
**Community assembly and food web interactions across pond
permanence gradients**

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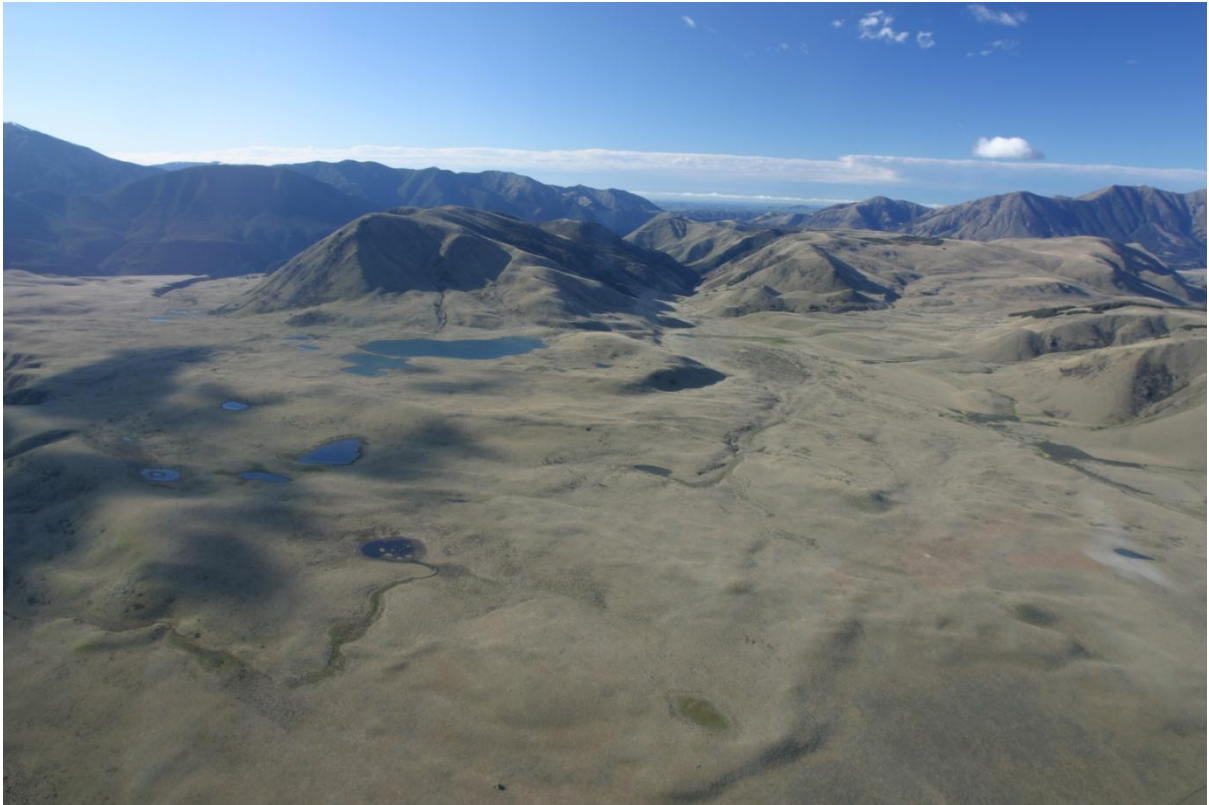
To my family

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Abstract

Ecological communities along gradients of environmental stress are thought to be structured by trade-offs between resisting biotic interactions in physically benign habitats and successfully exploiting physically stressful habitats. However, these trade-offs are likely to be affected by the predictability of abiotic stressors, and variation in the strength of biotic interactions. I investigated community assembly and food web interactions in ponds across an unpredictable gradient of water inundation (pond permanence) in Canterbury, New Zealand. Pond community composition and species richness were strongly influenced by pond permanence. However, species in temporary ponds were a nested subset of generalists that were also found in permanent ponds, rather than a unique assemblage of temporary pond specialists. Subsequent experiments indicated predator impact decreased with pond permanence, partially due to the foraging suppression of predatory invertebrates in permanent ponds by fish. Weak predation in permanent ponds combined with unpredictable drying regimes likely selected for generalist traits, and resulted in community assembly being driven by a gradient of drying stress rather than trade-offs between biotic interactions and drying. Furthermore, predator impact increased over time in temporary ponds. In predictable snow-melt ponds in the Colorado Rocky Mountains, seasonal windows of weak predation were exploited by vulnerable species, leading to increased diversity within habitats. However in unpredictable systems like Canterbury, temporal increases in predation risk that depend on drying history are likely to increase variability in the spatial arrangement of suitable habitats for particular species. This should further favour the evolution of generalist traits and reduce the importance of trade-offs between predation and drying in the assembly of communities. Considering the predictability of disturbance regimes and the spatial and temporal variation in biotic interactions will greatly enhance understanding and management of communities in heterogeneous landscapes.



Frontspiece: Aerial view of kettle ponds on Blackwater Moraine, Canterbury, New Zealand (top), and a final instar *Procordulia grayi* dragonfly larvae consuming a *Rhantus* beetle larvae (bottom). Photo credits: Angus McIntosh (top) and Amy Whitehead and Michelle Greenwood (bottom).

Chapter One

General introduction

Introduction

The earth is experiencing unprecedented levels of pressure on natural ecosystems, including climate change, pervasive alterations to habitats, invasions and overexploitation of primary resources (Vitousek et al. 1997, Foley et al. 2005, MEA 2005), especially in aquatic ecosystems (Angeler 2007, Smol and Douglas 2007). These factors are already having considerable impact on ecosystems (Menzel et al. 2006, Rosenzweig et al. 2008), and managing and predicting the response of biological communities at such a broad scale requires robust and integrative ecological theory (Kerr et al. 2007). However, a recent review identified significant “gaps” in current ecological knowledge that limit the predictive abilities of ecological theory, and called for an integration of ecological sub-disciplines (Agrawal et al. 2007). Agrawal et al. (2007) highlighted the lack of empirical studies addressing the relative importance of factors that structure ecological communities, and how these factors change across different habitats. They identified three key questions for empirical ecologists to address: 1) how do abiotic and biotic contexts influence species interactions, 2) how do abiotic and biotic factors interact and 3) how do abiotic and biotic influences vary in space and time?

Environmental gradients as a model system

Environmental gradients occur when abiotic factor(s) vary within habitats, or across habitat patches within a landscape. Consequently, habitats at one end of an environmental gradient can be considered stressful (or harsh) in the abiotic constraints imposed on organisms, and are considered benign at the opposite end of the gradient (Grime 1977, Peckarsky 1983, Lubchenco 1986, Callaway et al. 2002, Chase 2007). Environmental gradients provide a particularly useful context for addressing the key questions outlined by Agrawal et al. (2007) for three major reasons. First, they provide the opportunity for natural experiments where the strength of biotic interactions and other components of community assembly can be

investigated along gradients that differ in abiotic and biotic context. Thus, experiments replicated along environmental gradients will be particularly profitable for identifying mechanisms structuring communities (Crain et al. 2004, Agrawal et al. 2007). Second, gradients of abiotic factors are pervasive aspects of habitat heterogeneity across a wide range of landscapes, for example, ocean floors and marine intertidal zones (Lubchenco 1980, Micheli et al. 2002), lotic and lentic freshwater ecosystems (Power et al. 1996, Schneider and Frost 1996), estuaries (Huckle et al. 2000, Crain et al. 2004), and a multitude of terrestrial landscapes (Grime 2001, Callaway et al. 2002). Thus enhancing the understanding of community dynamics along particular environmental gradients is transferable to a wide range of ecosystems. Finally, many environmental gradients are closely associated with climatic and/or hydrological processes. Thus, effects of anthropogenic global change such as altered temperature patterns, precipitation regimes, and sea level height, are likely to have pervasive effects on these systems, especially their disturbance regimes. Disturbances in this context are relatively discrete events in time of high abiotic stress which disrupt ecological processes at some level and alter habitats (White and Pickett 1985). Hence, there is considerable applied benefit to understanding factors influencing the assembly of communities along environmental gradients.

Variation in disturbance across habitats or habitat patches within a landscape constitutes a subset of environmental gradients that have received considerable theoretical attention (Sousa 1979, 1984, White and Pickett 1985, Menge and Sutherland 1987, Poff 1992, Power et al. 1996). Variation in disturbance frequency and/or magnitude among habitats is important in determining species richness within habitat patches (Connell 1978, Sousa 1984, Pickett and White 1985). Furthermore, because disturbances often reduce species abundance and disproportionately influence higher trophic levels, competitive and predator-prey interactions may decrease in strength with increased disturbance. Consequently, communities across these gradients are influenced by the joint effects of disturbance and biotic stressors, and their relative influence changes with disturbance (Fig 1a) (Grime 1977, Connell 1978, Peckarsky 1983, Lubchenco 1986, Menge and Sutherland 1987, Menge and Farrell 1989). Species face trade-offs between traits that confer resistance to biotic interactions and resistance or resilience to abiotic stress because traits facilitate persistence in disturbed habitats often increase a species vulnerability to predation or competition (Power et al. 1996, Wellborn et al. 1996, Grime 2001). Consequently, the assembly of local communities across gradients of disturbance is often strongly related to the conditions of habitat patches.

Variation in pond duration as disturbance gradient

I investigated the influence of abiotic stress on the spatio-temporal dynamics of community assembly and the strength of species interactions across an environmental disturbance gradient of pond inundation.

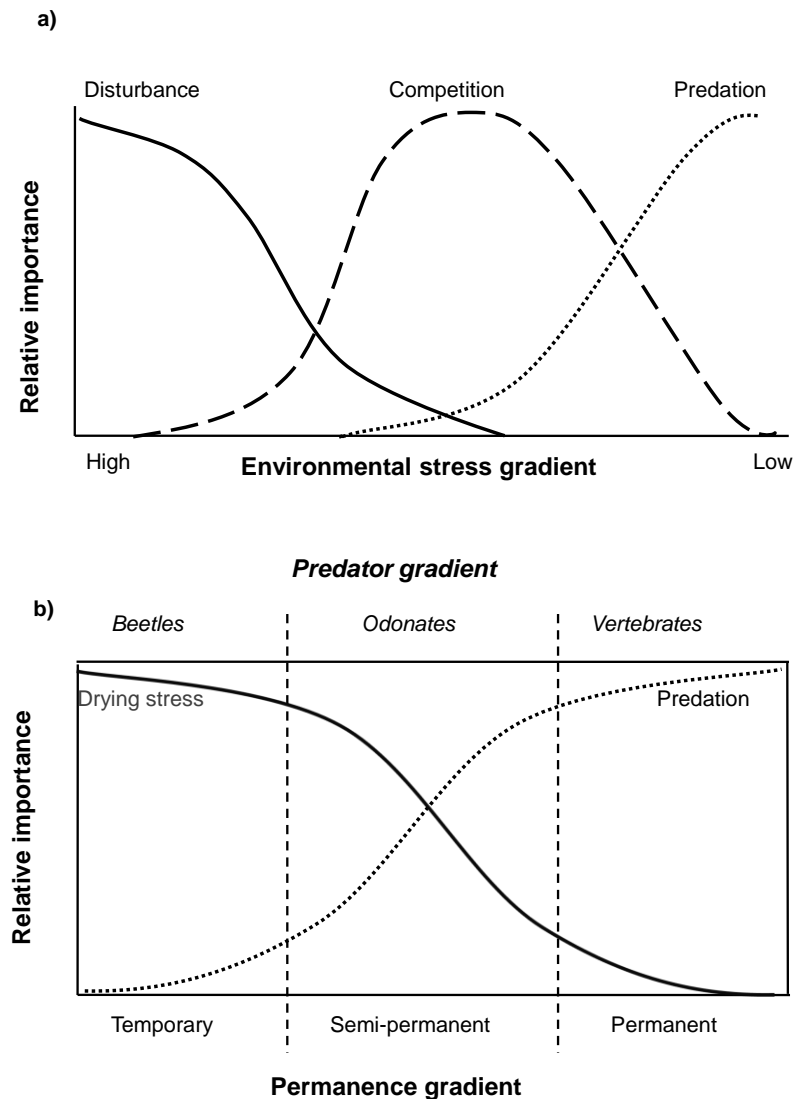


Fig. 1 Conceptual models of processes determining community structure along gradients of environmental disturbance. (a) Shifts in the relative importance of disturbance, competition and predation in determining community structure in local habitats along gradients of environmental stress (modified from Menge and Sutherland 1987). (b) The pond predator-permanence model of community assembly (Wellborn et al. 1996), where enhanced predation risk associated with increased habitat permanence leads to a shift in community control from drying stress in temporary ponds to top-down control by predators in permanent ponds. The dashed vertical lines indicate important transitions along this permanence gradient (Wellborn et al. 1996, Stoks and McPeck 2006) with associated top predators identified in *italics*. Vertebrate predators refer to fish and/or salamanders.

An additional benefit in addressing these important general ecological issues in pond systems was to generate primary ecological knowledge of the dynamics of temporary pond

communities in New Zealand, which have been vastly understudied compared to streams and lakes (Harding et al. 2004). Clusters of ponds within a landscape provide ideal systems to investigate the relative importance of abiotic and biotic factors in influencing community assembly because gradients of disturbance through pond drying are evident across multiple, discrete habitat patches (Schneider and Frost 1996, Wilbur 1997, Wissinger 1999). Pond communities are also dominated by mobile species, rather than the predominantly sessile taxa associated with communities across many other environmental gradients (e.g., marine intertidal and vegetation zonation) (Sousa 1984, Schneider and Frost 1996). As a result, competitive interactions which strongly influence the community assembly of sessile organisms may be less important in determining the assembly of highly mobile species common in pond communities. Consequently, models of community assembly across pond-permanence gradients predict the increasing influence of biotic interactions on community assembly in more permanent ponds is driven by changes in predation rather than competition (Fig 1b, Wellborn et al 1996).

The increased influence of predation on community assembly is largely due to the increased abundance and diversity of large predatory taxa (fish or salamanders) in more permanent ponds (Fig 1b). The rapid development, active foraging and minimal investment in defence characteristic of many temporary pond macroinvertebrate species increases their vulnerability to predation in permanent habitats, and as a consequence, species replacements of habitat specialists occur across this predator permanence gradient (reviewed by Wellborn et al. 1996, Wissinger 1999). These species replacements increase between habitat diversity (beta-diversity), as contrasting habitats across the permanence gradient contain unique subsets of the regional species pool (Wellborn et al. 1996, Skelly 1997, Urban 2004).

Despite the importance of local scale processes such as the strength of predator-prey interactions, regional processes operating at multiple levels likely influence communities along environmental gradients (e.g., Connolly and Roughgarden 1999, Connolly et al. 2001). At a broad regional scale, the interaction between biogeography and evolution influences the composition of species and their traits within the regional species pool, which in turn, is likely to affect community assembly (Cornell and Lawton 1992, Shurin et al. 2000, Amarasekara 2003, Leibold et al. 2004). For example, the majority of evidence for the predator-permanence model of pond community structure comes from systems with predictable hydrological regimes (e.g., snow melt) both within and between seasons (Wellborn et al. 1996, Wissinger 1999, Wissinger et al. *in press*). In these predictable systems, development that is synchronised with drying regimes underlies the success of many

temporary habitat specialists (Wiggins et al. 1980, Corbet 1999, Wissinger 1999). For example, the drying regime of high elevation ponds in the Colorado Rocky Mountains is very predictable, as all ponds are filled by snow melt every spring, and ponds dry in the same sequence every year (Wissinger et al. 1999a). Life history specialization to the predictable hydrology of temporary ponds and intense predation by salamanders in permanent ponds leads to the replacement of temporary pond specialists by closely related permanent pond specialists across the pond permanence gradient (Wissinger et al. 1999c, Wissinger et al. 2004, Wissinger et al. 2006b).

In contrast, life history theory predicts that systems with high inter-annual variability in pond drying and filling should favour the selection of generalist rather than specialist traits (Poff and Allan 1995, Winterbourn 1997, Lytle and Poff 2004). This is likely to alter patterns of community assembly in ponds across the permanence gradient, such as reducing the number of species replacements. In addition, regional differences in the species of top predator in permanent ponds (e.g., salmonids in New Zealand versus percoid and centrarchid fish in many United States comparisons; Wissinger et al. *in press*) may also influence community dynamics in ponds by altering the intensity of biotic interactions. Despite these apparent contingencies, the generality of the predator-permanence model of pond communities has received little attention, and in general community ecology, the influence of biogeographic-scale processes (such as climate regimes and phylogenies history) on the dynamics of community assembly is poorly understood.

Ponds in the Canterbury high country of New Zealand provide an opportunity to test the general applicability of the pond predator-permanence model because precipitation is seasonally unpredictable (Greenland 1977). This leads to high intra- and inter-annual variability in high country hydrological regimes (Clausen and Biggs 1997, Winterbourn 1997, Clausen and Biggs 2000). For example, from 1998-2006 there was no significant difference between the mean total rainfall in each month at the University of Canterbury's high country field station at Cass (Fig 1.2). Additionally, the fish fauna of New Zealand is dominated by native Eleotridae and Anguillidae, and native and introduced Salmoniformes, rather than Percidae, Centrarchidae (North America) and Cyprinidae (Europe) that are the top predators in many northern hemisphere lentic habitats (Diehl 1992, Wellborn et al. 1996, Pierce and Hinrichs 1997, Wissinger 1999). Previous work in ponds of the Canterbury high country indicates their community dynamics contrast with predictions of the predator-permanence model (Wissinger et al. *in press*). For example, Wissinger et al. (*in press*) observed that all the species found in temporary ponds in Canterbury were also present in

permanent ponds, indicating the absence of species replacements of habitat specialists. Addressing the mechanisms behind these different patterns requires the assessment of inter-annual predictability of drying regimes, the strength of predator-prey interactions across the drying gradient (Wissinger et al. *in press*) and the spatial context of the local pond communities.

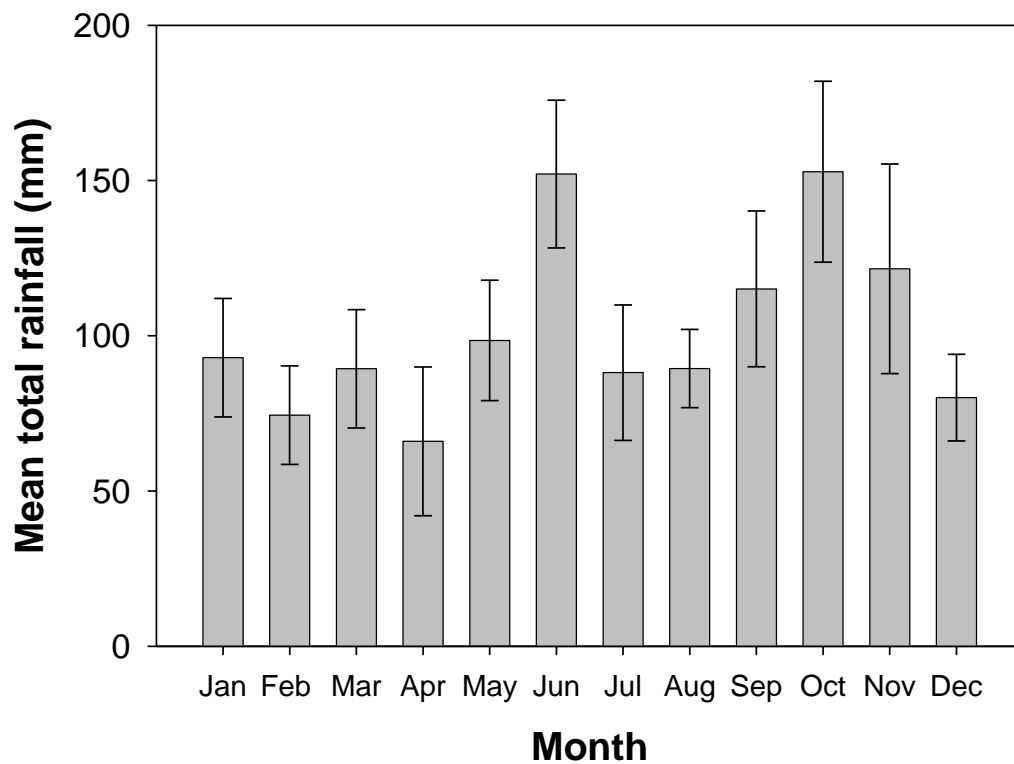


Fig. 2 Mean (\pm se) monthly rainfall at the University of Canterbury's Cass Field Station over 9 years (1998 – 2006). Rainfall did not differ significantly between months (One-way ANOVA blocked by year; month: $F_{11,88} = 1.64$, $P = 0.10$).

Assessing the effects of disturbance, interactions strength and spatial context of community structure needs to be done in relation to the scale and dynamics of the system. Local communities are rarely closed to dispersal, and the effects of local habitat properties on community assembly can be diluted by regional factors that influence the colonisation and emigration rates of taxa (e.g., recruitment density in marine communities; Connolly and Roughgarden 1999, Connolly et al. 2001, Menge et al. 2003). The metacommunity concept provides a useful framework to incorporate both regional and local controls of community assembly.

Metacommunities are aggregations of local communities linked by the dispersal of multiple, interacting species (Wilson 1992, Leibold et al. 2004). Models posed for the

structure of metacommunities can be divided into (a) niche assembly models that suggest species trade-offs interact with dispersal to influence local assembly in contrasting spatial or spatiotemporal habitat patches, and (b) neutral models that assume equivalence in both species traits and local habitat features, and suggest community assembly is governed by stochastic events and spatial effects on colonisation and emigration rates. Niche assembly models can be subdivided into three models that differ in the relative influence of dispersal on the assembly of local communities (Leibold et al. 2004). In species-sorting models, dispersal is sufficient to enable local communities to reflect the interaction between species traits and the environmental characteristics, but restricted enough to prevent strong source-sink dynamics (Leibold 1998). In contrast, mass-effect models suggest dispersal rates of migrants exceed rates of species extirpation by local factors, thereby reducing local species-environment matching in a pattern analogous to source-sink dynamics in metapopulations (Mouquet and Loreau 2003). Finally, patch-dynamic models suggest species colonisation-competition trade-offs structure local assembly across spatiotemporally variable habitat patches (Shurin and Allen 2001, Calcagno et al. 2006). Pond clusters are ideal examples of metacommunities as dispersal occurs between local habitats that vary in environmental conditions. Thus, incorporating the metacommunity framework should be particularly useful in assessing the relative importance of dispersal and environmental factors in the local assembly of pond communities (e.g., Cottenie and De Meester 2004, Urban 2004).

Thesis layout

This thesis is written as a series of stand-alone papers that will be submitted for publication, and as a consequence, some of the chapters share introductory material. In Chapter Two, I used the metacommunity framework to assess the relevance of the predator-permanence model to community structure across a pond permanence gradient in the Waimakariri catchment, South Island, New Zealand (Fig. 3, Plates 1-2). The variability of pond hydroperiods was quantified over three years and these data were combined with habitat and biotic surveys, and a mesocosm experiment to assess spatial, environmental and biotic influences on local pond assemblages.

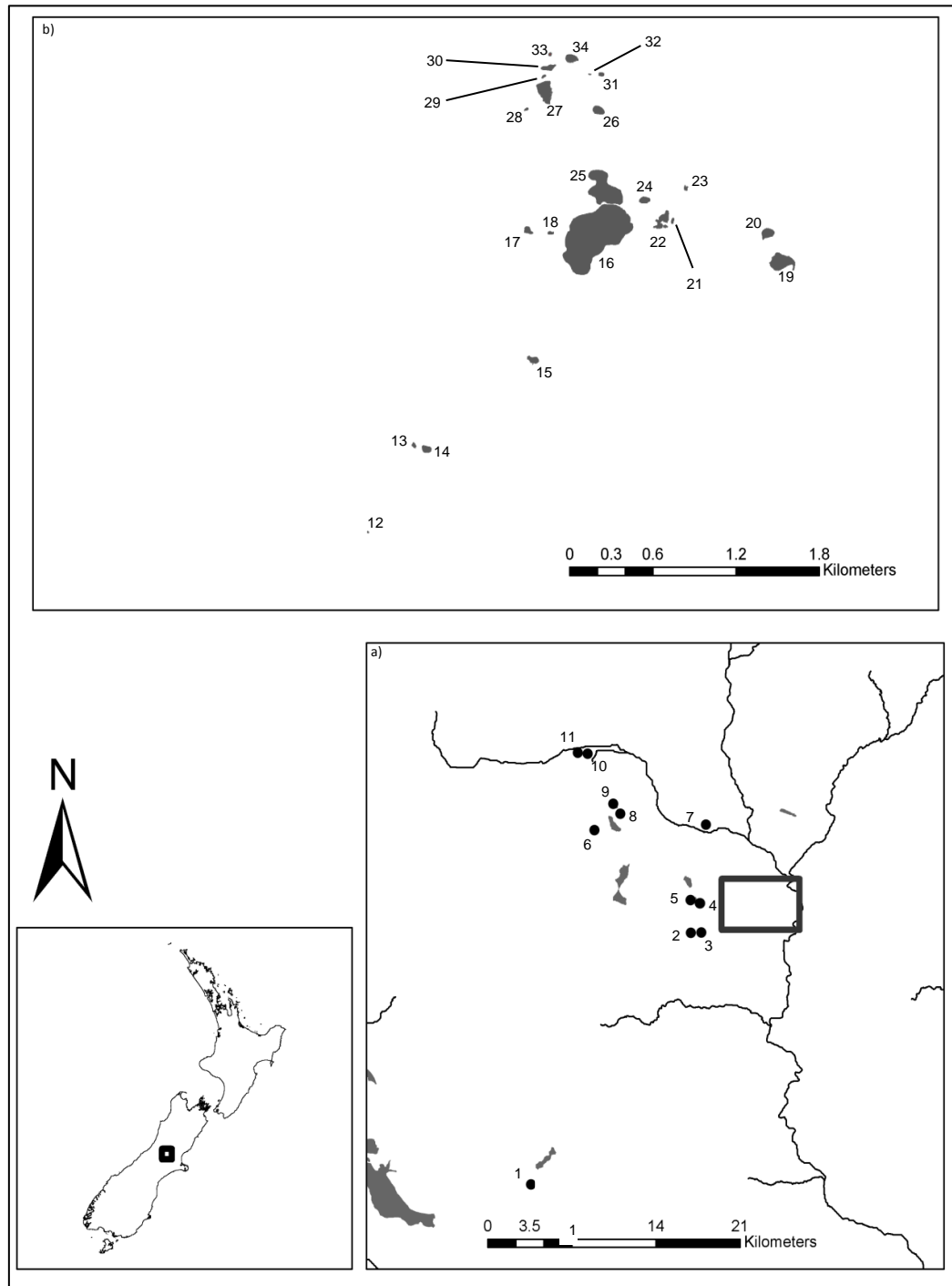


Fig. 3. Ponds and lakes in the upper Waimakariri River catchment, Canterbury New Zealand (a) and a detailed map of ponds across the Blackwater moraine (b). In (a), ponds sampled and their locations are indicated by numbers and black circles, with remaining unsampled lakes shown in grey. All ponds on the Blackwater moraine (b) were sampled. Pond names are 1 = Lyndon Tarn, 2 = Vagabonds West, 3 = Little Vagabonds, 4 = Craigieburn, 5 = Lake Marymere, 6 = Romulus, 7 = Gooseberry, 8 = Kettle, 9 = Lake Sarah, 10 = Goldney Saddle, 11 = Waimakariri Flat, 12 = T3, 13 = T1a, 14 = T1, 15 = T2, 16 = Lake Blackwater, 17 = BL16, 18 = BL15, 19 = BL1W, 20 = BL1, 21 = BL3, 22 = BL2, 23 = BL4, 24 = BL5, 25 = Little Blackwater, 26 = BL6, 27 = BL13, 28 = BL13A, 29 = BL12, 30 = BL7, 31 = BL9, 32 = BL11, 33 = BL14, 34 = BL10. Lake Blackwater and Little Blackwater are connected by a shallow stream when bank-full.

In Chapter Three, I experimentally investigated the effect of pond drying regimes on the strength of biotic interactions using *in situ* manipulations of predator biomass (both predatory fish and invertebrates) within replicate ponds across the permanence gradient. I then tested the mechanisms behind the results of the field manipulations with mesocosm experiments that assessed the consumptive effects of fish on prey biomass, and how changes in the density and diversity of predator guilds with pond permanence influenced community-wide predator-prey interactions.

Pond drying, like many other disturbance events, resets or substantially reduces community biomass, leading to post-disturbance succession processes (Connell and Slatyer 1977, Sousa 1984). Thus, colonisation and growth after ponds refill, and changes in habitat morphology as ponds dry, are likely to lead to substantial shifts in pond food webs and their interaction strengths. In Chapter Four, I used field surveys and *in situ* predator manipulations in cages within replicate temporary and permanent ponds over spring and summer to test whether predator-prey interactions intensify over time, and if this temporal change is stronger in temporary than permanent ponds.

Temporal shifts in biotic interactions may increase local diversity if the coexistence of taxa occur across temporal niches created by the seasonal dynamics of biota (Chesson 2000, Kneitel and Chase 2004). For example, taxa vulnerable to predation may be able to complete development and either emerge from ponds or enter a dormancy stage before biotic interactions intensify (Hairston 1987). This sort of adaptation might only be possible in systems with high inter-annual predictability of abiotic and biotic processes. In Chapter Five, I investigated whether temporal shifts in biotic interactions facilitate the broad distribution of a temporary-pond-specialist caddisfly, *Asynarchus nigriculus*, in a well described cluster of ponds in the Colorado Rocky Mountains. I followed the developmental phenologies of *Asynarchus* in short and long duration temporary ponds, and its major predator, *Dytiscus* beetles that are present in long duration ponds. I then used mesocosm experiments to assess size-dependent shifts in predation on *Asynarchus*, *Asynarchus* cannibalism and *Asynarchus* intraguild predation, to estimate phenological changes in vulnerability of *Asynarchus*.

In Chapter Six I integrate the results and conclusions of these studies to highlight the new insights to understanding of the community dynamics in Canterbury pond systems, and the generality of the predator permanence model of pond communities. I then discuss the contributions and implications of my work to general ecological theory.



Plate 1 Kettle ponds on the Blackwater moraine, Canterbury, New Zealand, filled after spring rains in 2004. The pond second from the left dried for the first time in > 5 years in December 2006.



Plate 2: Small ephemeral kettle pond in February, 2005, overlooking Lake Blackwater, Canterbury, New Zealand

Chapter Two

Variation in drying disturbance determines the structure of a pond metacommunity in Canterbury high country, New Zealand

Abstract

Community assembly along environmental disturbance gradients is thought to be determined by interplay between contrasting gradients of abiotic and biotic stress. For example, the ‘predator-permanence’ model of pond community assembly suggests species replacements occur along pond permanence gradients, driven by trade-offs at a local scale between coping with drying stress in temporary habitats and the resisting increased predation risk in longer duration ponds. However, evidence for the predator-permanence model is largely from systems with predictable hydrology, and the influence of regional scale processes is poorly understood. I investigated the generality of the predator-permanence model by investigating the metacommunity structure of Canterbury high country ponds with unpredictable pond drying and filling regimes. Pond communities were strongly associated with local scale factors rather than spatial position, indicating little effect of dispersal. While we observed declines in species richness with decreasing permanence, species present in the most temporary habitats were nested subsets of those present in permanent ponds, contradicting the species replacement hypothesis. Biotic interactions appeared weak in permanent ponds, with little effect of fish predators in field assays and mesocosms, and species that dominated temporary pond communities were no more vulnerable to fish predation than species that dominated permanent pond communities. Thus, nested community patterns in Canterbury ponds are likely to be driven by interplay between unpredictable drying and filling selecting for generalized traits, and weak biotic interactions in more permanent ponds preventing the biotic extirpation of temporary pond taxa.

Introduction

The assembly of local communities from a regional pool of species is influenced by both regional scale processes that influence colonisation, and the abiotic and biotic characteristics of local habitat patches (Cornell and Lawton 1992, Shurin 2001, Rajaniemi et al. 2006).

The metacommunity concept provides a useful framework to reconcile local and regional influences on communities, as it explicitly incorporates spatial processes that affect the exchange of individuals between habitats within a landscape (Leibold et al 2004). Species-sorting within metacommunities occurs where dispersal levels permit strong association of local habitat conditions and species traits (i.e., species-environment matching) but prevent source-sink dynamics (Leibold 1998, Chase and Leibold 2003, Urban 2004). Mass-effects occur when dispersal levels are sufficient to enable the persistence of species in unfavourable habitats in a process analogous to source-sink metapopulation dynamics (Mouquet and Loreau 2002, 2003). Alternatively, the patch dynamics model implies that dispersal limitation and colonisation-competition trade-offs determine assembly among temporally variable, but equally suitable, local habitat patches (Leibold et al. 2004, Calcagno et al. 2006). The importance of different species traits in these three niche assembly models contrast with neutral dynamics, which assume equivalence among species traits and local habitats, and that communities are assembled through the influence of spatial processes on stochastic colonisation and extinction events (Bell 2001, Hubbell 2001, Leibold et al. 2004).

Neutral metacommunity models have proved informative in some systems, such as streams (e.g., Thompson and Townsend 2006, Muneeppeerakul et al. 2008), but recent syntheses argue many communities should be structured by niche assembly at multiple scales (Chase and Leibold 2003, Kneitel and Chase 2004), especially those with pronounced abiotic gradients (Urban 2004, Pierce et al. 2007). In support, a meta-analysis of 158 studies found the majority of communities were structured by species sorting or combined species sorting and mass effects (Cottenie 2005). Here I investigate the role of local abiotic and biotic factors and spatial context in community assembly across a pond disturbance gradient.

Species-environment matching produced by niche assembly can occur through either a single strong axis of selection, or multiple, interactive filters of species traits. A well known example of interactive filters is the change in the strength of biotic interactions across gradients of environmental harshness. As habitats become more physically stressful, the strength of biotic interactions can decrease as disturbance events mediate competitive interactions (Grime 1977, Connell 1978, Lubchenco 1980, Crain et al. 2004) or disproportionately affect large predators (Lubchenco 1986, Menge and Sutherland 1987, Menge and Farrell 1989, Wellborn et al. 1996). As a consequence of this pattern, opposing axes of physical and biotic stress can bring about trade-offs among species traits leading to adaptations that enable the successful exploitation of physically stressful habitats but increase the susceptibility of species to negative biotic interactions and vice-versa (Power et al. 1996,

Wellborn et al. 1996). This leads to species replacements across environmental gradients (Lubchenco 1980, Wellborn et al. 1996, Urban 2004).

Alternatively, if biotic interactions do not vary in strength along environmental gradients, community dynamics may be determined by a single, strong gradient of abiotic stress. In such cases, physically benign habitats can accommodate the range of species traits present in the regional species pool, and subsequent increases in disturbance or physical stress decrease species richness through the extirpation of long-lived or disturbance-susceptible species (Urban 2004). The species persisting in the most disturbed habitats are therefore nested subsets of those present in physically benign habitats.

The nested community patterns evident in systems with a single gradient of abiotic stress should result in lower between-habitat diversity (beta-diversity), as physically harsh habitats contain few unique species. In contrast, species replacements along environmental gradients that are produced by opposing biotic and abiotic stress should increase beta-diversity as stressful and benign habitats each support unique sets of species (Kneitel and Chase 2004). Thus understanding the mechanisms behind species-environment associations will increase knowledge of community assembly at regional as well as local spatial scales.

Ponds provide ideal model metacommunity systems as local habitats patches (individual ponds) are well defined within a landscape, vary extensively in physical characteristics (Kiflawi et al. 2003) and their communities are connected by dispersal (Wissinger 1997, Bilton et al. 2001b, Van de Meutter et al. 2007). The relative isolation of ponds can influence community dynamics (McAbendroth et al. 2005, Shulman and Chase 2007) but strong species-environment associations are often evident (Schneider and Frost 1996, Wissinger et al. 1999a, Kiflawi et al. 2003, Urban 2004).

There is considerable evidence that these strong species-environmental associations in ponds are driven by both the physical constraints of pond water permanence (hydroperiod) and an increase in predation risk associated with more diverse guilds of larger predators in longer duration ponds (the 'predator-permanence gradient'; reviewed by Wellborn et al. 1996, Wissinger 1999). According to this model, the rapid development of temporary pond specialists increases their vulnerability to predation, and they are extirpated by predators in long duration or permanent ponds. Consequently, species replacements within genera or families occur across permanence gradients (Wellborn et al. 1996, Stoks and McPeck 2006, Wissinger et al. 2006b) and lead to species turnover between ponds differing in hydroperiods (Urban 2004).

Recent work however indicates that ponds may exhibit nested subsets rather than species replacements across permanence gradients (Baber et al. 2004, McAbendroth et al. 2005, Werner et al. 2007), suggesting that community assembly may be influenced primarily by pond duration limiting species developmental traits. Nested subsets may occur if selection favours generalist traits in a regional species pool (e.g., unpredictable pond filling and drying), or if biotic interactions do not limit the broad distribution of temporary pond specialists (Wissinger et al. *in press*). However, the maintenance of nested subsets could, in theory, be facilitated by mass-effects dynamics, where immigration of temporary pond taxa maintains the persistence of species highly vulnerable to predation or competitive exclusion. For example, many beetle species move reciprocally between permanent and temporary habitats (Roff 1994, Wissinger 1997). Thus, considering spatial context even with strong species-environment relationships is important for understanding assembly mechanisms.

I examined metacommunity dynamics in 29 ponds and lakes in the Canterbury high country, New Zealand (Fig. 2, Chapter One). Preliminary work in this system provided no evidence of species replacements as temporary pond fauna were a completely nested subset of species present in permanent ponds (Wissinger et al. *in press*). To investigate the mechanisms underlying this pattern I monitored pond hydrology for three years to quantify the variability of hydroperiods, and surveyed several physical and biotic properties of ponds across one season. This enabled the assessment of the relative importance of spatial position and local abiotic and biotic factors on the assembly of local communities. I also investigated the relative vulnerability to predatory fish of species dominating temporary and permanent lentic habitats to further address the role of predation in determining patterns of species occurrence.

Methods

Study sites

The study was based in the upper Waimakariri River valley which contains numerous lentic habitats within depressions in glacial- and fluvioglacial-formed landscape (Gage 1959, Timms 1983). Rainfall in the area is largely aseasonal, and averages 1300 mm per annum (Chapter One, Greenland 1977). Valleys are vegetated by semi-modified tussock grassland dominated by native *Festuca* and *Poa*, and introduced *Agrostis* and *Anthoxanthum* grasses, intermittently dispersed with short woody shrubs (*Discaria*, *Ozothamnus*, *Leptospermum*, *Hebe*, *Coprosma* and *Dracophyllum*) (Burrows 1977). Ponds were surrounded by emergent *Juncus* spp., *Chionochloa rubra*, *Carex secta* and *Typha orientalis*, especially the longer

duration ponds. Submergent vegetation varied in occurrence across the permanence gradient, but also between ponds of similar hydroperiods. Temporary ponds had zones of *Myriophyllum*, *Glyceria* and *Potamogeton* in the centre of the basins, then *Eleocharis*, *Hydrocotyle* and *Juncus articulatus*, which transitioned to a diverse, but short (< 4 cm), structurally simple turf community at shallow edges. In addition, extensive beds of vascular plants (*Elodea*, *Myriophyllum*, *Potamogeton*, *Ranunculus*, *Isoetes*) and characea algae (*Chara* and *Nitella*) formed within permanent ponds.

Sampling centred on 23 kettle-hole lakes and ponds on a terminal moraine and outwash terrace (Gage 1958, 1959) surrounding Lake Blackwater. However, the regional scale of sampling was expanded to include six more distant habitats (three temporary ponds and three small permanent lakes) selected based on their similarity of size and surrounding land-use to ponds in the Blackwater cluster. Fish were present in permanent lentic habitats in the area, and included koaro (*Galaxias brevipinnis*), upland bullies (*Gobiomorphus breviceps*) brown (*Salmo trutta*) and rainbow (*Oncorhynchus mykiss*) trout and longfin eels (*Anguilla dieffenbachii*).

Environmental characteristics

Pond hydrology was monitored from March 2005 to October 2007 with water height data loggers (Trutrack HT-100, Christchurch, New Zealand) installed in the majority of ponds, either at the deepest point or in the littoral zone. Some very temporary basins were monitored with air and water temperature recorders, from which periods of filling could be easily deduced. Ponds were mapped when all ponds were bank-full in September 2006 using differential GPS (Geo-XM, Trimble, Sunnyvale, CA, USA). In mid September 2006, habitat features of each pond were sampled using two perpendicular transects through the pond centre, or four parallel transects perpendicular to the shore of large, deep ponds. Water depth, surface area and height of plant morphotypes (Appendix 3), and inorganic substrate composition were estimated within a 1 m quadrat at 5 m intervals for transects < 50 m, and 10 m intervals for transects > 50 m. Conductivity and pH were measured with a calibrated hand held meter (Oakton 10 series, Oakton Instruments, Vernon Hills, IL, USA) in September and December 2006.

Biological surveys

Biological sampling was conducted in the austral spring (September) and summer (December). Rapid drying resulted in three ponds being sampled only once. Additional

qualitative samples were taken in long duration temporary ponds in March 2007 in order to detect late colonists normally restricted to permanent ponds. Qualitative samples were taken by repeatedly sweeping a standard D-net (1 mm mesh) through all habitats accessible from the shoreline in each pond, using real-time estimations of sampling efficiency (Chase 2003, Wissinger et al. 2006a, Wissinger et al. *in press*). The initial number of sweeps (three passes over 1 m x 0.3 m area) was scaled to \log_{10} pond area, with a minimum of 10 sweeps in the smallest pond. Sweep contents were transferred to a white sorting tray and voucher specimens of each new taxon were preserved in 90% ethanol to confirm field identifications. Sampling continued beyond the initial sweeps until five successive samples returned no new taxa. Ten supplementary sweeps were taken with a 500 μ m mesh net to enhance the detection of small bodied species. Fish were sampled qualitatively with visual observations and 10 Gee-minnow traps, and three fyke nets (5m lead) set in a range of habitats for 24 h.

Subsequent quantitative sampling was designed to estimate the abundance, biomass and size of the most common taxa, and to measure the relative distribution of biomass and size among predators and prey. Three core samples were taken in each pond to estimate the abundance of small-bodied or very abundant taxa (snails, chironomids, worms, hydroptilid caddisflies and epibenthic microcrustacea). Each sample comprised of multiple sweeps of a 500 μ m mesh aquarium net within the sediment and water column contained within a 1 m high section of 0.02 m² PVC pipe. Samples were preserved in 90% ethanol and later washed over a 500 μ m sieve and sorted under 10x magnification. Four box samples (multiple sweeps of a 1 mm mesh D-net within a 0.16 m² mesh frame, 60 cm high) were taken to estimate the abundance of large-bodied taxa. These samples were sorted on-site, and invertebrates were preserved in 90% ethanol. Because ponds varied considerably in their degree of open substrate and emergent vegetation, quantitative samples were limited to areas of submergent vegetation which were consistently found across all ponds.

Invertebrates were identified to the lowest possible taxonomic level using standard keys and reference to original descriptions where necessary (Winterbourn 1973, Chapman and Lewis 1976, Winterbourn et al. 2006 and references therein). Microcrustacea and chironomids were sorted under 10x magnification into coarse taxonomic groups, from which subsets of individuals were mounted on slides for identification to genus or species. Where coarse taxonomic groups consisted of multiple species, abundance was determined based on the proportion of each species in the subsamples. Dry mass for all taxa (except oligochaetes) was determined from taxon-specific length-weight regressions (Appendix 1) after the body length of a subset of 10 individuals was measured using an eye piece micrometer.

Oligochaetes were dried at 60 °C for 48 h and weighed to the nearest 0.1 mg. Dry mass of all taxa was converted to ash free dry mass (AFDM) using taxon-specific correction factors (H.S. Greig unpublished data).

Taxa were classified as predatory or non-predatory, predators being considered those species with diets consisting of a majority of animal tissue based on literature searches (Appendix 1, Chapter Four). Omnivorous tax (e.g., Tanypodinae, and *Hudsonema*) were considered non-predators, as were predators that feed mainly on very small (body length < 500 µm) prey. Although this size 500 µm limit simplified our observed food webs (Woodward et al. 2005b) it prevented overestimation of the proportion of total abundance and richness attributed to predators by failing to detect and/or quantify all prey taxa (e.g., rotifers and copeopdites).

Mesocosm experiment

To investigate whether species that dominate the biomass of temporary ponds were more vulnerable to fish predation than permanent pond species, I exposed a prey community comprised of numerous permanent and temporary pond species to predation by koaro in mesocosms at the University of Canterbury's Cass field station. I also manipulated the presence of submergent vegetation to determine whether vulnerable species coexist with predatory fish by utilising spatial refugia. Treatments were arranged in a 2 x 2 factorial design, in four randomized blocks, each containing one replicate of each of the four treatment combinations. Koaro were chosen because they are the native predator in our study sites, are abundant in the shallow littoral zone, and they feed on a large range of macroinvertebrates (Rowe et al. 2002). Mesocosms were 800 cm² oval polythene cattle tanks (see Greig and McIntosh 2006) fitted with a central standpipe that regulated water depth to 25-28 cm. Groundwater (10 °C; pH = 7.7; specific conductance = 114 µs cm⁻¹) was fed through two water jets on opposite sides of each tank (facing upwards to prevent benthic disturbance or circular flow), at a rate of 10 mL s⁻¹ to compensate for evaporation and to dampen diurnal temperate fluctuations. Two clumps of *Myriophyllum* (squares 25 x 25 cm and 15 x 15 cm; stem height 15 cm) and a 15 x 15 cm clump of *Carex* sedge (40 cm height) collected from a fishless pond were rinsed of invertebrates and added to each tank (Plate 3a). After one day, any invertebrates accidentally introduced with the vegetation were removed, and then vegetation was cut to soil level in half the tanks to form the simple vegetation treatment (Plate 3b). In all treatments, the remainder of the tank floor was covered in a 1 mm layer of

fine mud; a 12 cm long section of 6.5 cm diameter PVC pipe was set horizontally into the substrate for fish cover.

The prey community was artificially assembled from the regional species pool, and included five species that dominated the biomass of permanent ponds (*Xanthocnemis* and *Procordulia* odonates, *Triplectides* caddisflies, *Diaprepocoris* water boatmen, *Potamopyrgus* snails) and six species that dominated temporary pond biomass (*Sigara* water boatmen, *Anisops* backswimmers, both larval and adult *Rhantus* and larval *Antiporus* beetles, and *Daphnia* cladocerans). Biomass (AFDM) of each invertebrate taxa was approximately equal, and total biomass fell within the range observed in permanent ponds. Small numbers of cyclopoid copepods and orthoclad chironomids were inadvertently added with the soil clumps. Prey were added on the morning of 28 Feb 2007, and allowed to acclimate for 10 h before fish (one koaro, mean fork length: 120 ± 5.4 mm) were added to eight randomly selected tanks. Fish were collected from a nearby pond (Romulus) using Gee-minnow traps set earlier that day.

After two weeks, fish were removed from tanks, measured and weighed. Then a cylinder sample was taken within the largest clump of *Myriophyllum* to measure small bodied prey (chironomids and crustaceans), using the same procedure as for the predator assay. Following this, vegetation was removed, shaken vigorously in the tank, and transferred to a tray for sorting. Remaining soil clumps were removed from tanks and searched for invertebrates, and water and mud were tipped into a 1 mm mesh net whose contents were then transferred to a tray for sorting. Invertebrates were processed and AFDM determined as for the pond surveys.

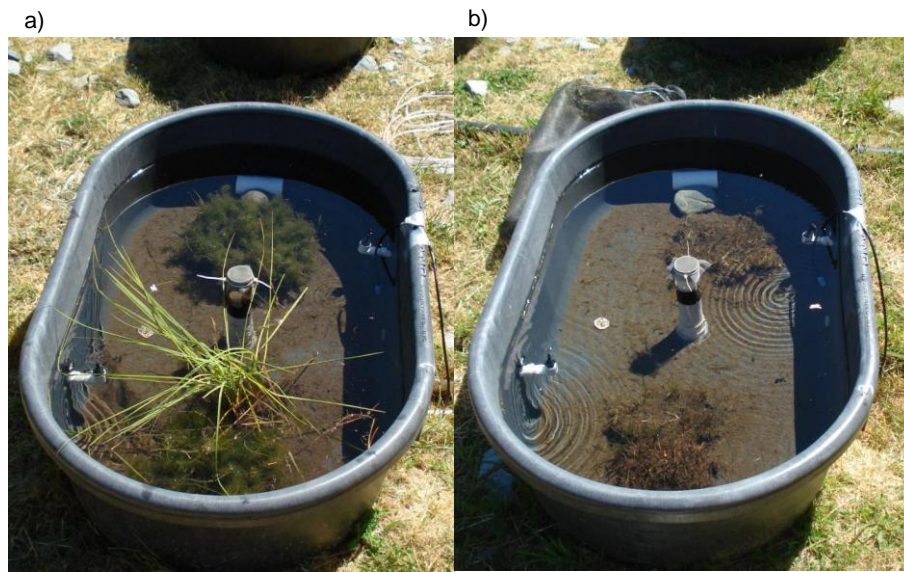


Plate 3 Mesocosms showing (a) complex treatment with clumps of *Carex* emergent vegetation and *Myriophyllum* submergent vegetation, and (b) simple vegetation treatment with vegetation cut to soil level of clumps.

Data analysis

I assessed spatial autocorrelation in species composition using Mantel tests to compare the community similarity matrix (Sorenson's index) with a matrix of inter-pond distances. Significance was tested with Z scores after 1000 Monte Carlo randomizations (MantelTester 1.1, based on Zt software; Bonnet and Van de Peer 2002). Inter-pond distances were calculated between the centroids of all sampled ponds that were defined from GPS polygon features. Pond centroids were appropriate given the scale of the landscape relative to pond size (Jeffries 1994, McAbendroth et al. 2005). The relative isolation of individual ponds was taken as the sum of distances to all other ponds sampled. Spatial autocorrelation was also assessed after accounting for environmental variation (three principal component axes explaining 77% of variation in 11 environmental variables) using partial Mantel statistics.

I used nested subset analysis to test whether community patterns I observed were determined predominantly by decreased pond duration causing the selective extirpation of taxa. Nestedness was calculated as a modified version of matrix temperature, T (Atmar and Patterson 1993), using the program 'Nestedness' (Ulrich 2006) which overcomes the inconsistencies in the Nestedness Temperature Calculator algorithm (e.g., Rodríguez-Girones and Santamaria 2006). Matrix temperature yields a number between 1 (perfectly nested) and 100 (perfectly non-nested) for entire communities, and also enables the calculation of an

index of the relative nestedness for each species. Thus, specific taxa contributing to nestedness or departure from nestedness can be determined (Atmar and Patterson 1993, McAbendroth et al. 2005). Significant nestedness occurs when observed T is significantly lower (using Z scores) than simulated T from multiple permutations of randomized, null models. I tested the significance of nestedness by comparing my pond matrix to 100 iterations of three alternative randomized null models that differed in their incorporation of underlying ecological structure (McAbendroth et al. 2005, Moore and Swihart 2007). The first model was fully randomized without constraints (Random 00). The second model employed randomizations with the probability of species presence determined by their number of site occurrences (Random 1 model), which controls for nestedness created by rare species being less likely to be sampled than common species (passive sampling; Fischer and Lindenmayer 2002, McAbendroth et al. 2005). Finally, randomizations within fixed column and row totals were employed (fixed-fixed model; Brualdi and Sanderson 1999), to randomize species composition while maintaining the integrity of observed matrix structure. This last model is the most conservative as it controls for nestedness produced by strong species richness gradients (Moore and Swihart 2007, Ulrich and Gotelli 2007). Environmental correlates of nestedness were evaluated by first ordering the ponds in the species matrix to maximize nestedness values (T packing algorithm). This pond order was then used as an ordinal response variable in best-subset multiple regression and hierarchical partitioning analysis (described below) to extract the environmental predictor variables that best explained the order of ponds that producing maximal nestedness.

The effect of environmental variables on multivariate community composition was assessed with constrained linear ordination (Redundancy Analysis, RDA) as short species gradients (< 2.7) observed in initial Detrended Correspondence Analysis (DCA) indicated the use of linear ordination was appropriate (Leps and Smilauer 2003). Forward selection following 199 permutations was used to extract significant environmental variables. Before analysis, environmental descriptors were centered by dividing by the mean (Quinn and Keough 2002) but retained moderate collinearity ($VIF < 9$). Subsequently, I used principal components analysis (PCA) to reduce within-pond habitat characteristics into two orthogonal principal components that explained 78.8% of the variation in habitat variables. Vegetation cover, % emergent vegetation and substrate index were significantly correlated with habitat PC1 ($r = 0.88, -0.83$ and -0.72 , respectively) and vegetation volume and the diversity of plant morphotypes were significantly associated with habitat PC2 (0.80 and 0.82, respectively). These two principal components, pond permanence, pond area, pH and conductivity (weak

colinearity: VIF 1.5 - 3.5) were included as environmental predictors in RDA and further analysis of univariate community descriptors.

The relationships between environmental variables and species richness and the proportion of predator species were assessed with best-subsets regression using second order Akaike's Information Criteria, AIC_c (Burnham and Anderson 1998), to select significant predictors. This process avoids the inconsistencies of stepwise selection procedures (Quinn and Keough 2002). Because best subset analysis does not provide information on the relative importance of moderately intercorrelated predictors (Werner et al. 2007), I performed hierarchical partitioning analysis to assess the independent, joint and total contributions of each predictor to variation in the response variable (Mac Nally 2000, Quinn and Keough 2002). The significance of contributions was assessed with Z-scores after 100 randomizations, and analysis was conducted with “hier.part” and “rand.hp” functions (Mac Nally and Walsh 2004) in R (R Development Core Team 2006).

The effect of hydroperiod on quantitative descriptors of food webs was first assessed using homogeneity of slopes tests that included date of sampling (spring or summer) as a covariate, days since refilling at date of sampling as a continuous predictor, and the date by hydroperiod interaction. Response variables with non-significant interactions terms in homogeneity of slopes tests were analysed subsequently by ANCOVA with date and hydroperiod as main effects. Variables with heterogeneous slopes were analysed with separate regressions. So as not to miss potentially important differences in biology between sampling periods (due to Type II statistical errors), I set alpha at 0.1 for the homogeneity of slopes tests. However, alpha was set at 0.05 for all subsequent tests (i.e., ANCOVAs and individual regressions if the interaction term was significant). Proportions were arcsine-square-root transformed and other variables were \log_e -transformed.

The effect of fish on the biomass of each species in the mesocosms was quantified as log-ratio interaction strength (Berlow et al. 1999):

$$IS = \ln (B_f/B_c)$$

where IS is interaction strength, B_f is prey biomass in the fish treatment and B_c is prey biomass in the control. I calculated IS separately for vegetation and no vegetation treatments, and fish and control treatments were paired within blocks. Data were analysed using nested, fixed-effects ANOVA with species nested within permanence, and vegetation nested within species.

Results

Pond hydrology

Pond filling dates and the length of time ponds contained water varied considerably between and within years, and were closely linked to rainfall events (Fig. 1). In 2005, a dry winter led to fewer than half of the ponds filling, and by early summer, all but the four permanent ponds had dried up. In 2006 a wet autumn and winter filled all the monitored ponds and high rainfall in late November and December (late spring-early summer) refilled even the most temporary ponds, and most retained water until February and March (late summer-early autumn). Spring rains in 2007 filled most of the ponds (Fig. 1), but many dried up in November and December (authors unpublished data). Additionally, numerous discrete rainfall events filled ponds for short durations, multiple times in a season over all three years.

Qualitative community structure

A total of 106 taxa was observed in the regional species pool, with 76% identified to species, 3% to genus and the remaining 11% to family level or higher. A Mantel test comparing community similarity and distance between ponds indicated marginally non-significant spatial autocorrelation across the 29 ponds ($r = 0.30$, $P = 0.055$; mean inter-pond distance = 5.7 km). The removal of one isolated outlier (Lyndon Tarn) had little influence on this marginal spatial correlation ($P = 0.056$; mean distance = 4.0 km), but no significant spatial autocorrelation was observed when the dataset was reduced to the 23 ponds on the Blackwater moraine ($P = 0.40$, mean distance 1.3 km). Eleven environmental variables were reduced to three principal component axes that explained 77% of the variation in environmental measures. These components were significantly, spatially autocorrelated ($P = 0.045$) and when their effects were removed with partial mantel tests, spatial autocorrelation of pond communities across all scales was not significant ($P > 0.10$).

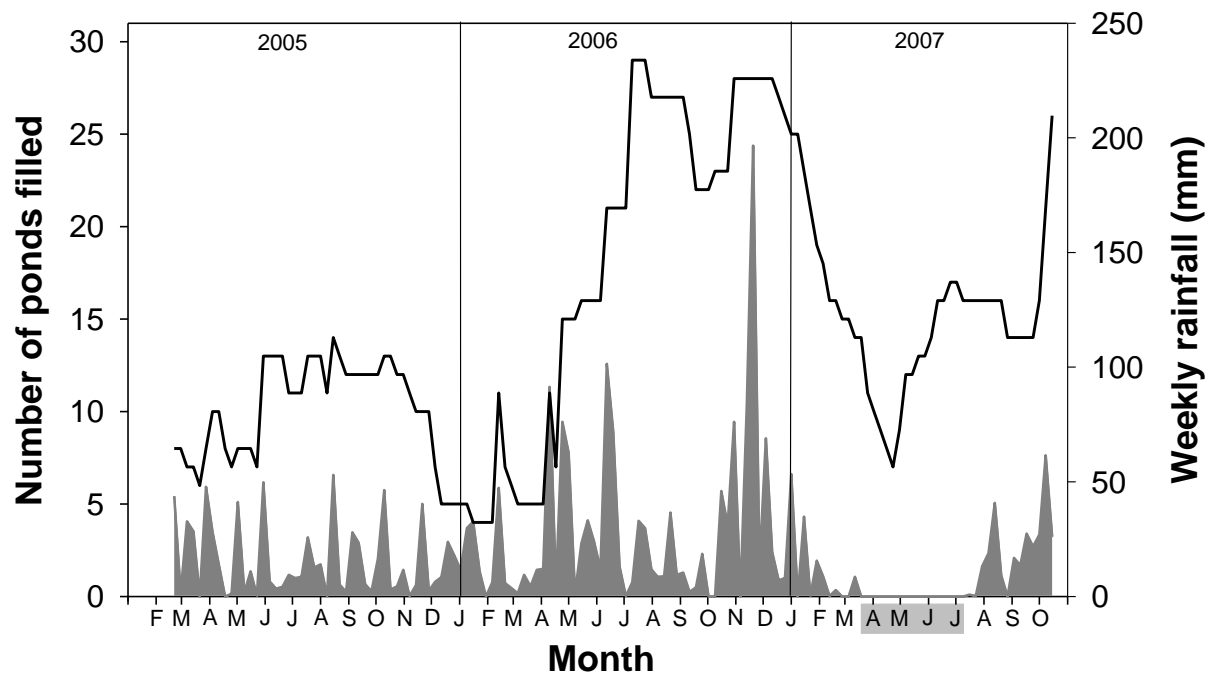


Fig. 1 The number of ponds (maximum of 29) containing water per week over a three year period from 2005 to 2007 (black line). Depth of ponds was measured continuously with water height recorders and a pond was considered filled if it contained water for at least seven days. Four permanent ponds (assessed across decades) represent the basal number filled. Total weekly rainfall at the University of Canterbury Cass Field Station over the same time period is shown in dark grey. Rainfall data were unavailable in the months shaded in light grey.

RDA revealed two significant axes of community composition, which together explained 31.1 % of qualitative species composition (Fig 2). Forward stepwise regression selected four variables with significant correlations with community composition. Long duration temporary ponds, and permanent ponds with moderate (although diverse) plant cover and coarse inorganic substrate clustered on the right side of axis one, and short duration temporary ponds with simple abundant vegetation and fine substrate aligned on the left side (Fig. 2). Along axis two, permanent basins with high conductivity and temporary ponds with little emergent vegetation separated from ponds with low conductivity and abundant emergent and tall submergent vegetation (Fig 2).

These environmental predictors were intercorrelated but were only moderate to weakly collinear ($VIF = 1.1 - 2.7$). Pond hydroperiod was significantly correlated with habitat PC1 ($r = -0.79$) and pond area ($r = 0.72$), habitat PC1 was correlated with area ($r = -0.62$), and pH was moderately correlated with conductivity ($r = 0.57$). The first ordination axis was also strongly correlated with species richness ($r = 0.97$; Fig 2).

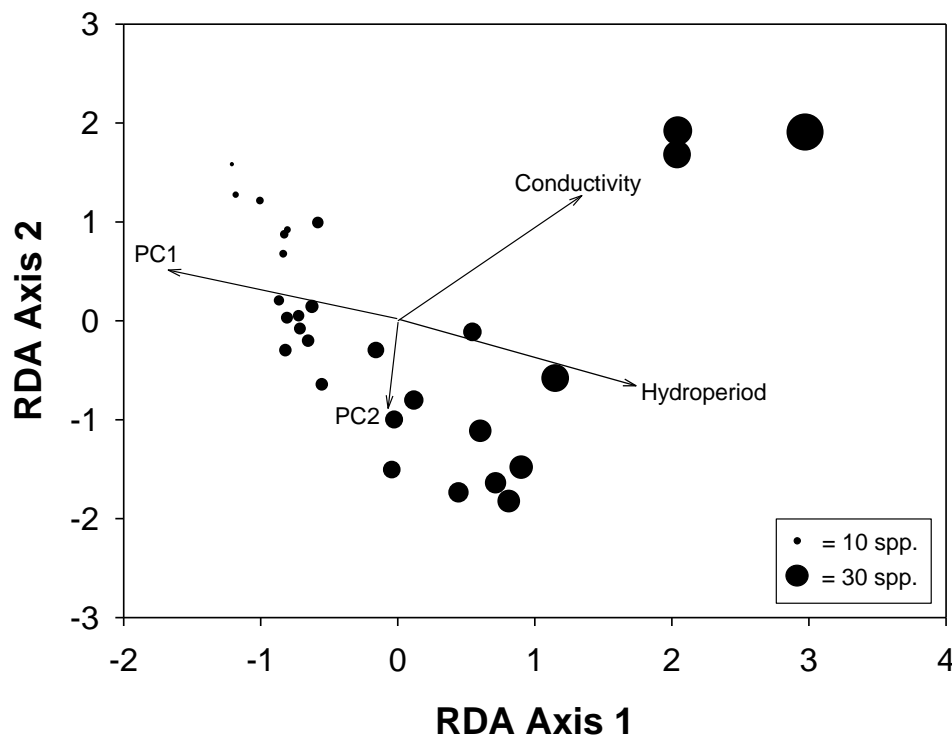


Fig. 2 Redundancy analysis (RDA) biplot of community composition in 29 ponds and four significant ($P < 0.05$) environmental predictors that were selected by forward stepwise regression. The area of circles indicates species richness (see legend) whereas the lengths of environmental vectors are proportional to correlation coefficients, multiplied by two for clarity. PC1 and PC2 are significant principal components describing within pond habitat heterogeneity (see text). Together RDA axes one and two explain 31.1% of the variation in species composition among sites (axis one: 22.5%, axis two: 8.6%).

Best-subsets model selection (AIC_c) revealed a three-variable model was the best predictor of species richness. It included a strong positive effect of permanence on species richness (Fig 3a), and additional positive and negative effects of conductivity and habitat PC1, respectively (Table 1a). Hierarchical partitioning analysis indicated permanence had the strongest independent effect on species richness (Table 1a). Habitat PC1, conductivity and pond area also had significant independent effects according to randomisations. Pond area was not selected in the model analysis, however (Table 1a), indicating its inclusion did not contribute significantly to the final model. Further analysis including spatial isolation (mean interpond distance) with the six other predictors did not alter the selection of predictors or their relative importance.

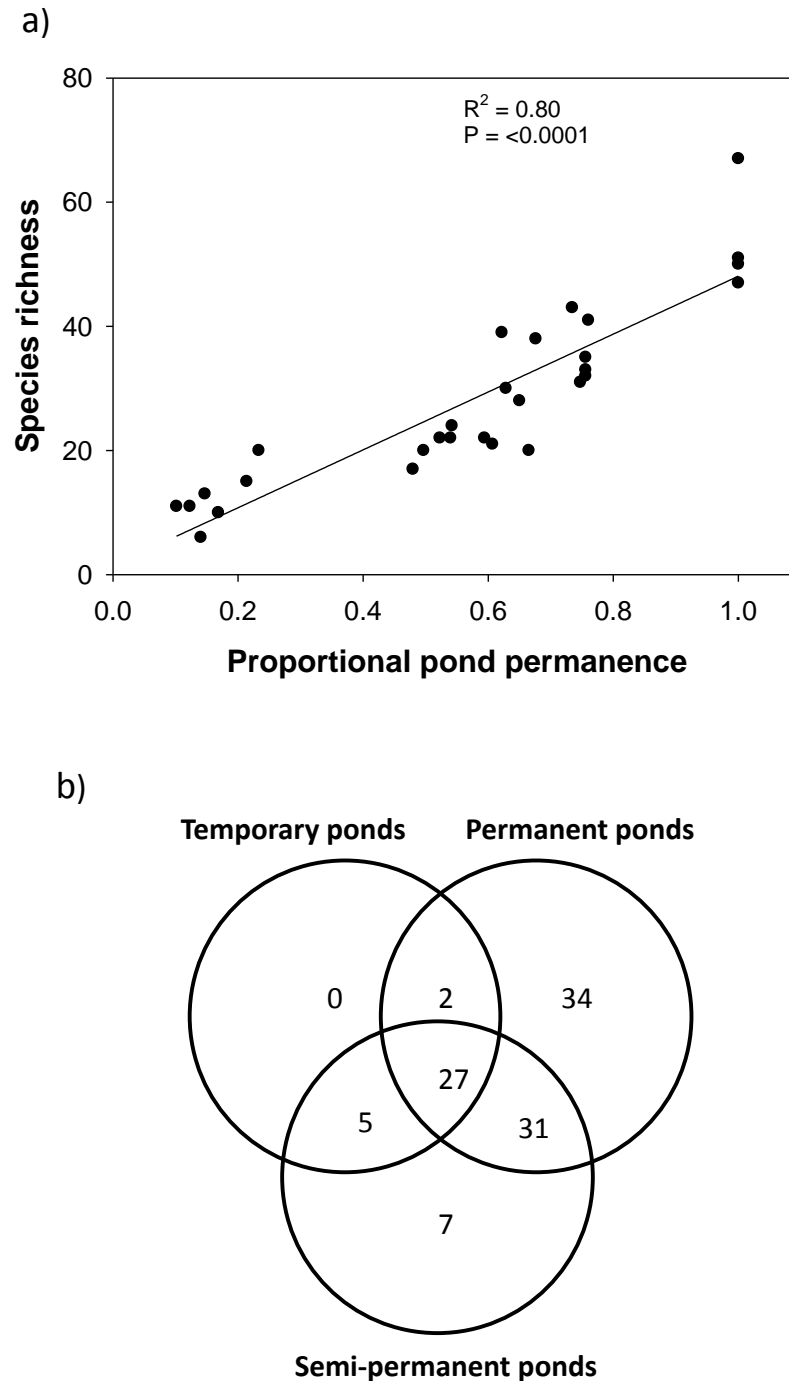


Fig. 3 Invertebrate species richness in 29 ponds spanning a gradient of pond permanence. In (a) relative pond permanence was calculated from the proportion of days filled during the monitoring after ponds initially filled in autumn/winter 2006 (460 days), and species richness was the total found across three sampling periods for a given pond. The regression equation is $y = 1.45 + 46.6x$. (b) Venn diagrams of species overlap from a regional pool of 106 taxa in ponds grouped in three permanence categories based on the separations seen in (a). Numbers are pooled counts of species across all ponds in a given category; numbers within overlapping circles are shared between categories.

Table 1 Generalized linear model selection and hierarchical partitioning analysis of six environmental predictors of species richness, proportional predator richness, and the order of sites to produce maximum nestedness. *P*-values were calculated from Wald's statistic on model parameters. Variables in bold were selected in final models based on AIC_c selection criteria. Asterisks indicate significant ($P < 0.05$) independent variance in the hierarchical partitioning analysis. PC1 was positively correlated with submergent and emergent vegetation cover, and negatively correlated with substrate index; PC2 was positively correlated with vegetation volume and the diversity of plant morphotypes.

Variable	Model selection		Hierarchical partitioning (R^2)		
	Parameter	<i>P</i>	Independent	Joint	Total
<i>a) Species Richness</i>					
pH	-2.67	0.24	0.02	0.05	0.07
Conductivity	0.25	< 0.0001	0.12*	0.17	0.29
Permanence	27.16	< 0.0001	0.35*	0.46	0.81
Area	0.98	0.073	0.17*	0.34	0.51
Habitat PC1	-3.47	0.004	0.26*	0.43	0.69
Habitat PC2	2.15	0.013	0.01	-0.01	0.00
<i>b) Predator richness</i>					
pH	-2.54	0.017	0.03	-0.03	0.00
Conductivity	0.03	0.14	0.03	0.05	0.08
Permanence	8.42	0.0001	0.34*	0.40	0.74
Area	0.45	0.074	0.18*	0.31	0.50
Habitat PC1	-0.52	0.34	0.21*	0.35	0.56
Habitat PC2	0.43	0.28	0.01	0.01	0.02
<i>c) Proportional predator richness</i>					
pH	-0.11	0.005	0.27*	0.11	0.38
Conductivity	-0.001	0.55	0.07	0.04	0.12
Permanence	0.06	0.48	0.02	0.00	0.02
Area	0.004	0.66	0.01	0.00	0.01
Habitat PC1	0.004	0.85	0.00	0.00	0.00
Habitat PC2	-0.01	0.48	0.07	0.06	0.12
<i>d) Nestedness</i>					
pH	0.29	0.883	0.02	0.05	0.07
Conductivity	-0.09	0.058	0.07	0.13	0.20
Permanence	-18.59	< 0.0001	0.35*	0.42	0.77
Area	-0.59	0.213	0.16*	0.32	0.48
Habitat PC1	1.49	0.152	0.23*	0.39	0.62
Habitat PC2	-1.41	0.060	0.02	-0.01	0.00

Based on degree of water permanence, ponds could be grouped into three identifiable clusters, with four permanent ponds, 18 ponds of intermediate hydroperiod (semi-permanent) and seven temporary ponds (Fig. 3a). The vast majority of species (88%) in the regional pool were observed in permanent ponds (Fig. 3b), and a quarter of the species in the regional pool were found in all three pond types. Permanent and semi-permanent ponds shared the most

species (29%) and only twelve species were not observed in permanent ponds. They were five crustaceans, five insects, one mite (*Hydrachna*) and the anuran *Litoria ewingi*; although two of these species were only found in a single pond. Nestedness analysis indicated strongly nested community composition (low matrix temperature), which was highly significant when compared to both simple and conservative null models (Table 2). However, comparisons of species-specific temperature with the combined matrix temperature revealed 38% of species exhibited distributions less nested than average (i.e., idiosyncratic distributions; McAbendroth et al. 2005). Crustaceans had a significantly higher proportion of species with idiosyncratic distribution than other taxa (crustacean mean proportion \pm se: 0.55 ± 0.09 ; other taxa: 0.32 ± 0.05 ; Binomial GLM, $P = 0.029$). When analysed separately, crustaceans were significantly nested according to all three null models investigated, but higher matrix temperature indicated crustaceans were less nested than other taxa. Furthermore, the order of sites producing highest nestedness was less correlated with pond hydroperiod than other taxa, indicating crustaceans were less nested along pond permanence gradients than other taxa (Table 2). Taxonomic resolution (species, genus or \geq family level) did not influence the relative nestedness of individual taxa (Binomial GLM: $P = 0.73$)

Table 2: Nested subset analysis of 29 ponds across a hydroperiod gradient using modified matrix temperature for all taxa, and separately for crustaceans and all other taxa. Observed matrix temperature was compared with simulated values from three randomised null models that differed in their structural constraints: the unconstrained Random00 model, Random1 model that controlled for passive sampling, and the fixed column and row total (FF) model that controlled for species richness (see text for more details). Significance was tested with Z scores after 100 permutations of each null model. Correlations of hydroperiod with the order of maximal nestedness are also shown.

Model	Matrix temperature	Z	P	Correlation with hydroperiod (r)
a) All taxa	8.76			-0.88
Random 00	60.47	-27.3	< 0.0001	
Random 1	18.93	-8.88	< 0.0001	
FF	10.87	-5.01	< 0.0001	
b) Crustacea	14.19			-0.71
Random 00	56.81	-13.3	< 0.0001	
Random 1	21.89	-4.26	< 0.0001	
FF	16.39	-2.71	0.003	
c) Other taxa	5.51			-0.90
Random 00	55.74	-26.4	< 0.0001	
Random 1	15.57	-8.31	< 0.0001	
FF	6.84	-3.02	0.0013	

Trophic composition of food webs

Fish were present in each of the permanent ponds. Koaro were found in Romulus and Lake Blackwater, and upland bullies in Lyndon Tarn and Lake Sarah. Low densities (< one per 50 m of visible shoreline) of large trout were also observed in Lakes Sarah and Blackwater during visual observations. Larval koaro were also observed in January in Little Blackwater, which had dried for the first time in more than 5 years the previous summer.

The diversity of predatory invertebrates, like total invertebrate species richness, was strongly and positively related to pond permanence (Table 1b). Pond permanence was the only predictor selected by AIC_c, and explained the majority of independent variation. As with predator richness, pond area and PC1 also made significant independent contributions to model R^2 . However, there was no relationship between predator diversity as a proportion of total richness (proportional predator richness), and pond duration. Rather, AIC_c revealed a weak relationship with pH (Table 1b). Further analysis for both predator richness and proportional predator richness that included spatial isolation (mean interpond distance) as well as the six other predictors did not alter the selection of predictors or their relative importance.

Patterns of quantitative trophic composition with days since refilling (pond duration) were similar to qualitative patterns, but relationships differed slightly among sampling periods. Both total invertebrate biomass and total density of invertebrate taxa increased with pond duration (Fig. 4a,b, Table 3), but total biomass was higher in short duration ponds in early summer than in spring, leading to a significantly lower slope with days since refilling in early summer (Fig 4a, Table 3). Predator biomass and predator density mirrored the trends for total biomass and density, increasing with pond duration (Fig. 4c,e). The slopes of the predator biomass to pond duration relationship were the same for both sampling periods (Fig. 4c, Table 3), but differed significantly between spring and summer for predator density (Fig. 4e, Table 3). These relationships changed when predator biomass and density were expressed as proportions. Proportional predator biomass was not affected by duration in September ($R^2 = 0.012$, $P = 0.57$) but increased with pond duration in December (Fig. 4d, Table 3). However, in September, ponds had a greater proportional predator biomass than in December (Table 3). Proportional predator density increased with pond duration, but this relationship did not differ between spring and summer (Fig 4f, Table 3). Finally, mean predator size (excluding fish) increased significantly with pond duration in both spring and summer and predators were larger in spring than in summer (Fig 4g, Table 3).

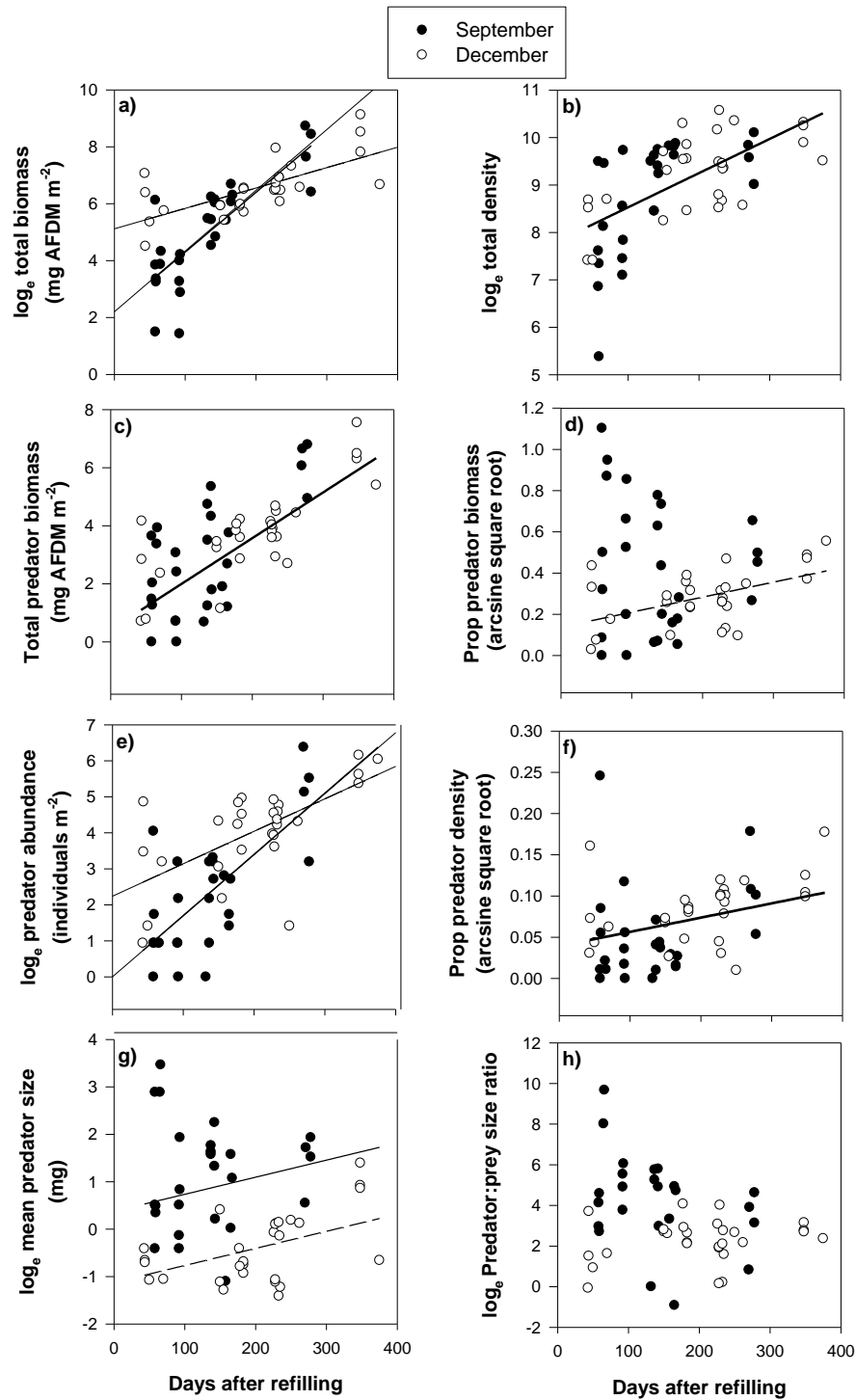


Fig. 4 Relationship between quantitative metrics of predator abundance and days after refilling in ponds over two sampling periods (September and December 2006). Regression lines were derived from homogeneity of slopes tests followed by ANCOVA when slopes were homogeneous (Table 3). Thick lines indicate regressions based on combined data from both sampling dates as indicated by no date or duration by date interaction. Thin lines are regressions for September (solid) and December (dashed), following a significant date effect in ANCOVA or duration by date interaction in homogeneity of slopes tests. Regression equations are: (a) September, $y = 2.20 + 0.021x$, $R^2 = 0.67$, $P < 0.0001$; December, $y = 5.12 + 0.007x$, $R^2 = 0.47$, $P < 0.0001$; (b) all dates, $y = 7.81 + 0.007x$, $R^2 = 0.37$, $P < 0.0001$; (c) all dates, $y = 0.087 + 0.015x$, $R^2 = 0.52$, $P < 0.0001$; (d) December, $y = 0.14 + 0.0007x$, $R^2 = 0.24$, $P = 0.007$; (e) September, $y = 0.004 + 0.017x$, $R^2 = 0.51$, $P < 0.0001$; December, $y = 2.24 + 0.009x$, $R^2 = 0.40$, $P = 0.0002$; (f) all dates, $y = 0.032 + 0.0002x$, $R^2 = 0.14$, $P = 0.005$; (g) September, $y = 0.38 + 0.004x$; December, $y = -1.13 + 0.004x$.

Table 3. Results of homogeneity of slopes tests and ANCOVA on the effect of duration since pond filling and date of sampling on the total biomass, density and trophic structure of 29 ponds in spring and summer. See text for further description of variables. α for homogeneity of slopes tests was set at 0.1.

Variable	df*	df	F	P
<i>Total biomass</i>				
Duration*	1, 50		80.08	< 0.0001
Date*	1, 50		26.53	< 0.0001
Duration x date*	1, 50		19.96	< 0.0001
<i>Total density</i>				
Duration		1, 51	25.92	< 0.0001
Date		1, 51	0.003	0.96
Duration x date*	1, 50		2.18	0.15
<i>Predator biomass</i>				
Duration		1, 51	33.10	< 0.0001
Date		1, 51	0.002	0.96
Duration x date*	1, 50		1.02	0.32
<i>Proportional predator biomass</i>				
Duration	1, 50		0.25	0.62
Date	1, 50		8.15	< 0.006
Duration x date*	1, 50		3.22	0.078
<i>Predator density</i>				
Duration*	1, 50		44.71	< 0.0001
Date*	1, 50		10.44	0.002
Duration x date*	1, 50		4.18	0.046
<i>Proportional predator density</i>				
Duration		1, 51	4.92	0.031
Date		1, 51	1.97	0.17
Duration x date*	1, 50		0.02	0.90
<i>Predator size</i>				
Duration		1, 51	5.97	0.018
Date		1, 51	34.03	< 0.0001
Duration x date*	1, 50		0.27	0.60
<i>Predator:prey size ratio</i>				
Duration*	1, 50		0.96	0.33
Date*	1, 50		8.68	0.005
Duration x date*	1, 50		3.31	0.074

* Obtained from homogeneity of slopes tests

Predator: prey size ratios were consistently greater in spring than in summer (Fig 4h, Table 3) and homogeneity of slopes test indicated a significant duration by date interaction. However, subsequent regressions indicated the negative and positive effects of duration on body-size ratios in September and December, respectively, were not significant (September: $R^2 = 0.12$, $P = 0.10$; December: $R^2 = 0.12$, $P = 0.21$).

Mesocosm experiment

Temporary pond taxa were not significantly more vulnerable to fish than permanent pond species (permanence effect: $F_{1,8} = 0.41$, $P = 0.54$; Fig 5b). However, fish significantly reduced the biomass of the common temporary pond predatory beetle larva, *Rhantus* (species [nested in permanence]: $F_{8,10} = 19.33$, $P < 0.001$; Fig 5a). The presence of submergent and emergent vegetation did not influence the impact of fish on *Rhantus* larvae or any other species (vegetation [nested in species]: $F_{10,60} = 0.32$, $P = 0.97$).

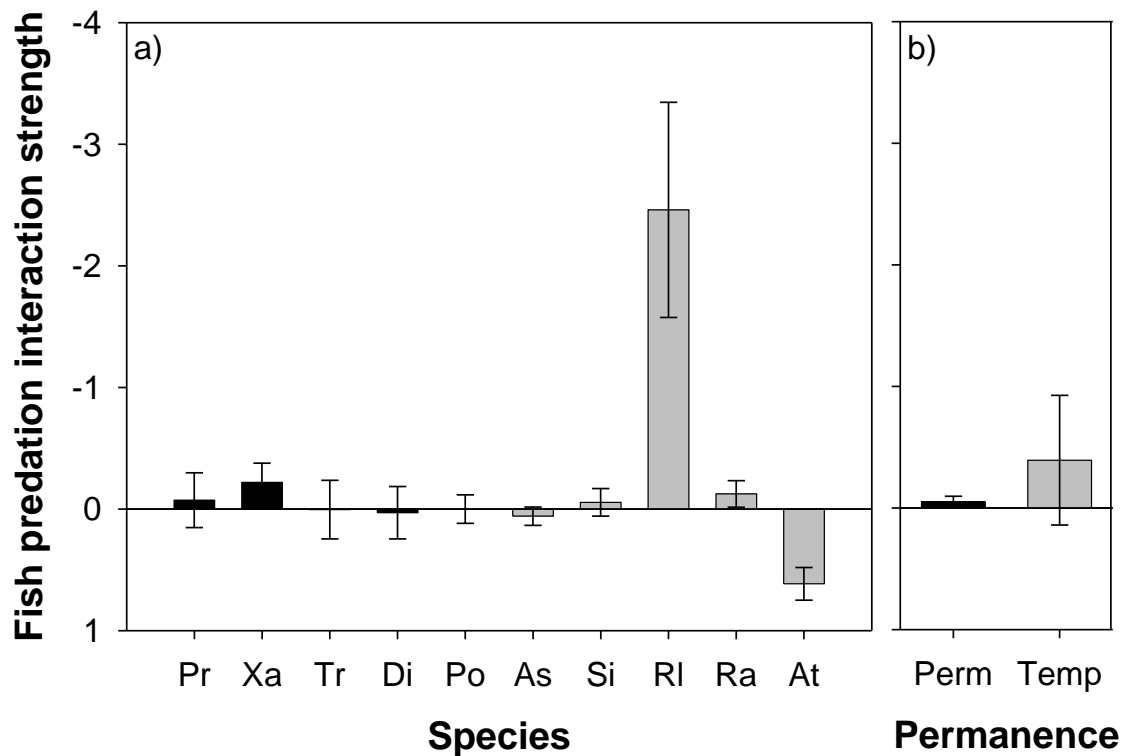


Fig. 5 The mean (\pm se) impact of fish (measured as log-ratio interaction strength) on (a) the biomass of ten prey species from permanent (black bars) and temporary (grey bars) ponds and (b) across all temporary and permanent pond species. Xa = *Xanthocnemis zelandica*, Pr = *Procordulia grayi*, Tr = *Triplectides cephalotes*, Di = *Diaprepocoris zealandiae*, Po = *Potamopyrgus antipodarum*, As = *Anisops* spp., Si = *Sigara arguta*, RI = *Rhantus suturalis* larvae, Ra = *Rhantus suturalis* adults, At = *Antiporus femoralis* larvae. Error bars are \pm one se.

Discussion

Absence of spatial structuring of communities

Strong species associations with the environmental gradient of pond duration observed in this study indicate niche-based assembly models that incorporate habitat variability better described pond metacommunity structure than neutral or patch dynamic models. First, I observed strong environment variation between ponds, largely with respect to habitat permanence, and species composition was strongly associated with those differences in habitat preference. Although some species were present across the permanence gradient, many were restricted to permanent habitats, and a minority appeared to be restricted to temporary habitats (Fig 3b). Thus species traits appear not to be equivalent as the neutral model predicts. Second, analysis of the nestedness of species distributions indicated significant departures from randomized null nestedness models, even when models were constrained by patterns of observed species occurrence and site richness (FF null models). Finally, there was little evidence for spatial structuring of communities. In particular, partial Mantel tests indicated there was little evidence for spatial autocorrelation, once covariance in environmental conditions was accounted for. This finding implies that the spatial orientation of habitats fell within the dispersal ranges of taxa, and that species presence was not limited by dispersal events. Similarly a number of studies have observed little spatial structuring of lentic communities within a landscape (Shurin et al. 2000, Jeffries 2003, Urban 2004), even among habitats connected by streams (Cottenie et al. 2003). However, some species, especially predators, may be slower to colonise newly created or recently refilled, isolated habitats (Wilcox 2001, McCauley 2006, Shulman and Chase 2007) indicating variation in species dispersal abilities may influence community structure (Van de Meutter et al. 2007), particularly in the short term (Chapter Four). Nevertheless, I observed no effect of isolation on predator richness or the trophic composition of communities in this study.

Spatial inferences that can be drawn from a study are limited by the scale of the investigation (Talley 2007) as regional species pools differ at different spatial scales (Shurin 2000). In my study there was some suggestive evidence of regional aggregation of species at the broadest spatial scale (mean interpond distance > 4 km) as three species were only found within ponds on the Blackwater moraine (*Microcyclops monacanthus* cyclopoids, *Ephydrella* dipterans and *Hydrophantes* mites) and others were only observed in the ponds outside the Blackwater moraine area (*Potamopyrgus* snails, *Simocephalus vetulus* cladocerans and *Candona aotearoa* and *Darwinula repoa* ostracods). These observations indicate that regional patchiness in species pools may occur at spatial scales beyond my sampling range.

Niche assembly models

The strong affinity of species for particular local habitat characteristics, and little evidence for spatial structuring of communities, implies community assembly in my study sites is influenced by interactions between species traits and local environments, rather than by dispersal. This is consistent with the species-sorting model of metacommunity dynamics, and similar dynamics of community assembly have been observed in numerous other pond systems (Schneider and Frost 1996, Skelly 1997, Wissinger 1999, Urban 2004, Werner et al. 2007, and references therein). Strong environmental gradients of pond permanence and associated changes in habitat structure underlay changes in community composition, nestedness, species richness, and trophic structure of ponds in the Cass basin. Conductivity also explained significant variation in community structure, but was largely due to high conductivity in three permanent ponds. RDA also implicated habitat PC2 (volume of submergent vegetation and % cover of emergent vegetation) as a significant predictor community of composition, possibly due to increased niche diversity and refugia, or more attractive habitats for oviposition or colonisation (Rowe 1987, Skelly 2001, Egan and Paton 2004, Williams et al. 2007). In contrast to studies of other pond systems (Ward and Blaustein 1994, Spencer et al. 1999, Rundle et al. 2002, Kiflawi et al. 2003), there was no evidence that pond area influenced community composition, and had, at best, a weak effect on species richness (Table 1a).

Niche assembly models such as species-sorting are particularly relevant to systems with strong environmental gradients such as groups of ponds, as species traits are often closely associated with local habitat conditions (Urban 2004, Cottenie 2005). The strong affinity of species composition to local habitats along environmental gradients may be a result of shifts in the balance of biotic and abiotic stressors interacting with species trade-offs between resisting biotic interactions and exploiting disturbed habitats (Menge and Sutherland 1987). These interacting biotic and abiotic stressors are implicit in the predator-permanence model of pond communities, where temporary pond specialists are extirpated by predation in long duration ponds, and species from long duration ponds with slow development rates and high investment in anti-predator traits cannot exploit very temporary ponds (Schneider and Frost 1996, Wellborn et al. 1996, Skelly 1997, Wissinger 1999, Wissinger et al. 2006b).

Consistent with the predator-permanence model, I observed an increase in the biomass, size, and proportional abundance of predators in the more permanent ponds, and vertebrate predators (trout, bullies and galaxiids) were only found in permanent habitats.

These patterns indicate that predation risk should increase with pond permanence. However, observed strongly nested patterns of community composition that was highly correlated with pond permanence, which contradicts predictions of the predator-permanence model. Moreover testing with multiple null models indicated that nestedness was not due to rare species being sampled less often than common species (passive sampling) or gradients in species richness (McAbendroth et al. 2005). This indicates selective extirpation of taxa based on developmental traits or colonisation ability probably occurs as pond duration decreases, and this has a greater influence on community assembly than trade-offs between abiotic stress and biotic interactions (Urban 2004, Werner et al. 2007). My observation that the vast majority of taxa in the regional species pool were found in permanent ponds (that contained fish), that a number of taxa appeared to be restricted to permanent ponds, and that a high proportion of generalists were present across the permanence gradient (Fig 2b) supports this argument. Similarly, Wissinger et al. (*in press*) found that temporary ponds in the upper Waimakariri catchment contained a completely nested subset of species present in permanent ponds, and that nested distributions were also evident in smaller historical studies comparing temporary and permanent ponds in other regions of New Zealand (Stout 1964, Barclay 1966).

There was some evidence that crustaceans exhibited species replacements across the permanence gradient as crustacean species were significantly less nested than other taxa, and comprised 40% of the species limited to temporary pools. High levels of planktivory among juvenile fish in New Zealand lakes (e.g., Staples 1975, Rowe et al. 2002) and vulnerability to predatory invertebrates may have led to some biotic limitation of crustaceans in permanent ponds at my study sites (see also Jeppesen et al. 1997, Jeppesen et al. 2000). Species replacements could also occur amongst small-bodied crustacean taxa (e.g., rotifers) that were below the sampling threshold of this study.

Factors producing nested communities

The absence of temporary pond specialists and the prevalence of habitat generalists likely reflects both historical selection pressures and present community filters. Wissinger et al. (*in press*) considered two, non-mutually exclusive hypotheses for the prevalence of habitat generalists in New Zealand pond systems: 1) unpredictable hydrological regimes select for generalist traits, and 2) the absence of strong biotic interactions in longer duration habitats permit the wide distribution of temporary pond taxa. The first hypothesis is similar to that posed for New Zealand's generalist stream fauna (Winterbourn et al. 1981, Winterbourn 1997), and attributes the lack of temporary pond specialists to the unpredictable hydrological

regimes that prevent the selection of specialized life history traits, such as synchronized development and oviposition to drying and filling regimes (Wiggins et al. 1980, Corbet 1999, Wissinger et al. 2003). In support of this argument, I observed considerable inter-annual variability in pond drying and filling dates, as well as multiple drying and filling events within years. Such variability in developmental time constraints produced by drying ponds may favour the evolution of bet-hedging life history strategies such as spatial partitioning of offspring, and also plastic behavioural and/or developmental responses to predators or disturbances that maximise fitness in unsuitable environments (Anderson et al. 1999, Lytle 2001, Lytle and Poff 2004). These developmental strategies have been observed in other systems with unpredictable hydrology, such as desert pools filled by flash floods (Anderson et al. 1999, Lytle 2002) and have potentially led to nested species distributions (Jocque et al. 2007).

Oviposition by semi-voltine, permanent pond species into temporary ponds that remain filled, or refill in summer (e.g., *Xanthocnemis zealandica*, *Procordulia grayi*, *Triplectides cephalotes*) may be a bet-hedging strategy by these taxa in my system. Some of these, largely permanent pond species, also appear to have strategies for dealing with drying. For example *Xanthocnemis* larvae appear to be able to persist for short periods in dry pond sediments (Rowe 1987) and *Austrolestes* can undergo rapid development in temporary ponds to emerge within 5-6 months (Barclay 1966, H.S. Greig unpublished data) compared to two year life cycles in permanent lakes (Rowe 1987). Despite possessing these traits, individuals of these species often experience mortality when ponds dry before metamorphosis (see also Suhling et al. 2004), although fitness benefits may be considerable if temporary ponds remain filled due to increased availability of palatable prey. These generalist species/traits are however, only likely to persist when there is a predictable presence of permanent pond refugia within the landscape. Regardless of the costs and benefits of generalist traits, the opportunistic colonisation patterns associated with generalist life histories are likely to lead to high among-year variability in temporary pond communities, depending on the recent history of drying and filling.

According to the second hypothesis considered by Wissinger et al. (*in press*), the prevalence of habitat generalists may be enhanced by the persistence in permanent ponds of species with specialist traits for temporary habitats, despite potentially strong biotic interactions associated with the increased size, biomass and abundance of predators in permanent ponds. Evidence for the exclusion of temporary pond taxa in permanent ponds was weak as only 12 of 106 species were not observed in permanent ponds. Of these 12 taxa, at

least three (*Daphnia carinata*, *Hydrachna* and Sciomyzidae) are found in permanent habitats beyond those sampled in this study (Chapman and Lewis 1976, Stout 1977, Chapman and Green 1987, Wissinger et al. 2006a, Wissinger et al. *in press*). Additionally, the majority of the crustaceans with desiccation resistant eggs or juvenile stages in the regional species pool were present in permanent ponds in this study (Appendix 2). The mesocosm experiment provided further evidence for the lack of biotic limitation; taxa that dominated the benthic biomass of temporary ponds were not consistently more vulnerable to fish than those dominating the biomass of permanent ponds. Predator effects on community assembly in this pond system may be weak due to generalist or flexible traits of prey species, traits of predators, or the complexity of habitats and food web structure (Wissinger et al. 2006a, Wissinger et al. *in press*). Further manipulative experiments in ponds across the permanence gradient will be required to address these alternative mechanisms (Chapters Three and Four).

Finally, dispersal from source habitats may enable the persistence of vulnerable species in permanent ponds (mass-effect dynamics), especially species that move cyclically between temporary and permanent habitats (e.g. some dytiscid beetles) (Wissinger 1997). Although I did not observe spatial partitioning of qualitative community parameters, I cannot rule out the influence of source-sink mass effects on the densities of species.

Conclusions and implications for models of community assembly

The strong species-environment relationships seen in this study are consistent with the prevalence of niche assembly models in pond systems (e.g., the predator-permanence model) and other habitats with explicit environmental gradients. However, my data indicate that niche assembly along environmental disturbance gradients can be produced by a single strong axis of selection, rather than those of opposing biotic and abiotic stress. If a single environmental gradient is the main avenue of niche assembly, and leads to nested distributions of species along that gradient, regional species pools should largely reflect the diversity of species within the most benign habitats. In contrast, if alternative, interacting gradients control niche assembly (e.g., those of biotic and abiotic stress), then the regional species pool will reflect the sum of the unique communities in contrasting habitats within the landscape (Chesson 2000, McPeck and Brown 2000, Kneitel and Chase 2004). Knowledge of the mechanisms behind species-sorting and other niche assembly models will therefore inform understanding of the maintenance of diversity at multiple scales.

The structure of metacommunities is also likely to be dependent on how species pools have evolved (Amarasek 2003, Leibold and Miller 2004) and this idea is central to the

hypothesis that historical selection among highly variable hydrological regimes has selected for generalists traits among the New Zealand lentic and lotic invertebrates (Winterbourn et al. 1981, Winterbourn 1997, Thompson and Townsend 2000, Wissinger et al. *in press*). Thus, in understanding and predicting the dynamics of community assembly, ecologists need to consider how biogeographical, evolutionary and phylogenetic processes have influenced the distribution and specialization of traits within the regional species pool (Shurin et al. 2000, Leibold et al. 2004) as well as the influence of contemporary biotic and abiotic filters.

Appendices

Appendix 1. Length – dry weight regressions (mg per mm body length) for common lentic taxa in New Zealand. Regression equations are in the form: $\log_e(y) = \log_e(a) + b * \log_e(x)$ or $\log_{10}(y) = \log_{10}(a) + b * \log_{10}(x)$. Standard errors of parameters are presented in brackets when available. In most cases regression equations were available for species or genera, but in some instances (mainly Diptera) family or ordinal regression equations were used. Larval beetle regression equations are denoted by “L”. n a = not available.

Taxon	Mass*	a [†]	b	R ²	Format	Reference
Ephemeroptera						
<i>Deleatidium</i> spp.		-5.38 (0.28)	3.06 (0.14)	0.91	log _e	1
<i>Coloburiscus humeralis</i>		-3.64 (0.47)	2.47 (0.19)	0.76	log _e	1
Odonata						
<i>Austrolestes colenstonis</i>		-8.20 (0.41)	3.58 (0.15)	0.95	log _e	2
<i>Xanthocnemis zealandica</i>		-1.84 (0.20)	2.30 (0.23)	0.87	log ₁₀	3
<i>Procordulia grayi</i>		-2.22 (0.16)	3.16 (0.17)	0.95	log ₁₀	3
Plecoptera						
<i>Zelandobius furcillatus</i> -group		-2.30 (0.26)	1.73 (0.43)	0.67	log _e	1
<i>Austroperla cyrene</i>		-4.79 (0.23)	2.59 (0.10)	0.95	log _e	1
Trichoptera						
<i>Pycnocentroides aureolus</i>		-4.87 (0.73)	2.50 (0.44)	0.58	log _e	1
<i>Triplectides cephalotes</i>		-2.13 (0.19)	2.84 (0.22)	0.90	log ₁₀	3
<i>Oecetis unicolor</i>		-2.05 (0.11)	2.58 (0.21)	0.68	log ₁₀	3
<i>Paroxyethira tillyardi</i>		-1.90 (0.04)	2.90 (0.14)	0.86	log ₁₀	3
Lepidoptera		1.01	2.92	n a	log ₁₀	4
Hemiptera						
<i>Sigara arguta</i>		-4.62 (0.33)	3.05 (0.19)	0.94	log _e	2
<i>Diaprepocoris zealandiae</i>		-6.30 (1.40)	4.07 (0.78)	n a	log _e	2
<i>Microvelia macgregori</i>			2.78	n a		5
<i>Anisops</i> spp.		-5.75 (0.08)	3.81 (0.05)	0.99	log _e	2
Coleoptera						
<i>Liodessus plicatus</i>	0.69 (0.02)					2
<i>Antiporus strigosulus</i>	3.94 (0.13)					2
<i>Antiporus femoralis</i>	2.71 (0.16)					2
<i>Antiporus</i> L		-7.53 (0.32)	3.95 (0.19)	0.92	log _e	2
<i>Lancetes lanceolatus</i>	18.98 (0.22)					2
<i>Lancetes lanceolatus</i> L		-5.94 (0.52)	2.80 (0.25)	0.90	log _e	2
<i>Rhantus suturalis</i>	33.70 (0.74)	-2.78 (0.73)	2.53 (0.29)	0.76	log _e	2
<i>Rhantus suturalis</i> L		-6.73 (0.32)	3.16 (0.15)	0.95	log _e	2
<i>Limnoxenus zealandicus</i>	15.93 (1.30)					2

Taxon	Mass*	a [†]	b	R ²	Format	Reference
Hydrophilidae L		-6.44 (0.58)	3.26 (0.33)	0.93	log _e	2
Diptera		-2.60	2.69	n a	log ₁₀	4
Stratiomyidae		-5.47 (0.34)	2.78 (0.14)	0.91	log _e	2
<i>Ephydrella</i>	0.35 (0.04)					2
Tanypodinae		-2.51 (0.10)	2.46 (0.15)	0.72	log ₁₀	3
Orthocladiinae		-2.83 (0.13)	2.82 (0.26)	0.80	log ₁₀	3
Chironominae		-2.68 (0.03)	2.47 (0.05)	0.84	log ₁₀	3
Ceratopogonidae Sp A		-8.42 (0.01)	2.87 (0.26)	0.91	log ₁₀	4
Acari		-2.02 (0.14)	1.66 (0.33)	0.48	log _e	6
Crustacea						
<i>Daphnia</i> [†]		1.21	1.66	0.97	log ₁₀	7
<i>Simocephalus</i> [†]		0.87	3.28	n a	log ₁₀	8
Chydoridae [†]		1.15	1.98	0.98	log ₁₀	7
<i>Bosmina</i>		-1.89	1.32	0.69	log ₁₀	9
<i>Ceriodaphnia</i> [†]		0.60	1.98	0.99	log ₁₀	7
Copepoda [€]		-2.00	2.27	0.88	log ₁₀	9
<i>Cypridopsis</i> (round-bodied) [†]		1.19	2.11	n a	log _e	10
<i>Physocypria</i> (oval-bodied) [†]		1.37	2.46	n a	log _e	10
Mollusca						
<i>Lymnaea stagnalis</i>		-4.69	2.62	0.98	log _e	11
<i>Hyridella menziesi</i>		-3.88 (0.29)	4.43 (0.18)	0.92	log ₁₀	3
<i>Potamopyrgus antipodarum</i>		-1.86 (0.07)	3.71 (0.11)	0.94	log ₁₀	3
<i>Gyraulus corinna</i>		-3.82 (0.30)	2.42 (0.17)	0.90	log _e	2
<i>Physella acuta</i>		-3.08 (0.21)	3.23 (0.11)	0.92	log _e	2
<i>Musculium novaezealandiae</i>		-1.85 (0.10)	3.57 (0.24)	0.71	log ₁₀	3
Turbellaria		1.01	2.20		log ₁₀	4
Amphibia						
<i>Litoria ewingii</i>		-5.07 (0.32)	3.26 (0.15)	0.98	log ₁₀	2

* Mean body mass of adult beetles was calculated from n > 8 individuals as body length was too similar between individuals (except *Rhantus*) to create meaningful length-weight regressions.

[†] Parameter either log_e or log₁₀ transformed (see "Format")

[†] Mass in micrograms rather than milligrams.

[€] *Boeckella* copepods assigned mass values based on life stage classifications in Jeppesen et al. (1997).

References: 1: Towers et al (1994); 2: This study; 3: Stoffells et al (2003); 4: Benke et al. (1999); 5: Smock (1980); 6: Baumgartner (2003); 7: Culver et al (1985); 8: Dunmont et al. (1975); 9: Rahkola (1998); 10: Anderson (1998); 11: Nystrom and Perez (1998).

Appendix 2 Species composition of 4 permanent, 7 semi-permanent and 18 temporary ponds in 29 ponds in the upper Waimakariri catchment, South Island, New Zealand. Permanence categories were derived from clusters evident along a continuous hydrological axis (see Fig 3a). Perm, permanent; Semi-perm, semi-permanent; Temp, temporary ponds. Shading indicates species present in qualitative sampling in at least one pond in the respective category.

Species	Perm	Semi-perm	Temp	Class/order
<i>Oxyethira albiceps</i>				Trichoptera
<i>Sigara arguta</i>				Hemiptera
<i>Liodessus plicatus</i>				Coleoptera
<i>Antiporus strigosulus</i>				Coleoptera
<i>Lancetes lanceolatus</i>				Coleoptera
<i>Rhantus suturalis</i>				Coleoptera
<i>Limnoxenus zealandicus</i>				Coleoptera
Scirtidae				Coleoptera
<i>Macropelopiini</i> sp.				Diptera
<i>Paratrachocladius pluriserialis</i>				Diptera
<i>Limnophyes</i> sp.				Diptera
<i>Chironomus zealandicus</i>				Diptera
<i>Tanytarsus funebris</i>				Diptera
<i>Eylais waikawae</i>				Acarina
<i>Simocephalus obtusatus</i>				Cladocera
<i>Ceriodaphnia dubia</i>				Cladocera
<i>Echinisca schauinslandi</i>				Cladocera
<i>Ilyocypris sordidus</i>				Cladocera
<i>Alona quadrangularis</i>				Cladocera
<i>Chydorus sphaericus</i>				Cladocera
<i>Boeckella dilatata</i>				Calanoida
<i>Acanthocyclops robustus*</i>				Cyclopoida
<i>Cypretta viridis*</i>				Ostracoda
Ostracoda sp A				Ostracoda
<i>Ilyodromus varrovillius*</i>				Ostracoda
<i>Cypricercus sanguineus*</i>				Ostracoda
Oligochaeta				Oligochaeta
<i>Ephydrella</i>				Diptera
<i>Daphnia carinata</i>				Cladocera
<i>Microcyclops monocanthus</i>				Cyclopoida
<i>Prinocypris marplesii</i>				Ostracoda
<i>Eucypris*</i>				Ostracoda
<i>Piona pseudouncata</i>				Acarina
<i>Herpetocypris pascheri*</i>				Ostracoda
<i>Austrolestes colenonis</i>				Odonata
<i>Xanthocnemis zealandica</i>				Odonata
<i>Procordulia grayi</i>				Odonata
<i>Triplectides cephalotes</i>				Trichoptera
<i>Oecetis unicolor</i>				Trichoptera
<i>Oecetis iti</i>				Trichoptera
<i>Paroxyethira hendersoni</i>				Trichoptera
<i>Microvelia macgregori</i>				Hemiptera
<i>Anisops wakefieldi</i>				Hemiptera
<i>Anisops assimilis</i>				Hemiptera
<i>Liodessus deflectus</i>				Coleoptera
<i>Antiporus femoralis</i>				Coleoptera
Hydrophilidae sp A (<i>Paracymus</i> sp)				Coleoptera
Hydrophilidae larvae				Coleoptera
Elmidae Adult				Coleoptera
Curculionidae larvae				Diptera
Muscidae				Diptera
Stratiomyidae				Diptera
<i>Corynoneura scutellata</i>				Diptera
<i>Polypedilum</i> sp.				Diptera
<i>Arrenurus lacus</i>				Acarina
Oribatei				Acarina
<i>Simocephalus vetulus</i>				Cladocera
<i>Leydiga australis</i>				Cladocera
<i>Cypridopsis vidua</i>				Ostracoda
<i>Cypretta</i> sp				Ostracoda
<i>Austropeplea tomentosa*</i>				Mollusca
<i>Gyraulus corinna</i>				Mollusca
<i>Cura</i>				Turbellaria
<i>Musculium novaezealandiae</i>				Mollusca
<i>Physella acuta</i>				Mollusca
<i>Deleatidium</i> spp.				Ephemeroptera
<i>Coloburiscus humeralis</i>				Ephemeroptera
<i>Procordulia smithi</i>				Odonata
<i>Zelandobius furcillatus</i> -group				Plecoptera
<i>Pycnocentroides aureolus</i>				Trichoptera
<i>Hudsonema amabile</i>				Trichoptera
<i>Triplectides obsoletus</i>				Trichoptera
<i>Hygraula nitens</i>				Lepidoptera
<i>Diaprepocoris zealandiae</i>				Hemiptera
<i>Zelandotipula</i>				Diptera
<i>Paralimnophila skusei</i>				Diptera
<i>Chironomus</i> sp A				Diptera

Species	Perm	Semi-perm	Temp	Class/order
<i>Tanytarsus verspertinus</i>				Diptera
Ceratopogonidae				Diptera
<i>Hydrophantes</i>				Acarina
<i>Piona uncata exigua</i>				Acarina
Acarina sp A				Acarina
Acarina sp B				Acarina
<i>Daphnia</i> sp B				Cladocera
<i>Neothrix armata</i>				Cladocera
<i>Bosmina meridionalis</i>				Cladocera
<i>Alona rectangula</i>				Cladocera
<i>Camptocercus australis</i>				Cladocera
<i>Eucyclops serratus</i>				Cyclopoida
<i>Darwinula repoa</i>				Ostracoda
<i>Candona aotearoa</i>				Ostracoda
<i>Candonocypris*</i>				Ostracoda
<i>Glyptophysa variabilis</i>				Mollusca
<i>Lymnaea stagnalis</i>				Mollusca
<i>Hyridella menziesi</i>				Mollusca
<i>Potamopyrgus antipodarum</i>				Mollusca
Glossiphonia				Hirundinea
<i>Oeconesus</i> sp.				Trichoptera
<i>Helicopsyche</i>				Trichoptera
Sciomyzidae				Diptera
Orthoclaadiinae 1				Diptera
Orthoclaadiinae 2				Diptera
<i>Culex pervigilans</i>				Diptera
<i>Hydrachna maramauensis</i>				Acarina
<i>Pseudomoina lemnae</i>				Cladocera
<i>Litoria ewingii</i>				Anura

* Species with desiccation resistant eggs or juvenile stages (Chapman and Lewis 1976, Authors unpublished data).

Appendix 3 Plant morphotype classifications and their constituent species used to assess vegetative cover and diversity in ponds across a permanence gradient in the Upper Waimakariri river catchment, Canterbury high country, New Zealand.

Morphotype	Dominant species
Tall rushes	<i>Juncus effusus</i> , <i>Shoenus</i>
Short rushes	<i>Juncus articulatus</i>
Sedge	<i>Carex secta</i> ,
Tussock	<i>Chionochloa rubra</i> , <i>Festuca</i>
<i>Typha</i>	<i>Typha orientalis</i>
<i>Eleocharis</i>	<i>Eleocharis acuta</i> , <i>Eleocharis sphacelata</i>
Terrestrial grass	<i>Agrostis</i> , <i>Poa</i>
Aquatic grass	<i>Glyceria aquatica</i>
<i>Myriophyllum</i>	<i>Myriophyllum propinquum</i> , <i>Myriophyllum triphyllum</i>
<i>Potamogeton</i>	<i>Potamogeton cheesmanii</i>
<i>Elodea</i>	<i>Elodea canadensis</i>
<i>Isoetes</i>	<i>Isoetes alpinus</i>
Prostrate submergent	<i>Limosella lineata</i> , <i>Glossostigma</i>
Ephemeral turf	<i>Isolepis</i> , <i>Hydrocotyle</i> , <i>Galium</i> , <i>Carex</i> spp.
Characea	<i>Chara</i> , <i>Nitella</i>
<i>Ranunculus</i>	<i>Ranunculus fluitans</i>

Chapter Three

Unexpected variation in predator impacts across a pond permanence gradient: a consequence of non-consumptive interactions?

Abstract

Predator size and diversity increase with pond permanence. Consequently, changes in benthic communities with pond permanence are thought to be driven by trade-offs between the ability to exploit short duration habitats and resistance to intensifying biotic interactions. However, few studies have explicitly tested how interactions between predators and prey change with pond permanence. Field manipulations in New Zealand ponds suggested an unexpected *decrease* in community-wide predator impact with increasing pond permanence, which could be driven by interference between predator species. I tested whether total predator impact was lower in permanent ponds with diverse predator guilds than in temporary ponds with simple predator guilds by conducting both substitutive and additive manipulations of invertebrate predator diversity and non-consumptive fish cues in mesocosms. Predator impact was enhanced by increasing invertebrate predator diversity and biomass (additive design), but the substitutive design (constant predator biomass with increasing diversity) confirmed that per-capita predator impact did not increase with diversity. The presence of fish cues reduced predator impact in the highest diversity treatment to less than or equal that of single species treatments in both models. These results indicate negative trait-mediated effects of fish on predatory invertebrates can reduce predator impacts in permanent ponds.

Introduction

Understanding how the strength of species interactions change with abiotic context is essential for predicting the dynamics of ecological communities (Agrawal et al. 2007), especially in response to altered disturbance regimes. Physical disturbances can mediate the strength of biotic interactions by reducing competitive interactions (Connell 1978, Lubchenco 1980, Grime 2001, Crain et al. 2004, Gerhardt and Collinge 2007) and disproportionately influencing higher trophic level species (Lubchenco 1986, Menge and Farrell 1989, Peckarsky et al. 1990, Wellborn et al. 1996, Wootton et al. 1996). Consequently, community

structure and biomass may be driven by colonization and growth after disturbance events in physically stressful habitats, and the outcomes of species interactions in physically benign habitats (Peckarsky 1983, Lubchenco 1986, Menge and Sutherland 1987). These shifts in the relative importance of abiotic and biotic stress contribute significantly to niche differentiation that promotes species coexistence across heterogeneous local habitats (Chesson 2000, Chase and Leibold 2003, Kneitel and Chase 2004). However, despite the importance of understanding the effects of abiotic gradients on the strength of biotic interactions, little is known of how concurrent shifts in habitat and food web structure along environmental gradients can modify the strength of community-wide biotic interactions.

Several non-mutually exclusive aspects of disturbed habitats may complicate abiotic controls on trophic interactions and potentially enhance biotic interactions. First, disturbance contracts the range of developmental traits of species able to persist in disturbed habitats (Power et al. 1996, Schneider and Frost 1996, Chase 2003). As a result, physically benign habitats often have higher species diversity (both within and across trophic levels), and a broader distribution of body size than disturbed habitats, thereby producing more complex food webs. A rich body of literature addresses the effects of food web structure on the outcome of species interactions (Power 1992, Polis and Strong 1996, Duffy et al. 2007, Schmitz 2007). The majority of studies suggest that increased food web complexity leads to diverse, but generally weak interactions (McCann et al. 1998, Emmerson and Yearsley 2004, Finke and Denno 2004). Conversely, food webs in highly disturbed habitats are likely to be characterised by low diversity, chain-like resource pathways and strong interactions (Power et al. 1996, Thompson and Townsend 1999). Surprisingly, food web complexity is not often integrated into studies of biotic interactions across environmental gradients. Secondly, organisms inhabiting physically stressful environments face time constraints or resource-stress constraints that force individuals to trade-off resistance to biotic interactions in order to increase development rates (Sousa 1979, Lubchenco 1986, Wissinger et al. 1999c). Such trade-offs result in more vulnerable prey communities in disturbed than benign habitats (Sousa 1984, Wootton et al. 1996). Finally, concurrent changes in habitat morphology such as shrinking size and reduced complexity may further complicate the community-wide outcome of biotic interaction across environmental gradients. Thus, if predators are able to exploit disturbed habitats through rapid colonisation, or by having home ranges that exceed the scale of disturbance events (e.g., migrating herbivores), then the simple food web and habitat structure of a disturbed habitat may lead to stronger predator-prey interactions than in benign habitats (e.g., Wootton et al. 1996).

I investigated the effect of disturbance regimes on the strength of predator-prey interactions in ponds that spanned gradient of water inundation. Abiotic stress from habitat desiccation varies among ponds, resulting in heterogeneous local habitat patches across a landscape, and species composition often strongly associated with the properties of local habitat patches (Cottenie et al. 2003, Kiflawi et al. 2003, Urban 2004). Species richness often increases with pond duration as long duration habitats support more diverse developmental traits (Schneider and Frost 1996, Williams 1996, Spencer et al. 1999, Wissinger et al. 1999a, Urban 2004). Moreover, pond drying has a greater impact on large predators (e.g. fish and salamanders) than other taxa because of their slow development (Brown et al. 2004, Woodward et al. 2005a) or slow colonisation rates (MacArthur and Wilson 1967, Pimm and Kitching 1987, Holt 1996). Consequently, predator diversity, biomass and size also increase with pond permanence (Woodward 1983, Werner and McPeck 1994, Schneider and Frost 1996, Bilton et al. 2001a, Richter-Boix et al. 2007). These shifts in predator guilds with pond permanence can lead to trait specialisation, as traits that enable the exploitation of temporary ponds (e.g., high activity, low investment in antipredator defence) often increase vulnerability to predation (Skelly 1995, Werner and Anholt 1996, Wissinger et al. 1999a, Stoks and McPeck 2003b). This often leads to the replacement of temporary pond specialists by permanent pond specialists as pond duration increases (reviewed in Wellborn et al. 1996, Wissinger 1999, Stoks and McPeck 2006).

The effects of changes in predator guilds with pond permanence on the strength of community-wide predator-prey interactions such as top-down control of prey biomass are largely untested (but see Schneider and Frost 1996). The interactive effects of increased pond size (Schneider and Frost 1996, Wissinger et al. 1999a, Hall et al. 2004), refuge availability (Chapter Two), and the complexity of food webs (through increased diversity, size-structure and number of trophic levels) (Wissinger et al. 1999a) in permanent ponds may lead to unexpected, weaker community-wide predator prey interactions in permanent ponds than temporary ponds (Blaustein 1990, Blaustein et al. 1995, Brendonck et al. 2002).

I used a combination of *in situ* experimental manipulations and laboratory mesocosm experiments to investigate community-wide impact of predators on prey biomass in montaine grassland ponds spanning a gradient of permanence in Canterbury, New Zealand. First, I manipulated predator biomass in cages within multiple ponds across this permanence gradient to quantify the effect of pond permanence on the effects of predators on prey biomass. Second, I manipulated the presence of macrophytes and fish in mesocosms to examine the hypotheses that refugia mediates predation on invertebrates in permanent ponds.

Finally, I altered the diversity of predatory invertebrates, and the presence of fish cues in mesocosms to investigate the hypothesis that negative interactions within diverse predator guilds may decrease total predator impact in permanent ponds.

Methods

Study sites and natural history

I studied predator and prey interactions in ponds and the littoral zone of small lakes in the upper Waimakariri and Rakaia catchments, South Island, New Zealand. The lentic habitats in this area range in size from 2 metre diameter ephemeral pools to large lakes (up to 179 ha) that have formed within a fluvio-glacial landscape vegetated by tussock and scrub (for more detail see Chapter Two, Wissinger et al. 2006a, Wissinger et al. *in press*). The degree of water permanence strongly influences species richness and community composition in the ponds, with predator species richness, size and biomass increasing with pond permanence (Chapter Two, Wissinger et al. *in press*). Most of the permanent ponds and lakes contain small (< 200 mm) native fish including koaro (*Galaxias brevipinnis*) and upland bullies (*Gobiomorphus breviceps*), and the larger lakes have low densities of introduced brown (*Salmo trutta*) and/or rainbow trout (*Onchorynchus mykiss*) and native longfin eels (*Anguilla dieffenbachii*) (Jeppesen et al. 1997, Kelly and McDowall 2004, Wissinger et al. 2006a). However, trout have little effect on epibenthic invertebrate communities in my study area (Wissinger et al. 2006a). Predatory invertebrate guilds are dominated by odonates in permanent ponds, and beetles and water bugs in temporary habitats (Chapter Two, Wissinger et al. *in press*). In contrast to many temporary pond food webs around the world (Wissinger 1999, Williams 2006), there are no salamanders, belostomatids or large notonectids in New Zealand (Winterbourn et al. 2006), and there were no large dytiscid species at my study sites.

I selected 15 ponds for predator removal manipulations based on their likelihood of retaining water throughout the duration of experiments, and the presence of submerged vegetation in shallow water (< 60 cm deep). Large lakes were unsuitable as wave action excluded shallow-water macrophytes, and very ephemeral ponds were too short in duration for experiments. Visual monitoring of pond hydrology began in March 2005 when the majority of the temporary ponds were dry. Water depth in each habitat was recorded hourly using stage height data loggers (HT-100, TruTrack Ltd., Christchurch, New Zealand) from 12 October 2005. Loggers were placed in the deepest point of the pond basin where possible, or in the littoral zone. Because these ponds dry and fill through unpredictable rainfall events, sometimes several times per season (Chapter Two), and because some permanent ponds can

fluctuate considerably in depth, I used a multivariate approach to quantifying hydroperiod. An index of pond permanence was derived from principal components analysis of three aspects of pond hydrology: days until first drying, maximum proportion of total depth lost and number of days inundated over 12 months (Appendix 1).

In situ assay of predator impact

I manipulated predator biomass in cages (1.5 mm mesh on a steel wire frame, 0.25 m² surface area, 50 cm height) pushed into the sediment within macrophyte beds with the bottom edges sealed where necessary with a mixture of clay and fine gravel. Three cages were placed 1 m apart in shallow water (mean \pm se: 26 \pm 3 cm) in each pond to form one replicate each of three treatments: ‘fish removal’, ‘all predator removal’, and an open frame (control) allowing access to all predators. Predators were removed from the water column and benthic layer within cages with five successive sweeps of a 1 mm mesh D-net. Predatory invertebrates and any fish were removed from samples in a white sorting tray, and remaining invertebrates and detritus were returned to the cage. This procedure left submergent vegetation intact and removed all fish biomass, and 56 \pm 10% (mean \pm se) of predatory invertebrate biomass based on analyses at the end of the experiment. Predatory invertebrates were defined as species that obtained the majority of their energy through the consumption of other macroscopic animals based on published dietary studies (Appendix 1, Chapter Four,) but excluded small bodied predators (*Liodes* Hydroporinae, mites and cyclopoid copepods) and omnivores. The open sided control cages, which represented ambient levels of predation, were covered in a temporary sleeve of mesh and sampled using the same procedures as above but without the removal of any animals to control for prey mortality during the predator manipulations.

Cages were installed in the 15 ponds over a period of four days and after two weeks were sampled and then removed from ponds in which they were installed. Sampling was by a combination of two methods: 1) To estimate the abundance of small bodied animals (crustaceans, chironomids, worms and molluscs), a 500 μ m mesh net was drawn up a PVC pipe (0.020 m²), pushed into the substrate in the centre of the cage, five times. Samples were preserved in 70% ETOH and sorted in the laboratory under 10x magnification. 2) To estimate the abundance of remaining taxa, cages were sampled using the predator removal procedure but all taxa were removed and preserved in 70% ETOH. Invertebrates were identified to tribe for Chironomidae, family or genus for Crustacea, and to the lowest possible taxonomic level (usually species) for snails and all remaining insects using standard keys (Winterbourn 1973, Chapman and Lewis 1976, Winterbourn et al. 2006). The body length of ten individuals from

each taxonomic unit in each cage was measured at 10-20X magnification using an eye piece micrometer to enable mean individual biomass of all taxa except oligochaetes to be calculated using published or specifically created length-dry weight regressions (Appendix 1, Chapter Two). Oligochaetes were dried at 60 °C for 48 h and weighed to the nearest 0.1 mg. Dry weights for all taxa were converted to AFDM using taxon specific % ash correction factors.

Predator impact on prey biomass was calculated using log ratio of effect size (Berlow 1999):

$$PI = \ln(B_a/B_r)$$

where PI is predator impact, B_a is total prey biomass in the ambient predator control treatment and B_r is total prey biomass in the removal treatments. Fish PI was determined by comparing prey biomass in the control treatment with total prey biomass (including predatory invertebrates) in the fish removal cages. Predatory invertebrate PI was determined by comparing prey biomass in fish removal cages with all predator removal cages. Finally, comparisons of prey biomass between control cages and ‘all predator removal’ cages produced total PI .

Three of the 15 ponds investigated dried during the experiment and were excluded from subsequent analyses. The effect of fish on prey biomass in permanent habitats was analysed by comparing deviations of predator impact from zero using one sample t-tests. The same procedures were used to test for cage effects by comparing control versus fish removal cages in fish free habitats. I compared fish predator impact between ponds with and without fish for three prey categories using MANOVA. Prey categories were all invertebrates, primary consumers, (i.e., excluding predatory invertebrates) and unprotected consumers (excluding snails and cased caddisflies). The effect of pond permanence on the strength of predatory invertebrate impact for all prey and unprotected prey was analysed with regression.

Manipulation of predatory fish and submergent vegetation

To provide a powerful test of fish impacts on prey, and to determine how they are mediated by submergent vegetation, I manipulated the presence/absence of koaro and simple/complex vegetation structure in mesocosms at the University of Canterbury’s Cass field station using a 2 x 2 factorial design with four replicates of each of the four treatment combinations. Koaro were chosen because they are the native predator in our study sites, are abundant in the

shallow littoral zone, and they feed on a large range of macroinvertebrates (Rowe et al. 2002). Mesocosms were 800 cm² oval polythene cattle tanks (see Greig and McIntosh 2006) fitted with a central standpipe that regulated water depth to 25-28 cm. Groundwater (10 °C; pH = 7.7; specific conductance = 114 $\mu\text{S cm}^{-1}$) was fed through two water jets on opposite sides of each tank (facing upwards to prevent benthic disturbance or circular flow), at a rate of 10 mL s⁻¹ to compensate for evaporation and to dampen diurnal temperature fluctuations. Two clumps of *Myriophyllum* (squares 25 x 25 cm and 15 x 15 cm; stem height 15 cm) and a 15 x 15 cm clump of *Carex* sedge (40 cm height) collected from a fishless pond were rinsed of invertebrates and added to each tank. After one day vegetation was cut to soil level in half the tanks to form the simple vegetation treatment. In all treatments, the remainder of the tank floor was covered in a 1 mm layer of fine mud; a 12 cm long section of 6.5 cm diameter PVC pipe was set horizontally into the substrate for fish cover.

The prey community was artificially assembled from the regional species pool, and included five species that dominated the biomass of permanent ponds, and six species that dominated temporary pond biomass. Biomass of all prey taxa was approximately equal, and total biomass fell within the range observed in permanent ponds (see Chapter Two for more details). Small numbers of cyclopoid copepods and orthoclad chironomids passively colonized the tanks from soil clumps. Prey were added on the morning of 28 Feb 2007, and allowed to acclimate for 10 h before fish (one koaro, mean fork length: 120 \pm 5.4 mm) were added to eight randomly selected tanks. Fish were collected from a nearby pond (Romulus) using Gee-minnow traps set earlier that day.

After two weeks, fish were removed from tanks, measured and weighed. Then a cylinder sample was taken within the largest clump of *Myriophyllum* to measure small bodied prey (chironomids and crustacean) using the same procedure as for the predator assay. Following this, vegetation was removed, shaken vigorously in the tank, and transferred to a tray for sorting. Remaining soil clumps were removed from tanks and searched for invertebrates and water and mud were tipped into a 1 mm mesh net whose contents were then transferred to a tray for sorting. Invertebrates were processed and AFDM determined as for the predator assay.

Recovery of zooplankton was negligible across all treatments, so all analyses were conducted on the 11 macroinvertebrate species (see Chapter Two). The effects of koaro and vegetation on prey survival were explored using 2 x 2 factorial ANOVA with fish and vegetation as fixed effects and log_e-transformed total AFDM the response. Treatment effects on prey community composition were assessed with PERMANOVA (Anderson 2001,

McArdle and Anderson 2001) on a Bray-Curtis dissimilarity matrix created from untransformed AFDM of the 11 macroinvertebrate species. Significance was tested ($P < 0.05$) after 999 permutations.

Multiple predator experiment

To test the effect of increased density and diversity of predators due to pond permanence on the strength of predator impacts on prey, I manipulated predatory invertebrate density and diversity, and non-consumptive fish cues in mesocosms using a hybrid design that included both additive and substitutive diversity manipulations (Griffen 2006, Schmitz 2007). The additive model reflected patterns of predator guilds across the permanence gradient in our study system, and held intraspecific interactions constant as diversity is manipulated. In contrast, the substitutive model held total density constant, and thus prevents the confounding of diversity with density. Predator treatments mimicked the increase in predator diversity and density with pond permanence (Fig. 1a) through manipulating three dominant predatory invertebrate taxa (*Rhantus suturalis* dytiscid larvae, *Xanthocnemis zealandica* damselflies and *Procordulia grayi* dragonfly larvae) and the combined, non-consumptive effects of two common predatory fish species (*Galaxias brevipinnis* and *Onchorynchus mykiss*) (Fig. 1b). I used subsets of possible treatment combinations that were relevant to the observed patterns in predator guilds seen along the pond permanence gradient to test three models: (a) additive density manipulations among a single predator species, (b) additive manipulations of multiple predator species in combination with all possible single species in low density treatments to enable the calculation of expected predation rates, and (c) a substitutive model at high predator densities. Each of the 11 treatment combinations (Fig 1b), including predator free control treatments with and without fish cues, was replicated four times.

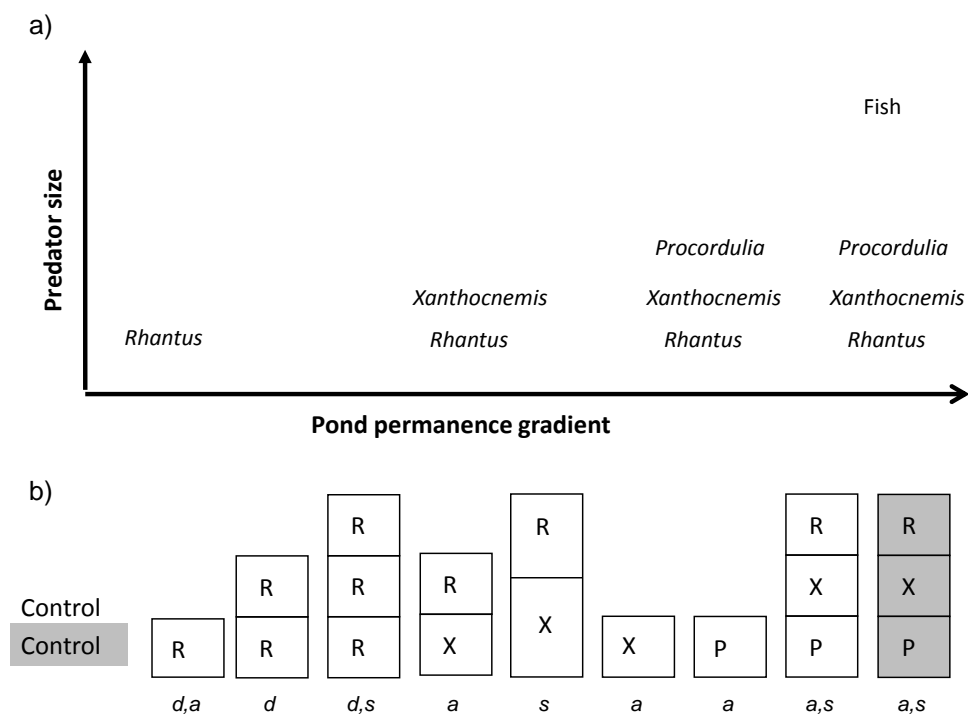


Fig. 1 (a) The distribution of predator biomass across the gradient of water permanence from short duration temporary ponds to permanent habitats in Canterbury, New Zealand. (b) Hybrid experimental designs used to investigate multiple predator effects along the permanence gradient. In (b) each box represents one treatment and box size is proportional to predatory invertebrate density: R = *Rhantus*; X = *Xanthocnemis*; P = *Procordulia*. Shading indicates the presence of fish chemical cues. Prey density was constant. Lower case letters denote treatment combinations used in the single species density manipulation (d), and additive (a) and substitutive (s) diversity manipulations. Two predator free controls (with and without fish cues) were also included.



Plate 4 Array of 44 tanks (surface area 0.35 m² each) used in the multiple predator experiment.

Manipulations were conducted in mesocosms, which were semi-translucent white plastic tubs (surface area 0.35 m²) filled with groundwater to a depth of 18 cm, regulated by four 1 cm diameter holes covered in 500 µm mesh (Plate 4). Substrate consisted of three clumps of 15 cm high plastic aquarium plants and three large cobbles, evenly distributed over a 5 mm thick base of fine sand. Prey were 100 late instar *Chironomus zelandicus* larvae per tank, collected from a fishless pond. *Chironomus* larvae were chosen as prey because they are a ubiquitous species that occurs in high abundance across the permanence gradient. Tanks were covered with 1 mm mesh to capture emerged adult chironomids. *Daphnia* and calanoid copepods were initially added as additional prey, but high background mortality precluded them from analyses.

Predator density varied between 4 and 12 individuals per tank, reflecting the range of predator biomass observed in all but the most densely populated habitats. Fish cues were added by dripping aerated groundwater from a single tank housing one koaro (145 mm fork length [FL]) and one rainbow trout (140 mm FL) into tanks assigned to fish treatments at a rate of $6.2 \pm 1 \text{ L h}^{-1}$ (mean \pm se). Fish were fed *ad libitum* on all three species of invertebrates used in the experiment to ensure the complete range of cues from fish feeding on conspecifics was present. A control drip from an identical tank without fish or invertebrates was fed at the same rate into the remaining tanks. Prey were added at 1600h on 31 October 2007, and allowed to acclimate for 24 h before predators were added.

After five days, adult chironomids that had emerged were hand-collected, cobbles and artificial plants were washed and removed, and invertebrates were collected by repeated elutriation of the tank contents through a 250 µm mesh net followed by an inspection of the remaining sand. Invertebrates were preserved in 90% ETOH, prior to processing. Predators and chironomids were counted and their AFDM determined as in the predator assay (above). Treatment combinations were grouped according to types of predator manipulation: 1) *Rhantus* density treatment, 2) additive diversity manipulations and 3) substitutive diversity manipulations. Significance of each predator manipulation was tested using one-way ANOVA with tanks as replicates, followed by Tukey's post-hoc comparisons to identify differences between (at $P < 0.05$) treatment means. To test for multiple predator effects while controlling for density in the additive model, I calculated expected predation rates for the two and three species treatments from species monocultures using an extended additive probability model assuming finite prey resources (Soluk and Collins 1988, Sih et al. 1998) modified for a three species guild (following Miller 2006:62):

$$\text{Expected prey consumption} = 100*(P_r + P_x + P_p - P_rP_x - P_xP_p + P_rP_xP_p)$$

where P_r , P_x and P_p the proportion of initial prey abundance eaten in the *Rhantus*, *Xanthocnemis* and *Procordulia* monocultures, respectively. The effect of density on intraspecific interactions in *Rhantus* monocultures was also tested using these models, with expected values based on *Rhantus* low density treatments. I tested the significance of departures of observed predation rates from expected values in these comparisons using one sample *t*-tests.

Results

In situ predator assay

I observed no consistent effect of fish on the biomass of prey in the *in situ* assays of predator impact (Fig. 2). The biomass of all invertebrates (Fig. 2a) and primary consumers (Fig. 2b) in control cages allowing access to fish in permanent ponds did not differ significantly from cages that prevented fish access (one sample *t*-tests $P > 0.25$). Also no influence of fish on unprotected prey biomass (species without cases or shells) was detected (Fig. 2c), indicating the overall lack of fish impact could not be explained by the high biomass of molluscs and cased caddis in permanent ponds. Comparisons of treatments in ponds without fish indicated a trend towards higher prey biomass in open (control) compared to closed cages (Fig. 2a), suggesting a possible cage effect. However, there was no significant difference in the fish impact index between ponds with and without fish across all prey types (MANOVA, Fish effect: Wilks $\lambda = 0.96$, $P = 0.925$, Univariate ANOVAs $P > 0.56$). This indicated that potential cage bias was not responsible for the lack of fish effects seen in permanent ponds.

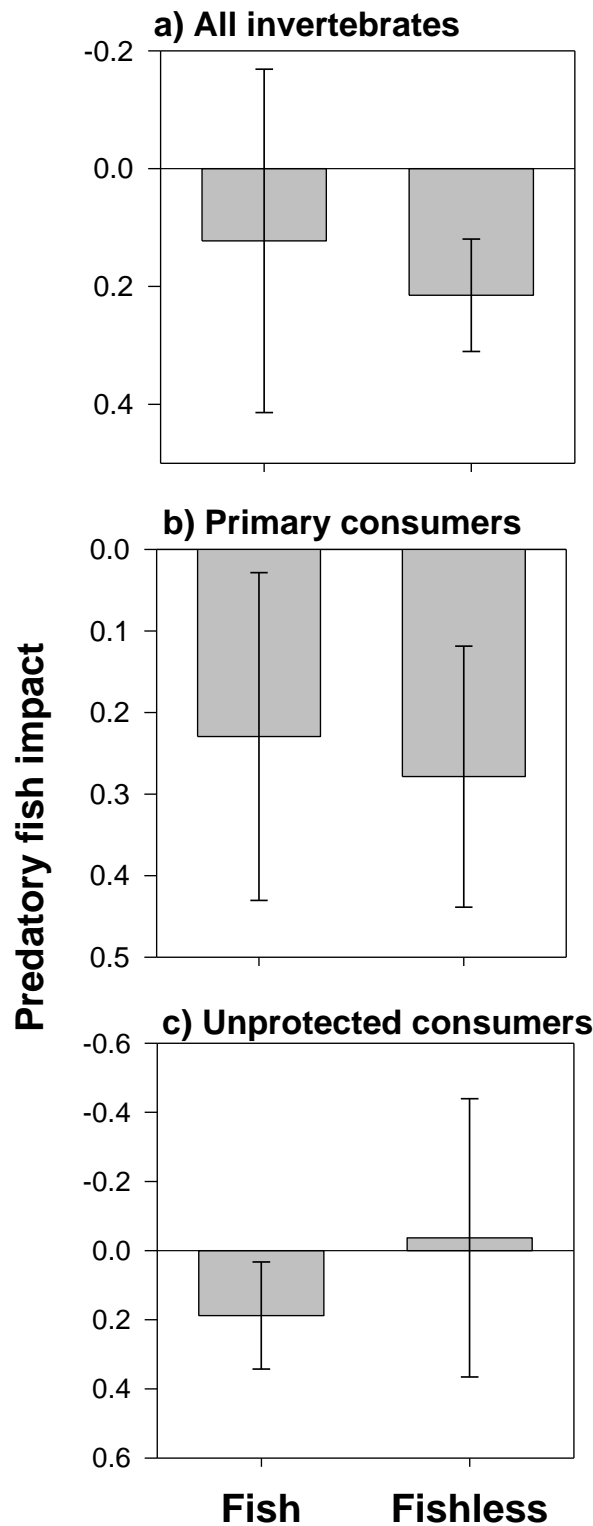


Fig. 2 The effect of fish exclusions on invertebrate biomass, expressed as the log-ratio of effect strength (see methods text), in ponds with and without fish. Negative values indicate a decrease in prey biomass in cages with fish access relative to cages that prevented fish access; positive values indicate a prey biomass increase in fish-access cages. In fishless ponds 'predatory fish impact' quantifies potential cage effects by comparing prey biomass in open versus closed, ambient predation cages. Prey were separated into (a) total invertebrate biomass, (b) primary consumers only, and (c) unprotected primary consumers (i.e., molluscs and cased caddis removed). Means (± 1 se) were calculated with ponds as replicates, and $n = 5$ and 7 for fish and fishless ponds, respectively.

Contrary to expectations, predatory invertebrate impacts on prey biomass decreased with increasing pond permanence (Fig. 3a). Again, this could not be explained by permanent ponds having more morphologically defended prey, as predator impact on unprotected prey biomass was stronger, and *PI* in permanent ponds did not increase (Fig. 3b). In summary, the absence of detectable fish effects, combined with the significant decrease in predatory invertebrate impact on prey biomass in permanent habitats indicates the strength of community-wide predator: prey interactions increased as ponds became less permanent.

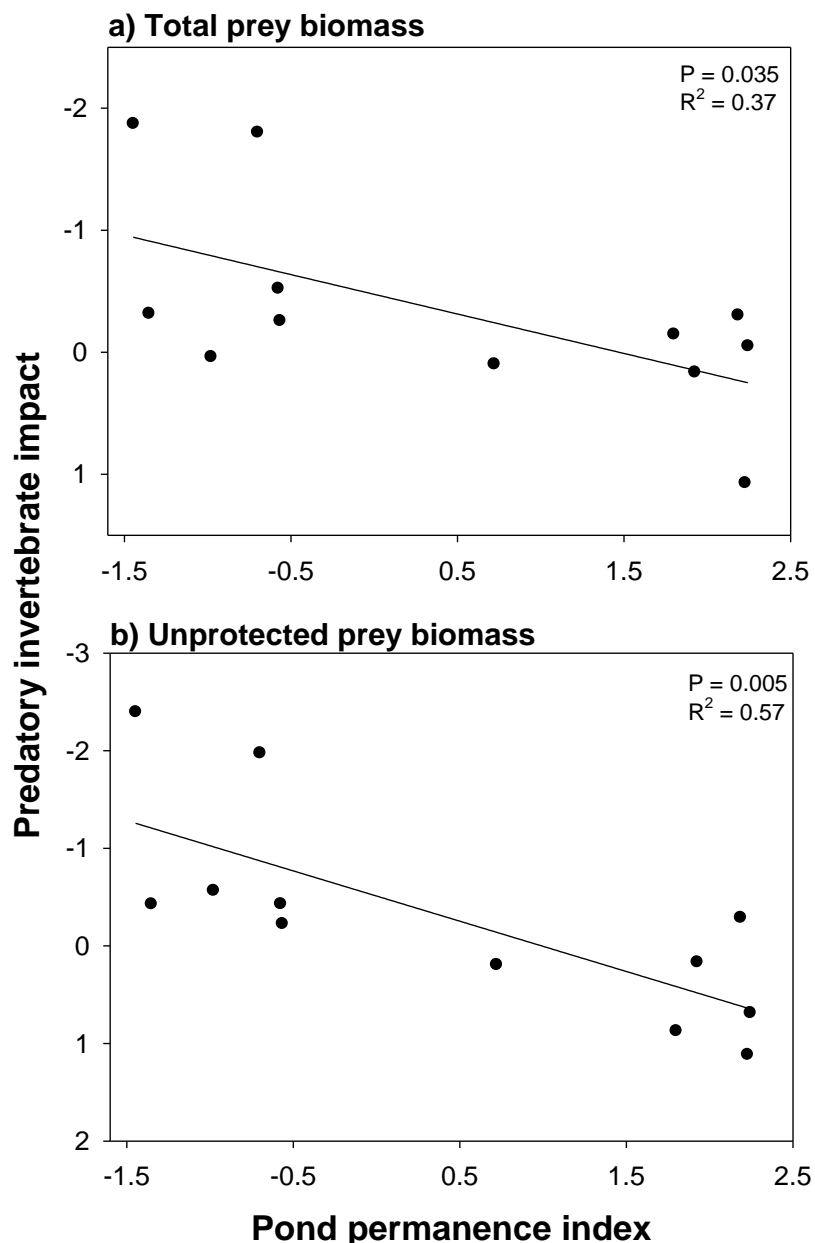


Fig. 3 Predatory invertebrate impact index on (a) total prey biomass and (b) unprotected prey biomass (i.e., snails and cased caddis excluded) in ponds varying in permanence due to drying. Negative predator impacts indicate a decrease in prey biomass relative to predator removal treatments; higher values on the x-axis indicate more permanent ponds. Regression equations are $y = -0.51 + 0.59x$ and $y = -0.56 + 0.92x$ for total prey biomass and undefended prey biomass, respectively.

Manipulating predatory fish and submergent vegetation

Galaxias brevipinnis exerted no detectable effect on prey biomass in the mesocosms, even when vegetative cover was absent (Fig. 4). Total prey biomass was not significantly different between fish and fishless treatments ($F_{1,12} = 0.29$, $P = 0.60$; Fig. 4), or between complex and simple vegetation treatments ($F_{1,12} = 2.74$, $P = 0.12$), and no fish by vegetation interaction was observed ($F_{1,12} = 1.03$, $P = 0.33$). Similarly, PERMANOVA indicated there were no treatment effects on the composition of the prey community (fish: $F_{1,12} = 0.84$, $P = 0.51$; vegetation: $F_{1,12} = 1.95$, $P = 0.11$; interaction: $F_{1,12} = 1.17$, $P = 0.28$). Lastly, fish had no effect on total biomass of predatory taxa (ANOVA, fish: $F_{1,12} = 0.52$, $P = 0.48$, interaction: $F_{1,12} = 0.87$, $P = 0.37$) indicating they did not release prey species by reducing the density of intermediate predators.

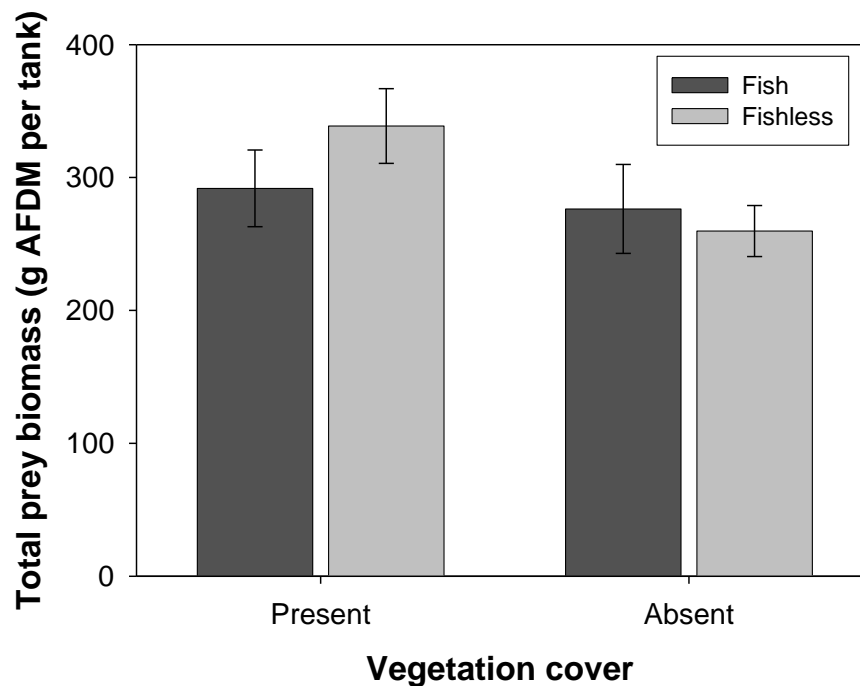


Fig. 4 Mean (\pm se) effect of predatory fish (*Galaxias brevipinnis*) and submerged vegetation on total biomass of 11 invertebrate species after 14 days in a mesocosm experiment. Means were calculated with tanks as replicates. Vegetation cover indicates the presence or absence of submergent and emergent vegetation in mesocosms.

Multiple predator experiment

Predation rates with *Rhantus* as the sole predator increased significantly with density (one-way ANOVA: $F_{2,9} = 7.26$, $P = 0.013$; Fig. 5). However, observed predation rates were significantly lower than expected based on additive probability models extrapolating

predation at low *Rhantus* density (Fig 5). This finding suggests that intraspecific interference increased with density. The additive manipulation of predator diversity, where total predator density increased, had significant impacts on the consumption of *Chironomus* (Fig. 5a, One way ANOVA: $F_{(5,18)} = 17.9$, $P < 0.0001$). In treatments with single predator species, predation by *Rhantus* and *Procordulia* larvae on *Chironomus* were almost identical, but *Xanthocnemis* was a significantly weaker predator (Fig. 5b). The two predator species treatment resulted in significantly higher predation rates than by *Xanthocnemis* alone, but was not significantly different from rates for *Procordulia* and *Rhantus* alone. In contrast to the single species density manipulation, increasing predator density by increasing diversity led to predation rates almost identical to expected values calculated from low density single species treatments (Fig. 5b). However, the addition of chemical cues from predatory fish, as a fourth level of predator complexity, significantly decreased predation rates in the three species treatment to a level similar to the two species treatment, and not significantly higher than for low density single species treatments of either *Rhantus* or *Procordulia* (Fig. 5a).

The substitutive manipulation of predator density (where total predator density was kept constant) significantly influenced predation on *Chironomus* (Fig. 5c, one-way ANOVA: $F_{3,12} = 4.29$, $P = 0.028$); however, this was due largely to the effect of fish chemical cues reducing predation rates in the three species treatment (Fig. 5c). Post-hoc tests indicated no significant difference between the one, two and three species treatments in the absence of fish cues ($P > 0.34$). Thus, the substitutive design also indicated a lack of risk reduction or enhancement with increasing predatory invertebrate diversity as seen in the additive experiment, and also revealed the negative impact of fish chemical cues on predation rates of predatory invertebrates.

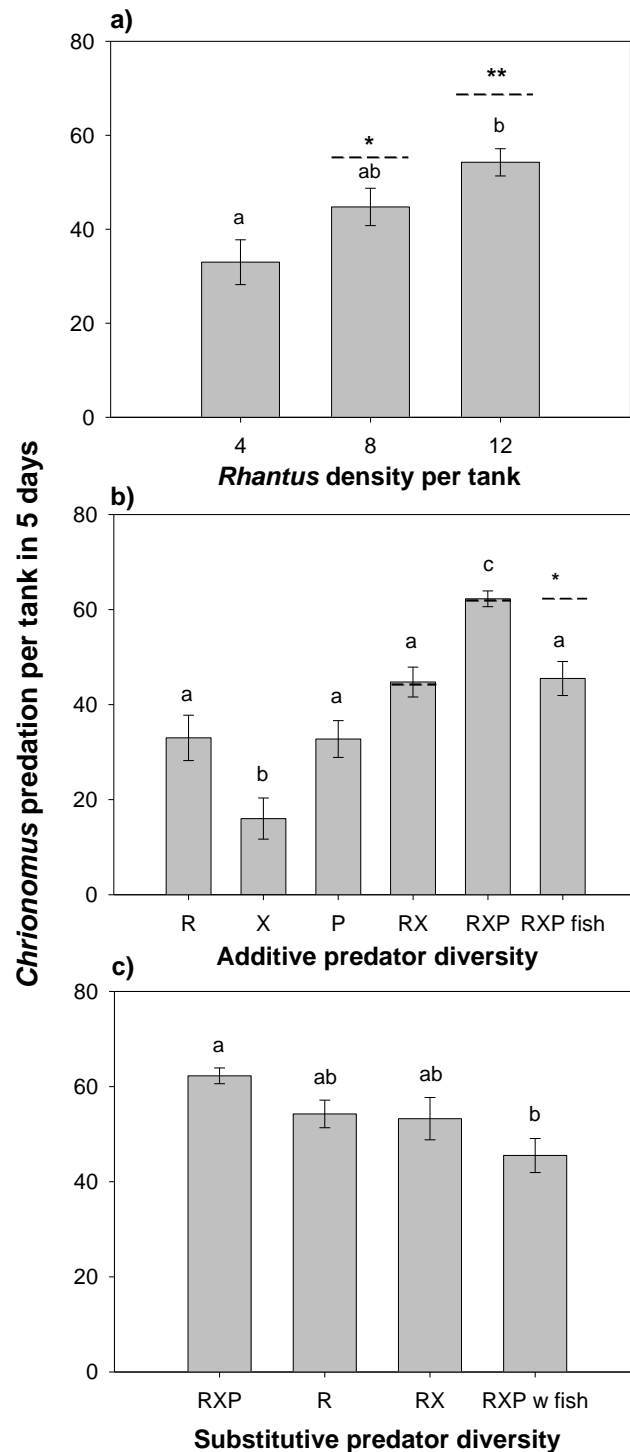


Fig. 5 Effect of a) larval *Rhantus* density, b) additive predator diversity and c) substitutive predator diversity on mean (\pm se) consumption of *Chironomus* larvae during a five day mesocosm experiment. X-axis labels for b) and c) are: R, *Rhantus* larvae; X, *Xanthocnemis* larvae; P, *Procordulia* larvae; and fish, presence of chemical cues from both rainbow trout (*Onchorynchus mykiss*) and koaro (*Galaxias brevipinnis*). See Fig. 1 for further description of treatments. Means were calculated with tanks as replicates; letters indicate significant differences ($P < 0.05$) between treatments (Tukey's post-hoc comparisons). Dashed lines indicate expected *Chironomus* predation calculated from additive probability models (adjusted for finite prey resources) of low density conspecifics in a), and from single species treatments in b). Asterisks indicate significant departures from the null model (* = $0.1 < P < 0.05$, ** = $P < 0.05$) based on one sample t-tests.

Discussion

Disturbance is thought to mediate the strength of competitive and predator-prey interactions. This produces variation in the relative importance of abiotic and biotic interactions along environmental gradients, thereby creating niche differentiation that enables species coexistence among habitats (Menge and Sutherland 1987, Wellborn et al. 1996, Chesson 2000). However, my field assays of top-down control of prey biomass across a pond disturbance gradient provided unexpected results indicating *stronger* predator-prey interactions in more physically stressful habitats. The reduction in predator impact with increasing permanence was likely to be a result of weak predation in permanent habitats due to non-consumptive effects of predatory fish, combined with simplified food webs in more temporary habitats. This indicates food web complexity can influence the patterns of predator-prey interactions along environmental gradients

Despite the increase in size, biomass and diversity of predatory invertebrates with increasing pond permanence, results of the field assay provided compelling evidence that the strength of community-wide invertebrate predator-prey interactions decreased with pond permanence. Variation in the properties of food webs and habitat morphology across pond permanence gradients provide some mechanisms for these unexpected results.

Changes in food web complexity from structurally simple food webs with chain-like dynamics in temporary ponds, to systems with a high prevalence of omnivory and intraguild interactions in permanent ponds, are likely to lead to more weak links and dampened top-down control (Strong 1992, Polis and Strong 1996, McCann et al 1998, Chase 2000). Moreover reductions in the aggregate effects of predators on prey can occur through both consumptive effects, such as intraguild predation and cannibalism (Snyder and Ives 2001, Vance-Chalcraft et al. 2007) and non-consumptive effects, such as foraging suppression (Werner and Peacor 2003, Prasad and Snyder 2006). The results of the predatory fish and invertebrate manipulations provide examples of these mechanisms.

Consumptive effects of predatory fish

Long lived vertebrate predators like fish and paedomorphic salamanders can only persist in permanent habitats. Consequently, they have been implicated the key drivers of community shifts along pond permanence gradients (Wellborn et al. 1996, Wissinger 1999, Van Buskirk 2005, Werner et al. 2007). Unexpectedly, our results indicate negligible consumptive effects of predatory fish on the biomass of prey communities. We observed no measurable effect of fish exclusion on the biomass of prey communities in permanent habitats but variability

between ponds led to low power (minimum detectable difference between mean fish and fishless biomass at $\beta = 0.8$ was 4-10 times greater than those presented in Fig. 2). However the mesocosm experiment showed that even in spatially confined environments, koaro did not depress prey biomass. In this experiment, power was sufficient (at $\beta = 0.8$) to detect a 15% difference between prey biomass in fish and fishless tanks, which is below the effects seen in other studies of fish predation on littoral benthic invertebrates (Morin 1984, Hershey and Dodson 1985, Diehl 1992). The effects of fish manipulations on the density and biomass of benthic prey communities in lentic systems have been equivocal (reviewed in Thorp 1986, Pierce and Hinrichs 1997). The structural complexity and density of plants within littoral zones of lentic habitats can weaken the lethal effects of fish by providing refuge space for invertebrates thereby reducing predator foraging efficiency (e.g., Gilinsky 1984, Hershey 1985, Diehl 1992, Baber and Babbitt 2004). Consequently, refugia are often invoked to explain weak fish effects (Pierce and Hinrichs 1997) and Wissinger et al. (2006a) argued that the prevalent stands of submergent aquatic vegetation in lakes at my study sites may have reduced the impacts of invasive salmonids. However, I also observed no measurable koaro predation in mesocosms without submergent vegetation, implying the presence of refugia within mesocosms was not responsible for the weak fish effects I observed.

A second explanation for weak fish effects is that size selective predation by fish leads to greater impacts on predatory invertebrates than primary consumers, and results in a net decrease in predation on herbivores (Carpenter et al. 1985, Strong 1992, Shurin et al. 2002). I did not observe disparate effects of fish on the biomass of predatory invertebrates in either the field assay or mesocosms experiment, however. A third possibility is that, antipredator behaviors of invertebrates in response to fish cues, as indicated in the multiple predator experiment, may have reduced consumptive effects of fish on predatory invertebrates and led to a positive, trait-mediated indirect effect of fish on primary consumers (e.g., Peckarsky and McIntosh 1998). Finally, high secondary production of invertebrates may reduce fish impacts if numerical responses by fish populations to prey resources are limited by other factors, such as spawning success.

Care must be taken when making conclusions based on the effect of fish removals within habitats, as the potential prey community may be a preselected subset of the regional species pool that is resistant to fish predation (Allan 1982, Thorp 1986, Wellborn et al. 1996). Nevertheless, there was no consistent effect of fish on unprotected prey species in the assay, indicating morphologically defended prey were not responsible for the lack of fish effects.

Furthermore, fish had no impact on prey communities assembled from the regional pool in the mesocosm experiment.

Dietary analysis indicates that the koaro of the size range used in the mesocosm experiment regularly feed on the taxa and size ranges of invertebrates included in the mesocosms experiment (Rowe et al. 2002). I observed koaro actively feeding in the experiment (Chapter Two) and the gut contents of two fish sacrificed at the conclusion of the experiment contained prey (*Rhantus*, *Antiporus* and *Xanthocnemis* larvae). These consumptive effects were probably obscured by predation and competitive interactions between species in the diverse prey community of the mesocosms. Regardless of the mechanism, my results and those of others (Chapter Two, Wissinger et al. 2006a, Wissinger et al. *in press*), indicate that the consumption of invertebrates by fish has weak impact at best on epibenthic invertebrate community composition in the lentic habitats of the Canterbury high country. However, fish may still exert a strong influence on food web interactions through non-consumptive effects on prey individuals (McPeck and Peckarsky 1998, Werner and Peacor 2003), and these were observed in the multiple predator experiment.

Predatory invertebrate impact across the permanence gradient

The multiple predator experiment provided strong evidence that the presence of fish (as indicated by fish odour) in permanent pond food webs led to a reduction in the foraging of predatory invertebrates. The presence of fish cues reduced chironomid predation in the three species treatment to levels more similar to those found in single species treatments (Fig. 6). Thus, if the lethal effects of fish are weak, as suggested by both the mesocosms experiments and *in situ* manipulations, then fish presence in our system reduces rather than enhances top-down control of prey biomass. This is likely to have contributed significantly to the weak effects of predatory invertebrates in permanent ponds that led, in part, to a decrease in the strength of predator prey interactions with increasing pond permanence. Also, reduced predatory invertebrate foraging rates provide a possible mechanism for the negligible effects of fish on invertebrate prey communities in the mesocosm experiment. My results provide further support for the notion that non-consumptive effects of fish in freshwater food webs can outweigh consumptive effects (e.g., McPeck and Peckarsky 1998, Peckarsky et al. 2001).

Like Grabowski and Kimbro (2005), our data did not provide evidence that interactions within benthic refugia were intensified as a result of predator-induced refuge use by intermediate consumers that potentially increased the spatial overlap predators and prey. However, if large size differences between predator species lead to asymmetric intraguild

predation (IGP) (e.g., fish can eat predatory invertebrates but invertebrates usually cannot eat fish), then risk reduction is likely, regardless of the amount of spatial overlap between predator and prey domains (*sensu* Schmitz 2007). Because body size often increases with trophic level (Woodward et al. 2005a), size asymmetry is most likely when increases in predator diversity in a food web come about through the addition of trophic levels, rather than through increased diversity within a trophic level (i.e., vertical rather than horizontal diversity; Duffy et al. 2007). Increased diversity within the predatory invertebrate guild had limited effects on predation rates. Furthermore, my experiments with the most abundant species of predatory invertebrates across the permanence gradient indicated the effect of predator diversity was substitutable (as opposed to enhancing or reducing predation rates). There is some indirect evidence that the addition of predator species may reduce negative interactions among conspecific predators at high densities (Griffin et al. 2008). I found that predation rates of *Rhantus* beetle larvae at high densities were significantly lower than the expected additive predation rate (adjusted for a finite prey resource) calculated from low density treatments; but predation rates in high density treatments of multiple predators almost equaled the expected predation rates (Fig 5). Additionally, decreased prey density may have decreased encounter rates in the high density *Rhantus* treatments, contributing to reduced predation rates.

Several other mechanisms may have also contributed to the decrease in predator impact with habitat permanence. First, because populations of predators in permanent ponds often have multiple cohorts because of semivoltine development, their broad size-structure can increase cannibalism and intraguild predation (IGP) (Polis 1991, Wissinger 1992, Padeffke and Suhling 2003, Chapter Five). Such size-structured interactions should be less prevalent in temporary ponds where drying and refilling should increase developmental synchrony within populations.

Secondly, the developmental costs of antipredator traits often result in the presence of more defended prey in physically benign habitats, and may reduce the ability of predators to suppress prey biomass (Sousa 1984, Wootton et al. 1996, Wissinger et al. 2006b). Permanent ponds contain a higher proportion of morphologically defended prey species (e.g., snails and cased caddisflies) than temporary ponds (Wissinger et al. *in press*) but they can still be vulnerable to predators (Stark 1981, Turner and Chislock 2007), and the negative relationship between predator impact and permanence actually strengthened when I excluded morphologically defended prey from my analysis (Fig. 3b).

Thirdly, prey behaviour may contribute to greater predator impact in temporary than permanent ponds. Most species (both predators and prey) present in temporary ponds exhibit active foraging to facilitate rapid development (Wiggins et al. 1980), and the potentially high costs of phenotypic plasticity (DeWitt et al. 1998, Relyea 2002) may constrain the evolution of plastic behavioural responses in temporary pond species. High activity rates are likely to increase predator-prey encounters and prey vulnerability in temporary ponds. Furthermore, temporary pond species are likely to exhibit rapid, inflexible metabolic rates (e.g., Stoks and McPeck 2003a) which can increase the strength of species interactions by increasing predator attack rates (McCann et al. 2005a). Finally, pond size was correlated with permanence at our sites (Chapter Two, Wissinger et al. *in press*) and the spatially confined interactions in the small temporary ponds may therefore have increased the connectance of spatially separate sub-webs (Krause et al. 2003), resulting in stronger predator-prey interactions (McCann et al. 2005a, McCann et al. 2005b, Rooney et al. 2006).

Inferences from this study are limited in two main ways. First, I did not manipulate the shortest duration habitats in the landscape (Chapter Two), and they are likely to have had fewer predators and potentially weaker interactions than the longer duration temporary ponds used (e.g., Schneider and Frost 1996). Consequently, across the entire range of ponds in our landscape, predation may follow a unimodal relationship with permanence, with predator impact strongest in intermediate duration ponds. Secondly, because temporary ponds follow a process of succession as species colonize and grow, the strength of species interactions is likely to be dynamic over time. Consequently the spatial pattern of predator-prey interactions across the landscape is also likely to be dynamic (Chapter Four).

Implications for community dynamics

Because disturbance resets community biomass and often has asymmetric effects on higher trophic levels (Connell 1978, Menge and Sutherland 1987), the composition and biomass of communities is often thought to be under stronger biotic control in physically benign than disturbed habitats. In contrast, my results indicate that community-wide predator-prey interactions were weaker in benign habitats, driven in part, by non-consumptive interactions among predators present in permanent ponds. This reinforces the idea that the local assembly of communities was driven largely by the environmental limitation of species based on their life history traits, rather than by biotic interactions in long duration ponds and abiotic stress in short duration ponds (Schneider and Frost 1996, Wellborn et al. 1996, Wissinger 1999, Urban 2004). The nested patterns of community assembly in ponds in my study area support this

hypothesis, as the vast majority of species present in temporary ponds also occur in permanent habitats (Chapter One).

My study has shown that changes in the properties of food webs and habitat along environmental gradients can produce unexpected relationships between the abiotic environment and the strength of species interactions. In particular, my results indicate the need to integrate recent advances in the understanding of interactions within complex food web, especially the effects of within and among trophic level diversity and non-consumptive interactions (Werner and Peacor 2003, Duffy et al. 2007, Schmitz 2007), with current models of assembly in order to develop a more realistic view of the controls of community organization across heterogeneous environments.

Appendices

Appendix 1 Principal components analysis of three metrics of pond hydrology derived from continuously recorded water depth. Days filled per annum, days until first drying and coefficient of variation (CV) of depth were reduced to one highly significant principal component (pond permanence index) that explained 91% of total variance. See Fig. 3, Chapter One, for pond locations.

Pond name	Days till first drying [‡]	Days filled per annum	CV depth (mm)	Pond permanence index (PC1)
Kettle*	20	29	1.70	-1.97
Vagabonds West*	26	65	1.82	-1.89
T3	61	97	1.62	-1.45
Goose	66	91	1.50	-1.35
BL1W	54	127	1.19	-0.90
Craigieburn	79	136	0.86	-0.56
BL10*	23	198	2.16	-1.60
Little Vagabonds	91	133	1.06	-0.70
Little Blackwater [‡]	53	246	1.33	-0.57
Goldney	142	334	0.66	0.71
Waimak Flat	365	365	0.57	1.79
Lyndon Tarn [‡]	365	365	0.42	1.92
Blackwater [‡]	365	365	0.11	2.18
Rhomulus [‡]	365	365	0.06	2.22
Marymere [‡]	365	365	0.04	2.24
Component loadings	0.97	0.94	-0.95	

* pond dried during experimental assay.

[‡] arbitrary start date of 12/10/05.

[†] ponds containing fish.

Chapter Four

Contrasting temporal variation in biotic interactions across an environmental disturbance gradient

Abstract

Models of community assembly across environmental gradients predict biotic interactions should be stronger in physically benign compared to stressful habitats. However there have been surprisingly few empirical investigations, especially of temporal variance in interaction strength. I investigated temporal shifts in predator-prey interactions in ponds that span a gradient of drying. The strength of predator-prey interactions are likely to increase in temporary habitats over time as predator size and biomass increase after colonisation, habitats contract, and individuals become more active as ponds dry. However, asynchronous development and multiple, overlapping cohorts of populations in permanent ponds may lead to invariable predator-prey interactions over time. To test the hypothesis that community composition and food web interactions show greater seasonal variation in temporary habitats than permanent habitats, I manipulated predator biomass in cages within multiple temporary and permanent ponds, three times over the season of filling and drying. Predator biomass in early season temporary ponds was two orders of magnitude lower than in permanent ponds; but there was no difference in predator impact between the two habitat types. Predator biomass and size and diversity increased dramatically over time in temporary ponds, but changed little in permanent ponds. Changes in the predator fauna were reflected in predator impact, which increased during the drying phase of temporary ponds, to be an order of magnitude higher than permanent ponds. These results indicate control of community assembly in ephemeral habitats is likely to shift from opportunistic colonisation to deterministic biotic interactions as time constraints approach. Furthermore, temporal shifts in the strength of biotic interactions over an environmental gradient may result in more intense interactions in physically stressful than benign habitats.

Introduction

Community assembly along gradients of environmental stress or disturbance is influenced by a well studied trade-off between resisting biotic interactions in physically benign habitats and

successfully colonising and completing development in physically stressful habitats (Lubchenco 1980, Menge and Sutherland 1987, Wellborn et al. 1996, Grime 2001). Therefore, understanding the influence of disturbance on biotic interactions is necessary to not only predict community assembly across environmental gradients, but also to manage the consequences of anthropogenic changes to natural abiotic stressors. Despite the importance of understanding abiotic constraints to species interactions, temporal variations in the strength of species interactions, especially their effects on metacommunity dynamics, have been largely overlooked.

Reviews of community dynamics have highlighted the importance of niche differentiation in facilitating species coexistence at local and regional scales (Chase and Leibold 2003, Kneitel and Chase 2004, Cottenie 2005). Consequently, spatial variations in trade-offs that lead to niche diversification have informed understanding of community assembly across heterogeneous environments (e.g., Menge and Farrell 1989, Crain et al. 2004, Urban 2004, Gerhardt and Collinge 2007). Temporal variation in the trade-offs that structure metacommunities are poorly understood, but are likely to have just as important consequences for community assembly (Kneitel and Chase 2004). Seasonal variation in trade-offs at the local scale may increase alpha diversity by facilitating coexistence across temporal niches if the local persistence of taxa is maintained by dormant phases or storage effects (Caceres 1997, Chesson and Huntly 1997, Chesson 2000). For example, the spatial coexistence of flowering plants that are strong and weak competitors for pollinators may be facilitated by the early flowering of weak competitors (Fargione and Tilman 2005, Kelly and Bowler 2005, Reineking et al. 2006). Furthermore, if the magnitude or direction of temporal variation in trade-offs differs among local habitat patches, then the spatial mosaic of favourable habitats for a given species is likely to be dynamic over a season, and influence source-sink dynamics and regional diversity patterns.

Food webs structure varies over time (e.g., Warren 1989, Winemiller 1990, Schoenly and Cohen 1991, Closs and Lake 1994) and structures are likely to be most dynamic in disturbed or seasonal habitats (Thompson and Townsend 1999) where succession after disturbances, or harsh seasonal events, lead to changes in species composition and abundance. Variation in food web structure can influence the strength of biotic interactions, especially if trophic asymmetry in colonisation (Pimm and Kitching 1987, Holt 1996) and growth rates (Brown et al. 2004) lead to changes in predator abundance and consumer: resource body ratios (Woodward et al. 2005a, Urban 2007). Moreover food web changes are likely to interact with seasonal or successional changes in habitat morphology and resource

availability (Williams 1996, Winemiller 1996), producing complex temporal variations in the strength of biotic interactions.

In this study I investigated temporal variation in biotic interactions within a pond metacommunity where local habitats (individual ponds) varied in water permanence. Pond permanence gradients are strong filters on community organisation, as only species with the appropriate morphological, behavioural or life history traits can successfully colonise and complete development in temporary ponds (Wiggins et al. 1980, Batzer and Wissinger 1996). Because predators are often slow to colonise habitats and typically have slower growth rates than non-predatory species, permanent ponds often support more diverse guilds of larger predators (Schneider and Frost 1996, Bilton et al. 2001a). Consequently local community structure is often influenced by trade-offs between avoiding predators in long duration ponds and exploiting short developmental windows in temporary ponds (Wellborn et al 1996). Such a trade-off is thought to facilitate coexistence of trait specialists across local habitat patches. However, because temporary ponds are dynamic systems, the nature of growth-predation risk trade-offs will vary over time. Thus, investigating temporal shifts in predator-prey interaction strength within ponds across this permanence gradient will enhance understanding of the mechanisms structuring pond metacommunities.

I used community surveys to investigate temporal shifts in predator-prey interactions in temporary and permanent ponds in the South Island, New Zealand, and then conducted in-situ manipulations of predator biomass designed to test four hypotheses. First, I predicted temporal shifts in community composition should be greater in temporary ponds than permanent ponds. Food webs in permanent ponds vary within and between seasons (Warren 1989), but food webs in temporary ponds may be more seasonally dynamic as their communities are reset each time they dry and fill. Upon refilling, the emergence and development of aestivating species, the variable influx of aerial colonisers and changes in the availability of basal resources are likely to cause pronounced shifts in the composition and abundance of species within temporary ponds (Lake et al. 1989, Jeffries 1994, Williams 1996). Second, I hypothesised that the trophic composition of food webs is likely to change more in temporary ponds, with predator species richness and biomass increasing over time in comparison to that of permanent ponds. Predators are likely to colonise refilled ponds more slowly than non-predatory species (Shulman and Chase 2007) because the majority of temporary pond predators recolonize aurally rather than from aestivating stages (Schneider 1999, Williams 2006) and predators require sufficient prey before successful colonisation (Pimm and Kitching 1987, Holt 1996). My third prediction was that predator: prey size ratios

should also increase over time because slow-growing predators tend to have single cohorts that increase in size, whereas rapidly developing prey species (e.g., Cladocera, Chironomidae) often have overlapping generations and so have a relatively constant mean size. Finally I expected the strength of predator-prey interactions to reflect these community changes. They were predicted to become stronger over time in temporary ponds due to increasing dominance of predator taxa, behavioural shifts associated with approaching time constraints, and because the contraction of habitats should result in increased encounters.

Materials and methods

Site description

Study sites were located in the upper Waimakariri and Rakaia river catchments (≈ 600 m asl) in the South Island high country. Numerous lentic habitats, from small temporary ponds to large lakes, form in depressions in this area on glacial and fluvioglacial landscapes dominated by tussock grassland interspersed with woody shrubs. Rainfall (≈ 1300 mm per year) is largely aseasonal (Greenland 1977), so the date and length of pond hydroperiods vary considerably within and between years (Chapter One). On average, most ponds fill during winter and dry at various stages from spring to autumn (for more detailed habitat descriptions, see Chapter Two, Wissinger et al. 2006a, Wissinger et al. *in press*). To compare temporal shifts in community structure and interaction strength across the pond permanence gradient, we selected four long duration temporary ponds (two on the Blackwater moraine [BL1W and BL10], Little Vagabonds and Gooseberry) and three permanent ponds/lakes (Lyndon Tarn, Romulus and a sheltered inlet of Lake Sarah) for intensive sampling and manipulation from a wider group previously sampled (Wissinger et al *in press*, Chapter One). Permanent ponds and lakes in this area often have a shallow littoral ring of wave-swept cobbles devoid of vegetation. We chose to sample these three permanent ponds because they were small or sheltered to contain areas of fine sediments and submergent vegetation at depths where it was possible to undertake cage manipulations comparable to those in temporary ponds.

Seasonal surveys of invertebrates and habitats

Temporary ponds were sampled on three occasions in the 2006-2007 austral spring: during colonisation in September 2006, in October 2006 during the growth phase of many taxa, and in January 2007 as ponds began to dry. This drying phase was delayed by heavy rainfall in November and December that refilled ponds to maximum levels. Permanent ponds were

sampled at the same times to allow comparison of seasonal trends. The shallow littoral zone of each pond (< 1 m deep) was sampled quantitatively during each time period using two complementary methods (after Wissinger et al. *in press*). First, the biomass and species richness of small highly abundant epibenthic species (microcrustacea, oligochaetes, dipterans, hydroptilid caddis and molluscs) were estimated from three core samples per pond, where a 500 μm mesh net was repeatedly drawn through the sediment and water column within a 0.020 m^2 PVC pipe pushed ≈ 5 cm into the substrate. Samples were preserved in 90% ethanol and sorted under a dissecting microscope at 10x magnification. Secondly the biomass and richness of large taxa were sampled with a 1 mm mesh D-net drawn repeatedly through a sampling box (surface area 0.16 m^2 , 60 cm high). These samples were sorted live, on-site, and invertebrates were preserved in 90% ethanol. Both types of samples were located within haphazardly selected patches of submergent vegetation. In total, this sampling protocol provided background information on temporal changes in community composition and basic food web structure relevant to the habitat and scale of associated experimental assays of predator-prey interactions.

Invertebrates were identified to the lowest possible taxonomic level using standard keys and reference to original descriptions where necessary (Winterbourn 1973, Chapman and Lewis 1976, Winterbourn et al. 2006). Microcrustacea and chironomids were sorted into coarse taxonomic groups under 10x magnification, from which subsets of individuals were mounted on slides for identification to genus or species. The abundance of each species in coarse taxonomic groups was estimated by dividing group abundance by the proportion of each species in the subsample. Dry mass for all taxa (except oligochaetes) was determined from taxon-specific length-weight regressions (Appendix 1, Chapter Two), after the body length of a subset of 10 individuals was measured using an eye piece micrometer. Oligochaetes were weighed to the nearest 0.1 mg after drying at 60 °C for 48 h. Dry mass was converted to ash free dry mass (AFDM) using taxon-specific correction factors (H.S. Greig unpublished data). Species were classified as predators if the majority of their diet consisted of living animal tissue, and non-predators if the diet consisted mainly of plant, fungal or bacterial tissue, or dead animal tissue (following Warren and Gaston 1992, Spencer et al. 1999, Shulman and Chase 2007) based on classifications from literature sources including published dietary analysis (Appendix 1). In some cases diets were inferred from descriptions of congeners. Species with diets consisting predominantly of prey smaller than 500 μm were classified as non-predators. This prevented the overestimation of the proportional abundance

and taxon richness of predators by failing to detect and/or quantify prey taxa inaccessible to my sampling protocols (e.g., rotifers and copepodites).

To quantify seasonal variation in prey refugia, I measured the cover of submergent vegetation along four transects. These radiated from the depth maxima in all but two ponds; in Lake Sarah and Lyndon tarn, the four transects were run perpendicular to the shore to maximum wading depth (~1.4 m). We used 1 m² quadrats at 5 m intervals on short transects (< 50 m) and 10 m intervals on long transects (> 50 m) to estimate the two- and three-dimensional cover of plant morphotypes (Appendix 3, Chapter Two). In each quadrat, plants were identified to morphotypes (Appendix 3, Chapter Two) and cover was estimated to the nearest 1%. Three dimensional cover of each morphotype was estimated by multiplying % cover scores by the plant height as a proportion of water depth. Vegetation sampling was conducted in mid October, and again along the same transects in late January. During these sampling periods, pH and specific conductivity (at 25 °C) was measured using a calibrated Oakton 10 series meter (Oakton Instruments, Vernon Hills, IL, USA)

Over the course of the study (September 2006 – February 2007) water depth and temperature in each pond was measured every 30 min using a TruTrack HT-100 data logger (TruTrack Ltd., Christchurch, New Zealand). Temporary ponds were mapped to allow surface area calculation with the aid of a hand held differential GPS (Geo-XM: Trimble, Sunnyvale, CA, USA) at each of the three sampling periods to quantify habitat contraction. Data loggers indicated that fluctuation in water depth, and consequently, surface area of the three permanent ponds was negligible.

Predator impact assays

To quantify temporal variation in the strength of predator-prey interactions I manipulated predator biomass in cages over each of the three sampling periods. Cages (steel frame; bottom surface area 0.25 m²; 50 cm - 100 cm high depending on pond depth; 1 mm mesh screen) were arranged into three blocks of two cages (with and without predators), and pushed through macrophyte beds onto the compacted layer of bottom sediments and sealed where necessary with clay. Cages within blocks were ~ one metre apart with at least two metres separating each block (Plate 5). Predators were extracted from one randomly selected cage in each block using three consecutive sweeps with a 1 mm mesh D-net (predator removal treatment). The contents of each sweep were transferred to a tray where all predatory taxa (mainly *Anisops* hemipterans, *Xanthocnemis* and *Procordulia* odonates, and numerous dytiscids) were sorted and removed, and the remaining detritus and non-predatory taxa were

returned to the cage. Comparisons of predator biomass in removal and control cages at the conclusion of each assay indicated the removal process significantly reduced predator biomass by $50.0 \pm 5\%$ (mean \pm se; one sample t-test, mean pond values at each time as replicates, $H_0 = 0\%$, $T_{20} = 9.10$, $P < 0.0001$). The success of predator removal (% reduction of predator biomass in comparison to control cages) did not differ significantly over time or between permanent and temporary ponds (repeated measures ANOVA, all effects: $P > 0.13$). Although not quantified, it is likely this predator removal process was more efficient for large-bodied than smaller taxa. To control for prey mortality during predator removal, the same protocols were followed in cages with ambient predation (ambient treatment), but after removal predators were immediately returned to the cages. The three permanent ponds contained low densities of fish, and these were removed from all cages during the predator removal and control manipulations. Thus, we only investigated the impact of predatory invertebrates with this manipulation. Previous experiments in cages and mesocosms in my study system indicated the lethal effects of fish on the biomass of prey communities were negligible over the same time periods used in this study (Chapters Two and Three).



Plate 5 *In situ* cages (50 x 50 x 50 cm) arranged in three blocks, each with a predator removal and control treatment. Pond is Little Vagabonds in October.

Cages were sampled after two weeks by taking a core sample from the centre of the cage (using the same procedure as in the surveys) and the large-bodied taxa (predators and

prey) were sampled using the predator removal protocols. Laboratory procedures also followed those of the surveys. For subsequent assays, cages were reset in new locations that were similar in vegetation and depth to those previously sampled.

Statistical analysis

I assessed spatial and temporal variation in community composition using ordination of mean biomass of species for each pond on each of the three sampling occasions. The larval and adult stages of beetle species were treated as separate taxonomic units for this analysis to reflect their different traits. The mean biomass of each species (square-root transformed to downweight highly abundant species) was used to create a Bray Curtis dissimilarity matrix which was subjected to ordination using non-metric multidimensional scaling (NMDS) with 20 random starts in both two and three dimensions. I retained two dimensions in the final model to simplify further analysis as adding the third dimension resulted in only a minor decrease in stress (0.08 vs 0.05). Spatial and temporal variation in community dissimilarity was analysed using repeated measures MANOVA on the scores of the two NMDS axes. The permanence main effect was tested between ponds, and time, and the time by permanence interaction tested within ponds. To compare the magnitude of temporal changes in community composition between permanent and temporary ponds, I performed *t*-tests on Euclidean distances calculated from the NMDS axis scores. Two distances were calculated: the sum of the movement from time September - October and October - January, and the straight line movement from September – January.

To further investigate change in community composition and trophic structure over time in permanent and temporary ponds, I calculated total species richness, and the proportion of total species richness, biomass, and density contributed by predators. Mean predator: prey size ratio was calculated from the mean size of each predator and prey taxon was adjusted for their relative abundance (after Urban 2007). I also investigated habitat parameters including pond area and depth, mean water temperature (calculated over the 14 day duration of the experiment), pH, conductivity, and the mean cover and volume of vegetation per m². These community and habitat metrics were analysed using repeated measures ANOVA with pond permanence tested between ponds and time, and the time by permanence interactions tested within ponds. Proportions were arcsine-square-root-transformed and predator body mass, density and biomass, and predator: prey body-size ratio were log_e-transformed. Habitat area was measured in temporary ponds only, and differences among times were assessed using one-way repeated measures ANOVA.

The effect of predatory invertebrates on prey biomass in the cage experiment was quantified using the log-ratio of effect size (Berlow 1999), with predator impact: $P = \ln(B_a/B_r)$, where B_a is total prey biomass in the ambient predator treatment and B_r is total prey biomass in the predator removal treatment. “Prey” were assumed to be all species not included in the predator removal process. Predator impact was calculated within each of the three blocks, and with pond means used as replicates in a subsequent repeated measures ANOVA. Ordinations were conducted using Primer 5, repeated measures ANOVAs in Statistica, and repeated measures MANOVA in R.

Results

Physical characteristics

Three of the temporary ponds refilled during a large rainfall on the 24 April 2006, with pond BL1W filling two weeks prior. Although a wet spring maintained near bank-full water levels until November, I observed a significant decrease in the depth (Time: $F_{2,8} = 9.10$, $P = 0.009$) and size ($F_{2,6} = 10.16$, $P = 0.011$; Fig 1a) of temporary ponds as they dried in summer. In contrast to temporary ponds, the depth of permanent ponds remained stable across the sampling period (time x permanence: $F_{2,8} = 9.42$, $P = 0.008$), indicating consistent habitat dimensions. Mean water temperature did not differ between permanent and temporary ponds (permanence: $F_{1,4} = 0.088$, $P = 0.78$; Fig 1b) and increased significantly over time in both habitats (Time: $F_{2,8} = 36.62$, $P < 0.0001$; time x permanence: $F_{2,8} = 0.80$, $P = 0.48$; Fig 1b). Conductivity was significantly higher in permanent than temporary ponds (permanence: $F_{1,5} = 54.6$, $P < 0.001$; Fig 1c), but did not differ over time in both habitats (time: $F_{2,10} = 0.28$, $P = 0.75$; time x permanence: $F_{2,10} = 1.38$, $P = 0.28$; Fig 1c). In contrast, pH was similar between permanent and temporary ponds (permanence: $F_{1,5} = 0.07$, $P = 0.79$; Fig 1d) but decreased over time in both habitats (time: $F_{2,10} = 8.93$, $P = 0.005$; time x permanence: $F_{2,10} = 0.02$, $P = 0.98$; Fig 1d). The surface area and volume of aquatic vegetation increased consistently over time in both permanent and temporary ponds (time: $F_{1,5} > 57.1$, $P < 0.001$; Fig 1e-f), but because percentage surface area of plants approached the asymptote of 100% in temporary ponds, we observed a significant time by permanence interaction ($F_{1,5} = 6.67$, $P = 0.027$; Fig 1e). Both plant surface area and volume were consistently greater in temporary ponds (Fig 1e-f), but the difference was only significant for plant volume (volume permanence effect: $F_{1,5} = 50.0$, $P < 0.001$; surface area permanence effect: $F_{1,5} = 4.24$, $P = 0.094$). During the drying phase of temporary ponds, over 85% of the water column contained vegetation.

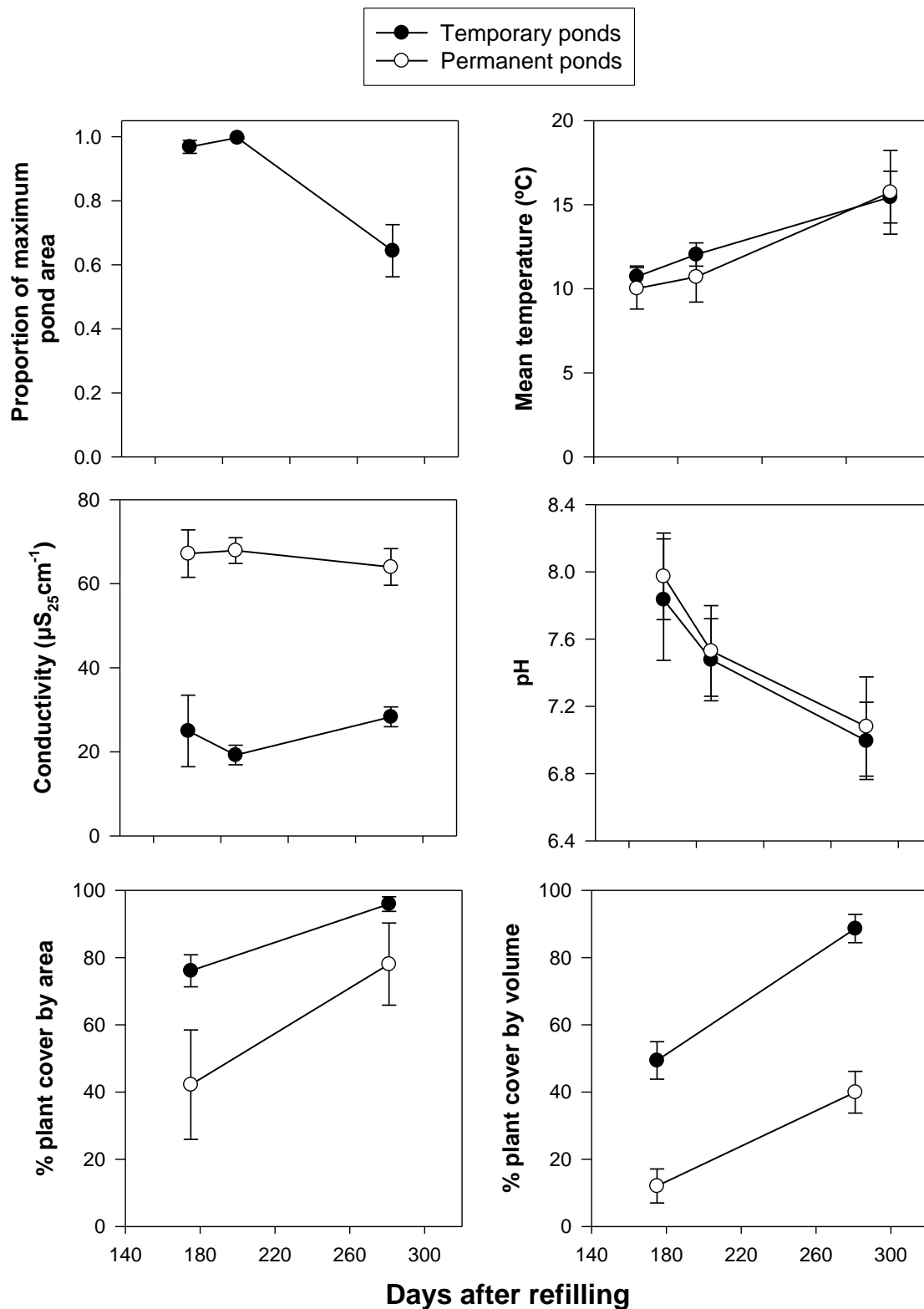


Fig. 1 Mean physical attributes of four temporary ponds (closed circles) and three permanent ponds (open circles) over three sampling periods after temporary ponds refilled. Means were calculated with ponds as replicates and error bars are ± 1 se. Vegetation cover was measured twice during sampling. Days after refilling are the mean of the four temporary ponds, which refilled within 2 weeks of each other.

Temporal shifts in community and food web structure

Ordination indicated clear spatial differences in community composition between permanent and temporary ponds across the three sampling periods (Fig. 2, Table 1a), largely through separation along axis one (Table 1b). The biomass of temporary pond prey communities was dominated by crustaceans, chironomids and oligochaetes, and predator communities were dominated by dytiscid beetles, and notonectids (Appendix 1). In contrast, prey communities in permanent ponds consisted mainly of molluscs, trichopterans, chironomids and oligochaetes and predator biomass was dominated by odonates (Appendix 1). Community structure was variable over time in both permanent and temporary ponds, but the nature and direction of change differed between the two types of habitats (a significant time x permanence interaction, Table 1b). Temporal changes in the composition of permanent ponds were indicated by short movements along axis one, whereas changes in all four temporary pond communities were more dramatic, as indicated by a consistent downward shift along axis two (Fig. 2). Change in temporary ponds was characterised by an increase in the biomass of chironomids (especially *Chironomus*), *Austropeplea tormentosa* snails and *Sigara arguta* water boatmen, as well as increases in most of the predators, especially *Anisops* backswimmers and adult dytiscids. There was also turnover in damselfly species, with *Austrolestes colenisonis* being replaced by *Xanthocnemis zealandica* later in the season.

Table 1 Repeated measures MANOVA and univariate ANOVAs on two axes scores from a non-metric multidimensional scaling (NMDS) ordination of the quantitative community composition of four temporary and three permanent ponds over three sampling dates.

Source of variation	Numerator df	Denominator df	Pillai Trace	<i>F</i>	<i>P</i>
a) Multivariate test					
Permanence	2	4	1.00	754	< 0.001
Time	4	20	0.88	3.9	0.016
Time x permanence	4	20	1.28	9.0	< 0.001
b) Univariate tests					
Axis 1					
Permanence	1	5		1865	< 0.001
Time	2	10		0.06	0.94
Time x permanence	2	10		18.1	< 0.001
Axis 2					
Permanence	1	5		0.12	0.74
Time	2	10		33.6	< 0.001
Time x permanence	2	10		23.6	< 0.001

The shift in community structure in ordination space over the three sampling periods was 2.3 - 3 times higher in temporary ponds than permanent ponds (analysis of Euclidean distance on NMDS scores; straight line distance: $t_5 = 4.80$, $P = 0.005$, aggregate distance: $t_5 = 4.46$, $P = 0.007$), indicating the magnitude of temporal shifts in community structure were significantly greater in temporary ponds.

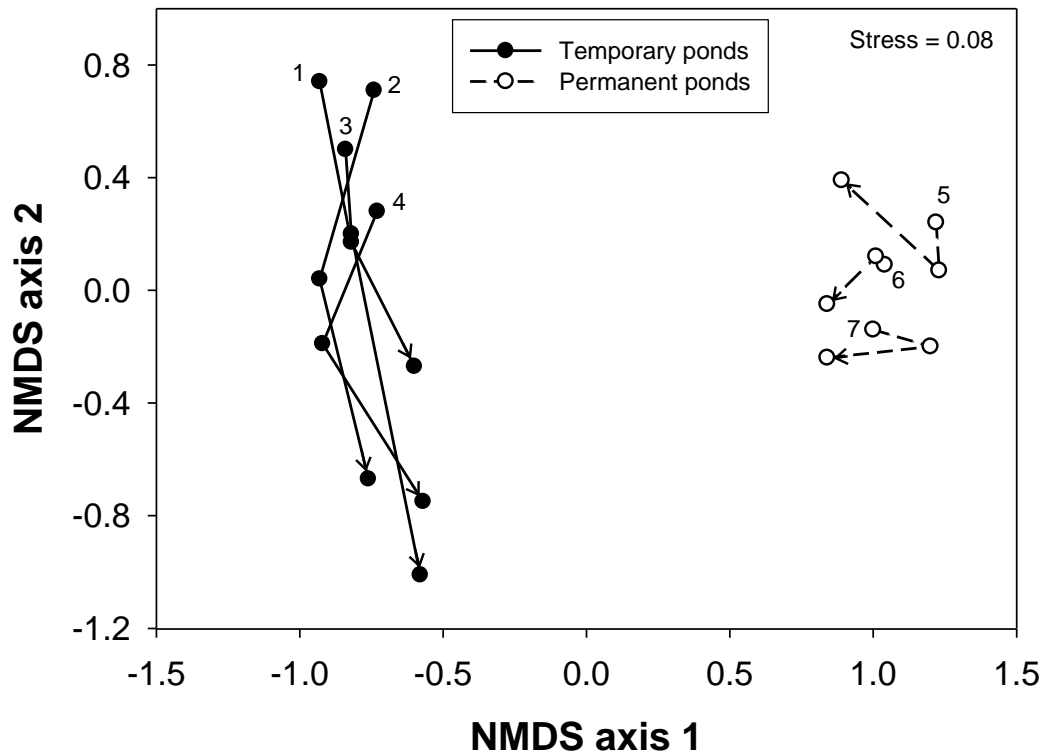


Fig. 2 Non-metric multidimensional scaling ordination of a Bray Curtis dissimilarity matrix of quantitative community composition in temporary (closed circles) and permanent ponds (open circles) across three sampling periods. Successive samplings of ponds are connected by arrows indicating the direction of community change since filling. Numbers adjacent to first sampling date indicate pond identity: 1 = Little Vagabonds, 2 = BL10, 3 = Gooseberry, 4 = BL1W, 5 = Lyndon Tarn, 6 = Lake Sarah, 7 = Romulus.

Species richness was consistently greater in permanent ponds than temporary ponds and did not differ significantly over time in either habitat (Fig 3a; Table 2). However, the proportion of predatory taxa increased with time in temporary ponds (Fig. 3b; Table 2), because of an increase in the number of predator species and a decline in prey species richness. Predator biomass increased with time in temporary ponds (Fig 3c; Table 2), and resulted in a greater proportional biomass of predators later in the season than on the first two sampling dates (Fig 3d; Table 2). In contrast, total and proportional predator biomass did not

change over time in permanent ponds (Fig 3c,d; Table 2). Despite these contrasting seasonal patterns, predator biomass was consistently greater in permanent ponds than temporary ponds (Fig 3c; Table 2). Predator density did not change over time in permanent ponds (Fig 3e), but increases in prey density lead to a decrease in proportional predator density over time (Table 2, Fig 3f). In contrast, proportional predator density in temporary ponds followed change in predator density (Table 2, Fig 3e) and increased significantly over time (Table 2, Fig 3f). The size of predators followed predator density trends with a significant increase in temporary ponds on the final sampling date; however in permanent ponds, predator size increased in late spring but decreased in summer to levels similar to those of early spring (Fig 3g; Table 2).

Prey size increased in temporary ponds and decreased in permanent ponds over time (time x permanence: $F_{2,10} = 8.45$, $P = 0.007$), but prey were consistently larger in permanent ponds (permanence: $F_{1,5} = 21.97$, $P < 0.001$). This temporal variation in both predator and prey size led to changes in predator: prey size ratios (Fig 3h). Body size ratios varied among permanent ponds, but mean size ratios across the three ponds remained similar over each sampling period. In temporary ponds, body size ratios were similar to those in permanent ponds in early spring and summer, but considerably lower during late spring. This pattern was masked in the combined repeated measures ANOVA by the high variability in body size found in permanent ponds (Table 2) but was significant when analysed in a separate repeated measures one way ANOVA ($F_{2,6} = 5.12$, $P = 0.042$).

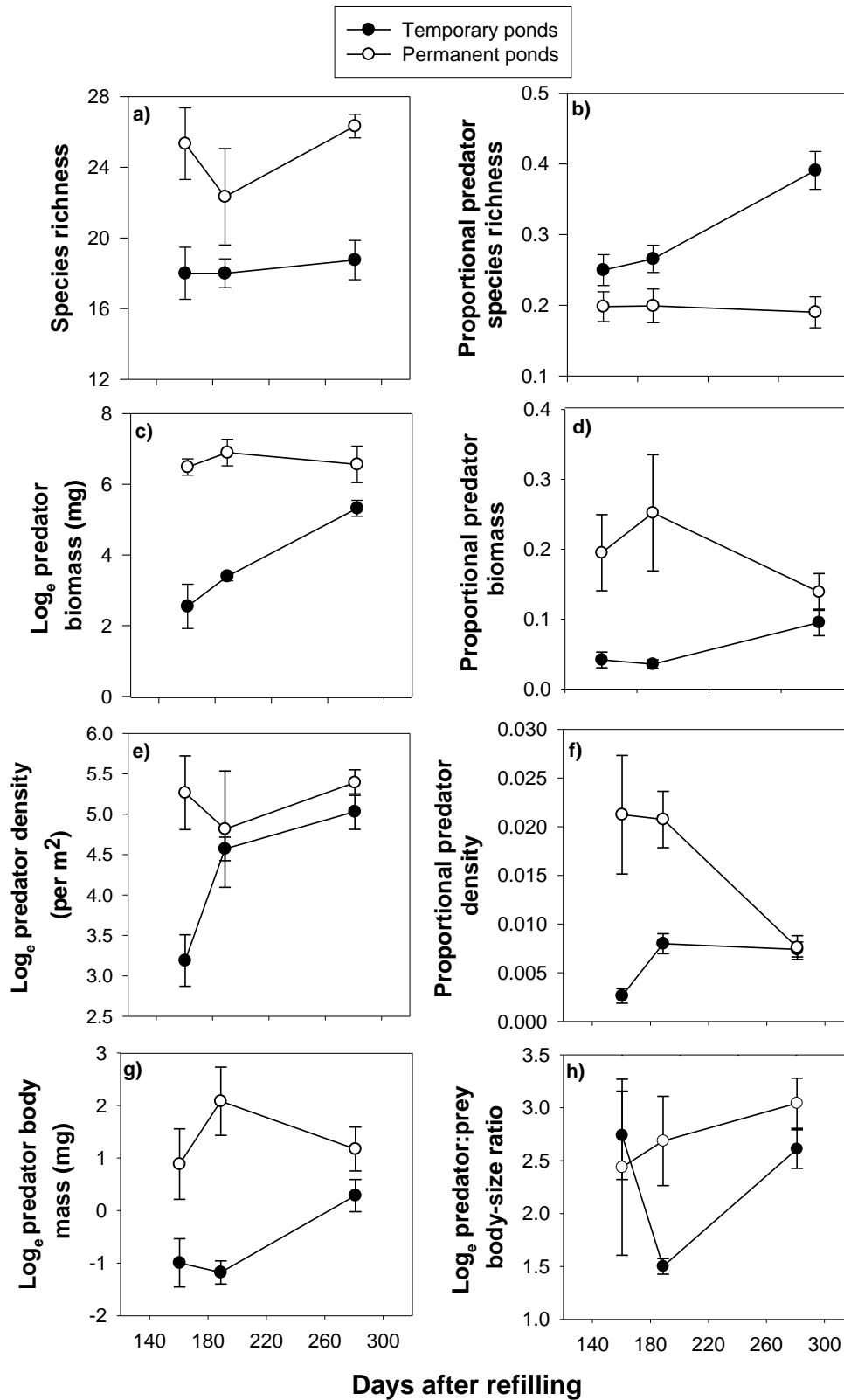


Fig. 3 Mean community attributes of four temporary ponds (closed circles) and three permanent ponds (open circles) over three sampling periods after temporary ponds refilled. Means were calculated with ponds as replicates and error bars are ± 1 se. Days after refilling are the mean of the four temporary ponds, which refilled within 2 weeks of each other.

Table 2 Repeated measures ANOVAs of community attributes from three permanent and four temporary ponds sampled over three dates from spring to summer. Permanence was tested between ponds and time and time x permanence interactions tested within ponds.

Source of variation	df	F	P
<i>Species richness</i>			
Permanence	1,5	13.65	0.014
Time	2,10	2.29	0.152
Time x Permanence	2,10	1.30	0.315
<i>Proportional predator species richness</i>			
Permanence	1,5	22.34	0.005
Time	2,10	1.67	0.236
Time x Permanence	2,10	8.47	0.007
<i>Predator biomass</i>			
Permanence	1,5	43.10	0.001
Time	2,10	10.64	0.003
Time x Permanence	2,10	10.94	0.003
<i>Proportional predator biomass</i>			
Permanence	1,5	25.05	0.004
Time	2,10	2.12	0.171
Time x Permanence	2,10	8.42	0.007
<i>Predator density</i>			
Permanence	1,5	4.91	0.078
Time	2,10	6.97	0.013
Time x Permanence	2,10	7.56	0.010
<i>Proportional predator density</i>			
Permanence	1,5	54.51	< 0.001
Time	2,10	4.27	0.046
Time x Permanence	2,10	10.01	0.004
<i>Predator body size</i>			
Permanence	1,5	22.25	0.005
Time	2,10	1.86	0.206
Time x Permanence	2,10	4.16	0.048
<i>Predator: prey body size ratio</i>			
Permanence	1,5	2.05	0.211
Time	2,10	1.67	0.235
Time x Permanence	2,10	1.66	0.238
<i>Predator impact</i>			
Permanence	1,5	9.26	0.029
Time	2,10	1.86	0.205
Time x Permanence	2,10	4.18	0.048

Predator-prey interactions

Predator impact on prey biomass did not change during the experiment in permanent ponds, but increased by two orders of magnitude over time in temporary ponds (Fig 4; time x permanence interaction, Table 2). In temporary ponds prey biomass was, on average, between 1% and 19% lower in predator-removal than control cages in early and late spring, respectively, and 75% lower in late summer as the ponds dried. On average, predator impact in temporary ponds was five-fold higher than in the permanent ponds (Fig 4; Table 2). However, across all sampling dates predators did not exert any significant negative impact on prey biomass in permanent ponds (one sample *t*-test, $H_0 = 0$: $t_8 = 1.20$, $P = 0.27$).

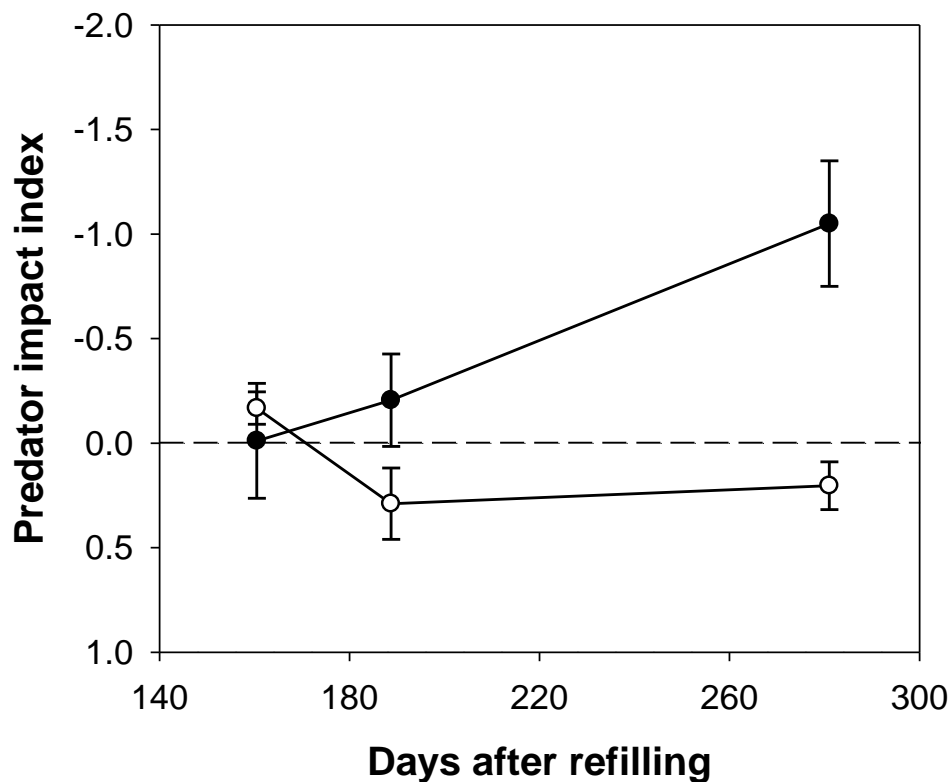


Fig. 4 Log-ratio index of predatory invertebrate impact on total prey biomass in a predator removal cage experiment in three permanent (open circles) and four temporary ponds (closed circles) following refilling. Means use ponds as replicates and error bars are ± 1 se. The dashed line denotes zero impact of predators on prey biomass, with negative numbers indicating predator reduction of prey biomass. Days after refilling are the mean of the four temporary ponds, which refilled within 2 weeks of each other.

Discussion

Addressing the spatial variation in biotic interactions within a landscape has enhanced our understanding of community assembly and coexistence across heterogeneous environments, especially along environmental gradients (Lubchenco 1986, Menge and Sutherland 1987, Wellborn et al. 1996, Chesson 2000, Callaway et al. 2002, Crain et al. 2004). However, empirical investigation of the temporal variation in the strength of biotic interactions has been often been overlooked (but see Settle et al. 1996, Corti et al. 1997, Gratton and Denno 2003, Agrawal et al. 2007), despite numerous studies that have documented the dynamic nature of food webs (Schoenly and Cohen 1991, Winemiller 1996, McCann et al. 2005a). The field surveys and in-situ experiments across pond permanence gradients in this study revealed seasonal shifts in food web properties in temporary ponds from refilling to drying that increased the strength of predator impact by two orders of magnitude. Thus, temporal shifts in the trophic structure of food webs resulted in a fundamentally important functional change in food web dynamics. In contrast, community structure and predator-prey interactions did not vary seasonally in permanent ponds, suggesting the nature of seasonal shifts in food web dynamics should vary between ponds across a permanence gradient. Below I evaluate the factors contributing to temporal changes in food web properties, and their effect on the strength of predator-prey interactions, and discuss the implications of these results for understanding of niche assembly models of metacommunity dynamics.

Temporal variation in food web properties

My comparative field data indicate that the community structure and trophic organisation of temporary pond communities is considerably more dynamic than in permanent ponds. In temporary ponds, I observed increases through time in the number of predator taxa, the proportion of predator species and biomass, and predator: prey body size ratios, all of which are important determinants of food web interactions (Warren and Gaston 1992, Wilson 1996, Emmerson and Raffaelli 2004, Woodward et al. 2005a, Brose et al. 2006).

Total species richness did not change, but colonisation by predators and turnover of prey species resulted in increased proportions of predator species in temporary ponds. Many studies report fixed predator: prey species richness ratios in lentic habitats (Jeffries 2002, Donald and Anderson 2003, Urban 2004) and other systems (Warren and Gaston 1992), which imply that constant predator prey ratios are potentially an emergent property of food web assembly (Warren and Gaston 1992). However, evidence for variable trophic ratios presented here, and in other studies investigating systems with local habitats that differ in

duration or isolation (Closs and Lake 1994, Spencer et al. 1999, Bilton et al. 2001a, Shulman and Chase 2007), suggests that differential dispersal rates between predators and prey in spatially or temporally constrained environments may preclude the assembly of fixed predator: prey ratios (Shulman and Chase 2007).

Seasonal shifts in the consumer-resource body-size ratios of food webs often occur because of variable colonisation and growth rates of species (Wilbur 1988, Woodward et al. 2005a, Urban 2007). We observed an increase in the size of predators late in the season in temporary ponds but the hypothesis that rapid generation times in temporary pond prey species result in stable prey size was not supported. An increase in prey size over spring and summer resulted in a quadratic rather than a linear change in predator: prey body size with time. High predator: prey body-size ratios in early spring were due to the presence of large, predatory adult beetles ovipositing after winter dormancy, combined with small crustaceans and early instar chironomids dominating prey communities. The subsequent loss of adult beetles and an increased density of larger prey (e.g., *Chironomus* larvae and the large cladoceran, *Simocephalus obtusatus*) contributed to lower predator: prey size ratios in late spring. Finally, the increased density of notonectids and both adult and late instar larval beetles dramatically increased mean predator size in late season temporary ponds, resulting in increased predator: prey size ratios despite concurrent increases in prey size. In contrast to temporary ponds, body-size ratios did not vary over time in permanent ponds and the small decrease in predator size over the season was balanced by a decrease in prey size. Such a pattern is consistent with asynchrony resulting from the multiple cohorts of semivoltine predator populations (e.g., dragonflies and *Xanthocnemis* damselflies) that dominate permanent lentic habitats in New Zealand (Stark 1981, Rowe 1987). Absolute and proportional predator density increased with time in temporary ponds, consistent with the slower colonisation of ephemeral habitats by predators. Interestingly, I also observed a decline in proportional predator density in permanent ponds, indicating some seasonality is present in permanent pond.

Temporal variation in predator-prey interaction strengths

The changes we observed in food web structure in temporary ponds are consistent with an increase in predation strength. First, increases in predator abundance (both biomass and density) are well known to increase the strength of top down control of prey, especially in systems with seasonal fluctuations in predator abundance (Settle et al. 1996, Walker and Jones 2001, Gratton and Denno 2003). Increases in predator biomass will be especially

important when predator biomass increases disproportionately to that of prey, as observed in my study.

Second, parallel increases in predator: prey body size ratios and interaction strength from late spring to summer were consistent with the theoretical expectations that predator size enhances predation risk, and that predator: prey size ratios are positively related to the strength of species interactions (Jennings and Warr 2003, Emmerson and Raffaelli 2004, Woodward et al. 2005a, Brose et al. 2006). However, predator: prey body size ratios in early spring that were similar to late summer ratios did not result in similarly high predator impacts. Other food web parameters such as low predator density and biomass are likely to have decoupled the predicted relationship between consumer: resource body-size ratios and interaction strength.

Third, the increased predator richness we observed through time in temporary ponds can increase predation rates (Sih et al. 1998, Schmitz 2007), particularly when diverse prey communities (as opposed to the one-or two-species prey guilds often used in experimental studies) encourage niche separation among predator species (Wilby and Thomas 2002, Cardinale et al. 2003, Snyder et al. 2006). These increases in predation rates are most probable at high predator densities where negative interspecific interactions among predators are weaker than competition among a comparable density of conspecific predators (Chapter Three, Griffin et al. 2008). Additionally, an increase in the diversity of predators relative to prey may decrease the potential for increases in the abundance of invulnerable prey in response to losses of vulnerable, competing prey (compensatory dynamics; Duffy et al. 2007), and reduce the benefits of species-specific anti-predator defences (Hoverman and Relyea 2007). This should lead to stronger, and more unstable food web interactions (Kondoh 2007). Thus, the increased proportional predator richness with time in temporary ponds is likely to have contributed to the observed increase in top-down prey suppression.

Changes in the trophic structure of temporary pond food webs that occurred as ponds dried were almost certain to have been affected by the changing physical properties of habitats and associated behavioural changes of individuals. Pond contraction increases the density of both predators and prey, and should lead to higher predator-prey encounter rates (Winemiller 1990). Pond contraction may also influence the presence and connectivity of spatially distinct sub-webs within the broader food web (food web compartments; Krause et al. 2003) that act to weaken interaction strength by enhancing asynchrony between predators and resources and promoting compensatory dynamics across compartments. Even in spatially confined, small, drying ponds (< 0.25 ha) like those at my study sites, food webs have open

water (pelagic) and littoral (epibenthic) food web compartments that can be linked by mobile invertebrate predators (Warren 1989). Three dimensional pond contraction during drying may reduce food web compartmentalization, or increase connectivity of compartments by members of higher trophic levels, and consequently lead to stronger interactions and more unstable food webs (McCann et al. 2005a, McCann et al. 2005b, Rooney et al. 2006). Thus, the contraction of pond habitats with drying, combined with continuing vertical growth of aquatic vegetation, is likely to have contributed to the strong interactions we observed. However water temperature does not appear to have contributed to increases in predation in temporary ponds, as seasonal patterns of temperature in permanent ponds were identical.

The increased vegetative cover in temporary ponds did not appear to provide effective refuge for prey from the effects of increased predator abundance, possibly due to the relative discrepancies in size of predators and prey. When predators are much larger than their prey, a disproportionate ability to exploit refuge space may weaken predation rates. For example, macrophytes often reduce the impact of predatory fish on benthic invertebrates (reviewed in Pierce and Hinrichs 1997). However, habitat complexity may have little effect on predation rates among similar sized predators and prey (as in our temporary ponds) as both groups are equally able to exploit complex habitats (James and Heck 1994, Alto et al. 2005), and predation may even be enhanced if cover is provided for ambush predators (Flynn and Ritz 1999, Hampton 2004).

Consequences of temporally variable biotic interactions to community dynamics

Regardless of the underlying mechanism, temporal shifts in the strength of predator impacts on prey are likely to have important consequences for the stability of food webs and the balance of trade-offs that influence community assembly across ponds and other environmental disturbance gradients. Disturbed habitats, because of their simple food web architecture and the vulnerability of prey (Power et al. 1996), are likely to be predisposed to strong interactions that potentially destabilise food webs. The temporal increases in strength of predator-prey interactions observed in my study indicate that food webs of disturbed habitats could become more unstable over time, inducing chaotic population dynamics, the loss of species, and shifts to alternative states. Because many prey species in temporary ponds are resistant or resilient to desiccation, periodic drying is likely to alleviate these strong interactions by disproportionately affecting predators, thus creating long term asynchrony between the dynamics of predator and prey populations. Consequently, changes in the timing and/or intensity of abiotic stress in disturbed habitats are likely to result in different

community trajectories depending on how they favour or disfavour particular predators and prey (Chase 2007).

Community assembly across ponds of differing permanence, and many other systems with pervasive environmental disturbance gradients, is often influenced by the contrasting pressures of biotic interactions and abiotic stress (Menge and Sutherland 1987, Wellborn et al. 1996, Crain et al. 2004). Hence, temporal changes in the strength of biotic interactions are likely to influence niche-based trade-off models of community assembly, such as species sorting and mass effect dynamics (Chase and Leibold 2003, Leibold et al. 2004) and affect local and regional diversity. At the local scale, seasonal increases in predator impact in temporary ponds may produce temporal shifts in the balance of trade-offs between rapid development versus biotic interactions. Theoretically, this should enhance within habitat (α) diversity by facilitating coexistence across temporal niches, as long as species can endure unfavourable conditions in dormant phases (either within or between generations) (Caceres 1997, Chesson and Huntly 1997, Chesson 2000, Kneitel and Chase 2004). For example, in pond systems, species vulnerable to predators may develop within temporal windows of low predation risk brought about by phenological time lags of predator populations (as in Hairston 1987, Chapter Five). However, if α -diversity is inflated by enabling the broader distribution of habitat specialists, diversity between local habitats (β diversity) will decrease. The effects on regional (γ) diversity are more complex and likely dependent on the predictability of trade-offs within and between seasons (Chapter Six).

Because biotic interactions showed little apparent change in permanent ponds during the course of my study, the seasonal variation in species interactions in temporary ponds should alter patterns of spatial variation in biotic interactions that promotes regional coexistence. That is, for a given species, the landscape mosaic of favourable habitats is likely to be variable within a season as well as between seasons. Moreover, altered disturbance regimes are likely to modify the intensity of interactions within local habitats, and alter the spatial orientation of trade-offs. My results indicate that the integration of temporal dynamics into our current, largely spatial, models of metacommunities is essential for both enhancing mechanistic understanding of the assembly at both local and regional scales, and for predicting the consequences of altered disturbance regimes that are likely with global change.

Appendix 1 Mean biomass (mg m⁻²) of species in four temporary and three permanent ponds across three sampling periods from pond filling to drying. Coleopteran larvae are indicated by “L”. Trophic groups are “P” for predators, “N” for non-predators (including omnivores). Trophic groups were determined from published accounts of diet and feeding mode, with specific references indicated by superscript numbers.

Taxon	Trophic group [€]	Temporary pond biomass			Permanent pond biomass		
		Sept	Oct	Jan	Sept	Oct	Jan
Ephemeroptera:							
<i>Deleatidium</i> spp.	N ¹	--	--	--	0.58	--	0.06
Odonata:							
<i>Austrolestes colenstonis</i>	P ^{2,3,4}	0.03	3.39	--	0.18	--	0.87
<i>Xanthocnemis zealandica</i>	P ^{2,3,4}	--	--	1.76	380	377	200
<i>Procordulia grayi</i>	P ^{4,5}	--	--	--	299	752	595
Trichoptera:							
<i>Hudsonema amabile</i>	N ^{5,6}	--	--	--	0.26	0.67	5.72
<i>Triplectides cephalotes</i>	N ^{5,6}	--	--	--	81.5	304	61.1
<i>Triplectides obsoletus</i>	N ^{1,5,6}	--	--	--	0.05	--	--
<i>Oecetis unicolor</i>	N	--	--	0.09	36.9	8.53	10.7
<i>Oecetis iti</i>	N	--	0.05	--	--	--	3.69
<i>Paroxyethira hendersoni</i>	N ⁵	--	--	--	23.4	11.3	97.2
Lepidoptera:							
<i>Hygraula nitens</i>	N ⁵	--	--	--	0.73	4.01	5.50
Hemiptera:							
<i>Sigara arguta</i>	N ³	1.29	4.11	465	12.6	6.54	80.1
<i>Diaprepocoris zealandiae</i>	N	--	--	--	113	58.2	57.8
<i>Anisops wakefieldi</i>	P ³	--	--	7.91	--	--	--
<i>Anisops assimilis</i>	P ³	--	--	108	2.79	--	35.3
Coleoptera:							
<i>Liodessus plicatus</i>	P ^{3,7}	1.03	1.29	3.62	--	--	--
<i>Liodessus</i> L	P ^{3,7}	--	0.01	0.02	--	--	--
<i>Antiporus strigosulus</i>	P ^{3,7}	0.75	--	4.50	2.00	12.6	14.0
<i>Antiporus femoralis</i>	P ^{3,7}	--	--	--	--	--	--
<i>Antiporus</i> L	P ^{3,7}	0.18	15.1	36.4	0.26	--	1.45
<i>Lancetes lanceolatus</i>	P ^{3,7}	3.51	--	7.02	--	--	--
<i>Lancetes lanceolatus</i> L	P ^{3,7}	0.71	6.14	11.1	--	--	--
<i>Rhantus suturalis</i>	P ^{3,7}	8.04	--	24.9	--	--	--
<i>Rhantus suturalis</i> L	P P ^{3,7}	1.71	1.81	13.4	--	--	--
Hydrophilidae L	P ⁸	--	0.02	0.51	--	--	--
Diptera:							
Stratiomyidae	P ⁸	0.66	2.73	--	0.46	--	--
Macropelopiini sp.	N ^{3,5,9†}	109	121	239	170	71.1	209
<i>Paratrichocladus pluriserialis</i>	N ^{5,9}	1.28	--	12.7	22.8	8.27	14.0
<i>Lymnophyes</i> sp.	N ^{5,9}	3.04	4.66	29.1	3.34	6.31	77.2
<i>Corynoneura</i> sp.	N ^{5,9}	--	--	4.95	--	--	--
Orthocladinae 1	N ^{5,9}	--	0.03	--	--	--	--
<i>Chironomus zealandicus</i>	N ^{5,9}	57.8	197	420	0.16	--	68.9
<i>Polypedilum</i> sp.	N ^{5,9}	--	--	--	50.6	43.9	--
<i>Tanytarsus funebris</i>	N ^{5,9}	0.35	--	--	--	--	--

Taxon	Trophic group [€]	Temporary pond biomass			Permanent pond biomass		
		Sept	Oct	Jan	Sept	Oct	Jan
Acarina:							
<i>Eylais waikawae</i>	P	--	--	0.48	--	--	--
<i>Hydrachna maramauensis</i>	P ¹⁰	--	--	--	--	--	0.83
<i>Piona pseudouncata</i>	P ^{10,11}	--	--	--	5.68	6.33	65.0
<i>Arrenurus lacus</i>	P ¹⁰	--	--	--	6.10	6.92	--
Oribattei	N ¹⁰	13.1	--	--	--	--	--
Cladocera							
<i>Daphnia carinata</i>	N ^{10,11}	8.85	12.7	--	--	--	--
<i>Daphnia</i> sp. B.	N ^{10,11}	--	--	--	--	0.32	--
<i>Simocephalus vetulus</i>	N ^{10,11}	--	--	--	5.61	0.43	37.4
<i>Simocephalus obtusatus</i>	N ^{10,11}	14.0	74.0	5.57	--	--	--
<i>Pseudomoina lemnae</i>	N ^{10,11}	1.96	1.69	--	--	--	--
<i>Echinisca schauinslandi</i>	N ^{10,11}	0.34	0.41	2.94	--	--	0.01
<i>Alona</i> spp.	N ^{10,11}	2.44	11.7	36.5	0.15	2.81	19.7
<i>Ilyocryptus sordidus</i>	N ^{10,11}	1.09	3.48	1.81	0.21	3.30	4.57
<i>Ceriodaphnia dubia</i>	N ^{10,11}	3.53	0.16	4.01	--	--	--
Calanoida:							
<i>Boeckella dilatata</i>	N ^{10,11}	5.52	3.05	0.01	0.07	--	--
Cyclopoida							
<i>Acanthocyclops robustus</i>	N ^{12†}	1.34	1.89	16.49	0.42	3.32	2.99
<i>Eucyclops serrulatus</i>	N ^{10,11}	--	--	--	0.03	0.27	0.23
Ostracoda:							
<i>Cypricercus sanguineus</i>	N ¹⁰	11.2	2.89	--	--	--	0.01
<i>Herpetocypris pascheri</i>	N ¹⁰	--	--	--	0.56	0.14	0.46
<i>Ilyodromus varrovillius</i>	N ¹⁰	2.94	2.15	0.58	--	0.16	--
<i>Candonocypris</i> sp.	N ¹⁰	--	--	--	0.23	1.77	2.04
<i>Darwinula repoa</i>	N ¹⁰	--	--	--	0.78	0.76	0.38
<i>Cypretta viridis</i>	N ¹⁰	0.58	0.54	0.24	--	0.01	--
<i>Cyprodopsis vidua</i>	N ¹⁰	--	--	--	0.01	0.01	--
<i>Candona aotearoa</i>	N ¹⁰	--	--	--	0.30	0.06	0.16
Mollusca:							
<i>Glyptophysa variabilis</i>	N	--	--	--	17.70	1.18	--
<i>Austropeplea tomentosa</i>	N	--	--	554	--	--	3.74
<i>Lymnaea stagnalis</i>	N	--	--	--	2.80	--	110
<i>Potamopyrgus antipodarum</i>	N ^{1,5}	--	--	--	541	1559	2124
<i>Gyraulus corinna</i>	N	--	--	--	356	438	174
<i>Physella acuta</i>	N	--	--	--	78.8	226	531
<i>Musculium novaezelandiae</i>	N	--	--	1.59	160	196	406
Amphibia:							
<i>Litoria ewingii</i>	N [*]	--	0.48	--	--	--	--
Oligochaeta	N	133	424	68	1404	1180	830

‡ Tanypods are often considered to be predators, but dietary analysis^{3,5} on the genera abundant in the Cass basin indicates omnivorous diets dominated by diatoms and detritus.

† *Acanthocyclops* is considered predatory (Li and Li 1979) but the majority of the prey species (rotifers and copepodites) fall below the 500 µm size threshold (see methods).

* Own observations.

€ References: 1 = Winterbourn (2000), 2 = Crumpton (1979), 3 = Dowdle (1981), 4 = Rowe (1987), 5 = (Stark 1981), 6 = Cowley (1978), 7 = Winterbourn et al. (2006), 8 = Merritt and Cummins (1996), 9 = Berg (1995), 10 = Chapman and Lewis (1976), 11 = Chapman and Green (1987), 12 = Li and Li (1979).

Chapter Five

Multiple time constraints facilitate the broad distribution of a trait specialist across an environmental gradient

Abstract

The contrasting selection pressures present in habitats along environmental gradients often result in habitat specialization; however, some species maintain broad distributions despite such gradients. Phenotypic plasticity enables some habitat generalists to persist, but it does not explain the wide distribution of some species with fixed traits. I investigated the role of multiple selection pressures in facilitating the broad distribution of a cased caddisfly, *Asynarchus nigriculus*, in ponds across a permanence gradient of wetland habitats in the Rocky Mountains. In short-duration vernal ponds, slowly developing larvae had increased risk of mortality from desiccation, suggesting that abiotic time constraints should select for rapid development. Surprisingly, larval development was significantly faster in long duration, autumnal ponds than in vernal pools; emergence occurred well before pond drying, and coincided with the appearance of larger instars of a predatory beetle (*Dytiscus*) larvae. Laboratory trials revealed that the last two instars of beetle larvae pose a significant mortality threat to *Asynarchus*, but that predation threat declines after caddisfly pupation. Rapid development also reduced cannibalism rates in both habitats and facilitated asymmetric intraguild predation of *Limnephilus externus* in autumnal ponds, providing a significant protein supplement for the detritus diet of *Asynarchus*. Thus, both intra and interspecific biotic time constraints select for rapid *Asynarchus* development in these habitats, even though drying pressures are relaxed. I did not observe antipredator responses (reduced activity, large cases, and accelerated development) by *Asynarchus* to *Dytiscus*, and caddisflies in predator-free ponds emerged as early as those in ponds with predators. This suggests that rapid development in *Asynarchus* is a fixed trait, regardless of habitat type. I propose that predictable convergent selection pressures across different types of habitats enable the broad distribution of a species with fixed specialised traits as an alternative mechanism to phenotypic plasticity.

Introduction

Different populations of the same species often occur across environmental gradients of abiotic stress. Increasing abiotic stress along environmental gradients often reduces herbivory (Rand 2002), competition (Lubchenco 1980, Grime 2001, Crain et al. 2004) and predation (Menge and Sutherland 1987, Wellborn et al. 1996) which can lead to an increase in the strength of biotic interactions in more physically benign habitats. Thus, broadly distributed species are simultaneously faced with changing abiotic and biotic selection pressures across their ranges. Phenotypic plasticity is one well-described evolutionary response to this type of spatial variation in selective pressures, and appears especially important in maintaining predator-prey coexistence (Lima and Dill 1990, Lima 1998, Tollrian and Harvell 1999). Phenotypic plasticity maximizes fitness in contrasting habitats by enabling the expression of alternative morphs, behaviours, physiologies, and/or life history traits to different environmental cues (West-Eberhard 1989, Nylin and Gotthard 1998, Schlichting and Pigliucci 1998). This trait plasticity enables the persistence of many habitat generalists, but it does not explain the wide distribution of some species with specialized, fixed traits (McPeck 1996).

Fixed traits often occur when selection pressures are predictable and vary dramatically between coarse habitat patches in a landscape (Futuyma and Moreno 1988, Van Tienderen 1991, Tufto 2000, Alpert and Simms 2002). Reciprocal specialization driven by trade-offs between traits that enable persistence in habitats with different abiotic and or biotic selection pressures, often result in species replacements along environmental gradients (e.g., Lubchenco 1980, Wellborn et al. 1996, Huckle et al. 2000). Despite an abundance of evidence for the existence of habitat specialization among species with fixed traits, some species appear to maintain broad distributions across environmental gradients, potentially by possessing intermediate rather than extreme levels of traits (Levins 1968, McPeck 1996, McCauley 2006). However this mechanism is poorly understood (McCauley 2007). Understanding the broad distributions of species along environmental gradients will require consideration of trait plasticity and the extremity of traits, relative to selection pressures within patches across habitat gradients (Levins 1968, McPeck 1996).

Drying in lentic (standing fresh water) habitats exerts considerable stress on aquatic animals. As a consequence, major shifts in community structure occur along a gradient from short duration ephemeral pools to long duration temporary ponds and permanent lakes. These community shifts reflect contrasting selection pressures between traits that facilitate the exploitation of habitats with frequent and harsh drying, and those that facilitate coexistence

with permanent-habitat predators (Wellborn et al. 1996). Permanent habitat specialists are replaced by temporary habitat specialists along these predator-permanence gradients for nearly all freshwater orders (Wellborn et al. 1996). These replacements often reflect specialization to cope with drying time constraints (investment in rapid growth) or predator defense (Skelly 1995, Wissinger et al. 1999a, Stoks and McPeck 2003a, Johansson and Suhling 2004); but can also occur among species with specialized anti-predator traits that are alternately effective against different types of predators present across the permanence gradient (Werner and McPeck 1994, Wellborn 2002, Stoks and McPeck 2006, Wissinger et al. 2006b).

Despite the well documented prevalence of habitat specialists in ponds, other species are present across more than one habitat type along the permanence gradient (McPeck 1996, De Block and Stoks 2005, McCauley 2007). However, the mechanisms facilitating the broad distribution of these species is less well understood (McCauley 2007). The purpose of this study was to investigate the mechanisms that enable the broad distribution of the caddisfly, *Asynarchus nigriculus*, which appears to exhibit fixed specialized traits.

Asynarchus is the only caddisfly species at our study sites that can complete its life cycles in vernal pools that dry in < 60 days. The exploitation of vernal pools by *Asynarchus* occurs through rapid larval development that is facilitated by high levels of activity and aggression, including group cannibalism (Wissinger et al. 1999a, Wissinger et al. 2004), and minimal investment in case construction compared to permanent habitat caddisflies (Wissinger et al. 2006b). These traits increase the vulnerability of *Asynarchus* to predators, and salamanders typically eliminate *Asynarchus* from permanent habitats (Wissinger et al. 1999a, Wissinger et al. 2006b). However *Asynarchus* is abundant in late drying autumnal ponds despite the presence of large predatory invertebrates, such as *Dytiscus dauricus* that prey heavily on it under experimental conditions (Wissinger et al. 2006b).

Asynarchus does not appear to have a longer period of larval development in autumnal ponds, despite relaxed time constraints compared to those in vernal habitats. This was unexpected given that adults do not feed, and extending larval growth should theoretically have direct, positive effects on adult survival and fecundity (see reviews by Peckarsky et al. 2001, Jannot et al. 2007). Rapid development in the absence of drying time constraints is also curious because it implies that *Asynarchus* larvae do not alter their “fast life-style” behavioural traits (Sih 1987) in the presence of predatory invertebrates in autumnal ponds.

To explain the apparently fixed, “fast life-style” traits of *Asynarchus* larvae, I hypothesized that the rapid development in autumnal habitats facilitates early emergence thereby reducing the time exposed to beetle predation. I also hypothesized that rapid, synchronous development reduces the potential for cannibalism among larvae, regardless of drying time constraints, and that rapid development might facilitate intraguild predation on small larvae of a confamilial species (*Limnephilus externus*) with which it often co-occurs in autumnal ponds (Wissinger et al. 1996, Wissinger et al. 2003).

To test these hypotheses, I first compared larval development of *Asynarchus* in adjacent vernal and autumnal habitats, and evaluated the timing of its life cycle in relation to that of *Dytiscus* in the autumnal ponds. Subsequently I designed microcosm experiments to determine size-specific vulnerability of *Asynarchus* to *Dytiscus* predation, and the effects of body size on cannibalism, and intraguild predation by *Asynarchus* on *Limnephilus*. Finally, I reared *Asynarchus* in mesocosms with and without beetle predators to investigate whether the success of *Asynarchus* in autumnal habitats could be explained by beetle-induced phenotypic plasticity in development rate or foraging behaviours. Together, my comparative data and experimental results provide evidence for a variety of reinforcing selective pressures that are likely to simultaneously operate on *Asynarchus* across different types of temporary habitats.

Methods

Comparative Life Histories

Surveys of natural populations of *Asynarchus* were conducted at the Mexican Cut Nature Preserve in the Elk Mountains, Colorado. The nature preserve includes a mosaic of > 60 numbered ponds spanning a pond permanence gradient (inundation period range: 40-365 open water days pa) within an area of 40 ha (see Wissinger et al. 1999b, Wissinger et al. 2003, for a detailed habitat description). Nearest neighbour distances between ponds are typically 10 - 20 m, and because recolonisation rates are high after population crashes (S.A. Wissinger unpublished data), adult dispersal among ponds is assumed to be high. I assessed the rate and timing of *Asynarchus* development from weekly samplings of four autumnal basins (ponds 6,8,10,11), one permanent basin (9) and five vernal ponds (7,13,15,21,22) beginning a week after snowmelt (15 June 2006) until pupation ended (17 July 2006). The vernal pools selected were known to have annual populations of *Asynarchus* and regular drying time constraints (Wissinger et al. 1999b, Wissinger et al. 2003). Pond 9 had few salamanders and community composition similar to the autumnal basins and provided the 5th replicate of non-time constrained ponds with large invertebrate top predators. Each pond was

sampled on each date by taking four non-destructive, quantitative, 1 m long sweeps with a standard 30 cm wide D-net (1 mm mesh). Sampling was restricted to littoral vegetation and benthos adjacent to pond edges where caddisfly larval densities were the highest. Larvae were sorted into instars in the field, with voucher specimens collected to confirm field-identified instar categories (body mass and instar metrics given in Wissinger et al. 2003). Pupae attached to the substrate were counted within the sample area before sweeps were taken. Emergence periods for each pond were estimated by repeatedly (every 2-3 days) counting and removing pupal exuvae that had accumulated on emergent boulders placed near the edge of the ponds. In autumnal ponds, *Dytiscus* phenology was inferred by taking a succession of ten 0.33 m² quantitative sweeps commencing after the appearance of first instar larvae on 22 June 2006, until beetle pupation began on 24 July 2006. The three larval instars of the beetles were easily identified in the field.

I tested differences in the development rate of caddisfly larvae between vernal and autumnal basins with repeated measures ANOVA on mean larval stage. Permanence was tested between ponds and date and the permanence by date interaction was tested within ponds. Mean larval stage was calculated by assigning each individual from a given sample to a category from 1-7, with 1-5 assigned to the respective larval instars, and prepupae and pupae assigned 6 and 7, respectively. Caddisfly pre-pupae were 5th instar larvae that have begun to add stones to their cases in preparation for pupation, but have yet to seal the ends of their cases and affix them to the substrate (Wissinger et al. 2003). Difference in mean caddisfly emergence date (in Julian days) between vernal and autumnal ponds was analysed using a *t*-test with pond means as replicates.

Size predation experiment with beetles and Asynarchus caddisflies

To determine how the size of caddisfly prey and beetle predators affects predation rates, I conducted survival trials by manipulating different size combinations of the two species. Experiments were conducted in plastic microcosms (W x L x D: 39 x 54 x 11 cm) to which detritus (1000 cm³) (with caddisflies and beetles removed), and a large cobble (long axis ~ 20cm) were added to mimic pond substrate. Microcosms were housed within a portable field shelter at Mexican Cut. I added fifteen 4th, 5th or prepupal (½ to ¾ of case covered in stones) *Asynarchus* caddisfly larvae to tanks 30 minutes prior to the addition of one 1st, 2nd or 3rd instar *Dytiscus* larva that had been starved for 20 hours. I also included a control treatment for each caddisfly stage without beetles to assess caddisfly cannibalism. Caddisfly developmental synchrony within ponds and the natural time lag of beetle phenologies

necessitated collecting caddis from ponds at relatively high elevations at our study site (3400-3800m) at the Mexican Cut and beetle larvae from a pond at a lower elevation (2900m). I ran two replicates of each of the 12 treatment combinations over two successive nights yielding a total of 4 replicates of each treatment. Experiments began in mid afternoon and ran for 19 hours overnight with survival assessed the following morning.

Mortality rates were corrected for larval cannibalism prior to analysis by subtracting the mean mortality value obtained in control tanks from mortality in each beetle tank for each instar. I tested the effect of beetle instar and caddisfly stage on untransformed mean caddisfly mortality using two-way ANOVA with time as a randomized block. Initial exploration of block interactions with both beetles and caddisflies revealed no significant interactions, so the final model was collapsed to include the block main effect alone. Scheffe's post-hoc comparisons were used to compare treatment means (after Day and Quinn 1989).

Non-consumptive effects of beetle predators on caddisflies

To investigate the degree of flexibility in the behavioural or developmental responses of *Asynarchus* larvae to *Dytiscus* larvae, I reared caddisfly larvae in large plastic wading pools (1.5 m²) with and without beetles. Tanks contained snowmelt water maintained to a level of 15cm, 3000cm³ of detritus collected from a beetle-free experimental mesocosm, and two large rocks added for pupation substrate. Forty 3rd instar caddis larvae were collected from an autumnal pond before beetles appeared and added to each mesocosm on 21 June 2006. The next day one 3rd instar beetle larva, inside a perforated floating container (two-way guppy breeder, Lee's Aquarium & Pet Products, CA; L x W x D: 14 x 8 x 8 cm) with a twig and several sedge leaves, was added randomly to half of the 14 tanks. Identical floating containers without beetles were added to the control treatments. Beetles were fed *Asynarchus* larvae added at a rate of 12 individuals every 2 days for the duration of the experiment. Tanks were checked every 2-3 days for pupae, and when found, were transferred to individual emergence chambers (Wissinger et al. 2004) that floated in a wading pool adjacent to the experimental array. Emerged adults were hand collected and frozen. Later their sex was determined, right wing length measured (nearest 0.05 mm) using an ocular micrometer, and thorax (with legs and head attached), abdomen and wing dry mass determined after drying at 60 °C for 24 hours by weighing on a Cahn C-31 microbalance to the nearest 0.001 mg.

Twice during the experiment (12 and 18 July 2006), 5 min focal animal observations of 5th instar larvae (excluding prepupae) were conducted mid-morning to assess foraging behaviour in the presence and absence of predator cues. I recorded time spent moving and the

number of encounters with conspecifics. Seven observers worked simultaneously in different tanks, alternating observations between treatments until two caddisfly larvae in each tank had been observed in total. Mean time spent moving and number of encounters in each tank were used in analyses. Mean time spent moving and mean number of encounters were analysed with randomized block ANOVA and Binomial GLMs, respectively. No observer bias or block by predator interaction was found, so, the final models included the block main effect only. Mean emergence date and adult size metrics (total mass, thorax mass and forewing length) were analysed by split-plot ANOVA and MANOVA, respectively, with beetle presence tested between tanks and caddisfly sex and beetle by sex interaction tested within tanks.

As *Asynarchus* larvae may be unable to detect non-mechanical predator cues, I conducted additional behavioural trials with unconstrained *Dytiscus* beetles in microcosms identical to those used in the size predation experiments. Ten 5th instar caddisfly larvae were introduced to each of the 12 microcosms 30 minutes prior to the introduction of one 3rd instar beetle to half of the tanks. Caddisflies were allowed to acclimatise for 30 minutes before trials began. Two observers worked in synchrony with one predator and one control tank, respectively. Focal animal sampling followed the same protocol as above but with 10 minute focal samples. One focal animal sample was taken from each tank during the observation period, yielding six independent replicates of each treatment.

Cannibalism and predation experiments with caddisflies

I knew that *Asynarchus* larvae engaged in cannibalism and intraguild predation (IGP) on *Limnephilus externus* (Wissinger et al. 1996), but the degree to which the proclivity for these interactions varied as a function of relative size was not known. I assessed size-specific cannibalism rates by manipulating instar combinations of *Asynarchus* in microcosms (30 x 16 cm plastic storage containers containing 2.5 cm of spring water with detritus placed on insect screen cut to fit the base of the chambers) housed in a portable field shelter at the Rocky Mountain Biological Laboratory. Ten prey individuals were added to each container, and allowed to acclimate for 30 min before 10 potential cannibals were introduced. Six replicates of the 10 pair-wise size combinations of 2nd – 5th instar larvae were randomly allocated to containers. As in the size-predation experiment, we collected animals from populations at different elevations to obtain all necessary size combinations for the experiment. In a second experiment, I manipulated instar combinations of *Asynarchus* and *Limnephilus* in microcosms to investigate size specific IGP rates throughout *Asynarchus* larval development.

Experimental venue and protocol were the same as in the cannibalism experiment. For both experiments, data were analysed using non-linear regression with treatment means as replicates.

Results

Comparative life histories in vernal and autumnal ponds

Asynarchus developed extremely rapidly and synchronously in vernal ponds, progressing from 2nd instar larvae to adults in less than 50 days during spring and early summer (Fig. 1). On average only 21 ± 2 % (pond mean \pm SE) of larvae were larger or smaller than the modal instar on each sampling occasion.

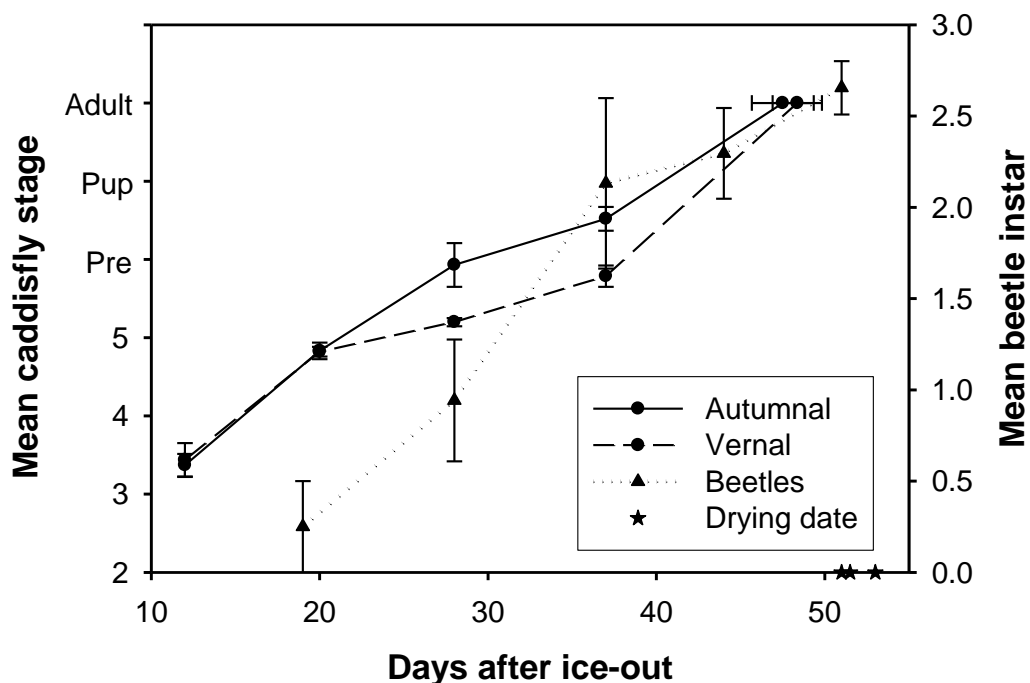


Fig. 1 The developmental phenology of *Asynarchus nigriculus* in vernal (dry early in spring) and autumnal (dry late in summer) ponds and *Dytiscus dauricus* larvae, which are only present in autumnal ponds at the Mexican Cut, West Elk Mountains, Colorado. The drying date of the vernal pools studied is shown on the x-axis. Ice-out occurred on 3 June 2006. Error bars represent one se with pond means as replicates. Horizontal errors are one se of mean adult emergence date. Prepupae were defined as 5th instar larvae that have begun to add stones to their cases in preparation for pupation.

Despite this rapid development, emergence in three of the four ponds was constrained by pond drying. Inspection of pupae remaining in ponds after drying revealed 21.0 ± 0.06 % (pond mean \pm SE) of individuals that reached the pupal stage perished from desiccation before emergence occurred. Although autumnal ponds dried two months later than vernal

pools, caddisfly larval development was actually faster in them than in vernal ponds (Fig. 1; Split-plot ANOVA: pond effect, $F_{1,8} = 26.93$, $P < 0.001$) with a divergence in growth over time (date x pond interaction, $F_{3,24} = 3.09$, $P = 0.046$) resulting in an earlier transition to prepupal and pupal stages in autumnal ponds (Fig 1). However, mean emergence date did not differ significantly between autumnal and vernal ponds ($t_9 = 0.225$, $P = 0.83$). *Dytiscus* larvae were observed only in the autumnal ponds, where their developmental phenology lagged behind that of caddisflies (Fig. 1). Much of the larval development of caddisflies in autumnal ponds occurred before beetles had reached the second larval instar. By this time, the caddisflies were adding stones to their cases in the pre-pupal phase, and had pupated and emerged before beetles developed into the 3rd and largest instar.

Size specific vulnerability of caddisflies to beetle predation

Predation by *Dytiscus* larvae on *Asynarchus* increased dramatically with predator size (Fig. 2, beetle effect, $F_{2,26} = 95.11$, $P < 0.001$), and varied with caddisfly stage (caddisfly effect, $F_{2,26} = 25.73$, $P < 0.001$; caddisfly x beetle interaction, $F_{4,26} = 12.69$, $P = 0.024$). Predation by 1st instar beetle larvae was negligible, but 2nd instar beetles attacked and killed many more 4th and 5th instar caddisfly larvae (Fig. 2). Caddisfly larvae of all sizes were vulnerable to 3rd instar beetles, although pre-pupae had significantly lower mortality rates than 4th and 5th instar larvae (Fig. 2).

Non-consumptive effects of beetle predators on caddisflies

Male *Asynarchus* emerged significantly earlier than females across all treatments (sex effect: $F_{1,12} = 16.60$, $P < 0.0001$, Fig. 3), and the presence of beetle larvae had no effect on time to emergence of either sex (beetle effect: $F_{1,12} = 0.045$, $P = 0.836$; beetle x sex: $F_{1,12} = 0.003$, $P = 0.95$; Fig. 3). Emerging males had longer wings and were significantly lower in total mass and thoracic mass than females (univariate ANOVAs on significant MANOVA: $P < 0.0001$; Appendix 1), However beetle presence had no effect on these size metrics for either sex (MANOVA: $P > 0.72$; Appendix 1).

During observation trials, the activity rates of late instar *Asynarchus* (Fig. 4a, randomized block ANOVA, beetle effect: $F = 0.033$, $P = 0.857$), and number of encounters between larvae (mean \pm se, beetle: 0.43 ± 0.14 , control: 0.14 ± 0.10 ; Binomial GLM, $P = 0.095$), did not differ significantly between treatments with and without caged beetles.

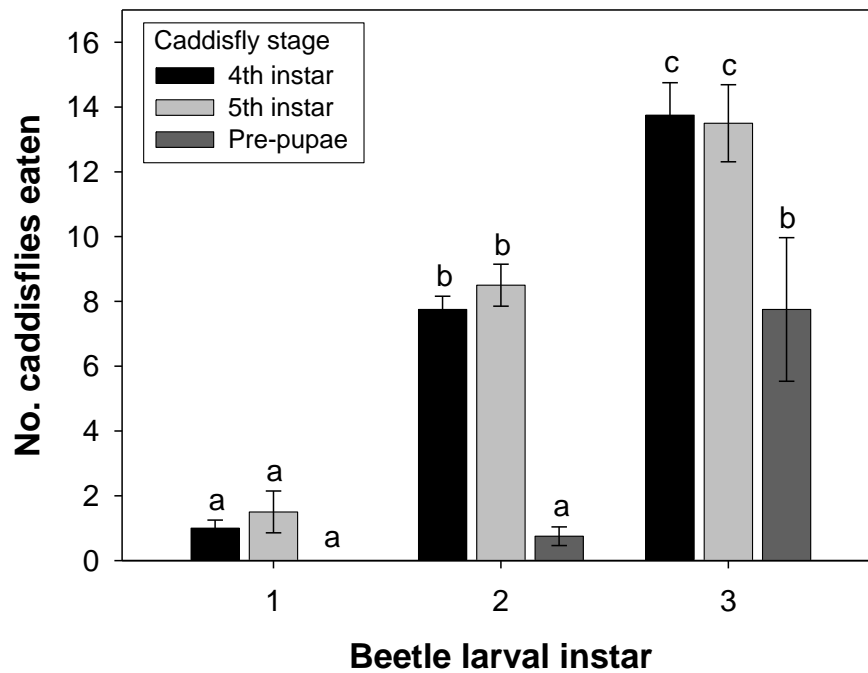


Fig. 2 Predation by three instars of *Dytiscus* on three developmental stages of *Asynarchus* in a 19 hour microcosm experiment. Lower case letters indicate significant differences ($P < 0.05$) indicated by Scheffe's post-hoc comparisons. Mean predation rates (\pm se) are adjusted for stage-specific cannibalism rates in *Dytiscus* free treatments (mean \pm se: 4th = 0.25 ± 0.25 ; 5th = 0, prepupae = 0.75 ± 0.25).

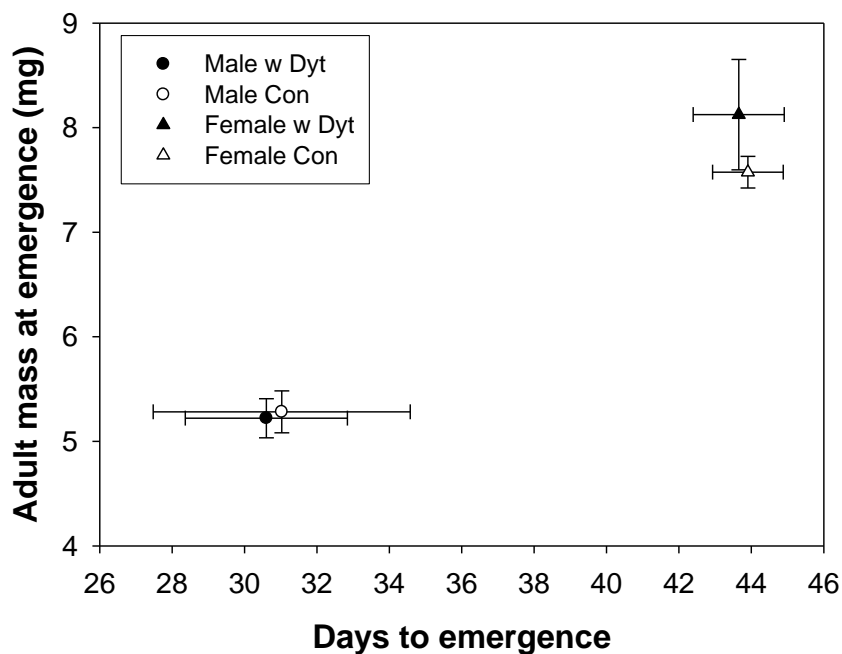


Fig. 3 Mean adult body mass and mean time of emergence for male and female *Asynarchus* reared in mesocosms with and without non-consumptive *Dytiscus* predation cues. Error bars are ± 1 se. Days until emergence were calculated from the beginning of the experiment when early 3rd instar larvae were added to the tanks.

This could not be explained by the inability of caddisfly larvae to detect beetles through chemical cues alone, as there was no difference in caddisfly activity level (Fig. 4b, $t_5 = 0.317$, $P = 0.757$), or the number of encounters between individuals (mean \pm se, beetle: 1.5 ± 0.43 , control: 1.0 ± 0.37 ; $\chi^2 = 0.60$, $P = 0.439$) when exposed to the suite of potential cues from unconstrained beetle larvae. Moreover in the trials with unconstrained beetles, caddisflies were regularly observed to collide with feeding beetles or even crawl between the open mandibles of the predators. In summary, I found no evidence for plasticity in caddisfly development or behaviour in response to the presence of beetles.

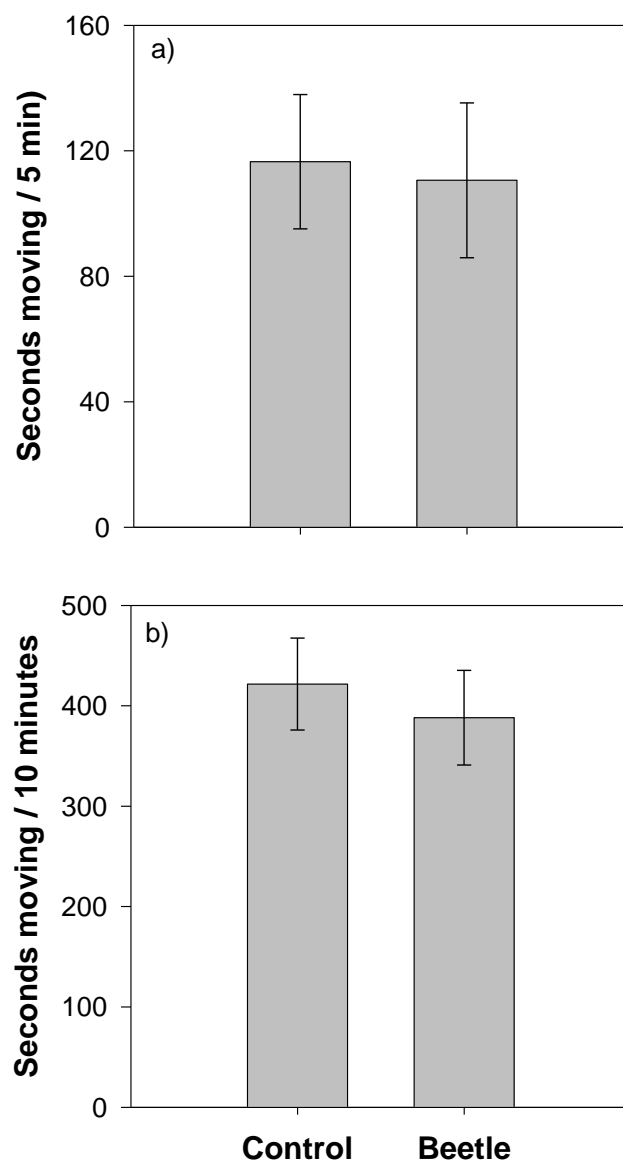


Fig. 4 Mean (\pm se) activity rate of *Asynarchus* 5th instar larvae exposed to (a) non-consumptive predator cues from caged *Dytiscus* in mesocosms (activity rate = seconds of movement per 5 minute focal animal study) and (b), predator cues from uncaged, unmanipulated *Dytiscus* (activity rate = seconds of movement per 10 minute focal animal study) in microcosms.

Size-specific cannibalism and intraguild predation among caddisflies

Both cannibalism and intraguild predation increased with the increasing size disparity between predators and prey (Fig. 5). Cannibalism rates of 15% occurred between individuals of the same size due to ‘mob’ cannibalism (Wissinger et al. 2004), and increased dramatically to a peak of 100% mortality of 2nd instar larvae when exposed to 5th instar cannibals (Fig. 5a). Observations made during the trials revealed that one-on-one cannibalism (as opposed to mob cannibalism among same-sized larvae) became increasingly common with the proportional size difference among *Asynarchus* instars.

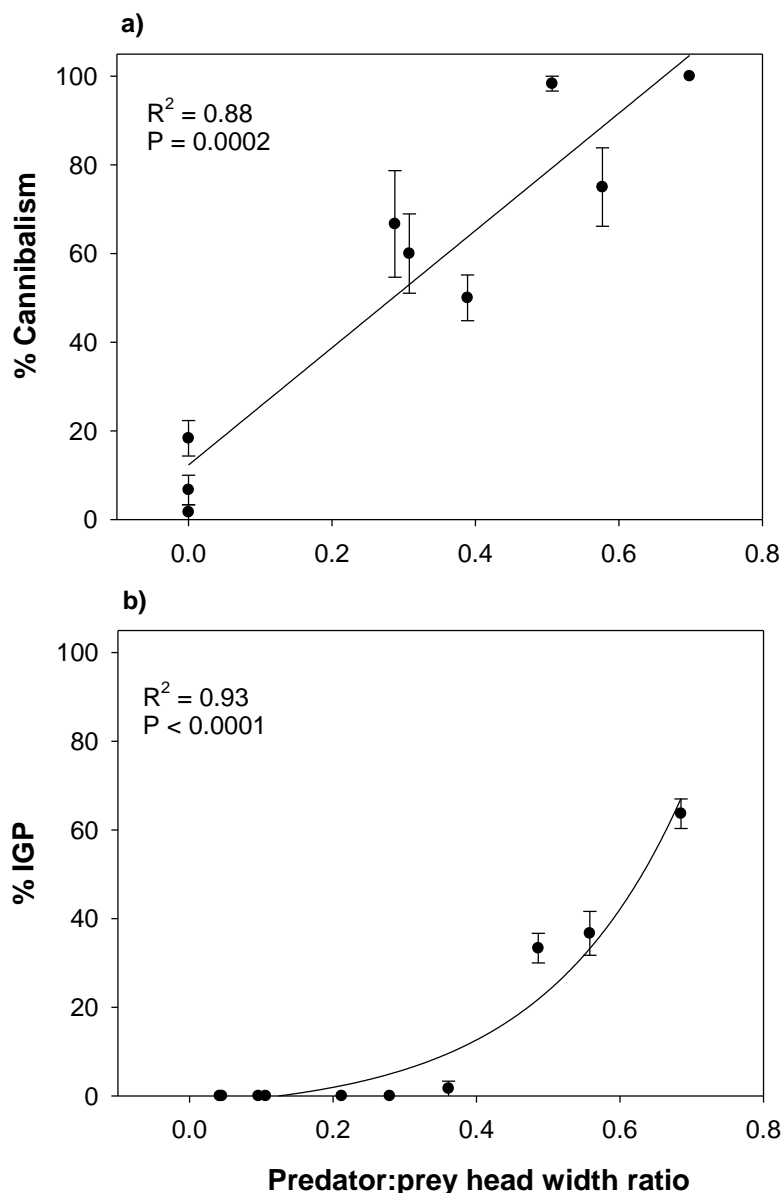


Fig. 5 Size-specific *Asynarchus* cannibalism (a) and intraguild predation on *Limnephilus externus* (b) in microcosm experiments. Error bars are ± 1 se, $n = 6$, R^2 and P -values from linear and non-linear regressions, respectively. Regression equations are: (a), $y = 12.31 * 132x$; (b), $y = 1.02 * 451^x$.

Intraguild predation of *Asynarchus* on *Limnephilus* was negligible when the proportional sizes of potential prey and predators were less than 0.5 (Fig. 5b). The size differences on the lower asymptote of Fig 5b corresponded to combinations of larvae that were the same instar, or differed by one instar (5th on 4th, 4th on 3rd, 3rd on 2nd instars). Above that lower threshold, IGP increased significantly with proportional difference in size (Fig. 5b). IGP was highest for 5th instar *Asynarchus* preying on 2nd instar *Limnephilus*, and intermediate when *Asynarchus* were 2 instars larger (5th on 3rd and 4th on 2nd) than *Limnephilus* (Fig. 5b).

Discussion

Phenotypic plasticity is often invoked as a mechanism facilitating the broad distribution of a species across contrasting habitats, especially those that differ in predation risk (Lima and Dill 1990, Lima 1998, Tollrian and Harvell 1999). However some species with fixed traits persist across contrasting habitats and the mechanisms facilitating these broad distributions are poorly understood (McPeck 1996, McCauley 2007). My results indicated parallel time constraints driven by both abiotic stress (drying) and biotic interactions (predation) across different habitat types facilitate the broad distribution of a species with rapid, fixed development, *Asynarchus nigrificulus*. Below I discuss the rationale for this explanation and address how convergent abiotic and biotic time constraints enhance the understanding of the persistence of habitat generalists across environmental gradients.

Reinforcing biotic and abiotic developmental time constraints

Within freshwater taxa, there are often species replacements across permanence gradients that reflect trade-offs between traits that lead to rapid development in temporary habitats, and traits that reduce vulnerability to predators in permanent habitats (Wellborn et al. 1996, Relyea and Werner 1999, Johansson and Suhling 2004). The caddisfly, *Asynarchus nigrificulus*, exhibits traits expected for a temporary pond specialist; i.e., rapid development is facilitated by a suite of “fast-life style” traits including high activity and foraging rates, protein supplementation through cannibalism and intraguild predation, and minimal investment in case building (Wissinger et al. 2004, Wissinger et al. 2006b). Not surprisingly, these traits increase vulnerability to predatory salamanders that typically eliminate them from permanent habitats (Wissinger et al. 1999c, Wissinger et al. 2006b). However this caddisfly species is also abundant in autumnal ponds that contain large-bodied predatory invertebrates, which are voracious predators of *Asynarchus*.

Selection pressures for this fast life style appeared to be ongoing; i.e., I observed that despite the rapidity with which *A. nigriculus* completes development in vernal habitats, slow-growing individuals perish when these habitats dry. My observations also revealed that larval development was as fast or faster in autumnal ponds than in vernal pools (Fig. 1). This is counterintuitive, because in the absence of drying time constraints, individuals were expected to extend larval development so as to accumulate more resources, thereby increasing adult body size, fecundity, and other fitness correlates (as in Nylin and Gotthard 1998, Johansson et al. 2001, Peckarsky et al. 2001). Field experiments with the dominant predator on *Asynarchus* in autumnal habitats, *Dytiscus* beetle larvae, indicate that caddisfly development was under biotic time constraints, even in the absence of drying time constraints. By comparing the phenologies of beetles and caddisflies in the ponds to the results of size- and stage-specific rates of predation in microcosm experiments, I was able to determine that even a short time lag (two to seven days) in caddisfly development relative to that of the beetles, would result in a substantial increase in larval mortality in autumnal ponds (Fig. 2). Most of the caddisflies in autumnal ponds emerge just before the beetles reach the size at which they become effective predators, and almost all of the caddisflies that have not emerged by that time pupate in stone cases that reduce beetle predation (Wissinger et al. 2006b).

A second biotic advantage of rapid development for *Asynarchus* in autumnal habitats is that it maintains a developmental size advantage over a potential detritivorous competitor and intraguild prey species, *Limnephilus externus*. Early hatching and rapid development of *Asynarchus* creates a phenological head start on *Limnephilus* of at least two instars that persists throughout larval development (Wissinger et al. 2003). My data show that this two-instar developmental size advantage is enough to facilitate intraguild predation (IGP). I found a sharp decline in IGP for slowly developing *Asynarchus* that had only a one-instar size advantage or were the same instar as *Limnephilus*. This type of developmental priority effect for facilitating asymmetrical interference competition and IGP is similar to that in guilds of competing predators (Wissinger 1989, Padeffke and Suhling 2003, Segev and Blaustein 2007).

A third potential selection pressure on *Asynarchus* development, even in the absence of drying time constraints, is associated with cannibalism. Cannibalism occurs at relatively low rates among same-sized *Asynarchus* via mob attacks on a vulnerable individual (e.g., those with damaged cases; Wissinger et al. 2006b). My experiments reveal that vulnerability to cannibalism increased dramatically with size disparities among conspecifics, as a result of both mob and one-on-one attacks. A two-instar difference in size resulted in an almost 10

fold increase in cannibalism compared to that among same-sized larvae. A threshold for cannibalism based on relative size has been observed in many species (Polis 1981) including other aquatic insects (Wissinger 1992). Moreover, when such size-thresholds occur within cohorts, according to theory cannibalism should select for rapid and synchronous development (Crowley and Hopper 1994).

In summary, the costs of slow development of *Asynarchus* in autumnal habitats are threefold: increased vulnerability to beetle predation, the loss of potential IGP on *Limnephilus*, and increased vulnerability to cannibalism by faster developing conspecifics. It is likely that these effects are interactive with positive feedback. That is, slow development should reduce the opportunity for IGP, which in turn should reduce growth rate and development, making larvae more vulnerable to beetle predation and/or cannibalism. My results suggest that even slight shifts in relative phenologies among *Asynarchus*, *Limnephilus*, and dytiscid beetles could have a dramatic impact on larval survival and adult fecundity of *Asynarchus*, and potentially their exploitation of autumnal habitats.

Most theoretical and empirical studies of time constraints have focused on the physical constraints of seasonality on development, such as habitat drying (Leips et al. 2000, Rudolf and Rodel 2007), onset of winter (Johansson and Rowe 1999, Johansson et al. 2001), timing of floods (Lytle 2001, 2002), and physiological temperature windows for emergence (Wohlfahrt et al. 2007). In the autumnal habitats at my study sites, those constraints are weaker, but selection for rapid development is replaced by biotic developmental constraints. The type of biotic time constraints that I have observed for this caddisfly are similar to those imposed by fish on copepods (*Diaptomus sanguineus*), which diapause before fish become active when water warms in spring (Hairston 1987). In both cases, it is the relative phenology of prey-predator development and activity that creates a time-specific change in life history events. In other situations, accelerated prey development reduces the cumulative costs of ongoing predation that occurs throughout an organism's life history (e.g., Laurila et al. 1998, Lardner 2000). These 'cumulative biotic time constraints' differ from the time-specific constraints in Hairston's and my study, which are driven by the seasonal onset of the threat of predation and/or availability of prey, and are therefore analogous to selection imposed by seasonal abiotic time constraints.

Reinforcing time constraints and the distribution of species with fixed traits

One of the implications of reinforcing biotic and drying time constraints in autumnal and vernal habitats, respectively, is that it appears to have led to the evolution of fast-life style

traits that are not flexible to predation risk. I observed no evidence for plasticity in the antipredator responses or high activity and foraging rates of *Asynarchus* in response to the presence / absence of predatory beetle larvae. Furthermore, despite high rates of predation by the beetles, there was no difference in development rate or size at emergence between caddisflies reared with and without beetle cues (Fig. 4), and caddisflies have been found to develop and emerge at the same rates in autumnal ponds without beetles and in ponds with beetles (Greig and Wissinger unpublished data). My results are consistent with previous work has shown that *Asynarchus* does not modify its behaviour, morphology, or activity levels in response to the presence of predatory salamanders (Wissinger et al. 1999c).

The selection pressures for rapid development in both vernal and autumnal habitats are likely to be predictable between years. Over the past 20 years, the sequence of drying among ponds and the lengths of the wet phase during summer have been remarkably constant (Wissinger et al. 1999b). Similarly, although there are fluctuations in densities, beetle predators are present in the same ponds each year, and the phenologies of beetles and *Limnephilus* are also predictable (Wissinger et al. 2003). Given both the predictability and reinforcing selection pressures across habitats, it is perhaps not surprising that fixed developmental strategies have evolved in the context of vernal and autumnal ponds. This is consistent with both theoretical and empirical results that suggest that predictability should lead to simple adaptive responses (Hairston 1987) and fixed traits (e.g., Alpert and Simms 2002).

Adaptations that underlie extant patterns of distribution and coexistence are likely to have occurred in both the context of current and historical ecological conditions and phylogenetic histories and constraints (Richardson 2001, Webb et al. 2002). Thus, the development of plastic antipredator traits may be constrained by either phylogenetic inertia from past selection in predator-free habitats for example, or genetic founder effects in isolated populations that impair the ability of species to adapt to novel, contemporary selection pressures (Van Tienderen 1991, Sih et al. 2000, Caudill and Peckarsky 2003). Several arguments suggest these mechanisms are unlikely to apply to our system: First, I have no reason to suspect that any of the taxa involved (caddisflies, beetles, salamanders) have recently invaded these habitats, making phylogenetic inertia unlikely. Second, co-occurrence patterns at the study site are representative of those observed across dozens of other study sites in the region (distance between sites > 10 km); thus the patterns I observed are unlikely a result of unique founder genotypes. Finally at a broader scale, developmental and behavioural phenotypic plasticity in response to both predators and drying has been

observed in other limnephilid species (e.g., Otto and Svensson 1980, Nislow and Molles 1993) suggesting that phylogenetic constraints on these traits are not characteristic of this group of taxa on the whole.

Conclusions and implications

Many studies have documented the behavioural, developmental, physiological, and morphological phenotypic plasticity that prey exhibit in predator-free and predator-present habitats (Sih 1987, Lima and Dill 1990, Lima 1998, Tollrian and Harvell 1999). Such flexibility allows species to have broader distributions across environmental gradients with contrasting selection pressures. The absence of plasticity in *Asynarchus* caddisflies has been somewhat puzzling, as they are found in two contrasting habitats (vernal and autumnal ponds) with contrasting selection pressures. My results indicate that reinforcing time constraints across habitat types enable a species with fixed traits to succeed in habitats that differ in their relative abiotic and biotic stressors. Traits that enable the exploitation of habitats under strong drying-time constraints also enable successful development in longer duration habitats. This occurs by these traits allowing emergence before time constraints imposed by seasonal shifts in predation (Hairston 1987) and by creating resources through phenological priority over intraguild prey (Suhling et al. 2005). It is not clear whether the fast-life style traits exhibited by *Asynarchus* are pre-adaptations or exaptations (sensu Gould and Vrba 1982) for any one of the four multiple benefits (escape from drying, escape from beetle predation, reduced cannibalism, increased intraguild predation) in different types of temporary habitats. Regardless, my data strongly suggest that together they facilitate the exploitation of both vernal and autumnal habitats. In that sense, fast life style traits are clearly adaptations. In this case, convergent abiotic and biotic time constraints create niche space for *Asynarchus* in both vernal and autumnal habitats (McPeck 1996). It is only in permanent ponds where predators (salamanders) are present year-round that these traits exact a high cost in terms of survival. Although fixed traits allow exploitation of adjacent habitats along environmental gradients where parallel selection pressures create convergent niche space, they are likely to result in species replacements (Wellborn et al. 1996) at opposite ends of environmental gradients.

Appendices

Appendix 1 Split-plot MANOVA and univariate ANOVAs testing the effect of non-consumptive *Dytiscus* beetle presence and caddisfly sex on three measures of the body size at emergence of *Asynarchus* caddisflies at emergence reared from 3rd instar larvae in mesocosms. The beetle effect was tested between pools, where the sex effect and beetle x sex interaction were tested within pools.

a) Multivariate test					
Source of variation	Numerator <i>df</i>	Denominator <i>df</i>	Pillai Trace	<i>F</i>	<i>P</i>
Beetle	3	10	0.081	0.29	0.830
Sex	3	10	0.962	84.83	<0.0001
Beetle x Sex	3	10	0.120	0.45	0.721
b) Univariate tests					
	Mean (se)				
	Total mass (mg)	Thorax mass (mg)	Wing length (mm)		
Male	5.20 (0.13)	2.62 (0.06)	12.5 (0.12)		
Female	7.89 (0.27)	3.16 (0.09)	10.9 (0.14)		
<i>P</i> -value	<0.0001	<0.0001	<0.0001		

Chapter Six

General discussion: towards a new model of pond community assembly

The relevance of the predator-permanence model to Canterbury high country pond communities

The predator-permanence model of pond communities (Wellborn et al. 1996) is similar to many other classical models predicting community assembly across gradients of environmental disturbance, in hypothesizing a shift from abiotic to biotic control of community structure as habitats become more physically benign (Connell and Slatyer 1977, Grime 1977, Peckarsky 1983, Menge and Sutherland 1987). However my results indicated the predator-permanence model did not predict community assembly in Canterbury high country ponds. Pond communities at my sites were dominated by generalist taxa, with the vast majority of species in even the shortest duration temporary ponds (< 65 days) being a nested subset of the species present in permanent ponds, rather than a unique set of temporary pond specialists (Chapter Two). These nested communities indicated the dominant influence on the diversity and composition of pond communities was the physical gradient of pond drying (Chapter Three). The distribution of species among ponds provided little evidence for the extirpation of temporary pond species in permanent ponds by predators, as predicted by the predator-permanence model. The nested distribution of generalist taxa across pond permanence gradients are likely to be produced by factors that constrain the evolution of specialist temporary pond taxa and factors such as weak predation that enable the persistence of habitat generalists in permanent ponds.

Much of the evidence for species replacements that underlie the predator-permanence model is from temperate continental Northern Hemisphere with predictable runoff through snowmelt or seasonal rainfall events (Wissinger 1999). In these systems, temporary pond specialists have developed life history strategies such as egg or ovarian diapause that are highly dependent on specific seasonal cues correlated with pond filling (Wiggins et al. 1980, Tauber and Tauber 1986, Corbet 1999, Wissinger 1999, Wissinger et al. 2003, Stoks and

McPeck 2006). The unpredictable drying regimes in New Zealand may preclude the evolution of these highly synchronized life history traits (Wissinger et al. *in press*). There is a well documented link between aseasonal precipitation regimes and unpredictable hydrology of lotic systems in New Zealand, especially on the South Island (Clausen and Biggs 1997, 2000). This unpredictability of flow disturbance has been identified as a key driver of the prevalence of generalist traits among New Zealand stream invertebrates (Winterbourn et al. 1981, Winterbourn 1997, Thompson and Townsend 2000). Moreover, theoretical models of life history also suggest the variable selection pressures that are likely to occur with unpredictable disturbance regimes should select for generalist traits (Lytle 2001, Satake et al. 2001, Lytle and Poff 2004), and these have received recent empirical support (Friedenberg 2003, Lytle et al. 2008, Shine and Brown 2008). Thus the same factors that seem to have driven life history evolution in New Zealand stream fauna may also be important in New Zealand ponds.

My data indicate unpredictable precipitation regimes at my study sites translate to unpredictable pond hydrology. I observed considerable inter- and intra-annual variation in the timing and duration of pond inundation over three years (Chapter Two). Furthermore, the pond filling events appeared closely linked to high rainfall events, which occurred at any time of the year and often multiple times within a season (Chapter Two). It is likely that these unpredictable hydrological regimes selected for generalist life history strategies, and precluded the evolution of life histories that are highly synchronized to the drying and filling regimes evident in many temporary pond specialists. Furthermore, the presence of numerous permanent ponds in the Canterbury landscape provide consistent refuges for species with generalist traits during dry years.

In addition to *in situ* evolution and diversification (e.g., McPeck and Brown 2000), the distribution of species and their traits within a regional species pool is likely to be influenced historical colonists that were successful in filling vacant niches within the region, but evolved elsewhere (Cornell and Lawton 1992, Ricklefs and Schluter 1993, Brown 1995). Thus, the traits present within a regional species pool are influenced by factors other than *in situ* adaptation and radiation. Nevertheless, the properties of a region that influence the evolution of traits within a system are also likely to act as a filter of the traits of potential colonists from elsewhere. Unpredictable pond drying and filling should favour the successful colonization of species with generalist life history traits over those with specialized life history traits, and thereby further contribute to the dominance of generalist traits within the regional species pool. These hypotheses suggest that considering the influence of the

predictability of hydrological regimes on species life history traits should increase the understanding of the dynamics of contemporary aquatic communities.

My results also provide strong support for the hypothesis that weak predator-prey interactions in permanent ponds enable the broad distribution of species with generalist traits. Although the size, diversity, biomass and density of predators increased with increasing pond permanence (Chapter Two), predator impact actually decreased (Chapter Three). Fish had no measurable effect on macroinvertebrate community biomass in the *in situ* cage experiment (Chapter Three) and in mesocosms (Chapter Two and Three), and species dominating the biomass of temporary ponds were also not more vulnerable to fish predation than those abundant in permanent ponds (Chapter Two). Additionally, the impact of predatory invertebrates on prey communities decreased with pond permanence (Chapter Three) partly due to the non-consumptive effect of predatory fish that reduced the foraging rates of predatory invertebrates (Chapter Three). Thus, the net result of the consumptive and non-consumptive effects of fish presence may actually be to reduce predation on benthic prey communities. Finally, I observed a considerable increase in the strength of predator-prey interactions in temporary pond with time after refilling that led to a divergence in predator impact between permanent and temporary ponds (Chapter Four).

In summary, both key factors structuring pond communities at the local scale, biotic interactions and pond permanence, appear to be fundamentally different in ponds in the Canterbury high country than in the Northern Hemisphere temperate regions for which the predator-permanence was developed (Wellborn et al. 1996). Although I have outlined two main hypotheses for the prevalence of generalists in Canterbury pond food webs, other factors may have had an influence. For example phylogenetic constraints within the New Zealand fauna may reduce the ability of specialist traits to evolve. Addressing these alternative hypotheses will need to involve replication beyond the scale of New Zealand and is beyond the scope of this thesis.

Species replacements or habitat generalists: a case for a new model?

The predator-permanence model did not predict the assembly of pond benthic communities or the strength of food web interactions in my study sites. Similarly, some recent studies have also detected nested distributions of taxa across pond permanence gradients, that are indicative of a significant proportion of habitat generalists in the regional species pool (e.g., Baber et al. 2004, Van Buskirk 2005, Werner et al. 2007). Although some species replacements were observed between habitats with and without fish (Van Buskirk 2005,

Werner et al. 2007) these studies observed weak effects of biotic interactions on the distribution of taxa among fishless ponds that differed in permanence, and the authors suggested that abiotic factors should exert primary influence on community structure in the absence of fish predation. However, in many other systems, species replacements do occur as a result of interactions between pond drying and predation by large invertebrate species or salamanders (Wellborn et al. 1996, Skelly 1997, Wissinger 1999, Wissinger et al. 1999a, Stoks and McPeck 2003b, Urban 2004, Wissinger et al. 2006b). These studies indicate that although species replacements may be observed more consistently in systems that contain permanent ponds with intense fish predation (e.g., when Percid and Centrarchid fish species are present), they are not restricted to these situations. Considering the effect of food web complexity and species identity on the strength of predator-prey interactions should contribute to the prediction of these differences community assembly patterns.

Spatial processes may also affect the broad distribution of species across the pond permanence gradient, if, for example, the density of dispersing individuals compensates for mortality from predation (i.e., mass-effect metacommunity dynamics; Leibold et al. 2004). For example, in my study sites, *Rhantus* dytiscid beetles appear particularly vulnerable to fish predation (Chapter Two), and their continued persistence in habitats containing fish may be a result of frequent dispersal from temporary ponds (Kholin and Nilsson 1998, Lundkvist et al. 2002, Jeffries 2003). These contingencies suggest a more integrative model of community assembly across pond permanence gradients is needed.

I suggest that pond community assembly be viewed as a continuum of the relative influence of drying disturbance and predator-prey interactions on local community assembly. The predator-permanence model could be considered to fall at one end of this continuum, as it suggests interplay between biotic and abiotic factors result in the dominance of species replacements in community assembly. In contrast, my results indicate the dynamics of benthic communities in ponds in Canterbury, New Zealand, lay towards the opposing end of this continuum, with nested communities a result of a single axis of abiotic stress. Assuming that single axes of abiotic stress produce nested communities, and interacting biotic and abiotic factors produce communities dominated by species replacements, assessing the *relative* nestedness of communities is likely to be a profitable tool in assessing the influence of biotic versus abiotic factors in determining pond community structure (e.g., Urban 2004).

Understanding the variation in the relative importance of these biotic and abiotic influences on pond community assembly in different regions is likely to require the incorporation of three scales of investigation. 1) The influence of broad-scale biogeographic

processes (e.g., factors influencing pond drying and filling regimes, or phylogenetic constraints) on the nature of species traits and the composition of predators in a regional species pool; 2) regional processes, such as pond isolation and the relative abundance of permanent and temporary ponds, that influence the rates of dispersal between local habitats and the presence of seasonal refugia for generalist taxa; 3) local-scale habitat morphology and biological context that influence the outcomes of species interactions within habitats. Separating the relative importance of these three scales will be a challenge as replication will need to be at the broadest scale. This can only be achieved by investigation across different biogeographic regions.

Interplay between biotic and abiotic forces and the implication for community dynamics

Environmental gradients are pervasive aspects of ecological communities. They can be formed by variation in the constraints imposed by constant abiotic stressors on species traits, for example elevation or salinity gradients in plant communities (Huckle et al. 2000, Callaway et al. 2002, Crain et al. 2004). Alternatively, environmental gradients may be produced by variation in the intensity or frequency of disturbance events that disrupt communities, for example pond drying events (Schneider and Frost 1996, Urban 2004) or flood disturbance in streams (Death and Winterbourn 1995). Lastly, they can be a mixture of constant abiotic stress and discrete disturbance events, for example wave disturbance interacting with tidal zonation (Sousa 1979, Menge and Sutherland 1987). Regardless of the underlying mechanism, abiotic stress along environmental gradients is likely to influence the strength of biotic interactions. Ecologists have considered this interplay between the relative influence of abiotic and biotic factors in determining local community assembly along environmental gradients, but empirical evidence is largely limited to communities dominated by sessile taxa (e.g., the marine intertidal zone). Furthermore, the understanding of factors that influence the relative importance of abiotic and biotic interactions is still poorly developed. The predator-permanence model is one example of a suite of models of environmental gradients that predict increases in the strength of biotic interactions with decreased abiotic stress or disturbance (Grime 1977, Connell 1978, Peckarsky 1983, Menge and Sutherland 1987, Wellborn et al. 1996). In contrast to these models, I observed that the strength of biotic interactions was actually greater in disturbed habitats.

In my study, non-consumptive effects within the complex food webs of stable habitats, the presence of vulnerable prey species in disturbed habitats (Chapter Three), and contracting habitat area in disturbed habitats (Chapter Four) all contributed to the unexpected

inverse relationship between interaction strength and disturbance. This indicates the importance of considering both the biotic and abiotic context of species interactions to fully understand the community-wide patterns of biotic interactions (Agrawal et al. 2007). Moreover, few studies have incorporated food web complexity (including non-consumptive species interactions) into assessment of community-wide predator-prey interaction along disturbance gradients, despite the well developed ecological literature on this topic (e.g., Polis and Strong 1996, Lima 1998, Werner and Peacor 2003, Duffy et al. 2007, Schmitz 2007). Changes in food web complexity are likely to occur along many environmental gradients, as variation in disturbance or other abiotic stress often has a strong influence on species diversity (Connell 1978, Sousa 1984, Pickett and White 1985). My results indicate that incorporating food web complexity, especially non-consumptive predator-prey interactions, into experiments investigating species interactions across environmental gradients should greatly enhance the ecological relevance of experimental outcomes. In addition, my results also indicate how integrating ecological sub-disciplines (Agrawal et al. 2007) can lead to a more complete understanding of community dynamics.

In Chapter Four, I showed that predator-prey interaction strength increased with time, but only in disturbed habitats. This suggests that within a habitat, the relative influence of abiotic and biotic factors are also likely to shift seasonally. Furthermore, biotic interactions often form an important component of trade-offs along many environmental gradients. Consequently, different patterns of seasonal variation in biotic interactions between habitats types in a landscape (e.g., between permanent and temporary ponds as seen in Chapter Four) are likely to result in seasonal changes in the spatial arrangement of suitable and unsuitable habitats for a given species. For example, a species vulnerable to predation can exist in temporary ponds soon after refilling, but may be forced to either enter a diapause stage (Hairston 1987) or disperse to an alternative habitat (Wissinger 1997) when biotic interactions intensify later in the season (Chapter Five). Therefore temporal variation in biotic interactions may lead to species replacements (turnover) within and between habitats over time. My results suggest incorporating temporal variation in trade-offs among landscape is essential to understanding the metacommunity dynamics of systems with periodic disturbances.

The potential influence of the predictability of disturbance on the development of species traits (Chapter Two) suggests that interactions between biogeography, evolution and historical colonization are likely to influence the species traits in a regional species pool, and consequently the structure of metacommunities (Cornell and Lawton 1992, Brown 1995,

Shurin et al. 2000, Amarasekara 2003, Leibold et al. 2004). Although there is a developing interest in the causes and consequences of evolution within metacommunities at a local scale (Bruun and Ejrnaes 2006, Urban and Skelly 2006, Loeuille and Leibold 2008, Venail et al. 2008), the effect of biogeographic variation that influenced the historical development of species traits on the dynamics of contemporary metacommunities is yet to be investigated. These insights, gained from observations that the pattern of pond community assembly across the drying disturbance gradient in Canterbury was different to those elsewhere (Chapter Two), highlights the value of testing hypotheses across broad biogeographic regions. The insights gained from investigating mechanisms responsible for biogeographic variation in the dynamics of similar ecosystem types, are likely to be particularly profitable for developing more integrative and predictive ecological models.

One of the major outcomes of human impacts on natural systems, especially climate change, is an alteration of natural disturbance regimes across a wide range of habitats. The results of my thesis indicate that in order to predict and manage the effects of these altered disturbance regimes (e.g., Smol and Douglas 2007), ecologists will need to consider contemporary factors, such as the abiotic and biotic context of species interactions, and historical factors that have influenced the distribution of traits within regional species pools. For example, regions with historically predictable disturbance regimes are likely to be the most vulnerable to changes in those regimes, as species are likely to have evolved specialist life histories that are strongly synchronized to seasonal cues associated with disturbances. This developmental specialization suggests anthropogenic influences on the disturbance regimes of these systems (e.g., altered precipitation regimes due to climate change) may lead to catastrophic impacts on populations or communities. Thus assessing the influence of biogeographic processes on the traits of species pools is likely to also inform regional conservation priorities.

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