Differential behaviour and shifts in genotype composition during the beginning of a seasonal period of diel vertical migration

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Abstract

During the first few weeks of a recurring seasonal period of diel vertical migration in Lake Maarsseveen (The Netherlands), part of the hybrid *Daphnia galeata* × *hyalina* population migrated, while another part remained in the epilimnion. In the epilimnion, 0+ perch prey upon daphnids during daytime. Gradually, the number of adult *Daphnia* in the epilimnion decrease until the epilimnion is nearly devoid of daphnids. The population as a whole may decrease, as in 1991, or may increase as in 1992. Genotype composition, as determined by allozyme analysis, changed substantially within a fortnight in 1992, and one genotype became dominant. Our data are in agreement with the hypothesis that predation on different genotypes (clones) occurs during the beginning of a seasonal period of diel vertical migration, though our data do not allow to exclude alternative explanations.

Introduction

Since the seminal paper by Zaret & Suffern (1976), diel vertical migration (DVM) has been generally considered to be a predator avoidance strategy. Although no definitive statement was made, the suggestion that "only those individuals that exhibited the appropriate behavioural response of vertical migration were able to survive to produce descendants" (p. 811) set the stage for considering genotype selection as a driving force. An equally important paper by Stich & Lampert (1981) demonstrated the existence of species-specific selection. The seasonal increase in migration amplitude in *Daphnia hyalina* was suggested to be generated by "selection pressures eliminating non-migrating animals from the population" (p. 398). By way of precaution, differential responses to changing (non-specified) environmental conditions were added. A third important paper by Gliwicz (1986) seemed to confirm that DVM in zooplankton was a genetically fixed behavioural trait. In an enthusiastic commentary by Huntingford & Metcalfe (1986, p. 682), diel vertical migration was called "a genetically pre-programmed

behavioural change". Since the publication of these papers, phenotypic induction has been demonstrated many times (Ringelberg, 1991b; Loose, 1993; Loose et al., 1993), and some researchers have explicitly recognised that a possible interaction between a genetic component and phenotypic plasticity in DVM behaviour needs to be studied (e.g. in marine habitats: Ohman, 1990; in freshwater systems: Neill, 1992; De Meester, 1993; 1996).

The rapid change from non-migrating to migrating *Daphnia* individuals in Lake Maarsseveen (The Netherlands), which occurs usually within one week, excludes genotype selection as an important factor. The co-occurrence of large shoals of 0+ perch (*Perca fluviatilis*) in the pelagic zone and an experimentally demonstrated enhanced responsiveness to light intensity changes in the presence of an exudate (kairomone) of these perch, made the conclusion of phenotypic induction inevitable (Ringelberg, 1991a; Ringelberg et al., 1991). In several papers, the active role of predator exudates in altering behaviour has been described (De Meester, 1993; Forward, 1993; Loose, 1993; Loose et al., 1993). Now, it is generally accepted that at least

some diel vertical migrations are reversible changes in behaviour of individuals and not irreversible changes in genotype. The role of causation by predators is moved to the evolutionary past and selective predation is held to be the ultimate cause of DVM. Ultimate causation is an historical event that can be neither proved nor disproved. However, if a strong trade-off is present, as in DVM, selective predation must be working continually to maintain the necessary traits. Depending on the values of factors that determine progeny, such as food availability and predation rate, the costs of a particular migration might exceed the benefits. The abundance of the migrating genotype(s) will then decrease and other genotypes will take over (Stich & Lampert, 1981; Gliwicz, 1986). For parthenogens with high reproductive rates, this might occur within a short period of time.

Daphnia populations consist of clones representing different genotypes (Lynch & Gabriel, 1983; Hebert, 1987; Lynch, 1987; Spaak, 1996). Some *D. magna* populations consist of genotypes with different (primary) phototactic behaviour (De Meester & Dumont, 1988; De Meester, 1990; 1996) while a genotype-dependent vertical distribution has also been shown for *D. galeata* × *hyalina* hybrids (De Meester et al., 1995). An earlier study on genetic variation in Lake Maarsseveen has indicated an appreciable genetic polymorphism (Spaak & Hoekstra, 1993). Clonal composition may change intra- and interannually, as intraspecific relative fitness may vary. When large numbers of 0+ perch prey upon *Daphnia* (Flik et al., 1997), such severe predation pressure may exert genotype-dependent selection, provided that genotypes differ in characters that determine predation risk. Several field studies (Weider, 1984; Müller & Seitz, 1993; King & Miracle, 1995) have shown indeed that different clones may exhibit different migration patterns. If strong selective predation occurs, the pattern of migration in a population could change rapidly. One could expect that the pattern of change, as well as the accompanying change in population size, varies from year to year, depending on the factors influencing relative fitness and, of course, the genotypic composition of the population. Although several studies addressed the problem of genotype-specific DVM (see above) very little work has been done on genetic shifts during the short period of DVM induction. In the present paper we want to focus on this aspect.

In Lake Maarsseveen, the hybrid *D. galeata* × *hyalina* has become the dominant taxon. Vertical migration occurs during a short period of six to seven weeks, starting in most years at the end of May

(Ringelberg et al., 1991). This migration was observed for the first time in 1988. In 1989, a yearly recurring study was started with a weekly sampling program during the crucial migrating period. Day-depth proved to be different from year to year. In the first two years, a large portion of the population stayed within the predation zone, which extended from the water surface to 7.5–8 m. 0+ perch are restricted to this water layer, which makes up the epilimnion (Flik et al., 1997), and we refer to this strata as the predation zone. In 1991, DVM of *D. galeata* × *hyalina* was delayed, indirectly due to a cold spring (Flik & Ringelberg, 1993), but the animals exhibited a much deeper migration. In 1992, a migration amplitude to 1991 was found at the height of the migration period (Ringelberg & Flik, 1994).

In the present paper, we present data on population size and vertical distribution of *D. galeata* × *hyalina* from 1991 and 1992 and on genotype composition of the population in 1992, to gain insight into whether and to what extent a change in genotype frequency contributes to the rapidly changing DVM pattern observed during the first two to three weeks of the seasonal migration period.

Methods

For a physical and chemical description of Lake Maarsseveen, see Swain et al. (1987). Vertical distribution and population size of the *D. galeata* × *hyalina* population were estimated from samples taken at noon and midnight along the length axis of the lake by towing simultaneously, seven (1991) or nine (1992) torpedo nets positioned at equal vertical intervals (2.5 m). The uppermost net was at a depth of about 1.25 m and the lowest one at 16.25 m in 1991 and at 21.25 m in 1992. Two runs were conducted per sampling bout. Samples were preserved in sugar-formalin and juveniles, adults with eggs and adults without eggs of the hybrid *D. galeata* × *hyalina* were enumerated. Numbers of ind. m⁻² were calculated for sections of 2.50 m. (2.5 m³). For the present study, numbers of adults from the three uppermost samples were taken together to represent individuals especially prone to predation by 0+ perch. The adults from all depths below 7.5 m were pooled, and represented individuals that were not exposed to predation by perch during the daytime. Sample sizes ranged from 286 individuals (noon day 184, 1991) to 6431 individuals (night day 161 1992) in both combined samples. The average sample size was 2035 individuals in both samples.

Figure 1. Ratio between total number of adults in the water column around noon and around midnight during a period of DVM in 1991 (closed symbols) and 1992 (open symbols). Day 120 is 30 April. Onset of DVM is on day 184 in 1991 and on day 162 in 1992.

The estimation of population size during a period of diel vertical migration has some problems. As is apparent from Figure 1, the total number of adults, caught at noon during a period of DVM, is often much smaller than the number caught during the night. This is because an increasing number of animals disappear below the depth at which the lowest torpedo net was operating in 1991. In 1992, when two torpedo's were added, more animals were caught during the day than in 1991, resulting in a smaller variation of the day/night ratio of abundance estimates (Figure 1). Although a large part of central Lake Maarsseveen has a depth of 25 m or more, shallower parts along the sampling trajectory prevented the torpedo nets from operating at depths greater than 21.25 m. In fact, the trajectory shown in Figure 1 nicely illustrates the period of DVM and of the change in migration amplitude during this period. Obviously, numbers from night-time sampling represent more closely total population size than those from noon samples. The day-time numbers in the lower portion of the water column (>21.5 m) were corrected by adding the difference between total night-time and daytime numbers. An estimate of the variance in total numbers of adults in the water column was derived from the two daytime and the two night-time sampling series obtained on three pre-migration and three

post-migration dates in 1991. Variance is expressed as coefficients of variation ($s/\bar{x}\%$) and as standard errors of the mean relative to the mean ($s.e./\bar{x}\%$). On average, the resulting values are 21% and 10%, respectively. In 1992, eight samples, taken between 02.00 h and 05.30 h, were also used to estimate the variance. The variance was 20% and the relative standard error was 7%.

We determined clonal composition of the *Daphnia* population in a vertical profile of the lake, by sampling at noon and midnight on 25 May and 10 June 1992. Animals were taken to the laboratory, adult females were frozen in liquid nitrogen and stored for subsequent electrophoretic analysis. Because of the low numbers in some torpedo net samples, we combined samples into five depth categories (0–2.5; 2.5–7.5; 7.5–12.5; 12.5–17.5; 17.5–22.5). Individual adult females were assayed using cellulose acetate electrophoresis following standard methods (Hebert & Beaton, 1989). Generally, 40 animals per depth per sample were assayed for three enzyme loci: phosphoglucumutase (*Pgm*, EC 5.4.2.2), phosphoglucose isomerase (*Pgi*, EC 5.3.1.9) and glutamate oxaloacetate transaminase (*Got*, EC 2.6.1.1). *Got* is a diagnostic marker for distinguishing between *D. galeata* and *D. hyalina* (Wolf & Mort, 1986). *D. galeata* is fixed for the F (fast) allele, while *D. hyalina* is fixed for the S (slow) allele. Interspecific hybrids can be identified as heterozygotes (SF) at *Got*. During the study period, only hybrid *D. galeata* × *hyalina* were found. Variation at the *Pgi* and *Pgm* loci made it possible to identify two-locus genotypes. $R \times C$ tests for independence (Sokal & Rohlf, 1995) were used to test if distributions of genotypes were different.

Results

Vertical distributions of *D. galeata* × *hyalina* at noon and midnight for three crucial dates in 1991 are presented in Figure 2. 1991 was exceptional because of a delayed start of the migration period (Flik & Ringelberg, 1993). On 12 June (day number 163), DVM had not yet started since a difference between night-time and daytime relative vertical distributions was not discernible (Figure 2A). Vertical distributions during day and night were completely different when the period of migration was in full progress, as on 3 July (day number 184, Figure 2C). Few individuals were then found in the upper water layers during the day. Adult animals started to arrive in these upper layers about one hour after sunset and had left one hour before sun-

Figure 2. The relative vertical daytime (open bars) and night-time (black bars) distributions of *D. galeata* $\times$ *hyalina* in Lake Maarsveen on three crucial dates in 1991.*

rise (J. Ringelberg, *pers. obs.*). June 26 (day number 177, Figure 2B) is of particular interest because it represents a transient state: part of the population (21%) performed a diel vertical migration, whereas 53% did not leave the epilimnion during the day. Adult numbers had decreased by 63% compared to the night-time estimate obtained two weeks earlier, on the 12th of June (Table 1). However, 26% of the adults were well below the metalimnion (7–9 m) and out of reach of predation during the day. One week later (3 July, day number 184), adult numbers had decreased again and few animals were left in the epilimnion during the day. Migration was at its maximum (Figure 2) and during the subsequent week, the number of adults did not change (Table 1; 11 July, day number 192). Part of the adult population (21–26%) remained in the lower part of the water column.

In 1992, the start of the migration period was at the beginning of June. On the first day of the allozyme analysis (25 May, day number 146), migration had not yet started, but DVM was in full swing during the second sampling period 16 days later (10 June, day number 162; Figure 3). Of the six *Pgi-Pgm* genotypes that were distinguished, two were dominant (MF-SF and MM-MF). We will focus our attention on these two genotypes. Before the migration period started, the genotypic depth distributions were not significantly different between noon and midnight ($R \times C$ -test, $G = 9.13$; $df=9$; $P = 0.43$; Figure 4). On 10 June, no analysis could be made for the uppermost 2.5 m during daytime, because no *Daphnia* were found. The MF-SF genotype had by far become the most dominant

genotype. The overall abundance of genotype MF-SF changed from 33% to 79% in two weeks. During the night, the MF-SF genotype had a significantly deeper distribution than the MM-MF genotype ($R \times C$ -test, $G=17.46$; $df=4$; $P<0.002$); the distributions were not different during the day.

In 1992, the *Daphnia* population density decreased for three weeks preceding day number 146 and adult numbers were very low on this date, just before the start of the migration period. Population size, however, was certainly underestimated on this date because a heavy *Dinobryon* bloom clogged the sieving surfaces of the torpedo nets. One week later (daynumber 153, 1 June) much higher numbers were found (Table 1). Despite the problematic estimate from the previous week, we conclude that the population had probably increased in size. This increase continued for an additional two weeks. On day number 153 (1 June), part of the population was migrating. Nine days later (day number 162, 10 June) nearly all adults had disappeared from the upper water column and 84% of the adults performed a diel vertical migration.

Discussion

In this study, we analysed the vertical distribution and genotype compositions in *D. galeata* $\times$ *hyalina* during the first weeks of a seasonal period of DVM. Monitoring of the population during the start of a seasonal period of migration is crucial for detecting the impact of predation by 0+ perch on the genetic structure of the

Table 1. Adult numbers in upper (U 0 to 7.5 m) and lower (L 7.5 to 16.25 (1991) or 21.25 (1992) m.) part of the water column and the total number (T) of adults in 1991 and 1992. When the number of adults in daytime samples was considerable smaller than that of night samples, it is presumed that this is because part of the animals reside lower than the deepest sampling depth during the day. The corrected number for the lower part of the water column and the corrected total are given between brackets. The percentage of adults that is supposed to be stationary in the upper and lower part, as well as the percentage of migrating animals are mentioned in the third column. * Numbers on day 146, 1992 are underestimated, see text

Day number	Number of adults		Type of behaviour	
	Daytime	Nighttime		
163, 1991	U: 50001	U: 24564		
	L: 20634	L: 28305		
	T: 70635	T: 52869		
177, 1991	U: 10483	U: 14536	53%	upper
	L: 13768	L: 4979	26%	lower
	T: 24251	T: 19515	21%	DVM
184, 1991	U: 105	U: 7093	1%	upper
	L: 6380 (9540)	L: 2552	26%	lower
	T: [9645]	T: 9645	73%	DVM
192, 1991	U: 17	U: 7792	0.2%	upper
	L: 2464 (9837)	L: 2062	21%	lower
	T: [9854]	T: 9854	78.8%	DVM
139, 1992	U: 38393	U: 39390		
	L: 9180	L: 9632		
	T: 47573	T: 49022		
146, 1992	U: 5479	U: 932		
	L: 2154	L: 4000		
	T: 7633*	T: 8932*		
153, 1992	U: 4566	U: 25786	6%	upper
	L: 48336 (68222)	L: 47002	65%	lower
	T: [72788]	T: 72788	29%	DVM
162, 1992	U: 366	U: 118424	1%	upper
	L: 118349 (139846)	L: 21788	15%	lower
	T: [140212]	T: 140212	84%	DVM

Daphnia population in Lake Maarsseveen. In order to detect selective predation in the field, a prey population must consist of different genotypes, that exhibit heritable behavioural differences. In Lake Maarsseveen, different genotypes were present in the *Daphnia* population in 1991 (Spaak & Hoekstra, 1993) and 1992 (this study). Furthermore, life table studies on Maarsseveen clones (Reede, 1995) have shown that genetic variation in life-history traits is available in this population.

Before the annual period of DVM started, daytime and night-time vertical distributions of the adults were the same in both years (Figure 2A and Figure 3A). This also holds for the vertical distribution of the six genotypes that could be differentiated, by allozyme

analysis in 1992 (Figure 4). As soon as 0+ perch attain a length of about 15 mm (Flik et al., 1997), or the total biomass of these fish surpasses a certain value (Ringelberg et al., 1997) (both variables are coupled), the number of *Daphnia* individuals remaining in the upper part of the water column during the day, starts to decrease (Table 1). This decrease has a two-fold origin. Firstly, *Daphnia* are eaten by 0+ perch that forage at high light intensities present in the upper part of the water column in daytime. Secondly, the *Daphnia* start to migrate. The latter is deduced from the fact that density shifts occur at sunrise and sunset. Since some adult *Daphnia* migrate and some do not migrate on a particular day, behavioural variability exists. The

Figure 3. The relative vertical daytime (open bars) and night-time (black bars) distributions of *D. galeata* $\times$ *hyalina* in Lake Maarsseveen on two dates in 1992. On both dates allozyme analyses were performed.

crucial point is, however, whether the migrating and non-migrating groups consist of different genotypes. Recently, De Meester et al. (1995) showed experimentally that genotypic variation exists for daytime vertical distribution of *D. galeata* $\times$ *hyalina* hybrids. In field studies, clonal variation for DVM behaviour in *Daphnia* has been shown (Weider, 1984; Müller & Seitz, 1993; King & Miracle, 1995). In 1992, during the period the epilimnion became devoid of adult *Daphnia*, the genotypic composition changed substantially: relative numbers of the MF-SF genotype increased while those of the MM-MF genotype decreased.

One might argue that this genotypic shift reflects differential behaviour by different genotypes. The decrease in the abundance of the MM-MF genotype would be explained by differential predation by perch (if this genotype migrates less) while the MF-SF genotype, which supposedly migrated to a greater extent, would have been less vulnerable to predation. If this interpretation of the data is correct, then a different probability of predation mortality caused a shift in the abundance of prey genotypes. However, alternative explanations are possible. For example, vertical migration (to the same extent by both genotypes) is accompanied by changes in environmental conditions such as food availability, temperature, light regime, etc. The new set of conditions may have promoted the relative competitive ability of the MF-SF geno-

type. The existence of interclonal differences in life histories (Reede & Ringelberg, 1995) within the *D. galeata* $\times$ *hyalina* population of Lake Maarsseveen may support this hypothesis. Under this scenario too, the presence of predators is the driving force behind the shift in clonal composition. The impact of fish is, however, indirect (a shift in clonal superiority associated with a shift in depth selection behaviour) rather than direct (genotype-dependent fish predation). The time needed for differential competition to become effective is, however, longer than for genotype-dependent predation. Whether the two weeks between our allozyme analyses suffice to bring about the large shift in genotype composition, is thus questionable. Also, these shifts as observed in the field can never be conclusive evidence for genotype-specific selective predation. Proof might be obtained by comparing the genotype composition of *Daphnia* in the stomachs of fish with that in the lake, similar to what Stich & Lampert (1981) did for the case of differential migration of two species. In their study, Stich & Lampert (1981) found more non-migrating *D. galeata* than migrating *D. hyalina* in fish stomachs compared to the relative abundance of these two species in Lake Constance.

In 1991, the density of the *Daphnia* population decreased during the first weeks of the migration period, while in 1992, the population increased (Table 1). This illustrates a point raised in the introduction:

Figure 4. Relative abundance of the two most abundant *Pgi-Pgm* genotypes just before and after the beginning of the seasonal period of DVM in 1992 by *D. galeata* $\times$ *hyalina* in Lake Maarsseveen. All other genotypes (MMSF, MFMF, MMFF, MMMM) are lumped together. Numbers above the bars indicate sample sizes.

the change in population size, accompanying DVM, may differ from year-to-year, depending on progeny-determining factors and on the genotypic composition of the population. Diel vertical migration decreases the probability of being eaten, but the animals are still prone to predation when they arrive in the predation zone after sunset, or when they remain too

long in the epilimnion at dawn. Year-to-year differences in phototactic behaviour exist (Ringelberg & Flik, 1994), and an increase in the amplitude of DVM was observed from 1989 to 1991 (Ringelberg & Flik, 1994). These differences may be genotype-specific and must be examined in future research.

Although genotype-specific predation was not conclusively shown to be operating in our study, our data are suggestive, and it may be (indirectly) responsible for the increased amplitude of migration during the first weeks of the migration period. An alternative hypothesis to explain the rapid shift in migration amplitude at the start of the migration period was also been proposed, i.e. that of an increased phenotypic induction caused by increasing fish kairomone concentrations (Ringelberg et al., 1997). During the first weeks of the migration period, the biomass of the 0+ perch gradually increases due to individual growth. Loose (1993) observed that the day-depth of an experimental *D. galeata* × *hyalina* population increased with increasing kairomone concentration as determined by the number of fish used to condition the medium. In Lake Maarsseveen, it is of course conceivable that both genotypic selection and phenotypic induction operate simultaneously.

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