Ecological genetics of Norwegian *Daphnia*. III. Clonal richness in an Arctic apomictic complex

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Arctic pond populations of *Daphnia pulex* on Svalbard, off the north Norwegian coast, were assayed for clonal richness. A total of 21 unique clones from 20 ponds were distinguished by allozyme electrophoresis at seven enzyme loci. Seventeen clones showed unbalanced electromorph banding patterns at certain enzyme loci, which suggests that they are polyploids. Each pond harboured an average of 1.7 clones (range 1–4). The most common clone was found in six ponds, and accounted for 23.5 per cent of all animals screened. Most clones were found only in one or two ponds. No discernible geographical patterns could be detected in clonal distributions, and all sampled areas held unique clones. The data suggest that our sampling effort has uncovered only a small subset of a much larger array of clones on this remote arctic archipelago, and indicates that the genetic structure of this apomictic complex is one of the most fragmented among asexual organisms.

Keywords: biogeography, clonal richness, *Daphnia*, parthenogenesis, polyploidy, Svalbard.

Introduction

The presence of substantial genetic (clonal) variation in populations of asexual organisms (Parker, 1979; Bell, 1982) has led to numerous attempts at explaining the mechanism maintaining clonal coexistence in these populations (Futuyma *et al.*, 1981; Lynch, 1984; Ayre, 1987; Christensen *et al.*, 1988), which can be directly related to the study of the evolutionary advantages/disadvantages of sexual reproduction (Bell, 1982).

Recent studies have revealed that pond populations of members of the freshwater microcrustacean, *Daphnia pulex* complex in North America contain high levels of genetic (clonal) diversity (Lynch, 1983; Hebert & Crease, 1983; Weider & Hebert, 1987a; Hebert *et al.*, 1988), which appear to be maintained by both biotic (Wilson & Hebert, 1992) and abiotic (Weider & Hebert, 1987b) factors. Contrary to earlier expectations of an attenuation of clonal diversity with increasing latitude (Weider *et al.*, 1987), arctic populations contain high levels of genetic (clonal) richness.

The predominant reproductive mode in this complex is via obligate parthenogenesis (Hebert *et al.*, 1988), particularly in the arctic (Weider *et al.*, 1987), while cyclic parthenogenesis prevails south of the Laurentian Great Lakes (Innes *et al.*, 1986; Hebert *et al.*, 1988). Within this broad geographic range, this species complex contains large numbers of electrophoretically distinct clones, which probably number in the tens of thousands. A fraction of these clones are polyploids, although this is not a prerequisite for their asexual reproductive mode (Beaton & Hebert, 1988). Molecular evidence indicates that the asexual complex has polyphyletic origins (Crease *et al.*, 1989; Hebert *et al.*, 1989), i.e. obligately parthenogenetic clones have arisen many times from cyclically parthenogenetic ancestors.

Although members of the *Daphnia pulex* complex have an even broader distribution in the Old World, much less is known about variation in their reproductive mode and clonal diversity outside North America (Ward & Geissler, 1988). Obligate asexuality was, in fact, first reported from the arctic islands of Svalbard (Olofsson, 1918), and is generally regarded as the predominant breeding mode in the arctic, based both on the scarcity or absence of males in arctic populations (Haney & Buchanan, 1987), and in the obligately

parthenogenetic production of diapausing eggs (Weider & Hebert, 1987b; Weider *et al.*, 1987).

The present study was undertaken to investigate clonal richness of members of the *D. pulex* complex in a remote, arctic area. Svalbard is an archipelago situated about 1000 km north of the European mainland, and about 500 km east of Greenland. If clonal diversity in Svalbard is comparable to that of North America, then one must consider the possibility that this apomictic complex extends over a vast range in a circumpolar fashion, and includes all of Siberia, the arctic islands, Iceland, Greenland and most of North America.

Materials and methods

Sampling was conducted on Spitsbergen (the largest island of the Svalbard archipelago) in August 1987. The field work was based at the Norwegian Polar Research Institute's research station at Ny-Ålesund on the western coast (79° 55′ N, 11° 56′ E). Twenty ponds were successfully sampled. Seventeen of them were situated along the Kongsfjord or its vicinity (Fig. 1). Along the Isfjord, another three ponds were sampled. Most ponds were less than 1 m deep, and all are situated along the coastline less than 2 km from the sea at altitudes below 50 m a.s.l. Some morphometric and physico-chemical characteristics of the ponds are given (Table 1).

Animals were collected and transported live in thermos bottles to the laboratory, where they were sorted individually into the wells of microtiter plates within 12 h of collection. Each animal was placed in 10 μl 0.001 M mercaptoethanol solution, and frozen at $-80°C$ for later electrophoretic analysis. Replicate samples from each pond were preserved in formalin for later identification and morphological analysis. Surface water samples from each pond were analysed for conductivity (μS cm^{-1}) and short-wave light absorption (at 254 and 384 nm).

Electrophoresis was undertaken using cellulose acetate gels (Helena Laboratories, Beaumont, TX), following the procedures of Hebert & Beaton (1989). The following enzymes were screened: aldehyde oxidase (AO); glutamate-oxaloacetate transferase (GOT); lactate dehydrogenase (LDH); malate dehydrogenase (MDH); mannose-phosphate isomerase (MPI); phosphoglucose isomerase (PGI); and phosphoglucomutase (PGM). For the remainder of the paper, the term 'electrophoretic clone' will be used to designate unique seven-locus genotypes as detected by electrophoresis. The use of marker animals propagated from clones isolated from the Canadian arctic allowed gel scoring and allele designations to be comparable

with results from Canada (Weider & Hebert, 1987a,b; Weider *et al.*, 1987). Data were obtained on a total of 1316 animals. In addition, we included 57 animals from pond E, which was resampled in July 1991.

Genetic relatedness between electrophoretic clones was analysed by computing a simple matching coefficient between each pair of clones (Innes *et al.*, 1986; Weider *et al.*, 1987); we assumed that all clones were tetraploid based on the criteria of Weider *et al.* (1987). Coefficients of similarity were converted to Euclidean distances by taking the square root of the complement of the coefficient (Sneath & Sokal, 1973). The genetic distance matrix was then subjected to a principal coordinate analysis (Gower, 1966), using the NTSYS-PC program (Rohlf, 1990).

A Mantel test (Mantel, 1967) was used to analyse for geographic patterns in clonal distribution, by first constructing a similarity matrix between the clonal arrays in each pond, based on Sorensen's index (Pielou, 1984), and then correlating this similarity matrix with a matrix of distances (km) between ponds.

Results

In the 20 ponds, we detected a total of 20 distinct electrophoretic clones in 1987 (Table 2). One additional electrophoretic clone was found in the 1991 sample from Pond E, for a total of 21 clones. Seventeen of the detected clones showed 'unbalanced' electromorph banding patterns (Weider *et al.*, 1987) at one enzyme locus (16 at *PGM* and 1 at *PGI*, Table 2), suggesting that they are polyploids (Beaton & Hebert, 1988). Heterozygosity values (measured as the fraction of heterozygous loci) ranged from 0 to 0.571 (mean = 0.327, S.E. = 0.030). Svalbard animals showed extensive allelic overlap with animals from the Canadian arctic. Nearly all the alleles from Svalbard are also present at Churchill, Manitoba (Weider & Hebert, 1987a) and/or Igloolik, N.W.T. (Weider *et al.*, 1987), with the exceptions of the slow (0) alleles observed at the *LDH* and *MDH* loci (Table 2).

The clonal composition of each pond is given (Table 3). On average, each pond held 1.7 electrophoretic clones (range: 1–4, S.E. = 0.9). There is no readily apparent pattern in the geographical distributions of clones or clonal groups. All the investigated areas held unique electrophoretic clones, although the more common clones occurred in several areas. Clone 1 was most common; it occurred in six ponds and constituted 23.5 per cent of all animals sampled. On average, each electrophoretic clone occurred in 1.6 ponds (S.E. = 0.25), and 13 clones were detected only in one pond each (Table 2). The Mantel test detected no significant geographical patterning (matrix correlation
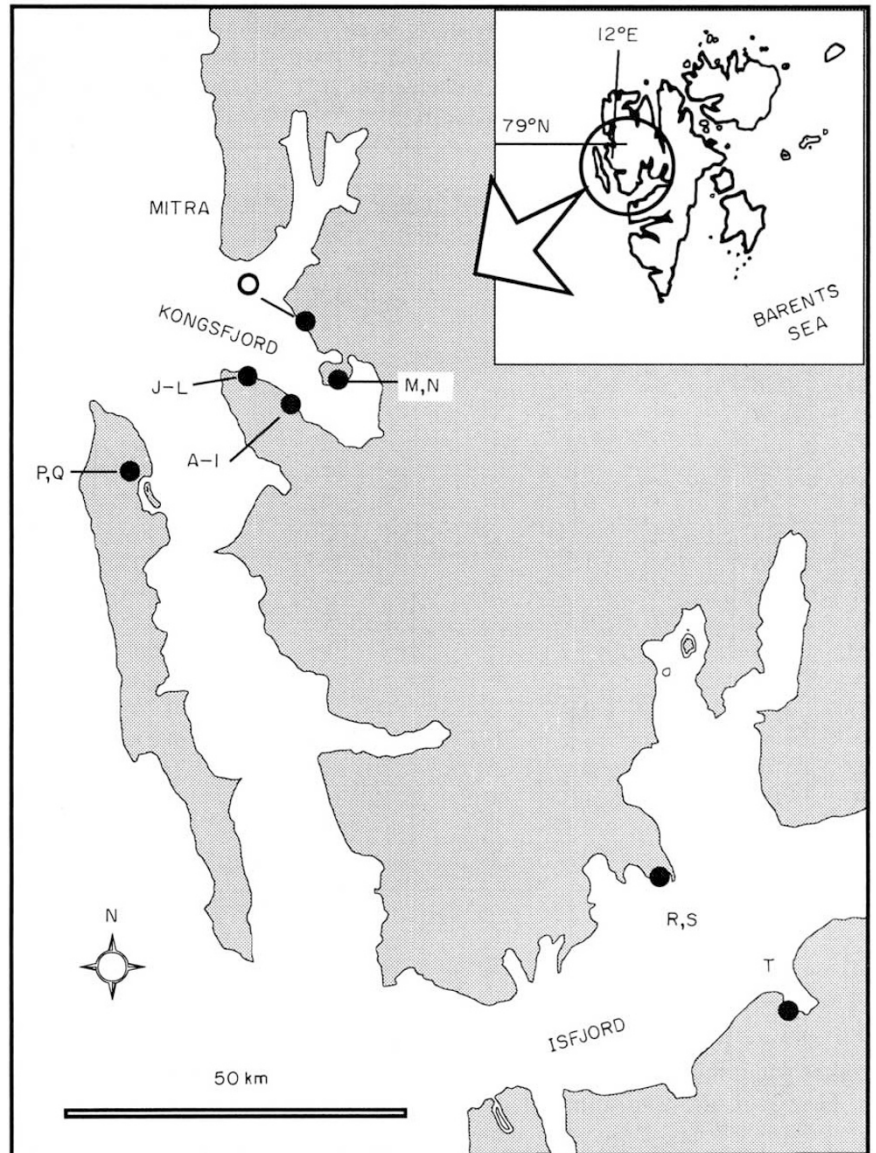
Fig. 1 Map showing the location of sampling areas (shaded dots) on Spitsbergen, Svalbard. The ponds located within each area are given, with designations as in Table 1.

$r = -0.0029$, Mantel $t = -0.036$, $P = 0.49$) of clonal arrays.

A principal coordinates analysis (Fig. 2) of genetic distances between Svalbard clones indicates that the first three principal axes explain about 73 per cent of the total variation. Electrophoretic clones 6 and 19 are both clearly separated from the others. The former is characterized by unique alleles at *LDH* (3) and *PGM* (0). A fairly distinct cluster was formed by clones 9, 13 and 20, which were distinct at the *MDH* locus and occurred only in Pond S. The bulk of clones fell within a diffuse group along principal axis 1.

Discussion

The clonal richness of *Daphnia pulex* (s.l.) in Svalbard ponds (mean 1.7 electrophoretic clones per pond, $N = 20$ ponds, 21 clones) is much lower than in similar habitats at a site in the Canadian high-arctic, Igloolik (mean 4.5 clones per pond, $N = 179$ ponds, total of 75 clones; Weider *et al.*, 1987a), but is similar to results from a low-arctic site, Churchill (mean 1.5 clones per pond, $N = 300$ ponds, total of 16 clones; Weider & Hebert, 1987a). In Ontario, Hebert & Crease (1983) found 3.6 clones per pond ($N = 11$ ponds, total of 22 clones), while Hebert *et al.* (1988) found an average of

Table 1 Localities investigated. Dimensions are field estimates. Vegetation surrounding the ponds is scored as none (0); sparse (1); moderate (2); and rich (3). Mosses dominate vegetation completely, except at pond T, where grasses and sedges dominate. Water quality is given as conductivity at 20 °C, and absorbance at 384 and 254 nm (unfiltered sample, 1 cm cuvettes)

Pond	Length (m)	Width (m)	Depth (m)	Surrounding vegetation	Conductivity (μS cm^{-1})	Absorbance 384 nm	254 nm
A	30	10	1.2	0	320	0.004	0.028
B	400	100	>2	1	145	0.004	0.018
C	60	20	1.5	1	61	0.005	0.026
D	100	30	1.0	1	175	0.012	0.082
E	90	50	0.8	3	335	0.017	0.147
F	15	8	0.4	0	220	0.003	0.016
G	3	2	0.4	0	148	0.004	0.033
H	250	70	0.6	0	142	0.007	0.045
I	600	400	>2	1	350	0.006	0.045
J	400	150	1.5	1	155	0.000	0.012
K	140	100	1.0	1	178	0.004	0.033
L	20	20	0.5	3	190	0.018	0.158
M	300	100	>2	2	95	0.006	0.049
N	80	50	0.5	1	180	0.006	0.062
O	150	100	0.8	1	132	0.005	0.049
P	80	50	1.0	1	200	0.016	0.077
Q	100	80	0.8	1	192	0.009	0.045
R	120	80	1.0	3	109	0.014	0.127
S	90	50	0.5	1	112	0.015	0.104
T	15	8	0.8	3	470	0.022	0.083

2.8 clones per pond from 200 ponds in the Great Lakes watershed.

However, the total number of clones at Svalbard is surprisingly high, especially when one considers the few localities sampled and the limited geographic extent of the survey. Extrapolating the data to larger areas is difficult. If the diversity patterns observed are typical of the whole archipelago, then the total number of clones present across the archipelago could be counted in the thousands. However, some clones could be widely distributed and more abundant than is evident from our data. Detection of new clones depends on the number of animals screened per pond, as well as the number of ponds surveyed and presumably the geographic distribution of ponds. By analysing the number of clones detected as a function of these parameters, Hebert *et al.* (1988) found that asymptotic levels were not easily reached. Moreover, the shape of a clone-area curve differs considerably between regions (Weider & Hebert, 1987a; Weider, 1989).

The present data set includes too few habitats to indicate this asymptotic level. Nevertheless, it should be noted that every area which was sampled yielded new electrophoretic clones. Data obtained from yet another area (the Mitra peninsula, Fig. 1) in 1986 (Hobæk & Wolf, unpublished) confirm this trend. Since the Mitra animals were run on starch gels, which produced poor resolution, they were not included in the present data set. At least one of the Mitra clones was not detected elsewhere. If the available data are representative, the present list of distinct clones must be a small subset of a much larger clonal array present in the archipelago.

The lack of geographical patterns in clonal composition of ponds is unexpected. By contrast, Weider (1989) found significant spatial patterns to individual clonal distributions at Igloolik, although many distributions were patchy. While the apparent randomness in distribution may be an effect of too few ponds surveyed, and perhaps too great a spatial scale (on the order of 100 km maximum distance), the Svalbard ponds are clearly distinguished from previous arctic

Table 2 Unique composite (7-locus) genotypes (clones) detected at Svalbard 1987 and 1991. Clones are ordered in numerical abundance. Unbalanced electromorphs (see text) are indicated by asterisks, with the 'overrepresented' allele preceding the asterisk. Enzyme abbreviations are given in Materials and methods. '—' denotes missing information

Clone no.	PGM	PGI	AO	GOT	LDH	MDH	MPI	N	%	No. of ponds
1	2*3	44	12	23	11	11	34	323	23.5	6
2	12*3	44	12	22	11	11	34	148	10.8	3
3	2*34	44	12	22	11	11	34	146	10.6	2
4	22	44	11	23	11	11	34	146	10.6	2
5	12*	44	12	22	11	11	34	167	8.4†	2
6	02*	14	22	22	33	11	33	77	5.6	2
7	2*3	45	11	22	11	11	34	73	5.3	2
8	2*3	44	11	23	11	11	34	71	5.2	1
9	22	44	11	23	11	00	22	63	4.6	1
10	2*3	44	12	22	11	11	33	61	4.4	1
11	2*3	44	12	22	11	11	34	56	4.1	1
12	2*3	44	22	22	11	11	33	11	0.8	1
13	22	44	11	23	11	11	22	8	0.6	1
14	12*3	44	12	22	11	11	44	6	0.4	1
15	2*3	44	22	22	11	11	34	6	0.4	1
16	2*3	14	12	22	11	11	44	5	0.4	1
17	12*3	44	11	22	11	11	34	2	0.1	1
18	12*3	44	12	23	11	11	44	1	0.1	1
19	22	14*	11	—	01	11	—	1	0.1	1‡
20	22	44	11	33	11	11	22	1	0.1	1
21	2*3	44	33	23	11	11	34	1	0.1	1

†Percentage calculated from sample size in 1987 (111 ind.).
‡Only detected in 1991.

surveys (Weider *et al.*, 1987; Weider, 1989) by containing fewer clones, whose distributions are much more restricted.

An important question remains: Does the observed clonal richness represent well-adapted genotypes that live in ponds with subtle, but important ecological differences, or just a small selection of a much larger clonal array each with rather restricted distributions? In the former case, one would expect a limited number of clones, each of which occurs scattered in ponds over large areas. Also, there should be pronounced differences between clones in competitive abilities, with competitive superiority varying with several ecological factors. Actually, there is considerable evidence that asexual clones of this complex display ecological differences. Such variation has been found in life-history traits like growth rate, reproductive rate, and age at reproductive maturity (Weider, 1987), in osmoregulation (Weider & Hebert, 1987b) and tolerance to short-wave radiation (Hebert & Emery, 1990).

In these cases, the distribution of clones among ponds is not random (Weider & Hebert, 1987b; Hebert & Emery, 1990). A parallel situation occurs in alpine pond populations of *D. longispina* (Hobæk & Wolf, 1991). Although we looked for similar patterns at Svalbard, they were not readily apparent. Ponds did not vary greatly in their conductivity, although absorption in the ultraviolet (UV) range differed markedly between ponds (Table 1). All clones had melanized carapaces, with the exception of clone 6, which occurred only in Pond M, where animals stayed below 1 m depth, and in Pond G, in which water was quite turbid (Table 1).

Although environmental heterogeneity may in part support the maintenance of multiclonal populations, it cannot explain all of the variation. For instance, the nearly identical ponds F and G, which are situated only 10 m apart, were inhabited by different clones (Table 3). The most parsimonious explanation for such apparently random occurrences is that stochastic processes (founder effects) coupled with low dispersal rates play an important role not only in structuring clonal distribution patterns in *Daphnia*, but appear to be critical in gene frequency divergence among other pond-dwelling organisms (Boileau *et al.*, 1991).

Coexistence of multiple, closely related clones in a given homogeneous habitat suggests that competition should be strong, and should presumably result in the competitive exclusion of all but the best competitor. This clearly is not the outcome in many cases (Hebert

Table 3 Clonal composition of *Daphnia pulex* pond
populations at Svalbard, August 1987. The localities are
shown in Fig. 1, and genotypes are listed in Table 2.
N = sample size

Pond	Genotype	*N*
A	3	69
B	1	71
	5	1
C	1	75
D	2	76
	17	2
E	5	166*
	19	1†
F	1	78
G	3	77
H	11	56
	1	22
I	2	68
	14	6
	16	5
	18	1
J	15	6
K	12	4
L	12	7
M	6	70
N	10	61
	2	4
O	1	76
P	4	77
	7	2
Q	7	71
R	4	69
	6	7
S	9	63
	13	8
	20	1
T	8	71
	1	1
	21	1

*Includes 56 animals sampled in 1991.
†Only detected in 1991.

Fig. 2 Three-dimensional plot of the first three principal
axes of a principal coordinates analysis of genetic similarity
of 21 *Daphnia pulex* clones. Numbers at each point refer to
clonal designations (Table 2).

& Crease, 1980; Wilson & Hebert, 1992). Recent evidence (Weider, 1992) suggests that competitive interactions among clones may be influenced greatly by environmental perturbations, which occur at low to intermediate frequencies, and result in the maintenance of multiclonal populations.

The distributional patterns of clones in different regions are likely a result of both deterministic (e.g. selection) and stochastic (e.g. passive dispersal, founder effects) forces. Given the contrasts in clonal distribution patterns between different regions, and among different organisms (Parker, 1979), further studies of
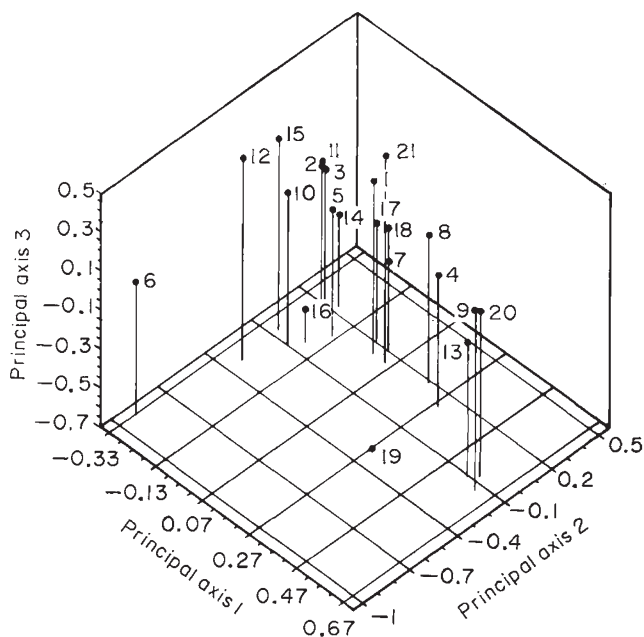
the factors controlling dispersal and coexistence in asexual complexes should yield interesting results. In particular, more direct measurements of dispersal rates in nature would be valuable (Slatkin, 1987).

One final consideration concerns the taxonomic controversies involving the Svalbard *Daphnia pulex* complex. The taxonomy of the species complex is presently under revision (Korínek, personal communication), including material from the present study. In the past, Svalbard *Daphnia* have been designated as *Daphnia pulex* Leydig (Olofsson, 1918; Thomasson, 1959; Meijering, 1972), *Daphnia tenebrosa* Sars (Amrén, 1964) and *Daphnia middendorffiana* Fischer (Brooks, 1957; Halvorsen & Gullestad, 1976). Based on morphological criteria, clone 6 is probably a true *Daphnia pulex* (Korínek, personal communication), while the remaining clones belong to *D. middendorffiana* and/or *D. tenebrosa*. Clone 6 is characterized by allele 3 at *LDH*, while all the other clones had slower alleles at this locus. However, the distinctiveness of these taxa is still uncertain, and must await further morphological and molecular characterization, which we are presently undertaking.

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