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Environmental challenges improve resource utilization for asexual reproduction and maintenance in hydra

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ABSTRACT

Variation in life history can reflect genetic differences, and may be caused by environmental effects on phenotypes. Understanding how these two sources of life history variation interact to express an optimal allocation of resources in a changing environment is central to life history theory. This study addresses variation in the allocation of resources to asexual reproduction and to maintenance of *Hydra magnipapillata* in relation to differences in temperature and food availability. Hydra is a non-senescent, persistent species with primarily clonal reproduction. We recorded changes in budding rate and mean survival under starvation, which indicate changes in the allocation of resources to asexual reproduction and maintenance. In constant conditions we observed a clear trade-off between asexual reproduction and maintenance, where budding increased linearly with food intake while starvation survival stayed rather constant. In contrast, an environment with fluctuations in temperature or food availability promotes maintenance and increases the survival chances of hydra under starvation. Surprisingly, asexual reproduction also tends to be positively affected by fluctuating environmental conditions, which suggests that in this case there is no clear trade-off between asexual reproduction and maintenance in hydra. Environmental stresses have a beneficial impact on the fitness-related phenotypical traits of the basal metazoan hydra. The results indicate that, if the stress occurs in hormetic doses, variable stressful and fluctuating environments can be salutary for hydra. A closer examination of this dynamic can therefore enable us to develop a deeper understanding of the evolution of aging and longevity.

1. Introduction

Organisms differ in their growth and breeding schedules, the extent of parental investment, the number of offspring, and the investments made in body maintenance and survival. A perfect match between these life history traits of an organism can never be attained because organisms must cope with constraints, changing environments and trade-offs (Roff, 1992). Thus, the question of how resources can be efficiently allocated among growth, reproduction and survival is of particular interest.

As anticipated by life history theory, a change in one phenotypic trait may occur together with a change in another; these are referred to as trade-offs (Roff, 1992): i.e., energy that is allocated to maintenance, which in turn increases the chances of survival, cannot be used for other processes, such as reproduction (Hercus et al., 2003; Le Bourg, 2009; Boggs, 2009). The presence of trade-offs between reproduction and survival is a central feature in life history theory, and affects the evolution of longevity (Le Bourg, 2009; Stearns, 1992). Trade-offs may change in response to environmental stresses (Parsons, 2005; Rattan, 2008), and this response may differ when stresses are applied as constant or fluctuating regimes (Rattan, 2008; Parsons, 2007; Gomez et al., 2009; Marshall and Sinclair, 2010). Thermal stresses (low or high temperature) and resource scarcity induce stress responses in organisms that can lead to increased longevity, but not necessarily at the expense of their reproductive output. The improvement in the survival of an organism following exposure to mild stresses is a response known as hormesis (Parsons, 2005; Calabrese and Baldwin, 2003), and has been observed in various species across the tree of life, e.g., in yeast (Minois, 2000), *Drosophila* (Semenchenko et al., 2004; Le Bourg and Minois, 1999) and nematode worms (Yashin et al., 2001; Lee et al., 2006).

Hydra (Cnidaria, Hydrozoa) deviates from typical life histories, and offers researchers the opportunity to gain insight into the role of trade-offs in shaping age-specific life histories. Hydra reproduces mostly clonally, through budding from the body tissues by a process of mitosis and cell migration. Asexual reproduction is the main reproductive mode in hydra, while sexual reproduction occurs less frequently. Therefore, hydra is ideal for studying neglected variations in life history traits based on environmental effects. The fact that the offspring are genetically identical facilitates the observation of phenotypic variation in the allocation of resources that depend exclusively on environmental conditions.

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In hydra, three distinct stem cell lineages have been found: the epithelial stem cells (endoderm and ectoderm) provide epidermal and digestive cells, while interstitial cells provide all of the remaining cell types. The epithelial cells have been shown to have a cell cycle time of approximately three days, and to be continuously cycling (Bosch and David, 1984), so that the epithelial tissue mass of the animal doubles every three to four days (David and Campbell, 1972). Thus, the pattern of cell turnover is highly dynamic, with differentiated cells persisting for only a short time before they are lost or destroyed through apoptosis and autophagy (Chera et al., 2009). Rather than investing energy into the repair of damaged cells, hydra instead replaces whole cells, presumably because doing so is more cost-effective. These cell dynamics are of great importance for the life history of hydra, and for decisions regarding resource allocation. Furthermore, because of this dynamic balance of cell loss and cell gain, hydra is a model of continuous regeneration, and is considered to be a non-senescent invertebrate (Martinez, 1998).

Another advantage of using hydra in our experiments is that individuals kept at a constant food level attain a relatively stable maximum size (which may be species-specific). At low food levels, the size of a polyp shrinks, and the use of dead cells from apoptosis as a food source increases, as does autophagy (Bosch and David, 1984; Chera et al., 2009). With these mechanisms, the polyps can maintain their body in perpetuity, and therefore survive very low food levels or starvation for several days. Once a polyp has grown to full size (for which a constant food level is necessary), most of the newly generated cells will be channeled into budding. At this stage, resources can be allocated to asexual reproduction as well as to maintenance, and maintenance will in turn influence survival. The rate of bud production is mainly governed by temperature and food intake.

The apparent lack of senescence, the efficient asexual reproduction mechanism and the regeneration potential of hydra suggest that the response of maintenance efficiency to changing environmental conditions may be crucial to understanding the evolution of longevity and non-senescence. In many organisms, mild environmental stresses have been shown to induce a higher degree of resistance against further or new stresses, and stressed organisms have been found to have better maintenance or longer life spans than unstressed organisms. A negative effect for maintenance could be observed in overfeeding experiments conducted by Bode et al. (1977): the polyps in the experiments died, suggesting a strong decline in somatic strength. However, all of the previous experiments in which food level change and starvation were combined with an analysis of budding rate and survival lasted fewer than 30 days (Chera et al., 2009; Bode et al., 1977; Otto and Campbell, 1977). Therefore, no clear pattern with respect to resource allocation and the trade-off between maintenance and asexual reproduction could be observed.

It is the aim of our study to examine the allocation of resources to asexual reproduction and maintenance in genetically identical individuals under both controlled and stressful environmental conditions, with respect to food availability and temperature. We explore the question of whether allocation strategies are phenotypically plastic within a lifetime of a polyp, and whether they vary in response to environmental conditions. We attempt to identify the mechanism that could play a crucial role in the optimal resource allocation between survival and asexual reproduction in hydra. We compare the nutritional costs of maintenance with the nutritional costs of asexual reproduction to examine whether either one is large enough to compete for a significant fraction of the resources allocated to the other.

2. Materials and methods

2.1. Species

There are similarities in life histories across the genus *Hydra*. In this study, we use the well-studied strain *Hydra magnipapillata* 105, as this line has been kept successfully in the laboratory for over 30 years where it reproduced exclusively by clonal budding. The strain 105 does not show any signs of sexual reproduction including production of gametes. We were able to follow standard proven laboratory procedures, which includes feeding a mono-diet of *Artemia salina* nauplii (1 day post hatching). We thus benefited from the long history and experience of researchers who have worked with this model system e.g. (Martinez, 1998).

2.2. Definitions

2.2.1. Asexual reproduction = budding

We measured budding (asexual reproduction) as a reproductive rate, expressed as the average number of buds produced per hydra per unit of time. We defined asexual reproduction as a developmental process with two states based on Sanyal (1966). 1. The development of a bud starts with the tissue recruitment from the parent polyp to the bud; both are genetically identical and all three independent stem cell lineages are involved in this process (Otto and Campbell, 1977; Sanyal, 1966). 2. This process ends at the time when the bud builds its first tentacle rudiments (bud hydranth morphogenesis) and the bud separates from the parent polyp. Asexual reproduction is strongly correlated with food concentration. Furthermore, the individual size (number of cells per hydra) and the individual budding rate depend on the food intake (Otto and Campbell, 1977). Therefore, it is very important to separate budding from polyp growth, which describes the change in the size or the cell number of a polyp. We predicted that, after a long period of constant food intake, the size of the polyps would stay constant over time and within treatment groups (Otto and Campbell, 1977). Furthermore, we predicted that the size could vary among groups with different food intakes. Under constant feeding regimes with a constant number of food items per day per hydra, individuals could reach a steady state in size (number of epithelial cells), which is proportional to the food intake (Bode et al., 1977; Otto and Campbell, 1977). The respective food concentration was held constant for more than three months to allow each individual to attain this stable maximum size. We thereby ensured that 1) at the beginning of each experiment, size effects between the polyps could be nearly excluded; 2) all polyps would have acclimatized to the respective condition; and 3) newly produced buds would have nearly the same size in each treatment.

2.2.2. Food utilization

We analyzed the efficiency of energy utilization. We quantified the number of *Artemia* needed to produce one bud by calculating the number of *Artemia* per bud per time for each individual. To do this, we integrated all of the *Artemia* fed, up to the day when the last bud separated from the mother. This is an indirect measure for detecting a change in resource allocation due to environmental stresses.

2.2.3. Survival under starvation

Another way to quantify changes in the pattern of resource allocation in hydra under environmental stresses is to assess the energy needed for maintenance; i.e., survival. In hydra, the identification of a relationship between environmental stresses and survival expansion, as observed in other species, is not directly possible due to its unknown and extraordinary lifespan. Thus, the indirect measurement of life expectancy under starvation in days, as it is used in our experiments, serves as a comparable approach. Significant differences in such an artificial mortality curve can then be explained as differences in the allocation of resources to maintenance. To avoid effects of cell number or size of polyps on this parameter (because survival can be positively correlated with the number of cells per polyp, as mentioned above) we started with an experiment in which we fed groups of polyps at different constant food levels (between 0.2