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Incidence of diapause varies among populations of *Daphnia pulicaria*

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Abstract Dormancy is a common way in which organisms survive environmental conditions that would be lethal to the active individual. However, while dormant, individuals forgo reproduction. Hence theory suggests an optimal time in which to enter dormancy, depending on risks associated with both remaining active and entering dormancy. When these relative risks differ among habitats, dormancy strategies are predicted to vary as well. For freshwater zooplankton, it has been suggested that sensitivity to the cues that initiate dormancy should be selected against when females have the opportunity to remain in the water column year round. We tested this prediction with 12 populations of lake-dwelling *Daphnia pulicaria* (Crustacea: Cladocera). Differences among lakes in basin morphometry, predators and resources create a gradient of risk for *Daphnia* in the water column. Some populations persist in high numbers year round while others are abundant only in spring. We used this difference in persistence ability as an estimate of risk in the water-column. For 3 years of field sampling we found consistent differences among the lake populations in the incidence of dormancy. In some populations, only a small fraction of females switched to producing dormant eggs each year whereas in others the majority of eggs produced in the late spring were dormant. In general, populations that experienced predictably low abundances in the active form exhibited higher incidence of dormancy than did populations that persisted in high abundance year round, but there were exceptions. Our results confirm that the

incidence of dormancy varies considerably among populations in a fashion consistent with general theory, but suggest that persistence in the water column is not the sole predictor of the diapause strategy found in any particular lake.

Keywords Diapause · Dormancy · Life-history · Resting eggs · Zooplankton

Introduction

Most organisms inhabit environments in which the probability of survival and reproduction varies both temporally and spatially. This variability has shaped the evolution of a wide array of risk-spreading traits including iteroparity, dispersal and dormancy (reviews by Stearns 1992; Hopper 1999; Roff 2002). For short-lived organisms such as annual plants and insects, dormancy is often incorporated into the life cycle as a way to persist during conditions that the active individual would not survive (Danks 1987; Leck et al. 1989; Cáceres 1997). However, entering dormancy is not without costs. While dormant, the individual may miss opportunities to reproduce, consume needed energy reserves, or fall victim to predators that specialize on the dormant stage (Garwood 1989; Ellner 1997; Soula and Menu 2003). A substantial body of theory has considered optimal dormancy strategies with annual plants (Cohen 1966; Venable and Lawlor 1980; Ellner 1985a, b; Rees 1994) and insects (Cohen 1970; Taylor 1980; Tuljapurkar and Istock 1993; Menu et al. 2000) serving as the primary model systems. In general, the relative incidence of diapause is predicted to depend at least in part on the frequency and magnitude of fitness declines in the active stage (Cohen 1970; Taylor 1980). This prediction has been observed in several insect species that show variation in diapause expression along a cline of season length (Dingle 1981; Istock 1981; Mousseau and Roff 1989).

In aquatic habitats, decades of limnological research has demonstrated that zooplankton in different lakes experi-

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Table 1 Among lake differences in morphometry and productivity influence the annual population dynamics of *D. pulicaria*. Values for total phosphorus (TP) are from spring turnover averaged for 2–5 years (Tessier and Woodruff 2002; Cáceres and Tessier 2004),

annual minimum density (± 1 SE) and CV (± 1 SE) are calculated from Fig. 1, average values for ephippial and male production are calculated from the data presented in Figs. 2 and 3

Name	Surface area (ha)	Max Depth (m)	Spring TP ($\mu\text{g l}^{-1}$)	Minimum density (no./m ²)	CV	Ephippia	Males
Cloverdale Lake	44.1	15	15	27 \pm 0	36 \pm 4	0.17 \pm 0.12	0.19 \pm 0.13
Baker Lake	23.8	9	25	45 \pm 18	38 \pm 0.3	0.003 \pm 0.002	0.007 \pm 0.006
Little Long Lake	67.6	9.5	8	45 \pm 24	35 \pm 6	0.15 \pm 0.01	0.15 \pm 0.02
Warner Lake	28.4	14	10	1,380 \pm 1,020	21 \pm 3	0.02 \pm 0.005	0.009 \pm 0.003
Pine Lake	27.6	10	5	1,450 \pm 480	15 \pm 3	0.003 \pm 0.002	0.008 \pm 0.003
Big Long Lake	121.7	15	13	1,480 \pm 560	17 \pm 2	0.02 \pm 0.02	0.02 \pm 0.01
Bassett Lake	18.8	11.5	15	1,540 \pm 860	17 \pm 3	0.03 \pm 0.01	0.02 \pm 0.009
Bristol Lake	62.8	15	11	1,540 \pm 860	18 \pm 5	0.05 \pm 0.03	0.02 \pm 0.004
Whitford Lake	10.0	8.5	9	1,770 \pm 840	17 \pm 6	0.03 \pm 0.004	0.02 \pm 0.006
Lawrence Lake	5.0	11.5	9	3,900 \pm 1,990	25 \pm 13	0.01 \pm 0.008	0.01 \pm 0.006
Three Lakes 2	21.2	10	12	5,140 \pm 2,290	9 \pm 1	0.01 \pm 0.005	0.09 \pm 0.04
Little Mill Lake	5.0	10	23	5,340 \pm 1,370	8 \pm 1	0.02 \pm 0.009	0.009 \pm 0.002

ence annual and inter-annual variability in the suitability of their habitat for survival and reproduction (Krantz et al. 1987; Kalff 2002). Because many species of zooplankton also produce a dormant stage (Hairston 1996; Cáceres 1997), lakes provide a parallel system in which to test general theory of diapause investment (Ellner et al. 1998, 1999). Even within the same geographic region, there can be considerable among-lake variation in the ability of the active form to persist seasonally. In one lake, a particular species may be abundant in the water column for only a few months each year whereas in another lake, that same species may be found in the water column year round. It commonly has been assumed that individuals from these different habitats should differ in their diapause strategies as well (Hutchinson 1967), yet few studies have compared use of dormancy among zooplankton populations.

Populations of the same *Daphnia* (Crustacea: Cladocera) species in particular exhibit considerable variation among lakes in many life-history traits (Lynch et al. 1999) but scant attention has been paid to variation in use of dormancy. Temporary ponds obviously require diapause for persistence, but in lakes, whether or not a particular population of *Daphnia* remains active year-round varies considerably. This variation in persistence ability raises the question of optimal investments in dormancy. If conditions never deteriorate in the water-column, why make dormant eggs? Lynch (1983) argued that when a *Daphnia* female allocates reproductive effort to the production of diapausing eggs, she does so at the expense of immediately-hatching parthenogenetic eggs. Because the time and energetic costs of making diapausing eggs are much greater, this trade-off is not advantageous in permanent lakes. However, *Daphnia* in permanent lakes do face ecological risks to remaining in the water-column year round (i.e., predation, competition, parasitism; see Kerfoot and Sih 1987; Sommer 1989; Ebert et al. 1997; Brendonck et al. 1998; for reviews). When these risks are realized, the abundance of a clone can be reduced by many orders of

magnitude within a few weeks (Lampert and Sommer 1997).

In this study, we chose 12 populations of *D. pulicaria* with which to investigate the prediction that the incidence of dormancy would be reduced in populations that experience only weak seasonal reductions in abundance and consequently, have a high probability of survival in the water column. We extend our studies over 3 years to capture both annual and interannual variation in abundance and production of diapausing eggs. Our results confirm that incidence of diapause varies considerably and consistently among populations and is often much higher in populations that experience high seasonal variation in abundance. However, exceptions to this generality were evident and suggest that the ability to persist in the water column is not the sole factor shaping diapause strategies in *Daphnia*.

Materials and methods

Study systems

We sampled 12 lake populations of *D. pulicaria* in southern Michigan (Barry and Kalamazoo counties). In all these lakes, *D. pulicaria* reproduce by parthenogenesis (i.e., females producing genetically identical daughters) for most of the year. During a brief period in spring, some females produce sons parthenogenetically, while other females produce haploid eggs that require fertilization. When a female produces haploid eggs, her carapace over the brood chamber is modified into a specialized structure known as an ephippium. After the female is inseminated and molts, one or two diapausing eggs are released into the ephippium. Any individual female may switch between production of parthenogenetic daughters and sons to diapausing eggs (and vice versa) in sequential molts (Kleiven et al. 1992), but these two types of eggs cannot be produced simultaneously. However, since multiple

copies of every genotype (clone) are simultaneously present in the water-column, a particular genotype may pursue a mixed strategy of immediately hatching parthenogenetic eggs and diapausing eggs.

We chose lakes that vary in surface area, maximum depth and trophic status so as to capture a gradient in seasonal abundance of *D. pulicaria* (Table 1). All lakes except Little Long stratify thermally during the summer. Thermal stratification creates a deep-water refuge in which the large-bodied *D. pulicaria* can avoid competition and predation (Wright and Shapiro 1990; Tessier and Welser 1991; Leibold 1991; Hu and Tessier 1995; Leibold and Tessier 1997; Dodson 2005). In these lakes, the active form is able to persist year round. In some lakes this refuge is unavailable, either because the lake does not stratify thermally (Little Long Lake), or because the deep-water becomes inhospitable by midsummer due to anoxia (Baker Lake and Cloverdale Lake). Without a refuge, fish predation and competition from summer species often result in severe population declines in large-bodied daphniids such as *D. pulicaria* (Table 1; see also Lynch 1978; Threlkeld 1979; Mills et al. 1987; DeMott 1989; Gliwicz and Pijanowska 1989; Geedey et al. 1996; Cáceres 1998; Tessier and Woodruff 2002; Steiner 2003). Hence, variation in basin morphometry, productivity and lake-specific interspecific interactions creates a natural gradient of persistence ability for the *D. pulicaria* in the water column (Fig. 1).

Field sampling

From 1999 to 2001, we sampled lakes using an 80- μm mesh Wisconsin-style bucket net to quantify total daphniid abundance and the annual timing and magnitude of diapausing egg and male production. We sampled in early April after ice-out, weekly from May until July, once in August and two or three times from September to November. Winter samples were also collected through the ice in early 2000 and 2001. Cloverdale Lake and Big Long Lake were not sampled in 1999. On each sampling date, we collected three vertical hauls from the deepest section of each lake. The three samples were combined, preserved in 70% EtOH and sub-sampled for population abundance estimates. To explore persistence ability in the water-column (our metric of risk), for each year we examined the spring maximum density, the fall minimum density and the annual coefficient of variation (determined from monthly average population densities). During late summer, we took temperature and oxygen readings at meter intervals with a YSI oxygen probe to confirm the absence of any measurable refuge in Little Long, Baker, and Cloverdale. Temperature and oxygen profiles in the other lakes confirmed the existence of an oxygenated deep-water refuge.

Each sample was also searched exhaustively for females carrying diapausing (ephippial) eggs and for males. We used both the production of ephippia and males as metrics of diapause among populations. First, we calculated the

fraction of clutches in each sample that were ephippial relative to the total number of clutches (ephippial and immediately hatching eggs). Estimates of annual ephippial production in each population were then approximated for each year by calculating the area under the plot of the fraction of clutches that were ephippial on each sampling date (see results). Because ephippial production in these populations was restricted to spring, the estimates of total ephippial production were divided by 91 days (number of days in April, May and June) to scale these numbers to a per day basis. We chose to consider the entire spring period (91 days) to capture ephippial production in all populations as well as the peak of male production. Incidence of male production was calculated similarly as the area under the plot of the percentage of the population composed of males on each sampling date during April, May and June, and dividing that number by 91 days.

Statistical analyses

We used MANOVA to compare the lake populations using the three descriptors of seasonal phenology (spring maximum population density, fall minimum density and the coefficient of variation across months). Results were interpreted subsequently with univariate ANOVAs for the three variables. Prior to analysis, the water column densities were $\log(x+1)$ transformed to normalize the residuals. The relationship between minimum population size and coefficient of variation was estimated by Pearson correlation. To further explore the life-history variation among the populations, we compared the annual timing of the onset of diapausing egg and male production. For each population in each year, we found the Julian dates of the first day that diapausing eggs and males were found in a sample and then used MANOVA to compare the timing of the onset of diapause. An additional MANOVA was used to investigate the relative magnitude of production of both diapausing eggs and males (relative to parthenogenetic daughters). The relationship between annual male production and annual ephippial production was investigated with a Pearson correlation.

Our primary hypothesis was that there would be a decreased incidence of diapause in populations that could remain active in the water-column year round. We had designed our sampling so as to analyze this relationship by regression, but the data did not conform to the assumptions of parametric statistics. Instead of falling along a continuum of minimum population sizes, we found that populations either had a minimum density of $<200 \text{ m}^{-2}$ or $>500 \text{ m}^{-2}$ (most values $>1,000 \text{ m}^{-2}$) and no transformation could equalize the variance in diapause incidence between the two groups. Hence, we divided our populations into a high risk group (average minimum density $<50 \text{ m}^{-2}$) or a low risk group (average minimum density $>1,000 \text{ m}^{-2}$) and then used a randomization test available in BLOSSOM (Cade and Richards 2001) to determine if the mean incidence of diapause varied between these two groups. We used three different metrics for our mean incidence of

diapause: production of ephippia, male production, and the product of ephippial and male production. All statistical analyses except the randomization test were performed in SYSTAT 10.0 (Wilkinson 2000).

Results

The populations of *D. pulicaria* differed in their seasonal dynamics (Wilks $\Lambda=0.11$, $df=33, 59$, $P=0.01$; Fig. 1). In all lakes, *D. pulicaria* reached annual maximum abundance in spring and annual minimum abundance in autumn. We found no difference in the maximum densities (number m^{-2}) attained by each population ($F_{11,22}=1.00$, $P=0.48$), despite among-lake differences in depth, surface area and productivity. These differences, however, contributed to variation in persistence ability throughout the year. While some populations remained abundant all year, other populations became rare in the water-column by late summer. These differences in seasonal dynamics were reflected in significant differences among populations in minimum population size ($F_{11,22}=3.36$, $P=0.006$) and annual coefficient of variation ($F_{11,22}=3.57$, $P=0.005$; Table 1). These metrics were significantly correlated ($r=-0.95$, $n=34$, $P<0.0001$); since the maximum abundance did not vary among populations, populations that had lower minima were also more variable.

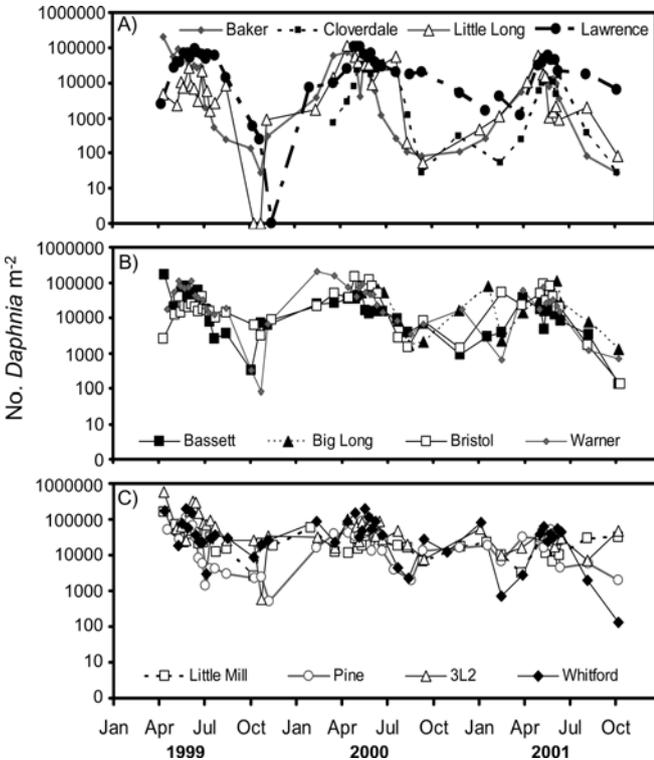


Fig. 1a-c Water-column abundances for 12 populations of *D. pulicaria*. For clarity, we plotted the seasonal dynamics of these populations in three panels (a-c). The four populations plotted in a occasionally (Lawrence Lake) or regularly (Baker Lake, Cloverdale Lake, Little Long Lake) experience drastic declines in water column abundances during summer. The tick marks on the x-axis represent the beginning of the month

We found no difference among populations in the timing of the annual onset of diapausing egg or male production (Wilks $\Lambda=0.12$, $df=22, 40$, $P=0.08$; Figs. 2, 3). Most ephippia were produced during May, and on average, males were found in the water column 2 weeks prior to the first ephippium (mean Julian date 113.6 ± 3.8 for onset of male production vs 129.2 ± 2.2 for onset of ephippial production). The timing of ephippial production was similar among populations, yet we found considerable differences in the relative incidence of diapause. Spring incidence of both ephippial (Fig. 2) and male production (Fig. 3) varied significantly across the lakes (Wilks $\Lambda=0.03$, $df=22, 42$, $P<0.0001$; ephippia $F_{11,22}=18.2$, $P<0.0001$; males $F_{11,22}=12.88$, $P<0.0001$). Populations that declined sharply such as Little Long and Cloverdale produced many males and ephippia whereas more persistent populations had relatively low incidence of diapause. Overall, the relative production of ephippia was correlated with the relative production of males ($r=0.78$, $n=34$, $P<0.0001$; Table 1).

Minimum abundance does not appear to be driven by incidence of diapause. Annual minimum density occurred in September and October, several generations after the production of diapausing eggs had ended (Figs. 1, 2). We found no relationship between the average water column

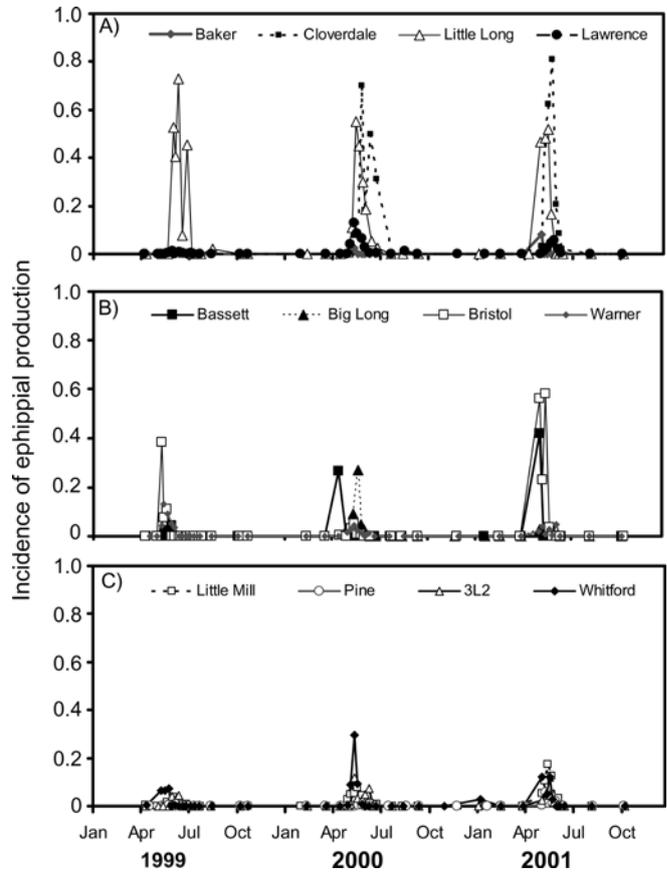


Fig. 2 Incidence of ephippial production, expressed as the proportion of clutches that were dormant on each sampling date. Cloverdale Lake and Big Long Lake were not sampled in 1999. For clarity, we plotted the 12 populations as in Fig. 1. The tick marks on the x-axis represent the beginning of the month

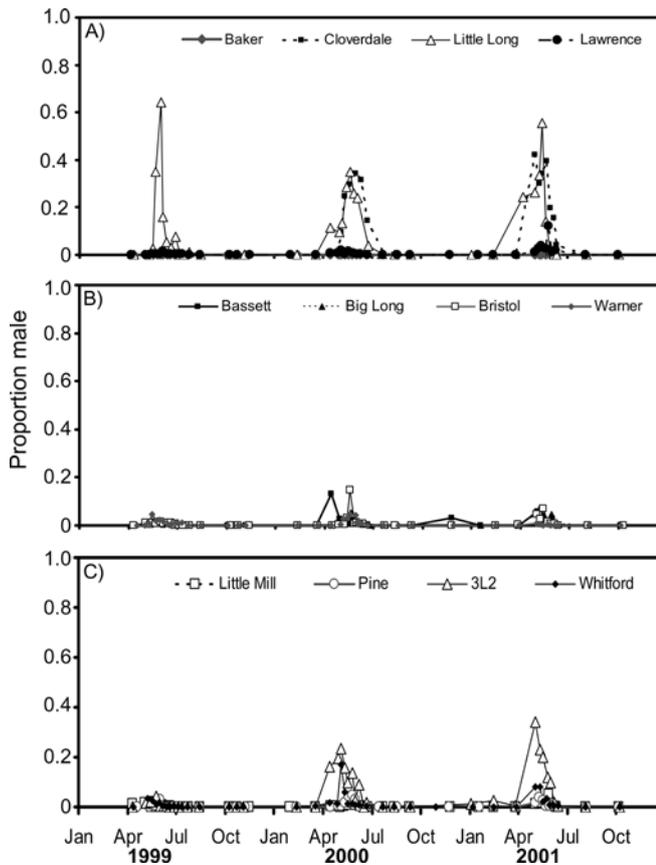


Fig. 3 Incidence of male production, expressed as the fraction of the population that was male on each sampling date. Cloverdale Lake and Big Long Lake were not sampled in 1999. For clarity, we plotted the 12 populations as in Fig. 1. The tick marks on the x-axis represent the beginning of the month

abundances in June (end of diapausing egg production) and the minimum population density ($r=0.26$, $n=34$, $P>0.1$). Most populations declined during May–June, regardless of their incidence of diapause. We compared the average number of parthenogenetic eggs per adult females between the high risk and low risk populations and found no difference in May ($t_{10}=1.18$, $P=0.27$), June ($t_{10}=0.64$, $P=0.54$) or July ($t_{10}=0.64$, $P=0.53$), suggesting that differences in population dynamics between the two groups during the summer was largely a result of variation in death rates (Edmondson 1968).

To investigate the relationship between diapause and risk in the water-column, we used a randomization test to examine potential differences between the high-risk versus low-risk groups in ephippial production alone (Standardized test statistic = -3.48 , $n=12$, $P=0.02$), male production alone (Standardized test statistic = -3.20 , $n=12$, $P=0.02$), and the product of male and ephippial production (Standardized test statistic = -4.30 , $n=12$, $P=0.01$). All combinations produced the same qualitative results, hence only the combined male and ephippial production versus the minimum population density is shown in Fig. 4. Populations that experienced a low risk in the water column never had a high incidence of diapause. However, populations that experienced a high risk in the water

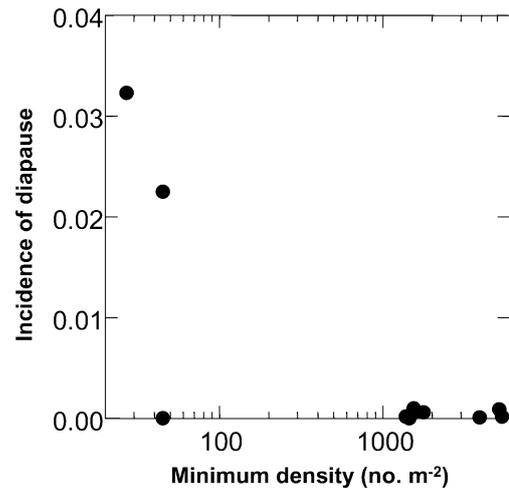


Fig. 4 Comparison of annual minimum population density in the water column and the incidence of diapause (see text for details) for *D. pulicaria*. Each point represents one population averaged over two (Big Long Lake and Cloverdale Lake) or 3 years

column may or may not have a correspondingly high incidence of diapause.

Discussion

We found large differences among *D. pulicaria* populations in water-column persistence and in relative incidence of diapause. However, the expected inverse relationship between these two metrics was only weakly supported. In accord with theoretical predictions (Lynch 1983), low incidence of diapause was characteristic of populations that persisted at high densities in the water column year round. Further, the highest incidence of diapause was observed only in those populations that inhabited lakes where abundances declined dramatically during summer. However, not all populations that faced such difficult summer situations displayed such a high incidence of diapause, suggesting that diapause was not predictable simply by seasonal variation in population size.

Males and ephippial eggs were found in all populations, including those where water column densities remained high year-round. It is clear that selection has not eliminated dormancy in populations inhabiting permanent lakes. Given that these eggs can remain viable for decades (Cáceres 1998) and accumulate in large numbers in sediment egg banks (Hairston 1996; Cáceres and Tessier 2004), the small cost incurred by producing a few diapausing eggs in place of immediately hatching eggs may be offset by a relatively large benefit obtained in years following extirpation from the water column.

The simultaneous production of both parthenogenetic and diapausing offspring has been viewed as a bet-hedging strategy in several species of insects (Walker 1980; Seger and Brockmann 1987; Dedryver et al. 2001). However, documenting that a particular genotype is bet-hedging in field populations is often complicated by the inability to track individual clones in nature (Hopper 1999). In

laboratory studies, we observed that some genotypes did employ a mixed strategy of producing both parthenogenetic and diapausing eggs, whereas other clones were gender specialists (Tessier and Cáceres 2004). More importantly, the incidence of diapause we observed by following individual clones in the laboratory mirrored the incidence of diapause we found at the population level in the field. Hence, these populations are genetically differentiated in their relative production of diapausing eggs.

Although populations characterized by low annual (and interannual) variation in abundance were never observed to have a high incidence of diapausing egg production, the opposite was not true. One population that experienced predictably high seasonal risk, (i.e., low minimum and high variance in abundance) produced few males or diapausing eggs. In theory, a female should switch to the production of diapausing offspring when the probability of survival and reproduction in the active stage falls below that of survival in the dormant stage (Cohen 1970). Currently, we cannot quantify the magnitude of the risks that diapausing eggs experience, but they are potentially substantial and are certainly variable among lakes. These risks include inbreeding depression, predation, infection, deep burial, lack of cues that terminate dormancy and difficulty reinvading the water column population (Innes 1989; De Meester 1993; Cáceres and Hairston 1998; DeMeester et al. 2002; Brendonck and DeMeester 2003; Cáceres and Tessier 2003). In short, in some lakes, the low incidence of diapause we observed may reflect the fact that the relative costs of entering dormancy outweigh potential benefits. In those cases, clones may achieve a higher fitness by remaining active in the water column, even in small numbers.

We suggest that to fully understand these patterns of dormancy variation we must focus simultaneously on risks in both the active and dormant stage (Evans and Cabin 1995). Because production of diapausing eggs requires sex, a better understanding of the links between the genetic structure of a population and the ecological features of each lake will help to resolve how selection may be shaping these diapause patterns (Rispe and Pierre 1998; Simon et al. 2002; Wilson et al. 2003). Further, because the diapausing eggs of *Daphnia* have the potential to survive for decades or centuries (Weider et al. 1997; Cáceres 1998), both short-term and long-term fitness consequences in both the active and dormant stage must be addressed. Studies addressing all of these aspects remain rare.

For both insects (Tauber et al. 1986; Hopper 1999) and annual plants (Templeton and Levin 1979; Leck et al. 1989), it is well known that dormancy influences both population cycles and community interactions. Until recently, however, the role of diapause in both short- and long-term plankton dynamics was rarely considered (Alekseev and Freyer 1996; Brendonck et al. 1998), and natural patterns of variation remain poorly described. We have demonstrated that different populations of *D. pulicaria* show considerable variation in their relative incidence of dormancy. Like some insect species that show latitudinal variation in the incidence of diapause (Dingle

1981; Istock 1981; Mousseau and Roff 1989) the variation in daphniid life-histories does seem to be explained, in part, by variation in the ecological factors experienced by the active form. However, only an understanding of the genetic structure of these populations, coupled with the particular ecological risks associated with water-column and sediment habitats will facilitate a fuller explanation of the short and long-term aspects that shape daphniid life-histories.

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