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**Regional and local processes
influencing establishment of zooplankton
communities in pools
(review)**

Regionální a lokální procesy ovlivňující strukturu
zooplanktonních společenstev malých vodních ploch
(literární rešerše)

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ABSTRACT

Pools are shallow aquatic habitats in the landscape with specific properties affecting colonization and survival of various organisms there. In this review I try to discuss most important regional and local processes regulating succession and structure of zooplankton communities in the pools, especially: 1) physical and chemical factors of the pools; 2) dispersal of zooplankton; and 3) biotic processes. I also discuss the definition of the term “pool” and its relationship to other expressions used for different water bodies.

Keywords: zooplankton; species diversity; dispersal; pools; ponds; abiotic factors; inducible defenses;

ABSTRAKT

Tůně jsou mělké vodní plochy se specifickými vlastnostmi, které ovlivňují organismy v nich žijící. V rámci této literární rešerše se zabývám regionálními i lokálními procesy ovlivňujícími vývoj a strukturu zooplanktonních společenstev tůní, a to zejména: 1) fyzikálními a chemickými aspekty tůní; 2) způsoby šíření zooplanktonu; a 3) ekologickými vazbami mezi organismy. Ve své práci se rovněž věnuji obsahovému významu anglického termínu „pool“ ve vztahu k jiným názvům používaným pro různé typy vodních ploch.

Klíčová slova: zooplankton; druhová diverzita; šíření organismů; tůň; abiotické podmínky; indukované obrany;

INTRODUCTION

Much attention of conservation biologists has been paid recently to protection of pools. Importance of these habitats for ecosystem functioning and regional aquatic species richness has been demonstrated many times. Pools and other small water bodies are specific habitats in the landscape balancing between isolation and connectivity, which may act for many species as a refuge from large predators of more permanent waters (Wellborn et al. 1996). Small water bodies, as patches of habitat with particular characteristics, are considered to behave as aquatic islands in the landscape (Figuerola and Green 2002). Among-habitat diversity (beta diversity) may be the key for high regional species diversity (Oertli et al. 2002, Rodrigo et al. 2003). Moreover, owing to the isolation, many pools are inhabited by regionally endemic species (Zedler 2003). Destruction of even relatively small part of a wetland biotope in the landscape may cause a rapid decrease of species diversity of unexpectedly high number of taxa (citation). Scientific knowledge and conservation of freshwater invertebrates fall far behind the knowledge and protection of vertebrates (Strayer 2006).

Research of biological succession in pools has achieved great attention of both the scientific community and active conservationists of wetlands all over the world (Oertli et al. 2004). Pools are suitable study models for biogeography, evolutionary biology, and ecology. Due to their small size, they are also excellent subjects for ecological experiments, because it may be relatively easy to manipulate their local communities, e.g., of zooplankton.

The aims of this review, which serves as my bachelor thesis, are 1) to summarise the main physical factors and biological interactions influencing zooplankton succession in pools; 2) to discuss the most important biotic processes controlling zooplankton species diversity in the pools; and 3) to review ecological functions of small water habitats in the landscape.

This review should provide me with the theoretical background, which I will then use in my diploma (MSc.) thesis, which will focus on the diversity of crustaceoplankton in a large set of pools in the Protected Landscape Area Kokořínsko, and on the main factors affecting the local species richness and composition. Most of the studied pools are located within the area enlisted as wetlands of international importance under the Ramsar Convention. I hope that this thesis will increase my understanding of ecology of small aquatic habitats, and that my research will also contribute to the conservation of these vulnerable wetland biotopes.

DEFINITION OF THE TERM “POOL”

There are a lot of different meanings of the term “pool “. Primarily, I will use the word “pool” simply for a small waterbody as a habitat¹. However, not every small water should be considered as a pool, especially as the meaning of “small” depends largely on the context. I would therefore like to compare this term against other terms describing waterbodies commonly used in ecological literature. Exact thresholds among the meanings of the expressions “pool”, “mere”, “pond”, “lake”, “puddle”, “wetland” or “marsh” do not exist. On the other hand, it is possible to order these expressions according to the basic physical parameters, such as the water depth or surface area. If these characteristics are considered, the order would be “puddle” < “pool” < “pond” < “mere” < “lake”.

The terms “wetland” and “marsh” have wider meanings, and are not usually used for describing a single water body but rather a part of the landscape with several, mostly shallow, waters. In conservation biology, the expression “wetland” is often used for wet region with shallow water bodies with maximal depth up to 6 meters (Anonymous, Ramsar Convention, 2007), usually with elevated groundwater level.

The expression “puddle” I use for very shallow and usually ephemeral water bodies, with surface area in order of magnitude of square meters (although, occasionally, much larger flooded areas with characteristics otherwise similar to small puddles occur). The term “lake” I use for larger permanent water bodies, with maximal depth usually of several meters and a large surface area (several hectares). The shallowest lakes may have very low depth (1-2 m), in that case, they should differ from “ponds” at least by the surface size (Cottenie et al. 2001).

“Pools” are main subjects of this review. The border between “pool” and “pond” is very unclear, and some authors do not distinguish them at all (Ebert and Balko 1987, Crosetti and Margaritora 1987). I will use the expression “pools” for small water bodies with surface area from approximately 1 m² to 1000 m², and with maximal depth usually not exceeding 2 metres. Ponds, being usually defined as water bodies with surface area from 25 m² to 2 ha (Biggs et al. 2005), would be therefore larger. For some examples of use of these terms, see Table 1. (Additionally, the term “pond” is often used instead of fishponds for extensive or

¹ (Additionally, I will of course use the expression “pool” in the sense of group of objects or subjects, e.g., regional species pool for a set of species in the regional scale, local species pool for all species within one habitat.)

intensive fish aquaculture. By their size and ecological characteristics, however, most fishponds, at least in Central Europe, would be classified like artificial and drainable shallow lakes.)

Pools and ponds may be both natural and man-made habitats, and may be both permanent and temporary. Defining any exact border without overlap would be undesirable and artificial, because many habitats would be sorted differently in different seasons of the year due to water level fluctuations.

| publication | surface area (m2) | maximum depth (cm) | term | objects | place |
|-------------------------------|--------------------------|---------------------------|-------------|----------------|------------------|
| Blaustein 1997 | 0.024 | 15 | pool | 16 | Israel |
| Bonner et al. 1997 | up to 1000 | up to 50 | pool | 5 | Mississippi, USA |
| Ebert et al. 2002 | 0.5-20 | 50 | pool | 507 | Finland |
| Eitam et al. 2004 | 0.01-166 | 0.1-80 | pool | 52 | Israel |
| Holland and Jenkins, 1998 | 1.8 | 30 | pool | 16 | Illinois, USA |
| Louette and De Meester 2005 | 35 - 825 | 65 - 200 | pool | 25 | Belgium |
| Mura and Brecciaroli 2003 | 9-500 | 28-80 | pool | 7 | Italy |
| Pajunen and Pajunen 2003 | 0.13-239 | 4-105 | pool | 507 | Finland |
| Spencer et al. 1999 | 0.15-13 | | pool | 24 | Israel |
| Tavernini et al. 2005 | 36-396 | 30-120 | pool | 13 | Italy |
| Crosetti and Margaritora 1987 | | up to 150 | pool,pond | 29 | Italy |
| Ebert and Balko, 1987 | 12-648 | | pool,pond | 54 | California, USA |
| Batzer, movements. 2004 | 0.03-0.08ha | | pond | 2 | Minnesota, USA |
| Cottenie et al. 2001 | 0.1-9.5ha | average 50 | pond | 33 | Belgium |
| Elgmork and Halvorsen 1976 | about 100 | up to 100 | pond | 2 | Norway |
| Jenkins and Buikiema 1998 | 405 | 210 | pond | 12 | Viriginia, USA |
| Kobari and Ban 1998 | 7000- 66000 | 2.5-4.7 | pond | 2 | Japan |
| Lim et al. 2001 | | up to 200 | pond | 32 | Canada |
| Louette et al. 2007 | 100-250 | 150 | pond | 11 | Belgium |
| Mura and Brecciaroli 2003 | 400-800 | 70-130 | pond | 2 | Italy |
| Oertli et al. 2002 | 6-95000 | mean 1.7 | pond | 8000 | Switzerland |
| Shurin 2000 | | 100-200 | pond | 7 | Michigan, USA |
| Steiner 2004 | 34-10558 | 160 | pond | 18 | Michigan, USA |
| Steiner and Roy 2003 | 700 | 160 | pond | 1 | Michigan, USA |
| Willey and Threlkeld 1993 | 4-40000 | 20-400 | pond | 28 | Illinois, USA |

Tab. 1. List of selected studies on zooplankton of shallow water bodies, with comparison of the terminology in use.

ABIOTIC FACTORS

Life conditions in the pools are strongly influenced by different physical and chemical factors. Many studies are based on estimation of the importance of individual factors (e.g., water depth, habitat age, productivity, disturbance etc.), which have usually unimodal relationships with species diversity when manipulated in isolation (Connel 1978, Wootton et al. 1998). The uniqueness of each pool, however, consists of the simultaneous combination of many environmental as well as historical factors (Gaston 2000, Ricklefs 1987, 2004). The impact of any single factor may influence similar zooplankton communities differently, depending on the state of other factors (Kneitel and Chase 2004, Östman et al. 2006, Worm et al. 2002, see Figure 1.). For example, disturbances and resource levels may significantly influence the effect of predation on rotifer communities (Kneitel and Chase 2004)

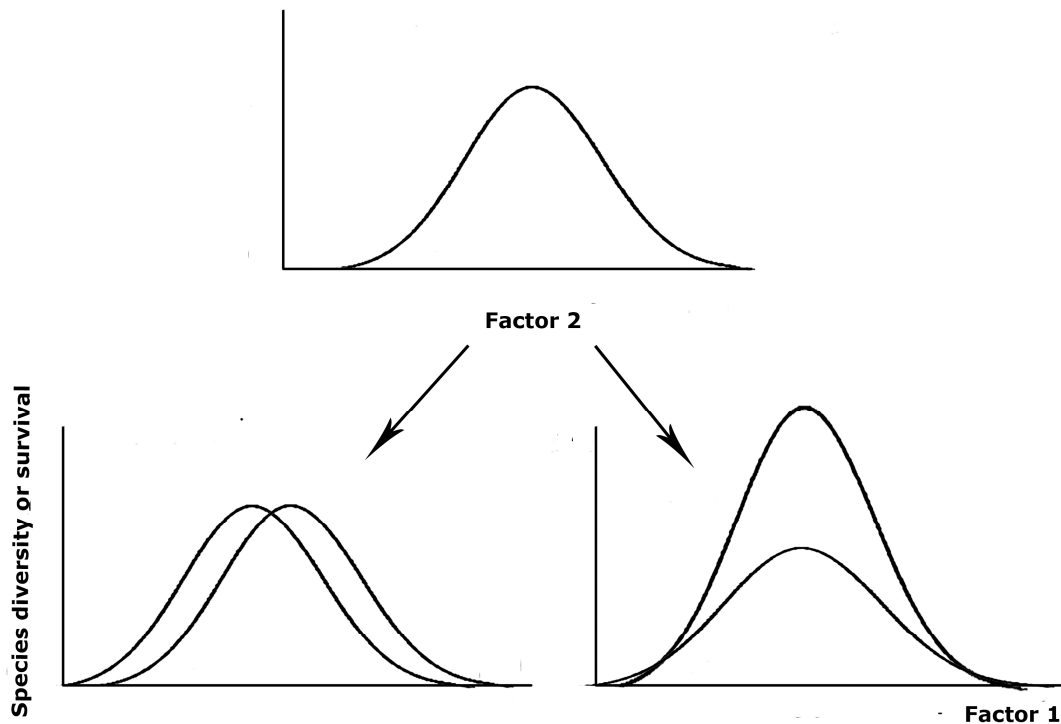


Figure 1. Factor 2 may shift a hump-shaped relationship between Factor1 and the species diversity or survival to the left or right, or may dampen or increase the magnitude of this relationship (Wootton 1998).

In nature, the life conditions are influenced by many factors, which are affected by the complex net of links (Drake 1991, Lampert 1987). Moreover, the relative contribution of factors structuring communities varies through time. On the other hand, the main factors and

processes controlling species richness are supposed to have a similar influence on different taxonomic groups in freshwater ecosystems (Holland and Jain 1981).

According to the scale on which an abiotic factor affects the community, it is possible to distinguish geographical factors (affecting both local and regional species richness) or physical and chemical factors (affecting the community within the habitat).

GEOGRAPHICAL FACTORS

The relative position of the habitat in relation to other suitable habitats in the landscape may strongly influence the colonization rate. Species richness of isolated pools may be effectively regulated by the dispersal (Angeler and Alvarez-Cobelas 2005) and so may be lower than in well-connected habitats (Shulman and Chase 2007). Species richness of individual well-interconnected pools may be regulated much more by local conditions than by dispersal. Isolation of the habitat may be caused by different geographical constraints according to the different dispersion ways, e.g., pools in a deep narrow canyon may be optimal for rivulet-provided dispersion of zooplankton but unsuitable for dispersion by waterfowl.

Connectivity

Connectivity is directly related to distance and potential dispersion rate. A pioneering study of holding data of the relative distances among the habitats for pool zooplankton communities was made by Michels et al. (2001). They studied a system of interconnected pools with rivulets and overflows functioning as pathways. They used data on flow rate, flow current and effective geographical distance to evaluate three different models in a GIS analysis of the studied area.

Flooding in floodplain areas represents a specific type of waterway connection. Passive dispersal of zooplankton by drift may occur during the aquatic phase (Frisch 2002, Havel et al. 2000) and thereby increase local species richness, e.g., of microcrustaceans (Fischer et al. 2000, Nielsen et al. 2002). On the other hand, flash floods may flush the whole zooplankton community from temporary pools in the deserts (Waard and Blaustein 1994).

Altitudinal and latitudinal gradients

Latitudinal and altitudinal gradients with their impact on the local climate affect all ecosystems, and small water bodies are no exceptions. Altitude clearly relates with

temperature and many other abiotic factors influencing zooplankton communities. High-altitude ponds usually have food chains of low complexity and are thought to support relatively low species diversity. The decrease of species richness with increasing elevation is obvious in many different taxonomic groups (Gaston 2000).

Temperature, decreasing with increasing elevation, may significantly influence zooplankton community structure and may also influence ontogenetic development and thereby the body size of zooplankton (Lock and McLaren 1970).

Latitudinal north-south gradient may also play an important role in regional variation in species richness (Holland and Jain 1981, Gaston 2000). Although both latitude and altitude affects the regional climate, local microclimate may also strongly affect the temperature conditions in pools – position in the landscape.

LOCAL PROCESSES

Ability of coping with the physical and chemical stress may be an important selection advantage for successful colonization and survival. Habitat size, maximum water depth, hydroperiod, disturbances and chemical properties of water (pH, salinity, nutrient state, etc.) belong among the most important local abiotic factors affecting the zooplankton community assemblage and structure.

Habitat size and maximal depth

Habitat size is the central unit in the island biogeography theory of McArthur & Wilson (1967), and plays a major role in species diversity (Dodson 1992). Variation in species diversity usually correlates with the habitat size, because larger areas experience fluctuations of many environmental variables of smaller amplitude, and are more likely to be invaded by immigrant species (McArthur&Wilson 1967, March & Bass 1995); larger habitats may also provide more diverse environment to host more species with different niches. Substantial part of species richness in temporary water bodies can often be explained by the pool size only (Biggs et al. 2005, Case 1990, Ebert and Balko 1987, Holland and Jain 1981, Spencer et al. 1999, Ward & Blaustein 1994). On the other hand, Scheffer and Geest (2006) formulated a hypothesis that small habitat size and isolation can promote species richness in lakes and ponds. The main idea is that shallow water bodies tend toward either of two alternative stable states; vegetated with clear water, or devoid of submerged plants and turbid. The vegetated state has a higher diversity in many animal groups, which is largely

explained through the key roles of fish and aquatic plants (Jeppesen et al. 1997, Scheffer et al. 1993, Smirnov 1996).

In small freshwater ecosystems, maximum depth may correlate with the habitat size, therefore the water depth may be an important predictor of zooplankton diversity. Water bodies are often divided into “shallow” and “deep” bodies; the main criterion of such classification in the temperate zone may be whether the water body can stratify during the year. In this sense, most pools would be typically classified as shallow habitats because permanent stratification is very rare. In shallow habitats, mixing by wind brings the whole water volume into contact with the bottom sediments, which may supply nutrients to the whole water column. Shallowness of the pools may also allow greater accessibility of benthic and littoral algae for calanoids; the water depth may therefore correlate with the calanoid body size (Smyly 1968).

Presence of sediment

Another factor affecting the zooplankton species richness in the pools is the presence of well-developed sediment. Sediments may be required for successful survival in the habitats, because they are an important repository for resting egg banks (Vandekerkhove et al. 2005). In the periodically drying habitats, egg banks in the sediment allow many populations to re-establish following previous local extinction caused by habitat drawdown (De Stasio 1990). In very early communities, egg banks may be important in the maintenance of species richness and genetic variation, although they are not as extensive as those in more mature habitats (Vandekerkhove et al. 2005). Specimens stored in the sediments are a part of the overall species diversity together with species present in the water column, and should not be overlooked in biodiversity monitoring (Crispim and Watanabe 2001). Detritus in the sediment may be also an important food resource for zooplankton (Rautio and Vincent 2006).

Habitat age

Another significant factor controlling species diversity in the pools is the habitat age discussed below. Generally, local processes are supposed to play a bigger role in more mature habitats and long-established communities usually have more species.

Permanence

Permanence (or temporality) of the habitat strongly effects communities of in small water bodies (Wellborn et al. 1996, Tavernini et al. 2005, Ebert and Balko 1987, Spencer et

al. 1999, Schell et al. 2001, Fischer et al. 2000). Organisms may also be sorted among habitats according to their predators, whose own distribution is related to the permanence (Wellborn et al. 1996, Spencer et al. 1999).

Extremely temporary water bodies with the shortest hydroperiod are often called “ephemeral”. While this term is often vaguely used, recently a study by Jocqué et al. (2007) attempted to define ephemeral water bodies also by the characteristics of their biotic community. In this sense, ephemeral habitats are those in which species replacement does not occur during the aquatic phase, i.e., the hydroperiod is so short that it does not allow species succession. Temporary waters with longer hydroperiods (“non-ephemeral”) show a characteristic succession in species composition between the filling and drying of the waterbody.

Temporary waters are usually shallow, with a large surface to volume ratio, so they are more susceptible to water fluctuations than permanent water bodies. Extinction due to pool drying is supposed to be a major driving force behind the structuring of microcrustacean communities in temporary pools. The main changes in hydrochemical parameters are usually observed during the pool drying, due to water evaporation and the small volume of remaining water and when habitats re-fill after a desiccation period accompanied by a flush of dissolved materials and their release from sediments or generally during significant water level fluctuations (Tavernini et al. 2005). Permanence can often significantly explain variation in zooplankton richness in temporary water bodies (Eitam et al. 2004, Holland & Jenkins 1998, Jocqué et al. 2007, Spencer et al. 1999, Tavernini et al. 2005). Species richness generally increases with the increasing hydroperiod in temporary freshwater habitats (Mahoney et al. 1990).

The local species diversity in temporary water bodies usually increases in time with linear slope (Jenkins and Buikema 1998). On the other hand, pools with a longer hydroperiod may attract or provide suitable conditions for more predator species (Spencer et al. 1999), which may eventually cause local extinctions of the preferred prey species (Murdoch and Scott 1984). Temporary habitats therefore favor organisms adapted well to both the habitat drying and predation press. Temporary pools can be also inhabited or even dominated by species which can survive only in an enemy/competitor free space and therefore are very rare in the surrounding landscape

Many adaptations of a very wide spectrum of organisms are associated with the hydroperiod. There are two most important ways how to cope with the habitat drying (Ebert

and Balko 1987). The first one is an “escape in space”, and usually involves a winged (insects) or terrestrial (amphibians) adult stage, which allows evading drawdown situations, and the second is an “escape in time”, i.e., entering the diapause or creation of persistent stages (Angeler and Alvarez-Cobelas 2005). The latter type of adaptation is much more common among zooplankters. A short wet cycle of temporary pools usually correlates with a fast development rate and a short life cycle, including resistant stages and propagules in life cycles and many other changes in life history. In temporary pools, interspecific differences in development time, and thus different dependence on the hydroperiod, often determine the structure of metapopulation patterns and dynamics in insects.

A lot of aquatic invertebrates solve the problem how to survive in the dry sediments.

Many different ways of coping with habitat drying were observed in copepods, especially in cyclopoids, which can stay alive in the soil for many months (Frisch 2002), but also for several tens of years. On the other hand, the duration of the dry period of the habitat appears to be inversely related to the number of copepod species that emerge from diapause, which is an important strategy for the persistence of copepods in short-hydroperiod wetlands (Bruno et al. 2001). Diapause may be necessary for survival, however, it brings many disadvantages such as extension of development time, potentially increased mortality and restriction of growth to only part of the year (Watson 1984).

Many temporary habitats dry out periodically, which makes them, at least partly, predictable. That’s why many copepods have evolved adaptive mechanisms that provide synchronization in time and space between growth, reproduction and favorable environmental conditions (Santer 1998).

On the other hand, many pools dry out much often and irregularly. This makes them much less predictable (Bonner et al. 1997). Especially vernal pools may be water-filled several times per year but some wet periods may be too short for completing of life cycle for most organisms (Wellborn et al. 1996, Tavernini et al. 2005, Eitam et al. 2004). Interesting adaptation on the unpredictability of the environment is prolonged dormancy of propagules in the sediment, e.g., mainly in branchiopods (Hairston and Cacéres 1996). The prolongation may be influenced both by the egg location (out of emerging signals) and just by the adaptation to environmental uncertainty. The adaptation to the environment unpredictability consisting of reaction of only a part of egg bank to hatching signal (or a seed bank to germination stimulus) is called “bet-hedging strategy” and be observed in aquatic as well as terrestrial ecosystems (Philippi 1993a, 1993b). Mechanisms which allow the variable

responses to the habitat drying are site-specific and may diverse among one species populations from different localities (Watson 1984).

The copepods may survive habitat drying in different ways, e.g. by making true diapausing and dormant eggs (Uye 1986), dormant copepodits (Elgmork 1967, Elgmork and Halvorsen 1976, Frisch 2002) or dormant and diapausing adults (Bruno et al. 2001).

Diapause may strongly influence the sex ratio of emerging copepods towards females (Bruno et al. 2001) in species diapausing as adult females. The males emerge often earlier than females, and are thereby assumed to be readily able to mate with emerging females.

Chemical properties of the water

Chemical properties of water may strongly affect the structure of zooplankton community, especially in small pools. Due to their small habitat size, water level may fluctuate much more than in larger habitats, and thereby concentrations of different ions may change rapidly during the season. In this way, salinity may be an important factor controlling species richness in the pools (De Los Rios and Contreras 2005, Nielsen et al. 2003). Many planktonic species are adapted to generally fluctuating or higher salinity of the small water bodies (Ortells et al. 2005, Rokneddine 2004). Every species have different salinity optimum, which allows their coexistence at the regional scale (De Los Rios and Contreras 2005).

Water acidity or alkalinity may effectively control local species diversity in the pools (Schell et al. 2001, Tavernini et al. 2005) as well as in the ponds (Biggs et al. 2005).

BIOTIC PROCESSES

Biotic processes play a major role in controlling zooplankton species richness in mature natural habitats (Shurin 2000, Urban 2004, Vanschoenwinkel et al. 2007, Cottenie and De Meester 2003, Cohen and Shurin 2003). The majority of biotic interactions in freshwater ecosystems are supposed to be antagonistic (Ricklefs 1987). In this way, predation and competition are supposed to play a key role in controlling species richness in the pools. The importance of parasitism in the pools hasn't be reliably evaluated yet; however, its influence is likely to be more important than currently supposed to be.

In recent years, much of interest has been paid to studying biotic processes influencing structure of zooplankton communities. Both natural observations and experimental studies are in focus of a number of studies, although there may be a substantial difference in the results between studying zooplanktonic biotic interactions in natural conditions and in artificial habitats (Elgmork and Halvorsen 1976).

Predation

Although the pools are assumed to act as refuges free of large top-predators occurring in more permanent and larger aquatic habitats, zooplankton communities in small water bodies must still face the risk of predation by various predators, including those absent from other habitats. In fishless water bodies, invertebrate predation may be an important factor regulating species richness of zooplankton (Vanni 1988, Steiner and Roy 2003). Predators in small water bodies can influence species diversity, abundance and biomass very effectively, especially at lower trophic levels. In some cases, predators can reduce the abundance of their prey to the point of exclusion (Murdoch and Scott 1984, Wilbur 1997). On the other hand, predation may allow local coexistence of competing species by reducing the superior competitor. In some cases, predation may also promote higher species richness by decreasing intermediate predators (Brooks and Dodson 1965, Vanni 1988).

It was recently shown that the predator:prey species richness ratio may be largely influenced by the isolation of the habitat and decrease with increasing isolation (Shulman and Chase 2007). Generally, proportion of predators increases with increasing pool size.

The most important invertebrate predators in pools in the temperate zone are phantom midge larvae (*Chaoborus*, Diptera), backswimmers (Notonectidae, Hemiptera), cyclopoids (Cyclopoida, Copepoda) and tadpole shrimps (Notostraca).

Phantom midge larvae (*Chaoborus*) are common predators in many small water bodies. *Chaoborus* larvae are gape-limited predators that select small planktonic invertebrate prey (Borkent 1979). In this way *Chaoborus* predation may have larger impact on rotifers than crustaceans (Hobæk et al. 2002). For review see Berendonk and Bonsall (2002).

Copepods are also important invertebrate predators in aquatic ecosystems. Among other prey, they can prey on small cladocerans (Chang and Hanazato 2003, El-Shabrawy and Dumont 2003, Kerfoot 1977). The most common interaction of copepods and cladocerans is the predation of large copepodites (CIV and CV) and adults on small, often new-born daphnids (Lampert 1987), as large-bodied cladocerans may be able to escape copepods more successfully (El-Shabrawy and Dumont 2003, Chang and Hanazato 2003). Unusual mechanism of size-selective predation may be observed in small copepodites, which may enter brood chambers of large *Daphnia* specimen and there prey on *Daphnia* eggs (Gliwicz and Lampert 1994). Cladoceran morphological responses to copepod predation exist as well (Kerfoot 1977).

Prey species cope with the predation by various ways. The best known are: 1) reduction of conspicuousness (e.g., transparent bodies or inconspicuously-coloured bodies), which is probably the most widespread defense against predation in zooplankton, and is common for “palatable” zooplankton prey (Kerfoot 1982); 2) aposematic coloration, which is very common for prey distasteful for fish predators, e.g., water mites (Kerfoot 1982); 3) inducible defenses (Dodson 1988) including both morphological, ontogenetic and behavioral adaptations.

INDUCIBLE DEFENCES OF PREY

In the presence of predator, many prey species try to avoid predation by specific responses. These predator-induced responses in plankton have elicited increasing research interest in the recent decades (Lass et Spaak 2003). They are an integral part of biological interactions among organisms of different taxonomical groups. Many types of prey defenses are info-chemical mediated. In these cases, the chemical substance carrying information is called kairomone (probably from Greek “*kairos*”, which means “foreign”). Kairomones are usually favourable for the receiver of the signal but not for its sender (Lass et Spaak 2003). In this way, prey is usually the receiver, while predator is sender (De Meester 1993, Dodson 1988, Tollrian 1994).

Kairomones are not necessarily produced by the predator itself (or only). For example, mucus-dwelling bacteria may produce chemical substances functioning as chemical cue

(Ringelberg and Gool 1998). Moreover, both fish and bacteria may interact in production of the so-called “fish kairomone”; this kairomone may therefore be some fish metabolite subsequently processed by bacteria living on the fish body (Beklioglu et al. 2006).

The responses of prey to predator are both predator- and prey-specific (Dodson 1988). Moreover, even different clones of the same species may have different response to the same predator (Dodson 1988, Weber and van Noorddwijk 2002).

On the other hand, freshly crushed conspecifics may also evoke various non-specific behavioral responses of the prey, e.g., in *Daphnia* (Laforsch and Beccara 2006, Pijanowska 1997). These responses usually have behavioral character. However, alarm cues from crushed conspecifics seem to be less effective than cues from predators (Laforsch and Beccara 2006).

Behavioral adaptations as inducible defenses against predation

Zooplankton may swarm, swim more uniformly and slower in the presence of kairomones indicating the predator presence (Jensen et al. 1998, Pijanowska and Kowalczewski 1997). Both swarming and slower swimming speed of the swarm are supposed to decrease predation efficiency. On the other hand, zooplankton swarms may be more vulnerable to a different kind of predators – aquatic carnivorous plants, e.g., *Utricularia* (Englund and Harms 2001). However, due to relative scarcity of those plants in most pools, this type of predation is not supposed to play an important role in regulation of zooplankton species richness in the pools generally.

Another induced behavioral defense against predation consists of continual alertness of the prey, i.e., increased sensitivity to any mechanic or light impulses. This type of increasing of evasiveness has been called the “last chance defense”, because it occurs when other defensive mechanisms did not substantially reduce spatial or temporal encounters of prey with predators (Pijanowska et al. 2006).

Another behavioral adaptation to the presence of predator is initiation of diurnal vertical migrations (DVM). DVMs are supposed to play a minor role in the pools due to shallowness of these habitats, although even in very small freshwater bodies *Chaoborus flavicans* are known to migrate in the water column to avoid fish predation (Berendok and Bonsall 2002).

Rather than DVM, diel horizontal migrations (DHM) may be important behavioral defenses against fish predation in shallow habitats. DHM may exist in horizontally structured

habitats, mostly due to well-developed littoral zone with macrophytes (Lauridsen et al. 1999), which may act as refuges for pelagic crustaceans against fish predation (Jeppesen et al. 1997). Generally, DHM should be more important in the habitats with fish than in fishless waterbodies, where they are considered to play a minor role (Lauridsen et al. 2001).

Ontogenetic adaptations as inducible defenses against predation

Rate of ontogenetic development of the prey may be substantially influenced by the presence of both invertebrate and vertebrate predators. Intensive research has been made especially on various *Daphnia* species. In these model organisms, several life-history parameters may change in the predator presence. For example, daphnids can reduce the period of greatest visibility and thus reduce their vulnerability to visually oriented predators, by shortening the period during which eggs are carried in the brood chamber (Mikulski et al. 2004) and decreasing the number and size of neonates released (Mikulski 2001).

Kairomone-induced specimens mature earlier and release their first clutch at a smaller size (Mikulski et al. 2004, Mikulski 2001, Weber and Declerck 1997). This is an adaptation to size-selective predators which select larger prey. Therefore, the probability of the prey survival increases with decreasing size at first reproduction.

Ontogenetic adaptations as inducible defenses are more commonly caused by vertebrate predators, such as fish. Interesting influence on the ontogenetic development of zooplankton may be caused by salamanders, which may locally act as important predators affecting the structure of zooplankton communities in small water bodies (Wilbur 1997). They may influence development of the crustacean eggs deposited in sediments of temporal pools. Salamanders can not prey upon these eggs, but can cause the strong delay of their hatching, very probably by chemical cues (Blaustein et al. 1996).

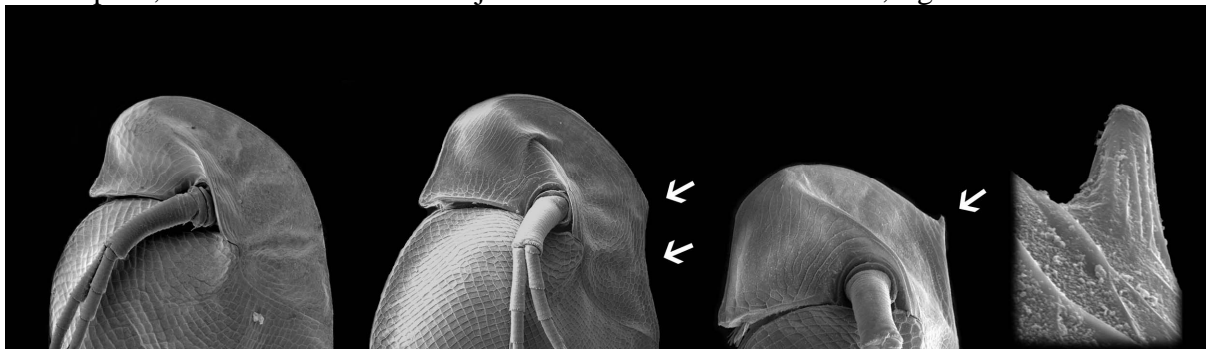
Morphological adaptations as inducible defenses against predation

Many zooplankton organisms produce various morphological defenses against predation. These morphological shapes decrease predator efficiency, as induced phenotypes are handled less efficiently by predators. Large variety of these shapes is known from *Daphnia*, the model organism for studies on inducible defenses.

Recently it was shown that morphological adaptations of induced phenotypes may be very complex mechanisms. Visible minute morphological changes may be only a part of the entire system. For example, induced *Daphnia pulex* specimens have specific shape of the dorsal part of carapace. This structure, called *neckteeth*, and its presence may be correlated

with significantly decreased effectiveness of predation on *Daphnia* by *Chaoborus* larvae. But the real mechanism of this morphological defense probably consists of the change of stability of carapace, which is several times higher in induced forms (Laforsch et al. 2004). *Neckteeth* may be observed also in several other species of *Daphnia*. These include two likely undescribed species from Czechia and Slovakia (Figure. 2.) occurring in pools. Currently we work on the formal description of these two taxa.

Figure 2. Inducible defense of *Daphnia n.sp.* against *Chaoborus* predation. Left: not induced adult female; second from left: induced adult female with specific “hump” on the dorsal part of carapace; third from left: induced juvenile female with neck-teeth; right: detail of neck-



teeth of juvenile female; Picture ©Petr Juračka

Kairomone-induced *Daphnia lumholtzi* specimens develop long helmets, which are supposed to be effective defense against fish predation (Tollrian 1994). However, most of morphological defenses in *Daphnia* are effective only against invertebrate predation.

The helmets of *Daphnia cucullata* have been studied largely for decades. Although production of this helmet is usually caused by the water turbulence, via the mechanical cues, the origin of this defense may be in kairomones as well. Moreover, turbidity and kairomones may act the production of helmet synergistically (Tollrian and Laforsch 2006). Great helmets are also developed by *Daphnia carinata* complex, as the defense against Notonectids (Grant and Bayly 1981), which often prey on daphnids (Steiner and Roy 2003, Murdoch and Scott 1984)

A special morphological inducible defense was observed in the *Daphnia atkinsoni* species complex as an adaptation against predation by notostracans (Petrušek 2007). These *Daphnia* are able to produce an “armor” looking like crown of thorns in the presence of *Triops*.

Competition

The competition among organisms is widespread both in terrestrial and aquatic habitats. Generally, two most obvious types of competition are defined as exploitative and interference competition. Both types may be intra- as well as interspecific. Exploitative competition involves indirect negative interactions arising from the use of a common resource (Case and Gilpin 1974), while interference competition involves direct negative interactions arising from territoriality, overgrowth or chemical competition (Schoener 1983).

Exploitative competition may negatively affect fitness of many zooplankters, e.g., increasing population density may have inverse relationship with fecundity in *Cyclops strenuus* (Elgmork and Halvorsen 1976). Competition may also affect species abundance, e.g. competition with large herbivores (e.g., *Daphnia*) contributes to the scarcity of small species (e.g., *Bosmina*) in fishless habitats (Vanni 1988).

Exploitative type of competition prevails in freshwater zooplankton communities, but interference competition exists in zooplankton as well, e.g., among cladocerans, ciliates and rotifers (Wickham and Gilbert 1991).

The competition among zooplankton may be largely influenced by its predators, because predation may decrease abundance of competitively superior species (Shurin 2001, Brooks and Dodson 1965, Paine 1966, Wilbur 1997). Several small-bodied zooplankton species coexist regionally with larger ones due to size-selective predation (Shurin 2001), e.g., *Holopedium gibberum* and *Daphnia parvula* are probably at least partly competitive species. They coexist in purely competitive system due to selective predation of *Chaborus* (Allan 1973).

Mutualism

Mutualism seems to be relatively rare and irregular among zooplankton, at least observations of possibly mutualistic relationships are scarce. An example of such may possibly be epibioses of certain green algae on *Daphnia*. Barea-Alco et al. (2001) described in detail such a system in a Spanish lake. This lake freezes regularly and production of ephippia is essential for survival of *Daphnia pulicaria* in this habitat. Ephippia production may be enhanced by the *Daphnia* epibionts (green algae), which are also largely grazed by *Daphnia*. This relationship is supposed to be mutualistic, as *Daphnia* provides on its body surface suitable habitat for algae, part of which become the food source for their host.

Interesting relationship may be observed in *Daphnia* gr. *obtusa* in shaded small waters. It was observed that they can have active plastids from sequestered cyanobacteria and from eukaryotic algae in the gut endocytes (Chang and Jenkins 2000). Senescence of the algal symbionts suggests that this relationship is not closely coevolved yet.

Parasitism

Parasitism also influences zooplankton communities. For example, infection of microsporidians may lead to evolutionary changes in the genetic composition of *Daphnia* (host) populations (Haag and Ebert 2004).

Epibionts

Many ciliates and algae are adapted on living on the bodies of some zooplankton species. Those organisms are called “epibionts”. They are usually host-specific, e.g., some species of the genus *Colacium* (Protozoa, Euglenophyta) live on the cycloids, and other ones on crustaceans (Chiavelli et al. 1993, Willey and Threlkeld 1993). Epibionts in general have negative influence on their host as they make zooplankton swimming more difficult (Barea-Alco et al. 2001). Another negative influence of epibionts may be increased susceptibility of their hosts to fish predation, due to increased visibility (Willey and Threlkeld 1993).

Relationships among terrestrial and aquatic organisms in the pools

Although biotic interactions among different taxonomic groups of freshwater invertebrates prevail, biotic processes between terrestrial and aquatic organisms in the pools exist as well. Many terrestrially derived detritivores (oligochaetes, millipedes, isopodes) might consume large amount of detritus in small water bodies, and terrestrially derived predators (arachnids, beetles) might prey on aquatic invertebrates aestivating in dry basins (Batzer 2004).

ZOOPLANKTON SUCCESSION IN POOLS

Small water bodies, such as pools, tend to have seasonal dynamics in aquatic environments during the year. The seasonality of the temporary habitats creates constraints for the length of life cycles and developmental time of organisms. Also, both succession and invasion of new species proceed much more quickly than in most terrestrial habitats, because the organisms must colonize the habitat and complete their life cycle before the habitat dries out. As the environmental conditions change during the season, the species diversity of the habitat changes as well.

Local zooplankton species richness is affected by both regional (geographical) and local processes. The terms “local” and “regional” are relative and their sense strongly depends on the scale used. In this context, I refer to the spatial scale at which ecological and biogeographical processes predominate. Predation, parasitism, competition and fluctuations of physical and chemical characteristics are mostly considered to be “local”, while dispersal and fluctuations in species distributions across broad geographic regions are considered to be “regional” ones.

In order to colonize the new habitat successfully, every newcomer must be able to arrive into the habitat and then to cope with local physical, chemical and biological conditions (Wellborn et al. 1996, Cornell and Lawton 1992, McPeck 1996). The final zooplankton assemblage therefore results from many biotic and abiotic processes.

Regarding the role of local interactions in controlling species assemblages, it is possible to distinguish between more and less “interactive” communities (Cornell and Lawton 1992). In the interactive ones, local conditions have large impact on the community, while in the non-interactive communities their impact is low or absent.

Real natural communities probably lie on a continuum from interactive to non-interactive systems (Ricklefs 1987, Shurin 2001), and the relative impact of ecological and biogeographical processes on the community composition depends both on the intensity of interactions within the local habitat (Cornell and Lawton 1992) and on the dispersal. For example, if dispersal events are rare, the local species composition largely depends on the site's colonisation history and local processes may play a minor role (Ricklefs 1987).

When the zooplankton community matures, local processes become more important (Wellborn et al. 1996), and the likelihood of successful invasion of new species decreases with increasing age of habitat (Holland and Jenkins 1998, Tilman 1997). In real communities, the local species diversity of one habitat may eventually reach the state when the successful colonisation of new species is unlikely, because all actually available microhabitats within the habitat have been already occupied: the so-called “species saturation” or “colonisation plateau”. Similarly, successful colonisation of a habitat may be low in areas with high dispersal rates, where the local species diversity is controlled mostly by local processes because all potential species arrive very early (Jenkins and Buikema 1998). This state is called “Quorum effect” and is also similar to “Equilibrium model of species number” in island biogeography, which is determined by the balance between immigration and extinction rates (McArthur and Wilson 1967).

A lot of zooplankton organisms produce resting stages, which may stay viable in the sediment for many years (Brendonck and De Meester 2003). These stages may have the most important influence on species richness especially in very isolated (Angeler and Alvarez-Cobelas 2005), often disturbed or in small ephemeral habitats (Hotový and Petrusek 2007). The main reason for producing persisting stages is rapid colonisation of temporary waters after habitat water re-filling. These communities of viable but inactive resting stages in the sediment are called “egg banks”. Although the majority of viable propagules occur in the upper centimeters, responsive eggs may be also in lower old layers (Hairston et al. 1995, Moritz 1987). The egg banks have large importance for evolution and ecology studies and for conservation biology, because the viable propagules in the sediment should be considered when evaluating the local species richness, or intraspecific genetic diversity.

Also the invasion history of a habitat by different species may be an important determinant of success or failure of further colonisation events as well (Drake 1991, Robinson and Edgemon 1988, Robinson and Dickerson 1987). Generally, colonisation rate and order have larger influence in sites where colonisation rates are relatively low (Jenkins and Buikiema 1998, Robinson and Edgemon 1988).

Some species may benefit from the earlier colonisation of the habitat, and may prevent later arrivals from the colonisation. The effects on the local species richness caused by the colonisation sequence are called “priority effects”. Similar effect, but affecting genetic structure of zooplankton communities, may be observed as well. It is called “founder effect” and it may efficiently prevent later arriving clones of successful colonization of yet colonized

habitat by the other clones of the same species (Louette et al. 2007). Founder effect simultaneously with rapid population growth and rapid local adaptation upon colonization of new habitat may result in the effective monopolization of resources yielding a strong priority effect. This effect may cause discrepancy between high dispersal rates of zooplankton and reduced rates of gene flow, and is called “Monopolization hypothesis” (De Meester et al. 2002). Large egg banks of well adapted clones play a big role in “monopolization process”, because they can effectively prevent newly invading genotypes from colonization, and thereby enhance priority effect. Also on the continental scale, repeated founder effects may cause important decrease of zooplankton genetic diversity (Boileau and Hebert 1991), especially when the populations are founded by a few individuals (Nei et al. 1975).

Although founder effects and monopolization of the habitat are ubiquitous in the nature, inverse process favouring immigrant genes exists as well. It is based on the fact that residents living the habitat are inbred. Thereby mating between immigrants and residents may result in offspring with fitness advantage from hybrid vigor (Ebert et al. 2002).

Though succession and final assemblage of zooplankton community depend on multiple variables and factors (Ricklefs 1987), many studies concentrated on either local processes or on the possibilities of dispersal and regional limitation of the species pool (Jenkins 1995). In any given study, one group of processes (local or regional) is usually more important predictor of the resulting species richness than the other one; the relative importance of regional and local factors strongly depends on the conditions and design of the experiment and on the taxa studied. In artificial experimental ecosystems, the limitation by dispersal is likely to be much more important for establishing zooplankton communities (Jenkins 1995; Jenkins and Buikema 1998; Jenkins and Underwood 1998; Holland and Jenkins 1998, Case 1990), while in mature natural habitats it seems to play a minor role (Shurin 2000, Urban 2004, Vanschoenwinkel et al. 2007, Cottenie and De Meester 2003, Cohen and Shurin 2003). However, evidence of dispersal limitations in natural ecosystems (Tilman 1997, Caley and Schluter 1997) as well as prevalence of local processes over dispersal in artificial ecosystems (Lukaszewski et al. 1999, Louette and De Meester 2005) exists as well.

Cohen and Shurin (2003) made an experimental test with zooplankton dispersion within small experimental area and they found that distance from the source pond (up to 60 meters) had a very weak effect on the rate at which new species arrived into experimental pools. Similar results were obtained by Shurin (2000) for a set of natural ponds. Dispersal

limitation is generally supposed to take a more important role within larger areas, of hundreds of square kilometers.

It is very difficult to quantify the dispersal rate for zooplankton organisms. Most studies focusing on zooplankton succession ignore this factor as being “rapid and frequent” (Lampert and Sommer 1997). Effective dispersal of zooplankton over large distances was generally accepted and its ecological importance neglected. Many zooplankton species have wide distributions, parthenogenetic life cycles and dormant life stages, which have been assumed to be the primary means of dispersal (McAtee 1917, Begon et al. 1990). The rapid spread of exotic zooplankton species also suggests effective dispersion of cladocerans across large distances (Mergeay et al. 2005, 2006, Havel et al. 1995, Louette and De Meester 2004, Havel and Medley 2006). On the other hand, detailed studies showed that many species distributions, supposed to be cosmopolitan, are actually much more restricted, and gene flow among populations may be limited (Boileau and Hebert 1991). Generally, copepods are regarded as inefficient dispersers over long distances, owing to absence of many species in formerly glaciated regions distant from unglaciated refugia.

Zooplankton dispersal among localities is considered to be mostly passive (apart from groups with a terrestrial or aerial phase, e.g., phantom midges *Chaoborus*) and thus it may be significant process controlling local species richness (Vanschoenwinkel et al. 2007). Understanding dispersion mechanism of particular zooplankton group should be crucial for understanding its ecology. This is especially true for metapopulations in temporary water bodies, where the dispersal may be an important factor for survival in the region. Among the common ways of passive zooplankton dispersion are animals, especially birds (Proctor 1964, Proctor and Malone 1965, Maguire 1959, Figuerola and Green 2002, Louette and De Meester 2004). Waterfowl may propagate zooplankton both on the body surface (ectozoochory) and in the intestinal tract (endozoochory) (Figuerola and Green 2002). In the areas with low bird abundances or in habitats not regularly visited by birds, dispersion by other animal vectors, such as insects (Bilton et al. 2001), fish (Jarnagin et al. 2000, Beladjal et al. 2007), amphibians (Bohonak and Whiteman 1999) and mammals, may be important as well. Man is also a significant disperser of zooplankton propagules, mostly unwittingly (Yan et al. 2002). Most known example of human-mediated of zooplankton invasion may be *Bythotrepes*. This species was probably introduced in the Great Lakes with the ballast water of the ships (Mills et al. 1993). Another example may be cladoceran *Cercopagis* dispersed by sport fishers in lakes (Jacobs and MacIsaac 2007). Human-mediated dispersal became recently an important

mechanism of dispersal among continents. Cases of deliberate introduction of zooplankton species, including intentional release by scientists (Kohout and Fott 2006), exist as well.

Passive dispersal by abiotic powers shouldn't be neglected; wind and rain (Brendonck and Riddoch 1999, Cáceres and Soluk 2002) or water flow (Michels et al. 2001) may be important dispersal ways of zooplankton. Waterway connections often cause the influx of the live animals and their propagules into connected habitats, and thus positively influence local species richness in the recipient pool (Michels et al. 2001). In very local scale, interconnected pools within a relatively small area can keep high α -diversity and support very differently developed zooplankton communities (Cottenie et al. 2001), while in regional scale pools connected by temporary overflows may host more similar communities of passive dispersers (Vanschoenwinkel et al. 2007).

Quantification of the zooplankton dispersal rate, although methodically complicated, may be important for our understanding of the ecology of pool communities. There are two main approaches how to evaluate the dispersion rate. First one consists of direct evaluation of the number of transported animals or their propagules in the specific dispersion way, e.g., counting number of dispersing eggs or individuals in the water flow (Michels et al. 2001), in wind or rainwater (Jenkins and Underwood 1998), or counting viable propagules in the intestinal tract or droppings of waterfowl (Proctor and Malone 1965, Figuerola and Green 2005).

Secondly, dispersion rate may be assessed indirectly from the colonisation success (Jenkins 1995) or from intrapopulation genetic diversity (Boileau et al. 1992). Study of gene frequency within the population seems to be more suitable for estimating dispersion rate and colonization success. Data of gene frequency provides also the possibility of including colonisation success of later arrivals of already colonized species.

Extended period, over one year, is probably necessary for dispersal to new habitats for most zooplankton species (Jenkins 1995). However, several studies have shown that the plateau of species diversity may be reached in much shorter time scales. Six months to saturation are reported by Jenkins and Buikema (1998), just one year by Cáceres and Soluk (2002) and by Pajunen (1986). The period needed to reach colonisation plateau probably depends also on the season when the experiment or observation started (Cáceres and Soluk 2002). In the theoretical perspective, species saturation of the habitat is possible only in non-interactive communities, while in real interactive communities the species saturation is

possible, but probably without hard limits to the diversity over evolutionary time-scales (Cornell and Lawton 1992).

Local diversity may not be limited only by number of available niches within the structured habitat but also by regional species richness (Cornell and Lawton 1992, Mouquet et al. 2003). The relationship between local and regional species richness is approximated to be linear among many diverse groups of organisms in many studies (Gaston 2000, Louette and De Meester 2005). However, this probably changes during the zooplankton community maturation (Louette 2005, Mouquet et al. 2003, Srivastava 1999) and may be influenced by the choice of regional scale (Angermeier and Winston 1998, Shurin et al. 2000, Cornell and Lawton 1992, Naeslund and Norberg 2006).

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