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**Genetic structure of the *Daphnia longispina* complex in
European mountain lakes**

Ph.D. thesis

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Prague, July 2011

I declare that this thesis has not been submitted for the purpose of obtaining the same or any other academic degree earlier or at another institution. My involvement in the research presented in this thesis is expressed through the authorship order of the included publications and manuscripts. All literature sources I used when writing this thesis have been properly cited.

Prague, July 2011

Eva Hamrová

Acknowledgements

When I started my studies of aquatic biology, I chose *Daphnia* from a wide scale of offered topics and animals. *Daphnia* are really pretty and cute animals, and the more I studied them, the more I think so. When I started my PhD studies four years ago, I changed the topic and moved from the life history experiments to studies of genetic diversity in *Daphnia*. Although I spent four years mostly in the laboratory studying the populations of animals which are tiny and unknown to most people, I am glad. I learnt a lot about *Daphnia*, but I also met many interesting people and several good friends and this is the value I appreciate the most.

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Abstract

I studied the genetic structure of cladocerans from the *Daphnia longispina* complex in several European mountain ranges. The population genetic structure of the *D. longispina* complex was studied using mitochondrial (mtDNA; partial sequencing of the 12S rRNA gene) and nuclear markers (nine microsatellite loci).

Major part of the work was done in the Tatra Mountains; the genetic structure of populations of the *Daphnia longispina* complex from two parts of this range (the West and the High Tatras) was compared. The pattern of mtDNA confirmed multiple colonization of lakes from different source populations, detected haplotype diversity was high and haplotype sharing only within the West or the High Tatras was observed. The observed genetic differentiation indicates low level of gene flow and persistent founder effect, consistent with the monopolization hypothesis. The alternation of asexual and sexual reproduction in the life cycle of *Daphnia*, cyclical parthenogenesis, may affect genetic structure of their populations. This was the topic of a study described in the first chapter. A detailed analysis of population structure of two closely related *Daphnia* species (*D. galeata* and *D. longispina*) living in similar habitats (permanent dimictic mountain lakes) in the Tatra Mountains revealed that populations show strikingly different genetic composition depending on their reproductive strategy during unfavourable periods (overwintering as parthenogenetic females vs. ephippial dormant eggs). The next chapter focused on the past changes of taxonomic composition of a *Daphnia* population in a single Tatra Mountain lake, and shows the usefulness of paleogenetic methods for such a purpose. The use of internal primers amplifying only short fragments of the target mitochondrial gene overcame the problem of degraded DNA in the old ephippial eggs, and enabled the correct species determination from 80-years old sediments.

Daphnia populations from other European mountainous regions extended the scope of my studies. In the third chapter, populations of *Daphnia longispina* and *Eucyclops serrulatus* complexes from the Tatra Mountains were compared with populations from other mountain ranges in South-Eastern Europe. All studied lakes were inhabited by single lineages of the respective species complexes (one of the *Eucyclops* clades, and *Daphnia longispina* sensu stricto) and their sequence variation suggests that many of the studied regions were colonised multiple times by both species. *D. longispina* haplotypes were highly variable, representing a substantial proportion of the known haplotype diversity of the species. We detected six divergent lineages of *Eucyclops* cf. *serrulatus*, confirming that this taxon represents a diverse species complex. The last chapter deals with the population genetic and phylogeographic structure of *D. longispina* in Pyrenean lakes. The diversity in the sampled region is mostly the result of a single colonization event. The post-colonization gene flow has been very rare indicating that priority effects are major drivers of genetic structure at various spatial scales. Although the presence of cryptic lineages in the mountain lakes does not seem to be a general pattern, studies of the mountain populations of zooplankton may advance the knowledge on processes shaping the within- and among-population diversity in this group of organisms.

Abstrakt (in Czech)

Genetická struktura perlooček druhového komplexu *Daphnia longispina* v evropských horských jezerech

Ve své práci jsem se zabývala genetickou strukturou populací perlooček z druhového komplexu *Daphnia longispina* v horských jezerech. Populace perlooček *D. longispina* a *D. galeata* byly analyzovány mitochondriálními (část genu pro 12S rRNA) a jadernými markery (devět mikrosatelitových lokusů). Většina práce byla provedena v Tatrách, kde jsem porovnávala genetickou strukturu populací komplexu *D. longispina*, a to mezi dvěma částmi pohoří: Západními a Vysokými Tatrami. Dle variability mitochondriální DNA byla jezera kolonizována z různých zdrojových populací, zjištěná haplotypová diverzita byla vysoká a sdílení haplotypů bylo pouze v rámci Západních nebo Vysokých Tater. Tato pozorovaná genetická odlišnost mezi dvěma částmi pohoří naznačuje nízký genový tok a přetrvávající efekt zakladatele, což je v souladu s monopolizační hypotézou vysvětlující zdánlivý rozpor mezi značnou schopností disperze, ale zároveň značnými genetickými odlišnostmi mezi populacemi planktonních živočichů. Cyklická partenogeneze, tj. střídání pohlavního a nepohlavního rozmnožování během životního cyklu perlooček, může ovlivnit genetickou strukturu jejich populací. V první kapitole je popsán vliv strategie rozmnožování během nepříznivých podmínek (zda přezimují jako partenogenetické samice nebo jako dormantní vajíčka) na genetickou strukturu populací dvou blízce příbuzných druhů *D. galeata* a *D. longispina*. Detailní analýza ukázala, že populace druhů, žijící v podobných podmínkách prostředí (dimiktická horská jezera), vykazují odlišnou genetickou strukturu v závislosti na výběru strategie přezimování. Následující kapitola je zaměřena na změny v taxonomickém složení populací perlooček r. *Daphnia* ve Štrbském plese za použití paleogenetických metod. Použitím primerů amplifikujících pouze krátké fragmenty studovaného mitochondriálního genu jsme vyřešili problém degradované genetické informace ze starých trvalých vajíček a mohli jsme určit druhy z 80 let starého materiálu.

Práci jsem rozšířila o studium populací perlooček r. *Daphnia* z vybraných evropských pohoří. Ve třetí kapitole byly srovnány tatranské populace druhových komplexů *Daphnia longispina* a buchanek *Eucyclops serrulatus* s populacemi z pohoří jihovýchodní Evropy. Ve všech studovaných pohořích s výjimkou Tater, kde mají oba druhové komplexy vyšší diverzitu, byl každý komplex zastoupen jedinci pouze jedné linie (jedna linie *Eucyclops* a *Daphnia longispina* sensu stricto). Dle odlišnosti sekvencí se dá usuzovat, že řada pohoří byla kolonizována oběma druhy několikrát, ale v několika případech lze usuzovat, že někde po jedné kolonizační události došlo následně k disperzi do okolních jezer. U perlooček *D. longispina* byla prokázána velká haplotypová diverzita, představující podstatnou proporcii známé haplotypové diverzity tohoto druhu. Mezi buchankami určenými jako *E. serrulatus* bylo rozlišeno celkem šest divergentních linií, což potvrzuje domněnku, že tento taxon představuje bohatý druhový komplex. Poslední část práce se zabývá genetickou a fylogeografickou strukturou populací *D. longispina* v Pyrenejích. Diverzita v této oblasti je převážně výsledkem jedné kolonizační události. Ukázalo se, že po kolonizaci zde genový tok probíhal pouze v omezené míře, a že efekt priority měl hlavní vliv na genetickou strukturu zdejších populací. Podle výsledků z východoevropských hor a Pyrenejí je patrné, že kryptické linie studovaných skupin zooplanktonu nejsou v horských jezerech příliš běžné, jak by se dalo usuzovat ze situace v tatranských jezerech. Přesto jsou populace horského zooplanktonu vhodným objektem pro studium procesů ovlivňujících diverzitu na různých úrovních, od koexistence klonů až po interakce mezi příbuznými druhy.

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CHAPTER I

Strong differences in the clonal variation of two *Daphnia* species from mountain lakes affected by overwintering strategy

Hamrová, E., Mergeay, J. & A. Petrusek
in revision, BMC Evolutionary Biology

CHAPTER II

Identifying century-old long-spined *Daphnia*: species replacement in a mountain lake characterised by paleogenetic methods

Hamrová, E., Goliáš, V. & A. Petrusek
Hydrobiologia 643 (1): 97-106

CHAPTER III

Multiple colonization and cryptic diversity in *Daphnia longispina* (Cladocera) and *Eucyclops serrulatus* (Copepoda) species complexes in Eastern European mountain lakes

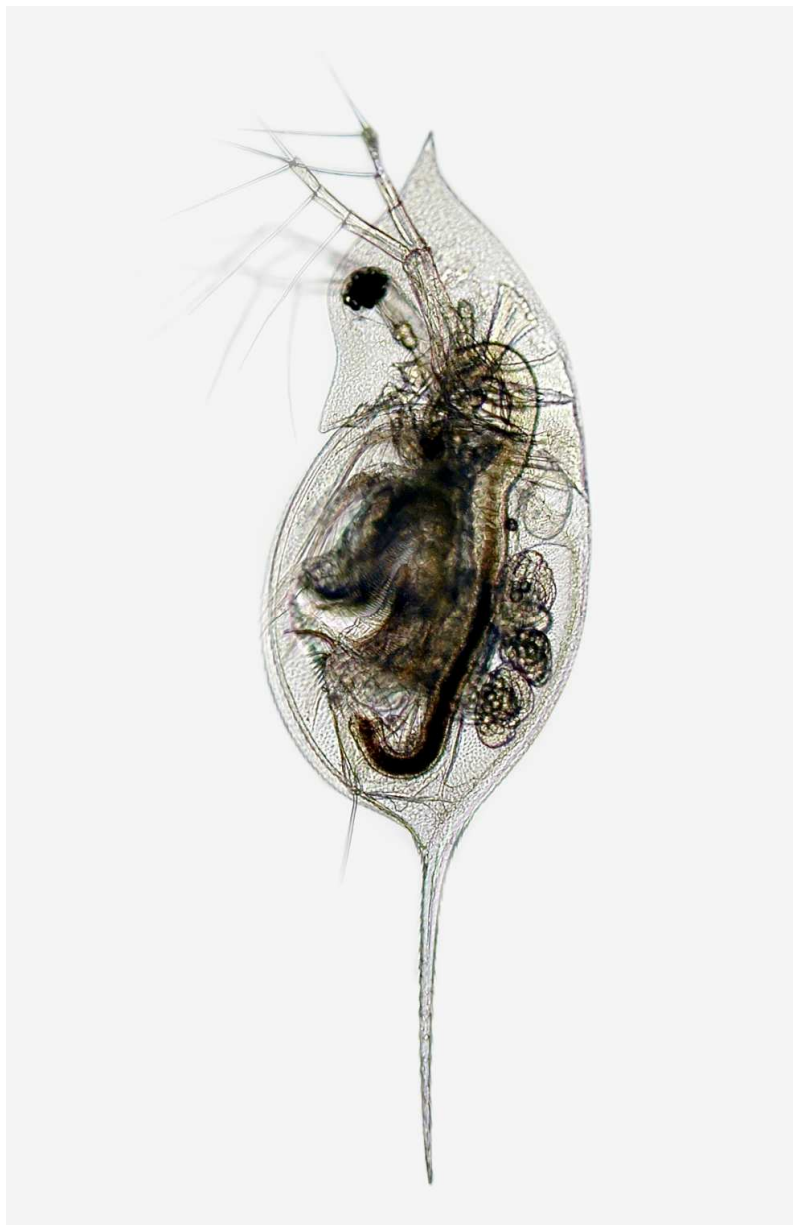
Hamrová, E., Krajíček, M., Karanovic, T. & A. Petrusek
unpublished manuscript

CHAPTER IV

Phylogeography, colonization dynamics and priority effects of *Daphnia longispina* in the eastern Pyrenees

Ventura, M., Hamrová, E., Miró, A., Petrusek, A., De Meester, L. & J. Mergeay
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GENERAL INTRODUCTION



Daphnia galeata, photo by Jan Fott and modified by Petr Jan Juračka.

Daphnia as a model organism

Daphnia (Cladocera) are small crustaceans representing an important component of freshwater zooplankton with many characteristics making them suitable model organisms (summarised in Seda & Petrusek 2011). They are common and geographically widespread almost all over the world. Their body size is species-dependent (mm ranges), large enough to be handled individually but small enough for large-scale experiments. *Daphnia* are easy to culture, can be easily kept in the laboratory as clonal lineages, have a short generation time; therefore large populations can be produced in short periods and populations respond to environmental changes quickly. They are keystone species in many aquatic habitats, with a central position in aquatic food webs as effective grazers of planktonic primary producers and prey consumed by both invertebrate and vertebrate predators.

Daphnia have been used in numerous studies in ecology (e.g., Alekseev & Lampert 2001; Gliwicz 1990), host-parasite interactions and coevolution (e.g., Decaestecker et al. 2007; Ebert 2008), studies of hybridization (e.g., Schwenk et al. 2001; Schwenk et Spaak 1997; Spaak 1995), evolution of asexuality (e.g., Hebert et al. 1988; Paland et al. 2005), microevolution (Jacobs 1990; Silva et al. 2010), phylogeography (e.g. De Gelas & De Meester 2005; Penton et al. 2004; Weider et al 1999), and recently also on global climate changes (Van Doorslaer et al. 2009).

In aquatic food webs *Daphnia* represent both, predator and prey. Various antipredator defences have evolved in *Daphnia* to escape predation of vertebrate and invertebrate predators and a lot of studies focused on the antipredator strategies, such as morphological defences (review by Tollrian & Dodson 1999), modifications of life-history traits, e.g. earlier reproduction (Dodson 1989; Macháček & Seda 2008) or changes in behaviour like diurnal vertical migration (e.g., King & Miracle 1995; Stich & Lampert 1981). As an important consumer of phytoplankton, *Daphnia* also has impact on its prey and causes inducible defences in algae (e.g. Van Donk et al. 1999).

Daphnia produce long-lived resting eggs preserved in lake sediments and resistant to various environmental factors. This has proven to be a powerful tool to study natural and anthropogenic changes in lake ecosystems. The introduction of molecular genetic methods increased the potential of using *Daphnia* resting eggs in paleoecological and paleogenetical studies to study long-term shifts in the genetic structure (Brede et al. 2009; Limburg & Weider 2002; Pollard et al. 2003; Reid et al. 2000). Resurrection of viable dormant eggs allowed also studying behavioural traits (e.g., Cousyn et al. 2001) or host-parasite interactions (Decaestecker et al. 2007) of past zooplankton populations.

Daphnia has currently become intensively used in genomic studies. Recently, an analysis of the whole *Daphnia pulex* s. l. genome, the first crustacean genome fully sequenced, has been published (Colbourne et al. 2011), and the genome sequencing and assembly of other model *Daphnia* species is in progress. So far, *Daphnia* is the animal with most known genes (of about 31 000 genes in comparison to 23 000 human genes). The

availability of annotated genome further expanded the potential of *Daphnia* as the research model to environmental genomics, to explore how organisms adapt genetically to environmental stressors, i.e. rising temperatures, heavy metals, or diseases (Ebert 2011).

Reproduction, diapause and dispersion

Daphnia reproduce via cyclical parthenogenesis, an alternation of asexual and sexual reproduction during the season (Fig. 1). Usually, *Daphnia* reproduce most of the time clonally and switch to the sexual reproduction under unfavourable environmental conditions. In that case, females start to produce sexual eggs and males are produced parthenogenetically. After fertilization, usually two eggs are encapsulated in a protective chitinous case called an ephippium (Zaffagnini 1987). Ephippia undergo a diapause, after which female offspring hatch from them. Production of resting eggs is caused by numerous environmental factors (reviewed in Alekseev 2007). There is an evidence of obligate parthenogenesis with asexual production of ephippia in the *D. pulex* group (Černý & Hebert 1993; Hebert et al. 1988; Hebert & Crease 1983) but this was never observed in the *D. longispina* group, on which this thesis focuses.

Production of ephippia has direct impact on ecology and evolution of *Daphnia* populations (Cáceres 1998). A fraction of dormant eggs can hatch the next season when favourable conditions are restored and the rest ensures the population dispersion in space and time. Burial of ephippia in the sediment forms a dormant egg bank, a reservoir of genetic variability (De Stasio 1989). Ephippia deep in the sediment represent an inactive dormant egg bank where chances for hatching decline because of low availability of hatching stimuli and decreased responsiveness to it of older eggs (De Meester & De Jager 1993).

Average ephippia abundance in pond and lake sediments can reach 10^3 - 10^6 ephippia per square meter (Brendock & De Meester 2003). Ephippia are able to remain viable or well-preserved in the sediment for a long time. An egg older than 100 years has been successfully hatched (Cacéres 1998) and successful DNA extraction was done from an egg 400 years old (Mergeay et al. 2005). However, neither the evolutionary potential nor genetic information in ephippial eggs is stored forever. The longer period is an ephippium buried in the sediment, the higher is risk of damage of resting eggs by mechanic or chemical damage, senescence (De Stasio 1989), predation (Mellors 1975), parasitism (Cáceres & Tessier 2004) or microbial and fungal activities (Cavarlho & Wolf 1989).

Such archivation of genetic and ecological diversity in the sediment is a good tool for paleolimnological and paleoecological studies, focusing on, e.g., temporal changes of species diversity (Mergeay et al. 2007; Vandekerkhove et al. 2005), impact of human activities on *Daphnia* populations during long periods (Brede et al. 2009; chapter II in this thesis), ecological and evolutionary responses to changes in trophic level and fish stock (Brede et al. 2009; Cousyn et al. 2001; Hairston et al. 1999; Jankowski & Straile 2003; Jeppesen et al. 2001), acidification (Pollard et al. 2003) or microevolution (e.g. Weider et al. 1997).

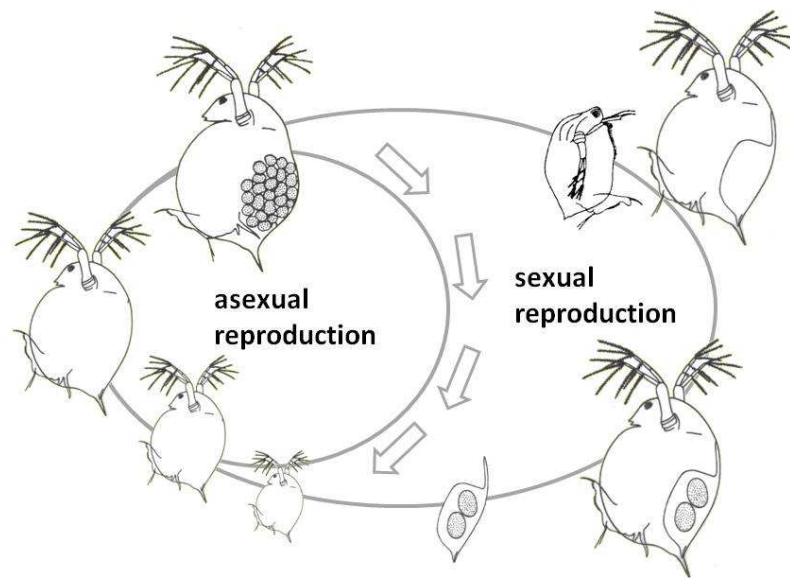


Fig. 1. Cyclical parthenogenesis - the reproductive mode of *Daphnia* with the alternation of asexual and sexual reproduction (drawings by Katleen Van der Gucht).

The main advantage that allows *Daphnia* to be particularly successful colonists is that a single ephippium is sufficient for founding a new population. Portion of diapausing eggs can disperse in space via environmental (Bilton et al. 2001; Cáceres & Soluk 2002) or animal vectors (Frisch et al. 2007; Green & Figuerola 2005; Melors 1975). Ephippia are able to resist desiccation (Davison 1969), freezing (Wood & Banta 1933) and mechanic and enzymatic effects (Proctor 1964; Proctor & Malone 1965). Successful long-distance dispersion of *Daphnia* individuals between continents was observed, both naturally and thanks to human activities (Adamowicz et al. 2009; Flössner & Kraus 1976; Mergeay et al. 2006).

Generally, the dispersal capacity in many zooplankton species, particularly cyclical parthenogens such as cladocerans and rotifers, is high due to the production of resting eggs. However, high dispersal ability does not warrant a successful colonization of a new habitat. The “monopolization hypothesis” (De Meester et al. 2002) describes mechanisms that may cause the often observed discrepancy between high dispersal ability and reduced gene flow. The hypothesis states that genetic structure of individuals reproducing via cyclical parthenogenesis is determined by colonization abilities, and gene flow is regulated by rapid monopolization of available sources, i.e., the build up of a dormant egg bank and rapid genetic adaptation to local conditions. Such processes were documented in Cladocera (De Gelas 2004; Louette et al. 2007), Copepoda (Zeller et al. 2006), Ostracoda (Schön 2007), as well as Rotifera (Gómez et al. 2007).

Genetic structure of Daphnia populations

Genetic structure in natural populations depends on founder effects, genetic drift, mutation, gene flow, natural selection and the type of reproduction (Avisé 1994). While genetic drift and mutations lead to the genetic differentiation of local populations, gene flow leads to the opposite pattern (Slatkin 1987). *Daphnia* population genetic structure has been an object of studies for more than 30 years. First works used allozyme electrophoresis (e.g. Hebert 1974; Wolf & Hobæk 1986) which still remains a useful tool (e.g. Piscia et al. 2006). Later, the DNA sequencing methods became a standard approach (e.g. Colbourne et al. 1998), often in combination with the preceding method (e.g. Adamowicz et al. 2004). Less than a decade ago, more variable high-resolution microsatellite markers have become available, and now are used widely (e.g. Mergeay et al. 2008; Thielsch et al. 2009; Yin et al. 2010).

Cyclical parthenogenesis has direct effect on the genetic structure of *Daphnia* populations because of alternation of asexual and sexual reproduction. Sexual reproduction increases genetic variation due to the gene segregation and recombination (De Gelas 2004). In cyclical parthenogens, high numbers of clones (and thus multilocus genotypes) are expected at the beginning of the growing season, followed by a decrease in genetic diversity during the period of parthenogenetic reproduction. The reduction of clonal diversity within the population is expected during clonal reproduction due to the clonal selection, which strongly impacts the genetic structure of populations (Vanoverbeke & De Meester 2010a). Clonal selection can result in the coexistence of a limited number of clones and lead to an erosion of clonal diversity, with the duration of the growing season and the size of the habitat being particularly important factors. The restoration of clonal diversity is ensured by sexual reproduction and subsequent hatching of resting eggs in the next season (Fig. 2).

Strong genetic differentiation among *Daphnia* populations has been observed in numerous studies (e.g., Haag et al. 2006; Thielsch et al. 2009; Vanoverbeke & De Meester 1997; chapter IV in this thesis). The among-population genetic differentiation, within-population genetic variation and the degree of clonality is determined mainly by the size of the dormant egg bank, length of the growing season, and strength of clonal selection (De Meester et al. 2006). Founder effects also play an important role in genetic differentiation among populations, and have persistent effect in shaping the genetic structure among cyclical parthenogenetic zooplankton populations (Boileau et al. 1992; De Meester et al. 2002). Several recent studies documented impact of the founder effect on the variation of natural *Daphnia* populations (e.g. Louette et al. 2007; Ortells et al. 2011).

Daphnia are present in wide range of different waterbodies, from small temporary pools to large permanent lakes, with different environmental conditions they have to face (e.g. the length of the growing season, food quality, predation pressure, size of the habitat). The resulting selection pressures lead to microevolutionary changes, and subsequently to population differentiation (De Meester et al. 2006). A particularly important factor I focused on in one part of the thesis is the length of the growing season, and severity of unfavourable

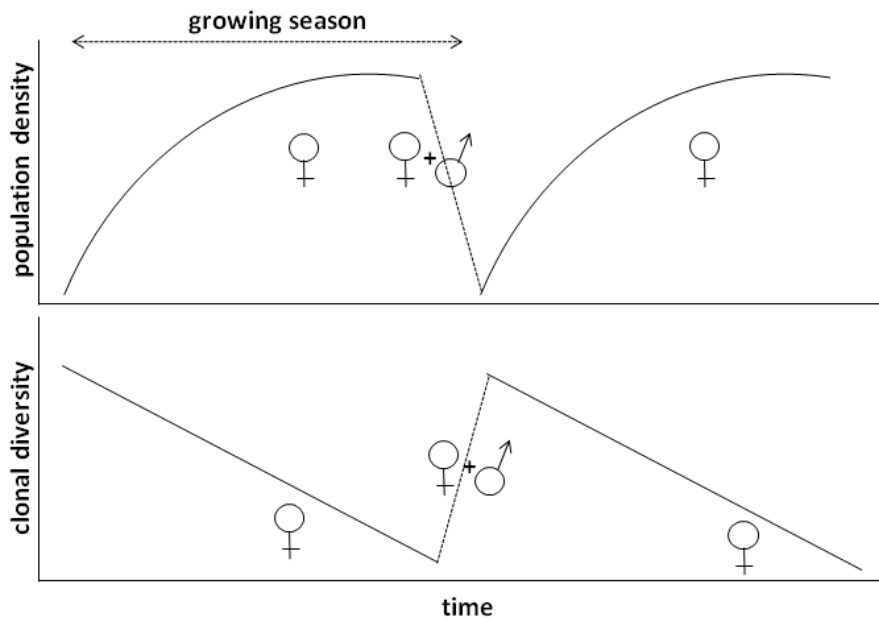


Fig. 2. Clonal erosion in a cyclical parthenogen population during the season. Parthenogenetic females reproduce clonally during the season, and different clones compete with each other for resources. Mating at the end of the growing season ensures the population survival of unfavourable period in a form of sexually-produced dormant eggs; hatching of these eggs then restores the clonal diversity. Drawings modified from Vanoverbeke & De Meester (2010b).

periods. Populations in intermittent habitats, or in permanent habitats with periods unsuitable for *Daphnia*, need to produce resting eggs to survive unfavourable conditions (e.g. freezing, drying, lack of food). The population is recovered from the dormant egg bank when conditions are favourable again. On the contrary, populations in permanent habitats can live for several years without a production and subsequent hatching of dormant eggs. Although *Daphnia* populations living in permanent lakes invest to the sexual reproduction and ephippia production (e.g., Keller & Spaak 2004; Spaak 1995, but see Jankowski & Straile 2004 or Gliwicz et al. 2001), some portion of individuals may overwinter as active females. Thus, the genetic structure between populations from intermittent and permanent habitats may differ strongly.

Populations from intermittent habitats show higher genetic diversity and clonal richness and genotype frequencies in good agreement with Hardy-Weinberg expectations due to the reestablishment from sexually produced dormant eggs. On the other hand, deviations of Hardy-Weinberg equilibrium and limited number of multilocus genotypes are often observed in populations inhabiting permanent habitats (De Meester 1996). The clonal erosion may result in strong heterozygote excess and extremely reduced clonal diversity (Vanoverbeke & De Meester 2010a; chapter I in this thesis).

Phenotypic variability in Daphnia

A huge morphological variability in many *Daphnia* species makes differentiation of these individuals, based on morphology only, very difficult. This has often resulted in pooling phenotypically similar lineages within species complexes under a single name. A cryptic species complex is usually defined as a group of species whose morphology is very similar, and thus their genetic and evolutionary distinctness remains “cryptic”; the most suitable method how to distinguish such species is by molecular tools (Pfenninger & Schwenk 2007; Taylor & Hebert 1992).

Daphnia are able to react to various environmental conditions by changing the phenotype within a single genotype, a phenomenon known as phenotypic plasticity. The most striking are transgenerational changes related to antipredator responses. These are induced by presence of kairomones, chemical signals indicating presence of invertebrate and vertebrate predators. Detecting kairomones in the environment leads *Daphnia* to the production of helmets or spines (e.g. Hanazato 1995), “crowns of thorns” (Petrušek et al. 2009), neckteeth (summarised in Juračka et al. 2011). However, responses to predators are not limited to phenotypic alterations, changes in life history (e.g. Bernot et al. 2006) and behaviour (e.g. Muluk & Beklioglu 2005; Dawidowicz & Wielanier 2004) are also common.

The interspecific hybridization known in several *Daphnia* groups (see Schwenk & Spaak 1995) also makes identification of particular taxa difficult. For example, common European members of the *D. longispina* complex, *D. longispina*, *D. galeata* and *D. cucullata* often coexist together and commonly hybridize, with some of the phenotypes particularly difficult to properly assign to the respective taxa (Dlouhá et al. 2010). Some of the hybridizing species within the complex are particularly divergent – for example, interspecies hybrids between *D. lacustris* and *D. galeata* with mtDNA divergence more than 15 % were found in nature (Hobæk et al. 2004).

On the other hand, many cases of phenotypic divergence in *Daphnia* are due to local adaptations to particular environmental conditions, resulting in dissimilar forms (e.g., Petrušek et al. 2008). All these sources of phenotypic variation result in often problematic interpretation of variation observed in natural localities. In my thesis, I tested some hypotheses related to the presence of cryptic diversity and proper identification of past *Daphnia* phenotypes in mountain populations of the *Daphnia longispina* complex.

The Daphnia longispina species complex

This species complex represents ecologically very important group of *Daphnia* in the Holarctic region. They are mostly inhabitants of pelagic environments of temperate waterbodies, from small fishless pools to lakes with various extent of fish predation. This complex includes in the Western Palearctic region several recognised lineages (see below) and Nearctic taxa *D. mendotae*, *D. dentifera* and *D. thorata* (which might be conspecific with

D. dentifera; Petrussek et al. 2008). Additional lineages within the complex still lack proper description or name assignment (Ishida & Taylor 2007; Petrussek et al. 2008). The taxonomy of the complex still remains partly unresolved, and different literature sources assign to it different taxa. For example, Benzie (2005) listed fewer species than presently recognised but also included into this complex *D. curvirostris*, *D. cristata* and *D. longiremis*, which are more divergent, and are separated to other species complexes by other authors (Adamowicz et al. 2009).

I studied populations from this species complex in European mountain ranges, thus I will focus to the current state of knowledge in Europe. Results published in the latest taxonomic reappraisal study by Petrussek et al. (2008) showed six clearly differentiated lineages in the Western Palearctic (*D. longispina*, *D. lacustris*, *D. cucullata*, *D. galeata*, “*D. umbra*” and an apparently undescribed Lake Berse lineage labelled *Daphnia* n. sp. A).

We can find several *Daphnia* taxa within the complex, the status of which changed several times within a relatively short time (Flössner & Kraus 1986; Petrussek et al. 2008). Also, numerous “species” were recognised in the past, often coexisting in a relatively small area (e.g. Litynski 1913), which more likely represented different morphs, not different evolutionary lineages. Some names within this complex which persisted in the literature and have been relatively widely used (e.g., *D. rosea*, *D. hyalina*) were shown recently to represent different forms with no genetic differentiation to support their recognition as a distinct species. Petrussek et al. (2008) thus suggested that morphologically and ecologically plastic but genetically uniform “*Daphnia hyalina-rosea-zschokkei* clade” should be identified as *Daphnia longispina* O. F. Müller, 1776.

Two species of the complex have primarily boreal distribution: *D. “umbra”* (a lineage requiring nomenclatural revision, known from Fennoscandia and North America), and *D. lacustris*. The latter species, described in 1862 from Norway, is widely distributed in Fennoscandia, with interesting disjunct records from two lakes from the Tatra Mountains in Central Europe. These represent the only known presently viable populations out of the Fennoscandia (Nilssen et al. 2007; Petrussek et al. 2007). The only other known locality for this species out of Fennoscandia is a lake in South Bohemia where it became extinct in the 20th century (Petrussek et al., unpubl.).

Incorrect use of species names, i.e. labelling different lineages by the same name (or vice versa), may lead to incorrect conclusions, make literature records incomparable for future analyses, and complicate further research. For example, *D. lacustris* was incorrectly labelled as *D. longispina* in a strict sense in some recent genetic studies (see Nilssen et al. 2007), which resulted in distorted view of the taxonomy and nomenclature of the whole species complex. We can find many examples of similar taxonomic confusions in the literature records, e.g., when comparing old and recent studies from mountain lakes (chapter II in this thesis).

Mountain lakes as a zooplankton habitat

High mountain lakes possess specific environmental conditions for local organisms. These lakes are usually oligotrophic, with low nutrient conditions and low water temperature, with these extreme conditions often lasting through the whole year. The ice or snow cover of high-altitude lakes is usually from late fall till the early summer and therefore the growing season is relatively short. In summer, high levels of UV radiation could have negative impact on some organisms, resulting in various special adaptations to protect from it (reviewed in Rautio & Tautarotti 2010). Thus, the biotic communities of high mountain lakes are simplified, due to the harsh environmental conditions organisms have to deal with (Starkweather 1990).

Mountain lakes are less influenced by pollution from agriculture and wastewater, compared to waterbodies from lowlands, but the atmospheric transport of pollutants is possible on long distances (Sommaruga 2001) with the particular risk of acidification of sensitive alpine habitats. Most mountain lakes are naturally fishless, but fish introductions happened frequently in the past (Schindler & Parker 2002; Pechlaner 1981) and usually strongly affected local zooplankton communities (Brancelj et al. 2000). Also, large invertebrate predators (e.g. *Chaoborus*) were replaced in many lakes by fish after their introduction, which affected the composition of zooplankton communities. Recently, eutrophication due to the increase input of nutrients together with the tourism into the mountain regions, and fish introductions changed the natural character of many mountain lakes (Gliwicz & Rowan 1984; Vreca & Muri 2006).

Mountain lakes could provide suitable conditions for cold-adapted species during warmer periods (such as the Holocene). Many zooplankton species have a boreoalpine distribution (Vekhoff 1997; Schindler 2000; Hořická et al. 2006; Jersabek et al. 2001). Morphologically or genetically unique populations are often found in mountain lakes (e.g., Marková et al. 2007; Mergeay et al. 2008; chapter II in this thesis) or harbour endemic species (Manca et al. 1994). A particularly conspicuous is the common occurrence of cuticular melanisation in *Daphnia* species in arctic and alpine regions, apparently a local adaptation to high UV doses (Černý & Hebert 1999; Hebert & McWalter 1983; Hebert & Emery 1990; Pelnaava-Arana & Manca 2007). Morphologically differentiated populations often represent to be more or less cryptic species, e.g. differently pigmented populations of *Daphnia* cf. *pulicaria* observed in the Tatra Mountains were shown to be divergent lineages (Marková et al. 2007; but see Dufresne et al. 2011).

Studied regions

I studied *Daphnia* populations from eleven mountain ranges in Europe (Fig. 3). Major part of work presented in this thesis was done in the Tatra Mountains, the highest region of the Carpathians situated on the border of Slovakia and Poland, which has been studied at our department for a long time. This mountain range is subdivided into three parts, the West

Tatras and the High Tatras with numerous lakes, and Belianske Tatras (with no major lakes due to different geology). There are more than 250 lakes of glacial origin in the Tatra Mountain range, the majority of which are located in the alpine region above 1800 m a. s. l. (Kopáček et al. 2000). Probably all of them were covered by glaciers during the last glaciations; glaciers finally retreated from the Tatra Mountains by the end of the pre-optimal part of the Holocene (Lindner et al. 2003). This mountain range had been strongly affected by anthropogenic acidification in the 20th century, resulting in extinction of crustaceans in many lakes above the timber line (Stuchlík et al. 1985). The recovery of lake chemistry started in the 1990s, followed by the return of zooplankton species to some lakes (Sacherová et al. 2006).

Three species from the *D. longispina* complex had been previously recognised in the Tatra Mountains by molecular methods: *D. longispina*, *D. galeata* and *D. lacustris* (Fig. 3); with no evidence of syntopic distribution or hybrids (Petrušek et al. 2007). The most common is *D. longispina*; *D. galeata* was confirmed at present in four lakes (Petrušek et al. 2007; Hamrová et al., unpubl.). The occurrence of the boreoalpine species *D. lacustris* (mentioned above) is particularly intriguing.

Apart from the *D. longispina* complex, populations of the *D. pulex* group identified as *D. pulicaria* inhabit some high-altitude lakes in the Tatra Mountains (e.g. Černý 1995). In most cases, these do not co-exist with the *D. longispina* complex. Although they also have very interesting ecology and evolutionary history (e.g., Gliwitz et al. 2001, Marková et al. 2007, Dufresne et al. 2011), they were not the study objects for my dissertation.

Daphnia populations from other European mountainous regions (ranges from Romania, the Balkan Peninsula, and the Pyrenees) extended the scope of my studies. These mountain ranges vary in the geology, most of them are calcareous, but there are some old granite-gneiss massifs such as the Rila. All lakes from these mountain ranges are of a glacial origin. There have been several researchers who studied different groups of freshwater zooplankton in Balkan Peninsula, but those investigations were mostly done unsystematically (see the review by Ostojčić 2010). Among *Daphnia*, Pljakic (1961) observed high morphological variability in the mountain lakes in the region of former Yugoslavia, which suggested possible occurrence of cryptic lineages similarly as in the Tatras.

I also contributed to one study on *D. longispina* from the Pyrenees, a range of mountains in southwest Europe that separates the Iberian Peninsula from the rest of continental Europe. The Pyrenees hold more than thousand lakes, the limnology of which was described by Catalan et al. (1992). In these mountains *D. longispina* is very common; other *Daphnia* species (*D. obtusa* and *D. cf. pulicaria*) can occasionally be found (Catalan et al. 2006).



Fig. 3. The distribution of eleven mountain ranges from which I analysed *Daphnia longispina* populations (1-Tatra Mountains, 2-Retezat, 3-Rila, 4-Pirin, 5-Sar Planina, 6-Bjelasica, 7-Prokletije, 8-Durmitor, 9-Zelengora, 10-Treskavica, 11-Pyrenees).

Genetic variation of the D. longispina complex in Tatra Mountains

One goal of my work was to compare the genetic structure of populations of the *Daphnia longispina* complex in Tatra Mountains. High mountain lakes represent relatively recently formed geographically separated systems open for colonization by zooplankton. Due to their glacial origin, several lakes, which may be isolated or interconnected by flowing water, are often situated within one glacier valley. Probably all lakes in the Tatra Mountains were colonized ca. 8000 years ago. The *D. longispina* complex inhabits mostly isolated but also some interconnected lakes in the Tatra Mountains.

Petrusek et al. (2007) brought some evidence for multiple colonization of Tatra Mountain lakes from different source populations. On a larger data set, we wanted to test whether there is some evidence of gene flow among lakes or whether all populations are distinctly differentiated. We predicted that due to quick monopolisation of resources (De Meester et al. 2002), relatively homogenous and significantly differentiated populations will be observed in lakes where independent colonization was assumed. Within a group of West Tatra lakes apparently colonised from the same source (likely due to one founding event followed by local dispersal), we expected higher genetic differentiation among lakes from different valleys than between stream-connected lakes situated in the same valley (where downstream ephippial dispersal and unidirectional gene flow is possible).

We studied the populations from two parts of this range, the West and the High Tatras. We analyzed *Daphnia* populations (*D. longispina* and *D. galeata*; Tab. 1) from isolated as well as interconnected lakes using the mitochondrial DNA and microsatellite markers (methods are in detail described in chapter I for microsatellites, and chapter II for mtDNA).

The pattern of mtDNA variation further supports the hypothesis by Petrušek et al. (2007) of a multiple colonization of lakes from different source populations. In *D. longispina*, 17 haplotypes among 12 populations (n=65) were detected. The detected haplotype diversity was high with haplotype sharing only within the West or the High Tatras (Fig. 4a). In the West Tatras, one dominant haplotype was observed, and several rare ones derived from it. In *D. galeata*, five haplotypes among four populations (n=39) were detected, no haplotype sharing was observed (Fig. 4b). Dominant *D. galeata* haplotypes in each lake differed from each other by two point mutations; together with relatively divergent patterns of microsatellite variation (see Chapter I) this suggests that each studied alpine *D. galeata* population was colonised independently.

The results of the factorial correspondence analysis (calculated in Genetix, Fig. 5a), as well as admixture analysis (performed in Structure, Fig. 5b) based on microsatellite variation suggest that the lakes of the High Tatra mountains are genetically clearly separated from the West Tatra lakes, as well as from each other. On the contrary, all analyses confirm that lakes in the West Tatra Mountains are genetically similar. Nevertheless, the extent of among-lake genetic differentiation (assessed by means of *Dest*; Tab. 2) within this region did not substantially differ between lakes separated in different valleys and those within a single valley, connected by stream. The difference between these two interconnected lakes (Ro2, Ro4) was not substantially lower than between some lakes in different valleys (Ro vs. Ra vs. VJ). On the contrary, the population from a downstream lake (Ro4) was more similar to a lake over the mountain ridge (Ra) than to a lake located upstream (Ro2), which might serve as a source of immigrants to Ro4.

The observed genetic differentiation among studied Tatra Mountain populations of *D. longispina* indicates low level of gene flow and persistent founder effect, consistent with the persistent founder effect (Boileau et al. 1992) and monopolization hypothesis (De Meester et al. 2002). As expected under such scenario, a more detailed analysis did not reveal any indication of substantial gene flow between the High and the West Tatras populations. The relatively higher similarity of West Tatra lakes might be explained by a single colonisation event. Even lakes, in which gene flow enhanced by downstream dispersal of ephippia could be expected, were genetically differentiated to an extent similar to that of some lakes located in different valleys. This suggests that immigration of genotypes within ephippia from upstream is not very effective, despite the fact that the populations are apparently re-established from ephippia every spring (see chapter I).

| lake | ID | Mt. range | altitude (m) | longitudo (E) | latitude (N) | max. depth (m) | area (ha) | N mtDNA | N hapl |
|-------------------------|-----|-----------|--------------|---------------|--------------|----------------|-----------|---------|--------|
| <i>D. longispina</i> | | | | | | | | | |
| Tretie Roháčské | Ro2 | WT | 1648 | 19.736 | 49.206 | 1.3 | 0.2 | 7 | 3 |
| Dolné Roháčské | Ro4 | WT | 1562 | 19.444 | 49.122 | 7.7 | 2.2 | 13 | 4 |
| Vyšné Račkové | Ra | WT | 1697 | 19.807 | 49.200 | 12.3 | 0.74 | 9 | 3 |
| Vyšné Jamnické | VJ | WT | 1839 | 19.738 | 49.207 | 3.6 | 0.4 | 1 | 1 |
| Vyšné Furkotské | VF | HT | 1698 | 20.031 | 49.144 | 2.4 | 0.41 | 9 | 1 |
| Vyšné Satanie | Sat | HT | 1894 | 20.064 | 49.171 | 3.5 | 0.2 | 8 | 2 |
| <i>D. galeata</i> | | | | | | | | | |
| Morskie Oko | MO | HT | 1395 | 20.072 | 49.198 | 50.8 | 34.5 | 11 | 1 |
| Nižné Žabie Bielovodské | NZB | HT | 1675 | 20.094 | 49.198 | 20.5 | 4.6 | 9 | 1 |
| Štrbské | SP | HT | 1346 | 20.330 | 49.719 | 19.7 | 6.6 | 18 | 2 |

Tab. 1. Basic morphometric and geographic information about the studied lakes: N mtDNA-number of analyzed individuals per population for mtDNA; N hapl-number of haplotypes identified in population. Abbreviations indicate mountain range: HT-the High Tatras, WT-the West Tatras.

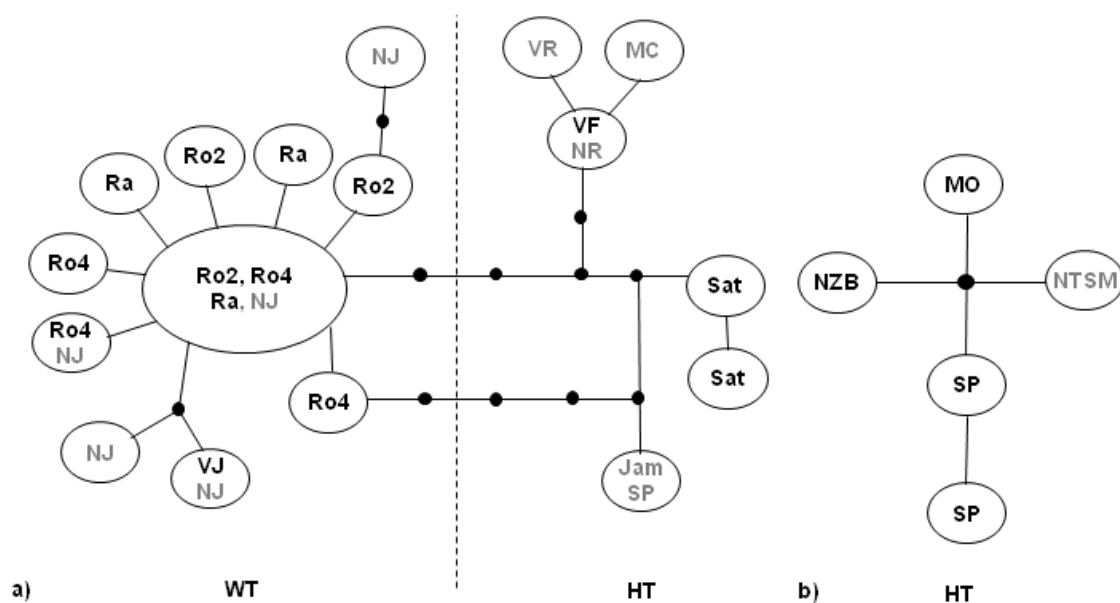


Fig. 4. Haplotype network of the 528 bp long 12S rDNA fragment from the taxon a) *Daphnia longispina* (65 sequences) and b) *Daphnia galeata* (39 sequences). Reference sequences from other Tatra lakes (n=19, Petrušek et al. 2007, Thielsch et al. 2009; GenBank acc. nos. DQ337926-39) to illustrate the overall haplotype variation of this species within the mountain range are in grey. Abbreviations indicate mountain range and lakes ID (Tab. 1; reference sequences from additional lakes: Jam-Jamské, MC-Malé Čierne, NJ-Nižné Jamnícke, NR-Nižné Rakytvske, NTSM-Nižné Temnosmrečinské, VR-Vyšné Rakytvské).

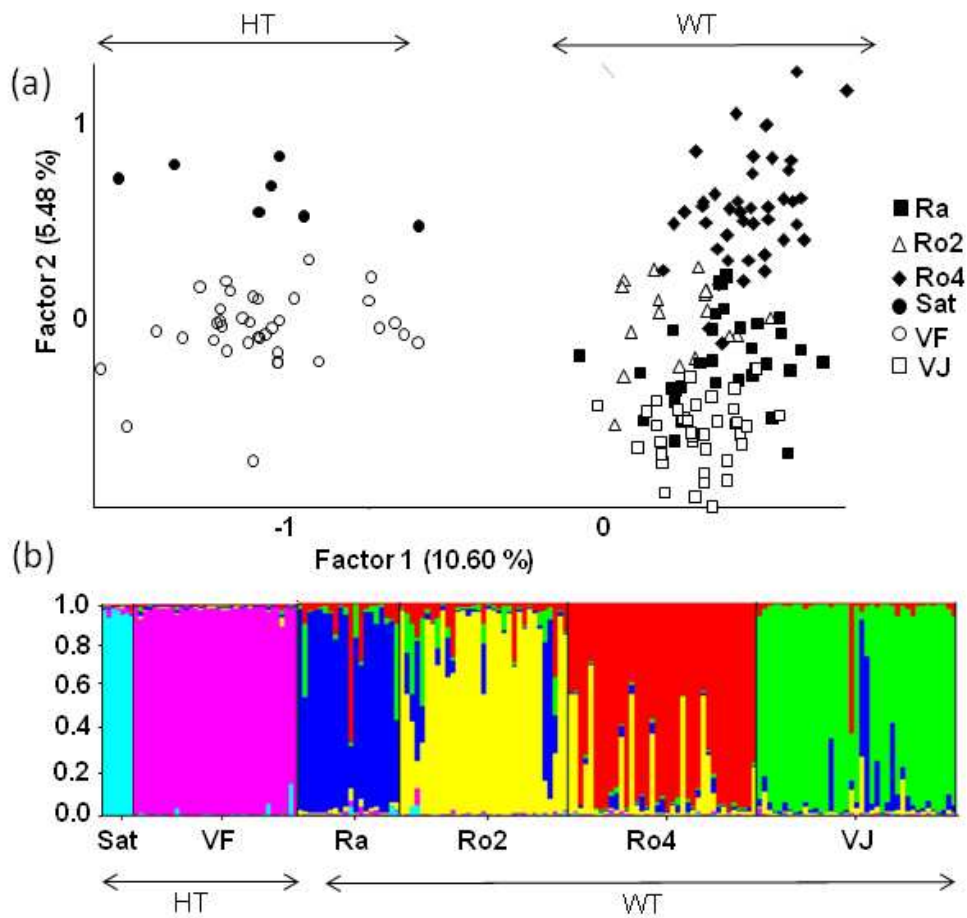


Fig. 5. (a) Factorial correspondence analysis based on microsatellite variation of six *D. longispina* populations. (b) Admixture analysis based on Bayesian analysis in Structure (K=6). (See Tab. 1 for abbreviations.)

| | VF | Sat | Ro2 | Ro4 | Ra |
|-----|------|------|-------------|-------------|-------------|
| VF | | | | | |
| Sat | 0.28 | | | | |
| Ro2 | 0.38 | 0.35 | | | |
| Ro4 | 0.34 | 0.45 | 0.10 | | |
| Ra | 0.29 | 0.26 | 0.07 | 0.21 | |
| VJ | 0.41 | 0.33 | 0.12 | 0.24 | 0.08 |

Tab. 2. Pairwise divergence based on microsatellite markers (expressed as *Dest* values) between analysed *D. longispina* populations from the Tatra Mountains. Lakes are indicated by their abbreviations (see Tab. 1). Comparisons of lakes within the West Tatra Mountains, which have been apparently colonised from the same source (see also Fig. 4), are highlighted in bold. Comparison of the two lakes within the same valley, in which a downstream water-mediated dispersal might be assumed (from Ro4 to Ro2), are in bold italics.

Outline of the thesis

The following four chapters in this thesis represent several results of my research on genetic diversity of the *Daphnia longispina* complex from mountain lakes that have been, or might be, separately published. Two of the chapters were studies restricted to the Tatra Mountains, one study dealt with populations from East European mountain lakes (in which we compared patterns observed in *Daphnia* with those observed in a similarly widespread copepod species complex), and the last study I contributed to focused on colonisation and diversification of *D. longispina* in the Pyrenees.

Detailed study of the among- and within-population genetic differentiation using microsatellite markers (briefly described above) revealed extremely pronounced differences in clonal variation among populations of two related *Daphnia* species occurring in Tatra Mountain lakes. We describe these patterns in chapter I, and ascribe them to different overwintering strategies of the local populations. Generally, *Daphnia* have two choices to survive winter unfavourable conditions (De Meester et al. 2006); as asexual females or as resting eggs. In harsh environmental conditions of mountain lakes, overwintering females have to face low water temperature and low food concentration (Gliwicz et al. 1990), but if overwintering clones survive these conditions, they are ready to reproduce as soon as conditions turn favourable again. Therefore, they are in competitive advantage over sexually produced clones in spring. Populations of the two studied species differ by their overwintering strategy in Tatra Mountain lakes, and this has a strong effect on the clonal richness and diversity of their populations. The supposed consequence of strong clonal erosion was observed in *D. galeata* overwintering as active females. Two out of three populations showed extremely reduced clonal richness (with an overwhelming dominance of a single clone; more clones were detected in the third population but two of them were rather common). On the contrary, *D. longispina* populations, apparently overwintering as sexually-produced dormant eggs, showed levels of genotype diversity comparable to obligately sexual species. The predictions by Vanoverbeke & De Meester (2010a) from a modelling of clonal erosion were thus supported in the natural *Daphnia* populations.

The second study from the Tatra Mountains did not focus on present patterns of population diversification but rather focused on the past changes of taxonomic composition of a specific *Daphnia* population. Petrušek et al. (2007) showed evidence based on comparison of present and past *Daphnia* phenotypes from Štrbské Lake, that a species replacement took place there, apparently due to the environmental changes during the twentieth century. Given the presence of unusually long-spined phenotypes remarkably similar to the boreal species *Daphnia lacustris*, we tested the hypothesis that this species had lived in the lake before anthropogenic impact. In this study, paleogenetic approach to study the resting egg bank showed to be a powerful tool. Although we obtained low number of ephippia containing preserved eggs suitable for genetic analysis, we obtained genetic data from two-thirds of all eggs found, unlike in previous studies from Central European mountain lakes (Faustová et al.

2004; Marková et al. 2006) that failed to amplify any DNA from subfossil eggs. The hypothesis that *D. lacustris* might have lived in this lake at the beginning of the 20th century seemed to be supported by the phenotypes of long-spined ephippia found in the sediment but was finally rejected by DNA analysis. The short fragment of DNA was sufficient to distinguish the species, and long-spined morphotypes were unambiguously identified as *D. longispina*, which was replaced by *D. galeata* due to the increase of trophic level and fish predation pressure in the second half of the 20th century.

The third study also originally focused on the search of cryptic *Daphnia* lineages, which was motivated by interesting phenotypes recorded in the historical literature. In comparison with the previous two, the chapter extends both the geographical and taxonomic coverage. It combines results from the Tatra Mountains and several other East and South-East European mountain ranges, and analyses the variation of mitochondrial DNA of populations of *Daphnia longispina* and *Eucyclops serrulatus* species complexes. While the genetic variability of *D. longispina* complex has been intensively studied and several cryptic lineages were confirmed in Tatra Mountains (Petrušek et al. 2007), the knowledge of genetic and cryptic diversity of the copepod *Eucyclops serrulatus* is still superficial. We predicted that cryptic diversity should be found in other European alpine lakes where morphological variation in *Daphnia* was reported (Pljakic 1961). Multiple colonization events by both taxa in several of the studied lakes was confirmed by our results. However, all analyzed *Daphnia* were confirmed genetically as *D. longispina*. On the contrary, six highly different lineages of *Eucyclops* were confirmed, two lineages in Tatra Mountains and four lineages from European lowland localities. Some lowlands populations also allied with mountain populations. Our results for *Eucyclops serrulatus* complex show that seemingly widespread copepod taxa harbour high cryptic diversity, a situation well known from *Daphnia* research but still not fully acknowledged for other crustacean taxa. In widespread mountain clades of both *Daphnia* and *Eucyclops*, we found evidence of multiple colonisation of some mountain ranges. However, contrary to our expectations, we did not observe any pattern that would suggest substantially more limited dispersal abilities of a copepod compared with a cladoceran.

The last chapter to which I contributed by genetic analyses is the study of detailed population genetic and phylogeographic structure of alpine *D. longispina* populations in the Pyrenees. In this study, we particularly focused on the role of spatial structure on *Daphnia* genetic variation, and on habitat shifts (lake–pond). Similarly to Balkan alpine lakes, all analysed individuals belonged to *D. longispina* and no other lineage of the species complex was found. The mtDNA showed that most Pyrenean lakes were colonized in a single colonization event at the end of the Pleistocene, followed by a spatial expansion throughout the Pyrenees. Within the eastern Pyrenees, high level of genetic diversity combined with a high degree of haplotype endemism, both at the level of individual valleys and at the level of individual water bodies, was observed. Priority effects and local adaptation were proven to be major drivers of genetic structure at various spatial scales.

Conclusions

In this thesis I have investigated the genetic structure of *Daphnia longispina* populations in mountain lakes. The comparison of haplotype variation of *D. longispina* populations throughout the Europe with the studied mountain ranges revealed an interesting pattern; within a small mountain region (Tatra Mountains), it was almost as high as within the whole continent. Other studied mountain ranges also hosted a wide array of haplotypes, confirming that mountain lakes may be reservoirs of genetic diversity of local species.

Detailed analysis of population genetic structure using microsatellite markers revealed another important result within my thesis. In relatively similar habitats, permanent dimictic mountain lakes of different sizes, *Daphnia* choice between two overwintering strategies had a strikingly different impact on the genetic structure and clonal diversity of the populations.

The genetic study of resting egg bank restricted to one lake helped to uncover the history of *Daphnia* species composition and replacement during the 20th century due to the anthropogenic changes. The paleogenetic approach allowed the reliable species determination, and the use of internal primers amplifying only short fragments of the target mitochondrial gene overcame the problem of degraded DNA in the old ephippial eggs.

The comparison of *Daphnia* and *Eucyclops* populations highlighted a very different level of taxonomic advances between the two groups. Although no cryptic lineages through the Balkans were found and all lakes were inhabited by a single *Daphnia* or *Eucyclops* lineage, the comparison with reference sequences revealed that *E. serrulatus* represent a species complex of high diversity. Tatra Mountains are particularly rich in diversity, they harbour three species of the *Daphnia longispina* complex, and two *Eucyclops* cf. *serrulatus* lineages. Further sampling in geographic regions in East and South-East Europe (e.g., Greece, Ukraine) would be beneficial for possible detection of cryptic lineages and also to extent the knowledge of colonization of European populations from the *Daphnia longispina* complex.

The detection of cryptic lineages is not the general pattern in mountain lakes was revealed by the study of Balkan lakes as well as in the Pyrenees, where all analysed individuals belonged to *Daphnia longispina*. The results of genetic structure of *D. longispina* populations from Pyrenees show that more attention to the role of priority effects in ecology and evolutionary biology should be paid.

Obviously, studies of the genetic diversity of mountain *Daphnia* species still bring new insights on the evolutionary history of these organisms. The application of genetic methods is also useful for studies of other zooplankton species that have not been so intensively studied so far (e.g. *Eucyclops serrulatus* complex) and can help us to understand the processes of shaping the within- and among-population diversity.

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