Genetic characterization of an arctic *zooplankter*: insights into geographic polyploidy

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SUMMARY

Species of *Bosmina* from the temperate regions of North America and Europe are diploid and reproduce by cyclical parthenogenesis. By contrast, this study provides evidence that the dominant bosminid taxon in High Arctic lakes reproduces by obligate parthenogenesis and is a polyploid derived from interspecific hybridization. *Sinobosmina liederi*, a species common in temperate North America, is likely to have been one parent of these hybrids, but the other parent is unknown. As neither parent was detected in the Arctic, it seems unlikely that the hybrid clones that now occupy arctic lakes were synthesized locally. Most habitats contained only one or two clones, despite a total of 38 clones in the region, suggesting that priority effects have been important in restricting diversity within single lakes. The high regional diversity of arctic bosminids could reflect either repeated hybridization between the parent taxa or the genetic instability of newly formed polyploid lineages. These processes would produce hybrid polyploids that are considerably more diverse than their sexual parent taxa, and this difference in genetic diversity may confer an advantage to the polyploid biotype. As many zooplankton taxa from the arctic possess genetic characteristics similar to those of bosminids, these processes may provide a general explanation for the widespread occurrence of polyploids in the Arctic.

1. INTRODUCTION

Polyploidy is particularly common in plants (Stebbins 1950), but it also occurs in a broad range of animal groups (Bell 1982). Although the evolutionary importance of polyploidy in animals is not entirely clear (Bell 1982; Beaton & Hebert 1988), its influence on plant evolution is well established, as perhaps 50% of all angiosperm species are of polyploid origin (Soltis & Soltis 1995). Hybridization appears to have been important in the generation of most polyploids and it has often been accompanied by transitions to asexual reproduction (Vandel 1928, 1940; Suomalainen *et al.* 1976; Dawley & Bogart 1989; Bell 1982). In addition, polyploid taxa are known to have different ecological attributes from their diploid counterparts. In particular, geographic surveys have suggested that polyploids are most common in harsh or unstable environments (Vandel 1940; Stebbins 1950; Bell 1982). However, the factors responsible for this patterning remain unclear. For example, several explanations have been advanced to account for the higher incidence of polyploids in arctic than in temperate floras. Stebbins (1950, 1984) attributed this pattern to the favourable conditions for the synthesis of polyploids in the Arctic, linking their origins to secondary contacts and hybridization between populations which diverged in isolated refugia during glacial maxima. However, other investigators have suggested that this pattern is due simply to shifts in plant growth form, attributing the rise in abundance of polyploids to the dominance of perennial shrubs in polar environments (Raunkiaer 1934; Lewis 1980).

As the factors underlying the abundance of polyploidy in arctic floras remain unresolved, studies on the geographical patterning of polyploidy in other taxa are needed to elucidate the ecological and evolutionary factors that differentiate polyploids from diploids. The freshwater zooplankton are a favourable target for these studies as numerous closely allied organisms have broad geographic distributions. Intensive genetic studies have so far been carried out on just one of the 100 or so genera of freshwater zooplankton, and this work has established the occurrence of polyploidy in the cladoceran genus *Daphnia* (Beaton & Hebert 1988). Polyploid lineages are so far only known from the *D. pulex* complex, and these are all obligate parthenogens that have arisen through hybridization (Weider *et al.* 1987; Beaton & Hebert 1988; Hebert *et al.* 1988; Dufresne & Hebert 1994, 1995; Van Raay & Crease 1995, Dufresne & Hebert 1997). It is significant that polyploid *Daphnia* are invariably restricted to the Arctic, while numerous studies of hybridization between *Daphnia* from a variety of species complexes in temperate regions have never detected elevated ploidy

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levels (e.g. Taylor & Hebert 1993; Spaak 1995; Schwenk & Spaak 1995). Even the obligately parthenogenetic *Daphnia* from the temperate zone, many of which are of hybrid origin, are also invariably diploid (Hebert *et al.* 1992; Hebert *et al.* 1989; Crease & Lynch 1991).

Although there remains a need to examine further the factors responsible for the latitudinal shifts of ploidy levels in the *D. pulex* complex, it also seems important to investigate if this pattern represents a generality in the Cladocera. Genetic surveys of other cladoceran taxa should be worthwhile, as all cladocerans possess traits (an apomictic phase in the life cycle, and no sex chromosomes) which simplify the transition to both obligate parthenogenesis and polyploidy (Dufresne & Hebert 1994). Although prior studies on several cladocerans outside of the genus *Daphnia* have failed to detect polyploids, this work has focused almost entirely on populations from the temperate zone. For example, all ten species in the genus *Bosmina* from temperate North America are diploid and reproduce by cyclic parthenogenesis (DeMelo & Hebert 1994*a*,*b*). In this study we extend the geographic scope of work on the genus *Bosmina* by examining the genetic characteristics and ploidy levels of populations in the High Arctic of Canada.

2. MATERIALS AND METHODS

Zooplankton collections were made from over 200 lakes on the Melville Peninsula, Baffin Island, Ormonde Island and Jens Munck Island, N.W.T., Canada, during August 1990, 1991 and 1994 (figure 1). Collections were made by oblique tows of a 200 μm mesh net from a float-equipped helicopter that taxied slowly across each lake. Bosminids were present in 26 of these lakes and, with the exception of a single population of *Eubosmina*, all belonged to the subgenus *Sinobosmina*, as indicated by the position of the lateral head pore between the rear branching of the forked lines of the fornix (Lieder 1983; DeMelo & Hebert 1994*b*). Sinobosminid population 18 is not indicated in figure 1 as the flight records for this excursion were lost. Following taxonomic assignment, individuals were either immediately electrophoresed or cryopreserved for later analysis.

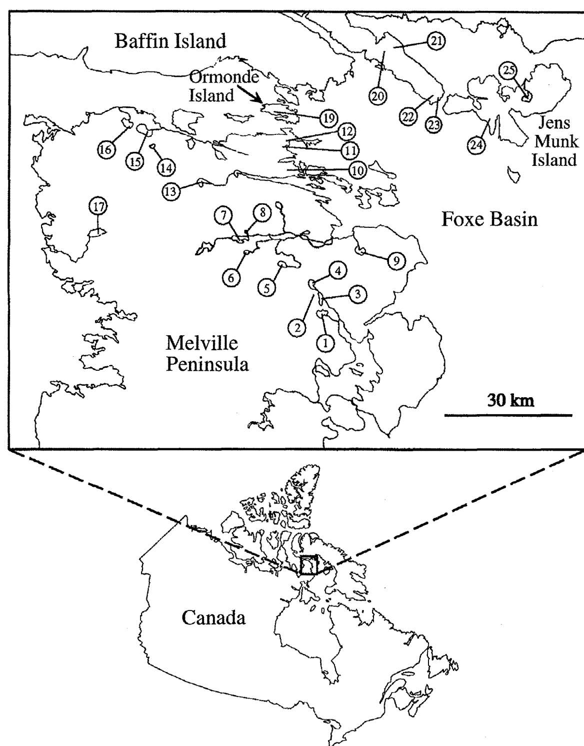

Figure 1. Locations of *Sinobosmina* populations on the Melville Peninsula, and Baffin, Ormonde and Jens Munck Islands, N.W.T., Canada.

Levels of genetic variability were characterized for each population using standard methods of cellulose acetate gel electrophoresis (Hebert & Beaton 1993). Wherever possible, at least 24 individuals from each population were screened for variation at eight enzyme loci known to provide adequate staining resolution in bosminids (DeMelo & Hebert 1994*a*). These loci included aldehyde oxidase (*AO*; EC 1.2.3.1) arginine phosphokinase (*APK*, EC 2.7.3.3), aspartate aminotransferase (*AAT*; EC 2.6.1.1), fumarate hydratase (*FUM*; EC 4.2.1.2), phosphoglucose isomerase (*GPI*; EC 5.3.1.9), lactate dehydrogenase (*LDH*; EC 1.1.1.27), malic dehydrogenase (*MDH*; EC 1.1.1.40) and phosphoglucomutase (*PGM*; EC 2.7.5.1). With the exception of *LDH*, all of the enzymes were polymorphic. However, as *MDH* and *AO* phenotypes could not be interpreted reliably, these loci were excluded from further analysis. Alleles at the remaining five loci were numerically designated, with the slowest migrating allele labelled 1, and faster migrating alleles numbered sequentially.

Analyses of genetic variability were performed using Biosys-1 (Swofford & Selander 1988) unless otherwise noted. Allele frequencies were determined by direct count for all populations. The genotypic information on each population was summarized by calculating the following parameters: observed and expected values of heterozygosity (H_o and H_e, respectively), the fixation index ($F = (H_e - H_o)/H_e$)), conformance to Hardy–Weinberg (HW) equilibrium (based on a χ^2 test), and the genotypic diversity ratio (GDR) (Hebert *et al.* 1988). Heterozygote banding patterns were often inconsistent with the known quaternary structure of the enzyme (Ward 1977), showing asymmetric or 'unbalanced' patterns of staining intensity typical of polyploids. To test the null assumption that these taxa are diploid sexuals, and that unbalanced phenotypes simply represented allelic differences in the activity of their enzyme products, balanced and unbalanced phenotypes were pooled into a single heterozygous class prior to performing the GDR and HW analyses. The GDR for each population was calculated using a BASIC computer program which compared the observed number of multilocus genotypes against the mean number expected (based on 100 Monte-Carlo simulations) in a sexual population with identical allele frequencies. The GDR approximates unity for populations whose genotypic frequencies are in both HW and linkage equilibrium, but is much less in populations that reproduce via obligate parthenogenesis. Thus, this ratio facilitates the diagnosis of reproductive modes by exploiting the paucity of unique multilocus genotypes commonly associated with ameiotic reproduction.

An analysis of the accumulation of unique multilocus genotypes detected in relation to the number of sites sampled was conducted using the combinatorial analysis outlined in Hebert *et al.* (1988). This estimation of clonal diversity was obtained using a computer program that counted the number of clones detected following the random sampling, without replacement, of 1, 2, 3,... *n* populations. This was repeated 100 times and the mean number of clones detected for each level of sampling effort was calculated. A G_{ST} analysis, and the *D*-statistic of Lynch & Crease (1990), were used to determine the relative importance of within and among population diversity.

Using Cavalli-Sforza & Edwards's (1967) chord distance, allelic frequencies were used to generate a matrix of genetic distances among populations. To assess the genetic relationships

among arctic and temperate populations of *Sinobosmina*, allele frequency data for 16 temperate populations of *S. liederi* and *S. freyi*, as well as a population of the closely related species *Bosmina longirostris* (DeMelo 1993), were included in the genetic distance analyses. Multidimensional scaling (Lessa 1990) of these genetic distances was performed to visualize genetic relationships among populations. As genome size analyses (P. Hebert, unpublished data) suggest that arctic bosminids are tetraploid, we repeated this distance analysis with allele frequencies in arctic populations estimated by assuming that all individuals were tetraploid. Therefore, a heterozygote with unbalanced staining activity was assumed to have three copies of the allele producing the stronger band, and one copy of the allele generating the weaker band.

3. RESULTS

Allozyme variation was detected at 5 enzyme loci (table 1), while the other reliably scorable locus (*LDH*) was monomorphic in all populations. A total of 38 unique multilocus genotypes were detected among the 25 populations (table 1), and the mean number of alleles observed per locus was 2.8. Both individual heterozygosities and the percentage of polymorphic loci were high, averaging 43% (s.e. $=0.03$) and 50.7% per population, respectively. In each population the multilocus genotypic diversity was significantly (one-tailed *t*-tests, $p<0.05$) less than expected in a sexually reproducing taxon with identical allele frequencies (average GDR $=0.18$ (s.e. $=0.04$)) (table 2). Moreover, HW deviations were detected in 60 out of 80 Bonferroni corrected tests (table 2). In all but one instance, the observed HW deviations were due to heterozygote excess, an observation reinforced by the high negative fixation indices (average $F=-0.79$ (s.e. $=0.04$)) for these populations.

Based on these genetic characteristics, as well as the absence of males, it was concluded that these bosminid populations reproduce by obligate parthenogenesis, and, therefore, each of the unique multilocus genotypes is hereafter termed a clone. Thirty-three of the 38 clones possessed, at one or more loci, heterozygote patterns typical of polyploids, while the remaining five clones (clones 3, 6, 7, 8, and 12; table 1) showed heterozygote banding patterns typical of those expected in diploids (Ward 1977).

The number of clones per lake averaged 2.4. The two most common clones (clones 1 and 9) accounted for 35% of the animals surveyed, and were detected in eight of the 25 populations (table 2). As many lakes contained just one or two clones (table 2), a significant fraction of the genetic diversity was due to inter-population differentiation ($G_{ST}=0.7$, s.e. $=0.003$, $D=562.8$, $p<0.01$). The combinatorial method used to generate a saturation curve of clonal diversity in relation to the number of lakes sampled (figure 2) did not reach an asymptote, indicating that this study has revealed only a portion of the clonal diversity in the eastern Arctic.

Cavalli-Svorza and Edwards's chord genetic distances between arctic populations averaged 0.12, and ranged from 0.00 to 0.49. Multidimensional scaling analysis of the distance matrix produced a graph suggesting a close genetic affinity between the arctic populations and temperate populations of *Sinobosmina liederi*, with genetic distances as low as 0.05 (figure 3). Two other taxa, *S. freyi*, and *B. longirostris*, were clearly distinct from the arctic populations, with minimum genetic distances of 0.39 and 0.38, respectively. The circles on figure 3 merely enclose all populations from a given species and are not the product of a statistical procedure. The version of the distance analysis which assumed tetraploidy produced an MDS diagram (result not shown) essentially identical to that in figure 3. Those clones (clones 3, 6, 7, 8 and 12) showing allozyme phenotypes suggestive of diploidy do not possess diagnostic alleles which distinguish them from clones that appear to be polyploids (see table 1); and a comparison of the genetic distances that separate arctic clones (i.e. a comparison among clones rather than a comparison among populations) revealed that putative diploid clones do not form a distinct cluster, but are instead

Table 1. *Unique multilocus genotypes (clones) detected for parthenogenetic* Sinobosmina *from the High Arctic*

(Asterisks represent the more intensely stained electromorph of an unbalanced heterozygous phenotype.)

	locus				
clone	*GPI*	*PGM*	*APK*	*AAT*	*FUM*
1	13*	33	2*3	33	13
2	13*	33	22	33	23
3	33	33	22	33	23
4	13*	33	22	34	13
5	13*	35	22	33	23
6	13	35	22	33	23
7	13	33	22	33	13
8	13	33	22	34	13
9	1*3	33	22	33	13*
10	13*	3*5	22	33	23
11	13*	3*5	22	33	23
12	13	35	22	33	13
13	1*3	35	22	33	13*
14	23*	35	22	23*	23
15	13*	35	12*	33	23
16	13*	33	22	33	13
17	1*3	33	12*	33	13
18	13*	33	12*	33	13
19	13*	3*5	22	33	13
20	13*	3*5	12*	33	23
21	13	35	22	23*	23
22	13*	33	22	33	23*
23	13*	3*5	22	33	13*
24	1*3	33	22	33	23
25	13	23*	22	33	13*
26	13*	33	22	33	33
27	13*	3*5	22	33	33
28	13	33	22	33	13*
29	33	33	22	33	23*
30	1*3	3*5	22	33	13*
31	13*	25	22	33	13*
32	13*	3*5	22	33	23*
33	13*	33	22	33	13*
34	33	23*	22	33	13*
35	33	23*	22	33	33
36	1*3	33	12	33	13*
37	1*3	33	12*	33	13*
38	13*	35	12*	33	23

Table 2. *Clonal frequencies and population genetic characteristics of parthenogenetic* Sinobosmina *populations from lakes in the Canadian High Arctic*

(HW denotes a significant (Bonferroni corrected; $p < 0.032$) Hardy–Weinberg disturbance at from one to five allozyme loci. GDR is the genotypic diversity ratio (see text). HET are individual heterozygosities. HW, GDR and HET analyses were not applied where the population sample size (N) was < 20.)

		clone	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
population	location	#clones																				
1	Melville Pen.	4	0.69				0.21								0.07	0.03						
2	Melville Pen.	3	0.38															0.50				
3	Melville Pen.	2	0.95											0.05								
4	Melville Pen.	1	1.00																			
5	Melville Pen.	1									1.00											
6	Melville Pen.	4											0.60								0.12	0.03
7	Melville Pen.	1			1.00																	
8	Melville Pen.	1																1.00				
9	Melville Pen.	2	0.91	0.09																		
10	Melville Pen.	5				0.18	0.09	0.27	0.27	0.18												
11	Melville Pen.	4																				
12	Melville Pen.	4																				
13	Melville Pen.	1					1.00															
14	Melville Pen.	3			0.05						0.90											
15	Melville Pen.	1																		1.00		
16	Melville Pen.	2																	0.81	0.19		
17	Melville Pen.	1															1.00					
18	Melville Pen.	4		0.53	0.17																	
19	Ormonde Is.	4																				
20	Baffin Is.	2																				
21	Baffin Is.	1																				
22	Baffin Is.	3											0.42									
23	Baffin Is.	1																				
24	Jens Munck Is.	1																				
25	Jens Munck Is.	4									0.85	0.11										
N (each clone):			117	19	17	2	51	3	3	2	132	9	44	1	2	1	22	15	50	4	7	2

Table 2. *(Cont.)*

		clone	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	N	HW	GDR	HET
population	location	#clones																						
1	Melville Pen.	4																			29	3	0.17	0.56
2	Melville Pen.	3							0.13												8			
3	Melville Pen.	2																			22	3	0.10	0.50
4	Melville Pen.	1																			44	2	0.05	0.50
5	Melville Pen.	1																			44	2	0.11	0.33
6	Melville Pen.	4	0.25																		60	4	0.11	0.55
7	Melville Pen.	1																			11			
8	Melville Pen.	1																			11			
9	Melville Pen.	2																			32	3	0.11	0.48
10	Melville Pen.	5																			11			
11	Melville Pen.	4										0.09		0.73	0.09	0.09					11			
12	Melville Pen.	4						0.36	0.52		0.06						0.06				33	2	0.40	0.26
13	Melville Pen.	1																			44	3	0.05	0.50
14	Melville Pen.	3																0.10			22	2	0.24	0.34
15	Melville Pen.	1																			33	3	0.05	0.50
16	Melville Pen.	2																			21	3	0.10	0.50
17	Melville Pen.	1																			22	4	0.03	0.67
18	Melville Pen.	4							0.27		0.03										30	0	0.68	0.17
19	Ormonde Is.	4			0.02		0.39			0.02					0.56						41	2	0.25	0.40
20	Baffin Is.	2				0.60		0.40													20	2	0.27	0.27
21	Baffin Is.	1			1.00																22	3	0.08	0.50
22	Baffin Is.	3																	0.16	0.42	19			
23	Baffin Is.	1			1.00																22	2	0.13	0.50
24	Jens Munck Is.	1		1.00																	22	2	0.13	0.33
25	Jens Munck Is.	4			0.02								0.01								81	2	0.44	0.36
N (each clone):			15	22	47	12	16	20	26	1	3	1	1	8	24	1	2	2	3	8	715			

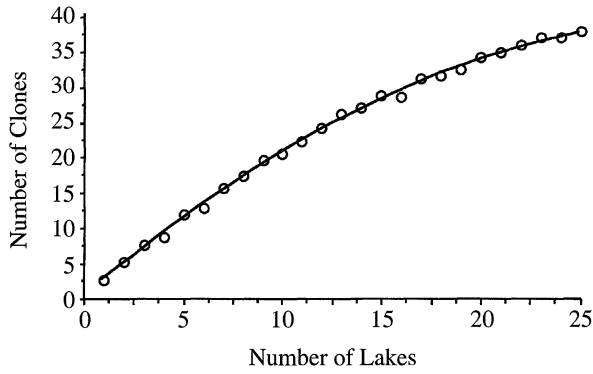

Figure 2. Graph showing the relationship between the number of lakes surveyed and the number of clones of *Sinobosmina* detected from the eastern High Arctic of Canada.

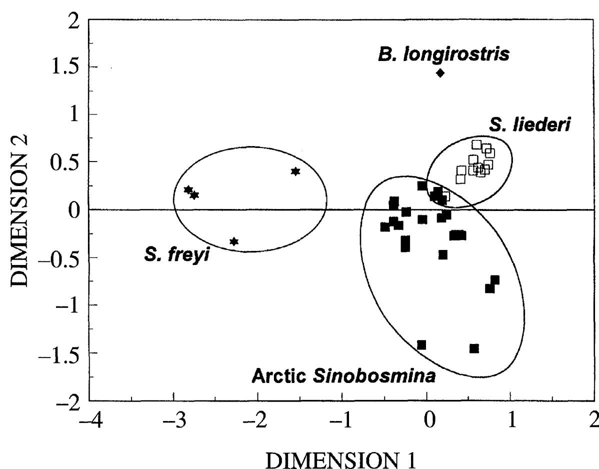

Figure 3. Multi-dimensional scaling ($r^2 = 0.980$, Kruskal test in two dimensions) of Roger's genetic distances between populations of *Bosmina longirostris*, *Sinobosmina freyi*, *S. liederi*, and arctic *Sinobosmina*.

evenly distributed throughout the genetic space occupied by arctic bosminids (result not shown).

Although the position of the lateral headpore assigned arctic populations to the subgenus *Sinobosmina*, further morphological analysis of individuals from ten arctic populations revealed their divergence from both known North American members of this subgenus. In particular, differences in body size and in the morphology of the taxonomically important proximal pecten on the post-abdominal claw were detected. Arctic *Sinobosmina* were substantially larger than their temperate zone counterparts with adults ranging in length from 528 to 628 μm, and averaging 584 μm ($n = 50$). By contrast, body lengths range from 324 to 480 μm in *S. liederi*, and from 389 to 590 μm in *S. freyi* (DeMelo & Hebert 1994*b*). Furthermore, the arctic animals possessed a proximal pecten that was more similar to that of *B. longirostris* than to other *Sinobosmina* (see DeMelo & Hebert 1994*b*).

4. DISCUSSION

The present study has established that most if not all bosminid clones in arctic Canada are polyploid. Thirty-three of the 38 clones in the eastern Arctic possessed unbalanced allozyme phenotypes which are indicative of polyploidy (Beaton & Hebert 1988; Little & Hebert 1994, 1997; Turgeon & Hebert 1994). In contrast, such phenotypes have never been reported in temperate zone populations (DeMelo & Hebert 1994*a*). Those arctic clones not showing aberrant allozyme phenotypes did not show any notable allelic differences from other clones, and may in fact also be polyploid, as normal phenotypes can occur in polyploids with an even number of gene copies (four, six, etc.) so long as each allele is represented by an equivalent number of copies. This possibility is supported by scanning microdensitometry studies, which have shown that arctic sinobosminids have a genome size twice as large as that of their temperate zone counterparts, suggesting their tetraploid status (P. Hebert, unpublished data).

For cladoceran populations, each type of breeding system produces a characteristic genetic architecture. Cyclic parthenogens possess genotypic arrays that approximate to those of sexual populations, as Hardy–Weinberg disequilibria and non-random associations of genotypes are rare (Hebert *et al.* 1989). Temperate bosminid populations possess this 'sexual' genetic structure (DeMelo & Hebert 1994*a*). By contrast, this study shows that bosminid populations in the Arctic have marked HW disturbances, and multilocus genotypic diversities are invariably lower than expected under sexual reproduction. These genetic characteristics, and our failure to detect males in any of the 25 populations analysed, indicate that sexual recruitment is either extremely rare or absent entirely, i.e. arctic bosminids are likely to be obligate parthenogens. A similar latitudinal shift from sexuality in temperate regions to obligate parthenogenesis in the Arctic has been documented in the genus *Daphnia* (e.g. Weider *et al.* 1987; Weider & Hobæk 1997).

The genetic characteristics of arctic bosminids are consistent with the expected results of interspecific hybridization. Individual heterozygosities are far higher than those of temperate bosminids (43% versus 10%; DeMelo & Hebert 1994*a*), and arctic populations were, on average, polymorphic at a substantially higher proportion of their loci (50.7% versus 15.8%). Interspecific hybrids ordinarily show fixed heterozygosity at loci where parental species possess diagnostic substitutions, and such a state is nearly achieved in arctic *Sinobosmina* at both the *FUM* and *GPI* loci. However, this fixed heterozygosity did not involve alleles which are taxonomically diagnostic in any two of the bosminid species (*S. liederi*, *S. freyi*, *B. longirostris*; see DeMelo & Hebert 1994*a*) used in our comparison of genetic identities. Moreover, arctic bosminids did not appear morphologically intermediate between any two putative parental species, as is often the case in other hybrids (see Gießler (1997) for a cladoceran example). Nevertheless, based on its close genetic affinity, *S. liederi* is likely to have been one of the parental taxa of these arctic animals, but the second parental species has eluded detection. Our inability to identify a second parental taxon, and the absence of both parents from the Arctic, suggests that arctic sinobosminid clones are not F1 hybrids that have been synthesized *in situ*. Instead, they probably represent

stabilized parthenoforms whose clonal diversity reflects either the generation of diversity through repeated hybridization events between the parent taxa, or substantial mutational and recombinational diversification that occurred after the generation of a unisexual hybrid.

This study revealed that, on average, most lakes contained only two of the 38 allozymically distinct clones detected in the region. The presence of only a small portion of the total regional clonal diversity in single habitats has been noted in other parthenogenetic microcrustaceans (e.g. Weider *et al.* 1987; Boileau *et al.* 1992; Van Raay & Crease 1995; Little & Hebert 1997). In some cases, selection has been shown to play an important role in restricting local clonal diversity (Weider & Hebert 1987; Wilson & Hebert 1993). Founder effects have also been implicated in curbing local diversity, and might be especially potent in cladocerans because single colonists can rapidly saturate an environment due to their parthenogenetic mode of reproduction. Secondary colonists will have little chance ($1/N$) of rising to fixation if they are ecologically equivalent to the resident clone. Such priority effects should be of particular importance in lakes because N will be large, and this may be the case for arctic sinobosminid populations as they are restricted to these habitats.

Despite this low diversity in single habitats, regional diversity in arctic bosminids is substantial. The present results are therefore concordant with studies on the cladoceran genus *Daphnia* (Weider *et al.* 1987; Hebert *et al.* 1988; Van Raay & Crease 1995) and on several genera of ostracode crustaceans (Havel *et al.* 1990; Little & Hebert 1997), which have established that polyploid taxa are particularly common in the Arctic and that their genotypic diversity is ordinarily high. Indeed, sympatric sexual and/or diploid species are often genetically impoverished in comparison (Weider *et al.* 1987; Beaton & Hebert 1989; Boileau *et al.* 1992; Taylor & Hebert 1994; Turgeon & Hebert 1994; Little & Hebert 1997). In the case of obligately parthenogenetic members of the *D. pulex* complex there is even evidence of a latitudinal increase in clonal diversity associated with the rise in frequency of polyploid hybrids in the far North (Weider *et al.* 1987; Beaton & Hebert 1988; Dufresne & Hebert 1997). This pattern in the Cladocera is compatible with Stebbins's (1984) hypothesis that the Arctic would provide the ideal setting for ploidy shifts due to extensive hybridization between sexual taxa formerly restricted to glacial refugia.

The subsequent displacement of sexual taxa by their polyploid derivatives might be attributable to a physiological advantage to polyploids at low temperatures (Thompson 1990), but this hypothesis is difficult to separate from the heterotic effects of hybridization. Towards a more comprehensive, although not mutually exclusive explanation, we emphasize the comparatively low genetic diversity of diploid sexuals in the Arctic. This low diversity has been linked to small sizes of populations restricted to refugia during glacial maxima (Stebbins 1984), and to founder events that occurred during colonization of the recently deglaciated habitats (Boileau *et al.* 1992). These recently 'bottlenecked' sexual taxa would have considerably less genetic diversity than the polyploid hybrids that form when pairs of colonizing species repeatedly hybridize. It is this difference in genetic diversity that may confer an advantage to polyploid hybrids in single habitats, and also allow them to colonize a greater range of habitats. In addition, recent work has shown that the genomes of newly arisen allopolyploids are very unstable and can diversify markedly over just a few generations (Soltis & Soltis 1993, 1995; Song *et al.* 1995). This segregation of genetic diversity might well be an additional source of clonal diversity in populations of arctic bosminids and other polyploids.

In summary, arctic bosminids appear to represent a new taxon that arose through the hybridization of two members of the subgenus *Sinobosmina*. This hybridization event apparently provoked the generation of polyploid clones, and the transition to an obligately parthenogenetic mode of reproduction. Polyploid speciation via hybridization is common in plants, and our results suggest that it has also been important in cladoceran crustaceans, perhaps because a pre-existing apomictic phase in the life cycle facilitated the shift to obligate parthenogenesis. The high clonal diversity that characterizes these forms may reflect either multiple hybrid origins, or genomic instability following polyploidization. Given such instability, polyploid speciation can rapidly create biotypes with ecological characteristics that are not only distinct from those of their parental taxa, but also the original polyploid derivative. These rapid adaptive 'mini radiations' may be of particular importance in newly arisen habitats, where extreme conditions or the loss of genetic diversity through population bottlenecks may constrain the pool of colonizing taxa.

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