Long-term changes in metapopulation genetic structure: a quarter-century retrospective study on low-Arctic rock pool *Daphnia*

Lawrence J. Weider^{1,*}, Dagmar Frisch^{1,†} and Paul D. N. Hebert²

¹Program in Ecology and Evolutionary Biology, Department of Zoology and Biological Station, University of Oklahoma, Norman, OK 73019, USA

²Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada

Population genetic surveys approximately 25 years apart examined the distribution and abundance of asexual clones of the freshwater zooplankton *Daphnia pulex* complex in rock pools near Churchill, Manitoba, Canada. In 1984–1985, melanic members of this species complex were present in 131 rock pools at this site, but were only detected in 90 of these pools in 2007–2008. Allozymic surveys conducted during these two time periods revealed that 59 per cent of these populations showed unchanged clonal composition. Total clonal replacement occurred in 8 per cent of the populations, while the others (33%) included a mixture of ‘resident’ clones and new ‘colonists’. We discuss these changes in light of shifts in biotic and abiotic factors. We also discuss the use of rock pool habitats as ‘sentinel’ systems for examining long-term environmental changes in the ecological genetics of aquatic organisms in the Arctic.

Keywords: climate change; zooplankton; Arctic; ecological genetics; time series

1. INTRODUCTION

A long-term perspective is critical to understand how organisms adapt to changing environmental conditions (Endler 1986; Ricklefs & Miller 1999). Several studies have examined long-term changes in metapopulation structure (Hastings & Harrison 1994; Moilanen *et al.* 1998; Hanski 1999; Pajunen & Pajunen 2003), primarily in temperate systems. The expansion of such studies is critical, especially in the Arctic, given its sensitivity to global climate change (ACIA 2005). Although Arctic systems might well serve as ‘sentinels’ of such changes, long-term Arctic studies are rare (Hanski 1999).

Natural microcosms (e.g. rock pools) are useful models for ecological and evolutionary studies (Srivastava *et al.* 2004). The small size of habitats, the short generation times of resident organisms and structural complexity can be tracked relatively easily are all advantages for analysis (Srivastava *et al.* 2004). Previous studies using rock pools as microcosms for studies in ecology and evolutionary biology (e.g. Hanski & Ranta 1983; Weider & Hebert 1987a,b; Bengtsson 1989) have shown their versatility in addressing major questions involving issues such as competition (Bengtsson 1989), predation (Wilson & Hebert 1993), maintenance of species diversity (Hanski & Ranta 1983) and genetic diversity (Weider & Hebert 1987a,b) and the role of biotic (Wilson & Hebert 1993) and abiotic (Weider & Hebert 1987a) processes on metapopulation dynamics (Pajunen & Pajunen 2003).

In particular, one system that has been studied extensively and might well serve as a good ‘model’

metapopulation system involves the microcrustacean fauna (i.e. zooplankton) that inhabit rock pools located on rock bluffs along the Hudson Bay coast near Churchill, Manitoba, a site in the Canadian low-Arctic (Weider 1987; Weider & Hebert 1987a,b). Much past work at this locale has centred on members of the microcrustacean genus, *Daphnia*, a keystone herbivore not only at this locality, but in many freshwater lentic habitats worldwide (Peters & de Bernardi 1987). A key feature of the life cycle of all daphniids is the production of diapausing (ephippial) eggs, which can be passively transported between habitats or remain dormant in the sediments (i.e. overwinter), and hatch to re-establish the population when conditions are once again favourable.

Previous genetic work, particularly focusing on the Churchill *Daphnia pulex* complex (Weider 1987; Weider & Hebert 1987a,b; Wilson & Hebert 1993; Dufresne & Hebert 1995; Weider *et al.* 1999a,b), has shown that this Arctic complex includes of a mixture of distinct lineages/species that are obligately parthenogenetic and that include both diploid (non-melanic) and polyploid (melanic) clones. Work on melanic clones in this complex (Weider 1987; Weider & Hebert 1987a,b) revealed microgeographic heterogeneity in their distributions that was strongly influenced by physico-chemical variation among rock pools, in particular salinity gradients. This has resulted in the evolution of distinct physiological ecotypes that are distributed non-randomly along salinity gradients across these rock bluffs.

The present study surveys the population genetic/clonal structure of these *D. pulex* populations to determine the changes in distribution and abundance of melanic clones after approximately 25 years. Further, we discuss the mechanisms that may be responsible for the changes detected in clonal composition. Ultimately,

* Author for correspondence (ljweider@ou.edu).

† Present address: Doñana Biological Station, Sevilla, Spain.

our goal is to present a long-term dataset that documents metapopulation dynamics and changes in genetic structure, which should inform the debate about long-term environmental effects on underlying genetic variation in natural populations, particularly in the Arctic.

2. MATERIAL AND METHODS

Earlier work (Weider & Hebert 1987*a,b*) described the rock pool system in great detail, and the genetic analyses that were conducted in 1984–1985 using cellulose acetate electrophoresis (Hebert & Beaton 1993). In 2007–2008, we resurveyed all 131 rock pools on three rock bluffs (A, B, C), which contained melanistic *D. pulex* at the time of the original study (Weider & Hebert 1987*a,b*). These three rock bluffs are located 20 km east of Churchill, Manitoba. No effort was made to ascertain whether melanistic *D. pulex* had colonized ‘new’ rock pools on these bluffs over the 25-year interval.

All rock pools were sampled from 14 to 20 July 2007, and again from 24 June to 2 July 2008, a time frame coinciding with the sampling bouts conducted in 1984 and 1985 (Weider & Hebert 1987*a,b*). Melanistic *D. pulex* were considered ‘absent’ from a habitat if they were not detected in consecutive years (i.e. 2007 and 2008). In 41 of the 131 rock pools (i.e. 31%), we did not detect melanics in these two years, and therefore classified these populations as ‘extinct’. This follows similar protocols by other researchers (e.g. Bengtsson 1989; Pajunen & Pajunen 2003).

The same four allozyme loci (aldehyde oxidase, EC 1.2.3.1; lactate dehydrogenase, EC 1.1.1.27; phosphoglucose mutase, EC 5.4.2.1; phosphoglucose isomerase, EC 5.3.1.9) employed in the original studies of Weider & Hebert (1987*a,b*) were again used to screen for multi-locus genotype (i.e. clonal) distributions. Sampling and laboratory methods followed those of Weider & Hebert (1987*a,b*). Sixty-six of the 131 rock pools contained melanistic *D. pulex* in 2008, and these populations were compared directly with the 1984–1985 allozyme survey.

In addition, a temperature–conductivity–DO meter (YSI model 90) was used to record pond water parameters. A Garmin 12CX GPS unit was used to record the latitude/longitude position of each rock pool, and field notes were taken to record other major zooplankton taxa in each pond (i.e. anostracans, copepods, other daphniid assemblages).

Jaccard’s coefficient of similarity (Ricklefs & Miller 1999) was used to determine similarity between the clonal composition for each rock pool sampled in 1984–1985 and in 2008.

We applied canonical correspondence analysis (CCA; ter Braak 1986) to examine clonal distributions in relation to temperature, conductivity and spatial location. For the CCA, we constructed a presence–absence matrix of the observed melanistic *D. pulex* clones as well as the presence–absence of non-melanics for the sampled ponds, and an explanatory variable matrix with the measured environmental factors—temperature and conductivity. Spatial location (i.e. presence of a given clone on bluffs A, B or C) was coded as a dummy variable. CCA was performed using the software CANOCO for Windows, v. 4.5 (ter Braak & Šmilauer 2002). A Monte Carlo permutation test (499 permutations) was performed to assess the significance of both the first canonical axis and all canonical axes together to allow the evaluation of the species–environment relationship.

In addition, ‘species’ response curves were fitted for clones and the environmental factors, temperature and

Figure 1. Distribution maps showing the presence/absence of melanistic *D. pulex* in 2007–2008 compared with the distributions in 1984–1985 on (a) bluff A, (b) bluff B, and (c) bluff C. Note: absent populations refer to those in which melanics were not detected in both 2007 and 2008. Filled circles, absent; open circles, present. (a) Scale bar, 50 m. (b,c) Scale bars, 100 m.

conductivity, measured in both 1984–1985 and 2007–2008. For this analysis, linear models with a binomial distribution of the response variable and a logit link function were constructed using the generalized linear model (GLM) modelling option of CANODRAW 4.0 (ter Braak & Šmilauer 2002). Previous work at Churchill (Weider 1987; Hebert & Emery 1990; Wilson & Hebert 1992; Ng *et al.* 2009) has shown the importance of environmental and biotic interactions in these habitats.

3. RESULTS

Melanistic *D. pulex* occurred in 131 rock pools on bluffs A, B and C in 1984–1985, but were present in just 69 per cent ($n = 90$) of these habitats in 2007–2008 (figure 1). Of the 34 rock pools on bluff A that contained melanistic *D. pulex* in 1984–1985, only 15 rock pools (44%) contained melanics in 2007–2008 (figure 1). On bluff B, 43 of the 54 rock pools (80%) contained melanics in

Figure 2. Pie diagrams showing (a) distribution of melanistic *D. pulex* clones on bluff A in 1984–1985 following the data of Weider & Hebert (1987a). Open circles, 1; circles with horizontal stripes, 2; filled circles, 3; circles with dots, 4. (b) Distribution of melanistic *D. pulex* clones on bluff A in 2008. Each pie depicts the frequency of each clone in a particular rock pool. Striped circles, 2; filled circles, 3; circles with dots, 4; shaded circles, other. Scale bar, 50 m.

2007–2008 (figure 1), while on bluff C (figure 1), 32 of the 43 rock pools (74%) contained melanistic *D. pulex*.

Allozyme analyses in 1984–1985 by Weider & Hebert (1987a) are depicted for bluffs A (figure 2a), B (figure 3a) and C (figure 4a). An allozyme survey in 2008 of melanistic clones for all ‘surviving populations’ ($n = 66$) revealed that 59 per cent ($n = 39$) showed either identical clonal frequencies or identical clonal compositions. By contrast, total clonal replacement was apparent in 8 per cent ($n = 5$) of the populations, while the other 22 populations (33%) included a mixture of ‘resident’ clones that were present in 1984–1985 as well as ‘new colonists’.

Jaccard’s coefficient of similarity among clonal assemblages in the 66 populations ranged from 0 to 1 (0.74 ± 0.34 ; overall mean ± 1 s.d.). On individual rock bluffs, the stability of these melanistic *D. pulex* populations over the past 25 years was quite variable (figures 2b, 3b and 4b). Jaccard’s similarity was substantially lower on bluff A (0.62 ± 0.38 ; $n = 14$) and bluff C (0.62 ± 0.37 ; $n = 21$) than on bluff B (0.88 ± 0.22 ; $n = 31$).

Bluff A showed a particularly dramatic turnover in clones (figure 2b). One of the four clones detected in 1985 (figure 2a), clone 1, was completely absent in 2008 (figure 2b), while clone 4 was greatly reduced in abundance and distribution (figure 2b). As well, two new clones (i.e. clones 8 and 11—listed as ‘other’; figure 2b), not detected on bluff A in 1985, but found at low frequencies on other rock bluffs at Churchill (Weider & Hebert 1987b), had become locally abundant. On bluff C (figure 4), one of the original five clones (i.e. clone 5) detected in 1985 (figure 4a) was

Figure 3. Pie diagrams showing (a) distribution of melanistic *D. pulex* clones on bluff B in 1984–1985 following the data of Weider & Hebert (1987a). Open circles, 1; filled circles, 3; circles with dots, 4; circles with oblique stripes, 6. (b) Distribution of melanistic *D. pulex* clones on bluff B in 2008. Each pie depicts the frequency of each clone in a particular rock pool. Open circles, 1; circles with horizontal stripes, 2; filled circles, 3; circles with oblique stripes, 6. Scale bar, 100 m.

not detected in 2008 (figure 4b), while clone 1 showed a dramatic decrease in its distribution and abundance in 2008 (figure 4b). Clones 3, 4 and 6 remained relatively ‘stable’ in their abundances and distributions during the intervening years (figure 4), while clone 13, which was not found previously on these three bluffs, but was detected elsewhere in the Churchill area (Weider & Hebert 1987b), and a completely ‘new’ clone (i.e. clone 17 had not been detected previously in the Churchill region; Weider & Hebert 1987b) became locally abundant in 2008 (figure 4b; both clones listed as other).

By contrast, clonal distributions and abundances on bluff B showed much greater stability (figure 3). Of the original four clones on bluff B (figure 3a), only clone 4, which was a minor component of the clonal assemblage in 1985 (figure 3a), was absent in 2008 (figure 3b). The three most abundant clones (1, 3 and 6) remained so in 2008, although clone 2 (not previously detected on bluff B) was found at low frequency in 2008 (i.e. less than 5% in one population; figure 3b). No other new clones were detected on bluff B.

Of the 41 populations that went extinct during the intervening 25 years, 23 had been uniclinal (11 for clone 1, six for clone 4, five for clone 3 and one for clone 2). The other 18 populations that went extinct had multiple clones, including an additional seven that contained clone 1, nine that contained either clone 2 or clone 3, four that contained clone 4, three that contained clone 6 and one that had clone 5 in it.

A retrospective comparison of the clonal diversity of populations that went extinct with those that persisted

Figure 4. Pie diagrams showing (a) distribution of melanistic *D. pulex* clones on bluff C in 1984–1985 following the data of Weider & Hebert (1987a). Open circles, 1; filled circles, 3; circles with dots, 4; circles with diamonds, 5; circles with oblique stripes, 6. (b) Distribution of melanistic *D. pulex* clones on bluff C in 2008. Each pie depicts the frequency of each clone in a particular rock pool. Open circles, 1; filled circles, 3; circles with dots, 4; circles with oblique stripes, 6; shaded circles, other. Scale bar, 100 m.

(figures 2–4) revealed no significant differences (paired *t*-test) in clonal diversity in 1985 sampling (i.e. extinct populations 1.49 ± 0.60 clones, $n = 41$; ‘persistent’ populations 1.52 ± 0.54 , $n = 90$; mean ± 1 s.d. number of clones). Likewise, we tested whether the coefficient of variation (CV) for conductivity/salinity was greater for populations that went extinct (implying that these populations were ‘less stable’) compared with populations that persisted. No significant differences in the CV for conductivity/salinity were detected (i.e. paired *t*-test).

Prior studies have established that competition plays an important role in determining clonal distributions (Hebert & Emery 1990; Wilson & Hebert 1993) and that melanics compete with non-melanics. Non-melanics coexisted with melanics in only 19 of the 131 rock pools in 1985. However, by 2008, non-melanics were present in 56 of these 131 rock pools. These additional colonizations by non-melanics coincide with the complete replacement of melanics by non-melanics in 17 of these 56 populations.

Results from the CCA (figure 5; table 1) revealed marked differences in the temperature and conductivity (salinity) patterns on the three bluffs between the two sampling periods (1984–1985 versus 2007–2008). On average, bluff A was associated with the highest conductivities, bluff C with intermediate values and bluff B with the lowest conductivities (figure 5a). Further, shifts to higher temperatures were observed for ponds sampled on bluffs B and C in 2007–2008, while bluff A ponds showed lower temperatures in 2007–2008 compared with the earlier sampling period (1985; figure 5a).

Mean (± 1 s.e.) temperature values for ponds on bluffs A, B and C in 1985 were 17.1 ± 0.3 , 11.8 ± 0.1 and $15.2 \pm 0.2^\circ\text{C}$, respectively. For 2007–2008, mean temperature values for ponds on bluffs A, B and C were 15.1 ± 0.2 , 20.6 ± 0.2 and $18.6 \pm 0.4^\circ\text{C}$, respectively. Mean (± 1 s.e.) conductivity values ($\mu\text{S cm}^{-1}$) for ponds on bluffs A, B and C in 1985 were 701 ± 210 , 266 ± 52 , and 498 ± 121 , respectively. For 2007–2008, mean (± 1 s.e.) conductivity values ($\mu\text{S cm}^{-1}$) for ponds on bluffs A, B and C were 930 ± 146 , 347 ± 57 and 625 ± 122 , respectively.

An examination of the distribution of clonal assemblages on the three bluffs and their association with temperature and conductivity revealed specific species (clone)–environment relations (figure 5). The first two canonical axes (table 1) explained 87.3 per cent of the variance of the species–environment relationship, with the first canonical axis showing significant discriminatory power (F -ratio = 14.99, $p < 0.002$). All canonical axes combined were significant (F -ratio = 6.49, $p < 0.002$), and jointly explained 10.7 per cent of the variance in clonal distributions.

Results from the individual clone (species)–response curve analysis using the GLM procedure (table 2) showed significant temperature effects (comparing presence/absence of clones between 1984–1985 and 2007–2008) for melanistic clones 1, 3 and 6 (all showing decreases in frequency—i.e. number of ponds inhabited; related to temperature increases in 2007–2008), while ‘non-melanics’ (a multi-clonal group), showed the opposite pattern (i.e. a significant increase in frequency with

Figure 5. Ordination biplots of the CCA for clonal composition. (a) Ponds in relation to temperature, conductivity and location (bluff). Circles, bluff A; triangles, bluff B; squares, bluff C. Grey symbols show ponds from 1985, and white symbols show those same ponds in 2007–2008. (b) Clonal association with the same explanatory variables. Axes 1 (*x*-axis) and 3 (*y*-axis) are plotted for clarity.

Table 1. Results of CCA for 127 of the 131 rock pools on bluffs A, B and C (data were missing for four pools), with 10 melanic clones and non-melanics as species, and temperature, conductivity and rock bluff as explanatory (environmental) variables. Test of significance of the first canonical axis (F -ratio = 14.99, p -value = 0.002); test of significance of all canonical axes (F -ratio = 6.49, p -value = 0.002).

axes	1	2	3	4	total inertia
<i>axis summary statistics</i>					
eigenvalues	0.367	0.162	0.053	0.025	5.646
species–environment correlations	0.765	0.512	0.283	0.247	
cumulative percentage variance of species data	6.5	9.4	10.3	10.7	
cumulative percentage variance of species–environment relation	60.5	87.3	95.9	100.0	
sum of all canonical eigenvalues					0.606

increasing temperature for 2007–2008). With respect to conductivity, only melanic clone 4 showed a significant response to increasing values (table 2). No other species–response curves were found to be significant.

4. DISCUSSION

This study has revealed that the melanic *D. pulex* complex at Churchill has contracted in distribution, disappearing from 31 per cent of the habitats that it occupied in 1984–1985. Within the habitats where it persisted, clonal composition was nearly stable in 59 per cent of

the rock pools. However, the remaining habitats showed either complete clonal replacement or the intrusion of new clones. The extent of this turnover varied among rock bluffs, with populations on bluff B showing much greater stability (as indicated by a Jaccard's similarity index (JSI) of 0.88) than populations on bluff A or C (JSI = 0.62 for both). The reasons for these differences are not clear, but previous work (Weider & Hebert 1987*a,b*) has shown that bluffs A and C are more exposed to Hudson Bay (i.e. salt spray, fluctuating conductivity/salinity levels) than bluff B.

Previous work by Dufresne & Hebert (1995) examined changes in clonal composition and clonal diversity in *Daphnia tenebrosa* populations (another member of the *D. pulex* species complex) in tundra ponds at Churchill. They found relatively stable clonal distributions and clonal compositions in these habitats over a 10-year (1981–1991) period. Clonal similarities (as measured by Renkonen's similarity statistic) were quite high (77.5%) for the period 1981–1987 and 87.5 per cent for the period 1987–1991, while a value of 64.3 per cent was recorded for the entire (1981–1991) 10-year period. Combined with our results, these data suggest that most populations of *Daphnia* at Churchill (60–65%) exhibit relatively stable clonal assemblages.

Although most populations showed stable clonal assemblages, we did observe distinct differences in the persistence of specific clones over the quarter-century. In particular, clone 1, which was the most common clone (35% of all isolates) in 1984–1985 (Weider & Hebert 1987*a,b*), saw its frequency decrease to 24 per cent by 2008. Conversely, clone 3 rose from 33 per cent of the clonal assemblage in 1984–1985 (Weider & Hebert 1987*a,b*) to 38 per cent in 2008. Clone 2 also increased from 11 to 16 per cent in the 25 years, while clone 4 decreased from 12 to 8 per cent. Clone 6, a minor member of the assemblage at 7 per cent in 1984–85, doubled in frequency to 14 per cent in 2008. Based on prior investigations, we expect that these shifts in clonal composition reflect changes in physico-chemical parameters (e.g. temperature, conductivity/salinity) or biotic (i.e. predators, competitors, parasites) factors (see below).

Table 2. Species response curves (results of GLMs for clonal presence/absence in response to temperature (temp) and conductivity (cond). Results are only shown for significant models. 'non-mel' refers to a group of various clones of the non-melanic *D. pulex* species complex.

environmental factor	clone	model coefficient B	s.e.	T-value	d.f.	F	p
temp	1	-0.1104	0.040	-2.757	252	7.76	0.006*
temp	3	-0.1401	0.039	-3.589	252	13.92	0.0002*
temp	6	-0.1519	0.061	-2.505	252	6.10	0.014
temp	'non-mel'	0.1359	0.041	3.289	252	11.53	0.001*
cond	4	0.0006	0.0002	2.813	252	8.73	0.003*

*Significant after Bonferroni correction ($p < 0.007$).

We noted an increase in the mean conductivity of the water in the rock pools from $453 \mu\text{S cm}^{-1}$ in 1984–1985 to $1252 \mu\text{S cm}^{-1}$ in 2007–2008. Most of this increase probably reflects a late October 2006 storm, which resulted in the inundation of many rock pools by a storm surge of salt water from Hudson Bay (M. Goodyear 2007, personal communication). This effect was indirectly a result of a longer ice-free period on Hudson Bay, which has occurred during the past several decades (ACIA 2005; Gagnon & Gough 2005). In past years, early formation of sea ice formed a barrier around the rock bluffs, protecting them from the surges of sea water driven by autumn storms.

Previous studies by Weider (1987) and Weider & Hebert (1987a,b) have shown that the major clones of melanic *D. pulex* in the Churchill rock pools show dramatic differences in salinity tolerance. In particular, clone 1 dominates low-salinity habitats near the back of the rock bluffs, and is found in habitats with a narrow range of conductivities/salinities ($85\text{--}1270 \mu\text{S cm}^{-1}$) and shows reduced survivorship when experimentally exposed to high salinities. Clone 1 showed a dramatic reduction in frequency over the past 25 years, and was only dominant in low-conductivity rock pools on bluffs B and C as depicted by the CCA ordination (figure 5). By contrast, as noted in §3, only clone 4 showed a significant response to increasing conductivities (table 2).

In addition to changes in conductivity, changes in mean water temperatures for most of these rock pools measured in 1985 and again in 2007–2008 closely mirror the approximately $4\text{--}5^\circ\text{C}$ air temperature increase at Churchill for the past 25 years (Environment Canada National Climate Data and Information Archive; http://www.climate.weatheroffice.ec.gc.ca/Welcome_e.html). These results are not unexpected given that temperatures in these small, shallow habitats are strongly influenced by ambient air temperatures. Further, the GLM analyses (table 2) support a significant negative association with temperature for three of the main resident (i.e. present in 1984–1985) melanic clones (1, 3 and 6), whereas non-melanics (as a group) showed a significant increase in frequency associated with higher temperatures. We have no data on whether there are differential thermal tolerances among the melanic and non-melanic *D. pulex* clones at Churchill, but previous work has shown that thermal tolerance differences are prevalent among clones in the *D. pulex* complex (Weider 1993; Palaima & Spitze 2004).

Above, we have focused on the likely role of abiotic factors in provoking the shifts in abundance and

distribution of melanic clones; biotic interactions are probably also involved. As noted, non-melanics have shown nearly a threefold increase in abundance in ponds with melanics since 1984–1985, leading to the displacement of melanics in 30 per cent of the ponds. If increasing temperatures explain this increase in non-melanic frequency, further increases in temperature should lead to further displacements of melanics in the future. Of course, this proposed association needs to be verified experimentally, as well as via long-term monitoring.

Interestingly, approximately 99 per cent of non-melanics are diploids, while all known melanic clones from Churchill are polyploids (Weider 1987; Dufresne & Hebert 1998). Dufresne & Hebert (1998) compared life-history features of diploid non-melanics with either weakly melanic or non-melanic polyploid clones under three temperatures ($10, 17, 24^\circ\text{C}$) in laboratory experiments. They found that polyploid clones matured more rapidly than diploid clones at the lowest temperature (10°C), but that diploids possessed the advantage at higher temperatures. This result follows other studies, which have shown that polyploids are favoured over diploids under low temperatures and vice versa (e.g. Zhang & Lefcort 1991; Otto & Whitton 2000). A note of caution needs to be mentioned in this diploid–polyploid comparison, given that there may be a confounding influence of the phylogenetic background of these different clonal lineages (i.e. multiple independent taxa have formed this assemblage through past hybridization events; Colbourne *et al.* 1998).

Churchill, like many other Arctic locales, has experienced dramatic increases in temperature over the past several decades. Therefore, our discovery that melanic polyploid clones have declined in abundance in the rock pools at Churchill, while non-melanics (primarily diploid) clones have shown a dramatic increase, parallels what might be predicted based on the earlier experimental work with polyploid–diploid lineages (Weider 1987; Dufresne & Hebert 1998).

Given the approximately 25-year sampling interval for this study, one might wonder about the magnitude of the annual metapopulation dynamics of rock pool *Daphnia* populations. Work done by Pajunen & Pajunen (2003, 2007) and colleagues (Haag *et al.* 2005, 2006; Altermatt *et al.* 2008) studied the dynamic nature of *Daphnia* metapopulations in a large set of Finnish rock pools ($n = 507$) scattered across islands in the Tvärminne archipelago over a 17-year period.

Interestingly, Pajunen & Pajunen (2003) found that 47 per cent of the *Daphnia* populations (consisting of three species—*Daphnia longispina*, *Daphnia magna* and *D. pulex*) in 1982 still persisted in 1998 in their original rock pools. They noted that each of the three *Daphnia* species could be characterized by unique niche characteristics, which undoubtedly played a role in reducing interspecific competition and maintaining a balance of patch (i.e. rock pool) occupancy by each species. Further, they noted that ‘pools with more persistent populations were deeper, in more sheltered places, and the vegetation of catchment area apparently buffered rapid changes’. Finally, they observed that rock pools near the sea more often lost their sediment (and thus their ephippial egg bank) owing to storms and winter ice scouring than inland rock pools. This suggests that populations in exposed rock pools had a higher probability of extinction.

Comparing the results from these Finnish rock pools with the Churchill populations, as noted above, we detected a 69 per cent pond occupancy rate of melanistic clones from 1984 to 2008. However, there appear to be no clear differences in the pond characteristics for persistent versus extinct populations at Churchill. As noted above, salinity/conductivity differences between ponds are dramatic, but no clear differences in salinity/conductivity were observed between these two sets of ponds. Extinct populations appeared to be haphazardly distributed across the rock bluffs (figure 1), although rock pool populations that contained clone 1 as the dominant clone appeared to have a high probability of going extinct (figures 2–4).

The results from our study strongly support the conclusion that rock pool metapopulations are good model systems for long-term research on environmental change. Such studies are critically needed, given the current evidence for global change (ACIA 2005; Altermatt *et al.* 2008). A recent study by Altermatt *et al.* (2008) in the Tvärminne rock pool *Daphnia* system has demonstrated that both metapopulation and metacommunity dynamics can be greatly affected by climate changes impacting these systems. Climate change, which influences local weather patterns, can cause long-term fluctuations not only in temperature but also precipitation. These authors noted that colonization rates among rock pool *Daphnia* populations increased fourfold with warmer, drier weather, presumably because drying of rock pools increases the passive transport of ephippial eggs. They also observed species-specific effects, which resulted in changes in the metacommunity structure through time. Results from such studies provide needed replication and more easily tractable documentation of long-term population (genetic) changes that may be related to concomitant changes in important environmental parameters.

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