HIGH DISPERSAL CAPACITY OF CLADOCERAN ZOOPLANKTON IN NEWLY FOUNDED COMMUNITIES

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Abstract. The relative importance of local and regional factors to community buildup is a key question in community ecology. Dispersal capacity is an important regional determinant but is very difficult to assess. Instead, measuring colonization rates in newly created habitats can provide a reasonable approximation of dispersal capacities. We monitored cladoceran zooplankton colonization rates in 25 newly dug and isolated pools. During the first 15 months, an average of 4.2 cladoceran species colonized each pool. In total, 20 different species were found during this period in the pools, representing 40% of the total species richness observed during summer in well-established cladoceran communities in water bodies in the immediate neighborhood (within 3 km) of the studied new pools. Our results reveal high colonization rates of newly created habitats by cladoceran zooplankton, reflecting a high dispersal capacity in this group of organisms. We discuss these results in light of the extent and ecological and evolutionary impact of dispersal in aquatic organisms.

Key words: Cladocera; colonization; Daphnia; dispersal; establishment success; local vs. regional factors; new habitat; pool.

INTRODUCTION

Community assemblage is a core issue in ecology. A key question is the relative importance of local and regional factors in determining community structure (Caley and Schlüter 1997, Shurin et al. 2000). Are communities determined primarily by local environmental conditions and biotic interactions with other resident species, or does dispersal limitation (i.e., the shortage of viable propagules arriving in the habitat) play a prominent role? Clearly, the relative importance of dispersal limitation and ecological interactions in determining establishment success will depend on the dispersal capacity of the organisms under consideration. In practice, however, dispersal rates are difficult to measure. There is also an important distinction to be made between dispersal rates, as quantified by the transport of propagules (dispersal capacity), and effective dispersal, which incorporates both transport and establishment success.

Recently, much work on the impact of local and regional factors has been carried out in freshwater zooplankton communities, both through a variance partitioning approach in field studies (Cottenie et al. 2003) and through experimental tests using enclosed units (Shurin 2000, Cottenie and De Meester 2004). Overall, the results of these studies indicate that local environmental control is very important in determining establishment success. Species sorting proved very efficient in a system with high dispersal rates (Cottenie and De Meester 2004) and establishment success of inoculated species of the regional species pool was found to be low in well-established communities (Shurin 2000). These findings contrast with data of a study monitoring the colonization of new habitats (Jenkins and Buikema 1998). In this latter study, species composition among habitats after one year differed substantially, even though the habitats were ecologically very similar. Jenkins and Buikema (1998) concluded that stochastic effects associated with low dispersal rates were important in these systems.

There are two reasons why the results of the study by Jenkins and Buikema (1998) suggest a different pattern than the results of Shurin (2000) and Cottenie and De Meester (2004). First, the degree of isolation (number of suitable habitats in the region) may differ among studies (see also Cohen and Shurin 2003, Havel and Shurin 2004). Second, dispersal limitation is expected to decline and the impact of local (biotic) interactions is expected to increase as the community matures and becomes more species rich. Therefore, studies on new habitats are expected to reveal more dispersal limitation than studies dealing with well-established communities.

Traditionally, and already noted by Darwin (1859), the dispersal capacity of aquatic organisms has been considered to be high thanks to the production of dormant stages. De Meester et al. (2002) listed several independent lines of evidence that dispersal capacity in zooplankton is indeed high, and their argument has since been reinforced by the results of a number of recent studies. Figuerola and Green (2002) have provided strong evidence that birds may carry a substantial amount of dormant stages of plants and aquatic organisms and thus may be potentially important vectors, at
least for regional dispersal. Long-distance jumps (e.g., 1000 km), which are not along flyways, seem to be linked instead to human activities. Cáceres and Soluk (2002) as well as Cohen and Sharin (2003) have provided independent experimental evidence that aquatic organisms can readily colonize containers covered with different mesh-sized nets. Yet, in a recent review, Bohonak and Jenkins (2003) argue that dispersal rates are not very high and question several of the arguments listed by the other authors. More specifically, they argue that most studies on the colonization of new habitats actually reveal low rather than high colonization rates. The major argument of Bohonak and Jenkins (2003) from this interpretation is that, even after one or two years, only a limited subset of the regional species pool is found in the local habitats. Given this controversy, we set out to assess dispersal rates of zooplankton under natural conditions by monitoring colonization of newly created pools through time.

So far, few studies have addressed in situ colonization of newly created aquatic habitats by zooplankton. Fryer (1985) mentions anecdotal evidence on the colonization of a few ponds and Jenkins and Buikema (1998) performed a detailed monitoring of the colonization of 12 neighboring ponds on a single location. We here report on the colonization rates of 25 pools during the first 15 months of existence. An important difference with the study of Jenkins and Buikema (1998) is that our pools are located over a wider geographic area, thereby sampling different regions with different patterns of regional species richness and density of source habitats. This is important, as differences in regional characteristics (e.g., species richness) are thought to strongly influence colonization rates (Sharin et al. 2000). Overall, our results support the idea of high dispersal capacity in cladoceran zooplankton and suggest that regional characteristics are important in explaining the differences in colonization rates reported among studies.

METHODS

Study sites

The pools studied are part of nature restoration projects that aim at creating suitable habitats for amphibian populations. Scattered over Flanders (Belgium) and financially supported by local and regional governments, numerous small pools are being created in nature reserves and agricultural land. Typically, the pools have a near-circular shape with a gentle slope on the northern side, have a surface area of ~100-250 m², and a maximum depth of 150 cm. Twenty-five such new pools, all constructed in late September 2001 and distributed over different regions in Flanders, were selected for our study (Fig. 1). We employed three criteria for pool selection. First, all of the studied pools were totally new and did not involve areas in which there was a pool, ditch, or swamp before. Thus, the soil of the pools contained no dormant egg bank. This expectation was confirmed by an analysis of the buildup of the dormant egg bank (J. Vandenbroekhove, G. Louette, L. Brendonck, and L. De Meester, unpublished data). The pools filled spontaneously by rain- and groundwater within two months after their creation. Secondly, all selected pools were isolated from any other water body, so that colonization could not occur by a direct connection. Instead, colonization had to occur through an overland process, such as by wind or with the help of animal vectors (Bilton et al. 2001, Figureola and Green 2002). Finally, in order to be able to assess the role of regional characteristics, we selected the pools such that they were located in different regions throughout Flanders.

Sampling local communities

Sampling of all 25 pools was performed monthly during one year (January–December 2002). On each sampling occasion, a number of environmental variables were measured: temperature, pH, conductivity, dissolved oxygen, water transparency, concentration of chlorophyll a, and the concentration of total suspended solids. These depth-integrated samples were collected during the day from the middle of the pool using a tube sampler (length 1.5 m; diameter 75 mm). Because pool depths were shallow, water transparency was determined using a Snell tube. A Snell tube consists of a hollow black cylinder (length 0.70 m; diameter 55 mm), which is closed at the bottom and filled with sample water. When measuring, a white disc attached at the side on a meter stick is lowered until the disc is not visible anymore, and then the disc is pulled up again until it becomes visible. The Snell depth is determined by averaging these two depths. Chlorophyll a concentrations were measured by filtering a 250-ml water sample through a GF/C filter and extracting the pigment in methanol (24 h) following the protocol of Talling and Driver (1963). Total suspended solids concentrations were determined by filtering a 250-ml water sample through a preweighed GF/C filter, drying it at 100°C for 24 h, and reweighing. The mean value of morphometric characteristics during the winter period and the average value of all the other environmental variables over all 12 months, are shown in Appendix A.

Cladocerans were collected bimonthly at eight randomly chosen locations within each pool. At each location, 6 L of water was collected with the tube sampler, and water from all locations was pooled. Of this combined sample, 18 L was filtered through a 64-μm plankton net and preserved in formaldehyde saturated with sucrose. To avoid contamination of pools, we used strictly separate sampling equipment for all pools that were sampled on a given day. In between sampling trips, all sampling material was thoroughly rinsed and dried (in a 30°C temperature room). All cladocerans in the local pool samples (50 mL) were counted and identified to species level, following Flössner (2000).
RESULTS

Ecology of the pools

All pools shared similar morphometric characteristics (Appendix A). Maximum surface area ranged from 35 m² to 825 m² and maximum depth ranged from 65 cm to 200 cm. However, water level fluctuations over the year varied considerably among pools, and thus conditions ranged from temporary to permanent. Water transparency tended to be high in most pools, with the exception of a few pools in which high concentrations of chlorophyll a (BI2), suspended clay particles (DA), and dissolved ferric ion complexes (HB2) led to a turbid water state. Nutrient concentrations of the pools were in the range of eutrophic waters (Appendix A). Submerged macrophytes (typical pioneer species like Callitriche spp., Chara spp., and Nitella spp.) first appeared in June 2002 and have since persisted. Submerged macrophytes were observed in 12 out of the 25 pools, but were only abundant in 5 of them (HE1, Chara globularis; KT, Callitriche sp. and Nitella flexilis; K01, Callitriche sp. and Chara globularis; MA2 and T2, Callitriche sp.).

Local community buildup

Table 1 shows the colonization history of each pool and the number of pools colonized by a given species. Within the first 15 months of existence, pools were colonized by an average of 4.2 ± 0.4 species (mean ± 1 std, range 2–8 species). A total of 20 cladoceran species were observed in the set of all 25 pools. Three species (Chydorus sphaericus, Daphnia obtusa, and Simocephalus vetulus) were observed in at least half of the pools. Strikingly, daphnids (Ceriodaphnia spp., Daphnia spp., Simocephalus vetulus, and Scapholeberis mucronata) represented almost 50% of the colonization events. This bias is even more pronounced during the first six months of the study, when more than 50% of the colonization events involved Daphnia species. Daphnia obtusa was observed in 11 of the 25
pools during the first sampling survey (January 2002). With the exception of *Chydorus sphaericus*, chydorid and macrothricid species tended only to be observed in the second half of the study, and none became very widespread.

A continuous and gradual increase in the average number of species was observed in the newly created pools (Fig. 2), with no indication that a plateau was reached after 15 months.

**The impact of regional species richness**

The regional survey, involving the analysis of subsamples of summer communities of a total of 135 water bodies, yielded a total of 50 species (listed in Appendix B). The average number of species observed per water body in the regional survey is $4.9 \pm 0.3$ (mean $\pm$ 1 SE). All species observed in the newly created pools in the present study were also observed in the immediate region (3 km) of the pools. There is a marginally positive linear relation between local (mean of all new pools located within a region) and regional species richness ($r^2 = 0.27$, $P = 0.07$; Fig. 3). Interestingly, of the 11 species that were found to be very common in the regional survey (occurring in more than 75% of the studied regions), two (*Disparalona rostrata* and *Daphnia parva*) were not observed in any of the newly created pools. Other very common species in regional species pools, such as *Ceriodaphnia pulchella* and *Bosmina longirostris*, were only found sporadically in the newly created pools and only colonized the pools relatively late.

**DISCUSSION**

The key observation of the present study is that newly created pools are readily colonized by cladoceran zooplankton. In particular, daphniid species showed a high colonizing ability, illustrated by the observation that almost half of the 25 pools were colonized by *Daphnia obtusa* within the first four months. If we take the July samples of the newly created pools into consideration, the average number of species found (1.6) is approximately one-third of the average number of species (4.9) that was observed in summer samples from older pools, ponds, and ditches in the region (radius of 3 km) surrounding the focal pools. Taking all 25 pools together yields a cumulative number of 20 species in a period of 15 months, whereas sampling of 135 standing water bodies in the immediate regions of the 25 pools yielded a total of 50 species. These results suggest that colonization rates are quite high and result in a substantial part (40%) of the regional species richness being captured in newly created habitats within 15 months. Furthermore, a mere species list is expected to underestimate the real number of successful colonization events, as each species could have colonized the habitat multiple times. Indeed, genetic analysis performed on 12 newly established *Daphnia* populations revealed on average 1.7 multilocus genotypes (range 1–3) per population (G. Louette, A. Wollebrants, and L. De Meester, unpublished data), supporting the hypothesis that multiple colonization events occurred.

A second important observation is that colonization rates differed among taxa, with daphniids in our study being better colonizers than chydorids or macrothricids. This result may be due either to an intrinsic difference in dispersal capacity or to a lower establishment success of chydorids and macrothricids. Consistent with the last interpretation is the fact that during this first growing season, the newly created pools had poor...
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The development of littoral zones, known to be the preferred habitat of chydorid and macrothricid species. Although our data suggest a high dispersal and colonization capacity for many cladoceran species, the data also show that the first 15 months of community buildup is strongly influenced by dispersal limitation. Two observations support this interpretation. First, there is a linear increase, without an asymptote, in the cumulative number of species observed (Fig. 2), indicating that local factors do not have a growing impact on observed colonization rates as the communities build up during this initial 15 months of colonization. Second, there is a positive relationship between local and regional species richness (Fig. 3), although the relationship is not very strong. The importance of the characteristics of the region is also illustrated by the fact that all species found to colonize one of the newly created pools were found in the immediate neighborhood (<3 km distance) of the focal pool. This result suggests that short-distance dispersal is a key process. Our results corroborate earlier findings, suggesting a high colonization capacity of zooplankton. Cáceres and Soluk (2002) reported more than 60% of the regional species pool captured in experimental mesocosms during a two-year survey on a single site, and Cohen and Shurin (2003) mentioned even more than 70% in a similar experimental setup during a few months of natural colonization. These results are in contrast with the general conclusions of Jenkins and Buikema (1998) (see also Bohonak and Jenkins 2003). This dissimilarity among the results of different studies is likely due to the importance of regional factors revealed by our study. The ponds studied by Jenkins and Buikema (1998) were likely much more isolated than the ones studied by us. Some preliminary evidence sug-

Fig. 2. Cumulative number of cladoceran species observed in the individual pools during the first 15 months of their existence. Values are averaged over all 25 pools; error bars represent one standard error ($Y = -0.84 + 0.37X; r = 0.59; P < 0.001$).

Fig. 3. Relationship between the regional (within 3 km) and mean local cladoceran species richness. Local species richness is determined as the cumulative number of species observed over a 12-months survey ($r = 0.27; P = 0.07$).
gests that artificial containers that were positioned in the neighborhood of species-rich ponds were readily colonized (Frank Van de Meutter, personal communication), whereas it took almost a year before similar containers set up in an area in which the nearest pond was at >1 km distance became colonized by cladocerans.

Our observations contrast with the general conclusion of a recent review by Bohonak and Jenkins (2003) that dispersal in zooplankton is not frequent on relatively short time scales. Obviously, the notion of rapid vs. slow and frequent vs. infrequent is a subjective one, but our data strongly suggest that, at least for many species of cladocerans, colonization rates of newly created habitats are surprisingly fast. We see three reasons for this discrepancy between the conclusion of Bohonak and Jenkins (2003) on the one hand and the results of our own and other recent studies (Cáceres and Soluk 2002, Figuerola and Green 2002, Cohen and Shurin 2003) on the other hand. First, colonization rates are habitat dependent and probably are strongly influenced by regional characteristics (e.g., the presence of source habitats), so that some studies (e.g., Jenkins and Buijema 1998) indeed reveal relatively slow colonization rates. One should note that the effects of scale on the dispersal rate of species are very important. Whereas dispersal on short spatial scales is rapid enough in order that local interactions restrict species diversity more than the supply of colonists, dispersal limitation over broader spatial scales (e.g., >20 km) might constrain geographic ranges and influence community structure (Havel and Shurin 2004).

Second, Bohonak and Jenkins (2003) ignore several lines of evidence illustrating the high dispersal capacity of zooplankton as listed by De Meester et al. (2002). For instance, strong evidence for high dispersal capacity in zooplankton is offered by the distribution patterns of clones of obligately parthenogenetic cladoceran species, such as occurs over very large areas across the Arctic (Weider et al. 1999). On a more local scale (3 km), clonal occurrence often strikingly reflects patterns of environmental heterogeneity (e.g., Weider and Hebert 1987, Wilson and Hebert 1993). This pattern can only be obtained when most clones can potentially reach all habitats, and after which clonal selection results in dominance of the one or few clones that are best adapted to the local conditions (Wilson and Hebert 1993). There is no way to explain these patterns when one assumes strong dispersal limitation. It does not require massive numbers of individuals being transported from one habitat to the other, but rather dispersal rates in the order of magnitude as reported in the present study, combined with strong clonal selection.

A third reason for the difference of our interpretation is that, even though Bohonak and Jenkins (2003) make the very important distinction between the potential for dispersal (here called dispersal capacity) and actual dispersal rates, they actually confound both concepts when they suggest that the limited geographic distribution (provincialism) of many zooplankton species indicates that these species do not have a high dispersal capacity. Given the high actual dispersal rates observed when considering the colonization of empty habitats, the conclusion rather should be that dispersal capacity is fairly high and actual movements of dormant propagules fairly frequent, but establishment success is constrained by local environmental features.

Dispersal rates are in general exceedingly difficult to quantify. One can estimate the number of propagules on certain vectors (Figuerola and Green 2002), but this only quantifies the capacity to be transported, and not whether suitable habitats are actually reached and colonized. Monitoring levels of gene flow using genetic markers is a second method, but strongly depends on the underlying assumptions (Bohonak and Jenkins 2003). Most importantly, however, gene flow only quantifies effective dispersal, which includes establishment success. Monitoring the colonization of empty habitats yields a better estimate of dispersal capacity, as establishment success in newly created habitats is not yet strongly impacted by biotic interactions imposed by the resident community. Nevertheless, as pointed out above, dispersal rate estimates based on the colonization of empty habitats may also underestimate true dispersal rates. Overall, the data on dormant propagule transport by animal vectors (Figuerola and Green 2002) and colonization rates (present study) strongly suggest a high dispersal capacity of zooplankton.

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LITERATURE CITED


HIGH DISPERsal CAPACITY OF CLADOCERANS


APPENDIX A

A table showing the average value of key environmental variables of the newly constructed pools is available in ESA's Electronic Data Archive: Ecological Archives E086-018-A1.

APPENDIX B

A table listing the cladoceran species present in each of the 13 investigated regions is available in ESA's Electronic Data Archive: Ecological Archives E086-018-A2.