

## Interclonal differences in age-specific performance in *Daphnia magna*

Barbara PIETRZAK

Department of Hydrobiology, University of Warsaw, Banacha 2, 02-097 Warszawa, Poland  
e-mail: b.pietrzak@uw.edu.pl

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### ABSTRACT

Clonal organisms are often characterized by indeterminate growth and it is more likely in these organisms that delayed senescence evolves. *Daphnia* is characterized by both clonality and indeterminate growth, yet evidence for its senescence has been collected. In addition, differences in the dynamics of age-specific parameters were seen between environmentally developed phenotypes within a genotype as well as between genotypes, including between sister species. The aim of the present study was to test for interclonal differences within a species and to examine the course of basic life history and age-specific fitness parameters throughout life of *Daphnia magna* females originating from two different habitats, pond and lake. Clones differed in size at subsequent reproductions, but this did not result in differences in fecundity, although number of offspring in a clutch increased both with size and age of a female. There were also interclonal differences in lifespan and age-specific measures of fitness, but apart from lifespan, habitat of origin did not have significant effects on life history traits.

*Key words:* life history, indeterminate growth, fecundity, age-specific fitness, aging, habitat

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### 1. INTRODUCTION

Senescence, defined as a decline in survival probability or reproductive performance with increasing age, is an unavoidable part of life history of those organisms, for which smaller offspring can be distinguished from larger parental individuals (Partridge & Barton 1993). Even bacteria that divide asymmetrically undergo senescence (Ackermann *et al.* 2003; Stewart *et al.* 2005). Although it seems that clonal organisms may delay or even escape senescence at the level of the genetic individual, i.e., the clone as a whole (Orive 1995; Gardner & Mangel 1997), single individuals, or modules or ramets in sessile animals and plants, may still experience senescence (Martínez & Levinton 1992; Watkinson 1992; Dudycha & Tessier 1999).

Many clonal organisms are characterized by indeterminate growth (Jackson 1977; Ally *et al.* 2010), and simultaneous growth and reproduction is exhibited by organisms as diverse as perennial plants, molluscs, echinoderms and some fish. Such organisms are more likely to evolve delayed senescence (Reznick *et al.* 2002; Vaupel *et al.* 2004), as the ability to grow throughout life entails, on one hand, the continuous presence of proliferating cells and telomerase activity, thus the capacity to replace old cells. This enables the maintenance of the body in a good shape and delays the increase of intrinsic mortality risk (Kishi *et al.* 2003). On the other hand, the indeterminate growth is accompanied by the rise of reproductive potential over time, as fecundity tends to increase with body size (Blueweiss *et al.* 1978; Honěk 1993; Fleming 1996; Reznick *et al.* 2002), to eventually reach a plateau in some species. Senescence is thought to be a by-product of natural

selection, and natural selection acts most effectively early in life, when many species have greatest reproductive value. In indeterminate growers, the rising reproductive potential counteracts the decline in natural selection that accompanies aging, thus allowing selection to remain effective even in late life (Vaupel *et al.* 2004; Ally *et al.* 2010). It was even hypothesized that individuals in species that at reproductive maturity attain size much smaller than maximum size, and that gain reproductive capacity as they grow, are characterized by negative senescence (Vaupel *et al.* 2004).

The pelagic crustacean *Daphnia* exhibits both, clonality and indeterminate growth. *Daphnia* are cyclical parthenogens, switching to sexual reproduction when conditions deteriorate (Zaffagnini 1987; Pijanowska & Stolpe 1996; Ślusarczyk 2004). Genetic evidence reveals also lineages of *Daphnia pulicaria* that reproduce by obligate parthenogenesis (Hebert *et al.* 1988; Ślusarczyk 2009), and some of these clonal lineages seem indeed long-lived and are estimated to be thousands years old (Lynch *et al.* 2008).

*Daphnia*, like all branchiopods and some other crustaceans, has indeterminate growth (Hartnoll 2001). The female may more than double in size after the age of first reproduction, increasing in length with each moult, and the number of produced eggs in a parthenogenetic brood (clutch) is strongly correlated with body size, if food is abundant (Taylor 1985). Yet, despite indeterminate growth, *Daphnia* has been shown to exhibit reproductive and tissular decline in its late life, starting with depletion of energy reserves in the fat body and continuing with damages of the digestive tract (Schulze-Röbbecke 1951, after: Vogt 2010). Several studies showed also survival curves characteristic for an

aging population (Dunham 1938; Vijverberg 1976; Lynch & Ennis 1983; Dudycha & Tessier 1999; Pietrzak *et al.* 2010a). Dudycha & Tessier (1999) showed evidence of senescence occurring in all populations of the species complex *Daphnia pulicaria* they studied: increasing mortality rates and declining fecundity rates over late life, together with the degradation of age-specific fitness in later life, estimated by summary measures combining survival and fecundity. Moreover, comparison of these closely related species revealed that individuals from populations experiencing in nature higher extrinsic mortality age faster than those experiencing lower mortality (Dudycha & Tessier 1999; Dudycha 2003).

It is predicted by the life history theory that genetic variation of senescence will be related to ecological variation of mortality risk (Williams 1957). Many ecological differences that influence the experienced by *Daphnia* mortality risk, associated with predation, resource availability, and abiotic factors, coincide with the habitat difference between lakes and temporary ponds (Wellborn *et al.* 1996; Dudycha 2001). Lakes present permanent, more stable environment (Geedey *et al.* 1996), with the expected death rates being lower than in temporary ponds, where ecological conditions change rapidly (Dudycha 2001). Interpopulation differences in experienced predation pressure or in habitat permanence were also proposed by Reznick (1993) to be followed by selection for alternate life history traits in crustaceans, including differences in the rate of aging.

The aim of the present study was to test for interclonal differences within a species and to examine the course of basic life history and age-specific fitness parameters throughout life of *Daphnia magna* females originating from two different habitats, a lake and a pond.

## 2. METHODS

Clones of *Daphnia magna* used in the study came from the clone library of the Department of Hydrobiology University of Warsaw. Of the four clones used, two (B1 and B2) originated from Grosser Binnensee, a hypertrophic coastal lake in northern Germany, and two others (M1 and M2) originated from an artificial temporary city pond Pole Mokotowskie in Warsaw, Poland. The clones were hatched from ephippia within a year prior to the study and were maintained in laboratory batch cultures at room temperature (19–22 °C) and fed with the green alga *Scenedesmus obliquus*. I selected a single female from each clonal culture to establish the experimental clonal lineage. To avoid maternal effect, I precultured clonal lineages for at least 3 generations prior to experiment (I took second-clutch offspring for further culture each time) under standard conditions, i.e., in the temperature-controlled water bath (20 °C ± 0.5 °C), summer photoperiod (16L:8D), fed daily with *S. obliquus* (1 mg C L<sup>-1</sup>), at the density of 20 ind. L<sup>-1</sup>. The culture medium was changed every two days.

For each clone, I started the experiment with 40 second-clutch neonates born within 12 h. The animals were kept individually in 100 mL glass vessels (20 °C ± 0.5 °C; 16L:8D) until their natural deaths. I fed them daily *S. obliquus* at concentration corresponding to 1 mg C L<sup>-1</sup> and changed into fresh medium every two days (conditioned and filtered lake water; food and medium were prepared as in Pietrzak *et al.* 2010b). I recorded deaths and removed and counted offspring of each experimental female daily. Until tenth reproduction, 10 females of each clone had all their offspring photographed under a dissecting microscope, and 10 of the 40 females of each B1, M1 and M2 clone, selected randomly at the start of experiment, were photographed at each reproduction. Photographing continued until five females of each clone remained alive. I measured the length of photographed animals from the top of the eye to the base of the spine with MultiScan software (CSS, Warsaw, Poland). Due to the presence of males among clone B2 neonates, this cohort was reduced to 33 females and only sporadic length measurements were taken in order to keep the cohort of 30 not-handled females.

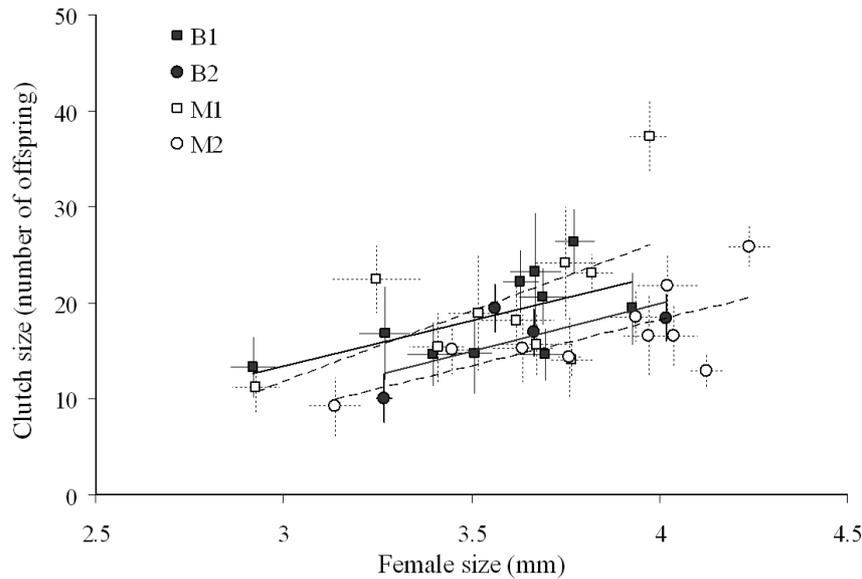
To check whether the not-handled and handled females can be pooled, I tested for the effects of handling. In none of the clones handling had any effect on lifespan (Kruskal-Wallis non-parametric ANOVA, parametric ANOVA applied to ranks statistics ranging from:  $F = 0.58$ ,  $df = 1$ ,  $p = 0.4492$  in B1, to:  $F = 0.02$ ,  $df = 1$ ,  $p = 0.8784$  in B2), nor on number of offspring in a clutch (ANOVA, ranging from:  $F = 3.29$ ,  $df = 1$ ,  $p = 0.0711$  in M2, where mean number of offspring in a clutch for handled females was insignificantly higher, to:  $F = 0.03$ ,  $df = 1$ ,  $p = 0.8680$  in B2). Thus the two groups of females were pooled and analyzed together.

To test for age and clone effects on number of offspring in a clutch, female size, and offspring size, I performed ANOVA of repeated measure design and linear regression when appropriate. To test for the effect of clone on survival, the Wilcoxon (Gehan) test was performed on survival data and for further interclonal comparisons. To test for the effect of habitat type, Kruskal-Wallis non-parametric ANOVA was performed. Daily mortality and fecundity data were used to calculate life-history parameters and summary fitness statistics.

From the data obtained, the age-specific cumulative survivorship,  $l_x$ , and age-specific *per capita* fecundity,  $m_x$ , were used to calculate individual reproductive success ( $R_0 = \sum l_x m_x$ ), and the rate of population increase,  $r$ , which was calculated by iterative approximation of Lotka's equation ( $1 = \sum e^{-rx} l_x m_x$ ). Generation time was then estimated as  $T = \ln R_0 / r$  (Slobodkin 1961). The mean expectation of life at birth,  $e_0$ , another parameter used for interclonal comparisons (de Bernardi & Manca 1982), was calculated as:  $e_0 = \sum p_x$ , where  $p_x$  is the probability of surviving to the next age class.

**Tab. 1.** Summary of life-history data for four *Daphnia magna* clones (B1, B2, M1 and M2). AFR: age at first reproduction (mean ± SD); SFR: size at first reproduction (mean ± SD); Offspring: total number of offspring per female (mean ± SD);  $R_0$ : individual reproductive success;  $r$ : estimated rate of population increase; T: generation time;  $e_0$ : mean expectation of life at birth; Lifespan: median lifespan.

	B1	B2	M1	M2
AFR (days)	10 ± 0.0	10 ± 0.2	10 ± 0.2	10 ± 0.0
SFR (mm)	2.87 ± 0.06	3.20 ± 0.08	2.90 ± 0.08	3.07 ± 0.07
Offspring	109.0 ± 44.7	143.8 ± 23.0	108.5 ± 44.4	98.0 ± 90.2
$R_0$	120.1	216.2	132.7	98.0
$r$	0.307	0.299	0.302	0.284
T (days)	15.6	18.0	16.2	16.1
$e_0$ (days)	52.1	90.0	62.9	66.4
Lifespan (days)	30.5	50	27	20.5



**Fig. 1.** Mean number of neonates in a clutch plotted against the mean length of the female of the four clones (black symbols: Binnensee clones; open symbols: Pole Mokotowskie pond clones). Regression lines (solid lines: Binnensee clones, dashed lines: Pole Mokotowskie clones).

One of the most widely used summary measures of age-specific fitness is reproductive value,  $v_x$ , which specifies the contribution of each age class to  $r$ , the rate of population increase, and which has been suggested as a useful measure for senescence studies (Partridge & Barton 1996). I calculated reproductive value according to the formula proposed by Goodman (1982):

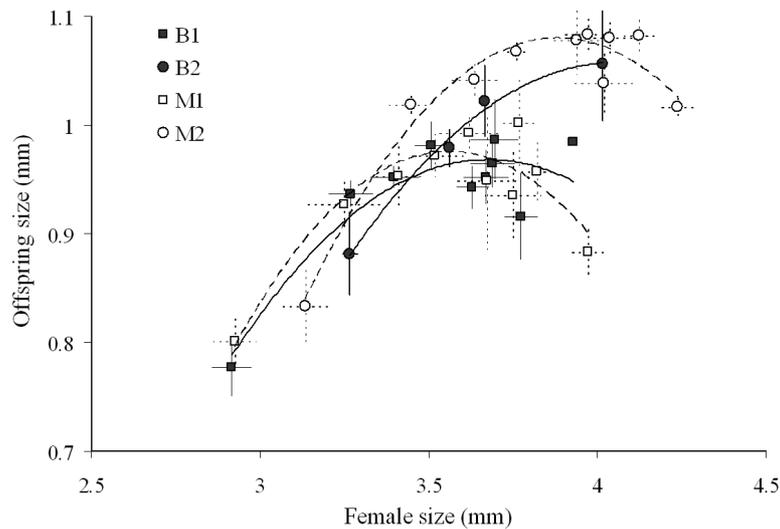
$$v_x = \frac{e^{r(x-1)}}{l_x} \sum_{j=x}^{\infty} e^{-rx} l_j m_j \quad (1)$$

As an alternative measure of age-specific fitness, I calculated intrinsic value,  $i_x$ , which is an unweighted contribution of each age class to the total lifetime reproduction and simplifies interclonal comparisons (Dudycha & Tessier 1999):

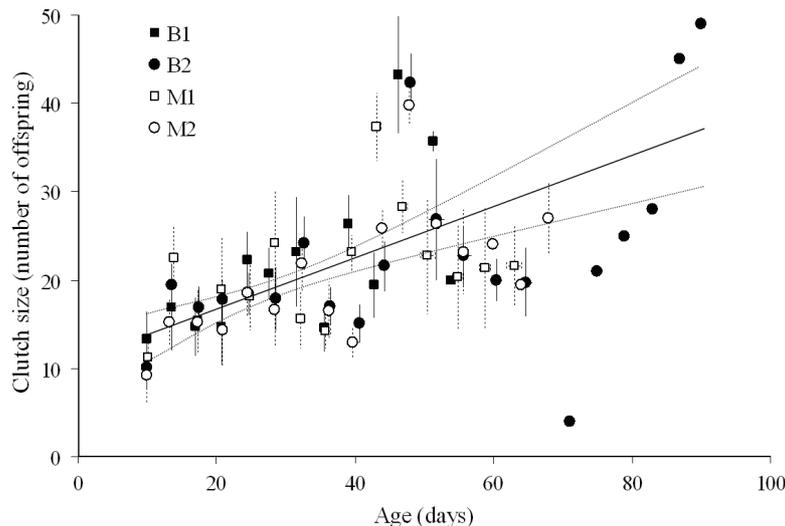
$$i_x = \frac{\sum_{j=x}^{\infty} l_j m_j}{\sum_{j=0}^{\infty} l_j m_j} \quad (2)$$

### 3. RESULTS

The *Daphnia magna* clones did not differ in the age at first reproduction (10 days), but differed in the number of offspring born at first reproduction (ANOVA:  $F = 15.07$ ,  $df = 3$ ,  $p < 10^{-4}$ ), mean clutch size ( $\pm$ SD) ranging from  $9.2 \pm 3.1$  neonates in M2 to  $13.3 \pm 3.1$  neonates in B1 (Tab. 1). Clones B1 and M1 started reproducing at smaller size than clones B2 and M2 (ANOVA:  $F = 43$ ,  $df = 3$ ,  $p < 10^{-4}$ ; Tukey *post-hoc* at  $\alpha = 0.001$ ; Fig. 1) and these differences in size were maintained in the measured clones at subsequent reproductions (repeated measures ANOVA: effect of clone:  $F = 33.97$ ,  $df = 2$ ,  $p < 10^{-4}$ ; clone  $\times$  reproduction interaction:  $F = 1.29$ ,  $df = 18$ ,  $p = 0.2078$ ). After the release of the first offspring, the length of the females increased linearly with age similarly in the three clones analyzed for body length (regression:  $F = 232.26$ ,  $p < 10^{-4}$ ; com-



**Fig. 2.** Mean length of a neonate in a clutch plotted against the mean length of the female of *D. magna* of the four clones (black symbols: Binnensee clones; open symbols: Pole Mokotowskie pond clones). Polynomial regression lines (solid lines: Binnensee clones, dashed lines: Pole Mokotowskie clones).



**Fig. 3.** Mean number of neonates in a clutch plotted against the mean age at subsequent reproduction of *D. magna* of the four clones (black symbols: Binnensee clones; open symbols: Pole Mokotowskie pond clones). Regression line and 95% confidence intervals.

parison of slopes:  $F = 1.70$ ,  $p = 0.1860$ ). As some clones reproduced at smaller sizes, the increase of the clutch size with the length of the female (regression:  $F = 27.85$ ,  $p < 10^{-4}$ ; comparison of elevations:  $F = 26.45$ ,  $p < 10^{-4}$ ; Fig. 1) did not result in differences in fecundity between clones (see below).

Offspring size could be better explained by female size than by number of offspring in a clutch, and the clones that reproduced at smaller size, B1 and M1, produced smaller offspring (repeated measures ANOVA: effect of clone:  $F = 3.87$ ,  $df = 2$ ,  $p = 0.05$ ). The mean size of offspring (neonate) increased with female size when females were small, but biggest offspring were born of medium sized females in the studied clones (degree 2 polynomial regressions for clones:  $R^2$

$> 0.8224$ ,  $F > 16.21$ ,  $p < 0.0025$ ; Fig. 2). However, when the first clutch, which was substantially different, was excluded from the analysis, the mean offspring size negatively correlated with the mean clutch size (Pearson's correlation:  $r = -0.5381$ ,  $p = 0.0012$ ).

Fecundity expressed as the number of offspring released at subsequent reproductive periods increased with age throughout the lifespan of the studied clones (regression:  $F = 42.61$ ,  $p < 10^{-4}$ ; slope coefficient  $a = 0.2872$ ,  $T = 6.53$ ,  $p < 10^{-4}$ ; intercept  $b = 11.1673$ ,  $T = 8.66$ ,  $p < 10^{-4}$ ), and this increase was similar in all clones (the slope of the regression line did not differ between clones:  $F = 0.52$ ,  $p = 0.6673$ ; Fig. 3). The time interval between reproductions did not differ between clones (ANOVA:  $F = 1.24$ ,  $df = 3$ ,  $p = 0.3037$ ), nor

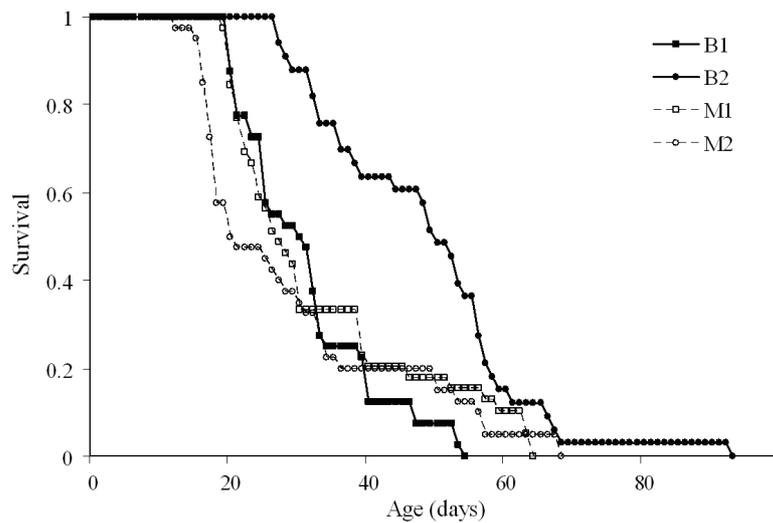


Fig. 4. Survival of *D. magna* of the four clones (black symbols: Binnensee clones; open symbols: Pole Mokotowskie pond clones).

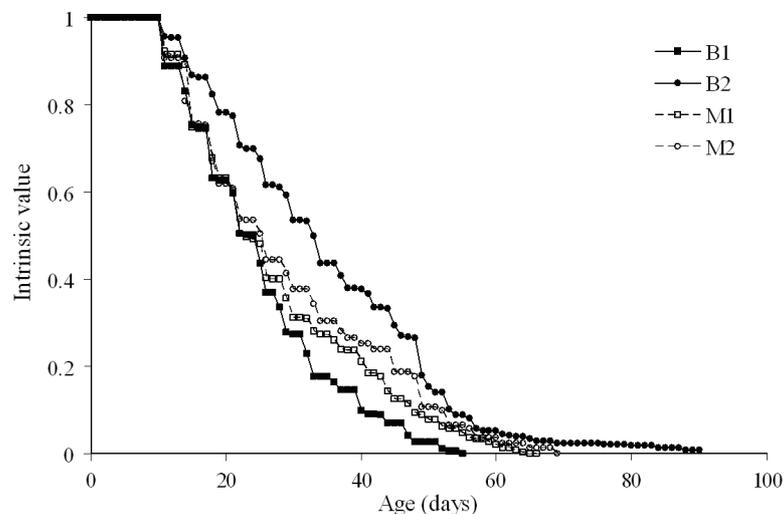


Fig. 5. Intrinsic value of *D. magna* of the four clones (black symbols: Binnensee clones; open symbols: Pole Mokotowskie pond clones).

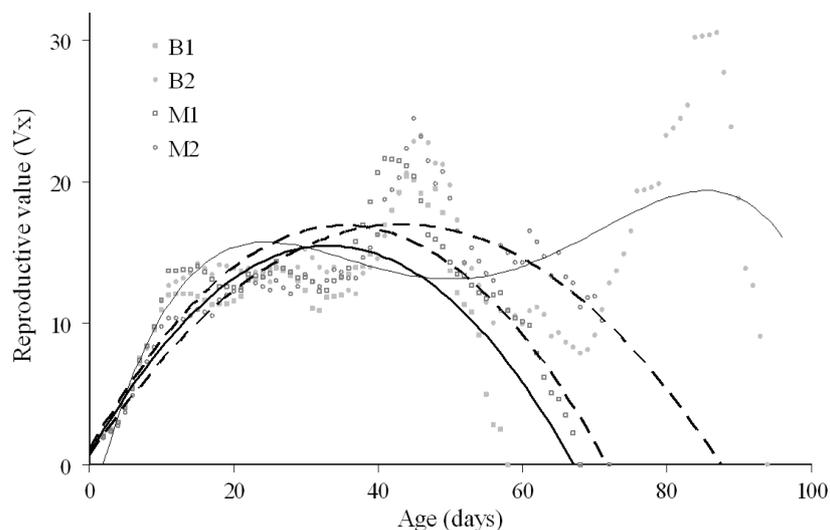
changed with time ( $F = 0.94$ ,  $df = 11$ ,  $p = 0.5153$ ; mean  $\pm$ SD:  $3.7 \pm 0.1$  days), thus the fecundity comparisons were not influenced by this factor. There was also no effect of clone on the mean number of offspring in a clutch ( $F = 0.30$ ,  $df = 3$ ,  $p = 0.8256$ ).

All experimental individuals survived to give the first offspring and none of them died before the age of 12 days. The studied clones differed in the intrinsic lifespan (Gehan-Wilcoxon test:  $\chi^2 = 34.41$ ,  $p < 10^{-4}$ ). Although Binnensee animals had longer lifespan than Pole Mokotowskie pond animals (Kruskal-Wallis test:  $F = 16.05$ ,  $df = 1$ ,  $p < 10^{-4}$ ; median = 33 days, maximum = 93 days, and median = 26 days, maximum = 68 days, respectively), it was in fact the long lifespan of the clone B2 that accounted for that difference (*post-hoc*,  $\alpha = 0.001$ ; Fig. 4). However, the ratio of the realized lifespan (median) to the expected life duration at birth ( $e_0$ ) was higher in both lake clones than in the pond clones (0.59 and 0.56 vs 0.43 and 0.31, respectively, Tab. 1).

Summary measures of age-specific fitness did not show significant between-habitat differences (repeated measures ANOVA:  $F < 0.18$ ,  $df = 1$ ,  $p > 0.7215$ ), although clones differed both in the course of intrinsic value ( $F = 235.87$ ,  $df = 3$ ,  $p < 10^{-4}$ ; Fig. 5) and reproductive value ( $F = 4.04$ ,  $df = 3$ ,  $p < 10^{-4}$ ; Fig. 6). These differences were partly due to earlier increase of mortality risk in the clone B1 on the one hand, and increasing fecundity of the last long-surviving individual from the clone B2 on the other. This analysis grouped the pond clones together and split the lake clones as having opposite extreme values of intrinsic value, or grouped B1, M1 and M2 together for reproductive value ( $\alpha = 0.001$ ).

#### 4. DISCUSSION

In animals with indeterminate growth, fecundity increases with age, and the same is to be expected in *Daphnia*. Yet, it has often been shown in different



**Fig. 6.** Reproductive value of *D. magna* of the four clones (black symbols: Binnensee clones; open symbols: Pole Mokotowskie pond clones). Polynomial regression lines (solid lines: Binnensee clones, dashed lines: Pole Mokotowskie clones).

*Daphnia* species that after an initial rise of fecundity following the maturity, fecundity levelled off or declined later in life (Dunham 1938; Kryutchkova & Sládeček 1968; Lei & Armitage 1980, de Bernardi & Manca 1982; Ebert & Jacobs 1991; Dudycha & Tessier 1999). In this study, no clear signs of reproductive senescence were seen. Despite fluctuations and temporal declines, fecundity showed an overall linear increase with age, suggesting *Daphnia* capability of increasing reproductive output throughout the whole life.

As it was expected, the number of offspring in a clutch increased with female size, but surprisingly, the interclonal differences in size at subsequent reproductions were not translated into differences in fecundity. It was clearly seen at the first reproduction, when smaller females gave birth to even more, although smaller, offspring than larger females. The two clones that started reproducing at a smaller size maintained the size difference and produced smaller, but equal in number, offspring to that produced by the bigger clones throughout the whole measurement period. Size at birth of the experimental females is not known, thus it cannot be distinguished whether the differences in size resulted from different size at birth or different juvenile growth rate. As no costs in later fitness or survival seem to be related to size, it is more likely that the size at birth accounted for the difference, because juvenile growth is expected to incur costs to late life fitness (Metcalfé & Monaghan 2001).

In later life, the size of offspring is inversely correlated with the number of offspring in a clutch. If offspring size substantially affects its fitness, the observed correlation raises the question whether the increased late life fecundity truly translates into increased fitness of the female. Such possibility is not very plausible, as gains in fitness diminish with increasing offspring size

(Tessier & Consolatti 1991), and for bigger offspring the relation of size to fitness is not straightforward (Guinnee *et al.* 2004; Fischer *et al.* 2006). Thus the initial increase of offspring size with female size would be important, and the differences in size of offspring born from large older, and fewer, mothers would be of less fitness consequences. On the other hand, older *Daphnia* females tend to exhibit per offspring overinvestment (Boersma 1997), and so the decreasing offspring size born of largest females is very likely not to affect their fitness. A point hindering any further speculations is that the mass of offspring is a better predictor of maternal investments than offspring length, and these two parameters are not always tightly related (Tessier & Consolatti 1991). Besides, there is no evolutionary reason for older mothers to produce higher-fitness offspring.

Although there was no age-related decline in the capability to produce offspring, mortality risk increased shortly after the onset of reproduction, suggesting that the capability to maintain the soma decreased when the females started reproducing. Such a decline in survival ability alone, with no decline in fecundity, is not necessarily an evidence of senescence and it may instead reflect a reallocation of effort between these two fitness components (Kozłowski 1993; Charnov & Downhower 1995; Dudycha & Tessier 1999). It would thus seem that as *Daphnia* ages, it trades off somatic maintenance for fecundity. Moreover, the cost of keeping the increase of fecundity might differ between clones and be reflected in differences in survival rates. Interestingly, Ebert & Jacobs (1991) found an inverse situation: groups of *D. cucullata* clones selected for differences in early life history traits exhibited different reproductive patterns, with either fecundity plateau or a sharp fecundity increase followed by a decline, but exhibited no differences in survival. Due to such reallocations between

fitness components, age-specific patterns of survival and fecundity should be examined jointly for among taxa comparisons. In the present study, I tested for interclonal and inter-habitat differences.

Evolutionary theory of senescence predicts that under high extrinsic mortality, when few individuals survive until older ages, there is strong selection for high investments in early fitness, which together with loosened selection for investments in late life fitness results in faster aging (Williams 1957). For *Daphnia* such conditions may be found in temporal ponds, where the populations experience high mortality due to both unpredictable and extreme changes of abiotic and biotic environment, e.g. food level, population density, predation pressure. Compared to such ponds, lakes are habitats of relatively stable environmental parameters and it can be expected that resident populations of these two types of habitat will differ in life history traits (Reznick 1993; Dudycha & Tessier 1999). In this study, I found significant clone effects for most life history traits in *Daphnia magna*, but contrary to expectations, these differences did not group the clones according to the habitat of origin. Only lifespan differed significantly between animals originating from the two types of habitat, animals from two lake clones living longer, both in terms of days and as the ratio to the expected life duration, than animals from two pond clones, which was in agreement with my expectations.

At the same time, the analysis of age-specific intrinsic value and reproductive value revealed interclonal differences and grouped all the clones with the lake clone B2 at the upper end of the values observed. Similar differences were revealed by basic life-history and population parameters: age and size at first reproduction, rate of population increase, generation time, and lifespan, and all these remained within the range of values previously observed for *Daphnia magna* (Korpelainen 1986; De Meester 1994; Arbačiauskas & Lampert 2003), and only individual reproductive success seemed to have exceptionally high values in the clone B2. More power could probably be added to the analysis of the population parameters by introducing variance through a resampling method (Meyer *et al.* 1986), especially as variance of intrinsic rate of increase and generation time was shown to be very low in *Daphnia* populations of similar size (Ponti *et al.* 2010). However, more definite conclusions would need more clones under study rather than further statistical analysis.

In general, I would expect lake clones to apply different life history strategies, whereas the temporary pond clones to be limited to a narrow optimum. The two Binnensee clones studied here appear more divergent in their life history traits than the two city pond clones. These lake clones differed in most parameters measured, the clone B1 resembling more the pond clones than the other lake clone, B2. The pond clones differed in reproductive success, however at a similar generation

time. Although the number of clone replicates does not allow for formal analysis, or for any conclusive generalisations, this could reflect the natural variation in the populations, resulting from both the longer time from colonization, and the presence of permanent egg bank in Binnensee and opens the questions on the divergence of *Daphnia* life histories in temporary and stable habitats, which could be tested in future studies.

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