

Absence of species replacements between permanent and temporary lentic communities in New Zealand

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Abstract. The species composition of lentic communities often shifts along hydroperiod gradients, in part because temporary-habitat specialists replace closely related permanent-habitat specialists. These replacements reflect tradeoffs between traits that facilitate coexistence with permanent-habitat predators and those that prevent desiccation. The evidence for species replacements and the underlying tradeoffs is considerable in North America, but few studies have explored this pattern in other regions. We compared benthic communities in permanent and temporary habitats on the South Island of New Zealand. Ordination across 58 sites showed that community composition was distinctly different between the 2 types of habitats. Assemblages in permanent habitats had $>2\times$ the number of species as those in temporary habitats. We found little evidence for temporary-habitat specialists; i.e., species in temporary communities were a nested subset of those in permanent communities. Quantitative sampling at 12 intensively studied sites revealed that chironomids, water bugs, beetles, and crustaceans accounted for 90% of the biomass in temporary, but only 14% of the biomass in permanent habitats, which were dominated by mollusks, annelids, caddisflies, and odonates. Damselflies, dragonflies, caddisflies, and several other large-bodied taxa common in permanent habitats were absent from most temporary habitats. We propose 2 explanations for the absence of species replacements in these groups in the New Zealand habitats that we studied. First, drying is unpredictable within and between years, perhaps precluding the evolution of temporary-habitat specialization. Second, fish predation on benthic invertebrates, a driver for phylogenetic diversification in North America, appears to be comparatively weak in New Zealand. Comparative studies across a range of climates and faunas will be needed to identify the ecological and phylogenetic contexts that favor evolution of generalists vs specialists along permanence gradients.

Key words: lakes, wetlands, invertebrates, permanence gradient, habitat specialists, drying, nestedness.

The species composition of standing-water communities often differs between permanent and temporary habitats (Batzer and Wissinger 1996, Wellborn et al. 1996). In part, this difference reflects the loss of species that cannot complete their life cycle in habitats that dry; thus, richness often declines toward increasingly ephemeral habitats (Schneider and Frost 1996, Williams 1996, 2006, Wissinger et al. 1999a, Whiles and Goldowitz 2005, Werner et al. 2007a). Community composition also changes along this gradient because temporary-habitat specialists replace closely related

permanent-habitat specialists. Literature reviews across a wide variety of habitat types provide comparative evidence for such replacements for nearly all groups of lentic taxa (Batzer and Wissinger 1996, Wellborn et al. 1996, Williams 1996). Experimental studies with hylid and ranid frogs and several groups of aquatic invertebrates (damselflies, dragonflies, caddisflies, amphipods) have revealed 2 general mechanisms that underlie these replacements. For some taxa, there is a tradeoff between the behavioral, morphological, or physiological traits that facilitate completing their life cycles in drying habitats (e.g., high activity and foraging rates) vs traits that reduce vulnerability to permanent-habitat predators (low activity rates, investment in antipredator morpho-

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gies) (e.g., Skelly 1995, Werner and Anholt 1996, Relyea and Werner 1999, Wissinger et al. 1999b, Johansson and Suhling 2004, Urban 2004). For other taxa, the tradeoffs are between traits that facilitate coexistence with the different competitors or top predators in permanent and temporary communities (e.g., McPeck 1990, McPeck et al. 1996, Werner and McPeck 1994, Wellborn 2002, Stoks and McPeck 2003, Wissinger et al. 2006b). Regardless of the underlying mechanism(s) for a particular group, replacements of genera within a family, or species within a genus, across a range of aquatic taxa lead to changes in community composition (Wellborn et al. 1996, Skelly 1997, Urban 2004). Despite evidence that species replacements underlie shifts in lentic community structure in North America (references above) and Europe (e.g., Richter-Boix et al. 2007), the generality of this pattern has rarely been tested beyond north-temperate climates and faunas (but see Suhling et al. 2005).

The purpose of our study was to compare the benthic invertebrate communities of permanent and temporary lentic habitats in New Zealand. Most research on lentic benthic communities in New Zealand has been conducted in large lakes and has focused on within-lake patterns of distribution among subhabitats and vegetation zones (reviewed by Kelly and McDowall 2004, Kelly and Hawes 2005). Few studies have characterized the invertebrate communities in wetlands, kettles, shallow tarns, and other temporary habitats that are common in landscapes dominated by glacial geomorphology (Stout 1964, Burns et al. 1984, Sorrell and Gerbeaux 2004). Our study provides a quantitative comparison of invertebrate communities in permanent and temporary lentic habitats in New Zealand to evaluate the generality of the community structure patterns reported for North America. We predicted that the combined effects of differences in the abiotic environment (permanent–temporary) and predator impacts (fish–no fish) between our study sites should lead to corresponding shifts in community composition that reflect species replacements within major taxonomic groups.

Methods

Qualitative taxonomic survey

In the 1st part of our study, we compared the species composition of benthic communities in the nearshore littoral zone of small lakes to those in adjacent temporary habitats (depressional wetlands, shallow kettles, and tarns) on the South Island of New Zealand. We restricted our study to the central mountains to the west of the Canterbury Plains to minimize the

complicating effects of shifts in regional species pools and differences in geology and water chemistry (Lowe and Green 1987, Timperly 1987). The 43 lakes in our comparison group originally were chosen to compare benthic communities in lakes with and without trout (map and more details in Wissinger et al. 2006a). Here, we compare the invertebrate communities in the nearshore littoral zone of those lakes to the communities in 15 temporary habitats near the subset of the lakes in the Cass District of the Canterbury Highlands. The temporary habitats were relatively small (mean area = 1.2 ha \pm 0.17 SD), shallow (average maximum basin-filled depth = 0.67 m \pm 0.33), depressional wetlands and tarns that dried completely during summer 2001–2002 (December–February). We excluded habitats of intermediate depth that might dry in some years, but did not during our study, to avoid erroneous inferences about the history of drying in the absence of long-term data.

We qualitatively sampled all of the habitats twice, once in spring (October–December) and again in late summer (February–March) to establish species lists that accounted for seasonal differences in life history and community composition. In 2001–2002, these sampling dates corresponded to before and after drying in all of the temporary habitats. We swept a standard D-frame net repeatedly through different types of substrate and vegetation until no new taxa were found. We sorted all macroinvertebrates from the detritus on-site and preserved them in 90% ethanol. Identification to genus and often species of most insects was based on the keys in Winterbourn et al. (2000) and other regional keys (Chironomidae: Boot-hroyd 2000, Oligochaeta: Brinkhurst 1971, Crustacea: Chapman and Lewis 1976, Mollusca: Winterbourn 1973).

Quantitative sampling for benthic biomass and species abundances

In the 2nd part of our study, we compared the biomass and abundance of invertebrates in 6 permanent lakes (Sarah, Hawdon, Grasmere, Marion, Romulus, Kaurapataka) to that of 6 temporary tarns and marshes (Kettle Tarn, Remus Marsh, Craigeburn Marsh, St Bernard Marsh, Goldney Saddle Tarn, Gooseberry Tarn) near Canterbury University's Cass Field Station (Table 1; Wissinger et al. 2006a). This group of adjacent temporary and permanent habitats did not differ in pH (permanent: 6.8 \pm 0.4, temporary: 7.0 \pm 0.4 SD; $t = 0.52$, $p = 0.61$), conductivity (permanent: 43.3 μ S/cm \pm 24.2, temporary: 54.1 μ S/cm \pm 22.2; $t = 0.81$, $p = 0.44$), or elevation (permanent: 570 m \pm 35, temporary: 600 m \pm 54; $t = 0.53$, $p = 0.61$).

TABLE 1. Summary of chemical and physical characteristics of the temporary and permanent lentic habitats in which we sampled quantitatively to estimate invertebrate biomass.

Site	Hydroperiod	Elevation (m)	Area (ha)	[P] ($\mu\text{g/L}$)	pH	Conductivity ($\mu\text{S}_{25}/\text{cm}$)	New Zealand map grid	
							Northing	Easting
Sarah	Permanent	577	20	9	7.4	60	5794630N	2410331E
Hawdon	Permanent	579	30	13	7.3	40	5788647N	2416386E
Romulus	Permanent	640	12	12	7.0	60	5792730N	2408440E
Grasmere	Permanent	584	63	17	7.3	70	5792962N	2410276E
Kaurapataka	Permanent	405	55	8	6.8	25	5823781N	2403384E
Marion	Permanent	640	17	36	7.0	50	5836371N	2447238E
Remus	Temporary	600	0.55	21	6.5	40	5795245N	2408610E
Kettle	Temporary	620	0.35	41	6.5	25	5794125N	2411130E
St Bernard	Temporary	620	0.50	32	7.1	90	5791905N	2412885E
Craigieburn	Temporary	600	0.60	23	7.2	50	5786795N	2417815E
Goldney	Temporary	660	0.25	15	7.3	60	5798715N	2407630E
Gooseberry	Temporary	500	0.65	21	7.5	60	5793080N	2417735E

Total P was slightly, but not significantly, higher in temporary ($25.6 \mu\text{g} \pm 9.3$) than in permanent habitats ($16.1 \mu\text{g} \pm 4.6$; $t = 2.73$, $p = 0.12$) (methods in Wissinger et al. 2006a). The water-chemistry data are consistent with previous studies that characterize lentic habitats in the region as circumneutral, oligotrophic to mesotrophic, and moderately soft (Stout 1969, Timperly 1987). The lakes all had ≥ 1 species of native fish (koaro [*Galaxias brevipinnis* Günther], bullies [*Gobiomorphus breviceps* (Stokell)], or eels [*Anguilla dieffenbachia* Gray]), and 4 had introduced brown (*Salmo trutta* Linnaeus) and rainbow trout (*Oncorhynchus mykiss* (Walbaum)). The original design of the study was balanced with respect to trout (3 with and 3 without), but we discovered trout in Kaurapataka late in the study. Trout and troutless lakes have nearly identical species composition and total biomass (Wissinger et al. 2006a); thus, the change in designation of Lake Kaurapataka had no effect on the conclusions drawn in this paper.

We used 2 types of quantitative sampling devices to sample the biomass and relative abundance of invertebrates in the temporary habitats and the littoral emergent zone of these lakes. At each of 4 sampling stations in each lake or wetland, we sampled the abundances of small-bodied macroinvertebrates (oligochaetes, chironomids, clams, snails, mites, epibenthic crustaceans) with a 0.01-m^2 corer (polyvinyl chloride pipe; 1-m length) that was pushed down over the vegetation and into the substrate. We transferred the contents of the corer to a standard D-frame net with a small net, washed the sample, sorted invertebrates from the substrate on-site, and preserved them in 90% ethanol. We sampled large-bodied taxa (caddisflies, odonates, beetles, water bugs, aquatic moths, mayflies) with a D-frame net that was repeatedly swept across a 0.33-m^2 area for a standard

time. We removed invertebrates and detritus from the net, sorted invertebrates from detritus, and preserved them on-site (Wissinger et al. 2006a).

In the laboratory, we identified and counted invertebrates and distributed them into major taxonomic categories for biomass determination. We obtained ash-free dry mass (AFDM) of each group by drying invertebrates at 50°C for 48 h, weighing them, combusting them at 500°C for 4 h, and reweighing them to the nearest 0.0001 g.

Statistical analyses

We analyzed the effects of basin area and hydroperiod status (permanent or temporary) using 1-way analysis of covariance (ANCOVA) with basin area as a covariate. We used Bray–Curtis ordination on presence/absence data for all taxa (Beals 1984) to summarize differences in community composition among habitats. We chose this ordination technique for our presence/absence data because of its nonrestrictive assumptions (does not assume random sampling, multivariate normality, unclustered observations) relative to the assumptions of eigenvector techniques (e.g., principal components analysis) (Gauch 1982, Austin 1985, McGarriegal et al. 2000). We based the original ordering of data on % dissimilarity (Gauch 1982). We conducted the ordination with PC-ORD (version 4; MJM, Gleneden Beach, Oregon).

We first compared biomass and abundance (no./m^2) for the various taxonomic groups using 1-way multivariate analysis of variance (MANOVA) for lakes without fish ($n = 2$), lakes with fish ($n = 4$), and temporary habitats ($n = 6$). We explored significant MANOVA effects with protected 1-way analysis of variance on the separate response variables, and we

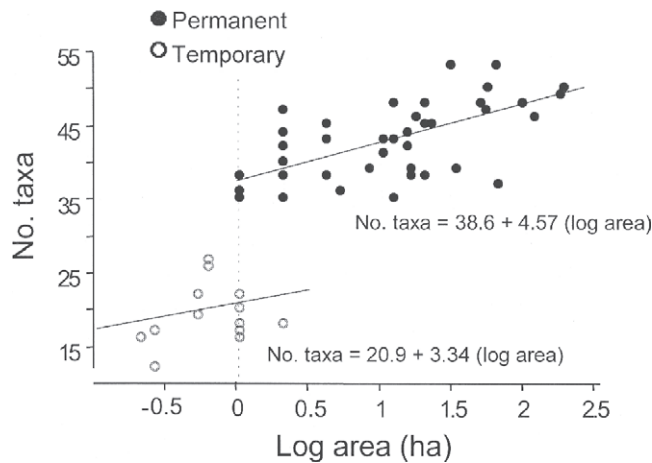


FIG. 1. Species richness of benthic invertebrates in temporary and permanent lentic habitats on the South Island of New Zealand as a function of habitat area. A nonsignificant analysis of covariance interaction term indicated the slopes of the species–area relationships for temporary and permanent habitats are not significantly different. Vertical dotted line indicates basins in the 2 habitat types for which area was comparable.

used Scheffé's a posteriori contrasts to identify pairs of treatments that differed (Day and Quinn 1989, Scheiner 1993). Neither density nor biomass differed between lakes with and without fish for any of the taxonomic categories; therefore, we conflated the lakes into 1 category ($n = 6$) for comparison with the temporary habitats ($n = 6$). We conducted these analyses with Statview (version 5.01; SAS Institute, Cary, North Carolina).

Results

Benthic invertebrate richness and community composition

Over 90 benthic and epibenthic invertebrate taxa were found in the 58 permanent and temporary habitats in the initial survey (Appendix; available online from: <http://dx.doi.org/10.1899/08-007.1.s1>). On average, species richness in permanent (43.6 ± 5.1) habitats was $>2\times$ that in temporary habitats (20.2 ± 4.2). ANCOVA analysis with area as a covariate revealed that the number of species differed significantly between permanent and temporary habitats ($F_{1,50} = 83.1, p < 0.001$) and that the effect of area was marginally significant ($F_{1,50} = 3.78, p = 0.057$). The ANCOVA interaction term was not significant ($F_{1,50} = 0.10, p = 0.75$), indicating the slopes for the 2 groups of habitats did not differ. For basins that were comparable in area (i.e., $\log_{10}[\text{area}] = 0.1\text{--}0.5$ ha), the number of species in permanent basins was greater than that in temporary basins (Fig. 1).

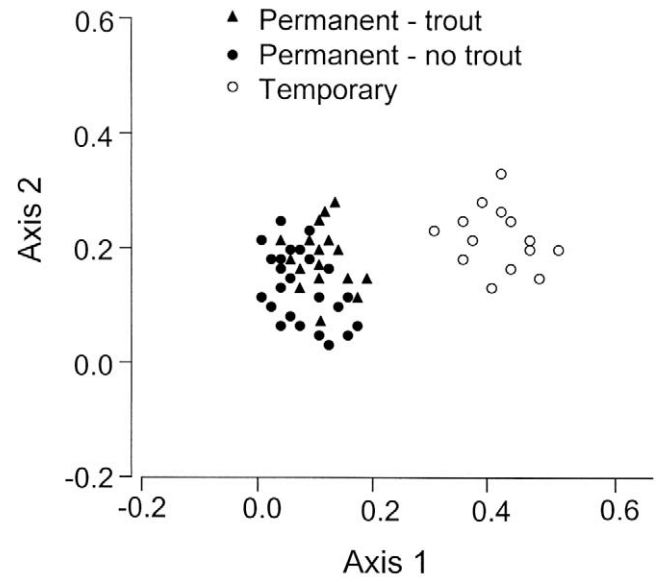


FIG. 2. Bray-Curtis unconstrained ordination based on presence/absence of 97 taxa in 43 permanent and 15 temporary habitats in the central South Island of New Zealand. The 2 dominant axes explain 72% (Axis 1 = 60%, Axis 2 = 12%) of the overall variation in the original data matrix.

Bray-Curtis ordination of the community composition data demonstrated that: 1) species assemblages of permanent and temporary habitats were distinct, and 2) differences between permanent habitats with and without trout were small compared to the relatively large separation between permanent and temporary habitats (Fig. 2). The 2 dominant axes explained 60 (axis 1) and 12.4% (axis 2) (total 72%; Fig. 2) of the variation in the original data matrix.

To analyze the underlying patterns of distribution that led to this difference in community composition, we focused on the subset of taxa for which we had sufficient taxonomic precision to ensure that we were not overlooking hidden species replacements (i.e., taxa identifiable to species or for which a genus was found in only one habitat type or the other [Tables 2, 3]). Caddisflies, which were the most diverse group of large-bodied taxa in the permanent habitats (2–5 leptocerid and 2–3 hydroptilid species present at all sites), were absent from all but 1 of the temporary habitats (Table 2). Nearly all lakes had 2 species of dragonflies (*Procordulia grayi* and *Procordulia smithi*) that were not encountered in temporary habitats. The damselfly *Xanthocnemis zealandica* was extremely abundant in all lakes, but was encountered only intermittently in low numbers in 2 temporary ponds (Remus, Gooseberry). A few early instar *Xanthocnemis* larvae were present in these 2 ponds in November, but

TABLE 2. Taxa found mainly in permanent New Zealand lentic habitats. VC = very common ($\geq 80\%$ sites sampled), C = common ($< 80\%$ but $> 20\%$ sites sampled), R = rare ($\leq 20\%$ sites sampled), blanks indicate taxon was absent.

Taxon	Permanent	Temporary
Ephemeroptera		
<i>Deleatidium</i> spp.	C	
<i>Nesameletus ornatus</i>	C	
Odonata		
<i>Austrolestes colenisonis</i>	VC	R
<i>Xanthocnemis zealandica</i>	VC	R
<i>Procordulia grayi</i>	VC	
<i>Procordulia smithi</i>	VC	
Plecoptera		
<i>Zelandobius furcillatus</i>	C	
<i>Austroperla cyrene</i>	C	
Trichoptera		
<i>Pycnocentroides aureolus</i>	R	
<i>Pycnocentria evecta</i>	R	
<i>Hudsonema amabile</i>	VC	
<i>Triplectides cephalotes</i>	VC	R
<i>Triplectides obsoletus</i>	VC	
<i>Oecetis unicolor</i>	VC	
<i>Oecetis iti</i>	C	
<i>Oxyethira albiceps</i>	VC	
<i>Paroxyethira tillyardi</i>	VC	
<i>Paroxyethira hendersoni</i>	VC	
Lepidoptera		
<i>Hygraula nitens</i>	VC	
Diptera		
<i>Cladopelma curtivalva</i>	VC	
<i>Parachironomus cylindricus</i>	C	
<i>Polypedilum pavidus</i>	C	
<i>Tanytarsus verspertinus</i>	R	
<i>Gressittius antarcticus</i>	VC	
<i>Cricotopus planus</i>	C	
<i>Cricotopus zealandicus utto</i>	VC	
<i>Metricnemus</i> sp.	C	
<i>Paratrichocladius pluriserialis</i>	VC	
<i>Kaniwhaniwhanus chapman</i>	R	
<i>Limonia</i> sp.	VC	
<i>Zelandotipula</i> sp.	VC	
Mollusca		
<i>Potamopyrgus antipodarum</i>	VC	
<i>Glyptophysa variabilis</i>	C	
<i>Physella acuta</i>	C	
<i>Musculium novaezealandiae</i>	C	
<i>Hyridella menziesi</i>	C	
<i>Lymnaea stagnalis</i>	C	
Annelida		
<i>Alboglossiphonia multistriata</i>	VC	
<i>Placobdelloides maorica</i>	VC	
<i>Aulodrilus pleuriseta</i>	VC	

not later in the summer (February) after the basins had dried and refilled. The other damselfly in lakes, *Austrolestes colenisonis*, which occurred mainly in emergent fringes, was also absent or rare in temporary habitats. Dipterans were abundant in both types of habitats, but temporary habitats were dominated by 1

TABLE 3. Taxa found in both temporary and permanent New Zealand lentic habitats. To avoid overlooking hidden species replacements, we used the subset of these taxa that were identified to species (or genus, when present in only 1 habitat) for ordination and inference about patterns of distribution between permanent and temporary habitats. VC = very common ($\geq 80\%$ sites sampled), C = common ($< 80\%$ but $> 20\%$ sites sampled), R = rare ($\leq 20\%$ sites sampled), blanks indicate taxon was absent.

Taxon	Permanent	Temporary
Hemiptera		
<i>Sigara arguta</i>	VC	VC
<i>Microvelia macgregori</i>	VC	VC
<i>Anisops wakefieldi</i>	VC	VC
<i>Anisops assimilis</i>	C	C
<i>Diaprepocoris zealandiae</i>	VC	R
Coleoptera		
<i>Liodessus plicatus</i>	VC	VC
<i>Liodessus deflectus</i>	VC	VC
<i>Antiporus strigosulus</i>	VC	VC
<i>Antiporus femoralis</i>	VC	VC
<i>Lancetes lanceolatus</i>	VC	VC
<i>Rhantus suturalis</i>	VC	VC
<i>Limnoxenus zealandicus</i>	C	C
<i>Huxelhydrus syntheticus</i>	R	R
<i>Onychohydrus hookeri</i>	R	R
Acari		
<i>Hydrachna maramauensis</i>	VC	VC
<i>Piona pseudouncata</i>	VC	VC
<i>Piona uncata exigua</i>	VC	VC
<i>Arrenurus lacus</i>	VC	VC
<i>Hydrozetes lemnae</i>	C	C
Diptera		
<i>Chironomus zealandicus</i>	VC	VC
<i>Polypedilum pavidus</i>	C	C
<i>Tanytarsus funebris</i>	VC	C
<i>Ablabesmyia mala</i>	VC	C
<i>Paratrichocladius pluriserialis</i>	VC	C
Mollusca		
<i>Gyraulus corinna</i>	VC	VC
<i>Austropeplea tomentosa</i>	C	C
Crustacea		
<i>Daphnia carinata</i>	C	C
<i>Simocephalus vetulus</i>	C	C
<i>Chydorus sphaericus</i>	VC	R
<i>Camptocercus australis</i>	C	C
<i>Herpetocypris pascheri</i>	VC	C
<i>Cyprretta viridis</i>	VC	R
<i>Cypridopsis vidua</i>	VC	R
<i>Cyprinotus incongruens</i>	VC	VC
<i>Candonocypris assimilis</i>	VC	R
<i>Acanthocyclops robustus</i>	VC	VC
<i>Boeckella triarticulata</i>	C	VC
Annelida		
<i>Lumbriculus variegatus</i>	VC	VC
<i>Limnodrilus hoffmeisteri</i>	VC	VC

species (*Chironomus zealandicus*), with low abundances of several orthoclads, and 1 tanypod, all of which were abundant in permanent habitats (Table 3). Mayflies, stoneflies, an aquatic moth (*Hygraula nitens*), and the

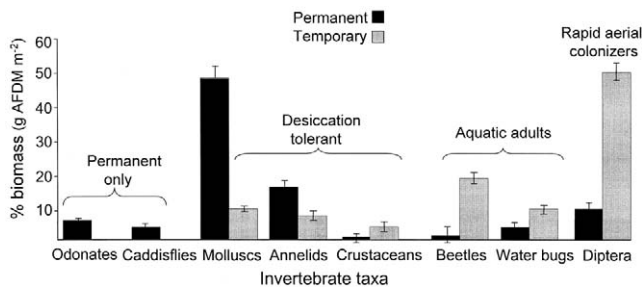


FIG. 3. Mean (± 1 SE) % biomass of benthic invertebrate taxa in permanent and temporary habitats in the Canterbury Highlands near the University of Canterbury's Cass Field Station on the South Island of New Zealand. The snail *Potamopyrgus antipodarum* accounted for $>95\%$ of the biomass of permanent habitat mollusks. Temporary-habitat taxa are grouped by mode of colonization (after Wissinger 1999).

snail *Potamopyrgus antipodarum* also were common in lakes, but absent in all or most temporary habitats (Table 2).

Temporary faunas were dominated by beetles, water bugs, mites, chironomids, annelids, and microcrustaceans (Table 3). Many of the beetles (*Antiporus strigosulus*, *Rhantus suturalis*, *Liodessus plicatus*, *Lancetes lanceolatus*), water bugs (*Sigara arguta*, *Anisops wakefieldi*), and most mites were found in every permanent and temporary habitat surveyed (Table 3). Epibenthic microcrustaceans were found in both types of habitats, but several species were reciprocally common in one and rare in the other, providing some evidence for specialization (Appendix). The dominant species of annelids and mollusks in temporary habitats also were common in permanent habitats. In summary, permanent and temporary communities differed (Fig. 2) because many permanent-habitat species were absent in temporary habitats, which were dominated by a subset of generalists that were common in permanent habitats (Table 3).

Benthic invertebrate biomass

MANOVA for the comparison of biomass (AFDM) of all taxonomic groups between permanent and temporary habitats was highly significant ($F_{12,8} = 7.75$, $p = 0.003$). Total biomass of benthic invertebrates in permanent habitats (5.74 ± 0.63 g AFDM/m²) was $>2\times$ that in temporary habitats (1.93 ± 0.39 g AFDM/m²; $F_{1,10} = 156.7$, $p = 0.001$). The largest contributor to that difference was the snail *Potamopyrgus antipodarum*, which was absent in temporary habitats, but accounted for almost $\frac{1}{2}$ of the biomass in the lakes (Fig. 3, Table 4). Snail densities in the littoral zone of lakes ranged from 50,000 to 200,000 ind./m² depending on

TABLE 4. Mean (± 1 SE, $n = 6$) invertebrate biomass (g ash-free dry mass/m²) in permanent and temporary lentic habitats. p -values are for protected 1-way analyses of variance in the context of a significant multiple analysis of variance.

Taxon	Permanent	Temporary	p
Odonata	0.332 ± 0.064	0.004 ± 0.003	0.001
Trichoptera	0.311 ± 0.034	0.004 ± 0.009	<0.001
Hemiptera	0.339 ± 0.125	0.240 ± 0.091	0.413
Coleoptera	0.068 ± 0.016	0.352 ± 0.041	<0.001
Diptera	1.164 ± 0.312	0.961 ± 0.059	0.500
Miscellaneous ^a	0.014 ± 0.004	0.001 ± 0.001	0.006
Mollusca	2.810 ± 0.876	0.208 ± 0.111	0.001
Crustacea ^b	0.003 ± 0.001	0.041 ± 0.006	<0.001
Annelida	0.880 ± 0.171	0.127 ± 0.280	0.001

^a Includes Lepidoptera, Ephemeroptera, and Plecoptera in permanent habitats and Hydracarina in both permanent and temporary habitats

^b Epibenthic microcrustaceans, mainly Ostracoda and Cladocera

the type and height of submerged vegetation (hence, vertical surface area). *Potamopyrgus antipodarum* was not found in the temporary habitats, but several other snails (*Gyraulus corrina* and *Austropeplea tomentosa*) typically were abundant in temporary habitats.

The invertebrate taxa that dominated the biomass differed between permanent and temporary habitats. The permanent ponds had higher biomass of snails, odonates, caddisflies, aquatic moths, stoneflies, mayflies, and annelids than temporary habitats (Table 4). In contrast, beetle and microcrustacean biomass was greater in temporary than in permanent habitats (Table 4). The biomass of water bugs and dipterans (mainly chironomids) did not differ between the 2 types of habitat. Water bugs, annelids, beetles, and microcrustaceans together accounted for $>90\%$ of the biomass in temporary habitats (Fig. 3).

Discussion

Comparative data, mainly from North America, provide evidence for species replacements between permanent and temporary habitats, and experimental studies have elucidated the tradeoffs that underlie replacements for several groups of taxa (reviewed by Wellborn et al. 1996, Urban 2004, Wissinger et al. 2006b). We found little evidence for species replacements in our study. Our data suggest that benthic invertebrate communities in the temporary wetlands and tarns that we studied in New Zealand are dominated by generalists that occur across a wide range of lentic habitats. All of the taxa identifiable to species in temporary habitats were encountered in the littoral zone of all or most of the lakes we sampled;

thus, by definition, temporary habitat communities are a completely nested subset of a more diverse permanent habitat fauna (see Baber et al. 2004, McAbendroth et al. 2005). Below we discuss our results in the context of previous studies that describe community change along permanence gradients, and then offer several potential explanations for the absence of species replacements at our study sites.

Species richness and biomass dominance in permanent vs temporary habitats

As has been reported in previous studies (Batzer and Wissinger 1996, Schneider 1999, Wissinger et al. 1999a, Williams 2006), we found that temporary habitats had fewer species than permanent habitats (Fig. 1). Because permanent basins tend to be larger than temporary basins, it is often difficult to separate the effects of permanence and area (see discussions by Wissinger et al. 1999a, Hall et al. 2004). We present evidence that both area and hydroperiod affect richness. The 2-fold difference in the number of species in permanent vs temporary basins of comparable area emphasizes that, independent of the area effect, temporary habitats tend to have fewer species than permanent habitats (Schneider and Frost 1996, Anderson and Smith 2000, Tarr et al. 2004).

Invertebrate biomass in the temporary wetlands and tarns was dominated by a different group of taxa than those that dominated in lake littoral zones (Fig. 3). Chironomids, beetles, water bugs, and microcrustaceans accounted for 90% of the biomass at temporary sites, but only 14% of the biomass in the nearshore zone of lakes. These taxa have the ability to colonize temporary habitats rapidly because they have: 1) desiccation-tolerant stages that aestivate within the substrate (e.g., microcrustaceans), 2) an aquatic winged adult stage (e.g., beetles and water bugs), or 3) rapidly colonizing adults with short generation times (7–14 d) (e.g., midges and mosquitoes) (Batzer and Wissinger 1996, Bilton et al. 2001, Williams 2006). The cyclic movement of beetles and water bugs between adjacent permanent and temporary habitats is well described (Roff 1994, Wissinger 1997, Williams 2006), and based on published dispersal distances, both groups probably migrate between the 2 types of habitat at our study sites (Young 1970, Larson 1985, Lundkvist et al. 2001, Davy-Bowker 2002).

Why are species replacements rare in New Zealand?

Perhaps the most striking result of our study was the absence of temporary-habitat specialists (Tables 2, 3). Such specialization often occurs at the level of genus within family or species within a genus in North

America (Wellborn et al. 1996); thus, studies that group taxa into families, tribes, or even genera might potentially overlook such replacements. We were able to identify most aquatic insects (except some chironomids), mollusks, and mites to the species level (Tables 2, 3); thus, we are confident that species replacements play, at best, a minor role in shifts in lentic community structure in the habitats that we studied in New Zealand. This result was most surprising for taxa for which this pattern is well described elsewhere. For example, we did not find the replacement pattern observed for damselflies in North America and Europe (McPeck 1990, De Block and Stoks 2005), where the evolution of alternative traits in fish vs fishless or temporary vs permanent habitats underlies an evolutionary history of regional diversification (Brown et al. 2000, McPeck and Brown 2000, Stoks and McPeck 2003, 2006). The damselflies in our study, *Xanthocnemis zealandicus* and *Austrolestes colonensis*, probably can complete their life cycles in long-duration temporary habitats (Barclay 1966, Crumpton 1979), and it appears, based on the demise of cohorts in drying ponds, that they might use bet-hedging strategies to colonize semipermanent basins (as in Anderson et al. 1999). However, it is clear that the recent (Quaternary) adaptive radiation of permanent (fish)- and temporary (fishless)-habitat damselflies in North America that is described by McPeck, Stoks, and colleagues (Brown et al. 2000, Turgeon et al. 2005, Stoks and McPeck 2006), has not occurred in New Zealand (Rowe 1987). Similarly, the patterns of species replacements across permanence gradients observed for lentic dragonflies in Africa (e.g., Johansson and Suhling 2004, Suhling et al. 2005) and caddisflies in North America (e.g., Wissinger et al. 2003, 2006b) were not found in our study.

One hypothesis for the absence of temporary habitat specialists in these groups of taxa is that the hydroperiods of New Zealand temporary habitats are seasonally unpredictable. Winterbourn (1997, p. 35) notes that "... rainfall is unpredictable and the pattern of storm events and dry spells can (and do) occur at any time of year." As a result, interannual variability in the hydrology of New Zealand streams is considerable, both in terms of when and to what extent they are disturbed by floods (Clausen and Biggs 1997). The effects of that interannual variability in hydrology on algal and benthic invertebrate community structure and diversity in streams are well described (Winterbourn 1997, Clausen and Biggs 2000, Biggs and Smith 2002). Recent data from our study sites indicate that this seasonal unpredictability in precipitation leads to considerable interannual variation in when temporary lentic habitats fill and dry and the duration of the dry

and wet phases of the hydroperiod (HG, unpublished data).

The taxa that dominate temporary habitats in New Zealand (Fig. 3) all rely on opportunistic colonizing strategies that are not tightly linked to seasonality; i.e., they either colonize as aquatic adults (beetles, water bugs), are rapid dispersers that oviposit in newly filled habitats within days to weeks (midges and mosquitoes), or have desiccation-tolerant stages that break diapause after hydration (microcrustaceans). In contrast, damselflies, dragonflies, caddisflies, mayflies, and other aquatic insects that colonize temporary habitats do so as a result of life histories that are finely tuned to seasonal schedules of basin filling and drying (Wiggins et al. 1980, Wissinger 1999, Williams 2006). For example, many north-temperate cased caddisflies spend the dry phase (late summer) of hydroperiods as adults in ovarian diapause and then deposit gelatinous, desiccation-tolerant egg masses that hatch upon re-inundation in autumn and winter (Wiggins 1973, Richardson and Mackay 1984, Whiles et al. 1999, Wissinger et al. 2003). Similarly, many temporary-habitat odonates (e.g., lested damselflies and symptetriniid dragonflies) deposit desiccation-resistant eggs inside plant stems where they diapause until habitats are filled with snowmelt or spring rains (Sawchyn and Gillott 1974, Corbet 1999). In these taxa, key life-cycle events (entering or breaking egg, larval, pupal or adult diapause, oviposition, emergence, dispersal) are triggered by seasonal cues (temperature, photoperiod) that are correlated with predictable changes in hydroperiod (Tauber and Tauber 1986, Corbet 1999, Wissinger et al. 2003). Unpredictable temporary habitats certainly exist in North America (e.g., Anderson et al. 1999), but a review of invertebrate communities across 38 different types of ponds and wetlands suggest that most have predictable hydroperiods associated with seasonal precipitation or snowmelt (Wissinger 1999).

Unpredictable drying does not explain why opportunistic colonizers of temporary habitats (e.g., midges, beetles, water bugs) also coexist with fish in New Zealand lakes (Table 3); i.e., tradeoffs do not appear to exist between the traits that allow species to cope with drying (rapid growth, high activity rates, modest investment in antipredator morphologies) and those that facilitate coexistence with fish (low activity rates, escape behaviors, investment in antipredator strategies) (McPeck et al. 1996, Wellborn et al. 1996, Wissinger et al. 2006b). One hypothesis to explain this result is that the strength of selection exerted by fish on benthic invertebrates is weak in New Zealand. Invertebrate specialization to fish and fishless habitats in North America appears to be driven mainly by predation by 2 groups of fishes (Percidae and

Centrarchidae) that do not occur in most New Zealand lakes. In contrast, the salmoniform fishes that dominate in lakes in New Zealand (native Galaxiidae and introduced trout) do not appear to have much effect on benthic communities, either because they feed mainly in the water column (as planktivores and piscivores) or because of the presence of extensive submerged macrophyte beds that serve as benthic refuges (Wissinger et al. 2006a). Whether these extensive macrophyte beds allow interactions between benthic invertebrates and demersal fish such as bullies (Eleotridae) has not been studied.

An alternative set of explanations for the absence of habitat specialization is that phylogenetic constraints on the New Zealand fauna have favored generalists or restricted the evolution of specialists. One such constraint described in other studies, the absence of "key innovations" within a lineage (McPeck 1996b), seems unlikely to explain the absence of specialization across so many different taxa. Phylogenetic constraints also could be related to how the history of glaciation has affected patterns of isolation and recontact of closely related species, hence rates of speciation or time for the evolution of habitat specialization between closely related species (Van Buskirk 2003). Hypotheses related to phylogenetic constraints focus on differences in the evolutionary history of faunas, whereas those above (unpredictable drying, predominance of salmoniform fishes, unique vegetation structure of New Zealand lakes) focus on the idea that the current habitat template (*sensu* Southwood 1977) in New Zealand differs from that in North America. Understanding geographic differences in the way extant communities shift along permanence gradients will require studies that address both components (habitat template and phylogenetic constraints) of community evolution (Losos 1996, McPeck and Miller 1996, Richardson 2002, Webb et al. 2002).

Conclusions and future study

In summary, differences in the species richness and types of taxa that dominate the benthos of the permanent and temporary lentic communities that we studied in New Zealand are similar to those observed in previous studies conducted in north-temperate habitats. However, we found little evidence for the species replacement pattern that contributes to shifts in community structure along this gradient in North America (Wellborn et al. 1996, Urban 2004). Instead, the species that inhabit temporary ponds in New Zealand are a nested subset of generalists that also occur in permanent habitats. The divergence of permanent and temporary habitat specialists from a

generalist ancestor should be most likely when: 1) traits that are beneficial for avoiding desiccation have a cost in permanent habitats (e.g., avoiding fish predation), and 2) traits that are beneficial in permanent habitats have a cost to avoiding desiccation. Such divergence is unlikely if fish exert weak selection in permanent habitats or the pattern of desiccation in temporary habitats is so unpredictable that it precludes the evolution of effective life histories, as appears to be the case for New Zealand odonates and caddisflies. Either of these 2 opposing forces should lead to divergence, and the apparent absence of both in New Zealand might make adaptive radiation between permanent and temporary habitats unlikely.

Several recent studies in North America (Baber et al. 2004, McCauley 2007, Werner et al. 2007a) and in Europe (Van Buskirk 2003, 2005) also have reported temporary-habitat assemblages that are dominated by a nested subset of permanent habitat species. Explanations for how these generalists are able to exploit a broad range of habitats include: 1) fixed intermediate antipredator or competitor traits, 2) phenotypic plasticity in traits that facilitates coexistence with different types of predators or leads to rapid growth in drying habitats, 3) habitat partitioning along axes embedded within the gradient, and 4) the presence of alternative genotypes across habitats (McPeck 1996a, Johansson et al. 2001, Relyea 2002, VanBuskirk 2003, 2005, McCauley 2007). Assessing the relative importance of these explanations for the New Zealand fauna will require: 1) measuring interannual patterns of drying across a range of hydroperiods (temporary, semipermanent, permanent); 2) documenting community turnover between years (Werner et al. 2007b); and 3) integrating comparative and experimental studies to assess the strength of selection exerted by predators and drying. Finally, understanding whether the replacement pattern along lentic permanence gradients observed in North America is the exception or the rule will require broadening the geographic scope of research on how drying regime and phylogenetics affect the evolution of generalists vs specialists.

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