Egg size and egg mass of Daphnia magna: response to food availability

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Abstract

The influence of different food availability on egg size and egg mass in Daphnia magna Straus was studied in long-term experiments using a flow-through system. Daphnia were either kept at constant high or low food levels or subjected to alternating periods of high food and starvation. Some animals were starved continuously after they had deposited their first clutch of eggs. Eggs were measured and weighed and their density (dry mass per volume) was determined. The results support the model of Glazier (1992), which defines a region of 'reproductive constraint' at very low food concentrations and a region of 'adaptive response' as food concentrations increase. Egg sizes were largest under continuously low food concentrations (0.1 mg C l⁻¹), which indicates that the maximum of Glazier's non-linear response curve is at very low food levels. Eggs produced during starvation were small, probably as a result of reproductive constraints. Egg density was about 0.37 mg dry weight mm⁻³ and did not differ between treatments.

Introduction

Egg size and neonate size in Daphnia are positively correlated (Glazier, 1992; Lampert, 1993). Therefore, the life-history consequences of varying egg size in Daphnia (Lynch, 1989) have become a topic of interest in the recent literature. Tradeoffs between offspring size and number (Ebert, 1993), the optimum amount of energy allocated per egg under varying food conditions (Glazier, 1992; Gliwicz & Guisande, 1992) and in the presence of predators (Stibor, 1992), and the determination of maturation size by maternal effects via egg size (Lampert, 1993) are especially interesting. The two most important factors in determining Daphnia egg size are probably size of the mother (Glazier, 1992; Lampert, 1993) and food supply (Guisande & Gliwicz, 1992). Ebert (1993) presented a very clear graph of the combined effect of clutch number and food level on neonate size – a close correlate of egg size – for D. magna.

The effect of food availability on egg size and neonate size has been particularly well-studied but with contradictory results. A number of studies found a positive correlation between egg size and food supply (Green, 1956; Brambilla, 1980; Urabe, 1988; Lynch, 1989; Tessier & Consolatti, 1991), others detected a negative relationship (Baichorov, 1992; Glazier, 1992; Guisande & Gliwicz, 1992; Taylor, 1985) or found no correlation (Glazier, 1992; Semenchenko & Semenjuk, 1988; Taylor, 1985). In a critical analysis of available data, Glazier (1992) proposed two main reasons for the conflicting results: the use of different ration levels and food conditions and the lack of consideration of maternal effects. There is also a genetic component in neonate size variability (Tessier & Consolatti, 1991; Ebert, 1993), i.e., one must expect differences in egg size responses to changing food availability between species and clones.

Glazier (1992) proposed a hypothetical model of the response of Daphnia egg size to food availability, which implies a maximum egg size at a relatively low food level. With decreasing food availability, egg size increases as larger neonates are more starvation resistant (Gliwicz & Guisande, 1992). However, when food availability decreases further, eggs will become smaller again due to energetic constraints. This mod-
el has not been tested quantitatively. It is possible that daphnids rarely reach the low-food region of the model when the food supply is low but constant. On the other hand, energy constraints may be effective if well-fed females are starved and use their limited amount of energy reserves to still produce some eggs. These eggs should then be small. One aim of this study is to test this hypothesis.

Direct measurements of egg dry mass are a rather delicate and time-consuming procedure, hence, egg mass is usually estimated from egg size. These estimates are based on microscopic measurements of egg size and calculation of egg volume. Egg volume is converted to wet egg mass assuming a density of 1 mg mm$^{-3}$ (Edmondson & Winberg, 1971). Then wet mass must be converted to dry mass. There is a surprisingly large variation in the applied conversion factors. They range from 0.1 (De Bernardi et al., 1978) to 0.4 (Ivanova, 1985). Although some of the variability may be due to measuring errors, another source of variation may be that the conversion factor is influenced by internal or external factors. For example, the ratio dry mass:volume of the eggs may depend on food availability or egg size. As this is an important factor in energetic consideration for constraints and tradeoffs, we use our data to calculate the dry mass:volume ratio of eggs in a clone of $D. magna$ and compared them with results from the literature.

Methods

Experiments were carried out with a clone of $D. magna$ that had been maintained in the laboratory for many years. Experimental animals were kept at 20 °C with unlimited food ($Scenedesmus acutus$ Meyen) under dim continuous light. Freshly born neonates were placed randomly in the chambers of a flow-through system (Lampert et al., 1988) and grown at constantly high (1.5 mg carbon l$^{-1}$) or constantly low (0.1 mg C l$^{-1}$) concentrations of $Scenedesmus$ in membrane-filtered (0.45 μm) lake water (10 animals per vessel; flow rate 1.5 l h$^{-1}$). The food suspension was freshly prepared every day. After the daphnids had produced their first clutch of eggs, they were transferred to clean vessels and were subsequently subjected to different feeding protocols. They were either fed continuously (1.5 or 0.1 mg C l$^{-1}$) or exposed to alternating periods of feeding and starvation until they had their eighth clutch. Only primiparae grown at the high food level were exposed to alternating food conditions. The alternating food regime started with a period of starvation. Daphnids were transferred to different food conditions (to starvation or 1.5 mg C l$^{-1}$) whenever they produced a new clutch of eggs. Thus, clutches 1, 3, 5, and 7 were produced after a period of feeding while clutches 2, 4, 6, and 8 were produced after a period of starvation. The maximum time between egg deposition and transfer to new food conditions was 12 hours. As this applied to transfers in both directions, we considered the effect of the delay on egg size negligible. Some primiparae from both the high-food and the low-food treatments were isolated and starved to death. During starvation, $Daphnia$ remained in the flow-through system but they received only membrane-filtered water.

Egg measurements were taken within a few hours of the deposition of a new clutch of eggs into the brood pouch (i.e., egg stage 1, Threlkeld, 1979). Eggs were carefully removed from the brood pouch with fine needles. Their diameter was measured to the nearest 0.01 mm under a dissecting microscope equipped with a semi-automatic measuring device (Wild MMS 235). Repeated measurement of individual eggs at different angles showed very little variability. Assuming the shape to be spherical, the egg volume was calculated from the diameter. Individual clutches were transferred to small aluminum containers, dried for 24 hours at 60 °C, cooled in a desiccator, and weighed to the nearest 0.1 μg on an electronic balance. Mean egg mass was calculated as dry weight of the clutch divided by the number of eggs. The density of an egg $d$ (mg mm$^{-3}$) was calculated from egg dry mass $W$ (mg) and volume $V$ (mm$^{-3}$):  

$$d = W / V.$$  

Assuming a density of 1, $d$ can be used for the conversion factor wet mass: dry mass.

Results

Experimental treatments started after the deposition of the first clutch, therefore the first eggs available for analysis came from clutch two. These eggs are smaller than those of the third and subsequent clutches but eggs of the third clutch differ only slightly from eggs of later clutches (Glazier, 1992; Ebert, 1993; Lampert, 1993). In order to eliminate the maternal effect (size of the mother) we analyzed two separate groups, the pooled eggs from clutches 3 to 8 and the eggs of the second clutch. Continuously starved $Daphnia$ produced no more than two additional clutches, thus they...