

The Monopolization Hypothesis and the dispersal–gene flow paradox in aquatic organisms

Luc De Meester^{a,*}, Africa Gómez^b, Beth Okamura^c, Klaus Schwenk^d

^aLaboratory of Aquatic Ecology, Katholieke Universiteit Leuven, Ch. De Beriotstraat 32, 3000 Leuven, Belgium

^bDepartment of Biological Sciences, University of Hull, Hull, HU6 7RX, UK

^cSchool of Animal and Microbial Sciences, University of Reading, Whiteknights, PO Box 228, Reading, RG6 6AJ, UK

^dDepartment of Ecology and Evolution, Zoological Institute, J.W. Goethe-University Frankfurt am Main, Siesmayerstraße 70, 60323 Frankfurt am Main, Germany

Received 1 September 2001; received in revised form 1 March 2002; accepted 2 March 2002

Abstract

Many aquatic organisms rely on passive transport of resting stages for their dispersal. In this review, we provide evidence pointing to the high dispersal capacity of both animals (cladocerans, rotifers and bryozoans) and aquatic macrophytes inhabiting lentic habitats. This evidence includes direct observation of dispersal by vectors such as wind and waterfowl and the rapid colonization of new habitats. Such high dispersal capacity contrasts with the abundant evidence of pronounced genetic differentiation among neighbouring populations in many pond-dwelling organisms. We provide an overview of the potential mechanisms causing a discrepancy between high dispersal rates and reduced levels of gene flow. We argue that founder events combined with rapid local adaptation may underlie the striking patterns of genetic differentiation for neutral markers in many aquatic organisms. Rapid population growth and local adaptation upon colonization of a new habitat result in the effective monopolization of resources, yielding a strong priority effect. Once a population is locally adapted, the presence of a large resting propagule bank provides a powerful buffer against newly invading genotypes, so enhancing priority effects. Under this Monopolization Hypothesis, high genetic differentiation among nearby populations largely reflects founder events. Phylogeographic data support a scenario of low effective dispersal among populations and persistent effects of historical colonization in cyclical parthenogens. A comparison of patterns of gene flow in taxa with different life cycles suggests an important role of local adaptation in reducing gene flow among populations. We argue that patterns of regional genetic differentiation may often reflect historical colonization of new habitats rather than contemporary gene flow. © 2002 Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

Keywords: Dispersal; Gene flow; Zooplankton; Bryozoans; Macrophytes; Aquatic organisms; Local adaptation; Sexual recombination; Resting propagule bank; Isolation-by-distance; Distribution; Phylogeography; Cyclical parthenogenesis

1. Introduction

Inland waters are often isolated from each other, providing an excellent example of island habitats. The resulting isolation is extreme in ephemeral ponds scattered in semi-arid regions, but also holds for streams and rivers belonging to different catchment areas. In addition, these environments offer only ephemeral and/or unpredictable habitats in an intermediate to long-term scale, as most ponds and lakes are geologically short-lived. Aquatic organisms inhabiting inland water bodies have, therefore, to rely on either active

flight (many aquatic insects) or passive dispersal mediated by resistant stages (Bilton et al., 2001). In this review, we will focus on organisms inhabiting lentic habitats (lakes and ponds) that disperse passively via resting propagules (Hairston and Cáceres, 1996; Colburne et al., 1997, 1998; Cáceres, 1997). These resting stages accumulate in the sediments of their habitats forming resting propagule banks that are in many aspects equivalent to plant seed banks (Hairston, 1996; Cáceres and Hairston, 1998). The wide geographical ranges of many aquatic taxa are testimony that passive dispersal by resting stages can be very effective, an observation made by both Lyell (1832) and Darwin (1859).

For a long time, it was thought that many aquatic taxa were essentially cosmopolitan. Mayr (1963), for instance,

* Corresponding author. Fax: +32-16-32-45-75.

E-mail address: Luc.DeMeester@bio.kuleuven.ac.be (L. De Meester).

wrote "...species (of freshwater organisms) that are successful in colonizing temporary bodies of water have in general such superb dispersal abilities that their entire world population may well be nearly panmictic". Although detailed morphological studies (Frey, 1982) and recent molecular work (Colbourne and Hebert, 1996; Schwenk et al., 1998; Gómez et al., 2000) have changed this view dramatically, it remains that many taxa are widespread. In addition, experimental work by Jenkins and Buikema (1998) has provided direct evidence for rapid colonization of newly formed habitats, supporting indirect evidence provided by a variety of more anecdotal records [see Bilton et al. (2001) for review]. However, studies employing neutral genetic markers have often reported strong genetic differentiation among zooplankton populations inhabiting nearby ponds, suggestive of low levels of ongoing gene flow [reviewed in Lynch and Spitze (1994), De Meester (1996a), and below].

We will argue that this apparent paradox of high dispersal and low gene flow can be explained by a combination of stochastic and selection-driven processes that have recently been shown to be particularly effective in populations of several aquatic organisms. First, rapid population growth rates after a historical colonization event from a few founding propagules prevent allele frequency changes due to gene flow (Boileau et al., 1992). The persistent effect of founding events is further enhanced by the presence of very large dormant propagule banks in these organisms (Hairton, 1996; Brendonck et al., 1998). In addition, rapid adaptation of resident populations to local conditions strongly reduces effective gene flow among populations (De Meester, 1993, 1996a; Okamura and Freeland, 2002), thus effectively increasing persistence of founder events. The present contribution integrates these processes into one hypothesis that we have termed 'the Monopolization Hypothesis', which can be viewed as an extension of the persistent founder effects hypothesis presented by Boileau et al. (1992).

Our aim is to examine recent findings that are relevant to the Monopolization Hypothesis. We start by critically reviewing studies that provide information concerning dispersal ability versus gene flow in lentic aquatic organisms. We subsequently review and discuss factors and processes that may play a role in solving this dispersal–gene flow paradox: the persistent influence of founding events (Boileau et al., 1992), the buffering against population crashes provided by resting propagule banks, and rapid local adaptation (De Meester, 1996a; Okamura and Freeland, 2002). First, we focus on cyclically parthenogenetic zooplankton. In the second part, patterns of gene flow and phylogeography are compared among aquatic taxa that differ in life cycle and investment in sexual reproduction. The comparative survey provides an insight into how the frequency and timing of sexual reproduction, as well as the production of propagules, may influence patterns of genetic differentiation among populations inhabiting ponds and lakes.

2. The dispersal–gene flow paradox

Many aquatic organisms seem well adapted for (passive) dispersal, whereas at the same time, genetic studies have reported clear-cut patterns of genetic differentiation and local adaptation, indicating low levels of gene flow (De Meester, 1996a). Recent studies have contributed substantial information relevant to this apparent paradox.

2.1. Evidence for efficient dispersal in aquatic organisms

Many aquatic organisms rely on passive dispersal, and various sources of information indicate significant potential for dispersal. Below we review five lines of evidence for efficient dispersal of these organisms.

2.1.1. Viable resting propagules or individuals are recovered from potential vectors for dispersal

There is a substantial amount of evidence that passively dispersed aquatic organisms, including cladocerans, copepods, anostracans, rotifers and bryozoans, among others, exhibit significant potential for dispersal. Their dormant propagules are resistant to adverse environmental conditions and allow for long-distance transport through wind, water or animal vectors such as waterfowl or aquatic insects. Viable resting propagules have been recovered repeatedly from waterfowl. Early observations (Maguire, 1963; Proctor, 1964; Proctor and Malone, 1965; Mellors, 1975) have been corroborated recently and extended by various studies carried out in the framework of the EU project LAKES (Charalambides et al., 2000). Waterfowl carry resting propagules of cladocerans and rotifers both in their digestive tract and in their feathers, a substantial proportion of which are viable (Proctor and Malone, 1965; Mellors, 1975; Charalambidou and Santamaría, 2002; Green et al., 2002). Internal transport of resting propagules (statoblasts) of bryozoans and seeds of aquatic macrophytes is also supported by their presence in waterfowl digestive tracts and the retrieval of viable statoblasts from waterfowl faeces (Brown, 1933; Charalambidou and Santamaría, 2002; Green et al., 2002; Charalambidou, unpublished). In macrophytes, it has even been demonstrated that mechanical treatment mimicking passage through a bird stomach enhances hatching efficiency (Santamaría, 2002; Santamaría, unpublished). Transport by wind is more difficult to quantify, but has been observed using sticky surfaces for resting propagules of anostracans (Brendonck and Riddoch, 1999a, b) and wind and rain traps for rotifers (Jenkins and Underwood, 1998). In water bodies that are connected to each other temporarily or permanently by direct water flow, transport can also be mediated through water. In that case, transport may not only involve resting propagules but also individuals of active populations. Havel et al. (2000) have demonstrated that rivers can act as very effective dispersal routes for zooplankton. Michels et al. (2001) quantified dispersal of zooplankton through overflows among a set of

neighbouring ponds, and observed dispersal rates of >10,000 zooplankton individuals per hour in some of the overflows.

2.1.2. Rapid colonization of newly available habitats

It has been repeatedly observed that newly created habitats are rapidly (within months) colonized by zooplankton species (Hebert and Moran, 1980; Fryer, 1985; Pajunen, 1986; Holland and Jenkins, 1998; Jenkins and Buikema, 1998; Havel et al., 2000b). One clone of *Daphnia magna* and one clone of *D. pulex* colonized a newly created pond in the city of Leuven within two months after its creation (Audenaert et al., unpublished). The study by Jenkins and Buikema (1998) indicates that colonization efficiency of new ponds is even greater in rotifers than in cladocerans. These results suggest a strong potential for regular input of resting propagules into new habitats, and we must assume that this will also occur on habitats harbouring established populations.

2.1.3. Wide geographical distribution of clonal lineages

Studies on the distribution of multilocus genotypes tracking particular obligately parthenogenetic clones indicate that single lineages can have distributions covering many ponds and distances over 1000 km (Weider and Hobaek, 1997; Weider et al., 1996, 1999b). Parthenogenetic ostracod clones have been found to be widespread in recently created farm ponds (Chaplin and Ayre, 1997). Similarly, in bryozoans, identical multilocus genotypes were retrieved from habitats that were more than 700 km apart (Freeland et al., 2000). Bryozoans undergo only limited sexual reproduction and disperse via asexual propagules. These results indicate that single clones have the potential to spread over entire continents. In addition, phylogeographic analyses have shown that mtDNA haplotype lineages have spread over vast areas after the last ice age from glacial refugia (*Daphnia*: Weider et al., 1999a; *Sida crystallinea*: Cox and Hebert, 2001; *Hyalodaphnia* taxa: Schwenk et al., 2000; K. Schwenk, unpublished] data; *Brachionus plicatilis* species complex: Gómez et al., 2000).

2.1.4. The rapid spread of exotic species

The documented rapid invasions of exotic cladoceran species is also testimony of their high dispersal capacity. The spread of *D. lumholzi* in south-eastern USA (Havel et al., 1995, 2000a; Havel and Shurin, unpublished) and of *Bosmina coregoni* (DeMelo and Hebert, 1994) in North America are spectacular and well-documented cases. Admittedly, human activities may have promoted the spread of these species (Havel and Stelzleni-Schwent, 2002). The spread of *D. ambigua* and *D. parvula* in Europe may be equally good examples of rapid colonization of a new continent, but these cases have been studied in less detail (reviewed in Maier, 1996).

2.1.5. Dispersal is not limiting for zooplankton community composition

Experimental work by Shurin (2000) has documented low success rates of artificial introductions of taxa from the regional species pool into zooplankton communities in isolated ponds, indicating that the community composition in these ponds is not determined by constraints in dispersal but rather by local interactions (see also Shurin et al., 2000; Hobæk et al., 2002). Jenkins and Buikema (1998) obtained evidence that initial colonization may strongly determine species composition through priority effects that appear to preclude subsequent colonization. These results are not in contradiction to those of Shurin (2000). The results of Jenkins and Buikema (1998) indicate that initial colonization effects may influence species composition through priority effects. The results of Shurin (2000), however, indicate that, in well-established communities, invasions by additional species are only occurring at appreciable rates when one reduces local interactions substantially, irrespective of dispersal rates.

2.2. Evidence for limited gene flow

We do not intend to provide a full review of studies on the population genetic structure of aquatic invertebrates, since a substantial part of that literature has been reviewed elsewhere (zooplankton: Hebert, 1987a, b; Lynch and Spitze, 1994; De Meester, 1996a; bryozoans: Okamura and Freeland, 2002). Given that dispersal capacity is high, it is striking that pronounced differences in genotype composition have often been observed among cladoceran and rotifer populations, even among neighbouring populations. Pronounced genetic differentiation among cladoceran populations has been observed for neutral markers as well as for ecologically relevant traits (Spitze, 1993; De Meester, 1996a; Lynch et al., 1999). Genetic studies involving neutral markers have often reported high G_{ST} or F_{ST} values, with greater genetic differentiation in small, than in large populations (cf. pond versus lake populations; Hebert, 1987a; Wolf, 1988; Jacobs, 1990; De Meester, 1996a; Vanoverbeke and De Meester, 1997). Even neighbouring pond populations often show F_{ST} values higher than 0.2 (Korpelainen, 1984; Wolf, 1988; Innes, 1991; Palsson, 2000). Such high differentiation among proximate populations may weaken the relationship between genetic and geographic distance (Innes, 1991; Lynch and Spitze, 1994; Vanoverbeke and De Meester, 1997), although clear-cut patterns of isolation-by-distance have emerged in a number of studies (Gómez et al., 2002; De Gelas, unpublished).

Several studies have reported genetic differentiation for ecologically relevant traits among populations. Some of this work has been reviewed by Carvalho (1994) and De Meester (1996a), and recent studies have added much to the evidence of local adaptation among zooplankton populations (see discussion in section on 'local adaptation' below). The emerging pattern points to a limited effect of gene flow

which otherwise would constrain genetic adaptation to local environmental conditions.

3. How to explain the high levels of genetic differentiation for neutral markers

The high levels of genetic differentiation (F_{ST} values) observed in studies using allozyme or DNA markers may be explained by three processes. First, observed levels of genetic differentiation in cyclically parthenogenetic zooplankton may be inflated by chance associations between neutral markers and successful genotypes (Vanoverbeke and De Meester, 1997; Palsson, 2001; see also Berg and Lascoux, 2000). Second, high F_{ST} values may be due to persistent founder effects. Third, gene flow may be impeded by local adaptation and competitive superiority of resident genotypes over immigrant genotypes. In the following sections we provide brief discussion on each of these three potential explanations. It should be noted that these mechanisms can and probably do act in concert. Local adaptation may indeed result in an enhancement of priority effects, resulting in a strengthening of founder effects.

3.1. Chance events associated with low clonal diversity: selection at linked loci

Part of the observed genetic differentiation in neutral genetic markers in cyclical parthenogenetic zooplankton may be due to a drift-like phenomenon associated with low clonal diversity. The variation at neutral markers may be affected by selection at linked loci, biasing estimates of genetic differentiation among populations (Palsson, 2001). Vanoverbeke and De Meester (1997) observed a striking negative correlation between the observed pairwise genetic differentiation between populations and their average diversity in multilocus genotypes. Populations with low multilocus genotype diversities tend to be highly differentiated from each other as measured by F_{ST} values. This is not merely a consequence of founder effects reducing genetic diversity, because populations are typically characterized by much lower multilocus genotype diversities than expected from allele frequencies (data given in De Meester and Vanoverbeke, 1999). Vanoverbeke and De Meester (1997) argued that genetic differentiation among populations might be upwardly biased in populations in which clonal selection results in a low clonal diversity during the course of the growing season. Under such conditions, allele frequencies at neutral loci may be significantly influenced by chance associations with successful genotypes. Because the whole genome constitutes a single linkage group during parthenogenetic reproduction, strong selection at particular loci may also influence allele frequencies at neutral markers (Palsson, 2001). A similar idea has been advocated in aphids by Rhomberg and coworkers (Rhomberg et al., 1985; Rhomberg and Singh, 1989). To the extent that the chance

associations build up during each growing season, the resulting pattern of allele frequencies is expected to be a very dynamic one. A partial test of the bias in estimates of genetic differentiation arising from chance associations with selected loci may lie in an analysis of temporal changes in allele frequencies within a given population over different growing seasons. If chance associations build up during each growing season and are partly broken up by sexual recombination, we expect that year-to-year genetic differentiation within a single population may be substantial (K. De Gelas, unpublished). Year-to-year variation in allele frequencies at neutral loci is thus expected to be higher in small populations with low multilocus genotype diversity than in large populations with high multilocus genotype diversity. In cases where the observed differences among populations are due to founder effects and genetic drift associated with bottlenecks in the past, we do not expect pronounced year-to-year variation in allele frequencies within a given population.

The notion that estimates of genetic differentiation among populations can be biased due to chance associations between markers and selected loci is relevant with respect to our discussion on the paradox between dispersal and gene flow. If chance associations between markers and selected loci are important, genetic changes during the growing season may be so strong as to overrule the effects of gene flow as measured by the markers used. Correcting for the effect of multilocus genotype diversity, Vanoverbeke and De Meester (1997) indeed observed an improved fit to isolation-by-distance expectations.

The bias due to linkage with selected loci cannot, however, explain all instances of pronounced genetic differentiation among populations. First, chance associations only become important in populations with low clonal diversity, and where linkage disequilibrium due to clonal selection has time to build up. Thus their effect is expected to be strongest in small populations and especially in small populations exhibiting extended growing seasons. Yet, even though populations inhabiting large lakes show lower levels of genetic differentiation than populations inhabiting small ponds, genetic differentiation is still substantial among these populations (Wolf, 1988; Jacobs, 1990; De Meester, 1996a). In addition, chance associations between neutral markers and selected traits obviously cannot explain the striking patterns of local adaptation among neighbouring populations (Declerck et al., 2001), which would not be possible in the face of the homogenizing force of massive gene flow.

3.2. Persistent founder effects

Boileau et al. (1992) proposed that the high levels of genetic differentiation at neutral markers in zooplankton populations may reflect the resilient effects of founder events. They also provided convincing evidence for the lack of correlation between dispersal ability and observed F_{ST} in 15 aquatic invertebrates including anostracans, copepods,

cladocerans and a notostracan. In addition, their theoretical model showed that in organisms, like zooplankton, that combine the potential to colonize whole habitats from a few propagules with the capacity for rapid population growth, allele frequencies established during initial founder events are resistant to decay for several thousands of generations, even with substantial rates of gene flow. As the initial colonizers have the capacity to increase rapidly to very high numbers, saturating the habitat in a few generations, the impact of subsequent migrants is strongly diluted, so that their effect on allele frequencies is negligible for many generations (Fig. 1). Such persistent founder effects as anticipated by Boileau et al. (1992) effectively reflect priority effects arising from the gross disparity in the numbers of residents and immigrants, resulting in a low probability of random increase in migrant genotype numbers due to drift alone. A consequence is that populations will take on the order of several thousands to millions of generations to reach migration-drift equilibrium, therefore effectively precluding the use of F_{ST} to estimate migration rates in most lentic habitats (see also Berg and Lascoux, 2000). Recent data have supported the strong effects of historical founding events in *Daphnia pulex* (Palsson, 2000) and rotifers (Gómez et al., 2002).

Many invertebrates found in lakes and ponds possess a life cycle that is expected to promote persistent founder effects. First, organisms like rotifers, cladocerans and large branchiopods have an impressive intrinsic capacity of population growth (Fig. 2). Second, the development of extensive resting propagule banks creates a powerful buffer against the impact of new invaders by maintaining population size at high levels and by increasing generation time,

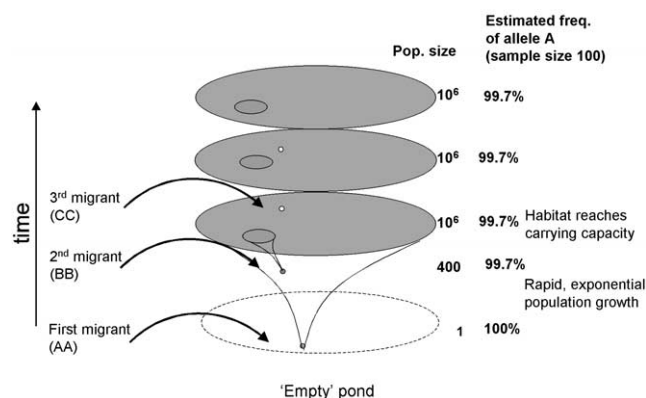


Fig. 1. Visualization of the persistent founder effects hypothesis for organisms with a high population growth rate as proposed by Boileau et al. (1992). The bottom of the figure depicts a colonizing propagule that arrives into an 'empty' pond and hatches at day 0. The clone thus originating then grows exponentially with an r of 1 day⁻¹ (rotifer intrinsic population growth rates (r) in the laboratory are well over 1 day⁻¹). As long as densities are not as high as to cause competitive interactions, the population will grow exponentially. Assuming equal fitness and one migrant per week, the ratio of migrants to residents will be 1 to 128 after 1 week, 1 to 8256 after 2 weeks, 1 to ca. 10⁶ after 3 weeks and 1 to ca. 1.35 10⁸ after 4 weeks. Note that these ratios will be even more in favour of the residents in cases of local adaptation.

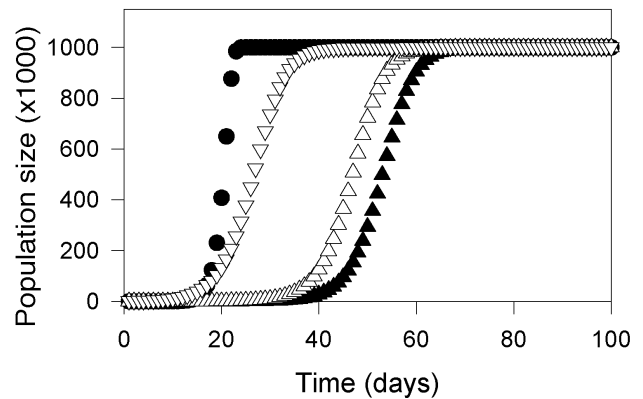


Fig. 2. Idealized scheme on the rate with which resources are monopolized in newly colonized habitats. We assume logistic population growth curves. Solid circles: population size with time of a lineage showing an intrinsic growth rate $r = 1$, a realistic value for rotifers. Solid triangles: $r = 0.3$, a realistic value for many cladocerans. Empty triangles: $r = 0.3$, five colonizing individuals on day 0. Upside down triangles: $r = 0.3$, 1000 individuals on day 0. The latter scenario simulates a situation in which there is hatching of propagules from a resting propagule bank at the beginning of a new growing season. Carrying capacity is set at 10⁶. The window of opportunity for an immigrant genotype to colonize the habitat depends on whether resources have been monopolized by resident genotypes, and thus depends on the intrinsic growth rate of the population, the carrying capacity and the number of colonizing propagules.

and therefore time to reach migration–drift equilibrium. The impact of the buffering effect of propagule banks depends on the dynamics of resting propagule production and hatching, but it is clear that in species with propagule banks, persistent founder effects are more likely than in taxa without resting propagules.

The hypothesis of persistent founder effects predicts that genetic differentiation among populations would decrease with increasing habitat size. The extent to which founder effects become 'frozen' is determined by the speed with which the habitat is fully occupied by the descendants of the first colonists in relation to the rate of arrival of new invaders (Fig. 2). Thus, if the arrival rates of resting stages to a given habitat are high, then multiple propagules may become established before the initial colonists have fully occupied the habitat. Assuming constant dispersal rates per area and time, the number of colonizers that reach a habitat before it is saturated will be higher in large, than in small habitats (Fig. 2). This will result in a more representative sample of the regional gene pool and thus in a reduced founder effect in large than in small populations. Naihong et al. (2000) developed a similar argument to explain the observed low levels of genetic differentiation between *Artemia* populations that inhabit very large lakes.

Given that resilience to changes in allele frequencies by immigrants is largely dependent on population sizes, effective gene flow may increase in perturbed habitats. Hairston et al. (1999b) documented the occurrence of *Daphnia exilis* in Onondaga lake (New York) based on an analysis of the resting propagule bank present in the lake sediments, and showed persistence of this non-indigenous species in the

lake during a period of industrial activity. In this case, however, it is likely that the industrial activities not only allowed the exotic species to get established through perturbation of the system, but were also responsible for introducing the species into the lake in the first place.

Interestingly, whereas population bottlenecks are expected to increase genetic differentiation among populations due to chance loss of allelic variation, a severe reduction in population size may also result in a lower genetic differentiation because it results in increased effective gene flow.

3.3. Local adaptation and low establishment success of new invaders

Another explanation of the pattern of strong genetic differentiation among populations in the face of high dispersal rates involves a substantial difference between the observed number of migrants and effective gene flow due to selection against migrants. Under this hypothesis, developed by De Meester (1996a) and Okamura and Freeland (2002), effective gene flow is reduced due to a low establishment success of invaders in a habitat that is already occupied. In addition to the persistent founder events discussed above, the establishment success of new invaders may also be reduced due to competition with locally adapted resident genotypes (De Meester, 1996a). Accordingly, an invading individual not only must cope with a high number of resident individuals, it often will, on average, be less well adapted to the target habitat. Korpelainen (1986) carried out an exploratory competition experiment in the field, and observed that a resident population of *Daphnia magna* was resistant to invasion by an artificially introduced clone from a different population. In addition to competitive superiority, establishment success of new invading genotypes may also be reduced by outbreeding depression. De Meester (1993) has indeed shown that the hatching success of interpopulational crosses is on average lower than that of intrapopulational crosses.

The hypothesis that local adaptation lowers establishment success extends the hypothesis of persistent founder effects developed by Boileau et al. (1992). Local adaptation increases priority effects and thus effectively retards the decay of founder effects. For the hypothesis to be important in explaining the observed levels of genetic differentiation, local adaptation should be widespread, and occur at a sufficiently fast rate. In the following, we will provide arguments for both these assertions.

Cyclical parthenogens show a high capacity for evolutionary change through natural selection (Lynch and Gabriel, 1983). On the one hand, recurrent sexual recombination generates a high genetic diversity at the beginning of the growing season. Given that the response to selection for a given trait is a function of selection differential and heritability, the release of hidden genetic variance after a bout of sexual reproduction (Lynch and Gabriel, 1983) has the potential to strongly boost opportunities for adaptive

change. In addition, subsequent parthenogenetic reproduction ensures that the genome is inherited as a whole, such that gene interaction effects are heritable, promoting an efficient response to selection during parthenogenesis. Evidence for an overwhelming genetic diversity at the beginning of the growing season comes from studies on the size of resting propagule banks. We illustrate this with a hypothetical but realistic example. Given that resting propagule densities in the sediments may easily amount to 10^4 to 10^6 propagules per square meter (Cousyn and De Meester, 1998; Brendonck and De Meester, 2002), this translates into 10^8 to 10^{10} propagules per hectare. In a moderately sized pond of about 1 ha, this would yield 10^6 to 10^8 different clones at the start of the growing season if we assume that only 10% of propagules is part of the active resting propagule bank (see Cáceres and Hairston, 1998), and only 10% of these propagules respond to the hatching stimuli at the start of the growing season. Lynch (1984) and Tessier et al. (1992) observed very high heritabilities for quantitative traits at the beginning of the growing season in *Daphnia*.

The recurrent bouts of high genetic diversity coupled with an efficient response to natural selection during the parthenogenetic phase is expected to promote local adaptation. Earlier studies on genetic differentiation in ecologically relevant traits have been reviewed by Carvalho (1994) and De Meester (1996a), and recent studies have substantially added to the evidence. Spitze (1993) showed that there is no association between genetic differentiation among populations for allozymes and ecologically relevant traits in a set of eight *D. obtusa* populations. Using genetic differentiation for neutral allozyme variants as neutral model, Spitze (1993) showed unequivocally that among population genetic differentiation for body size resulted from diversifying selection. Several studies have reported local genetic differentiation among *Daphnia* populations for traits related to predation risk: neck-teeth induction in response to the presence of the phantom midge larva *Chaoborus* (Parejko and Dodson, 1991), and phototactic behaviour (daytime vertical distribution and migration; De Meester, 1996b) as well as size at maturity in relation to fish predation pressure (Leibold and Tessier, 1991; Boersma et al., 1999). In a laboratory transplant experiment, Declerck et al. (Declerck et al., 2001) showed that two *Daphnia galeata* populations in ecologically contrasting ponds separated by only 5 m, perform substantially better in water from their own respective habitat.

To show local adaptation, one needs to demonstrate that the adaptive changes are the result of evolutionary change within the local population. Therefore, strictly speaking, the above-mentioned studies are consistent with the hypothesis of local adaptation, but do not provide direct evidence of adaptive changes. Such opportunities for exploring recent micro-evolutionary change are afforded by the study of hatchlings from propagule banks. Hairston et al. (1999a) provided evidence for a genetic change of the *D. galeata* population inhabiting Lake Constance in the tolerance to

cyanobacteria that paralleled a eutrophication event which was accompanied by an increase in cyanobacteria. Cousyn et al. (2001) showed that a *D. magna* population inhabiting a fish pond rapidly adapted to changes in fish predation pressure through genetic changes in inducible habitat selection (vertical migration) behaviour. Both studies provide strong and direct evidence for the capacity of *Daphnia* populations to adjust genetically to local environmental conditions. Such rapid adjustment to changing environmental conditions in the same trait as studied by De Meester (1996b) lends support to the interpretation that the among-population genetic differentiation observed arose by local adaptation.

Such a high incidence of local adaptation may apply to other cladoceran taxa and to rotifers, since they share a similar life cycle. Indeed, local adaptation might be enhanced in rotifers, given their shorter generation time.

In order for local adaptation to promote priority effects and therefore substantially increase the impact of founder effects, local adaptation should occur rapidly in relation to the arrival of new immigrants through dispersal. We have very few data on dispersal rates, but we now have convincing evidence that local adaptation can be achieved very rapidly. For instance, Cousyn et al. (2001) reported substantial genetic changes in predator-induced shifts in habitat selection behaviour in a time frame of 6 to 10 years. Given that a better resolution was not possible, the reported 6 to 10 years actually may hide a much faster response. The data by Declerck et al. (2001) suggest that local adaptation between two neighbouring *D. galeata* populations occurred rapidly (within 2 years) and on a fine spatial scale. Obviously, the speed with which populations may adapt to local environmental conditions will also depend on the type of adaptation, and to what extent there are genetic constraints involved. Local adaptation may be substantially slower or even impossible in the face of strong genetic constraints. In general terms, the speed of local adaptation will depend on the nature of the genetic variance-covariance structure for the traits involved (Roff, 1997; Lynch and Walsh, 1998).

It is possible that local adaptation may be hindered by a reduced genetic diversity resulting from a strong founder event. However, it is important to note that the impact of founder events may be more evident in traits resulting from single loci than on traits that are polygenic. Since most ecologically relevant traits are typically determined by many genes, even a single colonist may harbour substantial genetic variation for any given trait through heterozygosity at several of the loci concerned. This genetic variance is released after the first bout of sexual reproduction. No doubt genetic variation for ecologically relevant traits may be strongly reduced in cases involving very small numbers of founding propagules, but it is very likely that significant genetic variation will be present for selection to act on even under those circumstances. In addition, established populations with propagule banks will preserve a memory of past selective conditions which will speed up the rate at which

the population is able to track environmental change. Therefore, migrants will have to cope with both current and past adaptation.

In very small populations that undergo regular population bottlenecks and extinctions and are subsequently recolonized by only one individual, substantial inbreeding may occur. Under such circumstances, the immigrant genotype may have a strong fitness advantage both during the parthenogenetic phase (Ebert et al., 2002) as well as upon sexual recombination (hybrid vigour). This situation has been documented by Ebert et al. (2002) who studied *Daphnia* populations in small coastal rock-pools in Finland. The design of the experiments carried out by Ebert et al. (2002) artificially excluded the numerical advantage of resident genotypes, but does show convincingly that hybrid vigour may convey an advantage to immigrant genotypes in such populations. The pond populations studied by Ebert et al. (2002) share several characteristics that may lead to strong inbreeding: they are small, very unstable, there is an obligatory sexual phase every year (leading to extreme inbreeding if only one clone is present), and they often lack substantial resting egg banks. Most *Daphnia* populations that have been reported in the literature do not conform to this scenario, but show evidence that local adaptation may play a significant role in reducing colonization as discussed above and as evidenced by the observation of strong outbreeding depression (De Meester, 1993). More detailed studies on the genetic structure of cyclically parthenogenetic *Daphnia* populations inhabiting small habitats are needed in order to assess the relationship between habitat size and the transition between inbreeding and local adaptation (Berg 2001). With respect to this transition, it should be recalled that our contention that populations tend to be locally adapted refers to the average fitness of residents compared to immigrants. As such, the probability that populations are affected by selective sweeps by immigrant clones and genes that happen by chance to be better adapted to the specific habitat is low, yet this probability will be higher in very small, recently founded or bottlenecked populations.

3.4. Synthesis: the Monopolization Hypothesis

Given the above arguments and data, we can generate the following scenario on how genetic diversity is structured among populations of cyclical parthenogens (Fig. 3). First, colonization of new habitats in general will be rapid, with often a limited number of propagules. Prolific population growth and the build-up of a large resting propagule bank buffering against population crashes will result in very low genetic drift and a high resilience to the genetic impact of new immigrants. Founder effects will thus decay only slowly. The impact of new immigrants will be further reduced by selection, due to the rapid adaptation of the resident population to local environmental conditions, the effect of which may be significant after only a few growing

seasons. The fact that the resident population is on average better adapted to the local environment than immigrant genotypes may strongly constrain gene flow among populations. This is a self-reinforcing system, since incipient local adaptation will further reduce gene flow and thus promote even further local adaptation (De Meester, 1996a). As this process enhances priority effects, it results in founder effects being even more resistant to decay than predicted by the model developed by Boileau et al. (1992). Importantly, this scenario entails, as a consequence, a reduced rate of decay of the founder effect, as local adaptation becomes stronger. Rapid growth rate results in the monopolization of resources by descendants of the first immigrant, enhanced further by the fact that the resident population adapts to the local environment. We therefore suggest the term ‘monopolization’ to refer to the combined effects of a reduced impact of new immigrants by a dilution effect (neutral, drift-like process) and by local adaptation (selective process) (Fig. 3), resulting in a strong priority effect and thus persistent founder effects.

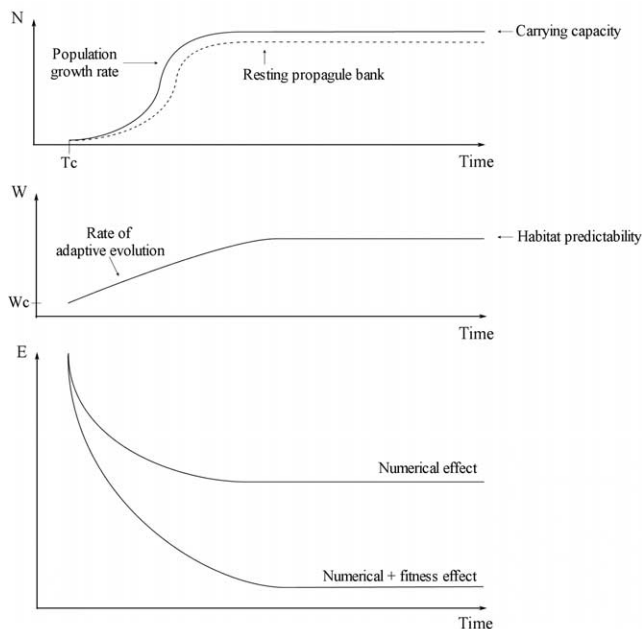


Fig. 3. Summarizing scheme illustrating the Monopolization Hypothesis. Upper graph: population size (N) of the active population at peak densities and the resting propagule bank in a local habitat with time following colonization (time T_c). The active population grows to carrying capacity with time and may be re-established from the resting propagule bank yearly. Note that the resting propagule bank grows to considerable size with time and can therefore substantially contribute to the population on an annual basis resulting in high densities at the start of the growing season. Middle graph: the average fitness (W) of the genotypes residing in a local population is expected to increase with time due to local adaptation (assuming no strong inbreeding, see text). The level of local adaptation reached is determined, amongst other factors, by habitat predictability. Note that on average (i.e., taken over many populations), the fitness of the invading genotype will be equal to the fitness of the first colonist (W_c ; assuming no rare-genotype advantage). The lower graph illustrates that establishment success (E) decreases with time following colonization by the first colonist due to a numerical effect (cf. upper graph) and a fitness effect (cf. middle graph). The exact shape of the curves is unknown.

In addition to the above process of monopolization of resources, in very small habitats in which growing seasons are sufficiently long for clonal selection to build up strong linkage disequilibria among markers, interpretation of genetic variation at multiple loci may be influenced by chance associations between variation at neutral markers and successful genotypes. Given the size of the resting propagule banks in most populations, it is expected that this latter pattern will be important only in very small populations. In such small populations, however, one should be attentive to the potential bias in the estimates of genetic differentiation caused by clonal selection. If genetic differentiation among populations is due to monopolization and priority effects, genotype frequencies within populations are not expected to change strongly from year to year, whereas patterns of genetic differentiation are expected to be more dynamic when chance associations are involved.

The above scenario focuses on the fact that gene flow is lowered substantially due to monopolization of the habitat by the first colonists in terms of numbers and due to local adaptation. This does not imply, however, that there is no gene flow at all. The message is that gene flow is less effective than in organisms showing lower population growth rates, small population sizes, no resting propagule banks or a reduced capacity for local adaptation. In fact, there are cases in which effective gene flow is potentially very high (Ebert et al., 2002), and several studies did report patterns of isolation-by-distance in cladocerans and rotifers [weak patterns in Lynch and Spitz (1994) and Vanoverbeke and De Meester (1997); stronger patterns in Gómez et al. (2002) and De Gelas (unpublished)], indicating that gene flow does contribute to the structure of genetic variation at a local scale. Yet, the Monopolization Hypothesis predicts that much of the structure in genetic variation that is seen at a larger scale may be shaped by colonization events rather than by contemporary gene flow. Importantly, the monopolization scenario also indicates that gene flow may be uncoupled largely from dispersal rates, since patterns of local adaptation and sizes of the resting propagule bank may determine effective gene flow. As such, it is not expected a priori that migration routes of birds, for instance, will strongly influence current patterns of gene flow for many freshwater taxa (see below for a comparison among taxa). Migration routes may be very important in structuring genetic variation of zooplankton at a continental scale, but rather through their impact on colonization patterns than through their impact on contemporary gene flow.

4. Taxon-dependent patterns of gene flow

Given the above arguments we expect greater gene flow amongst populations of organisms that show lower population growth rates, which lack or have relatively smaller resting propagule banks, and/or have a lower capacity for local adaptation than observed for cyclically parthenoge

Table 1
Comparison of taxa with respect to several traits that are thought to be positively associated with the capacity for monopolization of resources. (1) Population growth rate is considered to be high if clonal or vegetative reproduction is involved; this trait depends also on generation time and other characteristics. (2) Resting propagules are considered to provide a buffering effect against population crashes. (3) Various features associated with the capacity for rapid local adaptation: a 'yes' score for any of these traits will favour local adaptation. The overall score for local adaptation is indicative only, as the differences are in some cases qualitative in nature (OP do not locally adapt in the strict sense)

Trait	Cyclical parthenogens (CP)	Obligate parthenogens (OP)	Obligate sexuals	Bryozoans	Aquatic macrophytes
(1) Population growth rate	High	High	Lower than OP or CP	High	High
(2) Resting propagule banks	Yes	Yes	Yes	Yes	Yes
(3) Local adaptation					
• Regular generation of genetic variation due to sexual recombination	Yes	No	Yes	(Sporadic)	(Sporadic)
• Survival of harsh conditions associated with sexual recombination	Yes	No	Yes	No	Mixed
• Dispersal associated with sexual recombination	Yes	No	Yes	No	Mixed
• Phase of clonal selection	Yes	Yes	No	Yes	Yes
Score for capacity of local adaptation	5	2	4	2.5	3.5

netic zooplankton. A comparative survey among taxa may thus provide additional information on the processes that determine levels of genetic differentiation among populations of aquatic organisms. Here we briefly consider the case for obligately parthenogenetic zooplankton, obligately sexual zooplankton, bryozoans and aquatic macrophytes (Table 1).

4.1. Obligately parthenogenetic zooplankton

In obligately parthenogenetic zooplankton, patterns of population genetic differentiation are strikingly different from those characterized in cyclically parthenogenetic zooplankton. The occurrence and distribution of multilocus genotypes and mtDNA haplotypes have been extensively documented for several obligately parthenogenetic circum-arctic *Daphnia* taxa by Weider and coworkers (Weider and Hobæk, 1997; Weider et al., 1996, 1999a). There is clear evidence that certain genotypes can become widespread, occupying areas covering distances of more than 1000 km. Detailed studies on the distribution of multilocus genotypes on a local scale have provided strong evidence that the distribution of specific genotypes is strongly determined by environmental conditions within habitats (Weider and Hebert, 1987a, b; Wilson and Hebert, 1992, 1993). A striking example is given by the observation by Wilson and Hebert (1993) that the occurrence of two multilocus genotypes in ponds on a rock bluff almost perfectly matches the occurrence of a predator (the copepod *Hesperodiaptomus arcticus*): one clone seems to be able to coexist with the predator, whereas the other dominates the populations in the absence of the predator.

As argued by De Meester (1996a), the distribution of genotypes in obligate parthenogens should not be interpreted as a result of local adaptation, but rather as the result of selection of clones present in the regional clone pool on

the basis of their fitness to the given habitat. The internal dynamics of adaptation to local conditions is null or only weak in a population of obligately parthenogens. Rather, an increasing fit of the ecology of the resident population to the local environmental conditions results from immigration of pre-adapted genotypes. The strong correlation between environmental characteristics (salinity, predation regime) and the occurrence of specific clones indicates that, at the spatial scale considered (rock bluffs in the low-arctic), dispersal is not a limiting factor. It seems that at least some of the clones have the capacity to reach most of the ponds in a given area. The most striking difference between obligately parthenogenetic and cyclically parthenogenetic *Daphnia* is the absence of sexual recombination during formation of resting propagules in the former taxa. There is no evidence that the population growth rate is lower in obligate parthenogens, and they similarly have the capacity to build resting propagule banks (Table 1). However, the absence of sexual recombination limits the capacity for local adaptation in obligately parthenogenetic taxa. From a comparative point of view, evidence for broad distributions of clonal lineages in obligately parthenogenetic taxa suggests that local adaptation may be a key factor limiting effective gene flow in their cyclically parthenogenetic cousins. In addition, while local adaptation may constrain effective gene flow in cyclically parthenogens, local adaptation actually results from extensive effective dispersal in obligate parthenogens.

4.2. Obligately sexual zooplankton

Obligately sexual taxa are expected to show somewhat less rapid local adaptation than cyclically parthenogens, since they do not combine sexual recombination with an efficient response to selective factors during clonal selection. Their population growth rate also tends to be lower than that of

cyclically parthenogenetic taxa. It may therefore be predicted that these taxa show less strong interpopulational genetic differentiation than cyclically parthenogenetic populations. The few studies that have been carried out on copepods seem to substantiate this prediction. The values for genetic differentiation among populations reported by Boileau et al. (1992) for copepods are significant, but generally lower than values reported by various authors for pond-dwelling *Daphnia* and rotifers. Interpopulational genetic differentiation for ecologically relevant traits (Hairston and Olds, 1987; Hairston et al., 1990) as well as rapid evolutionary changes within populations (Hairston and Walton, 1986) have been reported in calanoid copepods. Genetic differentiation among anostracan populations is often high (Boileau et al., 1992; Bohonak, 1998; Brendonck et al., 2000). Brendonck et al. (2000) observed, however, that genetic differentiation among neighbouring ponds on the same rock bluff is low, whereas Bohonak (1998) reported a strong correlation between estimates of gene flow and ecological estimates of dispersal of propagules by salamanders. Bisexual *Artemia* are similarly characterized by the build-up of resting propagule banks and rapid population growth rates. Genetic differentiation amongst bisexual *Artemia* populations is moderate to low compared to freshwater anostracans (Abreu-Grobois, 1987; Gajardo et al., 1995; Naihong et al., 2000). This is probably due to the fact that the *Artemia* habitats studied are often considerably larger than those inhabited by freshwater anostracans. Naihong et al. (2000) observed very low levels of genetic differentiation among Chinese *Artemia* populations in very large habitats (>1 km²).

4.3. Freshwater bryozoans

Patterns of gene flow in the freshwater bryozoan, *Cristatella mucedo*, assessed through microsatellite analysis are more similar to those of obligately parthenogenetic zooplankton populations than to cyclically parthenogenetic rotifers and cladocerans (Freeland et al., 2000a; Okamura and Freeland, 2002). There is considerable evidence for low levels of ongoing gene flow in north-west Europe based on independent estimates. Indeed, one multilocus genotype was characterized in sites separated by >700 km (Freeland et al., 2000a). Notably, evidence for ongoing gene flow was obtained for populations sampled along a common migratory waterfowl route in Europe, but not amongst populations sampled along multiple and divergent waterfowl routes in North America (Freeland et al., 2000c, 2001).

As argued by Okamura and Freeland (2002), the major difference between bryozoans and zooplankton taxa may lie in the extent and timing of sexual reproduction. Thus, in bryozoans, a brief sexual phase occurs early in the growing season (Okamura, 1997). During this sexual period only a proportion of bryozoans in the population are sexual and it would appear that some populations forego a sexual phase in some years. In addition, the dormant statoblasts are

asexual products, and bryozoans are thus dispersed as clonal lineages (Table 1). After establishment in a new habitat, reproduction again is largely asexual (Okamura, 1994, 1997). As a result, bryozoans are expected to show diminished levels of local adaptation relative to facultatively parthenogenetic cladocerans or rotifers. High F_{IS} values have suggested substantial inbreeding in *C. mucedo* populations (Freeland et al., 2000a, b), although recent evidence has confirmed speculation that hatching of statoblasts from the resting propagule banks may also contribute to F_{IS} values via a Wahlund effect (Freeland et al., 2001, and unpublished). However, laboratory studies on viability of bryozoan statoblasts suggests that the longevity of statoblasts in sediments decreases with age, and is unlikely to exceed 8 years (Bushnell and Rao, 1974; Mukai, 1982; Wood, 1991) in comparison to decades, or even hundreds of years, for zooplankton propagules in sediments (e.g., Hairston et al., 1995, 1999a; Weider et al., 1997; Cousyn et al., 2001). Thus, statoblast banks may play similar but diminished roles to those of propagule banks as discussed earlier for zooplankton populations. Given their life histories, it may be expected that bryozoan populations would reveal intermediate levels of gene flow and local adaptation to the contrasting levels observed in obligately and facultatively parthenogenetic zooplankton populations (Table 1).

4.4. Aquatic macrophytes

Many aquatic macrophytes can be dispersed through both sexually produced seeds as well as vegetatively growing modules (leaves, pieces of stem, tubers; Sculthorpe, 1967; Santamaría, 2002). In certain taxa such as *Lemna*, dispersal is primarily mediated by actively growing modules. Another important difference with cyclically parthenogenetic zooplankton is that macrophyte populations often become re-established after an unfavourable period (e.g., winter) from vegetatively produced tubers, roots or shoots, rather than from sexually produced seeds. Overall, sexual reproduction is relatively rare compared to vegetative growth of new modules in many species of aquatic plants (Sculthorpe, 1967). This may substantially lower the rates of local adaptation in macrophytes compared to cyclically parthenogenetic organisms (Table 1). It is therefore expected that local adaptation may form a less strong barrier for gene flow in aquatic macrophytes than in cyclically parthenogenetic zooplankton. Overall genetic differentiation among populations of aquatic macrophytes is moderate to high, often with strong patterns of isolation by distance (Hollingsworth et al., 1996; Gornall et al., 1998; Santamaría, 2002). Mader et al. (1998) found evidence for higher levels of gene flow in *Potamogeton pectinatus* in areas visited versus non-visited by Bewick's swans, suggesting that gene flow is increased along bird migration routes.

The above comparative overview of patterns of gene flow across taxa reveals two main aspects. First, genetic differentiation among local populations is often significant in all

taxa considered, reflecting the importance of persistent founder events in populations inhabiting isolated ponds and lakes. Second, there is a tendency for lower levels of genetic differentiation and thus higher rates of effective gene flow in the various taxa considered compared to cyclically parthenogenetic zooplankton. As these taxa are characterized by a lower capacity for local adaptation than cyclical parthenogens, the results of this comparative survey suggest that local adaptation may be an important factor reducing effective gene flow among populations. We acknowledge that the comparative analysis given above is only indicative of general patterns and does not represent a test of the Monopolization Hypothesis.

5. Phylogeography and patterns of gene flow

The hypothesis that gene flow is strongly impeded by local adaptation of resident populations allows for specific predictions on phylogeographic patterns in aquatic organisms. In cyclical parthenogens, it is expected that the organisms spread rapidly from glacial refugia into newly available habitats, until they reach an area that is already occupied by populations of the same species that originated from a different refugium. The strong priority effects may then result in relatively sharp boundaries between genetically distinct lineages (i.e., 'provincialism' sensu Hebert and Wilson, 1994). Taxa that lack the potential of rapid local adaptation might exhibit phylogeographic patterns characterized by less sharp boundaries.

Since its inception in 1987, phylogeography, the study of the geographical distribution of phylogenetic lineages, has accumulated an exponentially increasing number of case studies and a varied array of technical, analytical and theoretical tools (Avice, 1999). In aquatic cyclical parthenogens, the first obstacle to effective phylogeographic study was confused taxonomies, often confounded by morphological stasis, sibling species complexes and hybridization (Schwenk, 1993; Hebert and Wilson, 1994; Lehman et al., 1995; Schwenk and Spaak, 1995; Taylor et al., 1996; Schwenk et al., 1998).

The phylogeographic study of zooplankton taxa is yielding an increasing number of insights into patterns of dispersal and gene flow. The first phylogeographic assessment on zooplankton used allozyme loci and focused on the broadly distributed North American cyclical parthenogen *Daphnia obtusa* (Hebert and Finston, 1996). The data showed pronounced allele shifts across the distribution, with no isolation by distance, pointing to strong population differentiation and little effect of gene flow. In a UPGMA analysis, populations clustered in three largely allopatric groups. The level and patterning of endemism strongly suggest population range contractions and subsequent recolonization of *D. obtusa* in North America from at least three glacial refugia (Atlantic, Central and Pacific). Interestingly, strong concordance with this scenario of three

refugia with north-wise colonization has been found in a phylogeographic analysis of *D. laevis*, in which mtDNA sequence variation was investigated (Taylor et al., 1998). In a recent investigation of mtDNA and allozyme variation in North American *Sida cristallina*, evidence for another refugium for freshwater fauna was found. *Sida* presented four deep, geographically segregated lineages, with the typical north–south range of North American species recolonizing after the Ice Ages (Cox and Hebert, 2001). These lineages could be ascribed to four refugia: Beringia, Mississippi, Pacific and Atlantic.

Results of recent genetic studies of European *D. galeata* (*Hyalodaphnia*) populations along avian migratory routes (high likelihood of dispersal) and populations distantly located from main migratory routes (low likelihood of dispersal) can be considered with regard to the predictions of current gene flow (mediated by waterfowl) versus colonization/local adaptation (and no current gene flow). If passive dispersal determines distributional patterns, we would expect that populations along main migration routes exhibit lower genetic differentiation than populations not connected by avian vectors. However, if the effects of current gene flow are buffered by persistent founding events and dispersers are not successful due to local adaptation, dispersal patterns will reflect historical colonization, and populations along migratory routes may be genetically differentiated despite high dispersal of resting propagules. Initial results using mtDNA variation of *D. galeata* revealed several haplotype groups of limited geographical distribution and two haplotypes that were found across large geographic distances (Schwenk, unpublished). In general, no pattern of isolation by distance was found, and overall population differentiation was high ($F_{ST} = 0.38$). Many *Daphnia* species seem to show a high degree of provincialism or even endemism (Hebert, pers. comm.), as is also illustrated by the Australian *Daphnia carinata* complex, which is composed of at least seven groups (Hebert and Wilson, 1994).

Rotifers have shown strong phylogeographic patterns at an even smaller scale. *Brachionus plicatilis* showed strong population differentiation in both mtDNA and microsatellite variation in the Iberian Peninsula (Gómez et al., 2000, 2002). Two allopatric lineages (called northern and southern) showed a level and pattern of differentiation suggestive of several episodes of population fragmentation from the beginning of the Pleistocene, and survival throughout the Ice Ages in at least two refugia. The data imply strongly that the northern refugium was located in the Iberian Peninsula, whereas the southern refugium may have been on the Iberian Peninsula or in Northern Africa.

Studies on obligately asexual *Daphnia* reveal different phylogeographic patterns than those found in cyclically parthenogenetic taxa. Taxa of the circumarctic *D. pulex* complex co-occur and are found across large areas (Weider and Hobaek, 1997; Weider et al., 1999a, b). In addition,

some haplotypes of *D. tenebrosa* have dispersed across immense geographic distances (Weider et al., 1999b).

Mitochondrial sequence data of the bryozoan, *Cristatella mucedo*, reveal three, closely related mitochondrial haplotypes present throughout north-west Europe and 16 widely distributed and divergent genetic lineages in central North America (Freeland et al., 2000c). The greater similarity of some of the North American lineages to European lineages than to other lineages in North America suggest relatively recent colonization of north-west Europe from North America, and the paucity and low degree of divergence of haplotypes in Europe strongly suggest a historical bottleneck. Populations on both continents are characterized by the presence of multiple mitochondrial haplotypes indicating repeated colonization events. The lack of population differentiation shown by mitochondrial data was, however, not mirrored by microsatellite data. Population specific microsatellite profiles have evolved in both continents as a result of the rapid mutation rates of microsatellite loci (Freeland et al., 2000a, b, c). Combined mitochondrial and microsatellite data for North American *C. mucedo* segregated into two classes, suggesting the presence of two cryptic species in North America. Population genetic studies thus suggest that bryozoans are characterized by multiple historical colonization events within sites, ongoing gene flow amongst populations in north-west Europe (see earlier discussion), and local divergence and cryptic speciation in central North America where populations lack evidence for gene flow.

Whereas studies using mitochondrial DNA have confirmed high levels of population subdivision found with nuclear markers in many cyclically parthenogenetic taxa, this is not the case in other taxa (e.g., bryozoans). In the former, the data suggest that an important part of the variation in neutral markers is due to a common colonization history, gene flow not having affected the resulting patterns to a great extent since the last glaciation. Thus, patterns of genetic homogeneity, initially attributed to gene flow, may be a result of rapid and recent colonization of the habitats made available after the ice retreated in these taxa. The reduced levels of gene flow resulting from the monopolization effect may thus prompt a re-interpretation of patterns of regional genetic differentiation, as these may not so much reflect patterns of gene flow, but rather patterns of colonization of new habitats.

6. Conclusions

The Monopolization Hypothesis reconciles the capacity to rapidly colonize empty habitats with low levels of effective gene flow in zooplankton. Rapid monopolization of resources through a dilution effect (neutral, drift-like process) and local adaptation (selective process) results in strong priority effects and thus in very resilient founder effects. A comparative survey of several aquatic taxa indi-

cates that effective gene flow may be more strongly reduced in cyclically parthenogenetic zooplankton than in taxa with other life histories. A similar conclusion emerges from a comparison of phylogeographic pattern among taxa, the results of which indicate that provincialism may be more strongly characteristic of cyclical parthenogens than of other aquatic taxa. Our comparative survey indicates that the process of local adaptation may be particularly important in explaining the striking patterns of genetic differentiation among populations of cyclically parthenogenetic zooplankton. Patterns of genetic differentiation among populations of aquatic organisms may in many cases reflect historical patterns of colonization rather than patterns of ongoing gene flow. The severity of founder effects will, in part, be determined by the arrival rate of new colonists compared to the speed with which local resources are monopolized. The rate of resource monopolization will be influenced by both population density and local adaptation for efficient exploitation of resources.

. Biblios non appelées

(Berg, 2001; Brendonck et al., 1998; Colbourne et al., 1998; Colbourne et al., 1997; Hairston and Cáceres, 1996; Hairston and Olds, 1987; Schwenk and Spaak, 1995; Weider and Hebert, 1987; Weider and Hebert, 1987)

Acknowledgements

We thank Luis Santamaría for organizing the most inspiring workshop on dispersal in aquatic organisms at Nieuwersluis (April 2001). The ideas expressed in the present paper benefited strongly from the many discussions associated with this workshop. Discussions with Paul Hebert proved particularly helpful. Gary Carvalho, John Havel, Lars Berg, Erik Michels and Koen De Gelas are thanked for the many critical but constructive comments on an earlier version of the manuscript. LDM acknowledges financial support from project OT/00/14 of the KULeuven Research Fund and EU project BIOMAN (EVK2-CT-1999-00046). BO gratefully acknowledges financial support from grant GR3/11068 from the Natural Environment Research Council. KS was supported by EU (project LAKES; ENV4-CT-97-0585) and Netherlands Science Organization—Section Life Sciences (805.41.043) research grants.

References

- Abreu-Grobois, F.A., 1987. A review of the genetics of *Artemia*. In: Sorgeloos, P., Bengtson, D.A., Declair, W., Jaspers, E. (Eds.), *Artemia* research and its Applications, Vol. 1: Morphology, Genetics, Strain Characterization, Toxicology. Universa Press, Wetteren, pp. 61–99.
- Avise, J.C., 1999. *Phylogeography: The History and Formation of Species*. Harvard University Press, Harvard.

- Berg, L.M., 2001. Genetic disequilibria and the interpretation of population genetic structure of *Daphnia*. PhD thesis, Uppsala.
- Berg, L.M., Lascoux, M., 2000. Neutral genetic differentiation in an island model with cyclical parthenogenesis. *J. Evol. Biol.* 13, 488–494.
- Bilton, D.T., Freeland, J.R., Okamura, B., 2001. Dispersal in aquatic invertebrates. *Annu. Rev. Ecol. Syst.* 32, 159–181.
- Boersma, M., De Meester, L., Spaak, P., 1999. Environmental stress and local adaptation in *Daphnia magna*. *Limnol. Oceanogr.* 44, 393–402.
- Bohonak, A.J., 1998. Genetic population structure of the fairy shrimp *Branchinecta coloradensis* (Anostraca) in the Rocky Mountains of Colorado. *Can. J. Zool.* 76, 2049–2057.
- Boileau, M.G., Hebert, P.D.N., Schwartz, S.S., 1992. Non-equilibrium gene frequency divergence: persistent founder effects in natural populations. *J. Evol. Biol.* 5, 25–39.
- Brendonck, L., De Meester, L., 2002. Egg banks in freshwater zooplankton: evolutionary and ecological archives in the sediment. *Hydrobiologia* (in press).
- Brendonck, L., De Meester, L., Hairston Jr, N.G., 1998. Evolutionary and ecological aspects of crustacean diapause. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 52.
- Brendonck, L., De Meester, L., Riddoch, B.J., 2000. Regional structuring of genetic variation in short-lived rock pool populations of *Branchiopodopsis wolfei* (Crustacea: Anostraca). *Oecologia* 123, 506–513.
- Brendonck, L., Riddoch, B.J., 1999a. Wind-borne short-range egg dispersal in anostracans (Crustacea: Branchiopoda). *Biol. J. Linnean Soc.* 67, 87–95.
- Brendonck, L., Riddoch, B.J., 1999b. Dispersal in the desert rock pool anostracan *Branchiopodopsis wolfei* (Branchiopoda: Anostraca). In: Von Vaupel Klein, J.C., Schram, F.R. (Eds.), *The biodiversity crisis and Crustacea*, AA. Balkema, Rotterdam. pp. 109–118.
- Brown, C.J.D., 1933. A limnological study of certain fresh-water Polyzoa with special reference to their statoblasts. *Trans. Am. Microsc. Soc.* 52, 271–314.
- Bushnell, J.H., Rao, K.S., 1974. Dormant or quiescent stages and structures among the Ectoprocta: physical and chemical factors affecting viability and germination of statoblasts. *Trans. Am. Microsc. Soc.* 93, 524–543.
- Cáceres, C.E., 1997. Dormancy in the invertebrates. *Invert. Biol.* 116, 371–383.
- Cáceres, C.E., Hairston Jr, N.G., 1998. Benthic-pelagic coupling in planktonic crustaceans: the role of the benthos. In: Brendonck, L., De Meester, L., Hairston Jr, N.G. (Eds.), *Evolutionary and ecological aspects of crustacean diapause*. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 52, pp. 163–174.
- Carvalho, G.R., 1994. Genetics of aquatic clonal organisms. In: Beaumont, A. (Ed.), *Genetics and Evolution of Aquatic Organisms*. Chapman and Hall, London, pp. 291–323.
- Chaplin, J.A., Ayre, D.J., 1997. Genetic evidence of widespread dispersal in a parthenogenetic freshwater ostracod. *Heredity* 78, 57–67.
- Charalambides, I., Comoli, P., Croft, J., Figuerola, J., Gornall, R.J., Green, A., Hobaek, A., King, A., Lurz, P.W.W., Manca, M., Preston, C.D., Rushton, S.P., Sand, A., Sanderson, R., Santamaría, L., Schwenk, K., Shirley, M.D.F., 2000. Long distance dispersal of aquatic key species. In: Sutton, M.A., Moreno, J.M., van der Putten, W.H., Struwe, S. (Eds.), *Terrestrial Ecosystem Research in Europe: Successes, Challenges and Policy*, European Commission. pp. 170–172.
- Charalambidou, I., Santamaría, L., 2002. Waterbirds as endozoochorous dispersers of aquatic organisms: a review of experimental evidence. *Acta Oecol.* (this volume).
- Colbourne, J.K., Crease, T.J., Weider, L., Hebert, P.D.N., Dufresne, F., Hobaek, A., 1998. Phylogenetics and evolution of a circumarctic species complex (Cladocera: *Daphnia pulex*). *Biol. J. Linn. Soc.* 65, 347–365.
- Colbourne, J.K., Hebert, P.D.N., 1996. The systematics of North American *Daphnia* (Crustacea: Anomopoda): a molecular phylogenetic approach. *Phil. Trans. R. Soc. Lond. B* 351, 349–360.
- Colbourne, J.K., Hebert, P.D.N., Taylor, D.J., 1997. Evolutionary origins of phenotypic diversity in *Daphnia*. In: Givnish, T.J., Sytsma, K.J. (Eds.), *Molecular Evolution and Adaptive Radiation*. Cambridge University Press, Cambridge, pp. 163–188.
- Cousyn, C., De Meester, L., 1998. The vertical profile of resting egg banks in natural populations of the pond-dwelling cladoceran *Daphnia magna* Straus. *Arch. Hydrobiol. Ergebn. Limnol.* 52, 127–139.
- Cousyn, C., De Meester, L., Colbourne, J.K., Brendonck, L., Verschuren, D., Volckaert, F., 2001. Rapid local adaptation of zooplankton behavior to changes in predation pressure in absence of neutral genetic changes. *Proc. Natl. Acad. Sci. USA* 98, 6256–6260.
- Cox, A.J., Hebert, P.D.N., 2001. Colonization, extinction, and phylogeographic patterning in a freshwater crustacean. *Mol. Ecol.* 10, 371–386.
- Darwin, C.R., 1859. *The Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. John Murray, London.
- Declerck, S., Cousyn, C., De Meester, L., 2001. Evidence for local adaptation in neighbouring *Daphnia* populations: a laboratory transplant experiment. *Freshwat. Biol.* 46, 187–198.
- De Meester, L., 1993. Inbreeding and outbreeding depression in *Daphnia*. *Oecologia* 96, 80–84.
- De Meester, L., 1996a. Local genetic differentiation and adaptation in freshwater zooplankton populations: patterns and processes. *Ecoscience* 3, 385–399.
- De Meester, L., 1996b. Evolutionary potential and local genetic differentiation in a phenotypically plastic trait of a cyclical parthenogen. *Evolution* 50, 1293–1298.
- De Meester, L., Vanoverbeke, J., 1999. Uncoupling of male and sexual egg production leads to reduced inbreeding in the cyclical parthenogen, *Daphnia*. *Proc. R. Soc. Lond. B* 266, 2471–2477.
- DeMelo, R., Hebert, P.D.N., 1994. Founder effects and geographical variation in the invading cladoceran *Bosmina (Eubosmina) coregoni* Baird 1857 in North America. *Heredity* 73, 490–499.
- Ebert, D., Haag, C., Kirkpatrick, M., Riek, M., Hottinger, J.W., Pajunen, V.I., 2002. A selective advantage to immigrant genes in a *Daphnia* metapopulation. *Science* 295, 485–488.
- Freeland, J.R., Noble, L.R., Okamura, B., 2000a. Genetic consequences of the metapopulation biology of a facultatively sexual freshwater invertebrate. *J. Evol. Biol.* 13, 383–395.
- Freeland, J.R., Noble, L.R., Okamura, B., 2000b. Genetic diversity of North American populations of *Cristatella Mucedo*, inferred from microsatellite and mitochondrial DNA. *Mol. Ecol.* 9, 1375–1389.
- Freeland, J.R., Rimmer, V.K., Okamura, B., 2001. Genetic changes within freshwater bryozoan populations suggest temporal gene flow from statoblast banks. *Limnol. Oceanogr.* 46, 1121–1129.
- Freeland, J.R., Romualdi, C., Okamura, B., 2000c. Gene flow and genetic diversity: A comparison of freshwater bryozoan populations in Europe and North America. *Heredity* 85, 498–508.
- Frey, D.G., 1982. Questions concerning cosmopolitanism in Cladocera. *Arch. Hydrobiol.* 93, 484–502.
- Fryer, G., 1985. The ecology and distribution of the genus *Daphnia* (Crustacea-Cladocera) in restricted areas: the pattern of Yorkshire. *J. Nat. Hist.* 19, 97–128.
- Gajardo, G.M., Conceicao, M., Weber, L., Beardmore, J.A., 1995. Genetic variability and interpopulational differentiation of *Artemia* strains from South America. *Hydrobiologia* 302, 21–29.
- Gómez, A., Carvalho, G.R., Lunt, D.H., 2000. Phylogeography and regional endemism of a passively dispersing zooplankton: mitochondrial DNA variation in rotifer resting egg banks. *Proc. R. Soc. Lond. B* 267, 2189–2197.
- Gómez, A., Adcock, G.A., Lunt, D.H., Carvalho, G.R., 2002. The interplay between colonisation history and gene flow in passively dispersing zooplankton: microsatellite analysis of rotifer resting egg banks. *J. Evol. Biol.* 15, 158–171.
- Gornall, R.J., Hollingsworth, P.M., Preston, C.D., 1998. Evidence for spatial structure and directional gene flow in a population of an aquatic plant, *Potamogeton coloratus*. *Heredity* 80, 414–421.

- Green, A.J., Figuerola, J., Sánchez, M.I., 2002. Implications of waterbird ecology for the dispersal of aquatic organisms. *Acta Oecol.* (this volume).
- Hairston, N.G., 1996. Zooplankton egg banks as biotic reservoirs in changing environments. *Limnol. Oceanogr.* 41, 1087–1092.
- Hairston, N.G., Cáceres, C.E., 1996. Distribution of crustacean diapause: micro- and macroevolutionary pattern and process. *Hydrobiologia* 320, 27–44.
- Hairston, N.G., Dillon, T.A., DeStasio, B.T., 1990. A field test for the cues of diapause in a freshwater copepod. *Ecology* 71, 2218–2223.
- Hairston Jr, N.G., Lampert, W., Cáceres, C.E., Holtmeier, C.L., Weider, L.J., Gaedke, U., Fischer, J.M., Fox, J.A., Post, D.M., 1999a. Rapid evolution revealed by dormant eggs. *Nature* 401, 446–446.
- Hairston, N.G., Olds, E.J., 1987. Population differences in the timing of diapause: a test of hypotheses. *Oecologia* 71, 339–344.
- Hairston, N.G., Perry, L.J., Bohonak, A.J., Fellows, M.Q., Kearns, C.M., 1999b. Population biology of a failed invasion: Paleolimnology of *Daphnia exilis* in upstate New York. *Limnol. Oceanogr.* 44, 477–486.
- Hairston, N.G., Van Brunt, R.A., Kearns, C.M., 1995. Age and survivorship of diapausing eggs in a sediment egg bank. *Ecology* 76, 1706–1711.
- Hairston, N.G., Walton, W.E., 1986. Rapid evolution of a life history trait. *Proc. Natl. Acad. Sci. USA* 83, 4831–4833.
- Havel, J.E., Colbourne, J.K., Hebert, P.D.N., 2000a. Reconstructing the history of intercontinental dispersal in *Daphnia lumholzi* by use of genetic markers. *Limnol. Oceanogr.* 45, 1414–1419.
- Havel, J.E., Eisenbacher, E.M., Black, A.A., 2000b. Diversity of crustacean zooplankton in riparian wetlands: colonization and egg banks. *Aquat. Ecol.* 34, 63–76.
- Havel, J.E., Mabee, M.R., Jones, J.R., 1995. Invasion of the exotic cladoceran *Daphnia lumholzi* into North American reservoirs. *Can. J. Fish. Aquat. Sci.* 52, 151–160.
- Havel, J.E., Stelzleni-Schwent, J., 2002. Zooplankton community structure: the role of dispersal. *Verh. Int. Verein. Limnol.* 27 (in press).
- Hebert, P.D.N., 1987a. Genetics of *Daphnia*. In: Peters, R.H., De Bernardi, R. (Eds.), *Daphnia*, Istituto Italiano di Idrobiologia, Pallanza. pp. 439–460.
- Hebert, P.D.N., 1987b. b. Genotypic characteristics of the Cladocera. *Hydrobiologia* 145, 183–193.
- Hebert, P.D.N., Finston, T.L., 1996. A taxonomic reevaluation of North American *Daphnia* (Crustacea: Cladocera). III. The *D. catawba* complex. *Can. J. Zool.* 75, 1254–1261.
- Hebert, P.D.N., Moran, C., 1980. Enzyme variability in natural populations of *Daphnia carinata* King. *Heredity* 45, 313–321.
- Hebert, P.D.N., Wilson, C.C., 1994. Provincialism in plankton: endemism and allopatric speciation in Australian *Daphnia*. *Evolution* 48, 1333–1349.
- Hobæk, A., Manca, M., Anderson, T., 2002. Factors influencing species richness in lacustrine zooplankton. This volume.
- Holland, T.A., Jenkins, D.G., 1998. Comparison of processes regulating zooplankton assemblages in new freshwater pools. *Hydrobiologia* 387, 207–214.
- Hollingsworth, P.M., Preston, C.D., Gornall, R.J., 1996. Genetic variability in two hydrophilous species of *Potamogeton*, *P. pectinatus* and *P. filiformis* (Potamogetonaceae). *Pl. Syst. Evol.* 202, 233–254.
- Innes, D.J., 1991. Geographic patterns of genetic differentiation among sexual populations of *Daphnia pulex*. *Can. J. Zool.* 69, 995–1003.
- Jacobs, J., 1990. Microevolution in predominantly clonal populations of pelagic *Daphnia* (Crustacea: Phyllozoa): selection, exchange, and sex. *J. Evol. Biol.* 3, 257–282.
- Jenkins, D.G., Buikema, A.L., 1998. Do similar communities develop in similar sites? *Ecol. Monogr.* 68, 421–443.
- Jenkins, D.G., Underwood, M.O., 1998. Zooplankton may not disperse readily in wind, rain, or waterfowl. *Hydrobiologia* 387/388, 15–21.
- Korpelainen, H., 1984. Genic differentiation of *Daphnia magna* populations. *Heredity* 101, 209–216.
- Korpelainen, H., 1986. Competition between clones: An experimental study in a natural population of *Daphnia magna*. *Heredity* 105, 29–35.
- Lehman, N., Pfrender, M.E., Morin, P.A., Crease, T.J., Lynch, M., 1995. A hierarchical molecular phylogeny of the genus *Daphnia*. *Mol. Phylogenet. Evol.* 4, 395–407.
- Leibold, M.A., Tessier, A.J., 1991. Contrasting patterns of body size for *Daphnia* species that segregate by habitat. *Oecologia* 86, 342–348.
- Lyell, C., 1832. Principles of Geology. Vol. 2. John Murray, London.
- Lynch, M., 1984. The limits of life history evolution in *Daphnia*. *Evolution* 38, 465–482.
- Lynch, M., Gabriel, W., 1983. Phenotypic evolution and parthenogenesis. *Am. Nat.* 122, 745–764.
- Lynch, M., Pfrender, M., Spitze, K., Lehman, N., Hicks, J., Allen, D., Latta, L., Ottene, M., Bogue, F., Colbourne, J., 1999. The quantitative and molecular genetic architecture of a subdivided species. *Evolution* 53, 100–110.
- Lynch, M., Spitze, K., 1994. Evolutionary genetics of *Daphnia*. In: Real, L.A. (Ed.), *Ecological Genetics*. Princeton University Press, Princeton, New Jersey, pp. 109–128.
- Lynch, M., Walsh, J.B., 1998. *Genetics and Analysis of Quantitative Traits*. Sinauer, Massachusetts.
- Mader, E., van Vierssen, W., Schwenk, K., 1998. Clonal diversity in the submerged macrophyte *Potamogeton pectinatus* L. inferred from nuclear and cytoplasmic variation. *Aquat. Bot.* 62, 147–160.
- Maguire, B., 1963. The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. *Ecol. Mon.* 33, 161–185.
- Maier, G., 1996. *Daphnia* invasion: population dynamics of *Daphnia* assemblages in two eutrophic lakes with particular reference to the introduced alien *Daphnia ambigua*. *J. Plankton Res.* 18, 2001–2015.
- Mayr, E., 1963. *Animal Species and Evolution*. Belknap Press of Harvard University Press, Cambridge, Massachusetts.
- Mellor, W.K., 1975. Selective predation of ephippial *Daphnia* and the resistance of ephippial eggs to digestion. *Ecology* 56, 974–980.
- Michels, E., Cottenie, K., Neys, L., De Meester, L., 2001. Zooplankton on the move: first results on the quantification of dispersal of zooplankton in a set of interconnected ponds. *Hydrobiologia* 442, 117–126.
- Mukai, H., 1982. Development of freshwater bryozoans (Phylactolaemata). In: Harrison, F.W., Cowden, R.R. (Eds.), *Developmental Biology of Freshwater Invertebrates*. Alan R. Liss, New York, pp. 535–576.
- Naihong, X., Audenaert, E., Vanoverbeke, J., Brendonck, L., Sorgeloos, P., De Meester, L., 2000. Low among-population genetic differentiation in Chinese bisexual *Artemia* populations. *Heredity* 84, 238–243.
- Okamura, B., 1994. Variation in local populations of the freshwater bryozoan *Cristatella mucedo*. In: Hayward, P.J., Ryland, J.S., Taylor, P.D. (Eds.), *Biology and Palaeobiology of Bryozoans*. Olsen & Olsen, Fredensborg, Denmark, pp. 145–149.
- Okamura, B., 1997. The ecology of subdivided populations of a clonal freshwater bryozoan in southern England. *Archiv für Hydrobiologie* 141, 13–34.
- Okamura, B., Freeland, J., 2002. Gene flow and the evolutionary ecology of passively dispersing aquatic invertebrates. In: Bullock, J.M., Kenward, R.E., Hails, R.S. (Eds.), *Dispersal*. Blackwell Scientific Publications, London (in press).
- Pajunen, V.I., 1986. Distributional dynamics of *Daphnia* species in a rock-pool environment. *Ann. zool. Fenn.* 23, 131–140.
- Palsson, S., 2000. Microsatellite variation in *Daphnia pulex* from both sides of the Baltic Sea. *Mol. Ecol.* 9, 1075–1088.
- Palsson, S., 2001. The effects of deleterious mutations in cyclically parthenogenetic organisms. *J. Theor. Biol.* 208, 201–204.
- Parejko, K., Dodson, S.I., 1991. The evolutionary ecology of an antipredator reaction norm: *Daphnia pulex* and *Chaoborus americanus*. *Evolution* 45, 1665–1674.
- Proctor, V.W., 1964. Viability of crustacean eggs recovered from ducks. *Ecology* 45, 656–658.

- Proctor, V.W., Malone, C., 1965. Further evidence of the passive dispersal of small aquatic organisms in the intestinal tract of birds. *Ecology* 46, 728–729.
- Rhomberg, L.R., Joseph, S., Singh, R.S., 1985. Seasonal variation and clonal selection in cyclically parthenogenetic rose aphids (*Macrosiphum rosae*). *Can. J. Genet. Cytol.* 27, 224–232.
- Rhomberg, L.R., Singh, R.S., 1989. Evidence for a link between local and seasonal cycles in gene frequencies and latitudinal gene clines in a cyclical parthenogen. *Genetica* 78, 73–79.
- Roff, D., 1997. *Evolutionary Quantitative Genetics*. Chapman and Hall, New York.
- Santamaria, L., 2002. Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment. This volume.
- Schwenk, K., 1993. Interspecific hybridization in *Daphnia*: distinction and origin of hybrid matriline. *Mol. Biol. Evol.* 10, 1289–1302.
- Schwenk, K., Posada, D., Hebert, P.D.N., 2000. Molecular systematics of European *Hyalodaphnia*: the role of contemporary hybridization in ancient species. *Proc. R. Soc. Lond. B* 267, 1833–1842.
- Schwenk, K., Sand, A., Boersma, M., Brehm, M., Mader, E., Offerhaus, D., Spaak, P., 1998. Genetic markers, genealogies and biogeographic patterns in the cladocera. *Aquat. Ecol.* 32, 37–51.
- Schwenk, K., Spaak, P., 1995. Evolutionary and ecological consequences of interspecific hybridization in cladocerans. *Experientia* 51, 465–481.
- Sculthorpe, C.D., 1967. *The Biology of Aquatic Vascular Plants*. Edward Arnold, London.
- Shurin, J.B., 2000. Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. *Ecology* 81, 3074–3086.
- Shurin, J.B., Havel, J.E., Leibold, M.A., Pinel-Alloul, B., 2000. Local and regional zooplankton species richness: a scale-independent test for saturation. *Ecology* 81, 3062–3073.
- Spitze, K., 1993. Population structure in *Daphnia obtusa*: quantitative genetic and allozyme variation. *Genetics* 135, 367–374.
- Taylor, D.J., Finston, T.L., Hebert, P.D.N., 1998. Biogeography of a widespread crustacean: pseudocongruence and cryptic endemism in the North American *Daphnia laevis* complex. *Evolution* 52, 1648–1670.
- Taylor, D.J., Hebert, P.D.N., Colbourne, J.K., 1996. Phylogenetics and evolution of the *Daphnia longispina* group (Crustacea) based on 12S rDNA sequence and allozyme variation. *Mol. Phylogenet. Evol.* 5, 495–510.
- Tessier, A.J., Young, A., Leibold, M., 1992. Population dynamics and body size selection in *Daphnia*. *Limnol. Oceanogr.* 37, 1–14.
- Vanoverbeke, J., De Meester, L., 1997. Among-population genetic differentiation in the cyclical parthenogen *Daphnia magna* (Crustacea: Anomopoda) and its relation to geographic distance and clonal diversity. *Hydrobiologia* 126, 135–142.
- Weider, L.J., Hebert, P.D.N., 1987a. Ecological and physiological differentiation among low-arctic clones of *Daphnia pulex*. *Ecology* 68, 188–198.
- Weider, L.J., Hebert, P.D.N., 1987b. Microgeographic genetic heterogeneity of melanistic *Daphnia pulex* at a low-arctic site. *Heredity* 58, 391–399.
- Weider, L.J., Hobaek, A., 1997. Postglacial dispersal, glacial refugia, and clonal structure in Russian/Siberian populations of the arctic *Daphnia pulex* complex. *Heredity* 78, 363–372.
- Weider, L.J., Hobaek, A., Colbourne, J.K., Crease, T.J., Dufresne, F., Hebert, P.D.N., 1999a. Holarctic phylogeography of an asexual species complex I. Mitochondrial DNA variation in arctic *Daphnia*. *Evolution* 53, 777–792.
- Weider, L.J., Hobaek, A., Crease, T.J., Stibor, H., 1996. Molecular characterization of clonal population structure and biogeography of arctic apomictic *Daphnia* from Greenland and Iceland. *Mol. Ecol.* 5, 107–118.
- Weider, L.J., Hobaek, A., Hebert, P.D.N., Crease, T.J., 1999b. Holarctic phylogeography of an asexual species complex II. Allozymic variation and clonal structure in Arctic *Daphnia*. *Mol. Ecol.* 8, 1–13.
- Weider, L.J., Lampert, L., Wessels, M., Colbourne, J.K., Limburg, P., 1997. Long-term genetic shifts in a microcrustacean egg bank associated with anthropogenic changes in the Lake Constance ecosystem. *Proc. R. Soc. London* 264, 1613–1618.
- Wilson, C.C., Hebert, P.D.N., 1992. The maintenance of taxon diversity in an asexual assemblage: an experimental analysis. *Ecology* 73, 1462–1472.
- Wilson, C.C., Hebert, P.D.N., 1993. Impact of copepod predation on distribution patterns of *Daphnia pulex* clones. *Limnol. Oceanogr.* 38, 1304–1310.
- Wolf, H.G., 1988. Differences in the genetic structure of pond-dwelling and lake-dwelling *Daphnia*. *Verh. Internat. Verein. Limnol.* 23, 2056–2059.
- Wood, T.S., 1991. Bryozoans. In: Thorp, J.H., Covich, A.P. (Eds.), *Ecology and Classification of North American Freshwater Invertebrates*. Academic Press, New York, pp. 481–499.