **14** 7, **13** 4, **12** 3, **8** 5, **9** 5, **15** 4	**9** 28, **12** 14, **13** 10, **15** 9, **11** 7, **8** 4, **10** 1, **14** 3
Predominant plant communities	Dominated by mats of *Spirogryra*, other plants sparse	Primarily *Chara vulgaris* or *Leptodictyum riparium* swards	Dense *Leptodictyum riparium* moss sward smothering substrate with emergent grasses & rushes.	Sparse but varied coverage primarily early colonists e.g. *Chara vulagris* & *Rancunculus aquatilis*

Table 3. Results of the GEE model of metacommunity incidence for the four metacommunity groups A-D, distinguished in Table 2. Firstly the overall model effects are given, then the thresholds delimiting membership of the four metacommunity groups defined by the model and finally the parameters estimates, *B*, and their lower and upper bounds for the individual predictor variables. Note that the plant communities were incorporated in the model as a single factorial variable with eight levels, 8-15. [a] The parameter estimates for each plant community are relative to the reference category, Plant community 15. Parameter estimate significance * P < 0.05, ** P< 0.01, *** P<0.001.

	Overall tests of model effects		
	Wald Chi-square	df	Significance
Plant communities	28.81	7	P<0.001
Length of previous summer dry phase	77.13	1	P<0.001
Length of previous winter inundation	24.50	1	P<0.001
Length of preceding spring dry phase	54.52	1	P<0.001
Distance X	5.10	1	P<0.05
Distance Y	14.08	1	P<0.01

	Thresholds delimiting membership of groups		
Group	*B*	Lower	Higher
A→B	0.127	-1.338	1.592
B→C	1.923	0.423	3.423
C→D	6.583	4.924	8.243

	GEE model equation parameter estimates		
	B	Lower	Higher
Factorial predictor			
Plant community 8	1.545.	-0.619	3.710
Plant community 9	5.257***	2.750	7.763
Plant community 10	0.881	-0.404	2.167
Plant community 11	0.315	-1.085	1.715
Plant community 12	2.930**	1.092	4.768
Plant community 13	-0.466	-1.568	0.635
Plant community 14	-0.360	-1.638	1.919
Plant community 15	0.0[a]		
Scale predictors			
Length of previous summer dry phase	0.064***	0.050	0.079
Length of previous winter inundation	-0.017***	-0.023	-0.010
Length of preceding spring dry phase	0.146***	0.107	0.184
Distance X	-0.055*	-0.102	0.007
Distance Y	0.089**	0.043	0.136

Table 4. Results of the metacommunity classifications given by GEE and multinomial models. The results of the GEE model are given first followed, in brackets, by the results from a standard multinomial model, which does not incorporate the adjustments needed for repeated-measures.

		Observed metacommunity group.			
		A	B	C	D
	Total in group	61	28	82	77
Predicted metacommunity group	A	59 (60)	0 (0)	1(0)	0 (1)
	B	1 (0)	15 (24)	15 (4)	0 (1)
	C	0 (0)	13 (4)	52 (72)	16 (5)
	D	1 (1)	0 (0)	14 (6)	61 (70)

Figure legends.

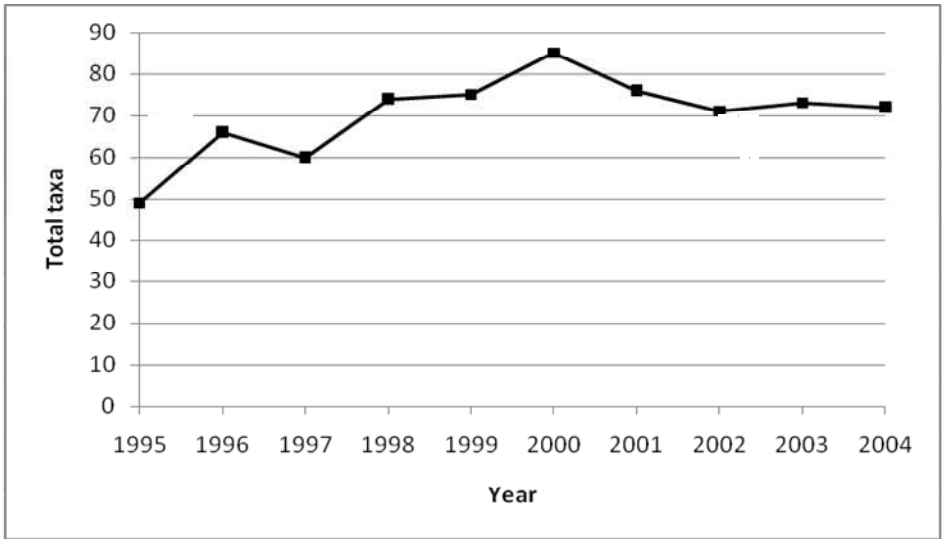
Figure 1. (a) Total taxa recorded from the Hauxley ponds each year, (b) mean number of taxa per pond ± 1 standard deviation. (N=28-30, except for 2004 when only 14 ponds were sampled).

Figure 2. RDA ordination summarising relationships between individual pond macroinvertebrate samples and predictor variables used in General Estimating Equation models of metacommunity incidence. (a) The 248 individual ponds have been combined into year groups and the mean ordination of the ponds from each year are shown, ± 1 standard deviation; (b) the mean ordination position, ± 1 standard deviation, of ponds in each of the four metacommunities, A-D is shown, ± 1 standard deviation. The predictor variables are described in Table 2. SU = length of summer dry phase, (note vector indicates relationship to increasingly short dry-phases) W = length of winter flooding, SP = length of spring dry phase, X and Y = northing or easting distance of ponds. Centroids are shown for the two plant communities which were significant predictor variables in the GEE equation of metacommunity incidence, the centroids shown by ▲

Figure 3. Examples of the frequency with which different taxa were recorded from the 30 ponds each year; y axis = number of ponds from which taxa was recorded. (a)-(c) Taxa associated associated with years following longer dry phases and shorter winter inundation, (d)-(f) taxa which colonised during the 97-99 wet-phase but were lost following the resumption of summer dry-phases, (g)-(i) taxa present thoughout the ten years, (j)-(l) later colonists. (N=28-30, except for 2004 when only 14 ponds were sampled, the 2004 results shown in ■).

Figure 1.

(a)


90
80
70
60
50
40
30
20
10
0
Total taxa
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
Year

(b)

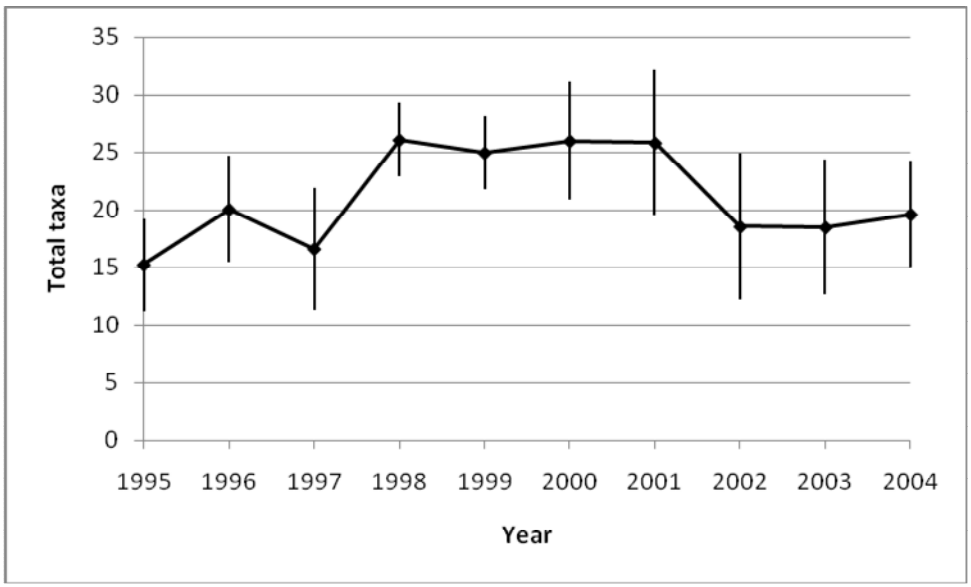

35
30
25
20
15
10
5
0
Total taxa
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
Year

Figure 2 (a)

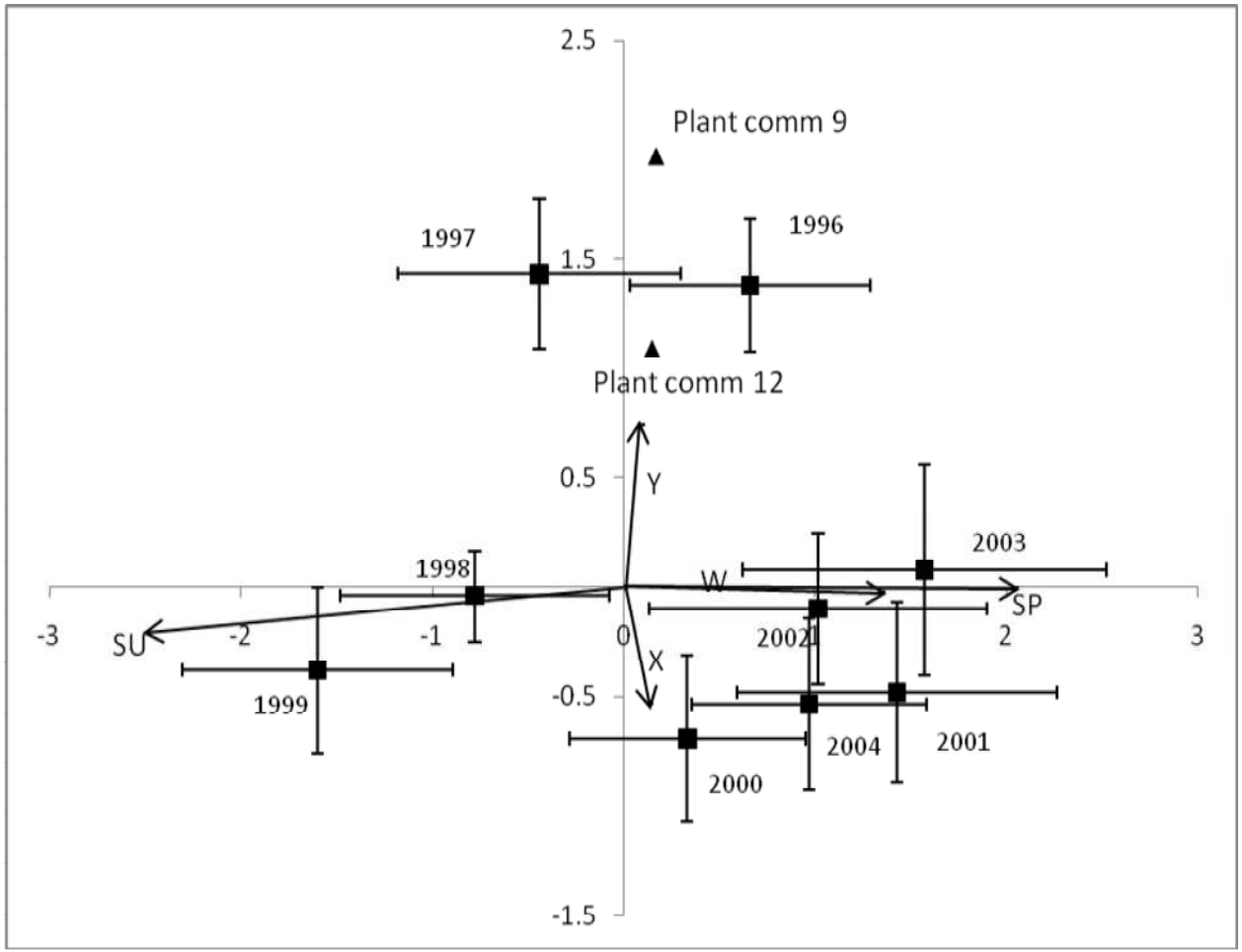

2.5
Plant comm 9
1997
1996
1.5
Plant comm 12
0.5
Y
2003
1998
W
SP
-3
SU
-2
-1
0
2002
2
3
X
-0.5
1999
2004
2001
2000
-1.5

Figure 2 (b)

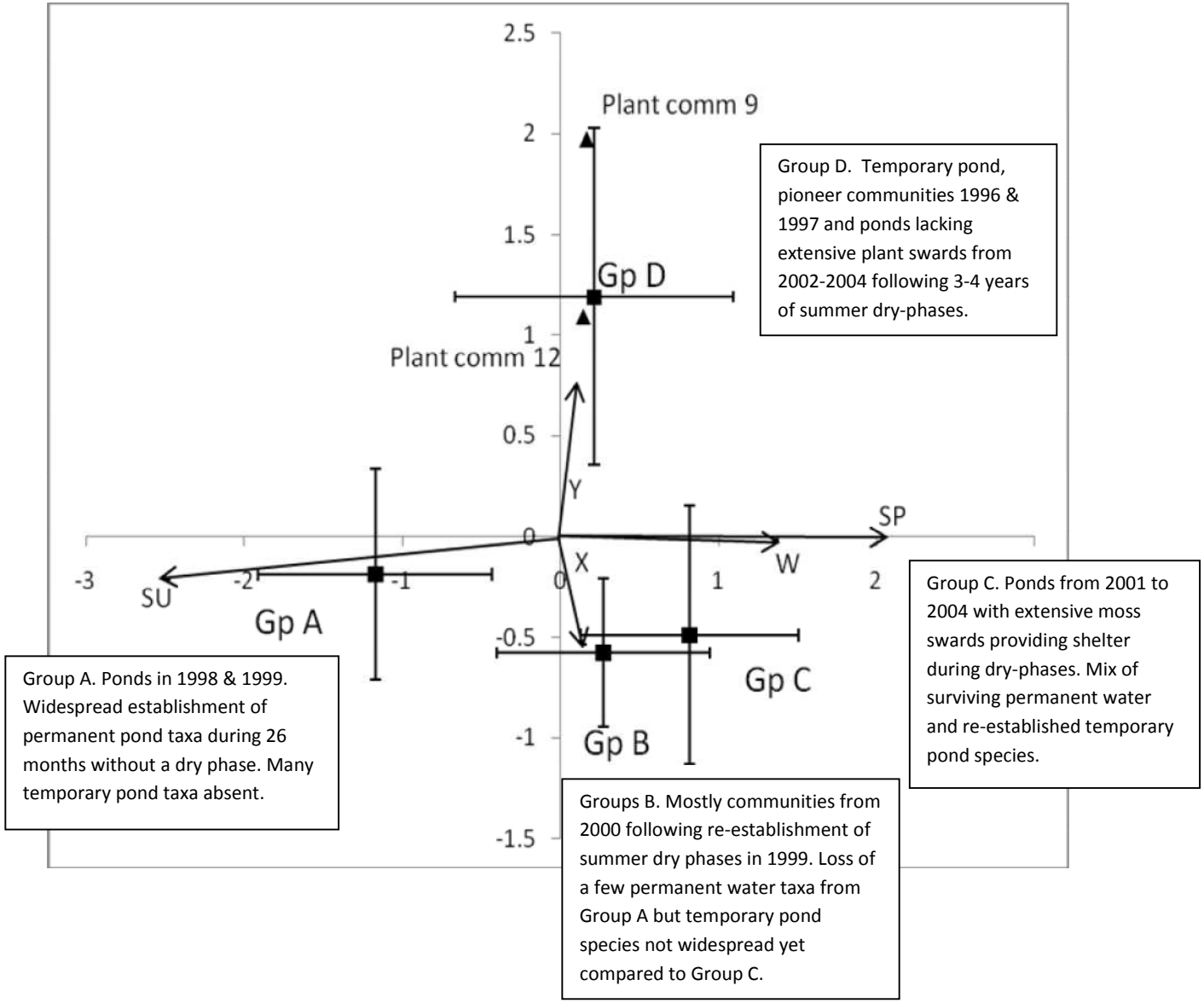
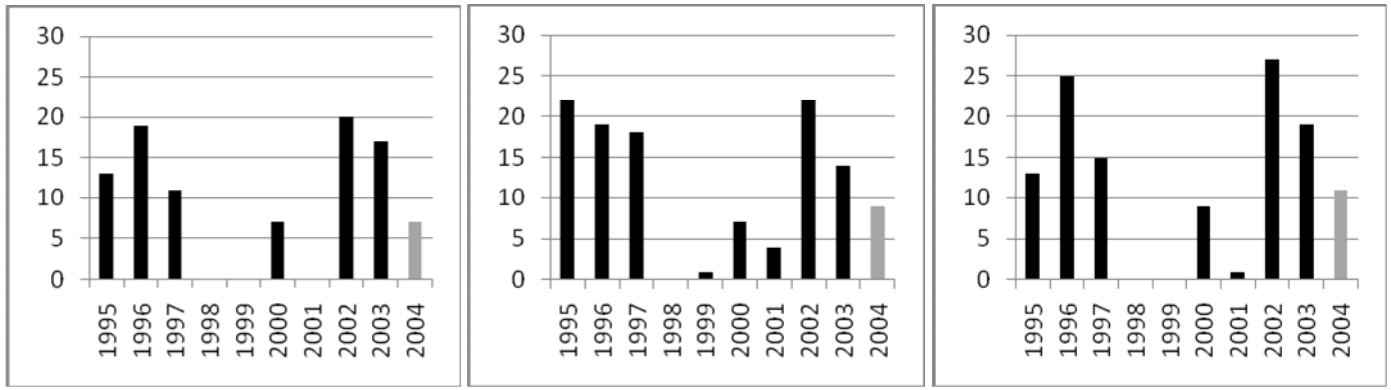

2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-3
-2
-1
0
1
2
Plant comm 9
Plant comm 12
Gp D
Gp A
Gp B
Gp C
SU
SP
W
X
Y
Group D. Temporary pond, pioneer communities 1996 & 1997 and ponds lacking extensive plant swards from 2002-2004 following 3-4 years of summer dry-phases.
Group C. Ponds from 2001 to 2004 with extensive moss swards providing shelter during dry-phases. Mix of surviving permanent water and re-established temporary pond species.
Group A. Ponds in 1998 & 1999. Widespread establishment of permanent pond taxa during 26 months without a dry phase. Many temporary pond taxa absent.
Groups B. Mostly communities from 2000 following re-establishment of summer dry phases in 1999. Loss of a few permanent water taxa from Group A but temporary pond species not widespread yet compared to Group C.

Figure 3.

(a) Heterocypris incongruens (b) *Hydroporus tessalatus* (c) *Helophorus grandis*



(d) *Cloeon dipterum* (e) *Dugesia lugubris* (f) *Chaoborus crystallinus*

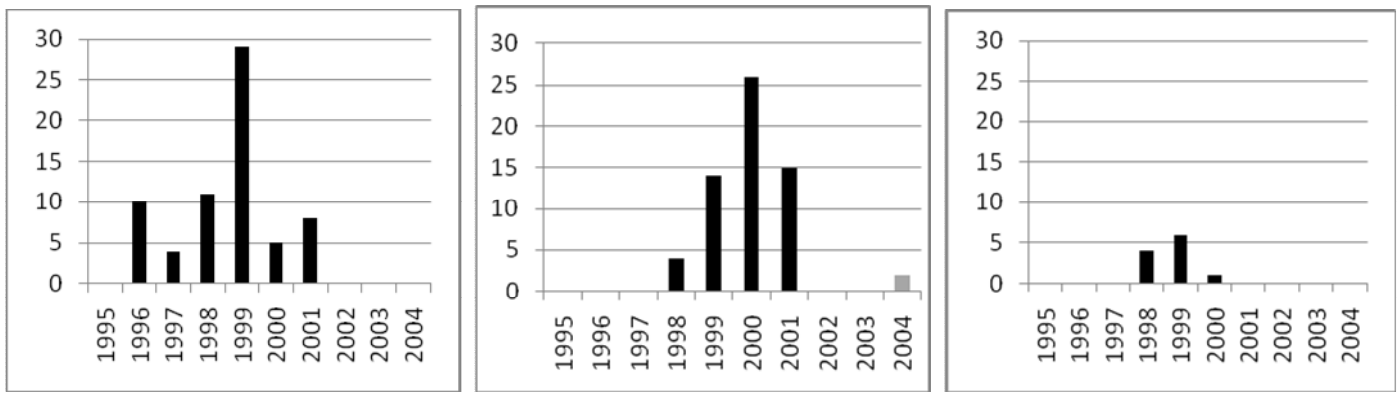
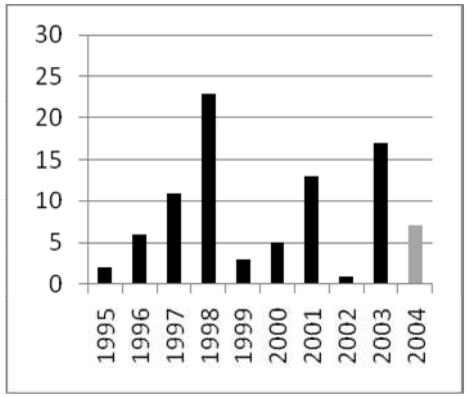
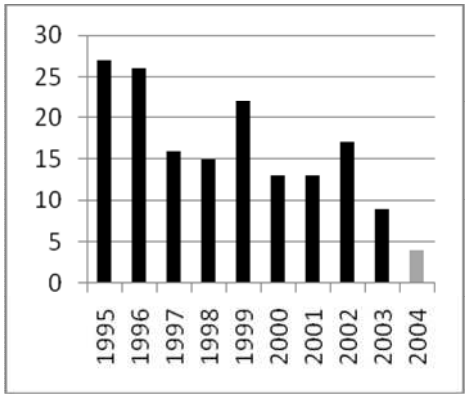


Figure 3, (cont.)

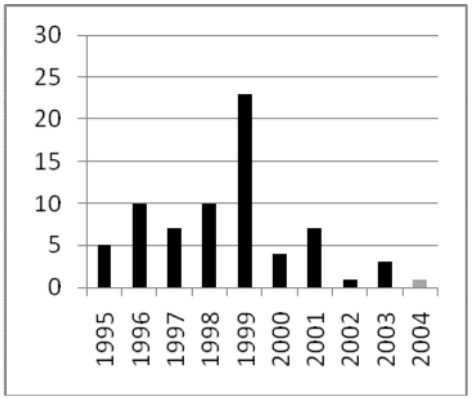
(g) *Microspectra* sp.



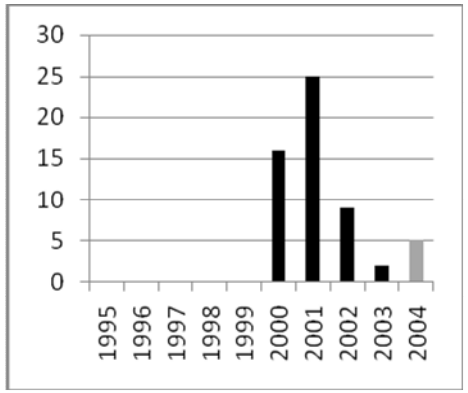
(h) *Daphnia obtusa*



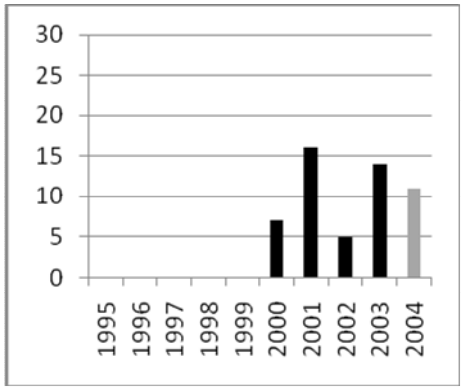
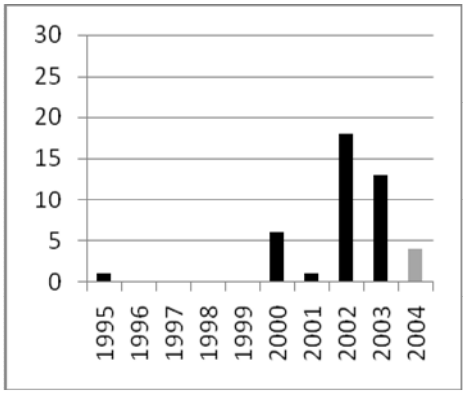
(i) *Agabus bipustulatus* larvae



(j) *Erpobdella octoculata*



(k) *Anacaena limbata*



(l) *Ilybius ater* (DeGeer)