UNIVERSITÉ DU QUÉBEC À RIMOUSKI

FACTEURS BIOTIQUES ET ABIOTIQUES INFLUENÇANT LES COMMUNAUTÉS DE

ZOOPLANCTON DES ÉTANGS SUBARCTIQUES ET LA RÉPARTITION

GÉOGRAPHIQUE DES CLONES DU COMPLEXE *DAPHNIA PULEX*

MÉMOIRE

PRÉSENTÉ

COMME EXIGENCE PARTIELLE

DE MAITRISE EN GESTION DE LA FAUNE

PAR

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Avertissement

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RÉSUMÉ

Ce projet de maîtrise visait à approfondir d'une part, les connaissances sur le fonctionnement des écosystèmes aquatiques subarctiques de l'est du Québec, et d'autre part, les connaissances sur la diversité génétique des daphnies du complexe d'espèces *pulex*. De plus, ce projet tentait d'évaluer les facteurs biotiques et abiotiques responsables de la distribution de ses différents génotypes à l'est de l'Amérique du nord.

Les étangs de la région de Kuujjuarapik et d'Umiujaq ont été caractérisés et l'assemblage des communautés zooplanctoniques décrites. Quatre facteurs physicochimiques (température, conductivité, altitude et COD) responsables de cet assemblage ont été identifiés. Dans la même étude, la diversité spécifique et génétique du complexe *pulex* ont été décrites. La conductivité, le pH et la profondeur des étangs expliquaient une grande proportion de la variation dans la distribution des clones.

Cette étude a également testé l'hypothèse selon laquelle les asexués et les polyploïdes avaient une distribution plus large et occupaient des régions froides et marginales grâce à une plus grande flexibilité métabolique et une plus grande tolérance physiologique aux conditions environnementales extrêmes que les diploïdes sexués. Deux expériences de laboratoires ont mis en évidence que la distribution géographique des modes de reproduction et des niveaux de ploïdie ne supportait pas cette hypothèse. Des facteurs historiques expliqueraient mieux la parthénogenèse et la polyploïdie géographiques. Finalement, ce projet a confirmé que les clones de daphnies sont spécialistes et occupent des niches écologiques différentes. Associé à une grande diversité génétique, cela pourrait expliquer la distribution cosmopolite des daphnies du complexe *pulex*.

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INTRODUCTION GÉNÉRALE

Structuration d'un écosystème

La complexité des écosystèmes a toujours fasciné les écologistes. De la théorie de la niche écologique à la théorie neutre de la biodiversité et de la biogéographie, de nombreuses hypothèses ont tenté d'appréhender cette complexité. Beaucoup d'attention a été portée sur la structure, la composition (Rautio 1998; Armengol and Miracle 1999; Swadling, Pienitz et al. 2000; Rautio 2001; Cottenie and DeMeester 2004; Young and Riessen 2005; Norlin, Bayley et al. 2006) ainsi que sur l'établissement (Louette, Mieke et al. 2006) et la résilience des communautés (Brock, Nielsen et al. 2003). Les paragraphes suivants sont une description non-exhaustives de ces hypothèses et des récents travaux effectués en écologie des populations.

La composition d'espèces et la structure des communautés dépendent de l'interaction de facteurs biotiques et abiotiques, communément classés sous deux niveaux de processus (Shurin 2000). Les processus locaux incluent la prédation, la compétition, l'acquisition des ressources et l'hétérogénéité environnementale de l'habitat, tandis que les processus régionaux comprennent l'extinction des populations locales et la colonisation via la dispersion (Cottenie and DeMeester 2004). L'importance relative de ces deux niveaux de processus générant des différences de composition spécifique varie parmi les types d'habitats et a suscité de nombreuses interrogations. Des auteurs ont montré que des effets stochastiques (histoires et séquences de colonisation des espèces, effets de priorité) associés à des taux de dispersion bas pouvaient déterminer le succès d'établissement et la composition d'espèces durant la phase initiale (1 an) d'assemblage des communautés zooplanctoniques (Jenkins and Buikema 1998). Shurin (2000) a effectué une étude sur la résistance aux invasions et la limite

de la dispersion du zooplancton dans des étangs et a démontré que plus la diversité spécifique est grande, plus la communauté est résistante aux invasions par de nouvelles espèces. Cela suggère que les facteurs locaux ont plus d'importance que la dispersion dans la structure et la composition des communautés établies. En effet, les habitats nouvellement formés sont colonisés par des espèces présentes dans la région par dispersion. Les premières espèces à coloniser l'habitat sont celles dont la capacité de dispersion et/ou l'abondance régionale sont les plus élevées. Un déclin dans le temps du nombre d'espèces colonisant l'habitat résulte de facteurs locaux, c'est-à-dire que l'augmentation d'interactions biotiques peut réduire le succès d'établissement de nouveaux immigrants, notamment par exclusion compétitive. Louette et coll (2006) confirment ces deux résultats en testant le succès d'établissement dans des communautés de cladocères de 1 an et 2 ans et portent une attention toute particulière sur l'importance de la prédation et de la compétition dans la détermination de la composition d'espèces des communautés zooplanctoniques.

Certains auteurs considèrent que ce sont les processus locaux qui sont responsables de la structure des communautés, alors que d'autres auteurs pensent que ce sont les processus régionaux. À cette dualité s'ajoute deux mouvements de pensée théorique qui divergent dans l'explication des patrons de compositions d'espèces. D'un côté, la théorie de la niche écologique suggère que les patrons de biodiversité sont étroitement reliés aux variations de nombreux paramètres écologiques locaux (conditions environnementales, compétition, prédation...). Par conséquent, la coexistence d'espèces est liée à la différentiation des niches écologiques de chaque espèce. De l'autre côté, la théorie neutre de Hubbell (2001) ignore les différences entre les individus dans leurs réponses aux conditions écologiques locales et considère la dispersion comme le principal facteur structurant les communautés locales, chaque individu étant équivalent. Les prédictions de la théorie neutre peuvent représenter des

hypothèses nulles pour expliquer les patrons de structure de communautés (Bell 2001). Si les théories de la niche écologique et neutre semblent s'exclure l'une de l'autre dans leur définition, des cas ont démontré leur possible coexistence. Récemment, Thompson et Towsend (2006), par exemple, ont mis en évidence le potentiel, aussi bien des processus de dispersion que des conditions environnementales locales pour expliquer les patrons locaux de diversité de communautés d'invertébrés de rivière. Une faible capacité de dispersion pour une espèce favorisait la théorie de la niche et une grande capacité de dispersion pour une autre penchait pour la théorie neutre.

Enfin, la taille et la structure de l'habitat peuvent également influencer le nombre d'espèces dans une communauté. Bien que la théorie de la biogéographie insulaire soit basée sur le fait que le nombre d'espèces est proportionnel à la taille de l'île (MacArthur and Wilson 1967), il a été démontré que de petits habitats peuvent présenter une grande richesse spécifique. C'est le cas des lacs peu profonds et des étangs (Scheffer, Geest et al. 2006).

L'écosystème aquatique subarctique

L'environnement abiotique

Les étangs sont des écosystèmes relativement isolés les uns des autres et représentent des 'îles' aquatiques dans un paysage terrestre. Par conséquent, chaque étang est une parcelle entourée d'une matrice hostile (où les individus ne peuvent se nourrir et se reproduire) comme le propose la théorie de la métapopulation (Hanski and Gilpin 1997). Les plans d'eaux de l'Arctique et du Subarctique sont parmi les écosystèmes qui réagiront en premier au

réchauffement global de la planète (Boer, Koster et al. 1990). Par conséquent, comprendre ce qui détermine les patrons actuels de distribution des espèces est essentiel afin d'évaluer les futurs changements de biodiversité et de structure de communautés qui pourraient résulter des changements climatiques. De plus, le nombre très élevé d'étangs nordiques dans une superficie relativement petite offre une grande opportunité de recherche écologique expérimentale et théorique sur le terrain. En effet, les lacs et les étangs sont formés de manière très dynamique. Année après année, le gel et le dégel font craquer le sol et agrandissent ces fissures, qui se comblent de neige en hiver. En été, la fonte des neiges et la pluie remplissent les trous d'eau (Bolen 1998). Parce qu'ils sont peu profonds, de petite superficie et dans un climat rude, ces microhabitats aquatiques, qui représentent 2% de la surface de la Terre, subissent de grandes fluctuations physico-chimiques (Rautio 1998; Rautio 2001). Ils gèlent complètement en hiver tandis que l'évaporation peut les assécher en été.

L'environnement biotique

La présence d'invertébrés aquatiques dans ces étangs temporaires est donc grandement liée à leur tolérance aux conditions variables de l'environnement (processus locaux) et à leur capacité de dispersion et de colonisation (processus régionaux) (Sheath 1986). La capacité de dispersion varie selon les espèces et peut être active ou passive. Cette dernière, utilisée par le zooplancton, est assurée par la formation d'œufs dormants durant le cycle de vie. Emportés par le vent ou attachés aux plumes d'oiseaux aquatiques, ils peuvent être transportés sur de grandes distances (Maguire 1963). La formation de ces œufs permet également de résister au gel et à la dessiccation et de rétablir les populations quand les bonnes conditions sont de retour au printemps. Ce phénomène, appelé résilience, se produit après chaque perturbation et les communautés repassent par tous les stades de colonisation et d'établissement. L'efficacité

d'éclosion des œufs et le temps très court pour compléter son cycle vital sont de grande importance. À l'échelle locale, les facteurs abiotiques qui semblent corrélés aux patrons de distribution du zooplancton incluent le pH, la taille des étangs et la proximité des autres étangs (Swadling, Gibson et al. 2001) tandis que les facteurs biotiques sont principalement la biomasse chlorophyllienne, la compétition et la prédation (Rautio 1998). Certains facteurs abiotiques peuvent également interagir avec des conditions biotiques ; la température peut avoir un effet négatif pour une espèce sur la capacité d'exploitation d'une ressource, par exemple (Steiner 2004).

Le zooplancton domine souvent dans les étangs peu profonds des hautes latitudes. On le retrouve même à des densités très élevées (Rautio and Vincent 2006), étant favorisé par l'absence de prédateurs vertébrés, résultant en une chaîne alimentaire simplifiée, à deux niveaux trophiques (Rautio 1998). Par contre, l'assemblage de prédateurs invertébrés joue un rôle important dans les étangs. Les larves de l'insecte *Chaoborus*, les copépodes carnivores tels *Heterocope* et plusieurs cyclopoïdes sont grandement responsables de la structure des communautés zooplanctoniques. Ces prédateurs se nourrissent de zooplancton herbivore tel que copépodes ou cladocères, qui eux, compétitionnent pour la nourriture, principalement composée de nanoplancton et de diatomées (Rautio 2001). Parallèlement, les rotifères, composante principale du microplancton, broutent la production primaire et consomme la production secondaire bactérienne (Rublee 1998). La biomasse algale de la colonne d'eau d'étangs peu profonds semble être une ressource insuffisante pour le nombre élevé d'espèces zooplanctoniques herbivores puisqu' une étude récente a montré que ces espèces pouvaient se nourrir substantiellement sur la biomasse algale benthique se trouvant dans le tapis microbien au fond des étangs (Rautio and Vincent 2007). Des études précédentes ont identifié six espèces de copépodes et cinq espèces de cyclopoïdes dans 37 étangs dans la région de

Kuujjuarapik. *Leptodiaptomus minutus* était l'espèce dominante dans la plupart des étangs, souvent co-habitant avec d'autres espèces de copépodes (Swadling, Gibson et al. 2001). Également, le cladocère *Daphnia middendorfiana* était présent dans tous les étangs étudiés dans cette même région en 2006 (Rautio and Vincent 2006). D'autres études ont montré que les cladocères du genre *Daphnia* dominent le zooplancton des étangs nordiques (Weider, Hobaek et al. 1999). Ces brouteurs sont principalement prédatés par les larves de l'insecte *Chaoborus* (Colbourne, Crease et al. 1998; Riessen and Young 2005). Louette et coll. (2006) ont montré que les compositions de communautés de cladocères sont principalement influencées par la compétition pour la ressource et la prédation par *Chaoborus*.

Parthénogénèse, polyploïdie et répartition géographique de *Daphnia pulex*

Les membres du complexe *Daphnia pulex* se reproduisent par parthénogenèse cyclique, comprenant une phase sexuée suivie d'une phase asexuée et par parthénogenèse obligatoire, strictement asexuée (Innes, Fox et al. 2000). Cette dernière est caractérisée par une descendance produite à partir d'œufs non fertilisés diploïdes ainsi que des œufs dormants ou éphippies, possédant un bagage génétique identique à celui de leur mère (Crease, Stanton et al. 1989). Pour plusieurs auteurs, la transition de la parthénogénèse cyclique à la parthénogénèse obligatoire est due à un allèle de suppression de la méiose limité par la femelle (Innes and Hebert 1988). La propagation de cet allèle dans une population à parthénogénèse cyclique a pour effet de figer sa variabilité génétique dans divers génotypes clonaux (Crease, Stanton et al. 1989).

Les daphnies se reproduisant par parthénogenèse obligatoire ou asexuées, dominent leurs congénères sexués sous des latitudes et des altitudes élevées. Le terme parthénogenèse

géographique a été avancé pour expliquer cette distribution spatiale disjointe entre les organismes sexués et asexués de la même espèce (Vandel 1928).

De plus, en Arctique, la parthénogénèse obligatoire est souvent associée à la polyploïdie (une augmentation du nombre de jeux de chromosomes) (Dufresne and Hebert 1994). La polyploïdie peut survenir suite à l'union de gamètes non réduits (2n) avec des gamètes réduits (n). Lorsque les unions de gamètes se font au sein d'une même population, on parle d'autopolyploïdie. Par contre, lorsque les unions se font entre gamètes provenant de génomes différents, on parle d'allopolyploidie (Otto and Whitton 2000). En zone tempérée, on retrouve presqu'exclusivement des daphnies diploïdes; dans le subarctique, plusieurs clones diploïdes co-existent avec des clones polyploïdes; et dans le haut Arctique, on note une prédominance de clones polyploïdes (Beaton and Hebert 1988). Le changement de niveau de ploïdie produit un isolement reproducteur qui empêche une réversion à la sexualité (Hebert, Schwartz et al. 1993). La combinaison de deux ou plusieurs génomes divergents entraîne souvent un taux élevé d'hétérozygotie chez les polyploïdes, ce qui peut les doter de nouvelles tolérances écologiques (Dufresne and Hebert 1998) pouvant expliquer leur grande répartition dans les milieux extrêmes (alpins et arctiques).

Problématique de l'étude

L'alliance de deux disciplines

De nombreuses études ont été effectuées sur la biologie des communautés et l'écologie du zooplancton (Rublee 1998; Armengol and Miracle 1999; Rautio 2001; Swadling, Gibson et al. 2001; Steiner 2004; Riessen and Young 2005; Norlin, Bayley et al. 2006; Scheffer,

Geest et al. 2006). Également, de nombreuses études ont été effectuées sur la diversité génétique de plusieurs espèces d'invertébrés aquatiques (Spaak 1997; Wilson, Sunnucks et al. 1999; Innes, Fox et al. 2000; Crease 2001; Hebert and Finston 2001; Palsson 2001; Winsor and Innes 2002; Michels, Audenaert et al. 2003; Weider and Hobaek 2003; Haag 2005; Paland, Colbourne et al. 2005). Par contre, rares sont les recherches qui allient ces disciplines sous un même objectif (Weider, Makino et al. 2005). Pourtant, les théories sur la diversité en génétique des populations et en écologie des communautés partagent plusieurs similarités frappantes. Ces deux disciplines montrent un intérêt commun dans l'explication des nombres et des fréquences relatives des variances biologiques trouvées en nature. Tandis qu'en génétique des populations, ces variances sont les génotypes ou les allèles, en écologie des communautés, ce sont les espèces. Vellend a fortement contribué à la mise en évidence d'une corrélation positive entre la diversité spécifique et la diversité génétique. En 2003, il teste ce qu'il nomme le SGDC, corrélation de la diversité spécifique-génétique, sur 14 bases de données compilées à partir de la littérature sur des oiseaux, des reptiles, des mammifères et des plantes, dans une grande variété d'archipels. La corrélation était généralement positive. En 2004, il trouve que la variation génétique de l'herbe *Trillium grandiflorum* est moins importante dans les forêts secondaires, poussant sur des terres agricoles abandonnées, comparativement aux forêts primaires, non perturbées. Également, la diversité spécifique dans les forêts secondaires était faible. Les facteurs expliquant le plus cette corrélation positive sont la surface et l'histoire d'utilisation de l'habitat combinées avec des variations autant dans la taille de la population (une espèce, en particulier), que dans celle de la communauté (toutes les espèces appartenant au même taxon) (Vellend 2003; Vellend 2004). Ces deux niveaux de diversité sont modulés par les mêmes facteurs (dérive des communautés ou génique, migration des individus ou des allèles, sélection sur les deux niveaux de diversité et spéciation/mutation). Ce projet de maîtrise vise donc à intégrer ces deux disciplines dans

l'étude des facteurs qui influencent la diversité des communautés de zooplancton, la diversité interspécifique des daphnies du complexe *D. pulex* ainsi que la diversité intraspécifique ou clonale.

La diversité clonale

La diversité génétique des daphnies a été beaucoup étudiée tant dans l'Arctique (Dufresne and Hebert 1995; Weider, Hobaek et al. 1999), que dans les régions tempérées d'Amérique du nord (Hann 1996; Hebert and Finston 2001) ainsi qu'en Argentine (Adamowicz, Gregory et al. 2002). La diversité clonale est plus grande dans l'Arctique que dans les régions tempérées (environ 4,5 clones pour moins de trois par étang, respectivement) (Dufresne and Hebert 1995). Également, les populations de la région de Churchill au Manitoba (Canada) à l'ouest de la baie d'Hudson sont très diversifiées (Wilson and Hebert 1993). Cependant, aucune information sur la diversité clonale des daphnies de la région à l'est de la baie d'Hudson, autour de Kuujjuarapik (Nunavik) n'est disponible. Lors du pléistocène, les glaces couvrant la quasi-totalité du continent nord-américain se sont retirées permettant aux espèces subsistant dans le refuge glaciaire de la Béringie (Alaska) de se propager à partir du nord-ouest vers le reste du continent. Kuujjuarapik étant plus éloignée du refuge glaciaire de la Béringie (Alaska) que Churchill, on peut prédire que la diversité clonale devrait être plus faible. De plus, la nature insulaire des étangs permet des différentiations génétiques et des adaptations locales entre les populations (DeMeester 1996). Vanoverbeke et DeMeester (2005) ont montré qu'il n'y avait pas de relation significative entre la distance géographique et la différentiation génétique de populations de *Daphnia magna* séparées de 100 m à 500 km. Ceci était expliqué principalement par le fait que les populations proches étaient déjà hautement différenciées génétiquement. Les populations avec peu de clones étaient les plus divergentes. Cette étude vise à combler les lacunes concernant la diversité clonale des

daphnies de la région subarctique de l'est de la baie d'Hudson et à tenter d'expliquer l'influence relative des processus locaux et régionaux sur la structure des communautés de zooplancton.

Répartition géographique des clones de Daphnia pulex

Si la répartition des clones en Amérique du nord a été bien décrite, les facteurs responsables de la distribution des modes de reproduction et de la polyploïdie sont moins bien compris. Peu d'études ont été conduites afin d'examiner les tolérances physiologiques et écologiques dans un taxon naturel où coexistent des individus sexués, asexués, diploïdes et polyploïdes. Le complexe d'espèce *Daphnia pulex* représente une belle opportunité de recherche sur cette problématique puisque l'on retrouve des diploïdes et des polyploïdes en sympatrie dans la région du subarctique et des sexués et des asexués en sympatrie, notament dans la région des Grands Lacs en Amérique du nord. Ses membres couvrent également un grand gradient latitudinal et sont présents dans des habitats dont les conditions environnementales peuvent être extrêmement divergentes. Enfin, la facilité de mise en culture et de manipulation font de *Daphnia* un organisme modèle en écologie expérimentale et permettent de tester des hypothèses sur la distribution des asexués/polyploïdes comparativement aux sexués.

Objectifs

Communautés zooplanctoniques des étangs subarctiques

Le premier objectif de ce projet de maîtrise est de caractériser les étangs subarctiques et d'en répertorier la biodiversité des macroinvertébrés dans la région de Kuujjuarapik et Umiujaq. Les différentes espèces d'invertébrés (larves d'insectes et crustacés) présents dans trois types d'étangs (rocheux, toundrique et thermokarst) ont été identifiées et quantifiées afin de décrire les communautés zooplanctoniques. Également, cet objectif vise à déterminer l'importance relative des processus locaux et régionaux influençant la distribution des différents taxons zooplanctoniques. Les facteurs à l'étude sont l'abondance des différentes espèces de prédateurs et de compétiteurs, la température, le pH, la salinité (mesures de conductivité de l'eau), la biomasse chlorophyllienne, le carbone organique dissous (DOC), les caractéristiques morphométriques des étangs, la transparence de l'eau ainsi que le pourcentage de végétation entourant les étangs.

Répartition géographique et diversité génétique des daphnies du complexe D. pulex

Le deuxième objectif tente d'estimer la distribution et la diversité génétique des daphnies du complexe *D. pulex*. Dans un premier temps, les communautés de daphnies de ce complexe présentes à l'été 2007 ont été décrites dans la région de Kuujjuarapik et Umiujaq. De plus, l'influence de divers facteurs biotiques et abiotiques sur les différentes espèces du complexe ainsi que sur les clones de ces espèces ont été testées lors de la campagne d'échantillonnage. Dans un deuxième temps, deux expériences de laboratoire ont été effectuées afin de comprendre la répartition géographique de différents génotypes de *Daphnia pulex*. Dans la première expérience, l'activité de trois enzymes impliquées dans les métabolismes aérobique et anaérobique (citrate synthase, système de transport des électrons et lactate déshydrogenase) on été mesurées sur quatre clones de daphnies qui diffèrent de niveau de ploïdie et d'origine géographique après une exposition de quatre jours à divers traitements

de température et de pH. Une plus grande flexibilité métabolique chez les polyploïdes pourrait expliquer leur succès dans les régions froides et extrêmes de la planète. Dans la deuxième expérience, la tolérance de clones diploïdes, triploïdes, sexués, asexués et issus de régions tempérées et nordiques a été comparée sous une température élevée, un pH basique, un pH acide, une faible conductivité et une conductivité élevée. Les différences de tolérances à ces conditions environnementales pourraient expliquer la différence de répartition des différents génotypes de daphnies.

CHAPITRE 1

Ecological factors influencing zooplankton assemblage and genetic diversity of the *Daphnia pulex* complex in subarctic ponds

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1.1 Abstract

Ecological functioning of subarctic ponds and the relationship between environmental factors and zooplankton community, species diversity and clonal diversity of the complex *Daphnia pulex* has been investigated in the Kuujjuarapik and Umiujaq region. Ponds showed great variation in environmental conditions and zooplankton abundance and structure. Among all the studied variables, temperature, conductivity, altitude, and DOC accounted for 69.7 % of the variation in zooplankton distribution. Copepods and *Daphnia* together dominated a high proportion of the ponds. At the interspecific level, depth influenced the different distribution of *D. pulicaria* and *D. pulex*, the latter preferring shallow waterbodies, thus excluding intercompetition. Clonal diversity of the *pulex* complex was 1.86 clones per pond. Conductivity, pH and depth accounted for a great percentage of the variation in clones distribution. Triploid clones were restricted to low conductivity water bodies while diploid clones of *D. pulex* were found mostly in rock ponds that exhibited relatively high conductivities. Clones inside each species had different ecological preferences and thus could be viewed as specialists. The large number of clones that have originated polyphyletically in this complex thus contribute to the wide distribution and ecological flexibility of this species.

Keywords: Subarctic ponds, zooplankton, environmental factors, *Daphnia pulex*, clonal diversity

1.2   Introduction

Shallow ponds are a major feature of high latitude landscape. As they are relatively isolated habitats, abundant, and have a spatial patchiness, they offer a great opportunity to study fundamental ecological processes in natural systems. Their species composition and community structure fall under two scales of processes (Shurin 2000). Competition, predation, pH and conductivity are included in local processes whereas dispersion and colonization act at a regional scale (Cottenie and DeMeester 2004). Great fluctuations of environmental conditions act yearly and seasonally on these ponds. They can dry in summer and freeze down to the bottom in winter. Moreover, the sunny season is very short for the phytoplankton growth and the quantity and quality of the primary production can have substantial repercussions on the diversity and abundance of taxa occurring in next trophic levels. Invertebrate species occurrence in these temporary or semi-temporary ponds is greatly influenced by their tolerance towards variable environmental conditions and dispersion and/or colonization capacities. Many zooplankton species possess developmental stages (resting eggs, ephippia) resistant to drought and freezing. They can therefore disperse by the way of wind, birds or human and colonize or re-establish when environmental conditions are favorable again. Zooplankton can be found in high densities in shallow subarctic ponds because of the lack of vertebrate predators but only few species are present in a single pond (Rautio and Vincent 2006). In fact, invertebrate predators play a substantial role in structuring zooplankton communities. Larval stage of the phamton midge *Chaoborus* and some cyclopoids feed on grazers like microcrustaceans. Cladocerans and copepods compete for phytoplankton (Rautio 2001) and rotifers graze primary and secondary production (Rublee 1998). A study reported 11 species of copepods in the Kuujjarapik region although species diversity ranged from 0 to 4 species per lake (Swadling, Gibson et al. 2001). This study

showed that conductivity, pH and dissolved organic carbon concentrations influence copepods distribution .

Members of the *Daphnia pulex* complex are abundant in subarctic ponds. They reproduce by cyclic parthenogenesis, an asexual phase followed by a sexual phase or by obligate parthenogenesis, strictly asexual (Innes, Fox et al. 2000). The resulting clones are genetically similar to their mother but numerous different clones have been identified in North America. The transition to asexuality is due to a sex-dependant meiosis-suppressor allele that is spread in populations and fixes genetic diversity in multiple clonal genotypes. The predominant reproductive mode of *Daphnia pulex* in north Canada is obligate parthenogenesis (Hebert, Schwartz et al. 1993). Moreover, polyploidy often occurs in high latitudes. In arctic regions, clones are polyploid while they are diploid in temperate regions (Dufresne and Hebert 1995). In the region of Churchill (Manitoba), clonal distribution of the *Daphnia pulex* complex has been correlated with salinity gradients that are a function of distance and location of pond with respect to Hudson Bay (Weider and Hebert 1987). Among numerous clones in this region, 2 dominated the ponds. Predator occurrence in these habitats determined presence of one and absence of the other clone (Wilson and Hebert 1993). No information on clonal diversity and distribution is available for sites in eastern Hudson Bay. The objective of this study was 1) to record and quantify biodiversity of macroinvertebrates of the subarctic shallow ponds of northern Québec and 2) to examine the influence of abiotic and biotic factors on zooplankton distribution, then more precisely on species of the *Daphnia pulex* complex distribution and finally on the genetic or clonal distribution of the latter species with a focus on clonal diversity. As subarctic and arctic ponds ecosystems will likely be the first to react to global warming (Boer, Koster et al. 1990), understanding actual biodiversity is necessary to assess future shifts due to climatic changes. This is the first study to compare zooplankton biodiversity and limnological data among the three pond formations encountered

in subarctic region, that are rock ponds, tundra ponds and thermokarst ponds, described in the next section. Also this study provides a first step to understand the ecological functioning of subarctic ponds through the relationships between environmental factors and zooplankton community and to assess the relationship between species diversity and clonal diversity in *Daphnia*.

1.3   Material and methods

1.3.1   Site description and sampling
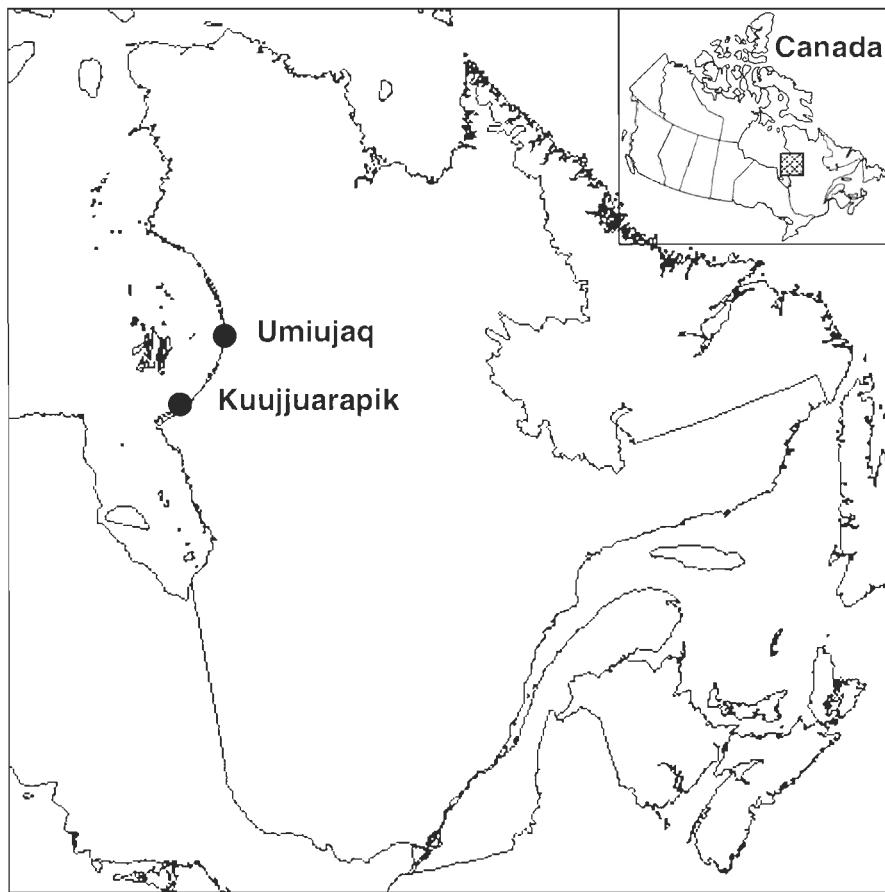
Figure 1   Location of the studied area.

Heterogeneity of the forest-tundra region geomorphology results in three pond formations. We named rock ponds those found on the carbonate-derived bedrock along the coast, tundra ponds those found inland on the Precambrian granite bedrock and thermokarsts those found on peatlands. Permafrost aggregation raises the peatland surface and creates two major features: palsas and peat plateau. Thawing of permafrost creates thermokarstic ponds at the bottom of palsas or on peat plateau. Vegetation varies greatly among these types of ponds, with essentially no or little vegetation in rock bluffs, small pruce trees, lichens and mosses in tundra landscape and *Sphagum* and mosses in peatlands. Zooplankton were sampled from the end of june to mid-july 2007. The main sampling location was in the Kuujjuarapik region (Nunavik) (55°17'N, 77°45'W) on both side of the Great Whale River. Two rock bluffs, two tundra sites on the north of the river and thermokarst ponds on the south of the river were sampled. Further samples were collected near the village of Umiujaq, on the tree line, on a rock bluff (56°33'N, 76°33'W) and in a palsa field inland (56°36'N, 76°12'W). Some ponds around Kuujjuarapik were sampled twice (at two weeks interval) to have an idea of temporal variability within the sampling period of community structure and environmental conditions of the ponds. Ponds sampled in this study were shallow (less than 1 m depth) and small (surface area between 0.5 and 348 m^2). Water temperature, pH, conductivity and total dissolved solids (TDS) were measured using CyberScan PC300 multimeter probes immerged in the 30 first centimetres from the surface water. Water samples were collected for the determination of the concentrations of dissolved organic carbon, chlorophyll *a* and phaeopigments. Filtration apparatus and sampling bottles were acid-cleaned (HCl 10%). Water samples used to DOC determination were filters onto pre-combusted 25 mm diameter GF/F Whatman filters (nominal pore size 0.7 μm). Filtrates were stored in glass tubes pre-washed according to Burdige & Homstead (1994) method and acidified with H_3PO_4 (25%) to a final pH of 2.0. DOC concentrations were finally obtained by high temperature oxydation

using a Shimatzu TOC analyser 5000A following Whitehead *and coll.* (2000) method. Water samples for the determination of chlorophyll a and phaeopigment were filtered onto 25 mm diameter GF/F Whatman filters (pore size 0.7 μm). Filters were then stored at $-$ 80 °C until analyses. Chlorophyll *a* and phaeopigment were determined by fluorometry, following the method developed by UNESCO (1994). Maximun depth, width and length of the ponds were measured and coordinates and altitude were noted. Water color was evaluated in the sampling container. We noted nine different colorations of water from crystal clear to brown opaque with a graduation of yellows and browns and then classed the nominal colors in numbers where 0 = crystal clear, 1 = light yellow, 2 = yellow, 3 = dark yellow, 4 = light brown, 5 = brown , 6 = dark brown, 7 = very dark brown, 8 = brown opaque.

Zooplankton samples were collected with a 7 L sampling container (or a 1 L hand pitcher for thermokarst ponds because of the harsh accessibility of the ponds) and filtered on a 104 μm mesh size net to have a quantitative sample. Volume of filtered water varied between 1 L and 70 L. In order to have a sample representative of the overall planktonic community, the container was held secured on a one-meter stick to allow sampling in the middle of large ponds and samples were collected at several points depending on the spatial variability of the pond. Between one to ten samples were collected per pond, depending on the size, the accessibility of the pond and the zooplankton abundance and then pooled. Zooplankton was transferred to borosilicate tubes of 50 mL and preserved with ethanol 95% until later counting and identification with a microscope. Zooplankton assemblages were characterized by placing taxa into seventeen categories. Cladocerans were identified to the species level except for the families of chydoridea, bosminidae and macrothrycidea. All daphnids belonging to the *D. pulex* group were pooled. Damaged cladoceran were classified into cladoceran spp. Copepods were classified as harpacticoids, calanoids and cyclopoids, except *Hesperodiaptomus arcticus*

that has been previously identified as a potential predator of *D. pulex*. Some damaged copepods were classified into copepod spp. The taxa ostracods and the insect *Notonecta* were included in a separate class. Insect larvae (Ephemeroptera, dyticidea, diptera, plecoptera, unknown larvaes and mosquito pupaes) were pooled into one class except for the larvae of the phantom midge *Chaoborus* which were placed a single class as it is an important predator of *D. pulex*.

1.3.2   Inter- and intraspecific diversity of Daphnia pulex

Twenty individuals of the *Daphnia pulex* complex from each pond were randomnly chosen to assess the genetic diversity of this complex. Individuals were genotyped at six microsatellite loci described by Colbourne *et al.* (2004). The loci used were Dpu45, Dpu502, Dpu183, Dpu30, Dpu6 and Dpu12.2. Forward primers were end-labeled with fluorescent dyes FAM or TET (Life Technologies, Univ. of Oklahoma, USA). Conditions for PCR were as described in Colbourne *et al.* (2004). PCR products were electrophoresed on 6% polyacrylamide gels and scanned with a FMBio III scanner (Hitachi, Tokyo, Japan). Allele sizes were assigned using a Fluorescent Ladder (Promega, USA). In order to assign clones discriminated in the microsatellite analysis to their species, a fragment (»850 bp) including part of the mitochondrial gene coding for the NADH dehydrogenase subunit 5 (ND5) was amplified by PCR following methods described in Colbourne *et al.* (1998) and Weider *et al.* (1999) and using primers DpuND5a and DpuND5b (Colbourne, Crease et al. 1998; Weider and Hobaek 2003). Further sequencing of this gene revealed lineages of the *Daphnia pulex* complex found in this study.

1.3.3   Statistical analyses

Relationships between the $\log_{10}$ (x+1) transformed abundance of the zooplankton groups described above and potential explanatory variables were analysed using redundancy analysis (RDA), a form of direct gradient analysis with CANOCO (TerBraak 1994). A total of eleven environmental measures were entered as explanatory variables in the RDA. These included altitude, temperature, pH, conductivity, chlorophyll a, phaeopigment, DOC, depth, water color, surface area and percentage of vegetation surrounding the ponds. Multivariate normality of data was tested in PAST vers. 1.81 with a Kurtosis test. Some variables including pH, conductivity, chlorophyll a, phaeopigment and DOC had to be Log-transformed to assess multinormality of the data set. Longitude and latitude had to be excluded from the analysis as their inflation factors were high (> 20). The type of pond (rock bluff pond, tundra pond and thermokarst) was decomposed in three dummy variables and added to the model as passive variables. The forward selection option in RDA was used to determine the minimum number of explanatory variables that could explain statiscically significant ($p \leq 0.05$) proportions of variation in the zooplankton data. The significance of the forward selection variables was assessed using Monte Carlo permutation tests (with 499 unrestricted permutations).

Another RDA was conducted in order to examine relationships between the square root transformed relative abundance of the clones of *D. pulex* and the same explanatory variables as the previous analysis. Three variables were added in the analysis to show interactions between the clones and their principal predators. These are $\log_{10}$ (x+1) *Chaoborus*, $\log_{10}$ (x+1) *Hesperodiaptomus arcticus* and $\log_{10}$ (x+1) notonecta abundances. Once again, the forward selection option was used. In addition to the type of pond, five passive variables

describing the relative abundance of the species of the *D. pulex* complex were added in the RDA triplot.

The number of genotypes, *ie* clonal richness and the Simpson's index of diversity were calculated for each pond. Simpson's index of diversity is an index of dominance and has values ranging from 0 to 1; 0 = community dominated by a single clone, 1 = community equally represented by all the clones.

1.4   Results

Table 1 summarizes the characteristics of the forty-one ponds used in this study. All other ponds were excluded from the analyses because of incomplete data. Ponds that were sampled twice showed great similarities in zooplankton composition, clonal diversity and environmental conditions and only the data of the first sampling occasion of these ponds were included in the analyses. Overall, the ponds varied greatly for all measured parameters. The pH of the studied ponds ranged from acidic (6.0) to alkaline (8.7) with a mean value of 7.2. Some exceptionally high values of DOC were found in thermokarsts that may be due to the large amount of *Sphagnum*-moss in decomposition in these ponds. The maximum DOC concentration was found in rock pond 13 (49.75 mg L^{-1}). This very high value can be explained by the occurrence of wings and a little of meat of a dead bird at the bottom of the pond that could have increased the DOC content. Conductivity had a wide range of values (from 14 to 28 800 μS cm^{-1}) and is very different between the three types of ponds (2887.9 μS cm^{-1} in rock bluff ponds, 130.1 μS cm^{-1} in thermokarsts and 47.1 μS cm^{-1} in tundra ponds). These values dropped quickly as ponds were far away from Hudson's Bay. Chlorophyll *a* varied considerably, ranging from 0.6 μg/L in the tundra pond 18 to 15.80 μg/L in the

thermokarsts 19 and 20. The number of zooplankton individuals per m^{-3} showed also great variation. The maximum value was found in the very small rock pond 13 (1 427 000 ind. m^{-3} with a surface area of 1.7 m^3) the same pond that had exceptional value of DOC. *Daphnia* and copepods together dominated the zooplankton community of 29 ponds ($\geq$ 75% of the total zooplankton.).

Table 1   Limnological characteristics of the ponds studied

Type of pond	No pond	Long	Lat	Alt (m)	Area (m^2)	Depth (cm)	Temp (°C)	Cond (μS cm^{-1})	pH	DOC (mg L^{-1})
Rock bluff	1	77.93	55.49	10.1	6.5	4.5	11.1	169.8	7.6	13.7
	2	77.93	55.49	10.1	80.2	40	9.7	159.6	8.6	13.1
	3	77.95	55.48	2.7	12.5	5	19.1	287.0	8.7	18.4
	4	77.94	55.48	2.7	26.0	9	16.4	315.0	8.8	14.2
	5	77.97	55.47	3.0	7.7	21	15.6	1375.0	8.7	13.0
	6	77.84	55.50	8.8	56.0	23	11.7	58.4	6.6	5.4
	7	77.84	55.51	8.2	6.1	27	12.1	52.8	6.0	12.2
	8	77.84	55.51	9.1	2.9	28	10.3	48.7	6.1	8.3
	9	77.83	55.50	10.4	5.6	24	10.7	55.3	6.5	9.3
	10	77.97	55.47	2.7	1.2	21	13	2620.0	7.3	25.8
	11	77.97	55.47	4.0	0.5	18	13.2	1573.0	7.6	31.2
	12	77.98	55.46	0.9	2.3	23	15.7	28800.0	8.2	12.4
	13	77.98	55.47	2.4	1.7	7	15	5680.0	7.2	49.7
	14	77.98	55.47	2.7	2.6	21	14.1	2750.0	7.9	14.8
	15	76.67	56.69	15.2	32.5	22	8.4	76.2	7.2	17.4
	16	76.67	56.69	0.0	5.2	25	9.7	202.0	7.1	14.5
	17	77.93	55.47	5.8	0.8	18	11	350.0	7.7	9.6
	18	77.97	55.47	2.4	27.1	28	12	7410.0	7.4	5.0
	Mean			5.6	15.4	20.3	12.7	2887.9	7.5	16.0
	(S.D.)			(4.2)	(21.9)	(9.1)	(2.8)	(6798.3)	(0.9)	(10.6)
Thermokarst	19	77.89	55.36	148.7	55.1	90	18	224.0	6.6	35.7
	20	77.89	55.36	149.0	37.8	90	18	337.0	6.6	37.5
	21	76.46	56.77	180.7	166.7	30	14.7	125.5	7.3	22.5
	22	76.45	56.79	186.2	86.7	60	15.5	24.7	6.0	15.9
	23	76.45	56.79	185.3	95.3	80	15.6	14.0	6.2	11.0
	24	76.44	56.77	211.8	3.5	8	15	88.9	7.0	12.1
	25	76.46	56.77	180.7	3.5	8	14.6	96.8	7.2	16.8
	Mean			177.5	64.1	52.3	15.9	130.1	6.7	21.7
	(S.D.)			(22.3)	(57.9)	(36.7)	(1.5)	(114.8)	(0.5)	(10.9)
Tundra	26	77.76	55.43	36.6	61.5	30	8.4	32.7	7.8	8.2
	27	77.78	55.44	60.4	62.1	52	8.0	36.4	7.7	13.9
	28	77.78	55.44	57.9	1.9	33	7.5	38.0	6.9	7.6
	29	77.74	55.44	46.0	27.3	48	9.3	58.5	7.6	10.1
	30	77.77	55.44	55.2	47.3	37	10.4	43.8	7.5	9.8
	31	77.79	55.44	52.1	57.2	28	11.2	47.2	7.3	15.9
	32	77.79	55.44	48.8	45.0	45	9.7	41.6	7.4	12.5
	33	77.80	55.31	60.4	78.1	76	7.2	37.6	7.5	6.9
	34	77.85	55.29	67.1	26.3	52	10.4	45.0	6.5	5.2
	35	77.88	55.32	65.8	24.6	30	10.1	33.8	6.5	9.2
	36	77.88	55.30	68.6	89.0	21	9.7	20.8	6.5	9.0
	37	77.84	55.54	49.7	120.0	48	17.1	52.4	7.4	9.6
	38	77.83	55.54	49.7	348.2	44	16.4	56.4	7.4	10.0
	39	77.93	55.51	91.7	62.4	57	14.9	64.1	7.3	5.5
	40	77.93	55.51	91.7	28.5	42	15	65.8	7.2	5.2
	41	77.84	55.30	94.2	5.6	30	10	80.0	6.5	18.1
	Mean			62.2	67.8	42.1	11.0	47.1	7.2	9.8
	(S.D.)			(17.2)	(80.9)	(13.8)	(3.2)	(15.0)	(0.4)	(3.7)
Total	Min			0	0.5	7	7.2	14.0	6.0	5.0
	Max			211.8	348.2	90	19.1	28800	8.8	49.7
	Mean			57.1	44.2	34.2	12.6	1308.5	7.2	14.5

End of Table 1   Limnological characteristics of the ponds studied (copep. = copepods;

Daphn. = daphnia and zoopl. = zooplankton)

Type of pond	No pond	Chl a (μg	Phaeo (μg L^{-1})	Water color	% vegetation	% Copep.	% *Daphn.*	Total Zoopl. (ind m^{-3})
Rock bluff	1	4.6	2.3	1	75	21.1	78.0	41402
	2	1.2	0.5	1	70	90.2	8.5	43991
	3	2.8	1.6	1	85	52.5	21.5	25286
	4	5.3	1.7	2	40	32.7	7.3	7857
	5	1.5	0.4	0	0	5.9	74.5	2429
	6	2.8	3.3	3	10	100.0	0.0	439682
	7	12.1	8.4	7	50	89.6	3.9	11000
	8	2.5	8.8	7	10	82.1	13.0	208843
	9	1.8	3.8	7	0	73.3	21.1	12857
	10	2.1	3.2	2	0	34.7	65.0	130612
	11	4.0	7.0	8	0	62.5	33.6	43429
	12	7.1	3.6	2	0	0.0	0.3	23286
	13	5.8	3.4	2	0	1.0	44.9	1426857
	14	6.5	2.3	2	0	9.3	9.5	337315
	15	0.8	0.7	3	85	8.2	91.5	44375
	16	0.9	1.8	2	15	1.6	0.0	50833
	17	1.3	2.9	4	10	28.3	38.2	44857
	18	1.2	1.3	3	0	2.2	80.8	35771
	Mean	3.6	3.2	3.2	25	38.6	32.9	162815
	(S.D.)	(2.9)	(2.5)	(2.6)	(32.9)	(35.8)	(31.8)	(337939)
Thermokarst	19	15.8	23.6	5	100	0.9	92.7	536000
	20	15.8	23.6	5	100	70.2	0.7	305000
	21	6.1	2.7	8	100	50.0	0.0	5875
	22	3.5	2.9	8	100	96.3	0.0	15571
	23	3.4	2.9	1	100	93.9	0.0	11000
	24	7.5	6.1	8	100	16.1	61.3	5167
	25	0.8	3.0	8	100	1.3	97.4	33778
	Mean	7.6	9.3	6.7	100	47.0	36.9	130342
	(S.D.)	(6.0)	(9.9)	(3.1)	(0.0)	(41.5)	(46.1)	(209350)
Tundra	26	9.5	8.4	3	5	47.0	51.3	3286
	27	3.7	1.7	3	50	85.1	10.9	63918
	28	2.8	6.6	6	0	65.2	21.7	120356
	29	2.4	0.8	1	90	6.7	82.2	3214
	30	1.2	0.8	2	50	12.5	87.4	20237
	31	2.2	2.1	5	90	6.3	90.0	100571
	32	2.2	1.7	5	50	27.6	72.3	33883
	33	1.5	1.3	2	0	9.1	89.9	2357
	34	1.6	1.9	2	100	17.1	78.8	4857
	35	2.5	2.4	3	100	10.8	85.0	59643
	36	2.9	2.5	2	80	0.0	20.0	571
	37	2.5	1.9	2	100	58.5	17.0	1514
	38	0.6	0.4	3	100	20.9	0.0	1229
	39	2.0	0.9	3	85	2.2	86.2	10343
	40	1.6	0.9	2	100	0.2	65.3	15536
	41	2.0	2.4	3	80	11.2	67.4	3179
	Mean	2.6	2.3	2.9	67.5	23.8	57.8	27796
	(S.D.)	(2.0)	(2.2)	(1.3)	(37.3)	(26.0)	(32.5)	(38170)
Total	Min	0.6	0.4	0	0	0.0	0.0	571
	Max	15.8	23.6	8	100	100.0	92.7	1426857
	Mean	5.0	3.9	3.6	54.4	34.3	43.1	104580

Zooplankton-environment relationship

The influence of 11 environmental variables on the distribution of zooplankton groups was assessed using RDA (Fig 2). The first two RDA axes, with eigenvalues of 0.189 and 0.066 for axis 1 and 2, respectively, accounted for 25.5 % of the variation in species data. However, RDA axes 1 and 2 explained a high proportion (86 %) of the variation in the species-environment relationship. The species-environment correlations for axis 1 (0.762) and axis 2 (0.787) were high, indicating a reasonably strong relationship between the zooplankton groups and the environmental variables. With forward selection and Monte Carlo permutation tests RDA identified a subset of four variables that explained significant ($p \leq 0.05$) proportion of the variation in the species data. These were temperature, conductivity, altitude and DOC which accounted for 69.7 % of the variation in zooplankton distribution. The triplot presented in Figure 2 shows clear divergence in community structure among the three types of ponds. For example, *Daphnia* seemed strongly correlated with the abundance of its predator *Hesperodiaptomus arcticus* in rock ponds and inversely correlated with *Holopedium gibberum*. Tundra ponds showed less diversity in species composition with only *Polyphemus pedicullus* and *Holopedium gibberum* being positively correlated with this type of ponds. Moreover tundra ponds had low DOC concentrations and low values of conductivity. Thermokarsts were found in higher altitude and were inhabited by cyclopoids, *Chaoborus*, *Scapholeberis* spp., chydoridae and ostracods. Rock ponds were less discriminated by environmental variables as the ranges of temperature, DOC and conductivity were wide. They supported the cohabitation of calanoids, harpacticoids, *Daphnia*, *H. arcticus*, Macrothricidae, Bosminidae, insect larvae and notonects.
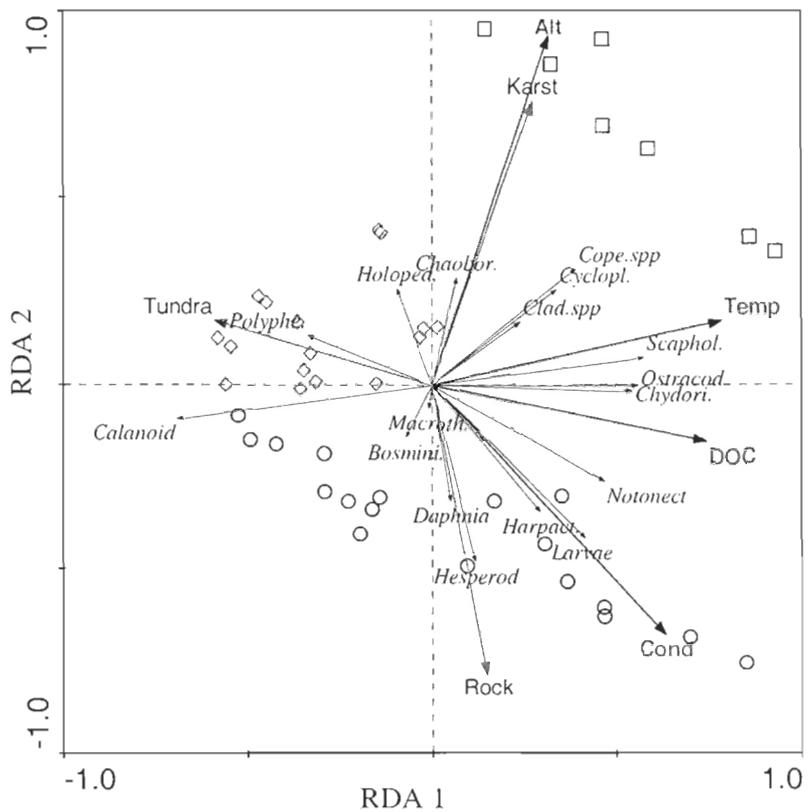
Figure 2   Triplot resulting from RDA with species as response variables and environmental factors as explanatory variables. The categorical variables describing the type of pond are added as passive variables. Samples are represented by circles (rock ponds), diamond-shaped (tundra ponds) and square (thermokarsts). Polyphe: *polyphemus pedicullus;* Holoped: *Holopedium gibberum*; Chaobor: *Chaoborus*; Cope.spp: Copepods *spp.*; Clad.spp: Cladocerans *spp.*; Cyclop: Cyclopoids *spp.*; Scaphol.: *Scapholeberis spp.*; Ostracod: Ostracods; Chydori.: *Chydoridae spp.*; Notonect: *Notonecta*; Harpact.: Harpacticoids *spp.*; Hesperod: *Hesperodiaptomus arcticus*; Bosmini.: *Bosminidae spp.*; Macroth.: *Macrothrycidae spp.*; Calanoid: Calanoids *spp.*

Daphnia pulex species and clones-environment relationship

Twenty-three of the ponds surveyed in the previous analysis were assayed for the species and genetic diversity of the *D. pulex* complex. A total of twenty-three clones were discrimated in the overall ponds studied from the microsatellite analysis. Eight clones belonged to the *D. pulex* species while two clones belonged to Western nearctic *D. pulicaria* and seven to Eastern nearctic *D. pulicaria* (*sensu* Colbourne *et al* 1998). One clone could not be discriminated between western and eastern *D. pulicaria* and four clones could not be identified to the species level. Differences in distribution of *Daphnia* species were observed (Fig 3). *D. pulex* clearly dominated in rock bluff ponds whereas eastern *D. pulicaria* dominated in tundra ponds and in thermokarsts. Eight clones were triploids and fifteen clones were diploids. Clonal diversity averaged 1.64 ($\pm$ 0.5) clones per rock ponds, 2 ($\pm$ 1) clones per thermokarsts and 2 ($\pm$ 1) clones per tundra ponds and 1.88 ($\pm$ 0.8) clones per pond in the overall survey (Table 3). None of the clones were present in all three types of ponds. Clone D1 was the most widespread clone occurring in 30 % of the ponds and representing 20 % of the total individuals of the survey. It was found mainly on one rock bluff and in one thermokarst and was the dominant clone of 57 % of the pond it inhabited. Eight clones were relatively common (D3, T4, D6, D7, D10, T11, D19 and T21). D3 co-ocurred with other clones in four ponds but had a low abundance compared to D7 which was present in three ponds but dominated in these ponds. Fourteen clones were found in a single pond, of them six comprised less than 5 % of the total individuals genotyped in the pond and were then considered as rare clones. In our study Simpson's index varied from 0 to 0.5 (Table 3). In general, one or few clones dominated the clonal community. Only five ponds (14, 17, 19, 24 and 39) had an index $\geq$ 0.4, indicating a similar abundance of individuals among the different clones.

Table 2   Description of clones, percentage of ponds in which each clone was detected, percentage of individuals belonging to each clone in all the survey and events of co-occurence with name of clones in the same pond (name of clone: D = diploid, T = triploid, the number are given in order of appearance).

| Clone	Species	% Occurence	% Abundance	Coexistence
D1	*pulex*	30	20	D7, D3, D3, D3, D2, D18
D2	*pulex*	4	2	D1
D3	*pulex*	17	5	D1, D1, D13, D1
T4	*western pulicaria*	17	9	D5, T6
D5	n. i.	4	1	T4
T6	*pulex*	9	8	T4
D7	*pulex*	12	13	D1, T4
T8	*pulex*	4	4	
D9	*eastern pulicaria*	4	3	D10
D10	*eastern pulicaria*	9	2	D9, D19
T11	*eastern pulicaria*	9	7	T21, T22
D12	*pulicaria*	4	4	
D13	*pulex*	4	3	D3
D14	*eastern pulicaria*	4	4	T15, D16, T17
T15	n. i.	4	0	D14, D16, T17
D16	n. i.	4	0	D14, T15, T17
T17	n. i.	4	0	D14, T15, D16
D18	*pulex*	4	0	D1
D19	*eastern pulicaria*	9	7	D10, D20, D23
D20	*western pulicaria*	4	0	D19, D23
T21	*eastern pulicaria*	9	5	T11, T22
T22	n. i.	4	1	T11, T21
D23	*eastern pulicaria*	4	0	D20, D19
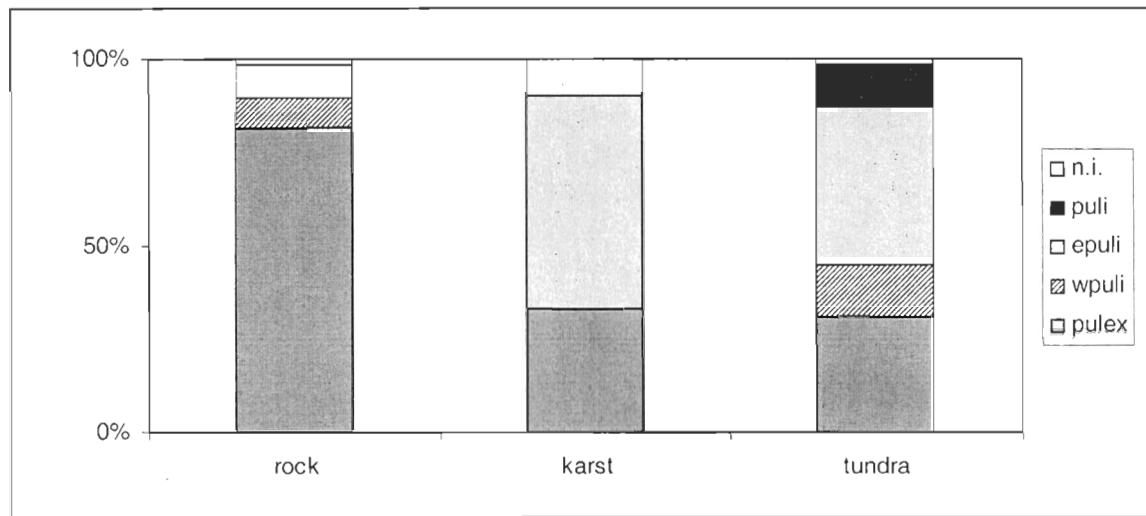
Figure 3   Relative abundance of *Daphnia* species in the three types of ponds. Puli: *Daphnia pulicaria*; epuli: Eastern *Daphnia pulicaria*; wpuli: western *Daphnia pulicaria*; pulex: *Daphnia pulex*

Table 3   Type of ponds, number of clones detected in each pond, ploidy levels and Simpson's index of diversity (1-D) on clones.

	No. of pond	Clone richness	Ploidy levels	1-D
	1	1	$2n$	0.0
	2	2	$2n, 3n$	0.3
	3	2	$2n$	0.3
	8	1	$3n$	0.0
	10	2	$2n$	0.3
Rock bluff	11	2	$2n$	0.3
	13	2	$2n$	0.1
	14	2	$2n$	0.4
	15	1	$3n$	0.0
	17	2	$2n$	0.5
	18	1	$2n$	0.0
	19	2	$2n$	0.5
Thermokarst	24	3	$3n$	0.5
	25	1	$3n$	0.0
	26	2	$2n, 3n$	0.1
	27	3	$2n$	0.2
	28	1	$3n$	0.0
	29	1	$3n$	0.0
Tundra	33	2	$3n$	0.3
	34	4	$2n, 3n$	0.3
	39	2	$2n$	0.4
	40	2	$2n$	0.3
	41	1	$2n$	0.0
Min.		1		0.0
Max.		4		0.5
Mean		1.88		0.2

The influence of 14 environmental variables on the distribution of clones was assessed using RDA (Fig 4). The first two RDA axes, with eigenvalues of 0.160 and 0.073 for axis 1 and 2, respectively, accounted for 23.3 % of the variation in species data. RDA axes 1 and 2 explained a high proportion (81.1 %) of the variation in the species-environment relationship. The species-environment correlations for axis 1 (0.89) and axis 2 (0.87) were high, indicating a reasonably strong relationship between the clones and the environmental variables. With

forward selection and Monte Carlo permutation tests RDA identified three variables that explained significant ($p \leq 0.05$) proportion of the variation in the clones data. These were conductivity, pH and depth, which accounted for 38.8 % of the variation in clone distribution. Low conductivity seemed to positively influence the distribution of triploid clones (all species included) and was correlated with tundra ponds whereas high conductivity, found notably in rock ponds, near the Hudson Bay, favoured the occurrence of diploid clones of *Daphnia pulex*. Low pH determined the occurrence of eight clones (T11, D12, T22, T15, T17, T21, D14, D16) all belonging to eastern *D. pulicaria* and non identified *Daphnia*. One can suppose that, according to the triplot and the small angles between their arrows, the non identified *Daphnia* belong to the eastern *D. pulicaria* species. High pH, feature of some rock ponds, determined the occurrence of D5 and T4 and in general, of western *D. pulicaria*. Six clones, all of eastern *D. Pulicaria* (D10, D9, D21, D23, D19 and D7) were clustered together and were correlated with depth. They occurred mainly in tundra ponds.
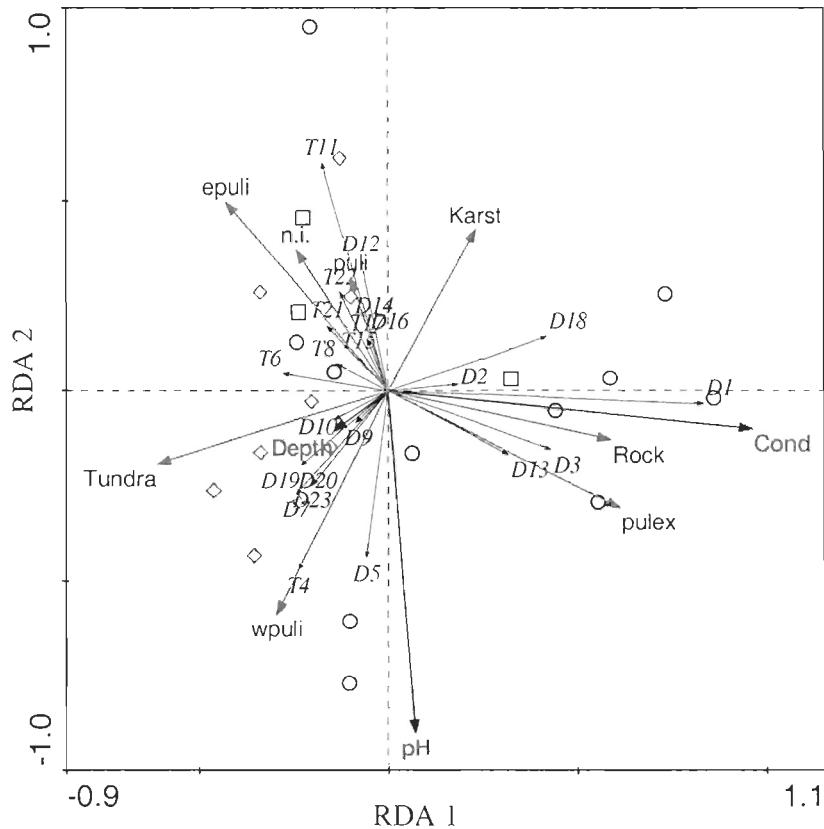
Figure 4   Triplot resulting from RDA with clones as response variables and environmental factors as explanatory variables. The categorical variables describing the type of pond and the species of *Daphnia pulex* complex are added as passive variables. Samples are represented by circles (rock ponds), diamond-shaped (tundra ponds) and square (thermokarsts). Puli: *Daphnia pulicaria*; epuli: Eastern *Daphnia pulicaria*; wpuli: western *Daphnia pulicaria*; pulex: *Daphnia pulex*

1.5 Discussion and conclusion

A growing interest has been devoted toward research on freshwater ecosystems at high latitude. Main limnological data on arctic and subarctic lakes and ponds have been recorded from Alaska to Finland (Rautio 1998; Swadling, Pienitz et al. 2000; Swadling, Gibson et al. 2001; Rautio and Vincent 2006). Heterogeneity of the forest-tundra region geomorphology in Subarctic Québec results in great variation of environmental conditions in shallow waterbodies. This represents a good opportunity to study fundamental species-environment relationships. This study aimed to characterize Subarctic Québec shallow ponds and examine the distribution pattern and abundance of zooplankton and its relationship with abiotic and biotic gradients under three scales of variation, community, interspecific and intraspecific.

In this study, the pH ranged from 6.0 to 8.7. Rock bluff ponds experienced the widest pH range as both minimum and maximum values of the survey have been encountered there but had a mean pH value higher than that of tundra or thermokarst pond. This can possibly result from dissolution of the carbonate bedrock that formed the basins, as proposed by Swadling and *coll.* (2001). In peatland ponds, it has been shown that high concentration of humic matter can be responsible for the more acidic waterbodies (Arlen-Pouliot and Bhiry 2005). Very high values of conductivity of some rock ponds are due to the salts carried in seaspray from nearby Hudson Bay where conductivity has been recorded as 38.3 mS cm^{-1} during the sampling period. Concentration of DOC in this study reached extremely high values in some ponds. Except for pond 13 which we mentioned above, the high values were mainly found in thermokarsts (mean 21.7 mg L^{-1}) with higher values in pond 19 (35.7 mg L^{-1}) and 20 (37.5 mg L^{-1}). These ponds are located at the base of a palsa and are completely surrounded by vegetation (mostly *Sphagnum*, pruces and mosses). Thus, input of DOC from

terrestrial surrounding vegetation must be relatively high. Moreover, the deep tea color of the water indicated that there was a lot of humic matter in suspension in the water column, also contributing to high values observed of dissolved organic carbon. DOC is an important abiotic factor in all aquatic ecosystems. It is a potential energy source for zooplankton (Salonen and Hammer 1986; Arlen-Pouliot and Bhiry 2005) and can be a protection against light penetration. It participates to the absorption of ultraviolet radiation through the water column and therefore helps protecting aquatic organisms from the damaging effect of UV wavelengths (Davis-Colley and Vant 1987). At high concentrations however, it can partly inhibit photosynthesis and primary production as it limits light penetration. Surprisingly, chlorophyll a concentrations reached their maxima values (15.80 μg L^{-1}) in those two thermokarsts (ponds 19 and 20). Those high values may be biased toward the input of tree leaves and peat-moss degradation in the ponds. In general, the chlorophyll a concentrations found in this study are comparable to those reported in a previous study in the same region (Swadling, Gibson et al. 2001). Zooplankton abundance also varied greatly (between 570 and 1 427 000 ind m^{-3}, in ponds 36 and 13 respectively); the maximum abundance was found in pond 13 that reached the maximum concentration of DOC and was constituted mainly of *Daphnia* and chydoridae. This high value may be due to an aggregation of individuals in the amount of water sampled. In fact, we often observed crowded 'clouds' of *Daphnia*. Detailed examination of zooplankton showed that *Daphnia* and copepods together dominated the community in the three quarters of the ponds sampled. Inside the copepod taxa, we found that *Leptodiaptomus minutus* was the dominant copepod species, following by *Hesperodiaptomus arcticus* and *Microcyclop rubellus*.

Zooplankton-environment relationship

The RDA analysis revealed that temperature, conductivity, altitude and DOC together explained 25.5 % of the variation in species composition. No other variable tested was statistically significant. The biotic factors tested here (chlorophyll a, phaeopigment) did not influence zooplankton assemblages. If the concentration of chlorophyll a can be a good estimator of phytoplanktonic biomass, it does not give information on food quality. The food particle size preference can be different among filter-feeding zooplankton species. For example, cladocerans of arctic and subarctic ponds grazed most efficiently on bacteria and picophytoplankton whereas copepods tended to feed on larger food particules (Rautio and Vincent 2006). Examination of the phytoplankton of few ponds in this study revealed that nanoplankton via small flagellates ($\leq 10 \mu$m) dominated the total biomass (data not shown). Moreover, it has been demonstrated that benthic algae represent a high proportion of food available for grazing taxa (Rautio and Vincent 2006; Rautio and Vincent 2007). Small value of percentage of variance explained by environmental variables is typical to species data and is due to large number of taxa and many zero values (TerBraak 1994). Moreover, other local or regional factors may play a significant role in species distribution. Testing for the effect of competition or predation in a whole zooplankton data set is a difficult task because each invertebrate predator as well as each potential competitor is a part of the zooplankton community. Excluding those species from the species matrix and including them in the explanatory variables matrix changed the overall analyses. However, during the data screening, even with this data set structure, we found no evidence of an affect of predation on the remaining species.

Temperature was the most important factor structuring zooplankton communities in the ponds surveyed. Water temperature is mostly a function of air temperature and volume of ponds. Larger and deeper ponds buffer temperature variation more efficiently than small

shallow ponds. As a result, the distribution of zooplankton taxa in habitats of different size can be dependant on the temperature tolerance range of species, range that can vary broadly among species, even closely-related. *Daphnia* are thought to be favoured by low temperatures (Steiner 2004), while increasing temperatures may favour small-bodied cladocerans (Bengtsson 1987). This was also seen in this study as Chydoridea were strongly associated with high temperature whereas *Daphnia* had medium temperature preference. Calanoid copepods and *Polyphemus pedicullus* preferred low temperatures. However, one must be careful with the effect of this parameter on zooplankton communities. Here, we evaluated a single measurement of temperature on species distribution. As it is highly correlated with air temperature, a several degree difference between days would most likely influence the results. Harpacticoids, insect larvae (except *Chaoborus*), notonects, *Daphnia* and *Hesperodiaptomus arcticus* were associated with increased conductivities. Conductivity has already been shown to be an important factor contributing to copepods (Swadling, Gibson et al. 2001) and *Daphnia pulex* (Weider 1987) distribution in this region.

Studies on the species distribution of zooplankton along an altitudinal gradient have demonstrated that species richness decreased with increasing altitude (Patalas 1964; Hebert and Hann 1986; Rautio 1998), which is in accordance with the prediction of island biogeography (MacArthur and Wilson 1967) that the more isolate the habitat is, the less it would have species able to colonize it. However, the altitude gradient in this study is relatively low (from sea-level to 211 m high) and high altitude ponds were not associated with less taxa here. Nevertheless, we have to keep in mind that species richness among certain taxa as copepods, chydoridae, macrothicidea and bosminidae were not evaluated here. The significant effect of altitude on species distribution may probably be a result of interactions with other factors (peatland catchment, vegetation type and water chemistry, for example)

rather than colonisation abilities of zooplankton taxa. Nevertheless, altitude gradient is a good discriminator of our types of ponds in this region; the rock bluff ponds being near the sea-level, tundra ponds between 30 to 100 m high and then thermokarts up to 210 m high. Finally, DOC was the fourth factor contributing significantly to the zooplankton community structure. Low DOC concentrations were tolerated by only few species, *Holopedium gibberum*, *Polyphemus pedicullus* and calanoid species. Except if they require low DOC concentrations as *Holopedium gibberum* (Leech, Padeletti et al. 2005), low protection from UV radiations offered by DOC in tundra ponds may be compensated by vegetation catchment of those ponds that can act as a refuge for these species.

Daphnia pulex species and clones-environment relationship

Clonal diversity of *Daphnia pulex* in the studied region was 1.86 clones per pond. Previous investigations of clonal diversity of the *D. pulex* complex on the other side of the Hudson Bay in the Churchill region (Manitoba) counted an average of 2.9 clones of *D. tenebrosa* (Dufresne and Hebert 1995), a species not found eastern of the bay and averages of 1.5 and 1.7 clones per ponds for pigmented and non-pigmented *D. pulex*, respectively (Weider and Hebert 1987). Southerly, Hebert *et al.* (1988) found a clonal diversity of obligately parthenogenetic populations of *D. pulex* of 2.8 clones per pond in the Great Lakes region. Our results are then in agreement with the general assumption that species (here, clonal) diversity decreases with increasing latitude.

In general, ponds were dominated by one or few clones. Local adaptation and local genetic differentiation may explain the ecological divergence between clones. Hebert *et al*. (1988) qualified clones as ecotypes because they differed physiologically and had different

ecological demands. The RDA showed interesting pattern in clonal assemblages. Of all the variables considered here, conductivity, pH and depth accounted for a great percentage of the variation in clones distribution. Triploid clones are restricted to low conductivity water bodies while diploid clones of *D. pulex* was found mostly in rock ponds that exhibited relatively high conductivities. These results contrast with previous works on *D. pulex* clones by Weider and Hebert (1987) and Wilson and Hebert (1992). In Churchill ponds, melanic clones, that are also polyploids, are found in rock bluff ponds and at much higher salinities than polyploids of the Kuujjuarapik region and diploid are restricted to ponds with high humic content. It seems that polyploids are not more tolerant to a broader range of ecological conditions but their apparent segregation may involve competitive abilities toward diploid clones. This competition can involve some of their life-history characteristics. For example, polyploid *Daphnia* are generally larger than their diploid counterpart. As invertebrate predator such as the larvae of the phantom midge *Chaoborus* prey on small *Daphnia*, this size-dependant invertebrate predation could partly explain the distribution of different cytotypes of *Daphnia*, though nothing in this study supports this assumption. Dufresne and Hebert (1997) demonstrated that in North America, *D. pulicaria* is divided into three distinct lineages that originated from different glacial refugia. We have seen that in this study region, Nunavut, two of those lineages are sympatric. However, despite their close taxonomic and phylogenetic relationship, western and eastern *pulicaria* species had different pH tolerance (see Fig. 4) that permits them to inhabit different habitats thus escaping from intercompetition. A similar pattern exists within *D. pulicaria* and *D. pulex*. In eastern Canada, it is admitted that *Daphnia pulicaria* is restricted in lakes whereas *D. pulex* is found in ponds (Cerny and Hebert 1993). However, in this study, *D. pulicaria* was found in more than half of the ponds studied. In opposition to the hypothesis that it occurs in large surface area water bodies (*ie.* lakes) because of higher environmental heterogeneity, here, we argue that depth is a determinant

factor in species distribution of the *D. pulex* complex. RDA shows that the occurrence and abundance of *D. pulicaria* is positively correlated with depth and that *D. pulex* is found mainly in rock ponds that are generally less deep than tundra ponds or thermokarsts.

This study provides a new integrative approach in fundamental ecology because it gives an insight of the relationship between different scales of biodiversity and its environment. Biotic and abiotic factors were explored to explain structure of community of the whole zooplankton, then we focused on one of its component, the *Daphnia pulex* complex and searched for ecological patterns among species and inside species, at the genetic level. At the three scales, physicochemical factors explained directly the distribution of organisms. If one environmental condition favours the occurrence of one species, it is difficult to attest for a better fitness under this condition or a better competitive ability or for the possibility that this species was the first colonizer of the pond and that no subsequent species had displaced it. Interactions between abiotic, biotic and historical factors can be analysed in experimental studies. Wilson and Hebert (1992) established the selective importance of abiotic factors, competition and predation in structuring clonal assemblages of *D. pulex* in a study combining observations of distributional patterns with experimental manipulations. *In situ* observations showed that physical factors such as salinity contributed to the spatial repartition of clones. In experiments, they highlighted the role of competition in limiting clonal richness in ponds and also found an interaction between competition and predation on the ability of certain clones to colonize and dominate habitats in their range of ecological tolerance.

The wide ecological tolerance associated with zooplankton of subarctic ponds and the more or less large overlap in taxa distribution may be explained by high species and genetic diversity. In this study, the genus *Daphnia* was absent from only six of the forty-three ponds

surveyed and distributed in all types of ponds over broad environmental conditions. However, interspecific distribution of *Daphnia* varied markedly. Species distribution was correlated with environmental gradients. The great variation in clonal distribution indicated that there was a strong genotype-environment interaction as proposed by Weider (1987). Ploidy level had certainly an effect on the distribution of clones, as diploids and polyploids rarely coexisted in ponds and triploids were segregated in low conductivities water.

From this study, we can hypothesize that the more genetic diversity a species has, the widest distribution and ecological tolerance it will have. In order to predict biodiversity changes resulting from climate warming in subarctic and arctic regions, it is thus necessary to have an insight on the genetic diversity of species and their interaction with the surrounding ecosystem. Further studies are needed on the other zooplankton taxa in order to have a better understanding of biodiversity in freshwater ecosystems from high latitudes.

and Hebert (1987) also revealed ecophysiological differences among *D. pulex* clones from the Churchill region (Manitoba) and suggested that those clones were not ecological equivalents.

Our results suggest no difference in aerobic and anaerobic capacity (estimated by ETS, CS and LDH enzyme capacities) among *D. pulex* clones after short-term acclimatization to stressful conditions as well as no ability to adjust metabolic capacities to these conditions. Studies that have observed different ETS activities among different crustaceans species had linked this variability to different environmental conditions tolerance and spatial distribution (Simcic and Brancelj 1997; Yurista 1999; Simcic 2004; Simcic 2006). In contrast to these studies which showed differences at interspecific level, the present work did not show any metabolic differences at the intraspecific level. Since body mass can affect metabolic rate and enzymatic capacity, mass must be considered when comparing metabolism capacities to avoid bias due to allometric factor. Here, apparent enzymatic differences were mostly explained by mass variability. Since enzyme capacities are not influenced by pH or temperature and did not differ among clones, it seems that differential distribution of *D. pulex* clones used in this work is poorly influenced by metabolic capacity. Our results stand in contrast to results from previous studies that noted a relationship between metabolic differences and species distribution (Simcic and Brancelj 1997; Simcic 2004; Simcic 2005; Simcic 2006). Since mass highly influences metabolic capacity it would be of great interest to revisit their conclusions considering the possible mass differences among species.

Briefly, metabolic capacity of *D. pulex* clones used in this study did not vary among pH and temperature treatments. Moreover, aerobic and anaerobic capacity did not differ among clones. In the light of our results, metabolism does not seem to explain geographic repartition pattern of *D. pulex* clones used. Other parameters such as body mass and life-history traits

could explain the distribution of polyploidy *D. pulex* clones. A previous study on *D. pulex* life-history traits has shown large inter-clonal variability in response to temperature shifts within each ploidy level (Dufresne and Hebert 1998). Thus, to confirm or infirm the influence of metabolism on the distribution of *D. pulex* clones, future research should examine more clones of each ploidy level and explore different enzymes affecting the different energetic pathways.

2.6   Acknowledgments

CHAPITRE 3

Differential survival among genotypes of *Daphnia pulex* differing in reproduction mode, ploidy level and geographic origin

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3.1   Abstract

The distributional pattern of geographical parthenogenesis has not been clearly explained yet. In *Daphnia pulex*, asexuals are found at higher latitude and in more marginal habitats than their sexual relatives. Some asexual lineages have also become polyploid. In order to understand this spatial disjunct distribution among different cytotypes of *Daphnia pulex*, this study aimed to test if polyploid clones were more resistant than sympatric diploid clones to a wide range of environmental factors and if asexual *Daphnia* (diploid clones) are more tolerant of extreme environmental conditions than sexual ones. We report significant differences in survivorships after short-term exposure to acute pH, conductivities, and temperatures in 12 clones of the *Daphnia pulex* complex. However, ploidy level and reproductive mode did not influence survivorship. Historical factors could play a substantial role in generating the pattern of geographical parthenogenesis. Local adaptation and the incomplete isolation of reproductive modes are indeed very important in explaining the ecological differences among clones.

Keywords: *Daphnia pulex*, geographical parthenogenesis, polyploidy, tolerance,

temperature, conductivity, pH

3.2   Introduction

Asexual organisms frequently dominate at higher latitudes and altitudes and in more marginal habitats than their sexual relatives, a pattern referred to as geographical parthenogenesis (Vandel 1928). Even though this disjunct spatial distribution has been known for almost a century, we still lack an adequate explanation for it. Different types of non mutually-exclusive hypotheses (historical, demographic, ecological, and evolutionary) have been proposed to explain geographical parthenogenesis. Demographic hypotheses refer to the fact that asexuals do not pay the twofold costs of sex (male production) and therefore have a numerical advantage over sexuals (Maynard-Smith 1998). Asexuals can establish populations from a single individual and hence can colonize remote areas more rapidly than sexuals (reproductive assurance hypothesis,(Baker 1955; Cuellar 1994)). They do not suffer from genetic bottlenecks at low population densities and hence may outcompete sexuals at the edge of a geographical range (Peck, Yearsley et al. 1998; Parker and Niklasson 2000; Haag and Ebert 2004). Under an ecological scenario, asexuals are better competitors or have fitness advantages over sexuals under certain ecological conditions (Glesener and Tilman 1978), owing largely to their frequent hybrid origins. Historical explanations refer to the association between parthenogenesis and environments that were strongly affected by the Pleistocene glacial cycles (Stebbins 1984; Kearney 2005). The repeated advances and retreats of glaciers has resulted in the creation of refugial races which were free to colonize new environments as glaciers retreated. Due to their better colonizing abilities, asexuals may have been able to follow glacial retreats faster than sexuals, hence the pattern of geographical parthenogenesis.

One important confounding factor of asexuality and geographical distribution is the frequent association of apomixis and polyploidy. All apomictic angiosperms are polyploid

(Asker and Jerling 1992) but not all polyploid plants are asexual. In the Animal Kingdom, the association between polyploidy and parthenogenesis is present in two thirds of taxa, mostly insects and reptiles (Suomalainen, Saura et al. 1987; Otto and Whitton 2000). « Geographical polyploidy » has been coined by zoologists to emphasize the role played by polyploidy in geographical parthenogenesis (Little, DeMelo et al. 1997; Stenberg, Lundmark et al. 2003). Genome polyploidization may result in unique gene combinations, an altered expression patterns, enlarged body, or cell size and elevated level of heterozygosity (Parker and Niklasson 2000). This has been argued to make polyploid clones more tolerant to abiotic stress and to possess wider ecological tolerances than their sexual ancestors (Lewis 1980) i.e. general-purpose genotype (Lynch 1984). Few studied have been conducted to examine ecological and physiological tolerances of natural asexuals/polyploids taxa with related sexuals.

Daphnia pulex, a cosmopolite freshwater microcrustacean, has a wide distribution in North America, being found from Mexico to the Arctic (Hrbacek 1987). Temperate populations of this species reproduce by cyclical parthenogenesis, that is an alternation between asexual (through the production of unfertilised subitaneous eggs in the summer) and sexual reproduction (through the production of sexual resting eggs in the fall). Some lineages have made permanent transitions to obligate parthenogenesis owing to genes that suppress meiosis in females but not in males(Innes and Hebert 1988). As a result males carrying these genes can mate with sexual females and most of the resulting offspring will reproduce by obligate parthenogenesis (Innes and Hebert 1988). Eastern populations of Daphnia pulex are strictly asexuals, mixed populations (both sexuals and asexuals) are found in Ontario whereas western populations reproduce by cyclic parthenogenesis. In addition, some asexual lineages have also become polyploid (i.e. more than two sets of chrosomosomes)(Beaton and Hebert

1988). These polyploid lineages are prevalent in arctic and some high alpine areas whereas diploid lineages dominate in temperate zones (Hebert, Schwartz et al. 1993; Weider, Hobaek et al. 1999; Hebert and Finston 2001; Adamowicz, Gregory et al. 2002; Weider and Hobaek 2003; Aguilera 2007). Ecological differentiations of these clonal lineages are not well understood. Subsistence of clonal diversity in environmental heterogeneous habitats suggests that clones have diverged physiologically into ecotypes, result of adaptive differentiation to diverse environmental conditions (Weider and Hebert 1987; Boersma 1999).

This study aimed to test if 1) polyploid clones are more resistant than sympatric diploid clones to a wide range of environmental factors and if 2) asexual *Daphnia* (diploid clones) are more tolerant of extreme environmental conditions than sexual Daphnia. We report significant differences in survivorships after short-term exposure to acute pH, conductivities, and temperatures in 12 clones of the *Daphnia pulex* complex.

3.3   Materials and methods

3.3.1   Origins of clones

Ploidy level, origin, reproduction mode and heterozygoty of the twelve clones are described in table 1. Heterozygoty of the clones was obtained by genetic typing using seven to nine microsatellite markers (Dpu 12.2, Dpu 12.1, Dpu 40, Dpu 6 Dpu 30, Dpu 45, Dpu 502 and Dpu 183).

3.3.2   Culture conditions

Ten adult females of each clone were kept in culture in environmental growth chambers (ThermoForma Diurnal Growth Chamber) (pH 7, 20 °C and 16 h light: 8 h dark diurnal cycle). Clones were cultured in 4L aquaria with filtered pond water. They were fed with an algal suspension of *Selenastrum sp.* twice a week (approx. concentration of 100 000 cells/L). Algal concentrations were standardized with a hematocytometer. The culture medium was changed weekly. Clonal lineages were raised during three generations, with all mothers sorted out at each generation to avoid maternal effect (Lynch and Ennis 1983).

3.3.3 Tolerance experiments

Acute tolerance experiments were performed following the USEPA method for daphnid acute toxicity test (USEPA 1982). Preliminary experiments were conducted to determine values of conductivities, pH and temperature that would result in gradual mortalities over a 48 hour period. Acute conductivities (80 and 1500 μS/cm), pHs (5 and 10) and temperature (30°C) were determined to be in the *Daphnia* tolerance interval ranges. PHs were adjusted with drops of NaOH or HCl and conductivities with distilled water and instant ocean salts. Ovigerous female were isolated in 40ml plastic cups. Thirty neonates (< 24h) were randomly removed, rinsed with pond water containing no algae, and transferred to each experimental solutions. Ten neonates were set-up per 40 ml plastic cups in triplicates. Ten additional neonates were transferred into a control solution (pond water, 20°C, pH 7 and 270 μS.cm^{-1}). Organisms were not fed during the experiments and dead ones were counted and removed after 12h, 24h, 36h and 48h. Death was assumed when organisms were immobile for 15s after they were gently shaked. PH test solutions were renewed daily to avoid buffer effect and changes in pH. Except for the temperature, all experiments were performed in the 20°C incubation chamber. The 30°C test was performed in an incubation chamber with a natural

diurnal light regime provided by external windows. For all tests, mortality in controls was less than 10%.

3.3.4 *Statistical analysis*

SAS software (9.1.3) was used for all statistical analyses. Kruskall-Wallis analyses were performed to test the effect of ploidy level, reproductive mode, geographic origin, clone, and heterozygoty on survivorship of all twelve clones (%) at each treatment. *Post hoc* comparison tests (non parametric Tuckey test) were used to determine which means differed significantly. Significance was assessed at the 0.05 (or lower) level for all tests.

Median lethal time (LT $_{50}$) were calculated using PROBIT procedure in SAS. When possible, 95% fiducial limits were used to compare values of LT $_{50}$ among clones.

3.4   Results

3.4.1 *Survival*

There was no significant effect of ploidy level, geographic origin, and heterozygosity on survival rates after a 48 h exposure at each treatment (Table 2). Reproductive mode had a significant effect on the survival of *D. pulex* clones with sexual clones suffering more mortality at $1500\mu S.cm-1$ and less at pH 5. Clone had a significant effect on survivorship at all treatments (table 2). Non parametric multiple comparisons Tukey test ($p \leq 0.05$) revealed differences between DAT-3 and DST-8 clones at 30°C. Also, there was important intraclonal variability according to their standard deviation (Figure 1, 2 and 3).

3.4.2   Median lethal time

Median lethal time (LT $_{50}$) differed among clones at each treatment and fiducial limits often overlapped (table 4). Some clones showed no or not enough variations in mortality so it was not possible to build a regression slope. Consequently, those clones, without 95% fiducial limits values, could not be considered.

Acute conductivities. At 80 uS.cm^{-1} PN-232 and DST-102 suffered no mortality. No differences in tolerance to low conductivity were observed among PN-9, DAT-41 and DAT-3 and between DAN-86 and DAN-52. Also these last two died sooner than DAT-41. PN-9 was more tolerant than DAN-52 and DAT-3 had similar mortality than DAN-86. At 1500 uS.cm^{-1} no mortality was noted for DAT-3, DAT-10, DAN-52 and PN-232. DAN-86 and PN-9 had greater high conductivity tolerance than DST-1.

Acute pH. DST-1, DST-102, DAT-41 and DAT-3 suffered no mortality at pH 5. PT-1-21 was the less tolerant clone at this treatment; all others having overlapping fiducial limits. At pH 10 no mortality was observed for DAN-86. DST-102 was the less tolerant clone; all others showed similar tolerance at acute high pH.

Acute temperature. At 30°C, no mortality was observed for DST-8. DST-1 with PN-95 and DAN-52 had greater tolerance than DST-102, DAT-41 and PN-232. PN-232 was less tolerant than DST-102.

Table 1   Distributions and reproductive characteristics of twelve clones of *Daphnia pulex*.

Clone	Ploidy level	Reproduction mode	Geographic origin	Latitude/Longitude	Heterozygoty
DST-1	2	Sexual	Minnesota, U.S.	45°11/93°34	0.89
DST-8	2	Sexual	Ontario, CA	42°34/80°15	0.33
DST-102	2	Sexual	Illinois, U.S.	40°07/88°12	0.33
DAT-41	2	Asexual	Quebec, CA	50°09/70°10	0.53
DAT-3	2	Asexual	Ontario, CA	43°44/80°57	0.89
DAT-10	2	Asexual	Michigan, U.S.	42°75/84°54	0.89
DAN-86	2	Asexual	Quebec, CA	55°18/77°55	0.78
DAN-52	2	Asexual	Quebec, CA	55°18/77°55	0.86
PN-95	3	Asexual	Quebec, CA	55°18/77°55	0.4
PN-232	3	Asexual	Quebec, CA	55°18/77°55	0.67
PN-9	3	Asexual	Quebec, CA	55°19/77°29	0.73
PT-1-21	3	Asexual	Ontario, CA	42°16/82°58	1

Table 2   Effect of clone and reproduction mode on survival rates after a 48 h exposition to each treatment according to Kruskal Wallis test.

	Treatment	d.l.	$\chi 2$	P
Reproduction	$1500\mu S.cm^{-1}$	1	8,1763	0,0042
	pH 5	1	7,7379	0,0054
Clone	$80\mu S.cm^{-1}$	11	20,6904	0,0367
	$1500\mu S.cm^{-1}$	11	29,0053	0,0023
	pH 5	11	21,4459	0,0290
	pH 10	11	21,7369	0,0265
	30°C	11	26,1530	0,0062
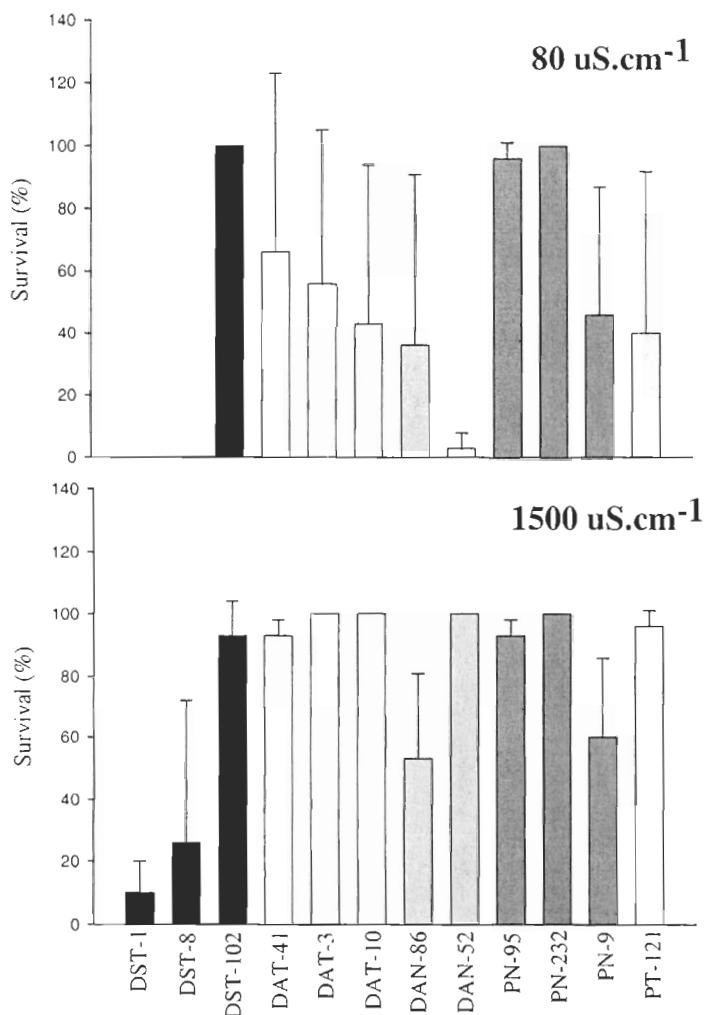
Figure 1　　　Mean (S.D.) survival (%) of twelve *Daphnia pulex* clones (n = 3) exposed to a 48 h acute conductivity. DST: diploid sexual clones from temperate regions; DAT: diploid asexual clones form temperate regions; DAN: diploid asexual from Nordic region; PN: polyploidy clones from Nordic region; PT: polyploidy clones from temperate regions.
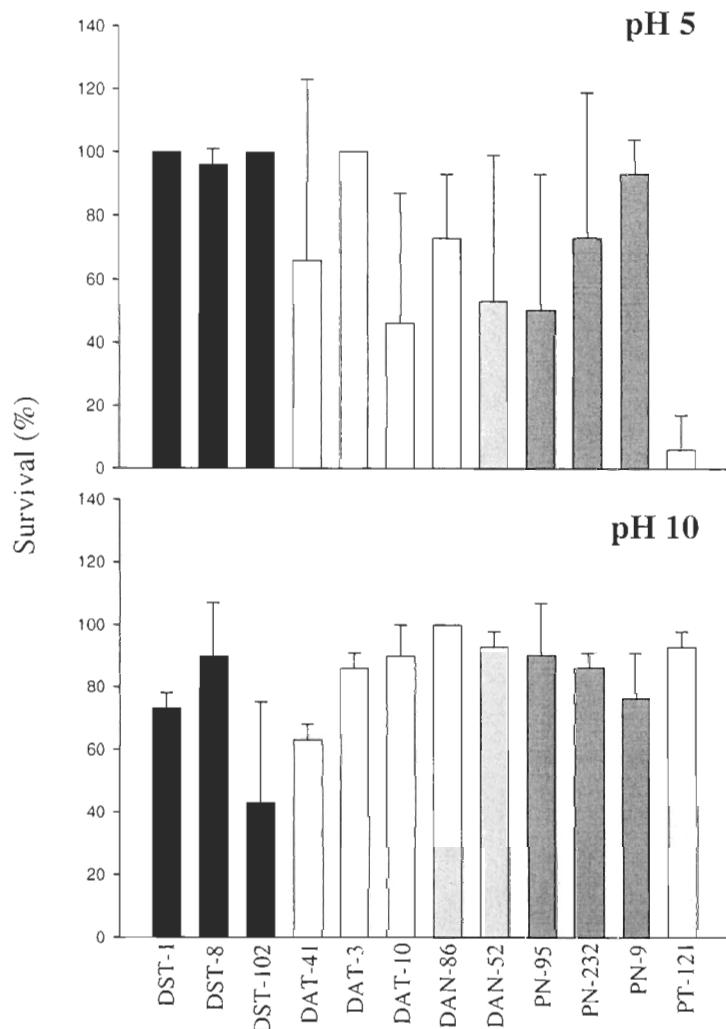
Figure 2   Mean (S.D.) survival (%) of twelve *Daphnia pulex* clones (n = 3) exposed to a 48 h acute pH. DST: diploid sexual clones from temperate regions; DAT: diploid asexual clones form temperate regions; DAN: diploid asexual from Nordic region; PN: polyploidy clones from Nordic region; PT: polyploidy clones from temperate regions.
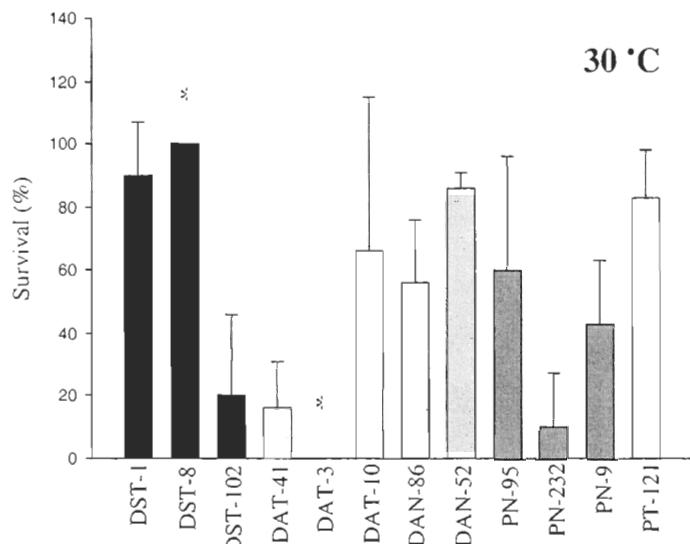
Figure 3   Mean (S.D.) survival (%) of twelve *Daphnia pulex* clones (n = 3) exposed to a 48 h acute temperature. DST: diploid sexual clones from temperate regions; DAT: diploid asexual clones form temperate regions; DAN: diploid asexual from Nordic region; PN: polyploidy clones from Nordic region; PT: polyploidy clones from temperate regions. * means statistical differences between treatment according to multiple comparisons Tukey test (p ≤ 0.05).

Table 3 Median lethal time (LT $_{50}$) and 95% fiducial limits for each clone at 80 and 1500 uS.cm^{-1}. 0 in parenthesis mean that no mortality was observed until 48h. Dashes in fiducial limits are present when there was just one point to make the regression slope.

Clone	LT $_{50}$ (h) 80uS.cm^{-1}	95% Fiducial limits		LT $_{50}$ (h) 1500uS.cm^{-1}	95% Fiducial limits	
DST-1	13.9	-	-	24.1	9.2	37.2
DST-8	6.0	-	-	30.2	-	-
DST-102	- (0)	- (0)	- (0)	51.2	-	-
DAT-41	58.8	49.0	85.8	51.2	-	-
DAT-3	47.8	41.6	59.4	- (0)	- (0)	- (0)
DAT-10	32.3	-	-	- (0)	- (0)	- (0)
DAN-86	37.3	33.0	42.9	47.1	42.9	54.6
DAN-52	25.0	8.8	37.5	- (0)	- (0)	- (0)
PN-95	52.0	-	-	172.7	-	-
PN-232	- (0)	- (0)	- (0)	- (0)	- (0)	- (0)
PN-9	46.2	39.8	57.8	51.3	44.5	65.8
PT-1-21	31.4	-	-	52.0	-	-

Table 4   Median lethal time (LT $_{50}$) and 95% fiducial limits for each clone at pH 5 and

pH 10. 0 in parenthesis mean that no mortality was observed until 48h. Dashes in fiducial

limits are present when there was just one point to make the regression slope.

Clone	LT $_{50}$ (h) pH 5	95% Fiducial limits		LT $_{50}$ (h) pH 10	95% Fiducial limits	
DST-1	- (0)	- (0)	- (0)	53.9	49.0	78.3
DST-8	93.9	-	-	83.9	59.5	3148.0
DST-102	- (0)	- (0)	- (0)	41.7	37.1	48.5
DAT-41	- (0)	- (0)	- (0)	55.3	46.4	77.0
DAT-3	- (0)	- (0)	- (0)	77.8	57.5	237.9
DAT-10	42.2	28.4	416.7	82.4	59.1	632.4
DAN-86	60.4	49.5	92.8	- (0)	- (0)	- (0)
DAN-52	45.2	39.5	55.0	140.1	-	-
PN-95	47.5	43.9	54.0	72.7	55.8	337.1
PN-232	49.4	-	-	63.3	52.6	615.3
PN-9	51.2	-	-	56.9	49.9	91.8
PT-1-21	25.5	22.2	28.8	94.6	-	-

Table 5   Median lethal time (LT $_{50}$) and 95% fiducial limits for each clone at 30°C. 0 in

parenthesis mean that no mortality was observed until 48h. Dashes in fiducial limits are

present when there was just one point to make the regression slope.

Clone	LT $_{50}$ (h)	30°C	95% Fiducial limits
DST-1	80.5	58.5	382.3
DST-8	- (0)	- (0)	- (0)
DST-102	42.8	40.4	45.4
DAT-41	23.3	-7.1	45.4
DAT-3	18.9	-	-
DAT-10	48.8	-	-
DAN-86	47.9	42.7	57.8
DAN-52	66.1	53.5	234.3
PN-95	52.4	46.2	67.0
PN-232	27.1	23.5	30.8
PN-9	43.5	38.2	52.0
PT-1-21	49.9	-	-

3.5   Discussion and conclusion

The results of the present study indicate that *Daphnia pulex* clones vary in their acute tolerance to all the different conditions met in this experiment. However, there was no evidence that polyploid clones are more tolerant to extreme conductivities, pH and temperature than diploid ones. Contrasting results have been obtained in previous studies on *Artemia* species. Zhang and Lefcort (1991) found a positive relationship between polyploidy and resistance to environmental stress in *A. parthenogenetica*. Polyploids had higher survival rates than sympatric diploids after a short-term exposure to cold and heat shocks. Similar results were obtained by Barata *et al.* (1996) with tetraploid *Artemia* strains having higher

survival at 15°C than the diploid ones although they had similar survival at 30°C. In contrast to the hypothesis that polyploidy confers greater tolerance to extreme environmental conditions because of higher heterozygozity and metabolic flexibility, Licht and Bogart (1989) found a similar thermal tolerance between diploid and triploid salamanders (*Ambystoma laterale-texanum*) and Schultz (1982) demonstrated that triploid fish (*Poeciliopsis monacha-lucida*) have lower resistance to cold stress than diploids. In this study, polyploid and diploid clones of *Daphnia pulex* have a similar tolerance to a range of environmental factors. Therefore their geographic distribution can not be explained by an increased tolerance to more extreme environmental conditions. It has been suggested that historical factors could explain the abundance of polyploid clones in arctic areas. During the last glaciation in the late Pleistocene, few zones were free of ice and served as refuges to many species in both the animal and vegetal kingdoms. Species in those restricted areas had to face harsh environmental conditions that led to the creation of new genetic and adaptive traits. The development of polyploidy might have been favoured as the ice sheet receded at the end of the Ice Age and polyploid organisms spread to those new habitats. Moreover, in the *Daphnia pulex* complex, high genetic diversity and clonal divergence in Arctic regions has been explained by recurrent hybridization events between different *Daphnia* species that occurred in different glacial refuges. After the retreat of glaciers, contact zones between refugial races favoured hydridization and subsequently polyploids formation (Dufresne and Hebert 1995; Weider and Hobaek 2003).

Asexuals neither did not have an increased tolerance to environmental extremes despite what has been suggested in previous studies (Beaton and Hebert 1988; Parker and Niklasson 2000; Schön and Martens 2003; Stenberg, Lundmark et al. 2003; Kearney 2005). Linking hybridization with parthenogenesis, Kearney (2005) suggested that the higher heterozygozity

of newly formed clones is advantageous in colonizing new habitats and facing new environmental challenges. Heterozygosity of the clones of this study ranged from 0.33 to 1 but beared no relationships with tolerance to a range of factors. Nonetheless, some differences between sexual and asexuals clones of *D. pulex* have been revealed in our experiment. Reproduction mode had a significant effect on survival of clones at $1500\mu S.$ cm^{-1} and pH 5. However, at pH 5 the pattern is inverted and under the other parameters tested, no significant difference was observed between cyclic and obligate parthenogens. So it is difficult in our study to attest for an effect of reproduction mode on the geographic repartition based on ecological tolerance differentiations. Those results are in concordance with a similar experimental study of Weider (1993) that tested the effect of reproduction mode on the tolerance to thermal and salinity stress among *Daphnia* clones. He found only one significant difference effect of breeding mode on salinity tolerance on four repeated experiments, the asexuals exhibiting a greater tolerance to salinity stress. In his three repeated experiments with temperature, he also found only one significant effect of breeding mode but then, the sexuals were more tolerant to thermal stress than the asexual clones. He concluded that parthenogens do not have a more broadly genotype that could have explained their wider geographical distribution. Lundmark (2006) also reported little evidence for asexuality as the main explanatory factor behind the success of clonal forms of arthropod species with geographical parthenogenesis. Lynch *et al.* (1989) found a large amount of genetic variation in life-history traits in obligate parthenogens of *D. pulex* and argued that associated with the potential for microevolutionary change within lineages, this variation can help to explain the broad geographic distribution of the asexual complex. They emphazised that obligate and cyclic parthenogens are not ecologically equivalent and remained that variation in asexuals is in great part a consequence of the polyphyletic origin of the clones as well as their incomplete

reproductive isolation from their sexual ancestors as was primarily hypothesized by Hebert *et al.* (1989) and Innes *et al.* (2000).

There are two leading exploratory models that have been advanced to explain geographical parthenogenesis. The 'general-purpose' genotype (GPG) refers to the notion that asexuals may possess a more broadly adapted genotype. As asexual genotypes are transmitted intact generation after generation, any favourable genes complexes will be selected to face broad ecological demands. On the other side, the Frozen Niche-Variation model (FNV) of Vrijenhoek (1979; 1984) states that multiple origins of asexuals produce an array of clones that capture and freeze genotypic variation of their sexual ancestors. Then, selection among clones would favour specialized genotype having minimal niche overlap with the established clones and their sexual ancestors. Several studies have tested for one or the other model on asexual organisms (Weider 1993; Vrijenhoek and Pfeiler 1997; VanDoninck, Schoen et al. 2002). Results do not converge on one model but some lead to the conclusion that clones are generalist (GPG) and others that clones are specialist (FNV). The main result of this study showed interclonal variability in response to acute environmental conditions. In all treatments, survivorship differed among clones. Also, all clones showed great variation in their response to the different treatments as demonstrated with the LT $_{50}$ values. In our results, no clone seemed to have an equal tolerance to all treatments. This may agree with the hypothesis that clones are specialist, each of them having different ecological demands. That is in agreement with the study of Weider (1993) mentioned above. His results did not support the notion that asexual clones of *D. pulex* possess a 'general-purpose' genotypes when compared with sexual clones.

Clones did not differ in their environmental tolerance according to their geographic origins. Temperatures of the regions covered in this study vary greatly. Mean annual temperatures are -4.4°C and 12 °C in northern Québec and in Illinois respectively (data are from the Gouvernement du Canada website and the NOAA website). One could hypothesize that clones from low latitude regions would have a greater tolerance to high temperature but no significant effect of latitude (ie, geographic origin) was observed among clones exposed to acute temperature. Some studies have demonstrated variation in response to environmental factors among clones that were similar in ploidy level, breeding mode and or geographic origin. For example, variation in response to salinity tolerance among obligate parthenogenetic clones of *D. pulex* near Churchill (Manitoba) has been showed. The authors exposed several clones to different salinity conditions and compare their response with the salinity they encounter in their ponds. The distribution of clones were concordant with the laboratory data suggesting that clones had evolved into ecotypes (Weider and Hebert 1987). Other studies demonstrated that local genetic differentiation and local adaptation may explain the distribution and the coexistence of clones. LaBerge and Hann (1989) found variation in acute temperature and oxygen stress among genotypes of *D. pulex* and could related the intraspecific differences to the temporal variation in environmental conditions experienced directly in the pond they originated from.

In this study, ploidy level and reproductive mode did not influence clonal survivorship under a wide range of environmental factors. Historical factors could however play a substantial role in the pattern of geographical parthenogenesis. Local adaptation and the incomplete isolation of reproduction mode are indeed very important in explaining the ecological differences among clones. Because freshwater habitats experienced a wide fluctuation of many environmental conditions in time and or in space, clones of *Daphnia* had

to specialize in order to be able to colonize new habitats. The great diversity of clones due to their polyphyletic origins has enabled species from the *Daphnia pulex* complex to have a wide distribution. Intraclonal variation in response to acute environmental stress have been observed in this study (see standard deviations in figures 1, 2 and 3). It would be very interesting to test for the magnitude of the intraclonal variation in response to different environmental conditions. Phenotypic plasticity may provide more ecological flexibility for a given genotype and could partly favour the 'general-pupose' genotype hypothesis.

CONCLUSION GÉNÉRALE

Le premier objectif de cette étude était de décrire les communautés zooplanctoniques dans la région de Kuujjuarapik et Umiujaq et de déterminer l'importance relative des processus locaux et régionaux influençant la distribution des différents taxons identifiés. Les conditions environnementales variaient énormément entre ces étangs. Les communautés zooplanctoniques des trois types d'étangs les plus fréquemment rencontrés au Nunavut (rocheux, thermokarstiques et toundriques) ont été comparées et l'influence des facteurs biotiques et abiotiques sur ces communautés a été testée. Seules quatre variables physicochimiques expliquaient significativement un quart de la variation dans la composition d'espèces. La température, la conductivité, l'altitude et le carbone organique dissous influençaient la structure des communautés de ces étangs. Il faut cependant être prudent quant à l'interprétation des résultats car il s'agit d'un échantillonnage ponctuel qui ne représente pas la structure des communautés de la saison estivale de 2007 et l'effet de la température doit être interprétée en gardant en tête la grande variabilité de ce type de paramètre dans une même journée et d'un jour à l'autre. Enfin, quelques espèces de copépodes et les daphnies du genre *Daphnia* dominaient une grande proportion des communautés recensées dans la région. Ces résultats concordent avec ceux d'autres études sur les écosystèmes aquatiques subarctiques (Weider 1987; Weider and Hebert 1987; Wilson and Hebert 1992; Rautio 1998; Rautio 2001) et apportent des compléments d'informations sur leur fonctionnement. Notamment, c'est à ma connaissance la première étude de ce type sur les mares thermokarstiques malgré l'abondance croissante de ce type d'étangs dû à la fonte du pergélisol dans ces milieux. Ils représentent une manne de nouvelles niches écologiques pour différentes espèces zooplanctoniques et peuvent servir de véritables laboratoires expérimentaux en milieu naturel pour étudier l'établissement des communautés, par exemple.

Finalement, cet objectif a permis d'établir une base de données sur ces écosystèmes dans la région de Kuujjuarapik et d'Umiujaq. Dans une perspective de changements climatiques, cette base de données était nécessaire à un éventuel suivi des communautés et des caractéristiques physicochimiques et morphométriques de ces trois types d'étangs. Étant donné le peu d'étude de ce type sur les plans d'eau des hautes latitudes et malgré leur abondance et leur sensibilité aux changements climatiques, il est nécessaire de poursuivre l'étude du fonctionnement de ces écosystèmes et d'échantillonner un plus grand nombre d'étangs et une plus vaste zone géographique dans le nord du Québec. De plus, une étude similaire mais incluant un suivi temporel sur la saison (étangs échantillonnés une fois par semaine durant toute la saison estivale) contribuerait à préciser nos résultats et à agrandir leur portée scientifique.

Le deuxième objectif visait à expliquer la distribution spatiale et la diversité génétique des daphnies du complexe *pulex*. Tout d'abord, les connaissances sur la diversité clonale à l'est de la baie d'Hudson ont été complétées. Ensuite, l'évaluation de l'influence de plusieurs facteurs biotiques et abiotiques a été effectuée dans la région de Kuujjuarapik et d'Umiujaq dans le but de comprendre les patrons de distributions de ces génotypes clonaux. Vingt-trois clones ont été recensés et les résultats montrent qu'ils possédaient des préférences écologiques différentes. La conductivité, le pH et la profondeur des étangs expliquaient une grande proportion de la variation dans la distribution des clones. Cette variation suggère une forte interaction entre le génotype et l'environnement. Il se peut donc que plus une espèce est diversifiée génétiquement, plus elle est tolérante à de grands gradients de facteurs environnementaux et plus sa distribution peut être étendue. Il serait très intéressant d'étudier la diversité génétique d'autres taxons dominants de cette région comme certains copépodes et d'autres cladocères afin de vérifier cette hypothèse. Cette étude apporte également des

éléments d'explication sur la distribution des daphnies polyploïdes. L'hypothèse selon laquelle la polyploïdie confère une plus grande tolérance aux variations des conditions environnementales n'est pas appuyée par nos résultats. Une faible conductivité semble favoriser les triploïdes qui sont absents des étangs où la conductivité est élevée. Également, une plus grande habilité des polyploïdes à compétitionner pourrait expliquer leur dominance sous de hautes latitudes et la rare coexistence entre les triploïdes et les diploïdes dans ces étangs. Il reste donc encore beaucoup d'études à effectuer pour expliquer la distribution géographique des triploïdes. Il faut notamment envisager d'autres pistes de réflexion telles que l'évitement du prédateur copépode *Hesperodiaptomus arcticus* qui semble préférer les eaux à conductivités plus élevées. Également, il serait intéressant d'évaluer la répartition spatiale des triploïdes de la région de Kuujjuarapik et d'Umiujak en mesurant la distance entre les étangs, notamment, afin de savoir si les triploïdes sont répartis de manière sporadiques dans la région ou s'ils sont concentrés dans des zones spécifiques. L'éparpillement des triploïdes comme il semble être le cas dans la présente étude, pourrait évoquer le fait que ce sont des clones qui ne parviennent pas à s'établir et sont exclus compétitivement mais qui sont régulièrement renouvelés par l'hybridation de leurs congénères diploïdes du même étang ou d'étangs voisins. Un suivi temporel régulier (intra- et intersaisons) des génotypes triploïdes dans une même région permettrait de vérifier cette hypothèse. Dans le cas de génotypes stables, une meilleure capacité compétitive pourrait expliquer leur présence.

Dans un volet expérimental, deux études sur la physiologie de différents clones de daphnies ont permis de confirmer les résultats obtenus sur le terrain et d'ouvrir la question de la distribution des clones sur une plus grande échelle spatiale, en utilisant des clones provenant de la région des grands Lacs (Etats-Unis et Canada) au Subarctique québécois. Une première étude exploratoire a permis de réfuter l'hypothèse selon laquelle les polyploïdes

possèderaient une plus grande flexibilité métabolique que les diploïdes, ce qui aurait pu expliquer leur grande distribution dans les milieux extrêmes. Une deuxième expérience a testé la tolérance de plusieurs clones à différents facteurs physicochimiques (température, pH et conductivités) extrêmes. Les résultats ont confirmé que les clones de daphnies possédaient des demandes écologiques différentes mais ni le niveau de ploïdie, ni le mode de reproduction (sexué vs asexué), ni l'origine géographique (latitude) n'ont eu d'influence sur la survie des clones. Encore une fois, les polyploïdes n'étaient pas plus tolérants aux conditions environnementales adverses que les diploïdes. De la même façon, les asexués n'étaient pas plus tolérants que les sexués. Une alternative à l'hypothèse de différences physiologiques entre les sexués, les asexués et les niveaux de ploïdie pour expliquer les patrons de distribution géographique des clones de daphnies reposent sur des facteurs historiques. L'avantage démographique de la reproduction asexuée aurait été favorisé lors de la colonisation de nouveaux habitats laissés vacant par le retrait des glaciers lors du pléistocène. Une fois les communautés établies, les ancêtres sexués n'auraient pas été capables de supplanter les asexués. Et finalement, le fait que les asexués et les polyploïdes ont des origines multiples et polyphylétiques chez *Daphnia pulex* peut expliquer que l'on ne détecte pas de différences écophysiologiques entre les sexués et les asexués, ni entre les niveaux de ploïdie. Par contre, les différences inter- et intraclonales confirment que les clones de daphnies sont spécialistes et occupent des niches écologiques différentes quelle que soit leur mode de reproduction et leur niveau de ploïdie. Par conséquent, le grand nombre de clones, en d'autres termes la grande diversité génétique des daphnies, pourrait expliquer la distribution cosmopolite de ce complexe d'espèces. Il serait pertinent de conduire des études comparables à celle-ci sur la diversité clonale et la répartition des modes de reproduction et des niveaux de ploïdie sur différentes espèces ayant des caractéristiques similaires aux daphnies du complexe

pulex afin de valider nos résultats ou d'apporter d'autres pistes de réflexion sur la parthénogenèse et la polyploïdie géographique.

En conclusion, ce projet de maîtrise contribue à l'avancement des connaissances sur les facteurs responsables de la biodiversité zooplanctonique des étangs subarctiques au niveau inter et intraspécifique. Non seulement il a permis de décrire les communautés zooplanctoniques dans la région de Kuujjuarapik et Umiujaq et de déterminer l'importance relative des processus locaux et régionaux influençant ces communautés, mais il apporte de nouvelles pistes sur la répartition des daphnies du complexe *pulex* du subarctique en intégrant une approche descriptive en milieu naturel et expérimentale en laboratoire. De nombreuses études comme ce projet seront nécessaires pour palier au manque de connaissances sur les écosystèmes aquatiques subarctiques et arctiques et sur la distribution de leur biodiversité, que ce soit présentement ou en marge des changements climatiques. Ces études devraient intégrer plusieurs disciplines complémentaires comme l'écologie des communautés, la physiologie et génétique évolutive, comme par exemple dans ce projet de maîtrise, dans le but d'élargir la compréhension des patrons de distribution des espèces.

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