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COMMUNITY ECOLOGY OF A LOW-ARCTIC *DAPHNIA PULEX* CLONAL ASSEMBLAGE

by

Christopher Carroll Wilson

A Thesis
submitted to the
Faculty of Graduate Studies and Research
through the Department of
Biological Sciences in Partial Fulfillment
of the requirements for the Degree
of Master of Science at the
University of Windsor

Windsor, Ontario, Canada

1989

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to my parents

ABSTRACT

Electrophoretic surveys of asexual Daphnia pulex populations in 150 coastal rock bluff ponds near Churchill, Manitoba in 1985 and 1989 revealed 36 unpigmented clones. Three clones dominated the assemblage in both years, comprising greater than 76% of all animals detected, and occurring in 135 of the 150 ponds. Clonal richness of the ponds ranged from 1 to 5 clones, and averaged 1.7 clones per pond in both years. Evidence from multiclonal ponds indicated that coexisting clones were not ecological analogues, and that coexistence in these ponds was facilitated by seasonal shifts in fitness as well as rescue effects from ephippial egg banks. Clonal distributions were both non-random and stable, suggesting that the system is at or near equilibrium. Distributions of individual clones were impacted by environmental variables including salinity, pH, and pond volume.

The three dominant clones were adapted to separate habitat types. Clone 1 occurred in high-salinity habitats, while clones 13 and 14 were found in lower salinity ponds. The latter two clones inhabited ponds with similar physicochemistry, but showed different sensitivities to the predatory copepod Hesperodiaptomus arcticus. Clone 13 rarely co-occurred with the copepod, whereas H. arcticus was found in 90% of the ponds dominated by clone 14. Clone 13's dominance of low-salinity ponds in the absence of H. arcticus suggested it was a superior competitor in these

habitats.

Experimental whole-pond manipulations examined pairwise competitive interactions among the three dominant clones in 1987. For the most part, clones were competitively superior in their native habitats and inferior away from them. Competitive interactions between clones 13 and 14 were asymmetric, with clone 13 showing competitive superiority regardless of habitat. Further competition experiments showed both clones 13 and 14 to be competitively superior to two less-abundant clones.

A second series of pond experiments in 1988 tested interactions between clones 13 and 14 in the presence of H. arcticus. Clone 13 was displaced in all ponds where the predator was introduced, while control ponds showed results similar to the 1987 experiments.

Reproductive differences among clones in multiclonal and experimental ponds showed varying predictive ability for clonal frequencies at the next sampling intervals. Clonal frequencies in multiclonal ponds fluctuated widely and showed poor predictability. Populations in experimental competition ponds showed the greatest consistency with predicted shifts in clonal frequencies, while changes in frequencies of clones in field predation experiments were largely uncorrelated with predictions from fecundity estimates.

Observations of natural distributions of clones in this pond system, as well as results from laboratory and

field experiments showed that environmental heterogeneity, competition and predation all influence the structure of this clonal assemblage.

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CHAPTER 1

CLONAL ASSEMBLAGES AS USEFUL MODEL SYSTEMS FOR COMMUNITY ECOLOGY

The study of factors underlying patterns of species assemblages in communities has been one of the main research thrusts in community ecology over the last three decades. A large number of hypotheses have been generated, which have gained mixed support from the scientific community. Southwood (1977) argued that environmental parameters determine species distribution patterns, and that interactions among members of a community are influenced by the species' relative positions within the habitat framework. A number of researchers (Diamond 1975, Richmond et al. 1975, Schoener 1982, 1986a,b, Roughgarden 1983) have argued that competition is the dominant factor operating among species within a trophic level, as opposed to colonization or stochastic events. This idea is supported by numerous field and laboratory studies (see Schoener 1983, Roughgarden 1983 for reviews), but difficulties do exist (Connell 1980, 1983, Simberloff 1982).

Although competition has been a central theme in community ecology for several decades, it has proven difficult to study directly in natural communities (Connell 1975, Pianka 1976). An alternate hypothesis that has received growing support in recent years is the predation hypothesis, which suggests that members of higher trophic levels exert strong selective pressures on the organisms that make up their food base, and that these pressures have a major effect on the composition of the prey community

(see Zaret 1980, Kerfoot and Sih 1986 for reviews). Differentiation of the processes responsible for observed species abundance and distribution patterns is often difficult, as the patterns of species occurrence which result from competition and predation may strongly resemble each other (Holt and Kotler 1987).

A number of different approaches have been employed in the effort to develop an understanding of factors responsible for community structure. A rich body of theoretical literature on the nature of species interactions and expected community patterns has been generated (see May 1976a,b, Wangersky 1978 for reviews), although the applicability of many models to natural systems is limited (Simberloff 1982). Attempts have been made to infer past competitive interactions from biogeographic studies (Diamond 1975, Moulton and Pimm 1983), but this approach has been criticized and is now primarily used as background inference for experimental studies (Connell 1980, Diamond 1986). Numerous laboratory experiments have been carried out on pairwise species interactions, but are prohibitively difficult when multiple species are considered. It is now generally accepted among ecologists that manipulative field experiments with appropriate controls are the best way to study interactions among species in nature (Diamond 1986), although reviews of the results obtained have been mixed (Connell 1983, Schoener 1983, 1986a).

Unfortunately, direct approaches to studying multi-species communities automatically introduce persistent sources of variation at both the inter- and intraspecific level. At the interspecific level, size differences among the species under study may affect dispersal abilities, choice of food, response to predation, and other traits. Species-specific differences in morphological, behavioural, and reproductive strategies, as well as responses to environmental stimuli, can easily affect the outcome of interactions among the species considered. All of these factors are potential sources of variation, and may obscure the meaning of results generated from experiments unless variation in each factor and its consequences are measured and weighted accordingly (Tilman 1987).

In order to discount these sources of variation, a detailed knowledge of the natural history of each species involved in the system is essential, requiring a great deal of background effort. Too often, studies are forced to conclude that patterns of species coexistence or exclusion observed in nature can be attributed to species-specific characters (Connell 1983, Schoener 1986b).

Efforts have been made to minimize life history differences among study organisms. For example, Diamond (1975) argued that members of a guild which share a common evolutionary past and have similar dispersal and reproductive habits should be excellent systems for evaluating the impacts of competition and predation.

Numerous microcosm studies using similar organisms from low trophic levels have been useful in elucidating issues in community ecology (Neill 1975, Maguire et al. 1980). Studies of this type, however, have serious limitations when extrapolating results back into natural communities (King 1980).

It is generally acknowledged that many experimental tests of community hypotheses have failed due to dissimilarities among the species under study (May 1976b, Connell 1983). For example, recent studies on ant communities (Cole 1983a,b) suggest that community patterns can be largely explained by differences in life history and dispersal ability of the species examined. In natural communities, it is quite difficult to find two or more very similar species co-occurring, which would enable researchers to measure or test competitive interactions and their outcomes (Pianka 1976). Moreover, when closely related taxa are identified, genetic variation within each species may affect the outcome of their interaction. For example, the indeterminacy observed in Park's (1948) classic competition experiments between two Tribolium species may have partially been due to founder events.

An alternative approach to investigations among different species is to use members of an asexual taxon as analogues to species in a community. By treating clones as separate "species" in a model system, interspecific sources of variation are eliminated. Instead of requiring detailed

information on a number of different species, research concentrates on just one. Conspecific clones typically have identical modes of dispersal, very similar body plans, food requirements, life histories, generation times, etc. Although their ecological strategies may vary, clones typically have much greater similarity than the most closely related species (Sebens and Thorne 1985). In addition, intraclonal variation is greatly reduced in comparison to its analog (variation within a species). Thus, by treating the various clones which comprise an asexual taxon as species analogues, one can study community-level interactions at a single trophic level, in a system which lacks several sources of complexity inherent in natural communities.

Although the idea of using clonal taxa to examine interspecific interactions has been suggested by a number of authors (Solbrig 1971, Parker 1979, Angus 1980, Hebert and Crease 1980, Jaenike et al. 1980, Loaring and Hebert 1981, Cook 1983, Jackson et al. 1985, Hughes 1987, Hebert et al. 1988), no studies have yet taken full advantage of the potential that such assemblages offer for manipulative field experiments (Bender et al. 1984). Opportunities for such research are plentiful: asexuality occurs in all five kingdoms and a sizable proportion of lower taxonomic groups (Bell 1982, Suomalainen et al. 1987).

Natural assemblages of clones occurring in spatially or temporally heterogeneous habitats are frequently diverse

(Selbrig 1971, Harper 1977, Hebert and Crease 1980, 1983, Hebert et al. 1988, Jaenike et al. 1980, Loaring and Hebert 1981, Lyman and Ellstrand 1984, Tucic et al. 1988, Weider 1989, Weider and Hebert 1987a,b, Weider et al. 1987, Young 1979). Such co-occurrence of large numbers of very similar but genetically distinct organisms is rarely equaled at the species level. Such clonal arrays largely remove the difficulties of testing theoretical models of multispecies communities (e.g. May 1976b, Pianka 1976). These model systems would also overcome many criticisms of field tests of multispecies systems (e.g. Connell 1983).

An additional advantage to using asexual organisms for experimental studies is the restricted distributions of many clones. Although parthenogenetic organisms often have larger ranges than their sexual relatives, many asexual organisms utilize passive dispersal and have limited vagility in their active or growing phase. Additionally, despite the widespread distribution of asexual taxa, specific clones usually occur over areas of much smaller geographic scale than do species (Sebens and Thorne 1985, Suomalainen et al. 1987). Experimental animals are therefore less likely to leave study areas than is the case when dealing with species assemblages. The limited natural distributions of most specific clones also decrease the possibility of a rescue effect occurring through immigration from outside the experimental system.

Another advantage of using clonal organisms for

experimental work is their ease of culture. In addition to being able to obtain large population sizes quickly, experimental manipulations can be established from small numbers of individuals without introducing founder effects which can complicate work with sexual species.

The analogy between a clonal complex and a multispecies community is not perfect. Many studies have shown that clonal and species abundance patterns differ (Sebens and Thorne 1985). Thus, studies of clonal diversity have consistently found a small number of extremely common clones, few clones with intermediate abundance, and greater numbers of rare clones than is usual for species assemblages (Jaenike et al. 1980, Hebert and Crease 1980, 1983, Lyman and Ellstrand 1984, Sebens and Thorne 1985, Weider and Hebert 1987a,b, Tucic et al. 1988, Weider 1989). The lognormal distribution (Preston 1948, May 1976b) characteristic of species assemblages is thought to arise from the interaction of multiple independent factors which produces an abundance pattern that resembles that expected by the Central Limit Theorem. The polarized clonal abundance patterns suggest that asexual taxa are exposed to more intense selective pressures than normally operate among species (Parker 1979, Hebert 1982, Sebens and Thorne 1985), which agrees with the theoretical argument of limiting similarity (Pianka 1976). If clones are ecologically equivalent, their extreme similarities should generate abundance patterns closely resembling Preston's

(1948) lognormal, based on the Central Limit Theorem of statistics. Polarized clonal abundances, however, indicate that these clonal populations are responding to strong selective pressures. Since genetic variability within clones is largely fixed, with mutation being the only source of variation, selection acts on the entire genome rather than upon additive effects of several gene loci (Wright 1977, Parker 1979, Templeton 1979, 1982, Hebert et al. 1988).

In theoretical considerations of competition, organisms compete for some limited commodity such as space or food, with the assumption that the intensity of competition varies in direct proportion to the degree of niche overlap (May 1976a, Pianka 1976). The Lotka-Volterra equations, classically used for examination of competition among species (May 1976a, Pianka 1976), may therefore apply more closely to clonal than species assemblages, due to the higher competition coefficients expected from the extreme similarity among clones. The intense competitive interactions among clones should drive selection in the experimental system more quickly than normal for species assemblages.

The ability of asexual organisms to rapidly increase their population size, coupled with the strong selective pressures exerted on clones by their biotic and abiotic environments, should enable researchers to achieve definitive experimental results in relatively short spans

of time. Indeed, prior work has shown that under stable environmental conditions, clones respond rapidly to selection (Solbrig 1971, Parker 1979, Lyman and Ellstrand 1984, Sebens and Thorne 1985) and that competitive exclusion typically occurs in less than ten generations (e.g. Snell 1977, Loaring and Hebert 1981).

When choosing a clonal assemblage for use as a model system, it is essential that the organisms are strictly asexual, as the generation of new clones from sexual relatives would confound the effects of selection on clonal diversity and abundance (Sebens and Thorne 1985). It would also be useful to know how the clones under consideration were formed, since clones derived from monophyletic and polyphyletic origins may exhibit qualitatively different competitive patterns (Parker 1979).

This type of model system has many potential applications. By correlating temporal patterns of clonal abundance with environmental parameters, for example, one should be able to closely examine genotype-environment interactions. Although this is highly desirable in community ecology, it is rarely accomplished successfully (Pianka 1976). Hypotheses examining evolutionary strategies of rare organisms (Rabinowitz et al. 1986) are also difficult to examine at the species level. Experimental and theoretical studies of rarity have frequently failed to explain observed species patterns (Levins and Culver 1971), although this type of study is

extremely simple using clones as species analogs. Asexual plant species such as dandelions (Solbrig 1971) are ideally suited for practical tests of frequency- and density-dependent selection, due to their ease of culture, large potential number of replicates, and the ability to construct appropriate controls. Indeed, observational studies on clonally-reproducing plant species have already provided some insight on how these processes operate in nature (Lyman and Ellstrand 1984, Tucic et al. 1988).

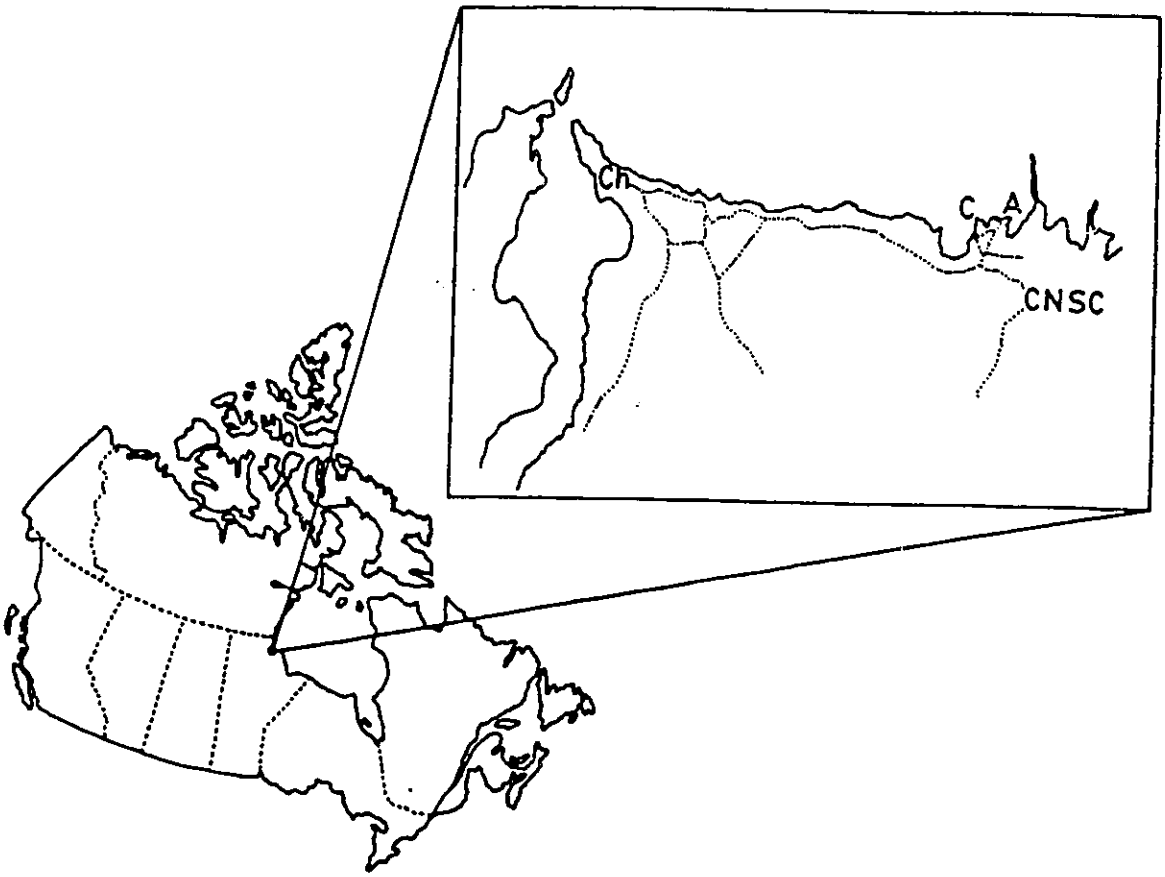
The freshwater cladoceran Daphnia pulex (Leydig) is an ideal organism for a model system of the type proposed here. The species occurs throughout the arctic and northern temperate zones (Reed 1963, Hebert and Hann 1986, Haney and Buchanan 1987, Hebert 1987), and is a common member of zooplankton communities in ponds and small lakes (Hrbacek 1987). Members of the genus Daphnia have been intensively studied, and an enormous body of literature exists on all aspects of their biology (De Bernardi and Peters 1987). The number and diversity of studies carried out on Daphnia pulex make it an excellent choice for studying fundamental questions such as community structure. The species' small size, simplicity of culture, and potential for rapid rate of population growth make it ideally suited for experimental studies (Schwartz 1984, Edmondson 1987, Peters 1987). Although some populations reproduce by cyclic parthenogenesis, populations in much of Canada reproduce by apomictic parthenogenesis (Hebert and

Crease 1980, Hebert 1981, Hebert and McWalter 1983, Innes and Hebert 1988). In those regions where it reproduces asexually, the species exhibits high levels of clonal diversity (Hebert and Crease 1980, 1983, Weider and Hebert 1987a,b, Weider et al. 1987, Beaton and Hebert 1988, Hebert et al. 1988).

The present study has investigated patterns of clonal diversity in populations of D. pulex at a site near Churchill, Manitoba (Figure 1). The Churchill area along Hudson Bay is characterized by quartzite rock outcrops rising up to 30 m above the shoreline, interspersed with areas of low-lying tundra. Many of these rock bluffs have hundreds of ponds in rocky depressions formed by glacial scouring and freeze-thaw action of ice. The ponds support a diverse assemblage of zooplankton species, of which D. pulex is one of the most common.

This pond system has already been the subject of a number of studies. Physical and chemical variation among ponds has been documented (Billington et al., in prep.), as well as zooplankton composition of the ponds (Hebert 1985, Billington, unpubl.). Patterns of genetic diversity have been analyzed in a number of taxa, including flatworms (Hebert and Payne 1985), copepods (Boileau 1989), and ostracods (Havel and Hebert 1989). Members of the genus Daphnia have been particularly well studied. Good (1981) examined biogeographic patterns among several daphniid species in the area, and Hebert and Loaring (1980) studied

Figure 1-1: Location of study area, showing relative positions of bluffs A and C in relation to Churchill, Manitoba (Ch) and the Churchill Northern Study Centre (CNSC).



the influence of copepod predation on daphniid distributions. Populations of D. pulex itself have been shown to reproduce by obligate parthenogenesis (Hebert and McWalter 1983, Hebert 1987), and to be comprised of two separate, diverse clonal assemblages - pigmented and unpigmented. The two assemblages differ in ploidy level: melanic or pigmented clones are tetraploid, while unpigmented clones are largely diploid (Beaton and Hebert 1988). Both clonal assemblages display high levels of genetic diversity, as indicated by both allozyme and mitochondrial DNA analyses (Stanton 1988). The pigmented clones are protected from near-ultraviolet radiation (NUV) by their melanic carapaces and occur in ponds with low humic content, while unpigmented clones are restricted to ponds with higher humic content because of their vulnerability to NUV radiation (Hebert and Emery 1990). Melanic D. pulex have been studied with respect to microgeographic distribution patterns of clones (Weider and Hebert 1987a), life history (Weider 1987), and ecological and physiological differences among clones (Weider and Hebert 1987b).

Previous work (Hebert et al. unpubl.) showed that populations of unpigmented D. pulex were also clonally diverse in ponds on the Churchill rock bluffs, and that clonal distributions and abundances varied greatly. My research has involved a description of the nature and stability of these clonal distribution patterns. In

addition, experimental studies were conducted to ascertain the selective forces responsible for the distribution patterns. Specifically, Chapter 2 examines stability of the clonal composition of D. pulex populations on rock bluffs A and C by comparing the results of analyses carried out in 1985 and 1989. The influence of habitat on clonal distributions is also considered by examining correlations between clonal distributions and environmental parameters. Most ponds contained only a single clone, but some contained up to five. Chapter 3 examines temporal shifts in clonal abundance and reproductive status in multiclonal ponds with a view towards gaining an understanding of the factors important in the maintenance of diversity. Chapters 4 and 5 examine the effects on clonal composition of interclonal competition and predation, respectively, using perturbation-type field experiments. Finally, Chapter 6 provides a synthesis of the results, and a summary of the factors involved in determining the distribution and abundance patterns of clones in this model system.

LITERATURE CITED

Angus, R.A. 1980. Geographic dispersal and clonal diversity in unisexual fish populations. Am. Nat. 115: 531-550

Beaton, M.J. and P.D.N. Hebert. 1988. Geographical parthenogenesis and polyploidy in Daphnia pulex. Am. Nat. 132: 837-845

Bell, G. 1982. The Masterpiece of Nature. Croom Helm, London.

Bender, E.A., T.J. Case and M.E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. Ecology 65: 1-13

Boileau, M.G. 1989. Biochemical genetic variation in the freshwater Copepoda: evolutionary consequences of passive dispersal in freshwater zooplankton. Ph.D. dissertation, University of Windsor, Ont.

Cole, B.J. 1983a. Assembly of mangrove ant communities: patterns of geographic distribution. J. Animal Ecol. 52: 339-347

_____. 1983b. Assembly of mangrove ant communities: colonization abilities. J. Animal Ecol. 52: 349-355

Connell, J.H. 1975. Some mechanisms producing structure in natural communities. p. 460-490 in Cody, M.L. and J.M. Diamond (eds). Ecology and Evolution of Communities. Harvard University Press, Cambridge.

_____. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35: 131-138

_____. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. Am. Nat. 122: 661-696

Cook, R.E. 1983. Clonal plant populations. Amer. Sci. 71: 244-253

De Bernardi, R. and R.H. Peters. 1987. Why Daphnia? p. 1-9 in Peters, R.H. and R. de Bernardi (eds). Daphnia. Mem. Ist. Ital. Idrobiol. 45, Pallanza.

Diamond, J.M. 1975. Assembly of species communities. p. 342-444 in Cody, M.L. and J.M. Diamond (eds). Ecology and Evolution of Communities. Harvard University Press, Cambridge.

_____. 1986. Overview: laboratory experiments, field experiments, and natural experiments. p. 3-22 in Diamond, J. and T.J. Case (eds). Community Ecology. Harper and Row, New York.

Edmondson, W.T. 1987. Daphnia in experimental ecology: notes on historical perspectives. p. 11-30 in Peters, R.H. and R. de Bernardi (eds). Daphnia. Mem. Ist. Ital. Idrobiol. 45, Pallanza.

Good, A.G. 1981. The ecology and biogeography of tundra zooplankton communities in the Churchill, Manitoba area. M.Sc. thesis, University of Windsor, Ontario.

Haney, J.F. and C. Buchanan. 1987. Distribution and biogeography of Daphnia in the Arctic. p. 77-105 in Peters, R.H. and R. de Bernardi (eds). Daphnia. Mem. Ist. Ital. Idrobiol. 45, Pallanza.

Harper, J.L. 1977. Population Biology of Plants. Academic Press, New York.

Havel, J.E. and P.D.N. Hebert. 1989. Genotypic diversity of asexual Ostracoda from a low arctic site. J. Evolut. Biol. (in press).

Hebert, P.D.N. 1981. Obligate asexuality in Daphnia. Am. Nat. 117: 784-789

_____. 1982. Competition in zooplankton communities. Ann. Zool. Fennici 19: 349-356

_____. 1985. Ecology of the dominant copepod species at a low arctic site. Can. J. Zool. 63: 1138-1147

_____. 1987. Genotypic characteristics of the Cladocera. Hydrobiol. 145: 183-193

Hebert, P.D.N. and T.J. Crease. 1980. Clonal coexistence in Daphnia pulex (Leydig): another planktonic paradox. Science 207: 1363-1365

_____. 1983. Clonal diversity in populations of Daphnia pulex reproducing by obligate parthenogenesis. Heredity 51: 353-369

Hebert, P.D.N. and C. Emery. 1990. Adaptive significance of cuticular pigmentation in Daphnia pulex. Funct. Ecol. (in review)

Hebert, P.D.N. and B.J. Hann. 1986. Patterns in the composition of arctic tundra pond microcrustacean communities. Can. J. Fish. Aquat. Sci. 43: 1416-1425

Hebert, P.D.N. and J.M. Loaring. 1980. Selective predation and the species composition of arctic ponds. Can. J. Zool. 58: 422-426

Hebert, P.D.N. and D.B. McWalter. 1983. Cuticular pigmentation in arctic Daphnia: adaptive diversification of asexual lineages? Amer. Nat. 122: 286-291

Hebert, P.D.N. and W.J. Payne. 1985. Genetic variation in populations of the hermaphroditic flatworm Mesostoma lingua (Turbellaria, Rhabdocoela). Biol. Bull. 169: 143-151

Hebert, P.D.N., R.D. Ward and L.J. Weider. 1988. Clonal-diversity patterns and breeding-system variation in Daphnia pulex, an asexual-sexual complex. Evolution 42: 147-159

Holt, R.D. and B.P. Kotler. 1987. Short-term apparent competition. Am. Nat. 130: 412-430

Hrbacek, J. 1987. Systematics and biogeography of Daphnia species in the northern temperate regions. p. 37-76 in Peters, R.H. and R. de Bernardi (eds). Daphnia. Mem. Ist. Ital. Idrobiol. 45, Pallanza.

Hughes, R.N. 1987. The functional ecology of clonal animals. Funct. Ecol. 1: 63-69

Innes, D.J. and P.D.N. Hebert. 1988. The origin and genetic basis of obligate parthenogenesis in Daphnia pulex. Evolution 42: 1024-1035

Jackson, J.B.C., L.W. Buss and R.E. Cook (eds). 1985. Population Biology and Evolution of Clonal Organisms. Yale University Press, New Haven.

Jaenike, J., E.D. Parker Jr. and R.K. Selander. 1980. Clonal niche structure in the parthenogenetic earthworm Octolasion tyrtaeum. Am. Nat. 116: 196-205

Kerfoot, W.C. and A. Sih. 1986. Predation: Direct and Indirect Impacts on Aquatic Communities. University Press of New England, Hanover.

King, D.L. 1980. Some cautions in applying results from aquatic microcosms. p. 164-191 in Giesy, J.P. Jr. (ed). Microcosms in Ecological Research. Technical Information Center, U.S. Department of Energy.

Levins, R. and D. Culver. 1971. Regional coexistence of species and competition between rare species. Proc. Nat. Acad. Sci. 68: 1246-1248

Loaring, J.M. and P.D.N. Hebert. 1981. Ecological differences among clones of Daphnia pulex Leydig. Oecologia 51: 162-168

Lyman, J.C. and N.C. Ellstrand. 1984. Clonal diversity in Taraxacum officinale (Compositae), an apomict. Heredity 53: 1-10

Maguire, B.Jr., L.B. Slobodkin, J.J. Morowitz, B. Moore III and D.B. Botkin. 1980. A new paradigm for the examination of closed ecosystems. p. 30-68 in Giesy, J.P. Jr. (ed). Microcosms in Ecological Research. Technical Information Center, U.S. Department of Energy.

May, R.M. 1976a. Models for two interacting populations. p. 49-70 in May, R.M. (ed). Theoretical Ecology: Principles and Applications. W.B. Saunders Co., Toronto.

_____. 1976b. Patterns in multi-species communities. p. 142-162 in May, R.M. (ed). Theoretical Ecology: Principles and Applications. W.B. Saunders Co., Toronto.

Moulton, M.P. and S.L. Pimm. 1983. The introduced Hawaiian avifauna: biogeographic evidence for competition. Am. Nat. 121: 669-690

Neill, W.E. 1975. Experimental studies of microcrustacean competition, community composition and efficiency of resource utilization. Ecology 56: 809-826

Park, T. 1948. Experimental studies of interspecies competition. I. Competition between populations of the flour beetles, Tribolium confusum Duval and Tribolium castaneum. Ecol. Monogr. 18: 265-307

Parker, E.D.Jr. 1979. Ecological implications of clonal diversity in parthenogenetic morphospecies. Am. Zool. 19: 753-762

Peters, R.H. 1987. p. 483-495 in Peters, R.H. and R. de Bernardi (eds). Daphnia. Mem. Ist. Ital. Idrobiol. 45, Pallanza.

Pianka, E.R. 1976. Competition and niche theory. p. 114-141 in May, R.M. (ed). Theoretical Ecology: Principles and Applications. W.B. Saunders Co., Toronto.

Preston, F.W. 1948. The commonness, and rarity, of species. Ecology 29: 254-283

Rabinowitz, D., S. Cairns and T. Dillon. 1986. Seven forms of rarity and their frequency in the flora of the British Isles. p. 182-204 in Soule, M.E. (ed). Conservation Biology. Sinauer Associates, Inc., Sunderland.

Reed, E.B. 1963. Records of freshwater Crustacea from arctic and subarctic Canada. Nat. Mus. Can. Bull. 199: 29-62

Richmond, R.C., M.E. Gilpin, S.P. Salas and F.J. Ayala. 1975. A search for emergent competitive phenomena: the dynamics of multispecies Drosophila systems. Ecology 56: 709-714

Roughgarden, J. 1983. Competition and theory in community ecology. Am. Nat. 122: 583-601

Schoener, T.W. 1982. The controversy over interspecific competition. Amer. Sci. 70: 586-595

_____. 1983. Field experiments on interspecific competition. Am. Nat. 122: 240-285

_____. 1986a. When should a field experiment be counted?: a reply to Galindo and Krebs. Oikos 46: 119-121

_____. 1986b. Mechanistic approaches to community ecology: a new reductionism? Am. Zool. 26: 81-106

Schwartz, S.S. 1984. Life history strategies in Daphnia: a review and predictions. Oikos 42: 114-122

Sebens, K.P. and B.L. Thorne. 1985. Coexistence of clones, clonal diversity, and the effects of disturbance. p. 357-398 in Jackson, J.B.C., L.W. Buss and R.E. Cook (eds). Population Biology and Evolution of Clonal Organisms. Yale University Press, London.

Simberloff, D. 1982. The status of competition theory in community ecology. Ann. Zool. Fennici 19: 241-253

Snell, T.W. 1977. Clonal selection: competition among clones. Arch. Hydrobiol. 8: 202-204

Solbrig, O.T. 1971. The population biology of dandelions. Amer. Sci. 59: 686-694

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? J. Animal Ecol. 46: 337-365

Stanton, D.J. 1988. Evolution of asexuality in Daphnia pulex: implications of mitochondrial DNA analysis. Ph.D. dissertation, University of Windsor, Ont.

Suomalainen, E., E. Saura and J. Lokki. 1987. Cytology and Evolution in Parthenogenesis. CRC Press, Boca Raton.

Templeton, A.R. 1979. The unit of selection in Drosophila mercatorum. II. Genetic revolutions and the origin of coadapted genomes. Genetics 92: 1265-1281

_____. 1982. The prophecies of parthenogenesis. p. 75-101 in Dingle, H. and J.P. Hegmann (eds). Evolution and Genetics of Life Histories. Springer-Verlag, Berlin.

Tilman, D. 1987. The importance of the mechanisms of interspecific competition. Am. Nat. 129: 769-774

Tucic, B., S. Milojkovic, S. Vujcic and A. Tarasjev. 1988. Clonal diversity and dispersion in Iris pumila. Acta Oecologia 9: 211-219

Wangersky, P.J. 1978. Lotka-Volterra population models. Ann. Rev. Ecol. Syst. 9: 189-218

Weider, L.J. 1989. Spatial heterogeneity and clonal structure in arctic populations of apomictic Daphnia. Ecology 70: 1405-1413

Weider, L.J. and P.D.N. Hebert. 1987a. Microgeographic genetic heterogeneity of melanic Daphnia pulex at a low-arctic site. Heredity 58: 391-399

_____. 1987b. Ecological and physiological differentiation among low-arctic clones of Daphnia pulex. Ecology 68: 188-198

Weider, L.J., M.J. Beaton and P.D.N. Hebert. 1987. Clonal diversity in high-arctic populations of Daphnia pulex, a polyploid apomictic complex. Evolution 41: 1335-1346

Wright, S. 1977. Evolution and Genetics of Populations. Vol. III. Experimental Results and Evolutionary Deductions. University of Chicago Press, Chicago.

Young, J.P.W. 1979. Enzyme polymorphism and cyclic parthenogenesis in Daphnia magna. I. Selection and clonal diversity. Genetics 92: 953-970

Zaret, T.M. 1980. Predation and Freshwater Communities. Yale University Press, New Haven.

CHAPTER 2

STRUCTURE AND STABILITY OF ABUNDANCE AND DISTRIBUTION PATTERNS IN A CLONAL ASSEMBLAGE

INTRODUCTION

Patterns of species abundance and diversity are of intense interest among ecologists, as community structure reflects interactions among component members and their responses to selection pressures (Connell 1975). Examination of community structure is therefore a necessary first step in any study attempting to examine species interactions within communities.

The optimal approach to the study of community structure has been hotly debated over the last decade. Natural experiments [as discussed by Connell (1975) and Diamond (1975)] and observational studies of *in situ* communities, while useful, are not sufficient to determine the forces which underlie community structure (Connor and Simberloff 1979, Diamond 1986). Null models based on natural abundances of species (Connor and Simberloff 1979, 1984, Lawlor 1980) have been attempted, but have largely failed due to their inability to simulate truly random natural assemblages (Diamond and Gilpin 1982, Gilpin and Diamond 1982, 1984, Case and Sidell 1983, Colwell and Winkler 1984).

The forces most dominant in structuring specific community types has also been argued extensively (see Chapter 1). Southwood (1977) has argued that habitat parameters provide a framework which largely influences community structure, such that species interactions occur within this framework. This idea has been further

developed by other authors (e.g. Greenslade 1983, Holm 1988). Talling (1951) has suggested that random events such as colonization are sufficiently important in some communities to obscure the outcome of deterministic processes such as competition and predation. Problems in assessing the relative importance of various selective factors also arise when different processes produce similar outcomes (Holt and Kotler 1987).

The debate over forces involved in community structure has been further complicated by the issue of ecosystem stability. Although numerous biotic and abiotic forces/processes are acknowledged to operate in communities, their structural effects are trivialized if the resultant species patterns do not persist over ecological time spans (Hutchinson 1961, Wiens 1984, Chesson 1986, Chesson and Case 1986). Any study attempting to understand the internal structure of an ecosystem is therefore incomplete without some knowledge of the long-term stability of that system (Wiens et al. 1986).

One of the most common approaches to the investigation of community structure has been to examine species abundances within a community. Abundance patterns can usually be described by simple mathematical models. Which model is chosen depends on how the underlying assumptions of each model correspond to natural processes operating within the community. Abundance patterns of species in a community may approximate logseries, lognormal, or "broken

stick" curves. The resemblance of species patterns to these models often provides insight into the selective forces operating in the community under study.

Aquatic systems are ideal for studies of community structure (Kerfoot 1980, Wetzel 1982) as their boundaries are sharply defined, in contrast to most terrestrial communities. The simple communities in small ponds are especially well-suited for ecological studies (Kerfoot 1980). Studies of ponds relating to MacArthur and Wilson's (1967) theory of equilibrium island biogeography have proved fruitful (Holland and Jain 1981, Good 1981). Ecological studies within a pond system are able to examine ecological processes on several scales. By studying a number of discrete local habitats (ponds) in close proximity, one can examine both local (within-pond) and regional processes, as well as temporal shifts in these patterns.

Environmental or abiotic characteristics of ponds are known to have a major effect on species composition (Langerspetz 1955, Hutchinson 1967). Likewise, studies have shown the importance of biotic influences such as predation (Hrabacek 1962, Brooks and Dodson 1965, Kerfoot and Sih 1986) and competition (Frank 1952, Neill 1975) in determining what species are present in a pond. Hall et al.'s (1970) classic experimental pond manipulations have shown that all of these factors contribute to community structure.

The present study aims to provide data on stability of distributional patterns of members of an asexual clonal complex at a low-arctic site. Prior studies of Daphnia pulex populations at this locality have shown that the species consists of two major morphological groups, melanic and unpigmented, both of which are clonally diverse (McWalter and Hebert 1983, Weider and Hebert 1987a,b, Hebert 1987). Unpigmented clones are restricted to ponds with high humic content that provides protection from ultraviolet radiation, while melanic clones are largely restricted to clear-water ponds (Hebert and Emery 1990). Previous work on the melanic assemblage has been fairly detailed and has shown that clonal distributions are non-random and are strongly related to pond salinity (Weider and Hebert 1987a,b). The unpigmented clonal complex has been much less studied, and is the subject of the current investigation.

This chapter examines the structure and stability of the unpigmented D. pulex complex by examining temporal and spatial shifts in the distributions of individual clones over a 5 year interval. This time interval represents a significant span of ecological time, as D. pulex populations pass through several generations each summer and are re-initiated each spring from resting eggs in the ponds. Similarities and differences between the two clonal censuses should give a clear indication of community stability within and between ponds, and hence an indication

of the equilibrial or nonequilibrial state of the system.

A number of environmental variables have been shown to affect Daphnia populations. Small rock pools of the type found at Churchill may show extensive heterogeneity in physicochemical variables (Ganning 1971, Billington et al., in prep.), which influence zooplankton distributions. Ranta (1979, 1982), for example, found that coexisting species of Daphnia differed in preference for pond volume, pH, and dissolved organic content. Ponds occupied by melanic and unpigmented D. pulex clones in Churchill have been shown to differ in absorbance, surface area, volume and conductivity values (Hebert and Emery 1990). Weider and Hebert (1987a) found that melanic Churchill D. pulex clones showed different physiological tolerances for salinity, and that clonal distributions corresponded with clinal shifts in pond conductivity. Gradients in a number of potentially important abiotic parameters measured by members of the Hebert lab in 1985 which are described by Billington et al. (in prep.) were therefore considered in relation to clonal distribution patterns on bluffs A and C. Biotic factors such as predation may also influence distributions (Kerfoot 1977, Zaret 1980): therefore, clonal distributions were also compared with the occurrence of two potentially important invertebrate predators, Hesperodiaptomus arcticus and Mesostoma lingua.

METHODS:

FIELD COLLECTIONS:

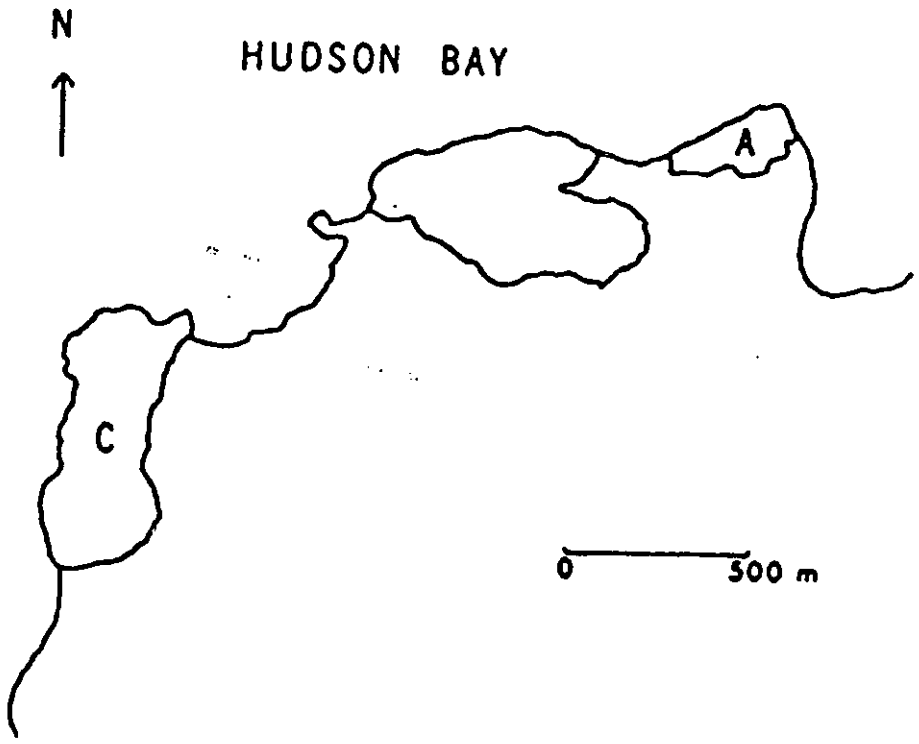
Surveys of ponds on rock bluffs A and C (shown in Figure 1) for unpigmented Daphnia pulex clones were conducted in mid-July of 1985 and late June of 1989. In both surveys, ponds were sampled using a 200 µm-mesh hand dip net. In ponds where unpigmented animals were detected, a random sample of 24 individuals was collected and returned to the CNSC lab for clonal identification. In 1985, all animals were kept in a refrigerator at 8°C until electrophoretic analysis was carried out later the same day. The 1989 samples were frozen at -170°C upon return to the lab in Taylor-Wharton 5 L dry shippers.

ELECTROPHORETIC IDENTIFICATION:

Clonal genotypes were identified using 6 enzyme loci known to be commonly polymorphic in D. pulex (Hebert et al. 1988). These loci include aldehyde oxidase (AO), amylase (AMY-1), glutamate-oxaloacetate transaminase (GOT), lactate dehydrogenase (LDH), phosphoglucomutase (PGM), and phosphoglucose isomerase (PGI). All electrophoresis was carried out on cellulose acetate gels with standard methods (Hebert and Beaton 1989).

An attempt was made to obtain clonal isolates, which were returned to Windsor for electrophoretic analyses at additional gene loci. Procedures largely followed those

Figure 2-1: Location of study sites near Churchill, Manitoba, showing relative sizes and distance between rock bluffs A and C.



described by Hebert and Beaton (1989), although modifications outlined in Richardson et al. (1986) were used for several enzyme systems. Where possible, multiple isolates of single clonal types were electrophoresed, in order to determine if groups identified in the field as "clones" were indeed distinct and specific genotypes, or instead represented groups of genetically similar subclones which could not be distinguished with the 6 loci used for field identification. The additional loci examined were: acid phosphatase (ACP), two additional amylase loci (AMY-2, AMY-3), arginine phosphokinase (APK), esterases (EST-1, EST-2), fumarate hydratase (FUM), glucose-6-dehydrogenase (G6PDH), glyceraldehyde-3-phosphate dehydrogenase (G3PDH), hexokinase (HEX), isocitrate dehydrogenase (IDH), leucyl-alanine peptidase (PEP-1), malate dehydrogenases (MDH-1, MDH-2), malic enzyme (ME), mannose phosphate isomerase (MPI), phenylalanine proline peptidase (PEP-2), triose phosphate isomerase (TPI), and xanthine dehydrogenase (XDH). The extent of genetic divergence among clones was quantified using Nei's (1972) genetic identity and distance estimates, using genotypes of individual clones as gene frequency data at each locus.

COMMUNITY ANALYSES:

Presence-absence data of clonal occurrences in all ponds were used to generate a Poisson distribution curve for unpigmented D. pulex in the bluff ponds, which was then

tested against the expected distribution using the chi-square goodness of fit statistics (Sokal and Rohlf 1981). The frequencies of individual clones in each of 150 habitats were pooled to determine the relative importance of each clone in both survey years, based on clonal abundances and relative ranking. Patterns of pooled clonal abundances were compared to lognormal and logseries distributions, again using goodness of fit tests.

The extent of temporal change in clonal community structure from 1985 to 1989 was tested in several ways. Overall clonal abundances were used to calculate percentage similarity coefficients (Pielou 1984) between the two years. Clonal diversity values for single ponds were calculated using the inverse of Simpson's (1949) index (Parker 1979) and Fisher's α coefficient (Krebs 1989), whereupon mean values for 1985 and 1989 ponds were compared. Finally, changes in pooled clonal rank abundances between 1985 and 1989 were tested using Spearman's rank correlation (Ludwig and Reynolds 1988).

Association coefficients among clones were tested using pond co-occurrence frequencies from presence-absence data. Multiple 2x2 contingency tables were tested for independence using Pearson's chi-square statistic and Fisher's exact probability estimate (Sokal and Rohlf 1981). Since these tests do not indicate whether clonal associations are positive or negative (Hubalek 1982), the direction of association was determined by comparing the

observed frequency of the present-present cell (a) of the contingency table with its expected value [E(a)]. Contingency tables with a > E(a) were interpreted as having a positive coefficient of association between clones, while those with a < E(a) were considered to have a negative association coefficient.

Multivariate analyses were used to study clonal relationships with respect to environmental parameters measured in 1985 (Billington et al., in prep.). Variation in maximum depth, mean depth, surface area, volume, water conductivity (as a measure of salinity), pH, light absorbance of water at 350 nm, and ephemerality were examined for all ponds on bluffs A and C. The raw data matrix of these physicochemical variables was log-transformed for all parameters except pH in order to normalize distributions. The correlation matrix resulting from within-pond correlations of the log-transformed variables was then subjected to principal components analysis (PCA). Individual pond scores were saved in order to determine variation within this pond system in the habitat space described by PCA axes with eigenvalues exceeding unity.

The influence of abiotic parameters on clonal diversity was examined using a number of different techniques. The effect of individual variables on diversity as reflected by clonal richness was explored by a series of one-way analysis of variance (ANOVA) tests. The

predictive ability of volume on within-pond diversity was tested using a log-linear regression model of pond volume against clonal richness and diversity. Effects of the predators Hesperodiaptomus arcticus and Mesostoma lingua on clone - volume relationships were also tested by linear regression.

To evaluate if the unpigmented D. pulex assemblage was restricted within the available habitat space, discriminant analyses were carried out for each PCA factor to determine the effects of associated environmental variables on occurrence of unpigmented clones in the ponds, using the 1985 distributional data set.

Potential differences in habitat utilization among clones were examined using presence-absence data of the clones within the ponds. Overlap of clonal types was plotted using PCA scores for ponds and presence-absence data of clones from the 1985 survey. A series of one-way ANOVA's utilizing Tukey's HSD test (Sokal and Rohlf 1981) tested differences in environmental parameters of ponds inhabited by medium- and high-abundance clones for significance. Mean values of abiotic parameters for clone-specific pond sets were compared among the clones for all variables with significant differences using the probability matrices produced by the Tukey test. All statistical tests were carried out using the SYSTAT statistical package (Wilkinson 1989) on an IBM-PC compatible computer.

RESULTS

Clonal diversity

Unpigmented clones occurred in 150 ponds on the two bluffs in 1985, and were found in 140 of these in 1989. Thirty five clones were detected in 1985. Sixteen of these clones were observed in ponds on bluff A, and 23 on bluff C; only 4 clones were shared by both bluffs. The 1989 survey resulted in the recognition of 1 new clone on bluff A. Phenotypes of these clones at the six polymorphic loci surveyed are given in Table 1, as well as ploidy levels for those clones which were determined by Beaton and Hebert (1988). Clones were numbered sequentially in order of detection.

Analyses of clonal isolates for 19 additional allozyme loci (listed in Appendix 1) revealed several more polymorphic loci. Specifically, ACP, APK, AMY-2, AMY-3, FUM, MPI, and TPI were variable. The remaining loci (EST-1, EST-2, G3PDH, HEX, IDH, ME, MDH-1, MDH-2, PEP-1, PEP-2, and XDH) were invariant among clones. Analysis of multiple isolates of the more common clones (1, 7, 13, 14, 15, 16, and 17) for these polymorphic loci did not result in their subdivision. Multiple within-pond isolates for these clones as well as for several other clones (9, 21, 25, and 27) also failed to reveal any new clones.

Table 2-1: Multilocus phenotypes for unpigmented Daphnia pulex clones on Churchill rock bluffs A and C. Loci where null activity occurs are indicated by --. Ploidy levels were inferred from heterozygote phenotypes, and confirmed (c) for 17 clones by scanning microdensitometry (Beaton and Hebert 1988). Numbers indicate relative mobilities of enzyme bands, with higher numbers representing proteins with more rapid anodal migration.

Clone	PGM	PGI	LDH	GOT	AO	AMY-1	Ploidy
1	22	14	11	23	22	22	2N c
2	22	44	11	23	11	44	2N c
3	22	44	13	23	11	13	2N c
4	22	14	11	22	33	23	2N c
5	22	14	11	23	22	--	2N c
6	22	14	11	24	22	22	2N c
7	22	44	11	23	22	23	2N c
8	22	14	11	23	22	12	2N
9	22	44	13	23	23	44	2N
10	22	11	11	23	33	23	2N
11	02	44	11	22	22	23	2N
12	22	04	11	23	22	22	2N
13	22	44	11	22	11	44	4N c
14	01	14	13	22	22	23	2N c
15	12	45	13	22	22	13	4N c
16	22	44	13	23	22	33	2N c
17	02	44	11	23	22	33	2N c
18	12	14	13	22	22	23	2N
19	22	44	13	23	22	22	2N
20	22	44	11	23	11	22	2N
21	22	14	13	33	22	22	2N c
22	12	45	13	22	22	22	2N c
23	22	44	13	23	22	23	2N
24	22	44	13	23	23	12	2N
25	22	44	11	23	22	22	2N c
26	22	44	11	02	11	44	2N
27	22	44	11	22	11	14	2N
28	12	44	11	23	22	23	2N
29	23	44	13	22	33	13	2N
30	22	44	11	23	22	44	2N
31	22	44	13	23	22	13	2N
32	22	14	11	22	33	22	2N c
33	22	11	13	23	33	23	4N c
34	22	14	13	33	33	22	2N
35	22	14	11	23	22	23	2N
36	22	44	13	23	22	34	2N
# alleles:	4	4	2	4	3	4 (+ null)	

Extent and factors influencing within-habitat diversity

The number of unpigmented clones per pond ranged from 0 to 5 and averaged 1.7 in both years for those ponds containing Daphnia (Figure 2). Patterns of clonal richness in ponds differed significantly from Poisson distributions in both years [$X^2(1985)=9.79$, df=4, $p<0.05$; $X^2(1989)=13.89$, df=4, $p<0.05$]. As well, the majority of "zero class" ponds included in the analysis were unsuitable habitats for unpigmented clones, and were occupied by melanic D. pulex.

Within-pond clonal diversity of inhabited ponds, calculated as the inverse of Simpson's (1949) index (C), was normally distributed among ponds in both years, averaging 1.26 ± 0.39 (SE) in 1985 and 1.29 ± 0.43 for 1989. Fisher's α was more sensitive to the number of clones present in each year, and produced values of 5.45 in 1985 versys 3.85 in 1989, with respective variances of 0.85 and 0.57. One-way ANOVA's testing the influence of the selected physicochemical variables from Billington et al. (in prep.) detected significant effects of surface area, pond volume and pH on clonal richness, but failed to detect any other significant effects on either clonal richness or diversity (Table 2). Log-linear regressions of pond volume against clonal richness (number of clones in a pond) and clonal diversity (Figure 3a,b) found that pond volume had no significant predictive ability on either measure [$r^2(\text{richness})=0.036$; $r^2(\text{diversity})=0.016$], suggesting co-

Figure 2-2: Bar graphs showing numbers of unpigmented clones detected in single ponds in 1985 and 1989.

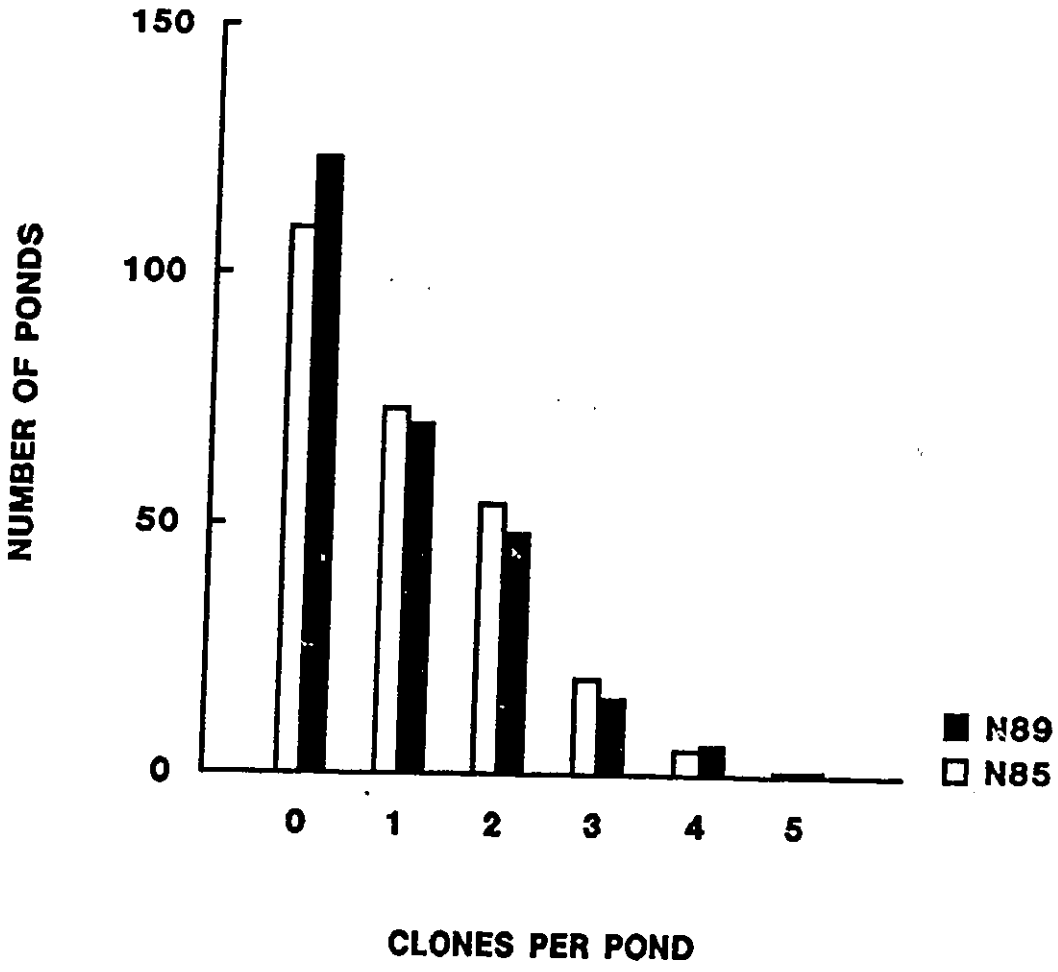


Table 2-2: Results of one-way ANOVA's of environmental variables on clonal richness and diversity values of ponds.

a) richness

variable		SS	MS	F
max. depth	regression	1.73	1.73	2.368
	residual	108.06	0.73	
mean depth	regression	1.64	1.64	2.249
	residual	108.15	0.73	
surface area	regression	5.18	5.18	7.334**
	residual	104.61	0.71	
volume	regression	5.05	5.05	7.135**
	residual	104.74	0.71	
absorb.	regression	2.80	2.80	3.867
	residual	107.00	0.72	
pH	regression	3.03	3.03	4.196*
	residual	106.77	0.72	
conduct.	regression	2.10	2.10	2.881
	residual	107.70	0.73	
ephem.	regression	1.53	1.53	2.087
	residual	107.19	0.73	

* $p < 0.05$
** $p < 0.01$

Table 2-2 (continued)

b) diversity

variable		SS	MS	F
max. depth	regression	0.55	0.55	2.926
	residual	27.60	0.19	
mean depth	regression	0.52	0.52	2.798
	residual	27.62	0.19	
surface area	regression	0.33	0.33	1.753
	residual	27.82	0.19	
volume	regression	0.46	0.46	2.460
	residual	27.68	0.19	
absorb.	regression	0.54	0.54	2.874
	residual	27.61	0.19	
pH	regression	0.21	0.21	1.101
	residual	27.94	0.19	
conduct.	regression	0.07	0.07	0.362
	residual	28.08	0.19	
ephem.	regression	0.06	0.06	0.305
	residual	27.92	0.19	

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occurrences of clones were not significantly influenced by pond volume. The presence of the predators Hesperodiaptomus arcticus or Mesostoma lingua [data from Boileau (1989) and Billington (in prep.)] also failed to account for either clonal richness or diversity (Table 3).

Clonal abundance patterns

Abundances of the clones were highly variable in the 1985 survey, with specific clonal abundances ranging from 1 to 971 individuals (Table 4). Clones 1, 13, and 14 dominated the assemblage in both abundance (76.2% of animals) and number of ponds occupied. Several other clones (2, 7, 11, 15, 16, 17, 19 and 29) occurred in fairly high proportions, but most were rare. Rare clones displayed several patterns of distribution and abundance. Type I clones (3,10,11,20 and 33) occurred in low numbers in several ponds, while types II and III were observed in single ponds. The latter two groups were separated on the basis of their abundance; Type II clones dominated the ponds in which they occurred, while Type III clones were represented by only a few animals (Figure 4). Six rare clones (21, 22, 23, 24, 27 and 31) were common in single ponds and were designated as Type II. The 13 remaining clones, designated Type III, were limited in both distribution and local abundance (4, 5, 6, 8, 12, 18, 28, 29, 30, 32, 34, 35 and 36). It is interesting that 9 of the 13 clones in this latter group were found on bluff A.

Table 2-3: Linear regressions of clonal richness and diversity values of ponds. a) all ponds included in the regression; b) ponds with H. arcticus present; c) ponds with M. lingua; d) predator-free ponds.

a) All ponds (n=150)

richness:	Y = 1.63 + 0.09 X	r^2=0.036
diversity:	Y = 1.26 + 0.03 X	r^2=0.016

b) H. arcticus present (n=58)

richness:	Y = 1.80 + 0.07 X	r^2=0.013
diversity:	Y = 1.35 + 0.01 X	r^2=0.001

c) M. lingua present (n=18)

richness:	Y = 1.41 + 0.16 X	r^2=0.065
diversity:	Y = 1.36 - 0.04 X	r^2=0.020

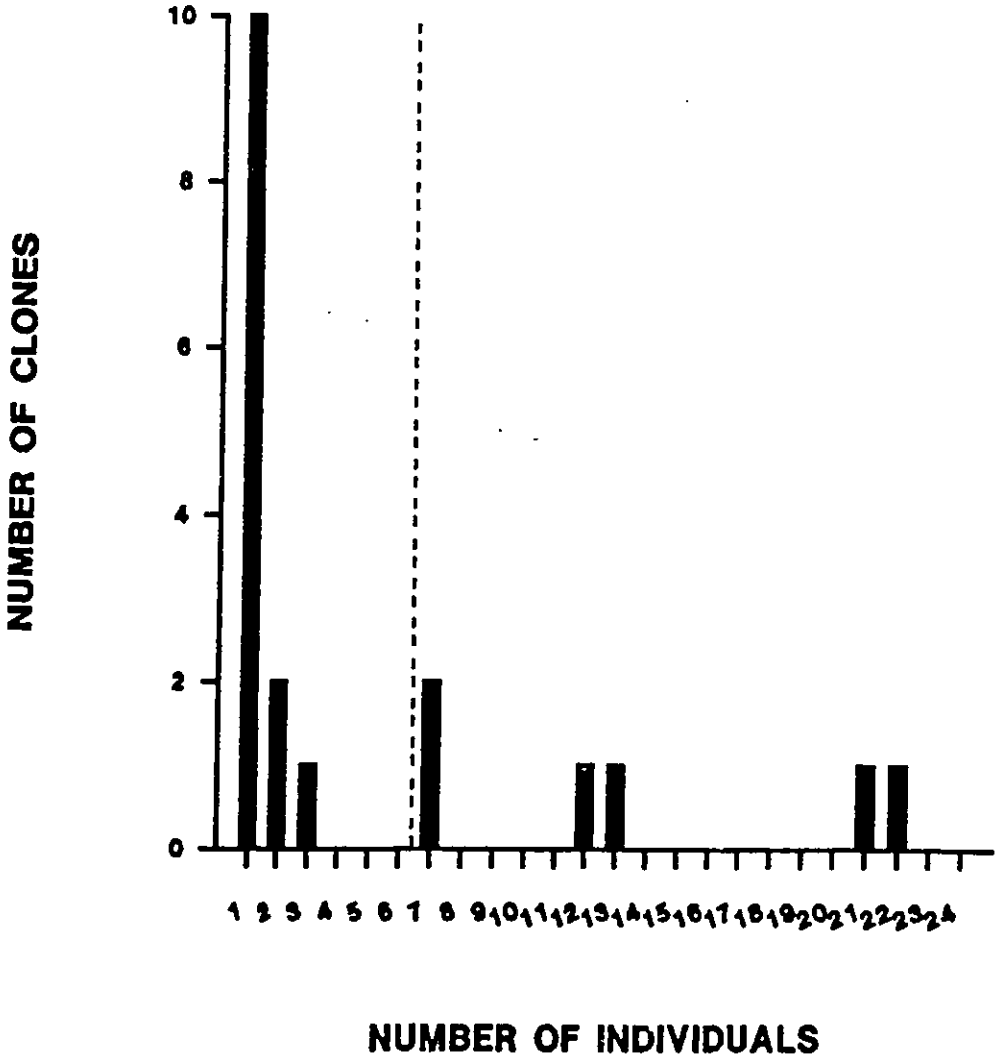
d) predator-free ponds (n=84)

richness:	Y = 1.58 + 0.09 X	r^2=0.029
diversity:	Y = 1.23 + 0.03 X	r^2=0.009

Table 2-4: List of Churchill unpigmented clones, showing 1985 site locations, number of individuals per clone, proportional frequency, number of ponds occupied, and mean frequency within home ponds (+/- 1 S.E.).

Clone	Site	N	P	No. ponds	$\bar{x}$ within ponds
1	A C	830	0.2493	49	0.77 (0.32)
2	A C	55	0.0165	9	0.24 (0.20)
3	A	4	0.0012	2	0.08 (0.06)
4	A	1	0.0003	1	0.04
5	A	1	0.0003	1	0.04
6	A	1	0.0003	1	0.04
7	A C	69	0.0207	7	0.41 (0.33)
8	A	1	0.0003	1	0.04
9	A	63	0.0189	4	0.66
10	A	13	0.0039	2	0.27 (0.09)
11	A C	4	0.0012	3	0.06 (0.02)
12	A	1	0.0003	1	0.04
13	C	738	0.2217	49	0.66 (0.40)
14	C	971	0.2918	60	0.67 (0.37)
15	C	110	0.0330	13	0.35 (0.30)
16	C	87	0.0261	10	0.36 (0.34)
17	C	182	0.0547	16	0.57 (0.42)
18	C	2	0.0006	1	0.08
19	C	60	0.0180	8	0.31 (0.36)
20	C	4	0.0012	2	0.08
21	C	21	0.0063	1	0.88
22	C	7	0.0021	1	0.29
23	C	7	0.0021	1	0.29
24	C	22	0.0066	1	0.92
25	C	21	0.0063	4	0.27 (0.22)
26	C	27	0.0081	3	0.38 (0.47)
27	C	13	0.0039	1	0.54
28	C	1	0.0003	1	0.04
29	C	3	0.0009	1	0.13
30	A	1	0.0003	1	0.04
31	C	12	0.0036	1	0.50
32	A	1	0.0003	1	0.04
33	A	8	0.0024	2	0.17 (0.18)
34	C	2	0.0006	1	0.08
35	A	1	0.0003	1	0.04

Figure 2-4: Plot showing abundances of clones restricted to single ponds.



The 1989 pond survey revealed little change from the patterns observed in 1985 (Appendix 3b, Table 5). Clones 1, 13, and 14 maintained their dominance, making up 75.9% of all animals. The greatest shifts in distribution and abundance occurred among clones of low to intermediate abundance, and were likely due to sampling error. Overall abundances of the unpigmented clones are summarized in Figure 5. Log-transformed clonal abundance curves from 1985 and 1989 data did not conform to lognormal distributions (Preston 1948), but closely resembled logseries distributions.

Clonal distribution patterns

Clone 1 dominated ponds on bluff A, being present in 38 of 39 ponds in 1985, and 35 of 36 ponds in 1989 (Figure 6). By contrast, clone 1 was found only on the seaward front of bluff C (Figure 7). Most of the ponds in the interior of bluff C were dominated by clones 13 and 14 in both 1985 and 1989 (Figure 7).

Distribution and abundance patterns varied greatly among the uncommon clones on both bluffs (Figure 8, Figure 9). Rare clones on bluff A were largely restricted to single ponds, whereas 6 of the 19 non-dominant clones on bluff C (15, 16, 17, 19, 25 and 28) were observed in several ponds.

Table 2-5: List of Churchill unpigmented clones, showing 1989 site location, number of individuals per clone, proportional frequency, number of ponds occupied, and mean occurrence within home ponds (+/- 1 S.E.). Blanks indicate clones which were not detected in the 1989 survey.

Clone	Site	N	P	No. ponds	$\bar{x}$ within ponds
1	A C	823	0.2485	46	0.771 (0.32)
2	A	18	0.0054	5	0.15 (0.12)
3	A	14	0.0042	1	0.58
4	...	.	.....	.	
5	A	1	0.0003	1	0.04
6	A	2	0.0006	1	0.08
7	A C	55	0.0166	5	0.46 (0.34)
8	...	.	.....	.	
9	A	65	0.0196	3	0.90 (0.13)
10	A	6	0.0018	1	0.25
11	C	8	0.0024	3	0.11 (0.05)
12	...	.	.....	.	
13	C	692	0.2089	47	0.61 (0.41)
14	C	1000	0.3019	61	0.69 (0.36)
15	C	94	0.0284	15	0.27 (0.33)
16	C	130	0.0393	13	0.42 (0.37)
17	C	218	0.0658	14	0.65 (0.37)
18	C	1	0.0003	1	0.04
19	C	54	0.0163	4	0.56 (0.38)
20	...	.	.....	.	
21	C	20	0.0060	1	0.83
22	C	1	0.0003	1	0.04
23	C	8	0.0024	3	0.11 (0.05)
24	C	20	0.0060	1	0.83
25	C	36	0.0109	3	0.50 (0.08)
26	C	27	0.0082	3	0.38 (0.54)
27	C	2	0.0006	1	0.08
28	C	12	0.0036	5	0.10 (0.07)
29	...	.	.....	.	
30	...	.	.....	.	
31	...	.	.....	.	
32	...	.	.....	.	
33	...	.	.....	.	
34	...	.	.....	.	
35	C	4	0.0012	1	0.17
36	A	1	0.0003	1	0.04

Figure 2-5: Log-transformed clonal abundances in 1985 and 1989.

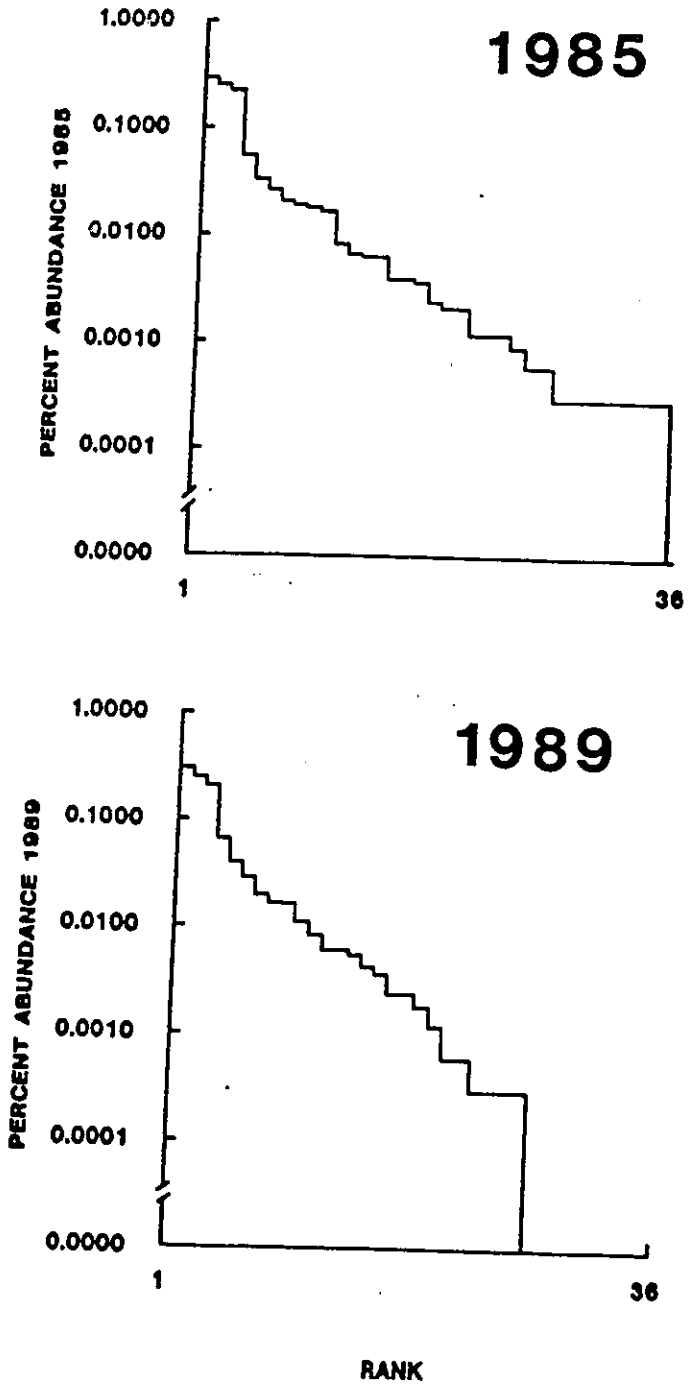


Figure 2-6: Distributions of unpigmented D. pulex clone 1 in ponds on rock bluff A in 1985 and 1989.

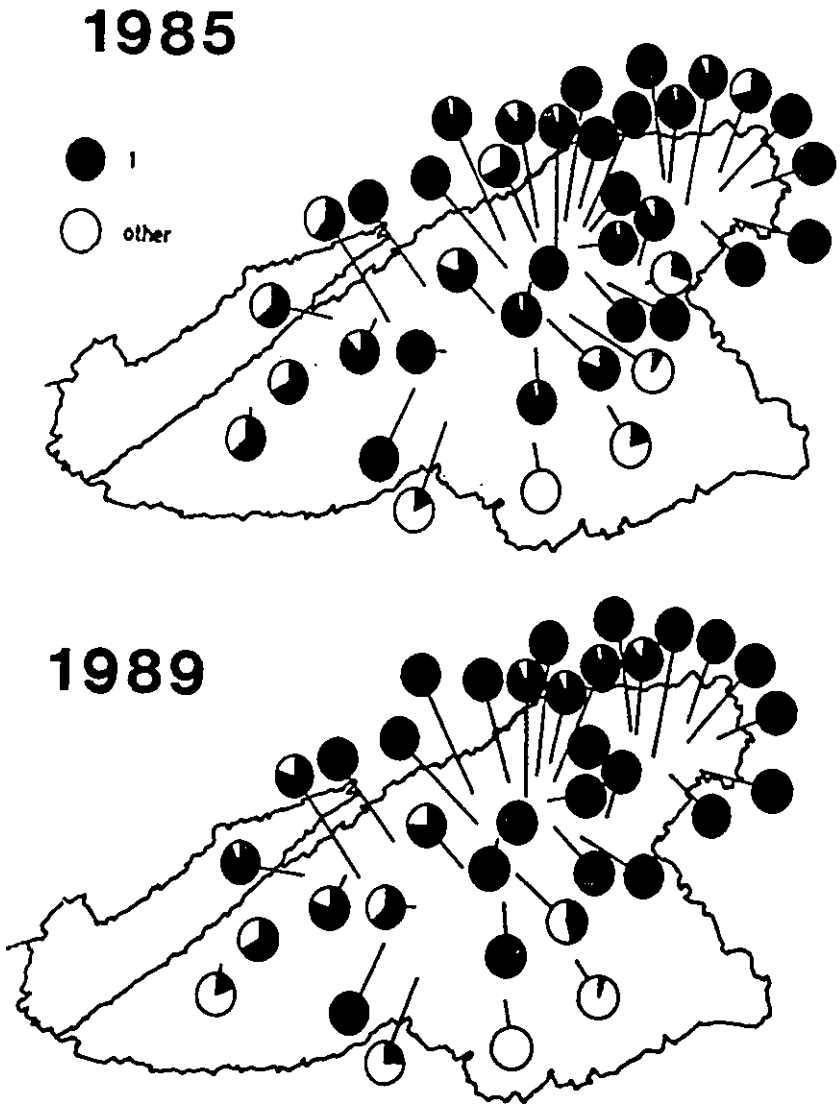


Figure 2-7: Distribution of common unpigmented D. pulex clones (1, 13 and 14) on bluff C in 1985 and 1989.

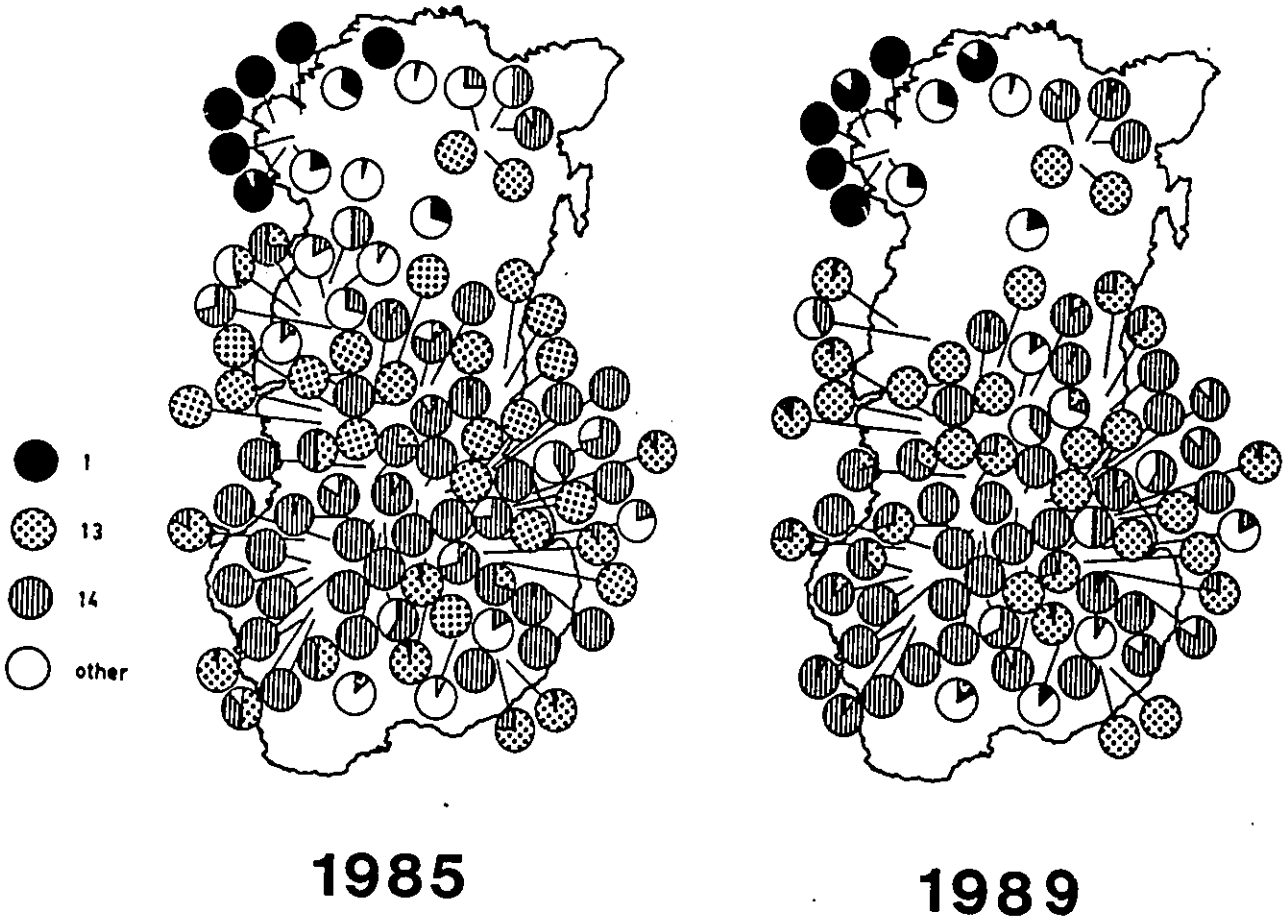


Figure 2-8: Distributions of non-dominant unpigmented D. pulex clones in ponds on rock bluff A in 1985 and 1989.

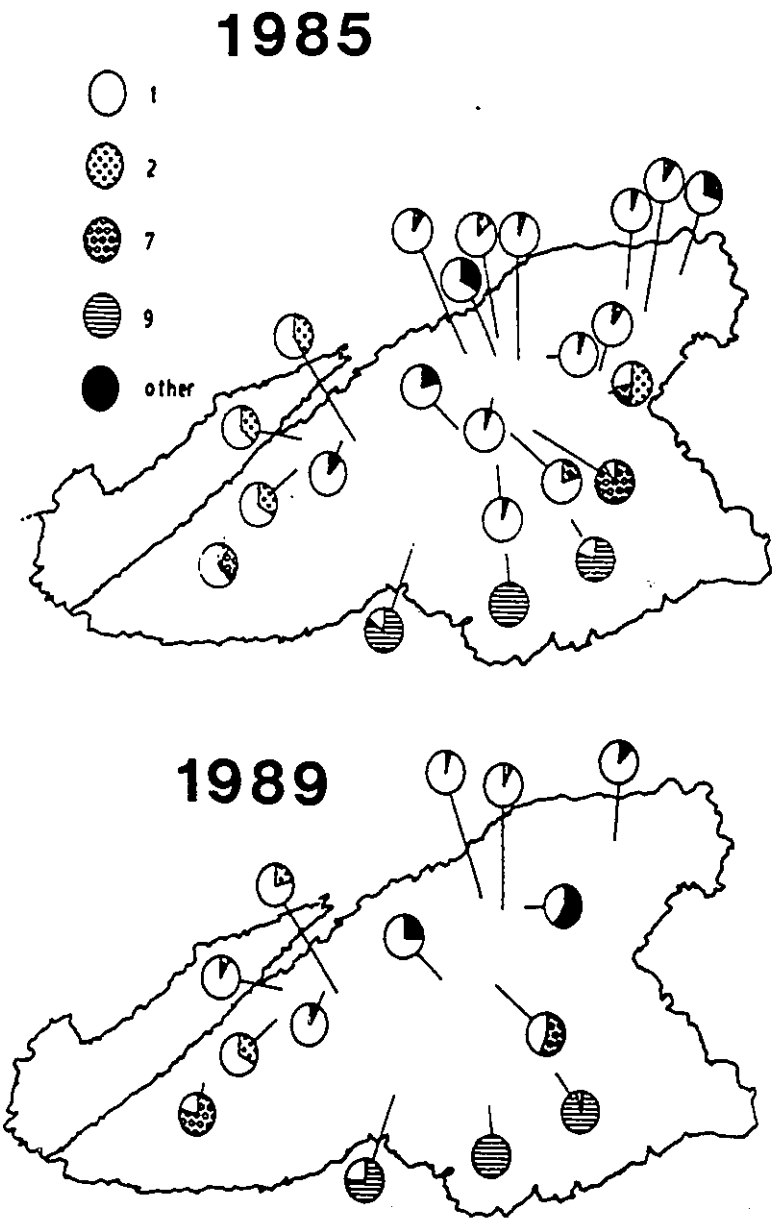
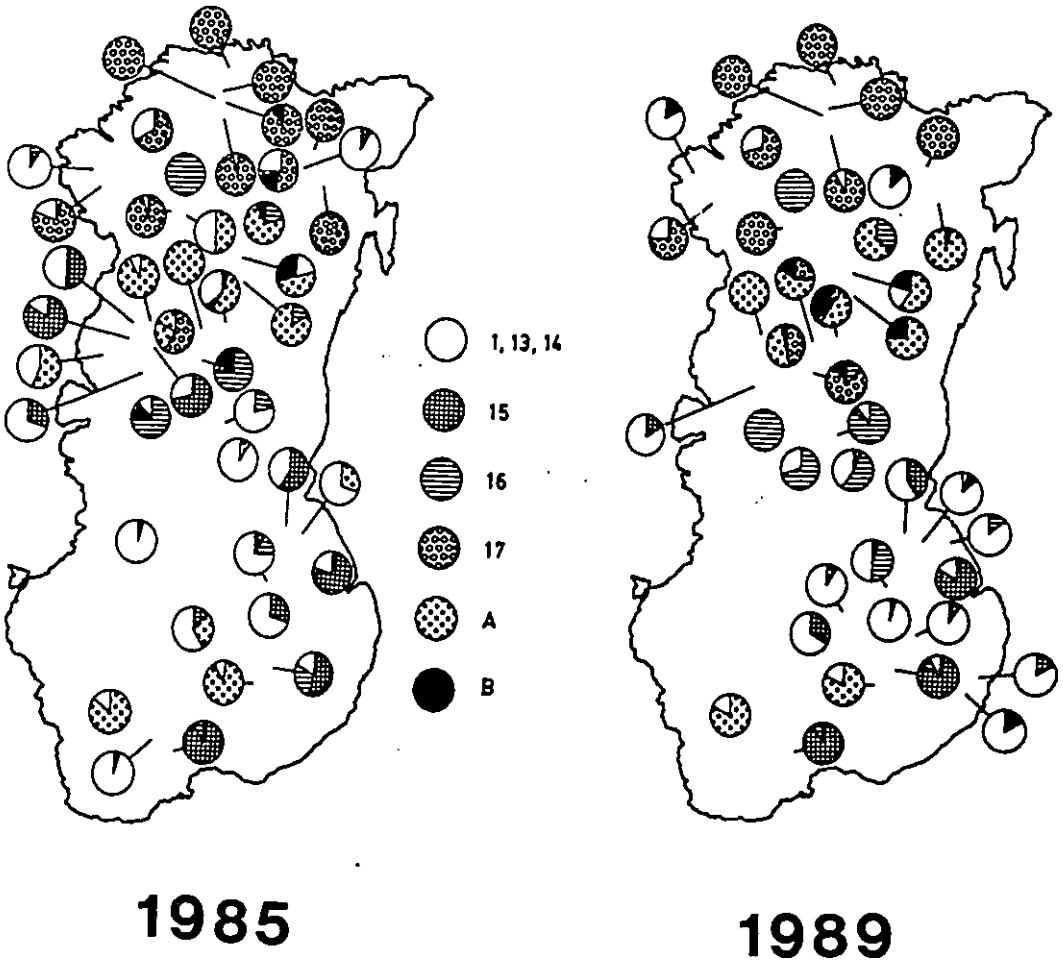


Figure 2-9: Distributions of non-dominant unpigmented D. pulex clones in ponds on bluff C in 1985 and 1989.



Patterns of clonal association

Significant pairwise clonal associations, based on 2x2 contingency tables using presence-absence data from Appendix 3, are presented in Table 6. Most associations were negative, suggesting that clones showed competitive exclusion or were limited to distinct habitats. Clones 1 and 2, and clones 14 and 15, showed the only positive associations in both bluff surveys. All clonal pairs not listed in Table 6 were not significantly associated, which was likely in part due to the limited numbers of ponds occupied by most clones.

The six most common clones in the assemblage (1, 13, 14, 15, 16 and 17) showed clear evidence of non-random distributional patterns. Thus, in 1985 clone 1 never co-occurred with clones 13, 14, 15, or 16 (Appendix 3a), and only rarely with clone 17. The remaining clones (13 to 17) co-occurred in 2- and 3- clone combinations, although clone 17 was a rare member. In 1989, clone 1 was found with clone 13 in one pond, with highly unequal numbers (pond C76, Appendix 3b). Again, clones 1 and 17 co-occurred, as did clones 13, 14, 15 and 16. If coexisting clones are ecologically independent, frequencies of clones in ponds where they co-occur should approximate a normal distribution, according to the central limit theorem, yet this was true only for clones 14 and 15 (Appendix 3). Clones 13 and 14 have been shown to have bimodal co-occurrence frequencies (Wilson and Hebert 1990), indicating

Table 2-6: Significant pairwise clonal associations among the six most abundant clones detected from 1985 and 1989 presence/absence data. Pearson chi-square values for 2x2 contingency tables for each clonal pair are given, as well as Fisher's exact probability for independent clonal association.

	1985		1989		Assoc.
Clones	X^2	P	X^2	P	(1985,1989)
1,13	32.69	0.000	30.29	0.000	-,-
1,14	45.40	0.000	51.38	0.000	-,-
1,15	6.83	0.009	6.64	0.010	-,-
1,16	2.46	0.085	7.01	0.008	ns,-
13,14	2.59	0.108	10.26	0.001	ns,+
13,17	8.60	0.003	7.86	0.005	-,-
14,15	16.42	0.000	17.48	0.000	+,+
14,17	5.54	0.019	11.67	0.001	-,-
15,16	6.23	0.013	6.03	0.014	-,+

that these clones are not independent. Co-occurrence distributions of the remaining clonal pairs could not be tested due to the limited sample sizes.

Occurrences in ponds containing the predatory species Hesperodiaptomus arcticus and Mesostoma lingua differed among the six most common clones (Table 7). Clone 1 never co-occurred with H. arcticus, while clones 14 and 15 showed positive associations with the predator. With the exception of clone 16, none of the clones showed any significant correlation with M. lingua. This clone, however, was able to coexist with the predator in the majority of ponds which the clone occupied.

Patterns in community stability

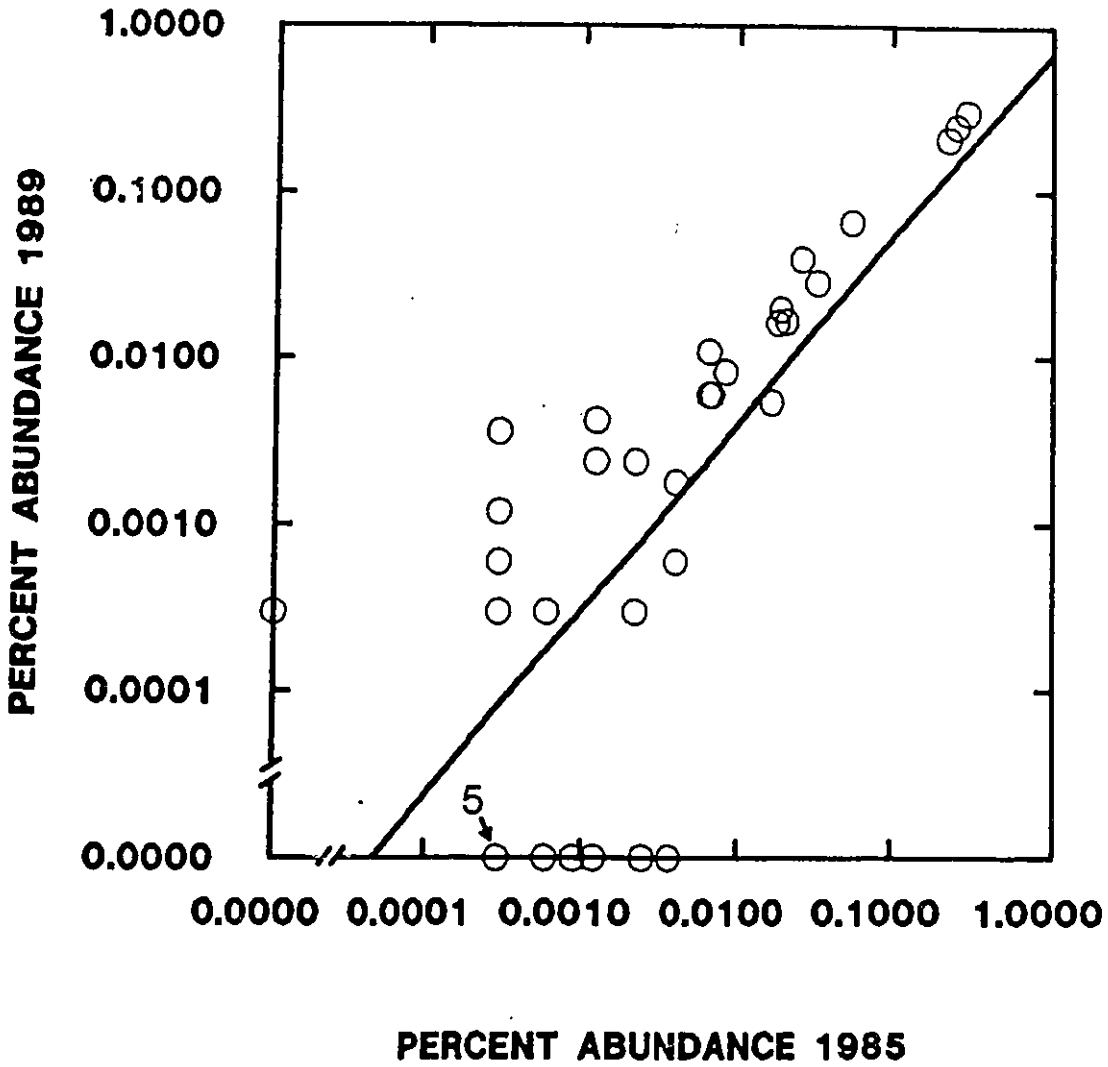
The strong similarity in clonal composition between the 1985 and 1989 assemblages (Figures 6 - 9) is supported by statistical analyses. Abundances of specific clones in the 1985 and 1989 surveys (Figure 10) were strongly correlated (r^2=0.99). Pielou's (1984) coefficient of community similarity, calculated by summing the lower occurrence frequencies of each clone between 1985 and 1989 (Tables 4 and 5), showed 95.4% similarity between the 1985 and 1989 communities. Spearman's rank correlation (Sokal and Rohlf 1981) on clonal abundances listed in Tables 4 and 5 tested for changes in clonal ranking from the two years, and determined that relative clonal abundances between the two years were highly correlated (R_S=0.90, df=36, $p<0.001$).

Table 2-7: Associations of the six most abundant unpigmented clones with the predators *Hesperodiaptomus arcticus* and *Mesostoma lingua* in the bluff ponds. N(*H. arcticus*) = 92; N(*M. lingua*) = 18

	H. arcticus			*M. lingua*		
Clone	present	absent	G	present	absent	G
1	0	49	33.72***	7	42	1.14
13	18	30	2.31	3	45	4.71
14	45	15	59.38***	7	53	1.03
15	10	3	8.84*	2	11	0.33
16	3	7	4.45	8	2	28.16**
17	12	4	1.71	3	13	0.91

Figure 2-10: Linear regression of clonal abundances in 1989 (Y) as predicted from 1985 values (X). 1989 abundances were described by the equation:

$$Y = 1.003\ X; \quad r^2 = 0.99$$



Factors responsible for stability of clonal distributions

The temporal stability but spatial differentiation of clonal distributions could be explained if each clone was adapted to a narrow range of environmental conditions, and habitat characteristics varied microspatially, but showed limited temporal heterogeneity. Prior studies have revealed conspicuous variation among the Churchill ponds in pH, salinity, volume and ephemerality (Billington et al., in prep.).

Principal component analysis (PCA) was used to examine correlations among measured habitat variables and levels of variation in the pond system, allowing the characteristics of the multidimensional habitat "hypervolume" to be collapsed onto a small number of relevant axes. Separate PCA's of environmental variables from ponds on bluff A and bluff C each produced three significant axes of variation (eigenvalues > 1), showing similar axial correlation coefficients on each bluff (Table 8). Data from both bluffs were therefore pooled to give an overall picture of variation in the selected physical and chemical parameters among the ponds. PCA axis 1 explained 40.8% of overall variation among the ponds, and was associated with measurements of pond size (volume, depth, and surface area). PCA axis 2 explained 23.7% of variation and was associated with pH and conductivity. Pond absorbance (dissolved organic carbon) and ephemerality showed correlations with PCA axis 3, which explained 16.5% of

Table 2-8: Correlation of 1985 abiotic variables/parameters with axes of variation generated by principal component analysis [PCA]. (A) Results from PCA using Bluff A pond data set only; (B) PCA results from data set of Bluff C ponds only; (C) PCA of pooled data set from all ponds on Bluffs A and C.

Bluff A:

variable	Factor 1	Factor 2	Factor 3
volume (m^3)	0.957	-0.065	0.033
mean depth (m)	0.888	-0.154	0.135
max. depth (m)	0.878	-0.111	0.128
surface area (m^2)	0.862	-0.019	-0.061
conductivity	-0.123	0.894	0.042
pH	-0.122	0.784	0.227
absorbance	0.007	0.727	-0.523
ephemerality	0.130	0.122	0.915
% variance	40.819	24.963	15.026

Bluff C:

variable	Factor 1	Factor 2	Factor 3
volume (m^3)	0.938	-0.119	0.150
mean depth (m)	0.922	0.011	-0.121
max. depth (m)	0.911	-0.070	-0.106
surface area (m^2)	0.829	-0.137	0.232
pH	-0.061	0.937	-0.032
conductivity	-0.005	0.897	0.052
absorbance	0.208	-0.583	0.346
ephemerality	0.001	0.062	-0.929
% variance	41.171	25.813	13.603

Bluffs A and C:

variable	Factor 1	Factor 2	Factor 3
volume (m^3)	0.945	0.068	-0.139
mean depth (m)	0.917	0.019	0.151
max. depth (m)	0.896	0.128	0.133
surface area (m^2)	0.835	0.039	-0.252
pH	-0.084	-0.954	0.029
conductivity	-0.062	-0.920	-0.097
absorbance	0.101	0.173	-0.816
ephemerality	0.065	0.296	0.723
% variance	40.753	23.708	16.536

variation within the pond set. Despite the similar PCA scores obtained in the separate analyses of bluffs A and C, results from the pooled data set showed a definite clustering of ponds from each bluff (Figure 11). This separation reflected the higher salinity and pH of bluff A ponds in comparison with those on bluff C.

Despite the extent of physicochemical variation among the ponds, D. pulex populations appeared to occupy ponds throughout the described habitat space. Discriminant analysis on PCA scores for presence or absence of D. pulex in the ponds, however, revealed that all three PCA axes had significant effects on presence or absence of Daphnia (factor 1: $F_{1,253}=20.421$, $p<0.001$; factor 2: $F_{1,253}=19.459$, $p<0.001$; factor 3: $F_{1,253}=5.361$, $p=0.021$). This indicates that all three axes should have some impact on clonal distributions in this habitat hypervolume.

Figure 12 shows occupancy of the six most common clones in the habitat space described by PCA axes 1 and 2, which jointly account for 64.5% of the variation in the environmental parameters. Clonal overlap is likely greater than shown, as the plotted ellipses encompass only the 50% Gaussian confidence areas for pond occupancy by each clone. Among the three dominant clones, habitats of clone 1 showed clear differences from those inhabited by clones 13 and 14. By contrast, the abiotic habitat spaces of the latter two clones were extremely similar. The three next most abundant clones (15, 16, and 17) also exhibited some

Figure 2-11: Vector co-ordinates of bluff A and C ponds in the habitat space described by axes of variation determined by principal component analysis.

○ = A

▲ = C

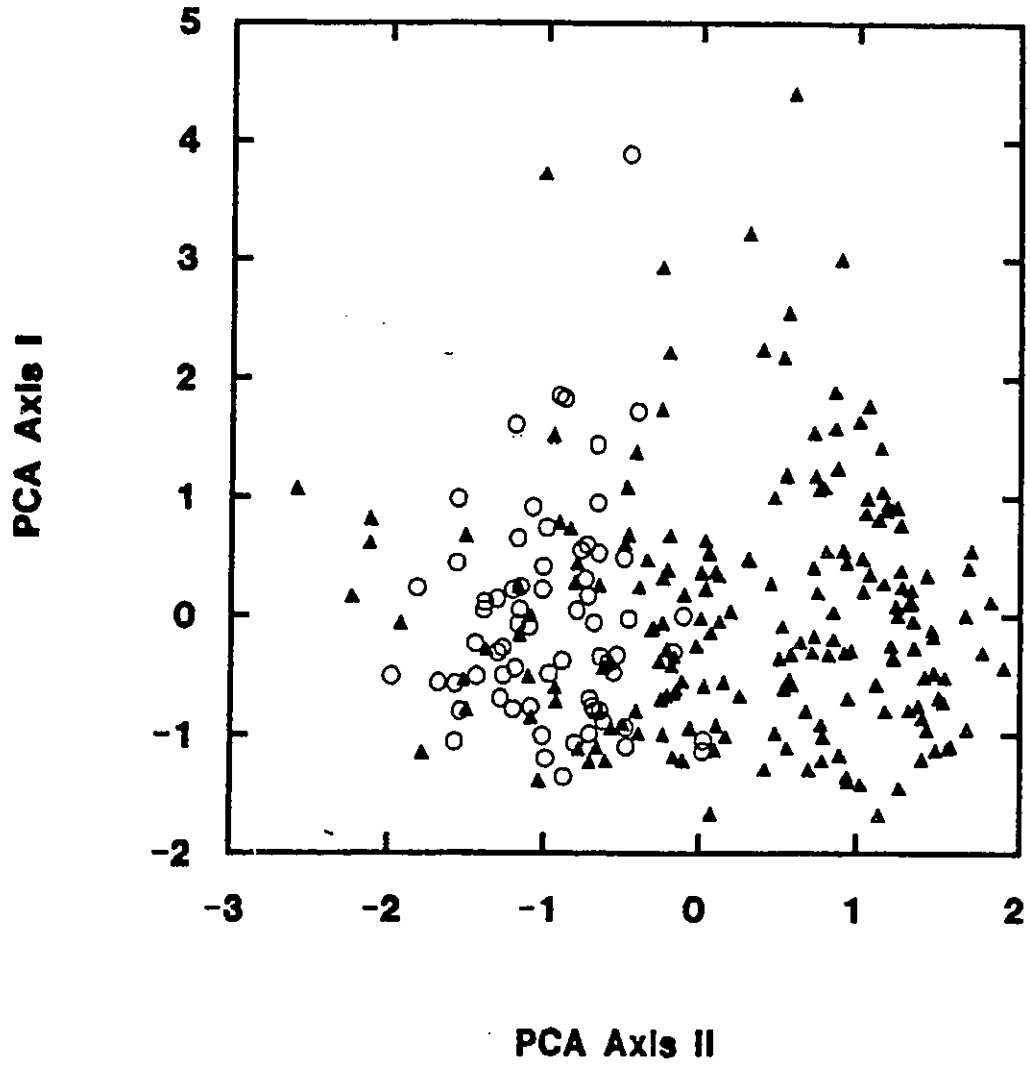
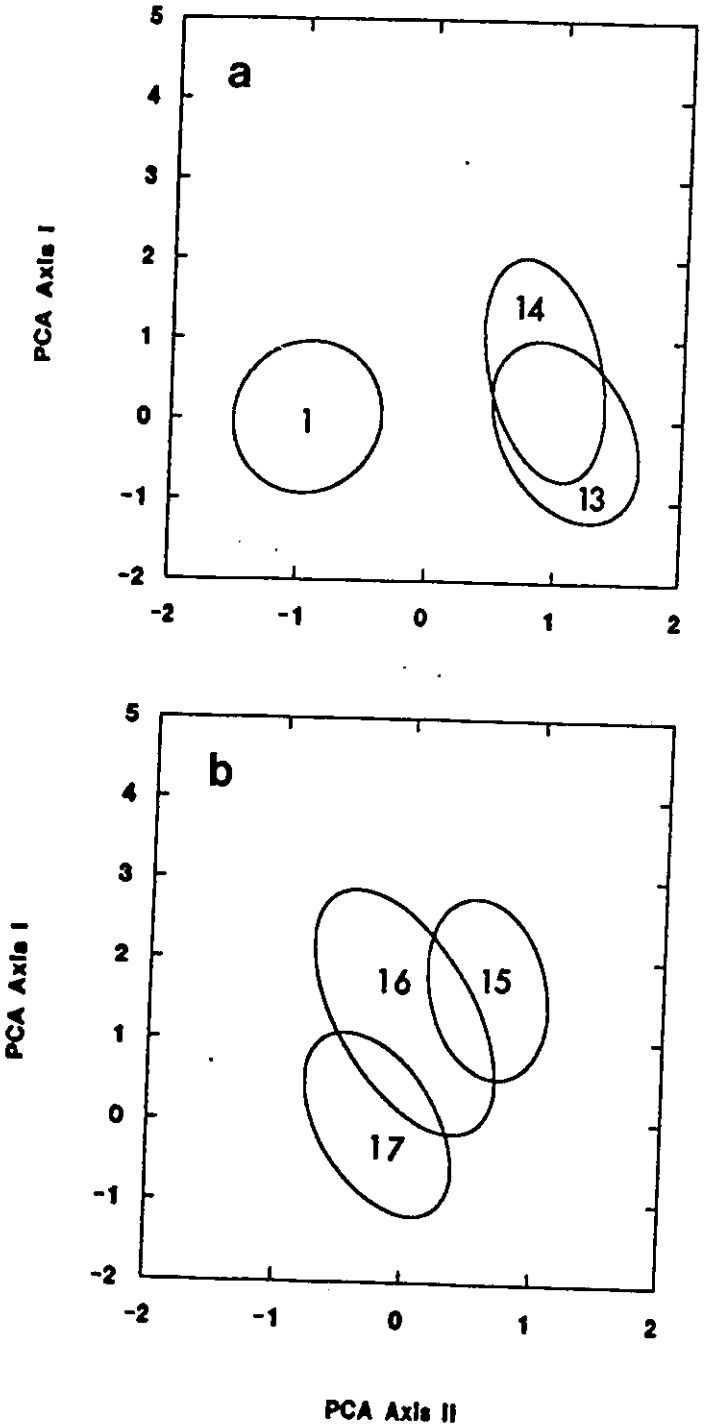


Figure 2-12: Distribution and overlap in habitat utilization of unpigmented D. pulex clones in environmental space described by PCA axes 1 and 2, using 1985 clonal distributions. (a) clones 1, 13 and 14; (b) shows habitat spaces occupied by clones 15, 16 and 17.



habitat overlap, although each clone was associated with a different habitat type (Figure 13b) with clone 17 showing the greatest similarity with clone 1's habitat preferences.

One-way ANOVA's using Tukey's HSD test of each abiotic variable used in the PCA showed that mean values of clone utilization of all habitat parameters except absorbance differed significantly (Table 9). Clones 14, 15 and 16 inhabited deeper, larger ponds than the other clones (Table 10). Pond pH exhibited the greatest variation among clonal habitats: clones 1, 16 and 17 inhabited alkaline ponds, while clones 13 and 14 dominated the most acidic ponds, with clone 15 intermediate between the two groups. Clones 1 and 17 showed a preference for saline habitats, while the other clones were found in ponds with conductivities less than 500 µS/cm. Differences in pond ephemerality among clones reflected the propensity of coastal ponds inhabited by clones 1 and 17 to dry out more quickly than those in the central portions of the bluffs. Absorbances of ponds inhabited by the different clones did not differ significantly. Although less numerous clones could not be tested, these results suggest that physicochemical variables strongly influence clonal distributions.

Table 2-9: Results of one-way analyses of variance for differences in habitat characteristics among ponds inhabited by the six most common clones in 1985.

Environmental variable	F	P
max. pond depth (m)	6.09	< 0.001
mean pond depth (m)	8.74	< 0.001
pond volume (m^3)	3.24	< 0.001
surface area (m^2)	4.32	< 0.001
absorbance	1.72	0.096
pH	81.79	< 0.0001
conductivity (µS/cm)	9.04	< 0.001
ephemerality (weeks)	5.68	< 0.001

Table 2-10: Results of Tukey's HSD test for differences among 1985 clonal means for habitat characters. Superscript letters show similarity of clonal means for the indicated parameter. Separate groups differ at the alpha=0.05 significance level.

Clone	max. depth	mean depth	surface area	pond volume	pH	conduct. (µS/cm)	ephem. (weeks)
1	0.39^{a}	0.23^{c}	16.75^{e}	4.39^{g}	8.54^{h}	1292.5^{j}	10.25^{m}
13	0.36^{a}	0.24^{c}	14.57^{f}	4.59^{g}	6.19^{i}	95.6^{k}	12.33^{n}
14	0.52^{b}	0.34^{d}	27.63^{e}	13.58^{h}	6.34^{i}	100.2^{k}	12.58^{n}
15	0.69^{b}	0.47^{d}	49.27^{e}	24.19^{h}	6.72^{i}	111.2^{k}	12.46^{n}
16	0.61^{b}	0.37^{d}	74.33^{e}	29.24^{h}	7.60^{i}	218.3^{k}	12.20^{n}
17	0.35^{a}	0.22^{c}	18.68^{e}	5.08^{g}	7.86^{i}	282.5^{j}	11.75

DISCUSSION

Clonal diversity

The present study revealed 36 different unpigmented D. pulex clones in the 150 ponds surveyed on the two bluffs. This number greatly exceeded the clonal richness of melanic D. pulex in the area: Weider and Hebert (1987a,b) found only 16 melanic clones in their survey of 147 ponds from 12 different bluffs and 6 tundra habitats. This difference may be more apparent than real, as the present study failed to detect within-clone electrophoretic variation at additional loci, while Weider and Hebert (1987a,b) detected subclonal groups within melanic "clones" identified in their survey. Most of the clonal diversity in D. pulex is thought to owe its origin to the polyphyletic loss of sex (Innes et al., 1989).

Extent and factors influencing within-habitat diversity

The lack of correlation between clonal richness or diversity and pond volume (Figure 3) contrasted with results obtained in studies of freshwater ecosystems at the species level. Fryer (1985) noted a positive relationship between lake volume and number of chydorid species, as did Holland and Jain (1981) for macrophytes. Good (1981) similarly found that the volume of rock and tundra ponds at Churchill accurately predicted the number of zooplankton species present. This suggests that selective inter- and

intraspecific interactions among the resident zooplankton may be qualitatively different, or differ in order of magnitude.

Clonal diversity might be expected to vary with environmental stress, with "soft" habitats supporting more diverse assemblages than rigorous environments (Connell and Orias 1964). The lower mean values of clonal richness and diversity in bluff A ponds listed in Appendix 4 may therefore be due to the higher pH and salinity of these ponds as compared with ponds on bluff C. The inability of habitat descriptors to predict clonal richness or diversity in the ponds, however, suggests that other selective processes also influence pond diversity values.

Clonal abundances

Clonal abundances in both years did not conform to a log-normal distribution (Preston 1949), as might have been expected, but rather fitted logseries abundance curves. This has some interesting implications, as the assumptions made for these two models are quite different (May 1975). The logseries model assumes that species essentially parcel off portions of a resource gradient, suggesting that one structural factor (usually inferred to be competition) is primarily responsible for the observed community structure. The canonical lognormal distribution of Preston (1949), in contrast, assumes that species abundances are the result of interactive effects of multiple independent

processes operating in the community. Species are thus assumed to be functionally independent.

May (1975) has argued that the lognormal distribution is primarily a mathematical artifact of generalized community patterns and has no biological meaning. Sugihara (1980) has shown, however, that the lognormal distribution is widespread in natural communities and reflects structural processes. He was also able to show that deviations from the lognormal curve should occur if species have strong interaction coefficients (i.e. influence each others' abundances).

The Churchill clones exhibited highly unequal abundances with clones 1, 13 and 14 dominating the clonal assemblage. Polarized abundance patterns of this type, comprised of several superabundant clones, few if any clones of intermediate abundance, and many rare members seem to be common in clonal organisms (Lyman and Ellstrand 1984, Jaenike et al. 1980, Hebert and Crease 1983, Sebens and Thorne 1985, Weider and Hebert 1987b), although no studies have yet examined this phenomenon. This abundance pattern is hardly surprising if one considers the concept of limiting similarity in conjunction with the extreme similarity in life history and resource utilization among conspecific clones (Parker 1979, Hebert 1977). Adaptations of clones to different selection scenarios should produce a small number of "best-adapted" clones to a given habitat type or niche strategy, with similar but less successful

clones occurring at much lower frequencies. This possibility is further supported by the logseries abundance patterns of the Churchill clones.

The clonal genotypes observed in Churchill appear to represent distinct ecotypes with markedly different ecological preferences, although some overlap existed. Ecological differences among genotypes of asexual organisms have also been documented in a number of other systems (Hebert 1974, Hebert and Ward 1976, Vrijenhoek 1978, Parker 1979, Loaring and Hebert 1981, Hebert and Crease 1983, Pace et al. 1984, Weider 1985, Tucic et al. 1986, Weider and Hebert 1987a).

Clonal distributions

The superabundance of a small number of clones has been explained by their having "general purpose genotypes" (Lynch 1983, Jaenike and Selander 1986). The dominant Churchill clones, however, did not exhibit generalized ecological strategies. Rather, the success of these clones was due to each being well-adapted for a common habitat type, similar to the results observed by Harshman and Futuyma (1985) in geometrid moths. Clone 1 dominated ponds with high conductivity (Weider 1987), and was exclusively found in high-salinity habitats on both bluffs. Clones 13 and 14 were found in ponds with low conductivity and similar physicochemistry, but differed in sensitivity to predation (Wilson and Hebert 1990). The dominance of low-

salinity ponds by clone 13 in the absence of predators indicates that this clone is a highly successful competitor (Wilson and Hebert 1990).

The general purpose genotype hypothesis also fails to account for the existence of ecological analogues among clones with lower abundances. Clones 2, 7 and 17 occupied habitats similar to those utilized by clone 1, and indeed clones 1 and 17 showed negative frequency-dependent distributions with respect to each other in bluff C ponds. Similarly, clones 9, 15 and 16 appeared analogous to clone 14, and were found only in ponds with D. arcticus. Thus, clonal distributions are better explained by adaptations to specific habitat types than by Lynch's (1984) general purpose genotype hypothesis.

Consideration of only the common clones may give a misleading picture of the nature of clonal adaptations, as the majority of clones were uncommon. Although statistical tests of habitat specificity/utilization of rare clones were not possible, to ignore these clones would neglect a major point of interest presented by this pond system. Rabinowitz (1980) described several patterns of rarity in plant species which encompass the types of rarity seen in the Churchill clones. Rare clones were assigned to one of three groups: (I) clones which occurred in several ponds, in low numbers; (II) clones largely restricted to single ponds, which they dominated; (III) clones represented by a few individuals in single ponds.

These patterns of clonal rarity may be due to a number of factors, such as limited dispersal, chance, or adaptation to specific but locally abundant resource types or niche spaces. Type II clones, (restricted distributions but locally abundant) are likely specialized clones which require rare or unique habitat conditions (Holm 1985). This argument has also been presented by Kolasa (1989), who pointed out that extreme specialization may not be adaptive and will likely cause rarity or extinction as a given habitat or resource type becomes scarce.

Type III clones may be recent mutational derivatives of other, sympatric clones. This hypothesis can be readily tested with genetic data. Although allozyme phenotypes for 8 of the 11 Type III clones did not show extreme similarity to co-occurring clones, Stanton (1988) has shown that 4 of 6 Type III clones examined had mitochondrial DNA types identical to those of sympatric clones.

The limited sample size used in both survey years restricts the resolution of determining clonal pond composition to detection of genotypes with occurrence frequencies of 0.10 or greater at the alpha=0.05 significance level (Gregorius 1980). The absence of many Type III clones in 1989 may be largely attributed to sampling effects.

Environmental gradients strongly affect clonal distributions in the bluff ponds. Ranta (1979) found that ranges of three coexisting species of Daphnia differed

along gradients of salinity, pH, and dissolved organic content in ponds on islands in the Finnish archipelago. In Churchill, Emery (1984) has shown that habitats supporting melanic and unpigmented clones may be distinguished by the absorbance values of the pond water, as determined by amounts of dissolved humic compounds. Weider and Hebert (1987a,b) also found melanic clones to have clinal distributions with respect to pond salinity.

Clonal associations

The relevance of clonal association coefficients in examining community structure is difficult to assess, as these statistical tests do not indicate the factors responsible for such associations. The positive association of two of the abundant clones (13 and 14) is misleading, as frequencies of the two clones exhibited bimodal distributions in ponds where both clones were detected (Wilson and Hebert 1990). Hastings (1986) has also shown that analysis of presence-absence data often fails to detect competitive interactions of species. This underscores the need for direct experimental tests *in situ* (Connor and Simberloff 1979). Weider (1987), however, has shown that unpigmented clones 1 and 17 are positively associated with saline habitats. Differences in mean values of clonal habitat characteristics (Table 8, Figure 13) suggest that adaptations of clones to differing habitats largely explains the majority of negative clonal

associations, although not all. Obviously, manipulative field experiments are required to fully address this issue, and will be described in chapters 4 and 5. Furthermore, it must be noted that the habitat characters considered in the principal component analysis may not represent limiting factors for the clones, nor may they accurately represent niche relationships among clones.

Patterns in community stability

The strong similarity between the two bluff surveys indicate that the clonal community in the ponds is extremely stable in both distribution and abundance patterns. This amount of structure might be expected if clonal distributions were rigidly controlled by a habitat "templet" (Southwood 1977) imposed by abiotic parameters. Abiotic parameters alone, however, cannot be the sole structural factors operating in this system, as the clones would be unlikely to exhibit such extensive overlap in habitat utilization. Ranta (1979) found that 3 regionally coexisting Daphnia species rarely co-occurred despite considerable overlap in habitat resources. Hanski and Ranta (1982) constructed a model to explain species composition in the ponds, and found competition to be the most likely process in generating the observed patterns.

Pajunen (1986) suggested that species composition of Daphnia populations in Finnish rock pools varied annually, with a small set of ponds with temporally stable species

composition acting as dispersal sources for populations found in other ponds, most of which showed little temporal stability. This was not observed in the Churchill ponds: 1985 maps of clonal distributions were accurate in predicting locations of specific clones in 1989.

The extreme similarity of clonal distribution and abundance patterns in 1985 and 1989 despite numerous opportunities for ephippial dispersal (Ranta 1979, Pajunen 1986, Weider 1989) indicate that clonal distributions in this community are at or near equilibrium. The presence of unpigmented D. pulex clones in virtually all suitable ponds further suggests that individual clones have likely had the opportunity to colonize most habitats. The low levels of gene flow noted among neighbouring Daphnia populations observed by other workers (Hebert 1974a, 1987, Hebert and Moran 1980, Korpalainen 1986, Weider and Hebert 1987b) likely represent a lack of success by dispersed individuals, rather than low dispersal rates.

The equilibrium state of most ponds was contrasted by ponds containing multiple clones. Diversity levels in these ponds was unexplained by abiotic factors or the presence of predators, but could arise through a number of processes. One (trivial) means could be the regular colonization of these ponds by ephippia of low-fitness clones from neighbouring populations. An alternate explanation could be that such sites represent environmental "cusps", where year to year habitat variation

results in shifting selective advantage among resident clones. These and other hypotheses are treated in greater detail in chapter 3.

Factors responsible for stability of clonal distributions

Hebert and Crease (1980) found that clonal composition of D. pulex populations in southern Ontario varied considerably between years, indicating that selective forces in these temperate ponds were not unidirectionally deterministic. By contrast, the stability of the Churchill populations can be better explained by strong, consistent selective pressures. With an annual cycle of pond freeze-up each winter, followed by the re-establishment of clones each spring, the ponds can be interpreted as continually striving towards an equilibrial state year after year, only to be disturbed and start again the following season.

Permanent or long-term exclusion of clones from ponds would be a slow process due to the ability of clones to produce resting eggs. Delayed germination of dormant seeds is well documented in plants (Harper 1977) and many invertebrate groups (Hanski 1988). The ability of Daphnia to produce diapause eggs, coupled with extended dormancy periods, should strongly buffer the effects of annual selective pressures on the membership of communities (Hanski 1988). Chesson (1983) has pointed out that this "storage effect" will facilitate prolonged coexistence of competitors, especially in stochastic environments.

The density-independent nature of environmental selective pressures should produce rapid results, quickly excluding clones from unsuitable pond habitats. As well as having low survival in environmentally-stressful habitats, incoming ephippia may have low hatching success in these ponds. Weider and Hebert (1987a) have shown this with melanic D. pulex, where clones from low-salinity habitats showed lower survival and ephippial hatching success in comparison with salt-tolerant clones under saline conditions. The asymmetric ability of salt-tolerant clones to thrive in the lab under low-salinity conditions suggests that other factors must be responsible for the lack of salt-tolerant clones in lower salinity ponds.

Although hatching of dormant ephippia could provide a "rescue effect", slowing changes in clonal distribution patterns, this alone is unlikely to explain the close maintenance of community patterns across a number of years. Such a storage effect would have little effect, however, on non-zero clonal abundance patterns. In addition, experimental studies described in chapters 4 and 5 indicate that biotic interactions within ponds cause dynamic, rapidly changing fluxes in clonal frequencies, which would argue against the yearly re-occurrence of a static pattern.

Environmental effects might also be responsible for observed differences in clonal patterns between the two years. The reduced numbers of clones observed in 1989 may be partly due to severe storms on Hudson Bay late the

previous year, which inundated many coastal ponds with salt spray from wave action (L. Foubert, pers. comm.). The increased pond salinity is likely responsible, as coastal ponds on both bluffs showed the greatest reduction of clonal occurrences (Appendix 3). Pajunen (1986) noted that salt input from sea spray was largely responsible for the disappearance of Daphnia species in Finnish rock pools. Despite the ability of some unpigmented clones (notably clones 1 and 17) to live in ponds with high salinities (Weider 1987), D. pulex cannot tolerate salinities exceeding 40,000 µS/cm (Hutchinson 1953, Langerspetz 1955). Incursion of salt water could therefore cause clonal extinctions in coastal ponds.

In conclusion, the distribution and abundance patterns of unpigmented Daphnia pulex clones in Churchill are both highly structured and stable. The pond system exists in a yearly cycle of dynamic equilibrium, where pond populations are re-established annually from resting eggs present in the pond sediments. Selective forces additional to environmental parameters influence clonal composition of the ponds, and likely operate within an interactive framework imposed by habitat characteristics.

LITERATURE CITED

Boileau, M.G. 1989. Biochemical genetic variation in the freshwater Copepoda: evolutionary consequences of passive dispersal in freshwater zooplankton. Ph.D. dissertation, University of Windsor, Ont.

Brooks, J.L. and S.I. Dodson. 1965. Predation, body size, and composition of plankton. Science 150: 28-35

Case, T.J. and R. Sidell. 1983. Pattern and chance in the structure of model and natural communities. Evolution 37: 832-849

Chesson, P.L. 1983. Coexistence of competitors in a stochastic environment: the storage effect. p. 188-198 in Freedman, H.I. and C. Strobeck (eds). Population Biology. Lecture Notes in Biomathematics 52. Springer-Verlag, Berlin.

_____. 1986. Environmental variation and the coexistence of species. p. 240-256 in Diamond, J. and T.J. Case (eds). Community Ecology. Harper and Row, New York.

Chesson, P.L. and T.J. Case. 1986. Overview: nonequilibrium community theories: chance, variability, history, and coexistence. p. 229-239 in Diamond, J.M. and T.J. Case (eds). Community Ecology. Harper and Row, New York.

Colwell, R.K. and D.W. Winkler. 1984. A null model for null models in biogeography. p. 344-359 in Strong, D.R., D. Simberloff, L.G. Abele and A.B. Thistle (eds). Ecological Communities: Conceptual Issues and the Evidence. Princeton University Press, Princeton NJ.

Connell, J.H. 1975. Some mechanisms producing structure in natural communities. p. 460-490 in Cody, M.L. and J.M. Diamond (eds). Ecology and Evolution of Communities. Harvard University Press, Cambridge.

Connell, J.H. and E. Orias. 1964. The ecological regulation of species diversity. Am. Nat. 98: 399-414

Connor, E.H. and D. Simberloff. 1979. The assembly of species communities: chance or competition? Ecology 60: 1132-1140

_____. 1983. Interspecific competition and species co-occurrence patterns on islands: null models and the evaluation of evidence. Oikos 41: 455-465

Diamond, J. 1975. Assembly of species communities. p. 342-444 in Cody, M.L. and J.M. Diamond (eds). Ecology and Evolution of Communities. Harvard University Press, Cambridge.

_____. 1986. Overview: laboratory experiments, field experiments, and natural experiments. p. 3-22 in Diamond, J. and T.J. Case (eds). Community Ecology. Harper and Row, New York.

Diamond, J. and M.E. Gilpin. 1982. Examination of the "null" model of Connor and Simberloff for species co-occurrences on islands. Oecologia 52: 64-74

Frank, P.W. 1952. A laboratory study of intraspecies and interspecies competition in Daphnia pulicaria (Forbes) and Simocephalus vetulus Muller. Physiol. Zool. 25: 178-204

Fryer, G. 1985. Crustacean diversity in relation to the size of water bodies: some facts and problems. Freshwater Biology 15: 347-361.

Ganning, B. 1971. Studies on chemical, physical and biological conditions in Swedish rockpool ecosystems. Ophelia 9: 51-109

Gilpin, M.E. and J.M. Diamond. 1982. Factors contributing to non-randomness in species co-occurrence on islands. Oecologia 52: 75-84

_____. 1984. Are species co-occurrences on islands non-random, and are null hypotheses useful in community ecology? p. 296-315 in Strong, D.R., D. Simberloff, L.G. Abele and A.B. Thistle (eds). Ecological Communities: Conceptual Issues and the Evidence. Princeton University Press, Princeton.

Ghilarov, A.M. 1967. The zooplankton of arctic rock pools. Oikos 18: 82-95

Good, A.G. 1981. The ecology and biogeography of tundra zooplankton communities in the Churchill, Manitoba area. M.Sc. thesis, University of Windsor, Ont.

Greenslade, P.J.M. 1983. Adversity selection and the habitat templet. Am. Nat. 122: 352-365

Gregorius, H.R. 1980. The probability of losing an allele when diploid genotypes are sampled. Biometrics 36: 643-652

Hall, D.J., W.E. Cooper and E.E. Werner. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnol. Oceanogr. 15: 839-928

Hanski, I. 1988. Four kinds of extra long diapause in insects: a review of theory and observations. Ann. Zool. Fennici 25: 37-53

Hanski, I. and E. Ranta. 1983. Coexistence in a patchy environment: three species of Daphnia in rock pools. J. Anim. Ecol. 52: 263-279

Harper, J.L. 1977. Population Biology of Plants. Academic Press, New York.

Harshman, L.G. and D.J. Futuyma. 1985. The origin and distribution of clonal diversity in Alsophila pometaria (Lepidoptera: Geometridae). Evolution 39: 315-324

Hastings, A. 1987. Can competition be detected using species co-occurrence data? Ecology 68: 117-123

Hebert, P.D.N. 1974. Ecological differences between genotypes in a natural population of Daphnia magna. Heredity 33: 327-337

_____. 1982. Competition in zooplankton communities. Ann. Zool. Fennici 19: 349-356

_____. 1984. Demographic implications of genetic variation in zooplankton populations. p. 195-207 in: Wohrmann, K. and V. Loeschcke (eds). Population biology and evolution. Springer-Verlag, Berlin.

_____. 1985. Ecology of the dominant copepod species at a low arctic site. Can. J. Zool. 63: 1138-1147

_____. 1987. Genotypic characteristics of the Cladocera. Hydrobiol. 145: 183-193

Hebert, P.D.N. and M.J. Beaton. 1989. Methodologies for allozyme analysis using cellulose acetate electrophoresis. Helena Laboratories, Beaumont TX.

Hebert, P.D.N. and T.J. Crease. 1980. Clonal coexistence in Daphnia pulex (Leydig): another planktonic paradox. Science 207: 1363-1365

_____. 1983. Clonal diversity in populations of Daphnia pulex reproducing by obligate parthenogenesis. Heredity 51: 353-369

Hebert, P.D.N. and C.E. Emery. 1990. The adaptive significance of cuticular pigmentation in Daphnia. Funct. Ecol. (in review)

Hebert, P.D.N. and D.B. McWalter. 1983. Cuticular pigmentation in arctic Daphnia: adaptive diversification of asexual lineages. Amer. Nat. 122: 286-291

Hebert, P.D.N. and R.D. Ward. 1976. Enzyme variability in natural populations of Daphnia magna. IV. Ecological differentiation and frequency changes of genotypes at Audley End. Heredity 36: 331-341

Hebert, P.D.N., R.D. Ward and L.J. Weider. 1988. Clonal-diversity patterns and breeding-system variation in Daphnia pulex, an asexual-sexual complex. Evolution 42: 147-159

Hebert, P.D.N., M.J. Beaton, S.S. Schwartz and D.J. Stanton. 1989. Polyphyletic origins of asexuality in Daphnia pulex. I. Breeding-system variation and levels of clonal diversity. Evolution 43: 1004-1015

Holland, R.F. and S.K. Jain. 1981. Insular biogeography of vernal pools in the central valley of California. Am. Nat. 117: 24-37

Holm, E. 1985. The evolution of generalist and specialist species. p. 87-93 in Vrba, E.S. (ed). Species and Speciation. Transvaal Mus. Monogr. 4. Pretoria.

Holm, E. 1988. Environmental restraints and life strategies: a habitat templet matrix. Oecologia 75: 141-145

Holt, R.D. and B.P. Kotler. 1987. Short-term apparent competition. Am. Nat. 130: 412-430

Hubalek, Z. 1982. Coefficients of association and similarity, based on binary (presence-absence) data: an evaluation. Biol. Rev. 57: 669-689

Hutchinson, G.E. 1953. The concept of pattern in ecology. Proc. Nat. Acad. Sci. 105: 1-13

_____. 1961. The paradox of the plankton. Am. Nat. 95: 137-145

_____. 1967. A Treatise on Limnology. Volume II. Wiley Press, New York.

Innes, D.J. and P.D.N. Hebert. 1989. The origin and genetic basis of obligate parthenogenesis in Daphnia pulex. Evolution 42: 1024-1035

Jaenike, J. and R.K. Selander. 1986. On the coexistence of ecologically similar clones of parthenogenetic earthworms. Oikos 44: 512-514

Jaenike, J., E.D.Jr. Parker and R.K. Selander. 1980. Clonal niche structure in the parthenogenetic earthworm Octolasion tyrtaeum. Amer. Nat. 116: 196-205

Kerfoot, W.C. 1977a. Competition in cladoceran communities: the cost of evolving defenses against copepod predation. Ecology 58: 303-313

_____. 1977b. Implications of copepod predation. Limnol. Oceanogr. 22: 316-325

Kerfoot, W.C. (ed). 1980. Evolution and Ecology of Zooplankton Communities. University Press of New England, Hanover.

Krebs, C.J. 1989. Ecological Methodology. Harper and Row, New York.

Kolasa, J. 1989. Ecological systems in hierarchical perspective: breaks in community structure and other consequences. Ecology 70: 36-47

Korpalainen, H. 1986. Temporal changes in the genetic structure of Daphnia magna populations. Heredity 57: 5-14

Langerspetz, K. 1955. Physiological studies on the brackish water tolerance of some species of Daphnia. Arch. Soc. Vanamo., Suppl. 9: 138-143

Lawlor, L.R. 1980. Structure and stability in natural and randomly constructed competitive communities. Am. Nat. 116: 394-408

Loaring, J.M. and P.D.N. Hebert. 1981. Ecological differences among clones of Daphnia pulex Leydig. Oecologia 51: 162-168

Ludwig, J.A. and J.F. Reynolds. 1988. Statistical Ecology. John Wiley and Sons, New York.

Lyman, J.C. and N.C. Ellstrand. 1984. Clonal diversity in Taraxacum officinale (Compositae), an apomict. Heredity 53: 1-10

Lynch, M. 1983. Destabilizing hybridization, general-purpose genotypes, and geographic parthenogenesis. Quart. Rev. Biol. 59: 257-290

May, R.M. 1975. Patterns of species abundance and diversity. p. 81-120 in: Cody, M.L. and J.M. Diamond (eds).Ecology and evolution of communities. Harvard University Press, Cambridge.

Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89: 583-590

Neill, W.E. 1975. Experimental studies of microcrustacean competition, community composition and efficiency of resource utilization. Ecology 56: 809-826

Pace, M.L., K. Porter and Y.S. Feig. 1984. Life history variation within a parthenogenetic population of Daphnia parvula (Crustacea: Cladocera). Oecologia 63: 43-51

Pajunen, V.I. 1986. Distributional dynamics of Daphnia species in a rock-pool environment. Ann. Zool. Fennici 23: 131-140

Parker, E.D. Jr. 1979. Ecological implications of clonal diversity in parthenogenetic morphospecies. Am. Zool. 19: 753-762

Pielou, E.C. 1984. The Interpretation of Ecological Data. John Wiley and Sons, New York.

Preston, F.W. 1948. The commonness, and rarity, of species. Ecology 29: 254-283

Rabinowitz, D. 1981. Seven forms of rarity. p. 205-217 in Synge, H. (ed). The Biological Aspects of Rare Plant Conservation. John Wiley and Sons, New York.

Ranta, E. 1979. Niche of Daphnia species in rock pools. Arch. Hydrobiol. 87: 205-223

Ranta, E. 1982. Animal communities in rockpools. Ann. Zool. Fennici 19: 337-348

Richardson, B.J., P.R. Baverstock and M. Adams. 1986. Allozyme Electrophoresis: A Handbook for Animal Systematics and Population Studies. Academic Press, New York.

Sebens, K.P. and Thorne, B.L. 1985. Coexistence of clones, clonal diversity, and the effects of disturbance. p. 357-398 in: Jackson, J.B.C., L.W. Buss, and R.E. Cook (eds.). Population biology and evolution of clonal organisms. Yale University Press, London.

Simpson, E.H. 1949. Measurement of diversity. Nature 163: 688

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. 2nd. ed. W.H. Freeman and Co., New York.

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? J. Animal Ecol. 46: 337-365

Stanton, D.J. 1988. Evolution of asexuality in Daphnia pulex: implications of mitochondrial DNA analysis. Ph.D. dissertation, University of Windsor, Ont.

Sugihara, G. 1980. Minimal community structure: an explanation of species abundance patterns. Amer. Nat. 116: 770-787

Talling, J.F. 1951. The element of chance in pond populations. The Naturalist 0: 157-170

Tucic, B., S. Milojkovic, A. Tarasjev and S. Vujcic. 1988. The influence of climatic factors on clonal diversity in a population of Iris pumila. Oikos 56: 115-120

Vrijenhoek, R.C. 1979. Factors affecting clonal diversity and coexistence. Amer. Zool. 197: 787-797

Weider, L.J. 1985. Spatial and temporal genetic hetterogeneity in a natural Daphnia population. J. Plankton Res. 7: 101-123

_____. 1987. Life history variation among low-arctic clones of obligately parthenogenetic Daphnia pulex: a diploid-polyploid complex. Oecologia 73: 251-256

_____. 1989. Spatial heterogeneity and clonal structure in arctic populations of apomictic Daphnia. Ecology 70: 1405-1413

Weider, L.J. and P.D.N. Hebert. 1987a. Ecological and physiological differentiation among low-arctic clones of Daphnia pulex. Ecology 68: 188-198

_____. 1987b. Microgeographic genetic heterogeneity of melanic Daphnia pulex at a low-Arctic site. Heredity 58: 391-399

Weider, L.J., M.J. Beaton and P.D.N. Hebert. 1987a. Clonal diversity in high-Arctic populations of Daphnia pulex, a polyploid apomictic complex. Evolution 41: 1335-1346

Wetzel, R.G. 1983. Limnology. 2nd ed. Saunders College Publishing, Philadelphia.

Wiens, J.A. 1984. On understanding a non-equilibrium world: myth and reality in community patterns and processes. p. 439-457 in Strong, D.R., D. Simberloff, L.G. Abele and A.B. Thistle (eds). Ecological Communities: Conceptual Issues and the Evidence. Princeton University Press, Princeton.

Wiens, J.A., J.F. Addicott, T.J. Case and J.M. Diamond. 1986. Overview: the importance of spatial and temporal scale in ecological investigation. p. 145-153 in Diamond, J.M. and T.J. Case (eds). Community Ecology. Harper and Row, New York.

Wilkinson, L. 1989. SYSTAT: the System for Statistics. Systat, Inc., Evanston IL.

Wilson, C.C. and P.D.N. Hebert. 1990. Impact of predation on distribution patterns of Daphnia pulex clones. Limnol. Oceanogr. (in review).

Zaret, T.M. 1980. Predation and freshwater communities. Yale University Press.

CHAPTER 3

MULTICLONAL PONDS IN A LOW-ARCTIC ECOSYSTEM: FREQUENCIES AND REPRODUCTIVE STATES AMONG SYMPATRIC *DAPHNIA PULEX* CLONES

INTRODUCTION

Interest in species diversity among aquatic biologists was first focused by Hutchinson's (1961) "paradox of the plankton", in which he noted the long-term coexistence of extremely similar species of phytoplankton. A number of potential explanations have been advanced to account for such coexistence (Richerson et al 1970, Peterson 1975, Jacobs 1977, Hebert and Crease 1980), but the issue has never been satisfactorily resolved (Ghilarov 1984).

Given that the coexistence of ecologically similar species is rare, one might expect coexistence among conspecific clones to be even less frequent. Many studies of clonal diversity have, however, shown habitats to contain a number of coexisting clones (Hebert and Crease 1980, 1983, Sebens and Thorne 1985, Weider 1985, Carvalho and Crisp 1987, Weider et al 1987, Hebert et al 1988, Tucic et al 1988).

Numerous explanations have been postulated for the coexistence of clones in single habitats. One trivial hypothesis is the generation of new asexual lines from a parent sexual population (Vrijenhoek 1978, Lynch 1983). In this situation, despite elimination of clones through competition, clonal richness would remain high due to the continual recruitment of new clones. Coexistence among members of an obligately asexual population, by contrast, presents more meaningful ecological questions. Clonal coexistence may be facilitated by differential microhabitat

utilization among clones (Solbrig 1971), high levels of disturbance (Sebens and Thorne 1985), extreme ecological similarity among clones (Angus 1980), or shifting competitive superiority among clones due to temporal shifts in habitat parameters (Hebert and Crease 1980, Lynch 1983).

Discrimination among at least some of these alternatives is possible. Ecologically analogous clones, for example, should show the same responses to selection pressures. Indeed, the results of competitive interactions would be indeterminate, as clonal frequencies would follow a random walk. Such competitive indeterminacy (Park 1948) has been observed in several sets of aquatic organisms (Ghilarov 1984), including Daphnia pulex (Hebert and Crease 1980) and represent neutral equilibrium states.

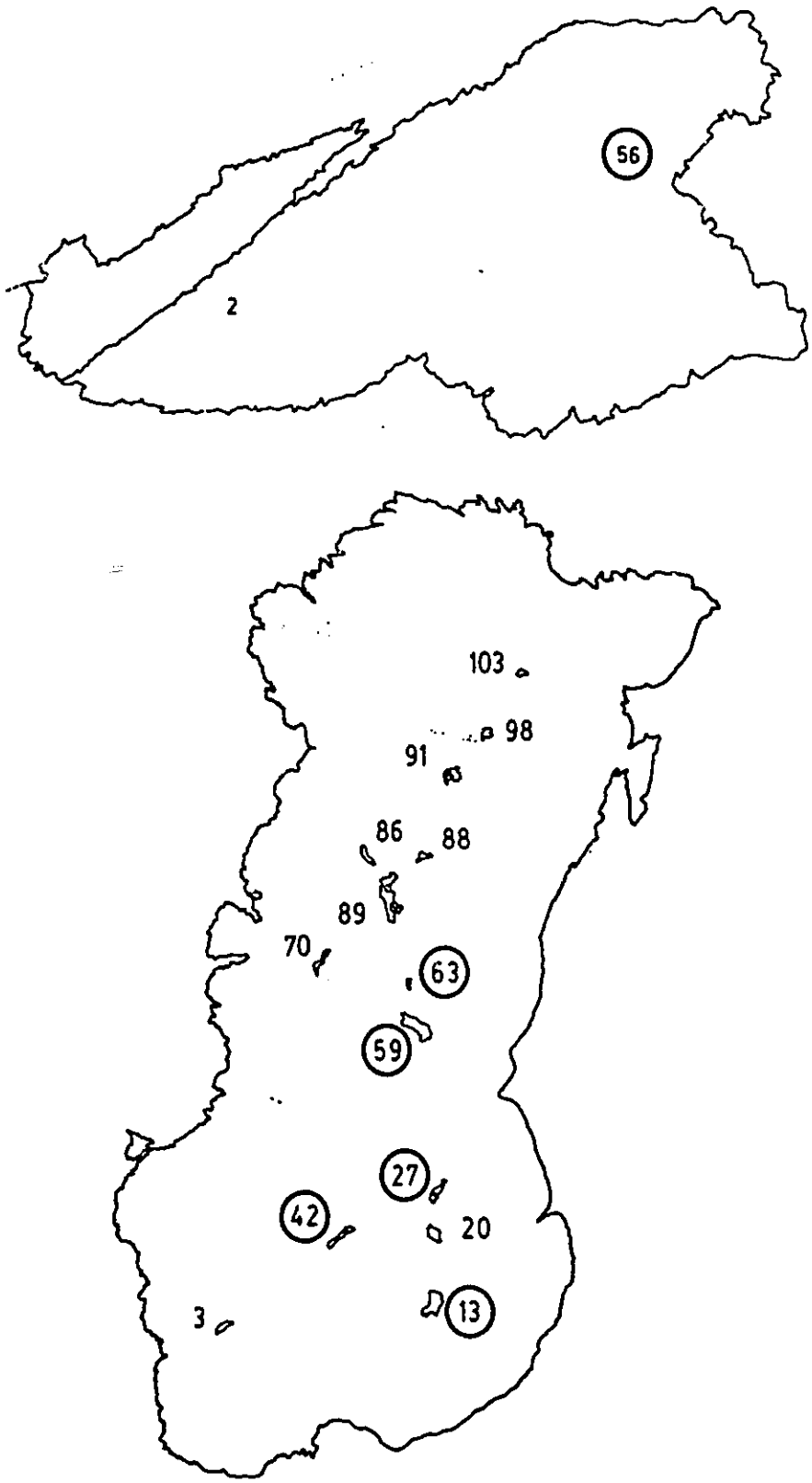
Alternatively, clonal diversity may be maintained despite ecological divergence among clones. In this case, two classes of explanation may be advanced for the persistence of multiclonal ponds. Non-equilibrium coexistence (Wiens 1984, Chesson 1986) could result from high rates of dispersal from neighbouring ponds (Ricklefs 1987, Ranta 1979, Pajunen 1986, Weider 1989), premature drying of ponds, or predation (Chesson and Case 1986). An additional possibility is that multiclonal ponds represent marginal habitats which are suboptimal for all clones present. Finally, clonal coexistence may be sustained by temporal shifts in habitat characteristics that favour different clones at different times throughout a season,

with less fit clones becoming re-established yearly from previously-laid ephippial eggs.

Alternatively, clonal coexistence would be possible in equilibrium habitats where clones occupy distinct microhabitats. Equilibrium multiclonal populations could also be possible through frequency-dependent selection on the member clones.

The present study attempted first to ascertain if clonal fitnesses in multiclonal ponds were similar by monitoring shifts in clonal frequencies in several ponds discovered to contain three or more clones in a 1985 survey (Figure 1). Attempts to assess the extent of ecological differences among coexisting clones were also carried out by assessing their relative reproductive status and hence long- and short-term fitness.

Figure 3-1: Locations of multiclonal ponds detected on rock bluffs A and C in 1985.



METHODS

Collections

The sixteen multiclonal ponds detected in the 1985 electrophoretic survey (Figure 1) were resampled in 1988 and 1989. In addition, six of these ponds were studied more intensively in 1988 via biweekly sampling of populations. Ponds were sampled with a 200 µm-mesh hand net, pooling the netted animals in a sampling tray and then returning all but a randomly chosen sample of approximately 100 individuals to the pond. In 1988 samples were stored at 8°C until processed, while 1989 samples were frozen in Taylor-Wharton portable freezers at -170°C and returned to Windsor for clonal identification.

Electrophoresis

Cellulose acetate electrophoresis was used to determine clonal identities of the animals. Methods followed standard protocols (Hebert and Beaton 1989) for the six polymorphic loci originally used in the 1985 bluff survey (AO, AMY-1, GOT, LDH, PGM, and PGI). Clonal frequencies in the ponds were arcsine square root transformed (Sokal and Rohlf 1981) to determine 95% confidence intervals, then back-transformed to give certainty estimates of clonal composition of the ponds.

Mean genetic distance among co-occurring clones was examined using Nei's (1978) unbiased genetic distance

estimation technique, presented in Chapter 2.

Clonal reproductive states

Prior to allozyme analysis, each animal was examined at 20X magnification to determine its reproductive status. Animals were classed as parthenogenetic (P), nonreproductive (NR) or ephippial (E), and brood sizes of parthenogenetic females were determined. Once clonal identities of individuals were determined, this information was used to test for differences in reproductive status between clones in individual ponds. Samples collected in 1989 were not examined for reproductive states of the animals, as the purpose of these samples was simply to determine clonal composition of the ponds.

Differences in reproductive status of clones were examined by comparing frequencies of the different reproductive states among clones. Frequencies of parthenogenetic adults were arcsine-square root transformed and differences between clones were tested using the G statistic (Sokal and Rohlf 1981). Clones with less than 9 individuals in a specific sample were excluded from this analysis, to reduce sample size bias of the statistical results. Differences in mean brood sizes among clones was tested using a t-test for means with unequal variances and sample sizes (Sokal and Rohlf 1981).

Yearly patterns in within-pond diversity

To examine temporal variation in clonal diversity, values from all multiclonal ponds at each sampling period in 1988 were plotted against time. In addition, similarities among initial clonal diversity values of the multiclonal ponds in 1985, 1988 and 1989 were examined using a correlation matrix in order to test the yearly stability of clonal diversity values in these ponds.

Clonal Reproduction

Short-term reproductive effort of clones, as represented by the production of subitaneous eggs in each sampling period (DeMott 1980), was used to predict relative clonal abundances in successive sampling periods. The absolute fitness of each clone was determined by multiplying the proportion of parthenogenetic females of each clone by the mean brood size observed among those females. Significant differences were examined by calculating 95% confidence intervals of the fecundity estimates. Significant differences in clonal fecundity were then compared against subsequent shifts in clonal frequencies.

The long-term fitnesses of clones were estimated by comparing their ephippial production. Proportions of ephippial adults for each clone were examined in each sampling period using log-likelihood independence tests (Sokal and Rohlf 1981).

RESULTS

Genetic diversity

Co-occurrences and genetic divergence among sympatric D. pulex clones in all multiclonal ponds observed in 1985, 1988 and 1989 are listed in Table 1. Clonal composition remained fairly constant in the majority of ponds: differences observed may in part be due to different sample sizes in 1985 versus later years. Genetic distances among co-occurring clones had a mean value of 0.387 and ranged from 0.095 to 0.704 for ponds with three or more clones in these years.

Yearly patterns in within-pond diversity

Clonal richness and diversity indices of the multiclonal ponds varied considerably among the 1985, 1988 and 1989 samples (Table 2). No between-year correlations in clonal richness of the ponds were detected. Similarly, the only significant correlation of clonal diversity between years was obtained from comparison of 1988 and 1989 values.

Clonal abundances

Patterns of clonal abundance varied considerably among the six ponds studied in 1988 (Figure 2). In pond C13 Figure 2a), clone 14 dominated the pond in mid-July but was subsequently replaced by clone 15. A similar pattern was

Table 3-1: Mean genetic distance (± 1 S.E.) of co-occurring clones in multiclonal ponds in 1985, 1988 and 1989, using Nei's (1978) unbiased genetic distance estimate. Ponds without D. pulex are indicated by blanks.

	1985			1988		
Pond	Clones	D	(S.E.)	Clones	D	(S.E.)
A2	1,7,11	0.134	(0.068)	1,7	0.095	
A56	1,2,7	0.348	(0.232)	1,2,4, 7,10	0.396	(0.200)
C3	13,14,15	0.704	(0.311)	13,14	0.833	
C13	14,15,16	0.370	(0.019)	14,15,16	0.370	(0.019)
C20	13,14,15	0.704	(0.311)	13,14,15	0.704	(0.311)
C27	14,15,16	0.370	(0.019)	13,14,15, 16	0.597	(0.252)
C42	14,15,22	0.281	(0.097)	14,15,22	0.281	(0.097)
C59	13,14,25	0.602	(0.245)	13,14,15, 25	0.609	(0.230)
C63	13,14,16	0.620	(0.252)	13,14,16	0.620	(0.252)
C70	14,16,19, 20	0.438	(0.228)	14,16,19, 23	0.230	(0.160)
C86	17,25,26	0.381	(0.160)	17,25,26	0.381	(0.160)
C88	7,17,25, 28	0.095	(0.061)	7,11,17, 25	0.113	(0.057)
C89	11,16,17, 19	0.197	(0.065)	11,16,17, 19	0.197	(0.065)
C91	1,11,19, 25,26	0.309	(0.249)	11,19,26	0.467	(0.225)
C98	16,19,20	0.342	(0.182)	16,19	0.213	
C103	14,17,18 19	0.264	(0.122)	14,17	0.324	

Table 3-1 (cont.)

Pond	Clones	1989 D	(S.E.)
A2	1,7	0.095	
A56	.....		
C3	13,14	0.883	
C13	14,15,16	0.370	(0.019)
C20	13,14,15	0.704	(0.311)
C27	14,15,16	0.370	(0.019)
C42	14,15,22	0.281	(0.097)
C59	13,14,25	0.602	(0.245)
C63	13,14,16,19	0.509	(0.235)
C70	16	0.000	
C86	17,25,26,29	0.319	(0.216)
C88	11,17,25,28	0.122	(0.046)
C89	11,16,17,28	0.154	(0.051)
C91	1,19,27,28	0.334	(0.219)
C98	16,19	0.213	
C103	7,14,17,18	0.232	(0.138)

Table 3-2: Comparison of clonal richness (N) and diversity (d) values of multiclonal ponds observed in 1985 for samples collected in early July of 1985, 1988 and 1989.

Pond	N	d	N	d	N	d
A2	4	2.17	2	1.60	2	1.49
A56	3	2.64	5	2.83	0	----
C3	3	2.17	2	1.18	2	1.09
C13	3	2.46	3	2.55	3	1.41
C20	3	2.07	3	1.19	3	1.77
C27	3	1.67	3	2.66	3	2.17
C42	3	2.27	2	1.82	3	1.88
C59	3	1.29	4	2.48	3	2.13
C63	3	1.69	3	2.00	4	1.42
C70	4	1.70	4	1.42	1	1
C86	3	2.32	3	2.27	4	2.55
C88	4	2.29	4	2.46	5	3.03
C89	4	1.68	4	2.17	4	1.70
C91	5	3.13	3	2.34	4	2.46
C98	3	1.81	2	1.60	2	1.80
C103	4	2.68	2	1.09	4	1.28

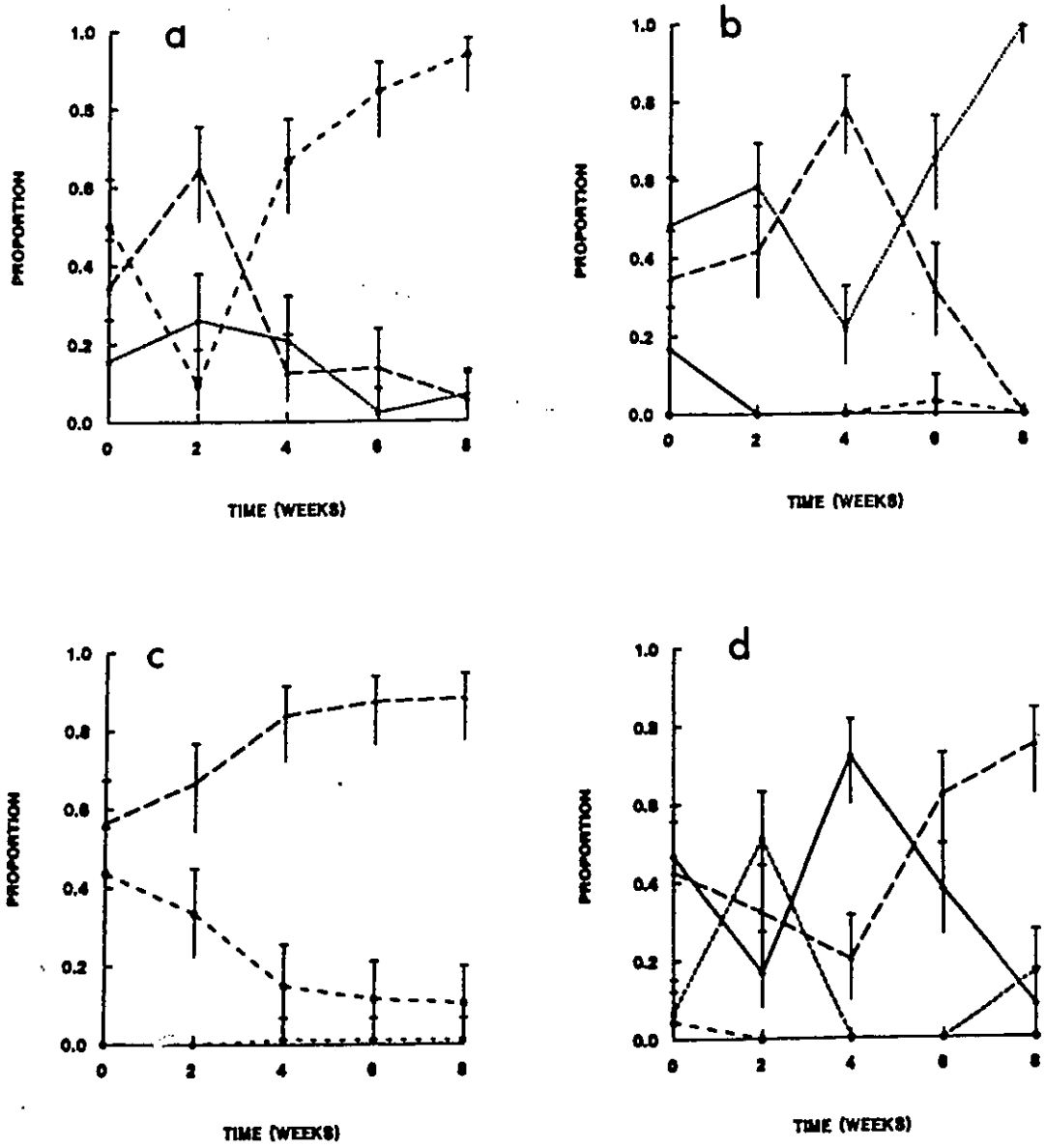
Between-year correlation matrix of pond diversity

	1985	1988	1989
1985			
1988			
1989			

Figure 3-2: Seasonal shifts in abundance of co-occurring clones in multiclonal ponds, sampled biweekly in 1988. (a) pond C13; (b) pond C27; (c) pond C42; (d) pond C59. Ponds A56 and C63 are not shown, as populations disappeared from these ponds in July. Vertical bars represent 95% confidence intervals of clonal frequencies.

LEGEND

—— = clone 13
--- = clone 14
---- = clone 15
—— = clone 16
.... = clone 22
—·— = clone 26



observed in pond C27 (Figure 2b), with clone 14 becoming dominant by mid-summer and subsequently displaced by clone 16. Clonal shifts were most consistent in pond C42 (Figure 2c), with clone 14 becoming increasingly dominant throughout the summer. Temporal succession of clones was observed in pond C59, with clones 26, 13 and 14 displaying sequential abundance peaks. D. pulex populations in ponds A56 and C63, in contrast, disappeared in July, although water was still present in these ponds. Five clones (1, 2, 4, 7 and 10) were initially present in A56, but could not be detected two weeks later. Similarly, clones 13, 14 and 16 occurred in pond C63, but were not found after the July 15 sampling period.

Seasonal changes in within-pond diversity are summarized in Figure 3. All ponds showed maximum diversities early in the summer, which declined as the season progressed. Linear regression of within-pond diversity values produced the equation:

Y (diversity) = 2.576 - 0.27 t (sampling period); r^2=0.66

Ponds A56 and C63 were not included in the regression, as D. pulex populations in these ponds disappeared prematurely.

Differences in reproductive status among sympatric clones

Reproductive status of the co-occurring clones in the multiclonal ponds at each sampling period are presented in Table 3, which shows proportional representation of

Figure 3-3: Shifts in clonal diversity values of multiclonal ponds in 1988. Diversity values are described by the equation:

$$Y \text{ (diversity)} = 2.58 - 0.27\ t \text{ (time)}; \quad r^2 = 0.66$$

LEGEND

..... = C13

— — = C27

- - - = C42

——— = C59

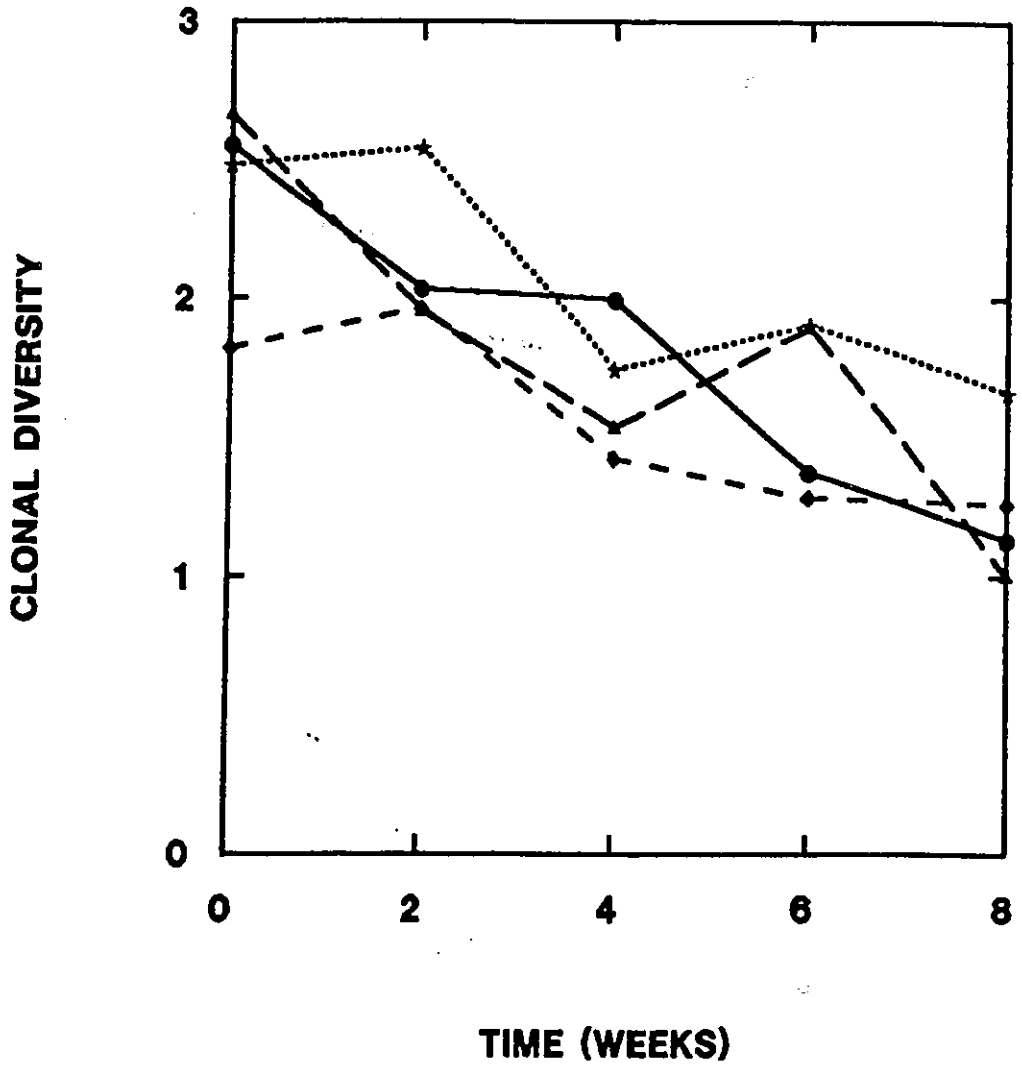


Table 3-3: Numbers and proportional reproductive status among clones in multiclonal ponds for samples collected in 1988.

		July 1				July 15				July 30			
Pond	Clone	N	NR	P	E	N	NR	P	E	N	NR	P	E
A56	1	45	0.53	0.20	0.27								
	2	33	0.48	0.52	....								
	4	8	0.75	0.25	....								
	7	9	0.56	0.44	....								
	10	1	1.00	....	....								
C13	14	33	0.39	0.45	0.15	62	0.13	0.85	0.02	12	0.25	0.58	0.17
	15	48	0.42	0.33	0.25	9	0.33	0.56	0.11	64	0.63	0.08	0.28
	16	15	0.60	0.13	0.27	25	0.52	0.44	0.04	20	0.60	0.20	0.20
C27	13	16	0.81	....	0.19	0	....	....	....	0	....	....	....
	14	33	1.00	....	....	40	0.50	0.30	0.20	75	0.57	0.17	0.25
	15	0	....	....	....	0	....	....	....	0	....	....	....
	16	46	0.87	0.02	0.11	56	0.13	0.77	0.11	21	0.14	0.76	0.10
C42	14	54	0.27	0.54	0.20	64	0.06	0.94	....	79	0.30	0.70	....
	15	42	0.48	0.29	0.24	32	0.13	0.69	0.19	16	0.19	0.81	....
	22	0	....	....	....	0	....	....	....	1	1.00	....	....
C59	13	45	0.27	0.73	....	16	0.63	0.06	0.31	67	0.25	0.39	0.36
	14	40	0.30	0.55	0.15	31	0.94	0.03	0.03	29	0.07	0.79	0.14
	15	2	....	1.00	....	0	....	....	....	0	....	....	....
	26	9	0.22	0.44	0.33	49	0.59	....	0.41	0	....	....	....
C63	13	9	0.78	....	0.22	13	0.85	....	0.15				
	14	24	0.50	....	0.50	0	....	....	....				
	16	63	0.76	....	0.24	83	0.69	....	0.31				

Table 3-3 (cont.)

		August 15				August 29			
Pond	Clone	N	NR	P	E	N	NR	P	E
A56	1								
	2								
	4								
	7								
	10								
C13	14	13	0.23	....	0.77	5	0.20	....	0.80
	15	81	0.52	0.12	0.36	90	0.68	0.19	0.13
	16	2	....	....	1.00	1	1.00	....	....
C27	13	0	....	....	....	0	....	....	....
	14	30	0.63	....	0.37	0	....	....	....
	15	3	1.00	....	....	0	....	....	....
	16	63	0.84	....	0.16	96	1.00	....	....
C42	14	85	0.80	0.07	0.13	84	0.37	0.63	....
	15	10	0.50	0.40	0.10	11	....	1.00	....
	22	1	1.00	....	....	1	....	....	1.00
C59	13	37	0.22	0.70	0.08	8	0.75	....	0.25
	14	59	0.07	0.93	....	72	0.97	....	0.03
	15	0	....	....	....	0	....	....	....
	26	0	....	....	....	16	0.63	....	0.37
C63	13								
	14								
	16								

nonreproductive (NR), parthenogenetic (P) and ephippial (E) states in each clone. Log-linear analysis of proportional parthenogenetic reproduction among sympatric clones detected significant differences 12 of the 18 cases where tests were possible (Table 4). Comparisons of mean brood sizes among sympatric clones, however, revealed few significant between-clone differences (Table 5). Several differences were observed, however: in all cases where clone 15 was tested, the clone had significantly smaller mean brood sizes than co-occurring clones. Significant differences in brood size were also detected between clones 14 and 16 in pond C27, with clone 16 producing larger broods.

Relative short-term reproductive investment of co-occurring clones are presented in Table 6. Significant differences in short-term reproductive effort among clones existed in 16 cases among the multiclonal ponds examined. Of these, 6 cases showed subsequent shifts in clonal frequencies in agreement with predictions from fecundity differences between the parthenogenetic clones, and 3 cases showed the reverse trend.

Contributions of clones to long-term fitness

Significant differences in investment towards long-term fitness were observed among clones in 10 of 20 samples where ephippial production occurred (Table 7). Neither clone-specific differences nor seasonal trends were observed.

Table 3-4: Multiple G-tests of relative proportions of parthenogenetic females in each clone in 1988. Clones with fewer than ten adults present were excluded. Blank lines (....) indicate cases where differences could not be tested.

	July 1	July 15	July 30	August 14	August 28
Pond	G	G	G	G	G
A56	8.54**				
C13	33.39***	16.05***	15.10**	3.61	2.42
C27	1.46	19.01***	25.40***	....	....
C42	6.22*	10.08**	2.93	10.16**	7.32*
C59	3.23	3.13	11.33**	9.30**	....
C63	....	....			

*** $p < 0.001$
** $p < 0.01$
* $p < 0.05$

Table 3-5: Comparison of brood sizes of parthenogenetic females of sympatric clones for 1988 sampling periods.

		July 1				July 15			
Pond	Clone	N	x	S.E.	t	N	x	S.E.	t	t
A56	1	9	8.66	3.28	0.25					
	2	17	9.06	2.99						
	4	2	6.00	1.41						
	7	4	5.25	1.26						
C13	14	15	5.47	2.45	2.11*	53	6.93	1.52	1.96	
	15	16	4.38	1.46		5	5.60	1.14		
	16	2	6.00	1.41		11	7.64	2.90		
C27	13									
	14					12	8.00	2.26	2.40*	
	16	1	1.00	....		43	10.33	3.19		
C42	14	29	19.93	4.76	3.79***	60	12.52	4.53	4.88***	
	15	12	11.58	2.94		22	7.73	1.60		
	22									
C59	13	32	20.16	14.47	0.20	1	1.00	....		
	14	22	17.59	10.51		1	1.00	....		
	15	2	6.00	1.41						
	26	4	11.00	1.63						

*** $p < 0.001$
** $p < 0.01$
* $p < 0.05$

Table 3-5 (cont.)

		July 30				August 14				August 28		
Pond	Clone	N	x	S.E.	t	N	x	S.E.	t	N	x	S.E.
A56	1											
	2											
	4											
	7											
C13	14	7	10.00	2.52								
	15	5	7.20	1.79		10	4.00	1.05		17	2.88	0.78
	16	4	5.50	3.11								
C27	13											
	14	13	8.62	3.10	5.25***							
	16	16	13.94	2.32								
C42	14	55	7.62	3.72	2.95**	53	7.49	4.15	1.98*	6	2.67	0.52
	15	13	4.31	1.65		11	4.27	1.49		4	5.50	1.00
	22					1	9.00	....				
C59	13	26	15.27	4.81	0.14	25	15.32	8.64	0.97			
	14	20	15.55	4.73		55	17.96	5.88				
	15											
	26											

*** $p < 0.001$
** $p < 0.01$
* $p < 0.05$

Table 3-6: Short-term reproductive fitnesses (E) (± 1 S.E.) of co-occurring clones. E = (proportion of parthenogenetic adults) x (mean brood size) for each clone. Clones with fewer than nine (9) parthenogenetic adults were excluded. Positive (+), negative (-) and nonsignificant (ns) shifts in clonal frequency are indicated for expected (e) and observed (o) proportional changes.

		July 1				July 15			
Pond	Clone	E	S.E.	e	o	E	S.E.	e	o
A56	1	1.73	0.31						
	2	4.71	0.76						
C13	14	2.46	0.31	+	+	5.89	0.13	+	-
	15	1.45	0.10	-	-				
	16					3.36	0.72	-	ns
C27	14					2.40	0.37	-	+
	16					5.88	0.48	+	-
C42	14	10.76	2.05	+	ns	11.77	0.44	+	ns
	15	3.36	0.72	-	ns	5.33	0.45	-	ns
C59	13	14.72	5.18	ns	-				
	14	9.67	3.43	ns	ns				

Table 3-6 (cont.)

		July 30				August 14			
Pond	Clone	E	S.E.	e	o	E	S.E.	e	o
A56	1								
	2								
C13	14								
	15					0.48	0.02		ns
	16								
C27	14	1.47	0.16	-	-				
	16	10.59	1.88	+	+				
C42	14	2.97	0.28	ns	ns	0.52	0.06	ns	ns
	15	3.40	0.32	ns	ns	1.71	0.53	ns	ns
C59	13	5.96	0.96	-	-	10.72	2.74	-	ns
	14	12.28	1.99	+	+	16.70	0.90	+	ns

Table 3-7: Differences in contribution to long-term fitness among co-occurring clones in multiclonal ponds for 1988 sampling periods.

Pond	July 1	July 15	July 30	August 14	August 28
A56	14.78***				
C13	1.41	1.79	1.09	11.32**	10.82
C27	7.83*	1.59	2.76	6.30*	----
C42	0.16	14.00***	----	----	0.34
C59	11.00***	17.17***	4.05*	5.98*	15.71***
C63	5.66	1.54			

*** $p < 0.001$
** $p < 0.01$
* $p < 0.05$

DISCUSSION

No single pattern of change in clonal abundances was common among the multiclonal ponds examined. Each pond exhibited unique characteristics, suggesting that the different ponds responded to a variety of selective regimes.

The multiclonal ponds were not restricted to any single geographic location on the rock bluffs (Figure 1), although several ponds were located in close proximity to each other (C86, 88 and 89). The two multiclonal ponds found on bluff A were at opposing ends of the rock bluff, and ponds on bluff C were separated by similar distances.

Despite the variety observed among multiclonal ponds, however, it is possible to examine the validity of several hypotheses proposed to explain their existence. Parker (1979) suggested that recent mutationally-derived clones could potentially coexist, as their ecological requirements and abilities would likely be identical. Conversely, Vrijenhoek (1978) has shown that clonal coexistence may result from continuous generation of new clonal types from parental sexual populations. Sebens and Thorne (1985) have documented a number of cases supporting this argument, and suggest that actual coexistence of individual clones is a short-term phenomenon balanced by the influx of new clonal types.

The electrophoretic data presented in Table 1, as well as Stanton's (1988) work on mitochondrial DNA of the

unpigmented clones, indicates that sympatric clones are not derived from recent mutational events, and display considerable genetic heterogeneity. The absence of male production in all but two of the clones (M. Beaton, pers. comm.) indicates that their ability to sexually reproduce was lost some time ago. Together, these observations suggest that neither Vrijenkoek's (1978) nor Parker's (1979) hypotheses are valid in explaining coexistence of these clones.

Indeterminate competition (Park 1948, Hebert and Crease 1980) is unlikely to be responsible for clonal coexistence in ponds. Competitive exclusion has been shown to occur among the Churchill clones (Chapter 4), including some clonal pairs that were observed to co-occur in the multiclonal ponds.

It is also unlikely that the co-occurrent clones are sufficiently dissimilar to facilitate their coexistence. The genetic similarity among these clones is still sufficiently high to predict strong competitive interactions (Hebert 1982). Although differences in habitat preference do exist among the clones (chapter 2), there is little reason to expect the clones to differ in their choice of food resources. Thus, it is extremely unlikely that clonal coexistence would be facilitated by differences among the component clones.

Examination of clonal richness and diversity versus pond volume (chapter 2) disproved the hypothesis that large

volume ponds might facilitate clonal coexistence through differential utilization of microhabitats by the different clones. Although Fryer (1985) showed an increase in species richness of chydorids with increasing volume of water bodies, no correlation was observed for either richness or diversity values of D. pulex clones with volumes of the Churchill ponds.

Similarly, data presented in chapter 2 showed that the presence of the predators Hesperodiaptomus arcticus and/or Mesostoma lingua in ponds failed to predict higher clonal diversity. This does not indicate that predators had no effect on richness or diversity indices of ponds, however, as most multiclonal ponds contained either one or both of the predators.

The temporal succession of clones in ponds C13, C27 and C59 (Figure 2) resembled results obtained by other researchers (Carvalho 1987, 1988, Carvalho and Crisp 1987), who observed seasonal succession among Daphnia magna clones. Similar results have been observed in clonal plant populations (Harper 1977, Sebens and Thorne 1985). Weider (1985) by contrast, found no consistent trends in clonal succession among D pulex clones examined across a 30-month period.

The initial high values and subsequent decay in clonal diversity observed in all the ponds during each annual cycle indicated that co-occurring clones did not have equal short-term fitnesses. Seasonal decreases in diversity were

likely caused by suppression or exclusion of clones responding to biotic selective pressures. The elimination of D. pulex from ponds A56 and C63 were likely caused by abiotic stress, suggesting that these ponds were not suitable habitats for any of the clones which appeared there.

A comparison of clonal diversity values from early July of 1985, 1988 and 1989 revealed that although clonal pond composition remained reasonably stable, diversity levels varied considerably among years. Almost all ponds retained two clones, but shifts in diversity values were pronounced. These results agree with Weider's (1985) findings that clonal diversities could not be predicted from values from the previous season.

The decay in clonal diversity in multiclonal ponds through 1988, shows that clones in these ponds are subjected to selective pressures such as competition which decrease clonal diversity throughout the summer. Carvalho (1988) observed a similar decrease in diversity between summer and winter clonal populations in a permanent pond. Clonal diversities in the Churchill ponds are re-established from the hatching of ephippial eggs each spring. Provided that each clone present is able to produce even a single successful resting egg, the high clonal richness of these ponds could persist indefinitely.

Stochastic events (Talling 1951) may play a large part in offsetting local (within-pond) selective effects

(Ricklefs 1987). High colonization rates of different clones would counteract decreasing diversity observed through the season. During the summer, this could be facilitated by flooding among ponds during periods of heavy rainfall (pers. obs.). Indeed, dispersal of clones likely accounts for the high diversities observed in several closely-spaced ponds (C86, 87 and 88) in 1988 and 1989.

Multiclonal ponds may represent environmental cusps or crucibles, where no single clone is ideally suited to the pond habitat, and all clones present are equally disadvantaged. This would explain multiclonal ponds such as A56, C70 and C103, which displayed inconsistent clonal compositions among the sampling years. Pond C70 changed completely from 1988 to 1989, with the number of resident clones dropping from 3 to 1. Similarly, pond C103 was found to support several clones in 1985, but proved difficult to collect from in later years. Repeated sweeps of the entire pond were required in order to obtain sufficient animals for gelling, suggesting that this pond habitat was suboptimal for the clones which occurred there. Pond 56 on bluff A was the most extreme example: when searched in 1988, the pond was dominated by Daphnia magna, with D. pulex occurring in very low numbers. A search of the pond in 1989 failed to detect any D. pulex whatsoever.

The observed differences in parthenogenetic proportions among sympatric clones suggests that clones are individually tracking changes in pond habitat. Hebert and

Ward (1976) observed differences in both brood size and proportion of parthenogenetic females in populations of D. magna, as did Carvalho (1987, 1988). The reduced brood sizes of clone 15 in comparison with co-occurring diploid clones were consistent with literature predictions of polyploid animals typically having reduced brood sizes with larger offspring than their diploid relatives (Beatty 1957, Sexton 1980), and agree with results of life-history studies among diploid and polyploid clones of D. pulex (Weider 1987).

The failure of clonal proportions and reproductive states to predict subsequent clonal frequencies was disappointing, but consistent with results from other field studies. Although Hebert (1974a) and Carvalho (1988) found that genotypic fecundities in permanent, cyclic parthenogenetic populations of D. magna were correlated with subsequent genotypic frequencies, clonal proportions in intermittent D. magna populations changed rapidly in an unpredictable fashion. Similarly, Korpalainen (1986) found that clonal proportions within populations of D. pulex underwent rapid changes and could not be related to reproductive states. The inability to accurately predict clonal composition in this study suggests that the multiclonal ponds are exposed to stochastic events which cause rapid and unpredictable changes in the clonal composition of the ponds.

In conclusion, the existence of multiclonal ponds on

the bluffs cannot be explained by any single hypothesis, although it was shown that co-occurring clones are not ecological analogues and differed in seasonal fitness.

LITERATURE CITED:

Carvalho, G.R. 1987. The clonal ecology of Daphnia magna (Crustacea: Cladocera). II. Thermal differentiation among seasonal clones. J. Animal Ecol. 56: 469-478

Carvalho, G.R. and D.J. Crisp. 1987. The clonal ecology of Daphnia magna (Crustacea: Cladocera). I. Temporal changes in the clonal structure of a natural population. J. Animal Ecol. 56: 453-468

Chesson, P.L. 1986. Environmental variation and the coexistence of species. p. 240-256 in J. Diamond and T.J. Case (eds). Community Ecology. Harper and Row, New York.

Chesson, P.L. and T.J. Case. 1986. Overview: nonequilibrium community theories: chance, variability, history, and coexistence. p. 229-239 in J. Diamond and T.J. Case (eds). Community Ecology. Harper and Row, New York.

DeMott, W.R. 1980. An analysis of the precision of birth and death rate estimates for egg-bearing zooplankters. p. 337-345 in Kerfoot, W.C. (ed). Evolution and Ecology of Zooplankton Communities. University Press of New England, Hanover NH.

_____. 1983. Seasonal succession in a natural Daphnia assemblage. Ecol. Monogr. 53: 321-340

Fryer, G. 1985. Crustacean diversity in relation to the size of water bodies: some facts and problems. Freshwater Biology 15: 347-361

Ghilarov, A.M. 1984. The paradox of the plankton reconsidered, or why do species coexist?

Harper, J.L. 1977. Population biology of Plants. Academic Press, New York.

Hebert, P.D.N. 1974. Ecological differences between genotypes in a natural population of Daphnia magna. Heredity 33: 327-337

_____. 1982. Competition in zooplankton communities. Ann. Zool. Fennici 19: 349-356

Hebert, P.D.N. and M.J. Beaton. 1989. Methodologies for allozyme analysis using cellulose acetate electrophoresis. Helena Laboratories, Beaumont TX.

Hebert, P.D.N. and T.J. Crease. 1980. Clonal coexistence in Daphnia pulex (Leydig): another planktonic paradox. Science 207: 1363-1365

_____. 1983. Clonal diversity in populations of Daphnia pulex reproducing by obligate parthenogenesis. Heredity 51: 353-369

Hebert, P.D.N. and R.D. Ward. 1976. Enzyme variability in natural populations of Daphnia magna. IV. Ecological differences and frequency changes of genotypes at Audley End. Heredity 36: 331-341

Hebert, P.D.N., R.D. Ward and L.J. Weider. 1988. Clonal-diversity patterns and breeding-system variation in Daphnia pulex, an asexual-sexual complex. Evolution 42: 147-159

Holt, R.D. and B.P. Kotler. 1987. Short-term apparent competition. Am. Nat. 130: 412-430

Hutchinson, G.E. 1961. The paradox of the plankton. Am. Nat. 95: 137-145

Jacobs, J. 1977. Coexistence of similar zooplankton species by different adaptation to reproduction and escape in an environment with fluctuating food and enemy densities. II. Field data analysis of Daphnia. Oecologia 30: 313-329

Korpalainen, H. 1986. Intraspecific variation in lifespan and fecundity under controlled conditions in the cyclic parthenogen Daphnia magna. Arch. Hydrobiol. 105: 321-327

Maly, E.J., S. Schoenholtz and M.T. Arts. 1980. The influence of flatworm predation on zooplankton inhabiting small ponds. Hydrobiologia 76: 233-240

Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89: 583-590

Pajunen, V.I. 1986. Distributional dynamics of Daphnia species in a rock-pool environment. Ann. Zool. Fennici 23: 131-140

Park, T. 1948. Experimental studies of interspecies competition. I. Competition between populations of the flour beetles, Tribolium confusum Duval and Tribolium castaneum. Ecol. Monogr. 18: 265-307

Parker, E.D. Jr. 1979. Ecological implications of clonal diversity in parthenogenetic morphospecies. Am. Zool. 19: 753-762

Peterson, R. 1975. The paradox of plankton: an equilibrium hypothesis. Am. Nat. 109: 35-49

Ranta, E. 1979. Niche of Daphnia species in rock pools. Arch. Hydrobiol. 87: 205-223

Richerson, P., R. Armstrong and C.R. Goldman. 1970. Contemporaneous disequilibrium: a new hypothesis to explain the paradox of the plankton. Proc. Nat. Acad. Sci. 67: 1710-1714

Ricklefs, R.E. 1987. Community diversity: relative roles of local and regional processes. Science 235: 167-171

Schwartz, S.S. and P.D.N. Hebert. 1982. A laboratory study of the feeding behaviour of the rhabdocoel Mesostoma ehrenbergii on pond Cladocera. Can. J. Zool. 60: 1305-1307

Sebens, K.P. and B.L. Thorne. 1985. Coexistence of clones, clonal diversity, and the effects of disturbance. p. 357-398 in Jackson, J.B.C., L.W. Buss and R.E. Cook (eds). Population Biology and Evolution of Clonal Organisms. Yale University Press, London.

Sexton, O.J. 1980. Polyploidy in animal evolution. p. 379-381 in W.H. Lewis (ed). Polyploidy: Biological Relevance. Plenum Press, New York.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. 2nd ed. W.H. Freeman and Co., New York.

Stanton, D.J. 1988. Evolution of asexuality in Daphnia pulex: implications of mitochondrial DNA analysis. Ph.D. dissertation, University of Windsor, Ont.

Stross, R.G. and D.A. Kangas. 1969. The reproductive cycle of Daphnia in an arctic pool. Ecology 50: 457-460

Talling, J.F. 1951. The element of chance in pond populations. The Naturalist 1951: 157-170

Tucic, B., S. Milojkovic, S.Vujcic and A. Tarasjev. 1988. Clonal diversity and dispersion in Iris pumila. Acta Oecologia 9: 211-219

Vrijenhoek, R.C. 1978. Coexistence of clones in a heterogeneous environment. Science 199: 549-552

_____. 1979. Factors affecting clonal diversity and coexistence. Am. Zool. 197: 787-797

Weider, L.J. 1989. Spatial heterogeneity and clonal structure in arctic populations of apomictic Daphnia. Ecology 70: 1405-1413

Weider, L.J., M.J. Beaton and P.D.N. Hebert. 1987. Clonal diversity in high-arctic populations of Daphnia pulex, a polyploid apomictic complex. Evolution 41: 1335-1346

Wiens, J.F. 1984. On understanding a non-equilibrium world: myth and reality in community patterns and processes. p. 439-457 in Strong, D.R., D. Simberloff, L.G. Abele and A. Thistle (eds). Ecological Communities: Conceptual Issues and the Evidence. Princeton University Press, Princeton NJ.

Wilkinson, L. 1988. SYSTAT: the System for Statistics. Systat, Inc., Evanston, IL.

Wilson, C.C. and P.D.N. Hebert. 1990. The impact of predation on distribution patterns of Daphnia pulex clones. Limnol. Oceanogr. (in review)

CHAPTER 4

COMPETITION IN A CLONAL ASSEMBLAGE

INTRODUCTION

Competition has long been considered to be one of the major forces responsible for structure in pond communities. Hutchinson (1951) argued that size differences among coexisting copepod species were the result of competition-induced niche differentiation. The notion of competitively structured zooplankton communities has been promoted by a number of researchers (Brooks and Dodson 1965, Ghilarov 1967, Hanspie and Polk 1974, Hebert 1982, Hanski and Ranta 1983, Schwartz 1984, Bengtsson 1986, Vanni 1986). Experimental studies have demonstrated the importance of competition in both the laboratory and the field (Frank 1952, Neill 1975, Jacobs 1978, DeMott and Kerfoot 1982, Bengtsson 1986, Hanazato and Yasuno 1987), with competitive exclusion frequently occurring.

Although life history and ecological differences certainly exist between conspecific clones (King 1972, Snell 1977, 1979, Loaring and Hebert 1981, Weider and Lampert 1985, Carvalho 1986, Weider 1988), clones typically have such similar ecological requirements (Hebert 1978, Loaring and Hebert 1981) that competition is particularly intense (Williams 1975). Competition among clones has been extensively demonstrated in plants (Harper 1977, Tucic et al 1988), but has largely been neglected in animal species. Rather, ecological relationships within asexual taxa have largely been inferred from distributional surveys of clones (Hebert 1974a,b, Hebert and Crease 1980, Jaenike et al

1980, Jaenike and Selander 1987, Weider and Hebert 1987a,b). Other studies have deduced interclonal competition by monitoring temporal shifts in clonal frequencies (Hebert and Crease 1983, Weider 1985, Korpalainen 1986a, Carvalho and Crisp 1987). Few experimental studies, have been carried out, although Snell (1977, 1979) found that clones of the rotifer Asplanchna brightwelli exhibited competitive exclusion in laboratory cultures. Similarly, Loaring and Hebert (1981) and Loaring (1982) observed competitive exclusion among clones of Daphnia pulex in 1 L jars and 500 L aquaria, respectively.

The usefulness of results from laboratory competition experiments has been questioned on the basis that laboratory microcosms oversimplify natural communities and force unnatural conditions on the experimental organisms (Hebert 1982, Simberloff et al 1982, Diamond 1986). Manipulative field experiments on natural populations are required to conclusively demonstrate the importance of competition in structuring communities (Connor and Simberloff 1979, Bender et al 1984).

Arctic pond habitats are well suited for manipulation experiments due to the simplicity of their resident communities (Ghilarov 1967, Hebert and Hann 1986). Most prior research on competition in arctic pond communities, however, has been limited to observational studies (Ghilarov 1967, Dodson 1979, Ranta 1979, Hobbie 1980, Hebert and Hann 1986).

The simple clonal composition of most ponds on the Churchill rock bluffs suggested strong competitive interactions among the unpigmented D. pulex clones. This possibility was further supported by the largely micro-allopatric distributions of the three dominant clones (chapter 2). In the present study, pairwise interactions among these three clones were examined using whole-pond manipulations. Experiments tested the hypothesis that clones were narrowly adapted to specific habitat types, and would hence be superior competitors in their native habitats and fare poorly away from them.

METHODS

Field experiments in July and August of 1987 and 1988 examined the hypothesis that competitive interactions among clones were responsible for their largely allopatric distributions. The intensity of competition was tested by establishing pairwise combinations of clones and monitoring shifts in clonal composition over the course of the summer. Experiments in 1987 examined competition among the three dominant clones (1, 13 and 14), while 1988 experiments examined competitive interactions between clones 13 and 14 and two less abundant clones (16 and 21).

Source ponds for clones 1, 13 and 14 were preliminarily identified from results of the 1985 bluff survey (chapter 2). Only ponds which were uniclonal for one of the three clones in 1985 were considered. Allozyme phenotypes of forty eight animals from each of eight ponds (2 ponds for each common clone, 1 pond per rare clone) were reanalysed using standard protocols (Hebert and Beaton 1989) in 1987 and 1988 to verify that no shifts in clonal composition had occurred. In all cases where no intrusion by new clones was observed, ponds were accepted as sources for the resident clone.

Ponds selected for use in the manipulation experiments were chosen to ensure congruence in size and bottom type. Specifically, experimental ponds ranged from 500 to 2,000 L in volume. Ponds underlain by permafrost, as opposed to rock, were avoided, since such ponds disappeared with

permafrost thaw. Eighteen experimental ponds were used in 1987, and an additional twelve in 1988.

In early July of 1987 and 1988, each experimental pond was drained, using a submersible pump powered by a portable electric generator. Water from the pond was filtered through a 200 µm-mesh Nitex screen to remove resident zooplankton and held in portable 500 L plastic storage pools at the site. The exposed pond sediments were allowed to dry for a period of 48 hours to kill any remaining zooplankters. The original pond water was then refiltered through the Nitex mesh and returned to its source pond. In this manner, the original habitat was restored, without the presence of any potential competitors or predators. Two weeks were required to complete preparatory manipulations of the ponds.

Reproductive adults were collected from the source ponds in mid-July and placed in separate holding pools containing a mixture of water from all source ponds. All animals introduced into the experimental ponds were thereby exposed to equally unfamiliar environments, reducing any "home field" advantage.

After a 24 hour holding period and just prior to their introduction into the manipulation ponds, the mean clutch size of each clone in the holding pools was determined, using 40 females from each clone. Sufficient ovigerous females of each clone were then introduced to ensure an initial density of 2 embryos per clone per litre. For

example, two clones having respective mean brood sizes of 6 and 4 eggs would have introduced populations of 667 and 1,000 animals for a 2,000 L pond.

Six ponds which were originally uniclonal for each of the three dominant clones were employed in 1987. The original clone was re-established in each pond, together with one of the other common clones. In this manner, each of the three possible pairwise combinations of the common clones occurred in six ponds, with each clone being the native inhabitant in three, and non-native in the other three. In 1988, six ponds were employed in further competition experiments, three native for clone 13 and three for clone 14. Of these, two of each type received introduced populations of clone 16 and the resident clone, and the other received clone 21 and the resident clone. The restricted distributions of these rarer clones prevented reciprocal introductions from being conducted. As well, two types of control ponds were established. Sham introductions were carried out where the non-native clone was introduced into ponds after removal of the native clone. Two of these ponds were established for each of the three common clones - one for each of the foreign habitats into which that clone had been placed in 1987. As well, empty controls were set up to determine the extent of post-spring hatching of ephippial eggs, in order to evaluate potential recruitment advantages of native clones throughout the season. Small-scale sham introductions were

conducted for the two rare clones in these latter ponds, using enclosures with a mesh sufficiently small to prevent escape of juveniles into the ponds.

In the event that more than 50% of water was lost from a pond, either from disturbance of the storage pools and/or evaporation later in the experiment, the pond volume was returned to its original level by addition of filtered water from the nearest pond with a pure stock of the clone native to the experimental pond.

Pond populations were sampled one week after initiation of the experiment and biweekly thereafter. Samples were collected and processed using the methods described in chapter 3. Analyses of clonal frequencies, short-term reproductive effort and relative fitnesses were also carried out as described in chapter 3. Reproductive states of animals collected in the first post-introduction sampling period were not considered, as only subadults were present.

RESULTS

Field experiments

All clonal combinations showed consistent shifts in clonal frequencies. For the most part, clones were competitively superior in their native habitats and were displaced in non-native ponds. Thus, clone 1 excluded clones 13 and 14 from its home ponds (Figure 1a,b), but was in turn displaced by clones 13 and 14 in their home ponds (Figure 1c, Figure 1e). One deviation from the general pattern was noted: clone 13 displaced clone 14 from its home pond (Figure 1f). Similar results were obtained in the studies with rare clones. Thus, clones 13 and 14 again displaced clones 16 and 21 (Figure 2a,b).

Sham introductions showed that clones 13 and 14 persisted in ponds originally occupied by clone 1, but ceased parthenogenetic reproduction within four weeks. By late August, clone 14 had disappeared from its control pond, while clone 13 was present only at low density. By contrast, clone 1 showed continual parthenogenetic reproduction and population growth in control ponds that were originally occupied by clones 13 and 14. Similarly, clone 13 was able to persist in clone 14 habitats and clone 14 in habitats formerly occupied by clone 13. Rare clones in the mesh enclosures also persisted and remained reproductively active throughout most of the summer. No recruitment of Daphnia from ephippial eggs was observed in

Figure 4-1: Seasonal shifts of abundance of clones 1, 13 and 14 in experimental competition ponds in 1987. (a) clone 1 vs. clone 13; (b) clone 1 vs. clone 14; (c) clone 13 vs. clone 1; (d) clone 13 vs. clone 14; (e) clone 14 vs. clone 1; (f) clone 14 vs. clone 13. Vertical bars represent sampling error of pooled clonal frequencies.

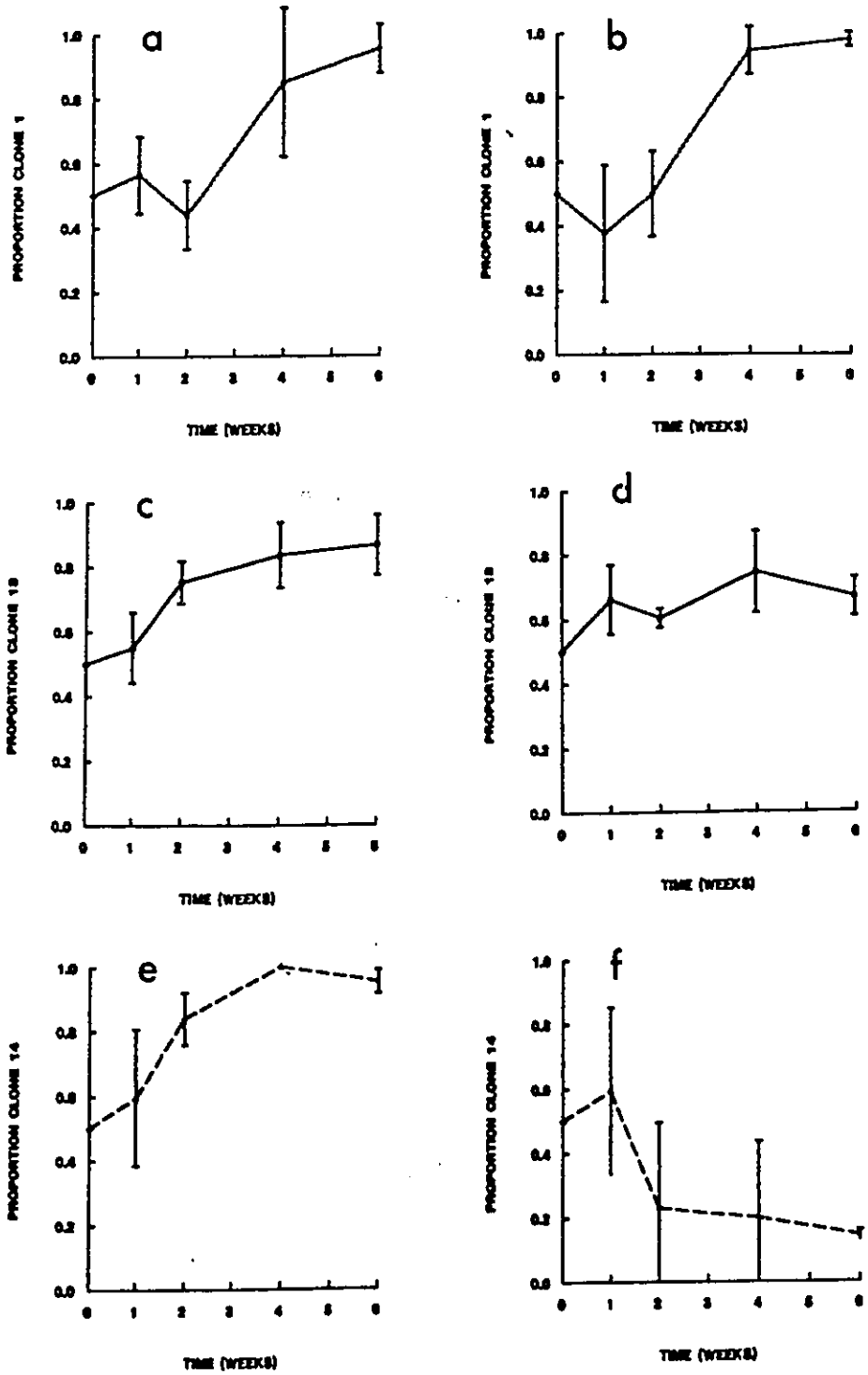
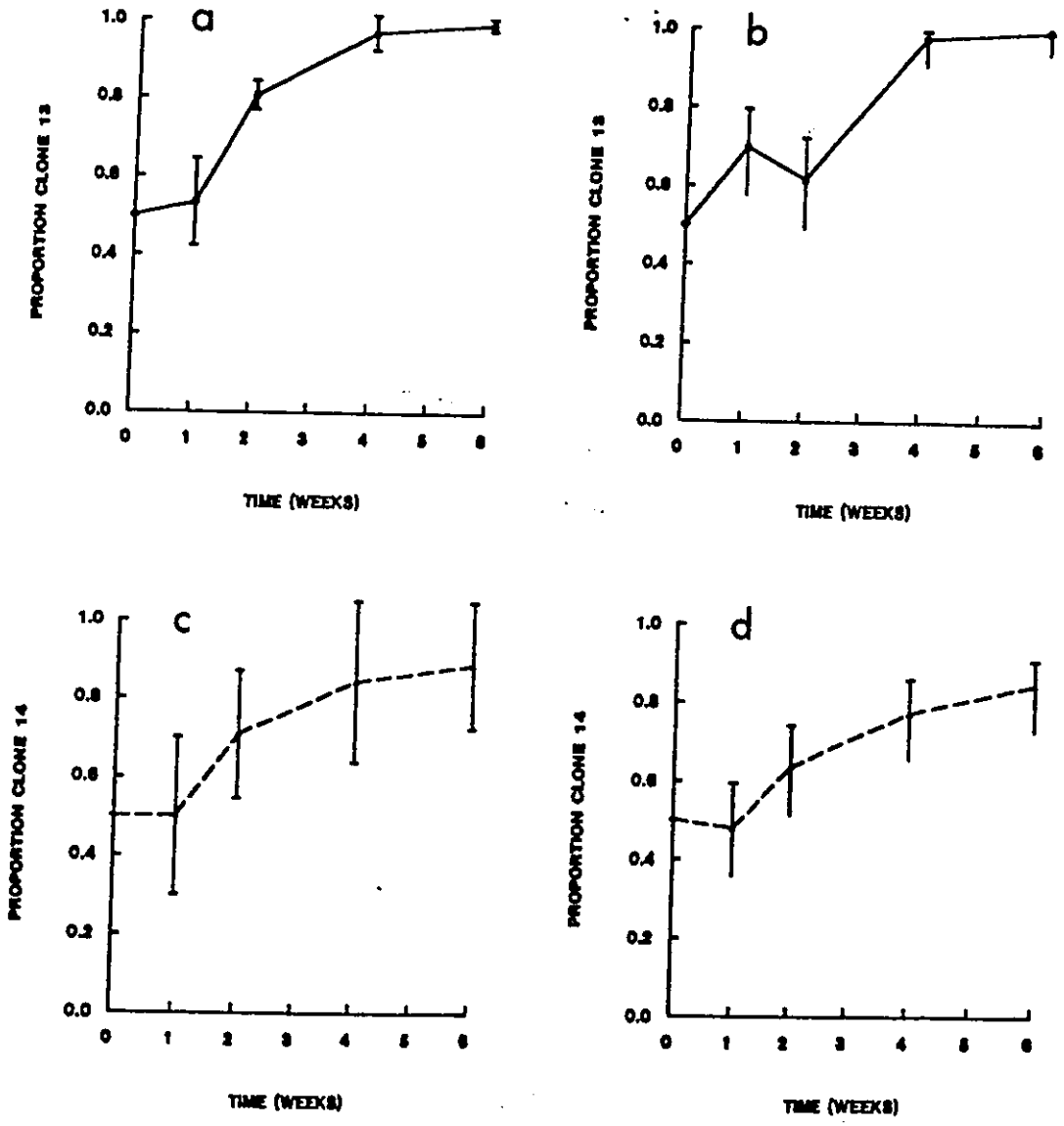


Figure 4-2: Seasonal shifts of abundance of clones 13 and 14 in experimental competition ponds in 1988. (a) clone 13 vs. clone 16; (b) clone 13 vs. clone 21; (c) clone 14 vs. clone 16; (d) clone 14 vs. clone 21. Vertical bars in (a) and (c) represent sampling error; (b) and (d) show 95% confidence intervals for single ponds.



the 1988 empty control ponds, as the ponds lacked animals all summer.

Reproductive status of all clones in the competition and control ponds are given in Table 1. The majority of populations showed decreasing proportions of parthenogenetic females and an increase of nonreproductive females as the season progressed, regardless of clonal type. Reproductive states of the clones also varied among ponds, as well as temporally.

Co-occurring clones showed significantly differences in the proportion of parthenogenetic females in 12 of the 44 samples which could be tested (Table 2). Of these, the resident clone had a significantly higher reproductive ratio in 9 cases. Tests of mean brood sizes between competing clones were further restricted (Table 3), as only 30 cases showed parthenogenetic reproduction of both clones. Statistical analyses of these samples was limited by the fact that in 24 cases one clone was represented by fewer than ten parthenogenetic females. Significant differences were, however, observed in 6 cases. In all 6 cases, clone 13 had smaller mean brood sizes than its competitor, regardless of habitat.

Differences in either proportions of parthenogenetic females or brood sizes of co-occurring clones alone were not accurate predictors of clonal frequencies at subsequent sampling intervals (Table 4). Of the 26 cases where shifts in clonal frequency could be predicted, 16 samples showed

Table 4-1: Reproductive status of clones in competition and control ponds, showing absolute numbers of each clone and proportional representation of each reproductive class at each sampling interval.

time		July 30				August 14				August 28			
Common vs. common clones (1987)													
Home	Clone	n	NR	E	P	n	NR	E	P	n	NR	E	P
1	1	53	.15	.55	.30	56	.63	.21	.16	83	.41	.39	.20
	13	43	.21	.47	.32	40	.58	.23	.20	13	.31	.54	.15
1	1	33	.42	.48	.09	93	.37	.53	.11	44	.41	.50	.09
	13	63	.38	.10	.52	3	1.00	.	.	2	.50	.50	.
1	1	57	.	.	1.00	86	.43	.45	.12	93	.53	.44	.03
	14	39	.10	.82	.08	10	.40	.60	.	3	1.00	.	.
1	1	39	.08	.33	.59	96	.27	.01	.72	96	.17	.27	.55
	14	57	.05	.89	.05	0	.	.	.	0	.	.	.
1	1	40	.33	.10	.58	96	.53	.04	.43	58	.57	.40	.03
	13	56	.25	.30	.46	0	.	.	.	0	.	.	.
14	14	75	.48	.31	.21	96	.81	.17	.02	94	.53	.44	.02
	1	21	.48	.33	.19	0	.	.	.	2	.50	.50	.
14	14	86	.37	.49	.14	96	.80	.20	.	89	.60	.40	.
	1	10	.10	.20	.70	0	.	.	.	7	.57	.43	.
13	13	76	.66	.22	.12	78	.96	.01	.03	84	.77	.18	.05
	1	20	.50	.35	.15	18	.72	.22	.06	12	.58	.42	.
13	13	65	.38	.43	.18	72	.89	.06	.06	74	.74	.16	.10
	1	31	.48	.52	.	24	.71	.29	.	22	.41	.55	.05
13	13	76	.46	.22	.32	91	.71	.01	.27	92	.78	.02	.20
	1	20	.55	.30	.15	5	.20	.	.80	4	.50	.25	.25
14	14	4	.75	.25	.	6	1.00	.	.	13	.92	.	.08
	13	92	.65	.35	.	90	.93	.03	.03	83	.83	.10	.07
14	14	40	.68	.	.32	35	.77	.17	.06	15	.53	.47	.
	13	56	.57	.18	.25	61	.87	.02	.11	81	.86	.10	.04

Table 4-1 (continued)

time		July 30				August 14				August 28			
Common vs. common clones (1987)													
Pond	Clone	n	NR	E	P	n	NR	E	P	n	NR	E	P
13	13	56	.70	.04	.27	83	.84	.07	.08	61	.70	.20	.10
	14	40	.83	.15	.03	13	.85	.08	.08	35	.51	.49	.
13	13	60	.42	.47	.12	60	.97	.02	.02	67	.97	.03	.
	14	36	.67	.28	.06	36	.89	.11	.	29	.46	.54	.
Common vs. rare clones (1988)													
Pond	Clone	n	NR	E	P	n	NR	E	P	n	NR	E	P
14	14	61	.38	.44	.18	74	.53	.36	.11	81	.32	.05	.63
	21	35	.40	.31	.29	22	.36	.59	.05	15	.13	.87	.
13	13	80	.22	.01	.78	90	1.00	.	.	94	.13	.04	.83
	16	16	.69	.06	.25	6	.83	.17	.	2	.	.	1.00
13	13	59	.93	.07	.	94	.54	.16	.30	96	.77	.23	.
	21	37	.38	.62	.	2	.	.	1.00	0	.	.	.
13	13	75	.35	.20	.45	96	.07	.04	.89	96	.39	.19	.43
	16	21	.38	.	.62	0	.	.	.	0	.	.	.
14	14	79	.91	.03	.06	95	.66	.33	.01	96	.03	.01	.96
	16	17	.71	.18	.12	1	1.00	.	.	0	.	.	.
14	14	57	.58	.23	.19	67	.70	.21	.09	74	.62	.18	.20
	16	39	.33	.26	.41	29	.69	.17	.14	22	.32	.68	.
Control ponds (1988)													
14	1	96	.52	.26	.22	96	.41	.43	.16	96	.73	.19	.08
13	1	96	.18	.38	.44	96	.73	.19	.08	96	.53	.34	.13
1	13	96	.28	.31	.41	96	.60	.38	.02	38	.63	.37	.
14	13	96	.39	.22	.40	96	.21	.48	.31	96	.74	.17	.09
1	14	96	.40	.44	.16	96	.72	.28	.	0	.	.	.
13	14	96	.66	.07	.27	96	.81	.05	.14	96	.60	.22	.18

Table 4-2: Multiple G-tests of relative frequencies of parthenogenetic females between competing clones in experimental ponds.

time		July 30	August 14	August 28
Home Clone		G	G	G
Common vs common clones (1987)				
1	1 13	0.06	0.25	0.19
1	1 13	19.72***	0.67	0.37
1	1 14	46.68***	2.33	0.19
1	1 14	35.84***	....	....
1	1 13	1.88	....	....
14	14 1	0.05	....	0.09
14	14 1	13.80***	....	....
13	13 1	0.14	0.37	1.09
13	13 1	10.16***	2.36	1.13
13	13 1	2.37	1.07	0.07
14	14 13	....	0.39	0.04
14	14 13	0.65	0.93	....

*** $p < 0.001$

Table 4-2 (continued)

time		July 30	August 14	August 28
Pond	Clone	G	G	G
Common vs. common clones (1987)				
13	13 14	12.07***	0.01	5.67*
13	13 14	1.06	0.95	....
Common vs. rare clones (1988)				
14	14 21	1.41	0.91	25.93***
13	13 16	15.95***	....	0.74
13	13 21	....	4.75*	....
13	13 16	1.82	....	....
14	14 16	0.54	0.02	....
14	14 16	5.35*	0.49	8.60**

*** $p < 0.001$
** $p < 0.01$
* $p < 0.05$

Table 4-3: Comparison of mean brood size between clones for all cases where both clones showed parthenogenetic reproduction, using Student's t-test for two samples with unequal sample sizes and variances.

time		July 30			August 14			August 28		
Home	Clone	$\bar{x}$	S.E.	t	$\bar{x}$	S.E.	t	$\bar{x}$	S.E.	t
Common vs common clones (1987)										
1	1	8.63	3.59	0.78	11.44	5.55	1.60	11.18	5.29	0.11
	13	7.43	3.16		4.75	1.67		9.50	0.71	
1	1	6.00	1.73	9.19***	8.30	2.67		7.50	1.91	
	13	2.33	0.99		....	....		....	....	
1	1	27.82	7.90	0.47	6.70	1.06		8.33	1.15	
	14	17.00	12.49		....	....		....	....	
1	1	12.04	3.95	0.40	9.69	2.66		9.77	2.09	
	14	14.33	3.06		....	....		....	....	
1	1	8.52	2.54	3.72***	11.98	4.85		7.00	....	
	13	6.04	2.13		....	....		....	....	
14	14	6.38	2.18	0.57	3.00	....		2.50	0.71	
	1	7.50	3.78		....	....		....	....	
14	14	15.00	9.98	0.52	....	....		....	....	
	1	7.29	1.50		....	....		....	....	
13	13	3.00	0.87	0.00	1.00	....		3.75	1.50	
	1	3.00	....		1.00	....		....	....	
13	13	3.42	1.62		1.00	....		1.29	0.76	5.80**
	1	....	....		....	....		6.00	....	
13	13	7.38	2.16	1.33	2.40	1.08	2.28*	3.33	1.46	2.45*
	1	5.67	1.15		3.25	1.50		7.00	....	
14	14	....	....		....	....		1.00	....	0.76
	13	....	....		2.00	1.00		3.00	1.41	
14	14	6.54	1.45	0.49	1.50	0.71	1.30	....	....	
	13	6.23	1.79		2.14	0.90		7.67	1.15	

*** $p < 0.001$
** $p < 0.01$
* $p < 0.05$

Table 4-3 (continued)

time		July 30			August 14			August 28		
Home	Clone	$\bar{x}$	S.E.	t	$\bar{x}$	S.E.	t	$\bar{x}$	S.E.	t
Common vs. common clones (1987)										
13	13	3.40	1.50	1.03	2.43	1.81	0.29	1.33	0.82	
	14	5.00	....		3.00	....		....	....	
13	13	3.86	1.86	0.84**	7.00	....		....	....	
	14	5.50	0.71		....	....		....	....	
Common vs. rare clones (1988)										
14	14	7.09	1.58	1.17	7.50	2.07	0.68	8.96	3.47	
	21	8.10	2.33		6.00	....		....	....	
13	13	8.08	1.88	1.48	....	....		10.96	3.45	1.50
	16	11.50	10.63		....	....		20.00	1.41	
13	13	....	....		1.89	0.88	0.01	....	....	
	21	....	....		2.00	....		....	....	
13	13	13.59	11.84	0.46	14.07	9.67		8.78	2.89	
	16	8.38	3.12		....	....		....	....	
14	14	6.20	3.03	0.04	7.00	....		17.73	7.81	
	16	6.00	1.00		....	....		....	....	
14	14	6.82	1.47	0.89	5.50	2.17	1.70	7.07	2.40	
	16	7.44	1.97		7.50	1.00		....	....	
Control ponds (1988)										
14	1	8.69	2.43		9.70	2.06		8.33	1.69	
13	1	7.31	2.78		7.75	2.38		6.83	2.33	
1	13	7.62	2.04		3.00	....		....	....	
14	13	8.30	2.09		7.45	1.36		9.89	5.13	
1	14	11.29	3.71		....	....		....	....	
13	14	7.79	1.64		6.76	1.78		10.25	3.84	

** $p < 0.01$

Table 4-4: Short-term reproductive efforts and significant differences among clones in competition ponds, using DeMott's (1980) egg-ratio (E). Dates where no parthenogenetic females were observed for a clone are indicated by (....). Blank lines (----) indicate that the clone specified was not detected. Positive, negative and nonsignificant shifts in expected (e) and observed (o) changes in clonal frequencies are indicated, and were determined using 95% confidence intervals of egg-ratios and clonal frequencies. Blank spaces indicate cells where shifts could not be predicted due to an absence of parthenogenetic adults or clones.

time		July 30				August 14			
Home	Clone	E	S.E.	e	o	E	S.E.	e	o
Common vs. common clones (1987)									
1	1	2.59	0.37	ns	+	1.83	0.40	ns	ns
	13	2.38	0.35	ns	-	0.95	0.10	ns	ns
1	1	0.54	0.10	-	+	0.91	0.08		ns
	13	1.21	0.03	+	-	....			ns
1	1	27.82	1.09	+	+	0.80	0.06		ns
	14	1.36	0.87	-	-	....			ns
1	1	7.10	1.14	+	+	6.98	0.25		
	14	0.72	0.18	-	-	----			
1	1	4.94	0.54	+	+	5.15	0.47		
	13	2.78	0.19	-	-	----			
14	14	1.34	0.10	ns	+	0.06	0.00		
	1	1.43	0.54	ns	-	----			
14	14	2.10	0.48	-	+	....			
	1	5.10	1.27	+	-	----			
13	13	0.36	0.01	ns	+	0.03	0.00	ns	ns
	1	0.45	0.06	ns	-	0.06	0.00	ns	ns
13	13	0.62	0.03	+	+	0.06	0.00		ns
	1	....		-	-	....			ns
13	13	2.36	0.18	+	+	0.65	0.02	-	ns
	1	0.85	0.21	-	-	2.60	0.70	+	ns
14	14	....		ns	+	....			ns
	13	....		ns	-	0.06	0.00		ns

Table 4-4 (continued)

time		July 30				August 14			
Home	Clone	E	S.E.	e	o	E	S.E.	o	e
Common vs. common clones (1987)									
14	14	2.09	0.25	ns	-	0.09	0.00	-	-
	13	1.56	0.14	ns	+	0.24	0.01	+	+
13	13	0.92	0.05	+	ns	0.19	0.01	ns	ns
	14	0.15	0.02	-	ns	0.24	0.05	ns	ns
13	13	0.46	0.03	+	ns	0.14	0.02		ns
	14	0.33	0.05	-	ns	....			ns
Common vs. rare clones (1988)									
14	14	1.28	0.13	-	ns	0.83	0.08	+	ns
	21	2.35	0.43	+	ns	0.30	0.08	-	ns
13	13	6.30	0.17	+	ns	....		ns	ns
	16	2.88	3.22	-	ns	....		ns	ns
13	13	....				0.57	0.01	-	ns
	21	....				2.00	0.01	+	ns
13	13	6.12	1.45	ns	ns	12.52	1.07		
	16	5.20	1.08	ns	ns	----			
14	14	0.37	0.03	+	ns	0.07	0.01	+	ns
	16	0.07	0.01	-	ns	....		-	ns
14	14	1.30	0.13	-	+	0.50	0.04	ns	ns
	16	3.05	0.38	+	-	1.05	0.24	ns	ns

agreement with predicted shifts, while 10 did not. Of the 10 cases where significant differences were observed but clonal frequency shifts were opposite to those predicted, the clone native to the pond increased in nine of the samples.

DISCUSSION

The variation observed among replicates of clonal competition pairs is not indicative of 'pseudoreplication' (Hurlbert 1978). Rather, variation was likely due to pond morphology and historically-induced effects such as sediment richness and pond productivity, as well as normal stochastic variation observed among zooplankton populations (Allan 1972).

Results of clonal competition in most of the experimental ponds supported the null hypothesis that clones were competitively superior in their native habitats. Clone 13 was, however, found to be competitively superior to clone 14 in the latter's home ponds. This suggests that some factor other than competition is responsible for clone 14's abundance.

The rapid changes in clonal frequencies in the experimental ponds demonstrated strong selective pressures. Because the clones' strong similarity should increase the intensity of competitive interactions (Williams 1975, Hebert 1982), these results were not unexpected.

Although the validity of the competitive exclusion principle (Hardin 1960) has been disputed (Cole 1960, Armstrong and McGehee 1974, Simberloff 1983), competitive exclusion was clearly observed in many of the experimental ponds. All ponds showed progressive, deterministic shifts in clonal frequencies as the season progressed. Exclusion of competitively-inferior clones would likely have been

observed in most or all of the ponds if the experiment had been continued until pond freeze-up. Certainly, competitive exclusion has been demonstrated in other zooplankton studies (Hauspie and Polk 1974, Loaring and Hebert 1981, Loaring 1982), and is a real phenomenon among the unpigmented Churchill clones.

The displacement of clones from the experimental ponds was not, however, entirely due to competitive interactions. Weider and Hebert (1987a) have demonstrated that melanic D. pulex clones represent distinct 'ecotypes' with differing physiological tolerances. In the present study, sham introductions showed that clone 1 was able to survive in low conductivity ponds from which it was ordinarily absent, but clones 13 and 14 fared poorly in the high salinity habitats. Exclusion of these clones from such ponds was therefore likely accelerated rather than determined (Cole 1960) by competition with clone 1.

As reciprocal transplants were not possible for experiments involving rare clones, no conclusive statements can be made regarding the influence of competition on the distribution of these clones. The joint results obtained from the competition and control ponds suggest, however, that these clones fare poorly in ponds containing clones 13 and 14 but are able to occupy these ponds in the absence of the dominant clones. The presence of the dominant clones may therefore be an important factor in limiting distributions of less abundant clones.

Significant differences in parthenogenetic reproduction were observed in 13 of 47 samples where both clones were present, suggesting that fitnesses were often unequal. Reproductive differences of clones in native versus non-native ponds were difficult to assess, due to rapid competitive exclusion. A crude generalization can be made, however, that clones showed lower proportions of parthenogenetic females and smaller brood sizes when placed in non-native ponds. Reduced brood sizes in zooplankton have typically been linked to low food levels (Green 1956, Lampert 1978). Differences in brood size between clones may therefore result from different foraging or assimilation efficiencies of the clones. Snell (1980) found that reproductive output of rotifer clones varied in response to blue-green algae as a food source. Similarly, Loaring (1982) observed differences in food source suitability among competing D. pulex clones. This supports the idea that clones are adapted to specific habitat types, rather than the general purpose genotype hypothesis of Lynch (1984).

The poor predictive ability between reproductive status and subsequent frequencies of competing clones suggests that differences in clonal fecundities are not the sole factor driving clonal replacement. Frequency shifts may instead be the result of differing mortality or development rates among the clones. This observation concurs with results obtained by Loaring (1982) and

Korpalainen (1986a). Hebert (1974a) observed a general association between reproductive status of D. magna clones in permanent English ponds, but found that patterns were less clear in intermittent populations (Hebert 1974b).

The smaller brood sizes observed for clone 13 are consistent with other studies which have shown lower brood sizes in polyploids than in their diploid relatives. Thus, polyploids typically have fewer but larger offspring, slower growth rates and larger adult body size (Beatty 1957, Sexton 1980). Weider (1987) has observed differences in life history traits among D. pulex clones of differing ploidy levels. Diploid clones matured earlier and at smaller sizes, and produced larger broods than tetraploid clones. The results reported by Weider are not conclusive, however, as the tetraploid clones examined produce melanin in their carapaces, which incurs considerable metabolic costs (Hebert and Emery 1990).

As clone 13 is a tetraploid, its competitive superiority in the low conductivity ponds is somewhat surprising, as other studies have shown that clones with slower growth rates are competitively inferior (Snell 1977, 1979, Loaring and Hebert 1981). The larger sizes of polyploids (Beatty 1957, Sexton 1980) may confer a competitive advantage, as larger daphniids are able to utilize a greater spectrum of food particle sizes (Burns 1968). In addition, it has been speculated that animals with higher ploidy levels suffer less physiological stress

under severe environmental conditions than their diploid relatives (Sexton 1979, Suomalainen 1971).

The poor predictability of shifts in clonal abundances indicates that selection in these ponds may be episodic (Wiens 1977). Loaring (1982) observed major fluxes in relative abundances of competing clones in 500 L aquaria. The comparable sizes of Loaring's "pools" and the Churchill ponds suggest that selection might operate in a similar fashion. Alternatively, frequency shifts and apparent competitive abilities of clones may reflect life history differences, as Bengtsson (1986) observed among co-occurring daphniids.

In summary, clear competitive differences existed among the clones, and competitive ability was strongly influenced by habitat type. Asymmetric competition between clones 13 and 14 suggests that some factor other than competition is responsible for clone 14's dominant status in many ponds. Although the mechanisms underlying competitive interactions remain undetermined, competition is clearly an important process influencing community structure among members of this clonal assemblage.

LITERATURE CITED

Allan, J.D. 1972. Life history patterns in zooplankton. Am. Nat. 110: 165-180

Armstrong, R.A. and R. McGehee. 1980. Competitive exclusion. Am. Nat. 115: 151-170

Beatty, R.A. 1957. Parthenogenesis and polyploidy in mammalian development. Cambridge Monographs in Experimental Biology 7, Cambridge University Press, London.

Bender, E.A., T.J. Case and M.E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. Ecology 65: 1-13

Bengtsson, J. 1986. Life histories and interspecific competition between three Daphnia species in rockpools. J. Animal Ecol. 55: 641-655

Brooks, J.L. and S.I. Dodson. 1965. Predation, body size, and composition of plankton. Science 150: 28-35

Burns, C. 1968. The relationship between body size of filter-feeding Cladocera and the maximum size of particle ingested. Limnol. Oceanogr. 13: 675-678

Carvalho, G.R. 1987. The clonal ecology of Daphnia magna (Crustacea: Cladocera). II. Thermal differentiation among seasonal clones. J. Animal Ecol. 56: 469-478

Carvalho, G.R. and D.J. Crisp. 1987. The clonal ecology of Daphnia magna (Crustacea: Cladocera). I. Temporal changes in the clonal structure of a natural population. J. Animal Ecol. 56: 453-468

Cole, L.C. 1960. Competitive exclusion. Science 132: 348-349

Connor, E.F. and D. Simberloff. 1979. The assembly of species communities: chance or competition? Ecology 60: 1132-1140

DeMott, W.R. and W.C. Kerfoot. 1982. Competition among cladocerans: nature of the interaction between Bosmina and Daphnia. Ecology 63: 1949-1966

Diamond, J. 1986. Overview: laboratory experiments, field experiments, and natural experiments. p. 3-22 in Diamond, J. and T.J. Case (eds). Community Ecology. Harper and Row, New York.

Dodson, S.I. 1979. Body size patterns in arctic and temperate zooplankton. Limnol. Oceanogr. 24: 940-949

Frank, P.W. 1952. A laboratory study of intraspecies and interspecies competition in Daphnia pulicaria (Forbes) and Simocephalus vetulus Muller. Physiol. Zool. 25: 178-204

_____. 1957. Coactions in laboratory populations of two species of Daphnia. Ecology 38: 510-519

Ghilarov, A.M. 1967. The zooplankton of arctic rock pools. Oikos 18: 82-95

Good, A.G. 1981. The ecology and biogeography of tundra zooplankton communities in the Churchill, Manitoba area. M.Sc. thesis, University of Windsor, Ontario.

Green, J. 1956. Growth, size and reproduction in Daphnia (Crustacea: Cladocera). Proc. Zool. Soc. London 126: 173-204

Hanazato, T. and M. Yasuno. 1987. Experimental studies on competition between Bosmina longirostris and Bosmina fatalis. Hydrobiologia 154: 189-199

Hanspie, R. and P. Polk. 1974. Some observations on harpactacoid populations, in relationship to the competitive exclusion principle. Hydrobiologia 45: 423-429

Hanski, I. and E. Ranta. 1983. Coexistence in a patchy environment: three species of Daphnia in rock pools. J. Animal Ecol. 52: 263-279

Hardin 1960. The competitive exclusion principle. Science 131: 1292-1298

Harper, J.L. 1977. Population Biology of Plants. Academic Press, New York.

Hebert, P.D.N. 1974a. Enzyme variability in natural populations of Daphnia magna. II. Genotypic frequencies in permanent populations. Genetics 77: 323-334

_____. 1974b. Enzyme variability in natural populations of Daphnia magna. III. Genotypic frequencies in intermittent populations. Genetics 77: 335-341

_____. 1978. The population biology of Daphnia (Crustacea, Daphniidae). Biol. Rev. 53: 387-426

_____. 1982. Competition in zooplankton communities. Ann. Zool. Fennici 19: 349-356

_____. 1985. Ecology of the dominant copepod species at a low arctic site. Can. J. Zool. 63: 1138-1147

Hebert, P.D.N. and T.J. Crease. 1980. Clonal coexistence in Daphnia pulex (Leydig): another planktonic paradox. Science 207: 1363-1365

_____. 1983. Clonal diversity in populations of Daphnia pulex reproducing by obligate parthenogenesis. Heredity 51: 353-369

Hebert, P.D.N. and C. Emery. 1990. Adaptive significance of cuticular pigmentation in Daphnia pulex. Funct. Ecol. (in review)

Hebert, P.D.N. and B.J. Hann. 1986. Patterns in the composition of arctic tundra pond microcrustacean communities. Can. J. Fish. Aquat. Sci. 43: 1416-1425

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54: 187-211

Hutchinson, G.E. 1961. The paradox of the plankton. Am. Nat. 95: 137-145

Jacobs, J. 1978. Coexistence of similar zooplankton species by differential adaptation to reproduction and escape in an environment with fluctuating food and enemy densities. III. Laboratory experiments. Oecologia 35: 35-54

Jaenike, J. and R.K. Selander. 1985. On the coexistence of ecologically similar clones of parthenogenetic earthworms. Oikos 44: 512-514

Jaenike, J., E.D. Parker Jr. and R.K. Selander. 1980. Clonal niche structure in the parthenogenetic earthworm Octolasion tyrtaeum. Am. Nat. 116: 196-205

King, C.E. 1972. Adaptations of rotifers to seasonal variation. Ecology 53: 408-418

Korpalainen, H. 1986a. Ecological genetics of the cyclic parthenogens, Daphnia longispina and Daphnia pulex. Hereditas 105: 7-16

_____. 1986b. Competition among clones: an experimental study in a natural population of Daphnia magna. Hereditas 105: 29-35

Lampert, W. 1978. A field study on the dependence of the fecundity of Daphnia species on food concentration. Oecologia 36: 363-369

Loaring, J.M. 1982. The ecological genetics of Daphnia species. M.Sc. thesis, University of Windsor, Ontario.

Loaring, J.M. and P.D.N. Hebert. 1981. Ecological differences among clones of Daphnia pulex Leydig. Oecologia 51: 162-168

Lynch, M. 1984. Destabilizing hybridization, general-purpose genotypes and geographic parthenogenesis. Quart. Rev. Biol. 59: 257-290 .pa

Neill, W.E. 1975. Experimental studies of microcrustacean competition, community composition and efficiency of resource utilization. Ecology 56: 809-826

Ranta, E. 1979. Niche of Daphnia species in rock pools. Arch. Hydrobiol. 87: 205-223

Persson, L. 1985. Asymmetrical competition: are larger animals competitively superior? Am. Nat. 126: 261-266

Pianka, E.R. 1983. Evolutionary Ecology. Harper and Row, New York.

Schwartz, S.S. 1984. Life history strategies in Daphnia: a review and predictions. Oikos 42: 114-122

Seitz, A. 1980. The coexistence of three species of Daphnia in the Klostersee. I. Field studies on the dynamics of reproduction. Oecologia 45: 117-130

Sexton, O.J. 1979. Polyploidy in animal evolution. p.379-381 in W.H. Lewis (ed). Polyploidy: Biological Relevance. Plenum Press, New York.

Simberloff, D. 1983. Competition theory, hypothesis-testing, and other community ecological buzzwords. Am. Nat. 122: 626-635

Strong, D.R. Jr., D. Simberloff, L.G. Abele and A.B. Thistle. 1984. Ecological Communities: Conceptual Issues and the Evidence. Princeton University Press, Princeton NJ.

Snell, T.W. 1977. Clonal selection: competition among clones. Arch. Hydrobiol. 8: 202-204

_____. 1979. Intraspecific competition and population structure in rotifers. Ecology 60: 494-502

_____. 1980. Blue-green algae and selection in rotifer populations. Oecologia 46: 343-346

Suomalainen, E. 1959. On polyploidy in animals. Proc. Finn. Acad. Sci. 1958: 105-119

Tilman, D. 1987. The importance of the mechanisms of interspecific competition. Am. Nat. 129: 769-774

Tucic, B., S. Milojkovic, S. Vujcic and A. Tarasjev. 1988. Clonal diversity and dispersion in Iris pumila. Acta Oecologia 9: 211-219

Vanni, M.J. 1986. Competition in zooplanktor communities: suppression of small species by Daphnia pulex. Limnol. Oceanogr. 31: 1039-1056 .pa

Weider, L.J. 1985. Spatial and temporal genetic heterogeneity in a natural Daphnia population. J. Plankton Res. 7: 101-123

_____. 1987. Life history variation among low-arctic clones of obligately parthenogenetic Daphnia pulex: a diploid-polyploid complex. Oecologia 73: 251-256

Weider, L.J. and P.D.N. Hebert. 1987a. Ecological and physiological differentiation among low-arctic clones of Daphnia pulex. Ecology 68: 188-198

_____. 1987b. Microgeographic genetic heterogeneity of melanic Daphnia pulex at a low-arctic site. Heredity 58: 391-399

Weider, L.J. and W. Lampert. 1985. Differential response of Daphnia genotypes to oxygen stress: respiration rates, hemoglobin content and low-oxygen tolerance. Oecologia 65: 487-491

Wiens, J.A. 1977. On competition and variable environments. Am. Sci. 65: 590-597

Williams, G.C. 1975. Sex and evolution. Princeton University Press, Princeton NJ.

CHAPTER 5

IMPACT OF THE PREDATORY COPEPOD *DIAPTOMUS ARCTICUS* ON DOMINANT CLONES OF *DAPHNIA PULEX* AT CHURCHILL

INTRODUCTION

The importance of predation in aquatic systems has been recognized since Hrbacek (1962) and Brooks and Dodson (1965) demonstrated the impact of fish predation on the species composition of zooplankton communities (see reviews in Zaret 1980, Kerfoot and Sih 1986). Although both vertebrate and invertebrate predators can structure zooplankton communities, vertebrates are often absent from ponds. In this latter habitat invertebrates play a dominant role. Past studies have shown that calanoid copepods are important predators in arctic ponds (Anderson 1970, Dodson 1974a, Stross et al 1980). The predatory copepod Heterocope septentrionalis, for example, has been shown to be responsible for the checkerboard distribution of Daphnia middendorffiana and Daphnia pulex in low arctic ponds (Hebert and Loaring 1980, Haney and Buchanan 1987). D. pulex, the competitive dominant, is excluded from ponds containing Heterocope, as it is extremely susceptible to predation. D. middendorffiana, in contrast, is well protected from predation by its larger neonate size, possession of a longer tail spine, and a harder carapace than D. pulex (Hebert and Loaring 1980, Luecke and O'Brien 1983, Dodson 1984). Other studies have also demonstrated the selective impact of invertebrate predators on their prey (Dodson 1974a,b,1975, 1984, O'Brien and Schmidt 1979, Krueger and Dodson 1981, Havel 1987).

Despite the recognized importance of copepod

predation, no studies have yet examined the impact of predators on genotypic composition of single prey species. Although Kerfoot (1977a) documented the occurrence of different Bosmina genotypes in the presence and absence of the copepod Epischurus nevadensis, it was later shown (Manning et al 1978) that these genotypes represented different species. O'Brien and Schmidt (1979) observed that natural populations of B. longirostris occurring with and without H. septentrionalis showed differing morphologies and vulnerability to predation, but their studies may again have involved a species complex.

Manipulative field experiments examining predator-prey interactions similar to those of Neill (1981) and Elser and Carpenter (1988) have rarely been carried out in arctic ponds. Rather, field experiments have been conducted by confining predators and prey in enclosures and monitoring the results (Dodson 1974b,1975, Hebert and Loaring 1980, Luecke and O'Brien 1983). While these studies have clearly shown an impact on structure of prey communities, the selective arenas are artificial (O'Brien 1988). Whole-pond manipulations of natural habitats, by contrast, enable the study of predator-prey interactions under more natural conditions.

The calanoid species Hesperodiaptomus arcticus is a common member of northern zooplankton communities (Hebert 1985, Hebert and Hann 1986), and is often an important predator in ponds where it occurs (Anderson 1970, Stross et

al 1980, Good 1981, Hebert 1985). In contrast to its prey, H. arcticus produces only one generation per summer. Early stages of H. arcticus are filter feeders, while adults are predaceous (Anderson 1967, 1970).

The objectives of this study were to examine the role of Hesperodiaptomus arcticus in limiting the distributions of the three dominant unpigmented clones (1, 13 and 14) of D. pulex at Churchill. Prior distributional studies (chapter 2) have shown that clone 1 never co-occurs with H. arcticus, while clones 13 and 14 show negative and positive associations with the predator, respectively. The present analysis involved both laboratory comparisons of the susceptibility of each clone to predation and field manipulation experiments involving the two dominant clones which occur with the predator.

METHODS

Lab experiment:

Hesperodiaptomus arcticus were collected in August 1987 from Churchill ponds and shipped to Windsor for laboratory experiments to examine the differential susceptibility of the three dominant *D. pulex* clones to predation. Lab populations of *H. arcticus* were held at 4°C and fed *D. pulex* neonates twice weekly, as well as 50 mL of a diluted aquarium algal culture (mostly *Scenedesmus* and *Ankistrodesmus* spp.) every second day.

Ten adult females from each of the three clones were individually placed in 120 mL plastic cups with 60 mL of synthetic pond water (SPW) (Hebert and Crease 1982). Animals were fed 5 mL of a chemostat-grown culture of *Scenedesmus quadricauda* every second day. Food levels were standardized by adjusting optical densities to a value of 0.80 at 650 nm, using a Pye-Unicam spectrophotometer. Cups were examined daily for neonates, which were immediately removed and placed in 1.5 l holding jars for use in the predation study. Neonates in each holding jar were fed 50 mL of algae every other day.

Predation experiments were carried out on neonates (instar I) and instars II and III of the three dominant clones, with twenty replicates per treatment. In each treatment, 24 similar-aged juveniles of two clones were placed in a 120 mL plastic cup filled with 100 mL of SPW at

room temperature, along with an adult H. arcticus which had been starved for 24 hours at room temperature prior to initiation of the experiment. Animals in cups were not given any algal suspension, to ensure maximal predation rates (Anderson 1970). Control cups were set up for each treatment, with all conditions duplicated, but with the absence of a predator. Each predation cup was visually monitored every eight hours until the number of Daphnia in each cup approached one-half of the initial total, which usually occurred after 24 hours. Thereafter, cups were checked hourly until 50% Daphnia mortality had occurred. The predator was then removed from the cup and clonal composition of the remaining Daphnia juveniles determined electrophoretically, using standard protocols (Hebert and Beaton 1989). Student's t-tests for differences between two means with equal variances (Sokal and Rohlf 1981) were carried out on age-specific mean clonal survivorship frequencies within predation treatments, using the SYSTAT computer package (Wilkinson 1989).

Field experiments:

Densities of H. arcticus were manipulated in 6 ponds to test the effect of this species on the composition of ponds dominated by D. pulex clones 13 and 14 on Bluff C. Ponds were selected and prepared using the same manipulation protocol described in Chapter 4. The experiment was initiated in mid-July of 1988 and ran until

August 30. It was assumed that predation could have a significant influence on clonal composition of the ponds during the initial stages of the experiment, when prey populations were still small. Introduced numbers of reproductive D. pulex adults were therefore scaled to produce an approximate initial density of 5 neonates per clone per litre. As sampling of undisturbed ponds showed H. arcticus densities ranging from 0.2 to 4.1 copepods per litre, the predator was introduced at densities of 1 animal per litre.

In addition to the predation experimental ponds, three control ponds were established where clones 13 and 14 were introduced together in the absence of H. arcticus. The sham introduction and empty controls described in chapter 4 were considered to be valid controls for this experiment also.

Samples were collected from the ponds as described in Chapter 3, with special care taken to return any copepods collected to the ponds immediately. Laboratory determination of reproductive status and clonal identities were performed as described in chapters 3 and 4, as were analyses of clonal frequencies and their relative fitnesses.

RESULTS

Laboratory experiments

Predation trials showed strong differences in vulnerability to the predator between clones (Figure 1). For instars I to III, clone 14 consistently exhibited lower mortality than clones 1 and 13. Differences in mortality between 14 and the other clones were significant for all three instars (instar I: $P < 0.05$; instars II and III: $P < 0.001$), but were most pronounced between 3rd instar juveniles. Clones 1 and 13 exhibited similar susceptibilities to predation by H. arcticus for all three instars. Control cups had negligible mortality, and nonsignificant clonal frequency differences at the end of 36 hours.

Field experiments

Shifts in clonal frequencies in the manipulation ponds were rapid. In ponds containing H. arcticus (Figure 2a), the frequency of clone 13 decreased dramatically, and the clone was nearly eliminated by the end of the season. By contrast, in the control ponds the pattern was reversed, with clone 13 dominating and clone 14 being displaced (Figure 2b).

Reproductive status

Reproductive status of clones 13 and 14 in the

Figure 5-1: Proportional survivorship (± 1 SE) of juveniles of clones 1, 13 and 14 following exposure to Hesperodiaptomus arcticus for instars I, II, and III.

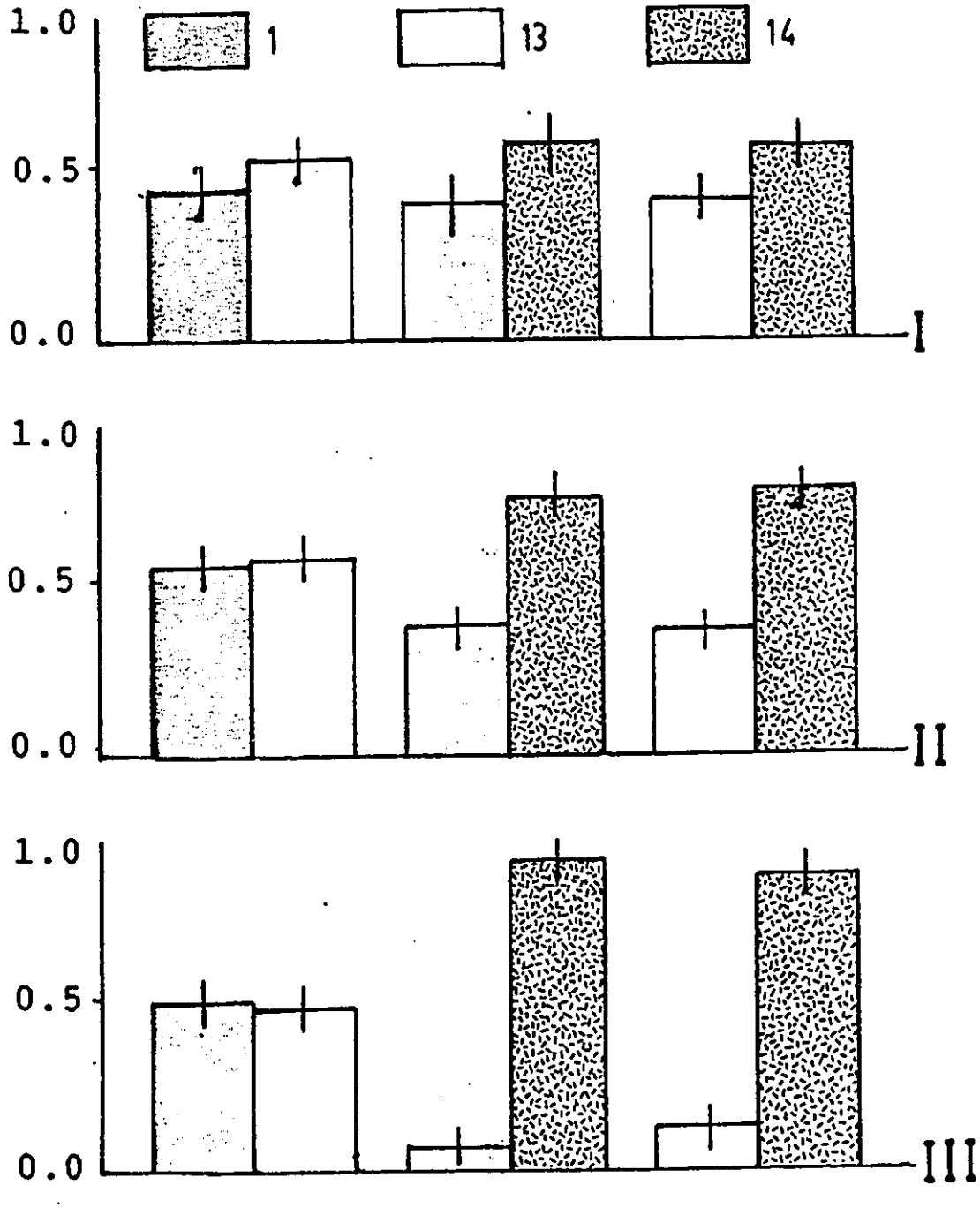
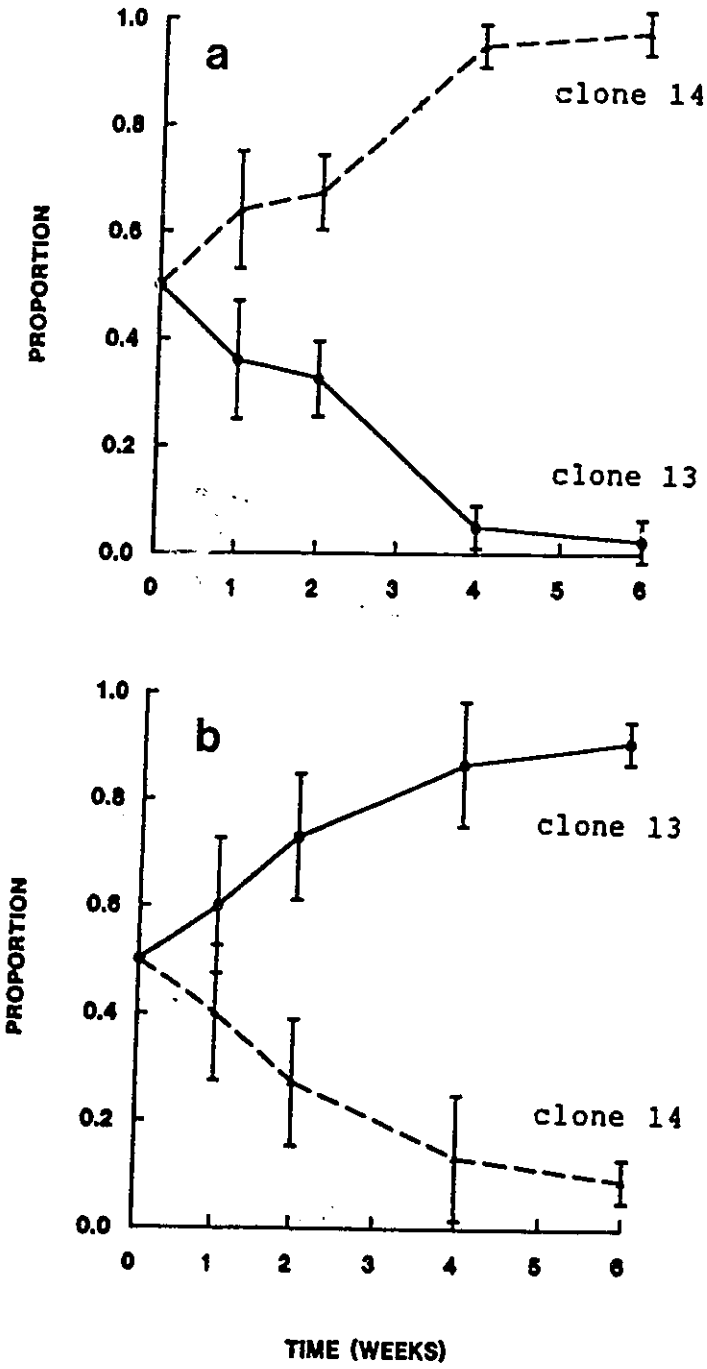


Figure 5-2: Shifts in frequency of clones 13 and 14 over time in experimental ponds with and without the predatory copepod H. arcticus in 1988. (a) ponds with H. arcticus; (b) control ponds (no predators). Vertical bars represent standard errors of pooled data.



manipulation ponds are summarized in Table 1. Relative frequencies of the different reproductive phenotypes varied between clones and sampling periods. Differences in the proportions of parthenogenetic females in the ponds were only detected in late July (Table 2), in part due to the rarity of one clone in each pond in later intervals. The interclonal differences in reproductive ratios were consistent, with clone 13 having a greater proportion of parthenogenetic females in all cases where a significant difference was detected. Brood sizes of the clones showed the converse pattern (Table 3), with clone 13 producing smaller broods than clone 14 in 4 of the 5 cases where significant differences were observed.

Table 4 shows the egg-ratio fecundities of the two clones (DeMott 1980) and the predicted and observed shifts in frequency. Fecundity data suggested 5 cases in which clone 13 should increase in abundance in predation ponds, but in all 5 cases the clone's abundance decreased. By contrast, in control ponds clone 13 had higher fecundities in all 6 samples, and showed an increased frequency in 5 of these cases.

Table 5-1: Reproductive status of clones 13 and 14 in predation and control ponds, showing absolute numbers of each clone and proportional representation of each reproductive class at each sampling interval.

time		July 30				August 14				August 28			
Pond	Clone	n	NR	E	P	n	NR	E	P	n	NR	E	P
(a) with *H. arcticus*													
C44a	13	27	.44	.52	.04	8	.75	.25	.	4	.75	.25	.
	14	69	.38	.51	.12	88	.81	.13	.07	92	.65	.32	.03
C45b	13	35	.34	.43	.23	2	1.00	.	.	.	.	.	.
	14	61	.43	.49	.08	94	.49	.38	.13	96	.97	.03	.
C48	13	21	.67	.	.33	.	.	.	.	.	.	.	.
	14	75	.37	.49	.13	96	.34	.32	.33	96	.75	.24	.01
C64a	13	31	.29	.13	.58	10	.70	.20	.10	9	.77	.22	.
	14	65	.48	.32	.20	86	.85	.08	.07	87	.70	.28	.02
C159	13	34	.53	.32	.15	5	.20	.60	.20	.	.	.	.
	14	62	.68	.26	.06	91	.79	.14	.07	96	.57	.43	.
C161	13	40	.68	.10	.23	4	.75	.25	.	.	.	.	.
	14	56	.55	.21	.23	92	.79	.21	.	96	.26	.70	.04
(b) without *H. arcticus* (control ponds)													
C45a	13	78	.27	.09	.64	86	.77	.17	.06	90	.70	.18	.12
	14	18	.61	.17	.22	10	.60	.40	.	6	1.00	.	.
C64	13	57	.63	.25	.12	71	.89	.08	.03	89	.65	.26	.09
	14	39	.41	.54	.05	25	.68	.32	.	7	.86	.14	.
C160	13	75	.48	.16	.36	93	.61	.23	.16	83	.49	.39	.12
	14	21	.62	.05	.33	3	1.00	.	.	13	.46	.38	.15

Table 5-2: Multiple G-tests of frequencies of parthenogenetic females of clones 13 and 14 in predation and control ponds.

time		July 30	August 14	August 28
Pond	Clone	G	G	G
(a) with *H. arcticus*				
C44a	13 14	1.68	1.08	0.26
C45b	13 14	3.92*	....	....
C48	13 14	4.02*	....	....
C64a	13 14	13.56***	0.11	0.40
C159	13 14	1.68	0.91	....
C161	13 14	0.01	....	....
(b) without *H. arcticus* (controls)				
C45a	13 14	10.67**	1.13	1.51
C64	13 14	1.50	1.22	1.27
C160	13 14	0.05	1.04	0.11

*** $p < 0.001$
** $p < 0.01$
* $p < 0.05$

Table 5-3: Comparison of mean brood size between clones in predation and control ponds for all cases where both clones showed parthenogenetic reproduction, using t-test for two samples with unequal sample sizes and variances.

time		July 30			August 14			August 28		
Pond	Clone	$\bar{x}$	S.E.	t	$\bar{x}$	S.E.	t	$\bar{x}$	S.E.	t
(a) with *H. arcticus*										
C44a	13	4.00	....	0.42	....	....		....	....	
	14	6.25	2.24		6.00	2.09		5.67	1.75	
C45b	13	3.00	0.93	4.06**	....	....		....	....	
	14	5.60	1.40		4.83	2.52		....	....	
C48	13	4.14	1.48	6.09***	....	....		....	....	
	14	7.10	1.37		8.16	2.81		5.00	....	
C64a	13	4.83	1.62	2.66*	3.00	....	0.75	....	....	
	14	6.38	2.63		4.33	1.28		3.50	0.71	
C159	13	4.20	1.78	0.90	4.00	....	1.75	....	....	
	14	5.00	1.63		8.83	1.60		....	....	
C161	13	7.11	1.36	2.16*	....	....		....	....	
	14	8.00	1.76		....	....		7.00	1.63	
(b) without *H. arcticus* (controls)										
C45a	13	6.76	3.06	0.10	5.48	1.41		5.45	2.34	
	14	7.00	1.63		....	....		....	....	
C64	13	3.00	1.24	1.06	2.50	0.71		8.75	3.77	
	14	4.00	1.00		....	....		....	....	
C160	13	5.15	1.52	2.32*	4.31	1.93		4.80	1.64	0.12
	14	4.29	1.70		....	....		5.00	....	

*** $p < 0.001$
** $p < 0.01$
* $p < 0.05$

Table 5-4: Comparison of short-term reproductive efforts and significant differences between clones 13 and 14 in predation and control ponds in 1988, using DeMott's (1980) egg-ratio (E) method. Dates where no parthenogenetic females were observed for a clone are indicated by (....). Blank lines (----) indicate that the clone specified was not detected.

time		July 30				August 14			
Pond	Clone	E	S.E.	e	o	E	S.E.	e	o
(a) with *H. arcticus*									
C44a	13	0.16	0.02	-	-	....		ns	-
	14	0.75	0.07	+	+	0.42	0.03	ns	+
C45b	13	0.69	0.05	+	-	....		ns	-
	14	0.45	0.04	-	+	0.63	0.04	ns	+
C48	13	1.37	0.21	+	-	----			
	14	0.92	0.08	-	+	2.69	0.18		
C64a	13	2.80	0.23	+	-	0.30	0.08	ns	-
	14	1.28	0.12	-	+	0.30	0.02	ns	+
C159	13	0.63	0.08	+	-	0.80	0.51	+	-
	14	0.30	0.03	-	+	0.62	0.06	-	+
C161	13	1.64	0.23	ns	-	....			
	14	1.84	0.22	ns	+	....			
(b) without *H. arcticus* (controls)									
C45a	13	4.33	0.21	+	+	0.33	0.02	ns	+
	14	1.54	0.50	-	-	....		ns	-
C64	13	0.36	0.02	+	+	0.08	0.00	ns	+
	14	0.20	0.02	-	-	....		ns	-
C160	13	1.85	0.09	+	+	0.69	0.03	ns	-
	14	1.42	0.24	-	-	....		ns	+

DISCUSSION

Field surveys suggested that H. arcticus had a significant effect on distributions of the dominant clones. Thus, clone 1 never co-occurred with the predator, and clone 13 had a negative association coefficient with it. By contrast, clone 14 showed a positive coefficient of association with the predator. Wilson and Hebert (1990) have shown these distributional associations were both significant and stable across years.

Clone 14's ability to coexist with the predator was supported by the results of the field experiments. The rapid elimination of clone 13 from the predation ponds showed the susceptibility of this clone to predation by H. arcticus. Clone 14's displacement from the control ponds, by contrast, suggested that it was a poor competitor. Such a tradeoff between defensive and competitive ability has been observed in a number of zooplankton species (Kerfoot 1977b, Dodson 1984, Havel and Dodson 1987).

The ability of a prey organism to coexist with a predator is often associated with lower fecundity in comparison with its more vulnerable relatives. Kerfoot (1977b), for example, observed that predator-resistant Bosmina genotypes produced small numbers of large eggs, while vulnerable Bosmina produced larger broods of small eggs, thereby boosting their fecundity in the absence of predators. Similarly, strains of Daphnia middendorffiana resistant to predation by Heterocope septentrionalis have

smaller broods of larger eggs than unprotected clones (Hebert and Loaring 1980) of D. pulex (Dodson 1984). By contrast, in the present situation the predator-resistant clone (14) produced more eggs than did clone 13. The smaller mean brood sizes produced by clone 13 are likely due to the clone's status as a tetraploid. The present study has shown that despite its smaller brood size, clone 13 often has a higher fecundity than clone 14 because of its higher reproductive ratio.

The modest fecundity advantage of clone 13, however, nay not be the sole basis for its competitive superiority over clone 14. Havel and Dodson (1987) found that individuals of a D. pulex clone with defensive structures induced by exposure to Chaoborus larvae had similar fecundity as those of noninduced individuals, but that juveniles had longer maturation times, significantly reducing their intrinsic rate of increase (r_m). This decrease in r_m in predator-resistant morphs despite similar clutch size was also seen by Mort and Kerfoot (1988), who observed that egg development took 30% longer in protected versus unprotected morphs of Ceriodaphnia cornuta. Intrinsic rates of clonal increase were not measured in the present study, but could easily be obtained from life history studies of the Churchill clones.

Differences in parthenogenetic reproduction of clones 13 and 14 in the ponds consistently failed to predict shifts in clonal frequency in the predation ponds, but

provided a good indication of the direction of clonal frequency shifts in the control ponds. As H. arcticus feeds on juvenile Daphnia (Anderson 1970), the predator's impact would be greatest among early instars of D. pulex and have a strong effect on clonal recruitment.

The differential susceptibility of early instars of D. pulex to predation was demonstrated for clones 1, 13 and 14 in the laboratory experiments. Differences in clonal survivorship were smallest for instar I, but were very pronounced by instars II and III. The mechanism by which clone 14 is able to defend itself from H. arcticus was not determined. Although morphological defenses such as body spikes or tail spines are common (Zaret 1980) and have been widely observed among arctic prey species (Dodson 1984, O'Brien and Schmidt 1979, Hebert and Loaring 1980), differences in tail spine length between juveniles of clone 13 and 14 failed to explain the relative susceptibilities of the clones (Wilson and Hebert 1990).

The greater susceptibility of clone 13 is even more puzzling when one recognizes that the clone is a tetraploid (Beaton and Hebert 1988), as polyploids typically have larger offspring and larger adult body sizes (Sexton 1979). Differences in life history characters have already been shown among melanic and unpigmented D. pulex clones differing in ploidy level (Weider 1987), with unpigmented diploids producing smaller offspring and maturing at smaller sizes. Indeed, juvenile instars of

clone 13 are consistenty larger than those of clone 14 (Wilson and Hebert 1990). On the basis of neonate and adult body size, one would therefore expect clone 13 to be less susceptible to copepod predation than clone 14, yet the reverse was true. Field results may perhaps be partially a result of the longer generation time of polyploids with respect to their diploid relatives (Sexton 1979, Weider 1987). With survivorship linked to growth rates among size-selected prey, the greater duration an individual must spend in the "predation window", the poorer its chances of survival (Zaret 1980).

In summary, Hesperodiaptomus arcticus has an important impact on clonal composition of Daphnia pulex populations. Natural distributions and both laboratory and field experiments showed large differences in susceptibility among the dominant unpigmented Daphnia pulex clones to this predator. It may be conclusively stated, therefore, that invertebrate predation has a significant effect on clonal distributions in the rock bluffs ponds.

LITERATURE CITED:

Anderson, R.S. 1967. Diaptomid copepods from two mountain ponds in Alberta. Can. J. Zool. 45: 1043-1047

_____. 1970. Predator-prey relationships and predation rates for crustacean zooplankters from some lakes in western Canada. Can. J. Zool. 48: 1229-1240

Beaton, M.J. and P.D.N. Hebert. 1988. Geographic parthenogenesis and polyploidy in Daphnia pulex. Amer. Nat. 132: 837-845

Boileau, M.G. 1989. Biochemical genetic variation in the freshwater Copepoda: evolutionary consequences of passive dispersal in freshwater zooplankton. Ph.D. dissertation, University of Windsor, Ontario.

Brooks, J.L. and S.I. Dodson. 1965. Predation, body size, and composition of plankton. Science 150: 28-35

Dodson, S.I. 1974a. Zooplankton competition and predation: an experimental test of the size-efficiency hypothesis. Ecology 55: 605-613

_____. 1974b. Adaptive change in plankton morphology in response to size-selective predation: a new hypothesis of cyclomorphosis. Limnol. Oceanogr. 19: 721-729

_____. 1975. Predation rates of zooplankton in arctic ponds. Limnol. Oceanogr. 20: 426-433

_____. 1984. Predation of Heterocope septentrionalis on two species of Daphnia: morphological defenses and their costs. Ecology 65: 1249-1257

Elser, J.J. and S.R. Carpenter. 1988. Predation-driven dynamics of zooplankton and phytoplankton communities in a whole-lake experiment. Oecologia 76: 148-154

Good, A.G. 1981. The ecology and biogeography of tundra zooplankton communities in the Churchill, Manitoba area. M.Sc. thesis, University of Windsor, Ontario.

Haney, J.F. and C. Buchanan. 1987. Distribution and biogeography of Daphnia in the Arctic. p.77-105 in Peters, R.H. and R. de Bernardi (eds.). Daphnia. Mem. Inst. Ital. Idrobiol. 45.

Havel, J. 1987. Predator-induced defenses: a review. p.263-278 in Kerfoot, W.C. and A. Sih (eds.). Predation: Direct and Indirect Impacts on Aquatic Communities. University Press of New England, Hanover.

Havel, J. and S.I. Dodson. 1987. Reproductive costs of Chaoborus-induced polymorphism in Daphnia pulex. Hydrobiologia 150: 273-281

Hebert, P.D.N. 1985. Ecology of the dominant copepod species at a low arctic site. Can. J. Zool. 63: 1138-1147

Hebert, P.D.N. and M.J. Beaton. 1989. Methodologies for allozyme analysis using cellulose acetate electrophoresis. Helena Laboratories, Beaumont,TX.

Hebert, P.D.N. and T.J. Crease. 1980. Clonal coexistence in Daphnia pulex (Leydig): another planktonic paradox. Science 207: 1363-1365

Hebert, P.D.N. and B.J. Hann. 1986. Patterns in the composition of arctic tundra pond microcrustacean communities. Can. J. Fish. Aquat. Sci. 43: 1416-1425

Hebert, P.D.N. and J.M. Loaring. 1980. Selective predation and the species composition of arctic ponds. Can. J. Zool. 58: 422-426

Hrbacek, J. 1962. Species composition and the amount of zooplankton in relation to the fish stock. Rozpr. Cesk. Akad. Ved., ser. mat. nat. sci. 72: 1-117

Kerfoot, W.C. 1977a. Implications of copepod predation. Limnol. Oceanogr. 22: 316-325

_____. 1977b. Competition in cladoceran communities: the cost of evolving defenses against copepod predation. Ecology 58: 303-313

Kerfoot, W.C. and A. Sih (eds). 1986. Predation: Direct and Indirect Impacts on Aquatic Communities. University Press of New England.

Krueger,D.A. and S.I. Dodson. 1981. Embryological induction and predation ecology in Daphnia pulex. Limnol. Oceanogr. 26: 219-223

Luecke, C. and W.J. O'Brien. 1983. The effect of Heterocope predation on zooplankton communities in arctic ponds. Limnol. Oceanogr. 28: 367-377

Manning, B.J., W.C. Kerfoot and E.M. Berger. 1978. Phenotypes and genotypes in cladoceran populations. Evolution 32: 365-374

Mort, M.A. and W.C. Kerfoot. 1988. Tropical zooplankton: phenotypic and spatial analyses of polymorphic Ceriodaphnia cornuta (Crustacea: Cladocera). Freshwater Biol. 19: 29-39

Neill, W.E. 1981. Impact of Chaoborus predation upon the structure and dynamics of a crustacean zooplankton community. Oecologia 48: 164-177

O'Brien, W.J. 1988. The effect of container size on the feeding rate of Heterocope septentrionalis, a freshwater predaceous copepod. J. Plankton Res. 10: 313-317

O'Brien, W.J. and D. Schmidt. 1979. Arctic Bosmina morphology and copepod predation. Limnol. Oceanogr. 24: 564-568

O'Brien, W.J., D. Kettle and H. Riessen. 1979. Helmets and invisible armor: structures reducing predation from tactile and visual planktivores. Ecology 60: 287-294

Reed, E.B. 1963. Records of freshwater Crustacea from arctic and subarctic Canada. Nat. Mus. Can. Bull. 199: 26-62

Sexton, O.J. 1979. Polyploidy in animal evolution. p.379-381 in Lewis, W.H. (ed). Polyploidy: Biological Relevance. Plenum Press, New York.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. 2nd edition. W.H.Freeman and Co., New York.

Stross, R.G., M.C. Miller and R.J. Daley. 1980. Zooplankton. p.251-296 in Hobbie, J.E.(ed). Limnology of Tundra Ponds. US/IBP Series, Vol. 13. Dowden, Hutchinson, and Ross, Inc., Stroudsburg, PA.

Weider, L.W. 1987. Life history variation among low-arctic clones of obligately parthenogenetic Daphnia pulex: a diploid-polyploid complex. Oecologia 73: 251-256

Weider, L.W. and P.D.N. Hebert. 1987. Ecological and physiological differentiation among low-arctic clones of Daphnia pulex. Ecology 68: 188-198

Wilkinson, L. 1988. SYSTAT: The System for Statistics. SYSTAT Inc., Evanston, IL.

Wilson, C.C. and P.D.N. Hebert. 1990. Impact of predation on distribution patterns of Daphnia pulex clones. Limnol. Oceanogr. (in review).

Zaret,T.M. 1980. Predation and freshwater communities. Yale University Press, London.

CHAPTER 6

SYNTHESIS OF COMMUNITY STRUCTURE IN A LOW-ARCTIC CLONAL COMPLEX

The results presented in the previous chapters have shown that a number of factors and processes significantly influence the distributions and abundances of unpigmented Daphnia pulex clones in bluff ponds near Churchill. The study utilized all three types of ecological experiments described by Diamond (1986). Passive studies involved mapping the distributions of clones in the ponds, and examining correlations with environmental variables. The large number of ponds provided opportunities for manipulative field experiments, and laboratory experiments were subsequently employed to confirm the influence of selective factors observed in the field.

Surveys of D. pulex populations on two rock bluffs in 1985 and 1989 revealed an assemblage of 36 clones (chapter 2). Clones 1, 13 and 14 were dominant, both numerically and in number of ponds occupied. The pattern of clonal abundances observed, with a few superabundant clones and many rare clones, was consistent with results obtained from other studies on asexual taxa (Jaenike et al. 1980, Hebert and Crease 1983, Sebens and Thorne 1985).

Clonal distributions appeared to be near equilibrium, as evidenced by the occupancy of virtually all suitable habitats, and by the stability of clonal composition of ponds across a five year interval. The study met all the criteria suggested by Connell and Sousa (1983) as necessary to determine the stability of populations and communities, although the question may still be asked as to whether the

observed clonal abundances and distributions mask yearly shifts in these patterns.

Results in chapter 2 showed the influence of abiotic variables on clonal distributions. These results disagreed with Lynch's (1984) general-purpose genotype hypothesis of parthenogenetic organisms, and more closely resembled Harshman and Futuyma's (1985) hypothesis that clonal assemblages are composed of a number of clones adapted to specific habitats. Indeed, the stability of clonal compositions in specific ponds is linked to the consistency of abiotic and biotic characteristics of the ponds.

Despite the general stability of clonal composition of ponds, clonal frequencies were not static. Significant shifts in clone frequencies occurred both between and within single seasons. Studies of multiclonal ponds, discussed in chapter 3, suggested that several different factors were responsible for the maintenance of diversity in polyclonal populations, including dispersal among ponds and the production of diapause eggs by lower-fitness clones before their competitive displacement. In addition, several ponds displayed temporal successions of clones, similar to results obtained by DeMott (1983) and Carvalho and Crisp (1987). The premature disappearance of D. pulex from some multiclonal ponds also suggested that some habitats are suboptimal so that no one clone is able to become dominant.

Chapter 4 demonstrated the importance of competition

in determining clonal composition of ponds and showed that clones were generally competitive dominants in their native ponds. The competitive superiority of clone 13 in home habitats of clone 14 indicated that some factor other than competition was responsible for clone 14's abundance. Distributional data in chapter 2 indicated that clone 14's distribution was strongly correlated with that of the predatory copepod Hesperodiaptomus arcticus. Chapter 5 described both laboratory and field experiments used to assess the impact of this copepod on the dominant D. pulex clones. Laboratory trials showed that juveniles of clones 1 and 13 were more susceptible to predation than clone 14, and the importance of predation was further confirmed by field experiments. In the presence of H. arcticus, clone 14 displaced clone 13, reversing the outcome from interclonal competition.

The nested effects of these different factors indicate that the selective framework operating in the pond system is similar to that suggested by Connell (1975) and Hall et al. (1976). The incidence of competition and predation is primarily determined by environmental patterns and historical effects such as dispersal. Both biotic factors operate within this framework, with predation on occasion masking competitive interactions among the clones. Tradeoffs in effectiveness of clonal adaptive strategies for competitive ability and resistance to predation (Allan 1974) were also demonstrated by clones 13 and 14.

The unpigmented Churchill clones clearly showed a range of adaptive strategies. The rarity of many clones may be due to their having lower fitnesses, or being adapted to less abundant habitat types. Although not tested in this study, adaptation to a specific habitat may cause organisms to become rare if that habitat type becomes uncommon (Kolasa 1989).

A number of questions remain unanswered. Why does clone 1 dominate ponds on bluff A so strongly, if the remaining clones on this bluff are also adapted to high salinity? What is the impact of ploidy level variation among the clones, and what enables a tetraploid clone to outcompete conspecific diploids? The study was also unable to determine the mechanism(s) responsible for competitive exclusion among the clones. Answers to these questions might be provided by life history studies of the clones. In addition, although the influence of copepod predation on clonal distributions was clearly shown, the effects of the flatworm Mesostoma lingua on the Daphnia clones has not yet been determined.

In conclusion, the study has clearly demonstrated the importance of abiotic habitat characteristics, as well as competition and predation, on clonal distributions in the bluff ponds. The study has also shown the utility of using clonal assemblages as analogous model systems for studies of community structure in multispecies communities.

LITERATURE CITED

Allan, J.D. 1974. Balancing predation and competition in cladocerans. Ecology 55: 622-629

Carvalho, G.R. and D.J. Crisp. 1987. The clonal ecology of Daphnia magna (Crustacea: Cladocera). I. Temporal changes in the clonal structure of a natural population. J. Animal Ecol. 56: 453-468

Connell, J.H. 1975. Some mechanisms producing structure in natural communities. p. 460-490 in Cody, M.L. and J.M. Diamond (eds). Ecology and Evolution of Communities. Harvard University Press, Cambridge.

Connell, J.H. and W.P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. Am. Nat. 121: 789-824

DeMott, W.R. 1983. Seasonal succession in a natural Daphnia assemblage. Ecol. Monogr. 53: 321-340

Diamond, J.M. 1986. Overview: laboratory experiments, field experiments, and natural experiments. p. 3-22 in Diamond, J. and T.J. Case (eds). Community Ecology. Harper and Row, New York.

Hall, D.J., S.T. Threlkeld, C.W. Burns and P.H. Crowley. 1976. The size-efficiency hypothesis and the size structure of zooplankton communities. Ann. Rev. Ecol. Syst. 7: 177-208

Harshman, L.G. and D.J. Futuyma. 1985. The origin and distribution of clonal diversity in Alsophila pometaria (Lepidoptera: Geometridae). Evolution 39: 315-324

Hebert, P.D.N. and T.J. Crease. 1983. Clonal diversity in populations of Daphnia pulex reproducing by obligate parthenogenesis. Heredity 51: 353-369

Jaenike, J., E.D. Parker Jr. and R.K. Selander. 1980. Clonal niche structure in the parthenogenetic earthworm Octolasion tyrtaeum. Am. Nat. 116: 196-205

Kolasa, J. 1989. Ecological systefms in hierarchical perspective: breaks in community structure and other consequences. Ecology 70: 36-47

Lynch, M. 1984. Destabilizing hybridization, general-purpose genotypes, and geographic parthenogenesis. Quart. Rev. Biol. 59: 257-289

Sebens, K.P. and B.L. Thorne. 1985. Coexistence of clones, clonal diversity, and the effects of disturbance. p. 357-398 in Jackson, J.B.C., L.W. Buss and R.E. Cook (eds). Population Biology and Evolution of Clonal Organisms. Yale University Press, London.

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? J. Animal Ecol. 46: 337-365

Stross, R.G. and D.A. Kangas. 1969. The reproductive cycle of Daphnia in an arctic pool. Ecology 50: 457-460

Threlkeld, S.T. 1987. Daphnia population fluctuations: patterns and mechanisms. p. 367-388 in Peters, R.H. and R. De Bernardi (eds). Daphnia. Mem. Ist. Ital. Idrobiol. 45, Pallanza.

Appendix 1: Multilocus genotypic identities of unpigmented Churchill *Daphnia pulex* clones. Asterisk at the AMY-2 locus for clone 15 indicates the clone has an unbalanced phenotype (1225) at this locus. Locus marked with -- indicates null activity. Loci where clonal genotypes were not determined are indicated by (.).

Clone	ACP	AO	APK	AMY-1	AMY-2	AMY-3	EST-1	EST-2	FUM
1	12	22	11	22	13	22	11	11	22
2	.	11	.	44	.	.	.	.	.
3	12	11	11	13	13	22	11	11	11
4	.	33	.	23	.	.	.	.	.
5	.	22	.	--	.	.	.	.	.
6	12	22	11	22	13	22	11	11	22
7	12	22	11	23	13	22	11	11	12
8	12	22	11	12	13	22	11	11	22
9	12	23	11	44	13	22	11	11	22
10	.	33	.	23	13	22	.	.	.
11	12	22	11	23	13	22	11	11	22
12	.	22	.	22	.	.	.	.	.
13	12	11	12	44	12	12	11	11	22
14	12	22	11	23	13	22	11	11	22
15	12	22	12	13	12*5	22	11	11	22
16	12	22	11	33	13	12	11	11	22
17	12	22	11	33	14	22	11	11	22
18	.	22	.	23	.	.	.	.	.
19	12	22	11	22	12	22	11	11	22
20	.	11	.	22	.	.	.	.	.
21	12	22	11	22	33	12	11	11	22
22	.	22	.	22	.	.	.	.	.
23	.	22	.	23	.	.	11	11	22
24	22	23	11	12	13	11	11	11	22
25	12	22	11	22	14	22	11	11	22
26	11	11	12	44	13	22	11	11	22
27	.	11	.	14	.	.	.	.	.
28	--	22	11	23	13	22	11	11	22
29	.	33	.	13	.	.	.	.	.
30	.	22	.	44	.	.	.	.	.
31	.	22	.	13	.	.	.	.	.
32	.	33	.	22	.	.	.	.	.
33	.	33	.	23	.	.	.	.	.
34	.	33	.	22	.	.	.	.	.
35	.	22	.	23	.	.	.	.	.
36	.	22	.	34	.	.	.	.	.

Appendix 1 (cont.)

Clone	G6PDH	G3PDH	GOT	HEX	IDH	LDH	ME	MDH-1
1	11	11	23	11	11	11	11	11
2	.	.	23	.	.	11	.	.
3	11	11	23	11	11	13	11	11
4	.	.	22	.	.	11	.	.
5	.	.	23	.	.	11	.	.
6	11	11	24	11	11	11	11	11
7	11	11	23	11	11	11	11	11
8	11	11	23	11	11	11	11	11
9	11	11	23	11	11	13	11	11
10	.	.	23	.	.	11	.	.
11	11	11	22	11	11	11	11	11
12	.	.	23	.	.	11	.	.
13	11	11	22	11	11	11	11	11
14	11	11	22	11	11	13	11	11
15	11	11	22	11	11	13	11	11
16	11	11	23	11	11	13	11	11
17	11	11	23	11	11	11	11	11
18	.	.	22	.	.	13	.	.
19	11	11	23	11	11	13	11	11
20	.	.	23	.	.	11	.	.
21	11	11	33	11	11	13	11	11
22	.	.	22	.	.	13	.	.
23	11	11	23	11	11	13	11	11
24	11	11	23	11	11	13	11	11
25	11	11	23	11	11	11	11	11
26	11	11	02	11	11	11	11	11
27	.	.	22	.	.	11	.	.
28	11	11	23	11	11	11	11	11
29	.	.	22	.	.	13	.	.
30	.	.	23	.	.	11	.	.
31	.	.	23	.	.	13	.	.
32	.	.	22	.	.	11	.	.
33	.	.	23	.	.	13	.	.
34	.	.	33	.	.	13	.	.
35	.	.	23	.	.	11	.	.
36	.	.	23	.	.	13	.	.

Appendix 1 (cont.)

Clone	MDH-2	MPI	PEP-1	PEP-2	PGM	PGI	TPI	XDH
1	11	11	11	11	22	14	11	11
2	.	.	.	.	22	44	.	.
3	11	11	11	11	22	44	11	11
4	.	.	.	.	22	14	.	.
5	.	.	.	.	22	14	.	.
6	11	22	11	11	22	14	11	11
7	11	22	11	11	22	44	11	11
8	11	22	11	11	22	14	11	11
9	11	11	11	11	22	44	11	11
10	.	.	.	.	22	11	.	.
11	11	11	11	11	02	44	11	11
12	.	.	.	.	22	04	.	.
13	11	11	11	11	22	44	11	11
14	11	22	11	11	01	14	11	11
15	11	11	11	11	12	45	12	11
16	11	11	11	11	22	44	11	11
17	11	11	11	11	02	44	11	11
18	.	.	.	.	12	14	.	.
19	11	11	11	11	22	44	11	11
20	.	.	.	.	22	44	.	.
21	11	11	11	11	22	14	11	11
22	.	.	.	.	12	45	.	.
23	11	01	.	.	22	44	.	.
24	11	11	11	11	22	44	12	11
25	11	22	11	11	22	44	11	11
26	11	22	11	11	22	44	11	11
27	.	.	.	.	22	44	.	.
28	11	22	11	11	12	44	12	11
29	.	.	.	.	23	44	.	.
30	.	.	.	.	22	44	.	.
31	.	.	.	.	22	44	.	.
32	.	.	.	.	22	14	.	.
33	.	.	.	.	22	11	.	.
34	.	.	.	.	22	14	.	.
35	.	.	.	.	22	14	.	.
36	.	.	.	.	22	44	.	.

Appendix 2: Matrix of Nei's unbiased genetic distance and identity estimates among unpigmented Churchill *Daphnia pulex* clones. Above diagonal = genetic identity; below diagonal = genetic distance.

	Clone							
Clone	1	2	3	4	5	6	7	8
1	****	.576	.535	.707	.809	.960	.910	.962
2	.551	****	.813	.576	.576	.528	.673	.610
3	.626	.207	****	.588	.535	.481	.695	.622
4	.346	.551	.531	****	.606	.707	.707	.695
5	.213	.551	.626	.500	****	.758	.809	.855
6	.041	.638	.732	.346	.277	****	.859	.909
7	.095	.397	.364	.346	.213	.152	****	.909
8	.039	.495	.475	.364	.156	.096	.096	****
9	.444	.207	.388	.444	.444	.531	.290	.388
10	.346	.733	.732	.095	.500	.420	.500	.364
11	.213	.551	.531	.346	.346	.213	.095	.221
12	.041	.551	.626	.420	.277	.095	.095	.096
13	.597	.041	.253	.443	.597	.597	.443	.540
14	.381	1.124	.863	.563	.563	.381	.381	.411
15	.668	1.124	.730	.786	.668	.668	.468	.507
16	.346	.551	.290	.500	.346	.420	.095	.290
17	.290	.340	.475	.531	.290	.364	.096	.234
18	.226	.837	.612	.381	.381	.226	.226	.244
19	.095	.551	.444	.500	.346	.152	.095	.156
20	.263	.196	.207	.397	.551	.328	.263	.340
21	.095	.733	.626	.683	.346	.213	.213	.156
22	.221	.900	.793	.531	.531	.221	.290	.308
23	.156	.495	.308	.444	.290	.221	.039	.165
24	.226	.431	.244	.301	.381	.301	.157	.170
25	.040	.447	.495	.397	.263	.091	.040	.089
26	.638	.042	.271	.551	.638	.638	.471	.582
27	.551	.091	.146	.397	.551	.551	.397	.415
28	.156	.495	.475	.444	.290	.221	.039	.165
29	.849	.677	.388	.221	.849	.849	.531	.675
30	.263	.196	.495	.551	.263	.328	.145	.207
31	.290	.495	.234	.531	.290	.364	.096	.165
32	.263	.601	.677	.040	.551	.263	.397	.340
33	.444	.900	.675	.156	.626	.531	.626	.475
34	.444	.677	.475	.290	.626	.626	.444	.475
35	.039	.495	.475	.290	.156	.096	.039	.039
36	.095	.397	.364	.420	.213	.152	.041	.039

Appendix 2 (cont.)

Clone	Clone 9	10	11	12	13	14	15	16
1	.641	.707	.809	.960	.551	.683	.513	.707
2	.813	.480	.576	.576	.960	.325	.325	.576
3	.679	.481	.588	.535	.777	.422	.482	.748
4	.641	.910	.707	.657	.642	.570	.456	.606
5	.641	.606	.707	.758	.551	.570	.513	.707
6	.588	.657	.809	.910	.551	.683	.513	.657
7	.748	.606	.910	.910	.642	.683	.626	.910
8	.679	.695	.802	.909	.582	.663	.602	.748
9	****	.535	.641	.641	.777	.482	.482	.748
10	.626	****	.505	.606	.459	.456	.285	.505
11	.444	.683	****	.809	.642	.854	.683	.809
12	.444	.500	.213	****	.551	.626	.513	.707
13	.253	.779	.443	.597	****	.414	.414	.551
14	.730	.786	.157	.468	.883	****	.706	.683
15	.730	1.256	.381	.668	.883	.348	****	.683
16	.290	.683	.213	.346	.597	.381	.381	****
17	.234	.732	.096	.290	.386	.324	.507	.156
18	.507	.563	.157	.301	.659	.038	.261	.226
19	.290	.683	.213	.095	.597	.381	.563	.213
20	.495	.551	.397	.263	.242	.837	1.124	.551
21	.444	.500	.500	.152	1.002	.563	.920	.346
22	.570	.849	.221	.221	.723	.170	.324	.444
23	.234	.626	.156	.156	.540	.324	.411	.039
24	.170	.468	.301	.226	.477	.549	.549	.226
25	.340	.551	.145	.040	.493	.431	.613	.263
26	.271	.838	.551	.638	.041	1.124	1.124	.638
27	.340	.733	.397	.551	.041	.837	.719	.551
28	.388	.626	.096	.156	.540	.244	.411	.156
29	.388	.531	.444	.849	.540	.612	.612	.444
30	.089	.733	.263	.263	.242	.613	.613	.263
31	.234	.732	.221	.290	.540	.411	.324	.039
32	.495	.145	.397	.328	.493	.613	.970	.733
33	.570	.039	.849	.626	.946	.730	1.200	.626
34	.388	.156	.849	.531	.946	1.018	1.423	.444
35	.388	.290	.156	.096	.540	.324	.507	.156
36	.290	.587	.152	.095	.443	.468	.468	.213

Appendix 2 (cont.)

Clone	Clone 17	18	19	20	21	22	23	24
1	.748	.797	.910	.769	.910	.802	.855	.797
2	.711	.433	.576	.822	.480	.407	.610	.650
3	.622	.542	.641	.813	.535	.452	.735	.783
4	.588	.683	.606	.673	.505	.588	.641	.740
5	.748	.683	.707	.576	.707	.588	.748	.683
6	.695	.797	.859	.721	.809	.802	.802	.740
7	.909	.797	.910	.769	.809	.748	.962	.854
8	.792	.783	.855	.711	.855	.735	.848	.843
9	.792	.602	.748	.610	.641	.565	.792	.843
10	.481	.570	.505	.576	.606	.428	.535	.626
11	.909	.854	.809	.673	.606	.802	.855	.740
12	.748	.740	.910	.769	.859	.802	.855	.797
13	.680	.517	.551	.785	.367	.485	.582	.621
14	.723	.963	.683	.433	.570	.843	.723	.578
15	.602	.770	.570	.325	.399	.723	.663	.578
16	.855	.797	.809	.576	.707	.641	.962	.797
17	****	.723	.748	.610	.641	.622	.848	.723
18	.324	****	.797	.541	.683	.904	.843	.706
19	.290	.226	****	.769	.910	.855	.962	.911
20	.495	.613	.263	****	.673	.610	.711	.758
21	.444	.381	.095	.397	****	.695	.855	.797
22	.475	.101	.156	.495	.364	****	.792	.723
23	.165	.170	.039	.340	.156	.234	****	.904
24	.324	.348	.093	.277	.226	.324	.101	****
25	.207	.277	.040	.196	.145	.207	.089	.143
26	.415	.837	.638	.253	.956	.900	.582	.518
27	.415	.613	.551	.196	.956	.677	.495	.351
28	.100	.170	.156	.340	.290	.234	.100	.244
29	.570	.507	.626	.677	1.137	.675	.475	.244
30	.089	.431	.263	.447	.397	.495	.207	.277
31	.165	.244	.156	.495	.290	.388	.039	.101
32	.677	.431	.397	.314	.551	.415	.495	.277
33	.927	.507	.626	.677	.444	.793	.570	.411
34	.675	.730	.444	.495	.290	.927	.388	.244
35	.165	.170	.156	.340	.156	.308	.100	.244
36	.156	.301	.095	.263	.213	.290	.096	.093

Appendix 2 (cont.)

Clone	Clone 25	26	27	28	29	30	31	32
1	.961	.528	.576	.855	.428	.769	.748	.769
2	.639	.959	.913	.610	.508	.822	.610	.548
3	.610	.762	.864	.622	.679	.610	.792	.508
4	.673	.576	.673	.641	.802	.576	.588	.961
5	.769	.528	.576	.748	.428	.769	.748	.576
6	.913	.528	.576	.802	.428	.721	.695	.769
7	.961	.625	.673	.962	.588	.865	.909	.673
8	.915	.559	.661	.848	.509	.813	.848	.711
9	.711	.762	.711	.679	.679	.915	.792	.610
10	.576	.432	.480	.535	.588	.480	.481	.865
11	.865	.576	.673	.909	.641	.769	.802	.673
12	.961	.528	.576	.855	.428	.769	.748	.721
13	.611	.960	.960	.582	.582	.785	.582	.611
14	.650	.325	.433	.783	.542	.541	.663	.541
15	.541	.325	.487	.663	.542	.541	.723	.379
16	.769	.528	.576	.855	.641	.769	.962	.480
17	.813	.661	.661	.905	.565	.915	.848	.508
18	.758	.433	.541	.843	.602	.650	.783	.650
19	.961	.528	.576	.855	.535	.769	.855	.673
20	.822	.776	.822	.711	.508	.639	.610	.731
21	.865	.384	.384	.748	.321	.673	.748	.576
22	.813	.407	.508	.792	.509	.610	.679	.661
23	.915	.559	.610	.905	.622	.813	.961	.610
24	.866	.596	.704	.783	.783	.758	.904	.758
25	****	.594	.639	.915	.508	.822	.813	.731
26	.521	****	.913	.559	.508	.776	.559	.548
27	.447	.091	****	.610	.661	.731	.661	.639
28	.089	.582	.495	****	.565	.813	.848	.610
29	.677	.677	.415	.570	****	.508	.679	.711
30	.196	.253	.314	.207	.677	****	.813	.548
31	.207	.582	.415	.165	.388	.207	****	.508
32	.314	.601	.447	.495	.340	.601	.677	****
33	.677	1.034	.900	.793	.475	.900	.675	.207
34	.495	.900	.900	.570	.475	.677	.475	.340
35	.089	.582	.495	.100	.675	.207	.165	.340
36	.040	.471	.328	.096	.531	.145	.096	.397

Appendix 2 (cont.)

Clone	Clone 33	34	35	36
1	.641	.641	.962	.910
2	.407	.508	.610	.673
3	.509	.622	.622	.695
4	.855	.748	.748	.657
5	.535	.535	.855	.809
6	.588	.535	.909	.859
7	.535	.641	.962	.960
8	.622	.622	.961	.962
9	.565	.679	.679	.748
10	.962	.855	.748	.556
11	.428	.428	.855	.859
12	.535	.588	.909	.910
13	.388	.388	.582	.642
14	.482	.361	.723	.626
15	.301	.241	.602	.626
16	.535	.641	.855	.809
17	.396	.509	.848	.855
18	.602	.482	.843	.740
19	.535	.641	.855	.910
20	.508	.610	.711	.769
21	.641	.748	.855	.809
22	.452	.396	.735	.748
23	.565	.679	.905	.909
24	.663	.783	.783	.911
25	.508	.610	.915	.961
26	.356	.407	.559	.625
27	.407	.407	.610	.721
28	.452	.565	.905	.909
29	.622	.622	.509	.588
30	.407	.508	.813	.865
31	.509	.622	.848	.909
32	.813	.711	.711	.673
33	****	.905	.679	.481
34	.100	****	.679	.588
35	.388	.388	****	.909
36	.732	.531	.096	****

Appendix 3a: Unpigmented clonal composition of *D. pulex* in ponds on Churchill Bluffs A and C in 1985.

Pond	clones(numbers)
A2	1(15), 7(6), 11(1)
A10	1(16), 2(8)
A11	1(15), 2(9)
A12	1(21), 2(1), 4(1), 5(1)
A17	1(24)
A19	1(24)
A20	1(6)
A21	9(24)
A21a	1(5), 9(19)
A23	1(19), 10(5)
A25	1(23), 9(1)
A27	1(23), 12(1)
A28	1(24)
A29	1(22), 2(1), other(1)
A30	1(23), 2(1)
A31	1(16), 10(8)
A32	1(20), 3(3), 32(1)
A34	1(24)
A35	1(10)
A36	1(24)
A37	1(23), 3(1)
A38	1(24)
A38b	1(24)
A38c	1(24)
A39	1(24)
A41	1(24)
A42	1(17), 33(7)
A42a	1(24)
A43	1(2)
A46a	1(24)
A47	1(23), 6(1)
A48	1(24)
A49	1(24)
A50	1(19), 7(5)
A51	1(2), 7(22)
A54	1(14), 2(10)
A55	1(4), 9(19), 35(1)
A56	1(7), 2(12), 7(5)
A58	1(22), 2(1), 8(1)
C1	15(17), 16(1), 34(2)
C3	13(12), 14(11), 15(1)
C4	13(3), 21(21)
C8	13(23), 14(1)
C8a	13(18), 14(6)
C9	14(24)
C10	14(24)
C12	14(24)
C13	14(4), 15(13), 16(7)
C14	13(2), 24(2)
C15	13(1), 14(23)
C16	13(7), 14(17)
C19	13(24)
C20	13(2), 14(15), 15(7)
C21	13(22), 14(2)
C22	13(24)
C23	14(5), 15(19)
C24	13(24)
C25	13(22), 14(2)
C27	14(18), 15(2), 16(4)
C28	14(24)
C29	14(24)
C30	14(17), 23(7)
C31	14(10), 15(14)
C32	14(24)
C33	13(24)
C34	14(24)
C35	14(24)
C36	14(24)
C37	14(24)
C38	14(24)
C39	13(2), 14(22)
C40	13(7)
C41	13(23), 14(1)
C42	14(14), 15(3), 22(7)
C43	13(23), 14(1)
C44	14(24)
C44a	14(24)
C45	14(24)
C45a	14(24)
C47	14(24)
C48	14(24)
C49	13(20), 14(4)
C50	14(24)
C51	14(24)
C52	14(24)
C52a	14(24)
C53	13(1), 14(23)
C54	13(6), 14(18)
C56	13(1), 14(19), 15(1)
C57	14(24)
C58	13(12), 14(12)
C59	13(1), 14(21), 25(2)
C60	14(24)
C61	13(1), 14(23)
C61a	13(24)
C62	13(24)
C63	13(3), 14(16), 16(5)

Appendix 3a (cont.)

Pond	clones(numbers)
C64	14(24)
C64a	13(24)
C67	13(2), 14(22)
C67a	13(3)
C68	13(24)
C69	13(24)
C69a	13(24)
C69b	13(24)
C70	14(3), 16(18), 19(1), 20(2)
C70a	13(24)
C73	14(17), 15(7)
C76	13(10), 14(1), 27(13)
C78	13(6), 14(18)
C82	14(4), 15(20)
C83	14(2), 15(5)
C84	14(1), 15(1)
C85	13(2), 26(22)
C86	17(7), 25(3), 26(2)
C87	25(3)
C88	7(9), 17(1), 25(13), 28(1)
C89	11(1), 16(18), 17(1), 19(4)
C90	7(20), 16(4)
C91	1(7), 11(2), 19(1), 25(11), 26(3)
C95	14(24)
C96	13(23), 14(1)
C97	13(12), 14(9)
C98	16(5), 19(17), 20(2)
C100a	13(24)
C102	13(24)
C103	14(3), 17(7), 18(2), 19(1)
C104	13(12), 14(12)
C105	14(22), 17(2)
C107	17(1), 19(23)
C108	17(24)
C111	2(12), 19(12)
C111b	1(1), 17(23)
C114	1(5), 16(1), 17(18)
C118	1(20), 17(1)
C120	1(7)
C123	1(8)
C124	1(24)
C127	1(24)
C134	1(8), 17(16)
C141	1(24)
C144	17(24)
C147	17(4)
C148	17(9)
C148a	17(21), 29(3)

Pond	clones(numbers)
C152	1(1), 17(23)
C156	16(24)
C159	13(24)
C160	13(24)
C161	13(24)

Appendix 3b: Unpigmented clonal composition of D. pulex in ponds on Churchill Bluffs A and C in 1989.

Pond	clones(numbers)
A2	1(5), 7(19)
A10	1(16), 2(8)
A11	1(22), 2(2)
A12	1(19), 5(1)
A17	1(24)
A19	1(24)
A20	1(15)
A21	9(24)
A21a	1(1), 9(23)
A23	1(18), 10(6)
A25	1(24)
A27	1(24)
A28	1(23)
A29	1(24)
A30	1(22), 2(2)
A31	----- (no animals)
A32	----- (no animals)
A34	1(23), 2(1)
A35	1(18)
A36	1(24)
A37	1(10), 3(14)
A38	1(24)
A38b	1(20)+
A38c	1(24)+
A39	1(24)
A41	1(24)
A42	1(23)
A42a	1(24)
A43	1(24)
A46a	1(24)
A47	1(21), 6(2), 36(1)
A48	1(24)
A49	1(24)
A50	1(11), 7(13)+
A51	----- (no animals)
A54	1(19), 2(5)
A55	1(6), 9(18)
A56	----- (no animals)
A58	1(20)
C1	15(22), 16(2)
C3	13(1), 14(23)
C4	13(3), 14(1), 21(20)
C8	13(24)
C8a	13(24)
C9	14(24)
C10	13(1), 14(19), 15(4)
C12	14(20), 23(4)
C13	14(2), 15(20), 16(2)
C14	14(3), 15(1), 24(20)
C15	13(1), 14(21), 15(2)
C16	13(1), 14(23)
C19	13(19), 14(4), 15(1)
C20	13(17), 14(6), 15(1)
C21	13(24)
C22	13(24)
C23	14(4), 15(20)
C24	13(24)
C25	13(22), 14(1), 15(1)
C27	14(12), 15(1), 16(11)
C28	13(3), 14(21)
C29	14(21), 16(3)
C30	14(21), 15(1), 23(2)
C31	14(14), 15(10)
C32	14(24)
C33	13(24)+
C34	13(24)+
C35	13(24)+
C36	14(24)
C37	14(24)
C38	14(24)
C39	14(24)
C40	13(23), 14(1)
C41	14(22), 23(2)
C42	14(16), 15(7), 22(1)
C43	13(24)
C44	14(24)+
C44a	14(24)+
C45	14(24)
C45a	13(3), 14(21)+
C47	13(9), 14(15)
C48	14(24)
C49	13(18), 14(6)
C50	14(24)
C51	14(24)
C52	14(24)
C52a	14(24)
C53	13(17), 14(7)
C54	13(18), 14(6)
C56	14(24)
C57	13(5), 14(19)
C58	13(8), 14(16)
C59	13(13), 14(1), 25(10)
C60	14(24)
C61	13(4), 14(3), 16(17)
C61a	13(24)*
C62	13(24)

Appendix 3b (cont.)

Pond	clones(numbers)
C63	13(1), 14(2), 16(20) 19(1)
C64	13(3), 14(21)+
C64a	13(1), 14(23)+
C67	13(1),*14(23)+
C67a	13(24)+
C68	13(24)+
C69	13(24)
C69a	13(23), 14(1)+
C69b	13(21), 14(3)+
C70	16(24)
C70a	13(24)
C73	14(10), 15(2)
C76	1(1), 13(23)
C78	----- (no animals)
C82	----- (no animals)
C83	----- (no animals)
C84	----- (no animals)
C85	26(24)
C86	17(11), 25(10), 26(2), 28(1)
C87	11(2), 17(6), 25(14), 28(2)
C88	7(4), 17(2), 25(12), 26(1), 28(5)
C89	11(2), 16(3), 17(18), 28(1)
C90	7(18), 11(4), 16(2)
C91	1(5), 19(14), 27(2), 28(3)
C95	14(24)
C96	13(1), 14(23)
C97	13(2), 14(22)
C98	16(8), 19(16)
C100a	13(24)
C102	13(24)
C103	7(1), 14(21), 17(1), 18(1)
C104	13(1), 14(23)
C105	14(24)
C107	16(1), 19(23)
C108	17(24)
C111	----- (no animals)
C111b	17(24)
C114	1(6), 17(18)
C118	1(24)
C120	1(18)
C123	1(24)
C124	1(20), 35(4)
C127	1(11)
C134	1(7), 17(17)
C141	1(20), 17(4)
C144	17(24)
C147	17(24)
C148	17(24)
C148a	----- (no animals)
C152	1(1), 17(21)
C156	16(24)+
C159	14(24)+
C160	13(16), 14(8)+
C161	13(18), 14(6)+

Note: ponds marked with + were used in 1987 and/or 1988 manipulation experiments.

* indicates empty control ponds.

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