Received: 25 June 2019 | Accepted: 17 June 2020

DOI: 10.1111/1365-2656.13287

RESEARCH ARTICLE

Journal of Animal Ecology | BRITISH ECOLOGICAL SOCIETY

Age-dependent plasticity in reproductive investment, regeneration capacity and survival in a partially clonal animal (*Hydra oligactis*)

Flóra Sebestyén | **Máté Miklós** | **Katalin Iván** | **Jácint Tökölyi**

MTA-DE Behavioural Ecology Research Group, Department of Evolutionary Zoology, University of Debrecen, Debrecen, Hungary

Correspondence
Flóra Sebestyén
Email: flora.sebestyen@gmail.com

Funding information
János Bolyai Research Scholarship of the Hungarian Academy of Sciences; Hungarian State and the European Union, Grant/Award Number: EFOP-3.6.1; ÚNKP New National Excellence Program of the Hungarian Ministry for Innovation and Technology, Grant/Award Number: ÚNKP-18-3, ÚNKP-19-3 and ÚNKP-19-4; NKFIH grant, Grant/Award Number: FK 124164

Handling Editor: Albert Phillimore

Abstract

1. Asexual reproduction diversifies life-history priorities and is associated with unusual reproduction and somatic maintenance patterns, such as constant fertility with age, extensive regeneration ability and negligible senescence. While age-dependent plasticity in relative allocation to sexual versus asexual reproductive modes is relatively well studied, the modulation of somatic maintenance traits in parallel with age-dependent reproduction is much less well understood in clonal or partially clonal animals.
2. Here, we asked how age-dependent investment into sexual and asexual reproduction co-varies with somatic maintenance such as regeneration in a partially clonal freshwater cnidarian *Hydra oligactis*, a species with remarkable regeneration abilities and experimentally inducible sex.
3. We induced gametogenesis by lowering temperature at two ages, 1 or 4 weeks after detachment from an asexual parent, in animals of a male and a female clone. Then we measured phenotypically asexual and sexual reproductive traits (budding rate, start day and number of sexual organs) together with head regeneration rate, survival and the cellular background of these traits (number of reproductive and interstitial stem cells) for 2 or 5 months.
4. Younger animals had higher asexual reproduction while individuals in the older group had more intensive gametogenesis and reproductive cell production. In parallel with these age-dependent reproductive differences, somatic maintenance of older individuals was also impacted: head regeneration, survival and interstitial stem cell numbers were reduced compared to younger polyps. Some of the traits investigated showed an ontogenetic effect, suggesting that age-dependent plasticity and a fixed ontogenetic response might both contribute to differences between age groups.
5. We show that in *H. oligactis* asexual reproduction coupled with higher somatic maintenance is prioritized earlier in life, while sexual reproduction with higher maintenance costs occurs later if sex is induced. These findings confirm general

life-history theory predictions on resource allocation between somatic maintenance and sexual reproduction applying in a partially clonal species. At the same time, our study also highlights the age-dependent integration of these resource allocation decisions with sexual/asexual strategies. Accounting for age-related differences might enhance repeatability of research done with clonal individuals derived from mass cultures.

KEYWORDS

eco-evo-devo, partial clonality, phenotypic plasticity, regeneration, resource allocation, senescence, sexual investment, stem cells

1 | INTRODUCTION

Living in a constantly changing environment poses a challenge for organisms. The optimal phenotype is expected to change with the environment (Endler, 1977), hence phenotypic plasticity may maintain absolute fitness (Chevin, Lande, & Mace, 2010). Plasticity might be especially important for clonal populations and species, because it can reduce the negative effects of low genetic variation, enable the occupancy of a wide range of habitats and allow sessile species to adapt to temporal environmental changes (Bruno & Edmunds, 1997). Theoretical studies suggest that phenotypic plasticity is favoured in varying environments, when costs of plasticity are low and reliable environmental cues are available (Fischer, van Doorn, Dieckmann, & Taborsky, 2014 and references therein). Cues for phenotype modifications can be both external abiotic agents such as temperature (e.g. for regeneration in corals; Lester & Bak, 1985), salinity (e.g. for reproduction in copepods; Chen, Sheng, Lin, Gao, & Lv, 2006) or space limitation (e.g. for growth in corals; Muko, Sakai, & Iwasa, 2001), or biotic factors like bacteria (e.g. for elemental composition in *Daphnia*; Frost, Ebert, & Smith, 2008), population density (e.g. for diapause in rotifers; Schröder & Gilbert, 2004) or presence of predators (e.g. for morphological defence in *Daphnia*; Tollrian, 1995).

In addition to external factors, West-Eberhard (2003) mentions *internal* environment as well in her definition of phenotypic plasticity, that is 'The ability of an organism to react to an internal or external environmental input with a change in form, state, movement, or rate of activity' (p. 33). Internal factors affecting phenotypic plasticity comprise body size and condition including energy reserves, immune system or nutritional status, among many other traits (McNamara & Houston, 1996). Age, as an internal environmental factor, correlates with condition, reproduction and survival and is part of an organism's state (McNamara & Houston, 1996). In addition, information acquisition with age can be crucial for decision-making in precarious environments (Fischer et al., 2014): if an organism does not have perfect information about its environment at birth, but can improve its estimate about the environment with time, phenotypic adjustment is expected to change with age in a nonmonotonic fashion (Fischer et al., 2014).

Allocation of resources to basic life functions often shows age- or life stage-dependent plasticity (Radchuk, Turlure, & Schtickzelle, 2013; Richardson & Smiseth, 2019). For instance, an increase in fecundity with age is common in both indeterminate and determinate growers (Berube, Festa-Bianchet, & Jorgenson, 1999; Clutton-Brock, 1984; Martin, 1995), because when growth stops or declines after maturity, it is optimal to direct the remaining resources into reproduction (Cichoń, 2001). Repair intensity of somatic damage (i.e. somatic maintenance) also varies with age but generally declines after maturity, being highest early in life, diminishing later and stopping completely well before the end of the maximum expected life (Cichoń & Kozłowski, 2000). Empirical evidence confirms this pattern in many taxa (e.g. reviewed in: Jones et al., 2013) and the decline in somatic maintenance is a decisive component in theories of senescence such as the 'antagonistic pleiotropy' or 'disposable soma' hypotheses (Kirkwood & Rose, 1991). Due to competition over limited energy or nutrients, age-dependent allocation strategies can shape all main life-history components responsible for growth, reproduction, somatic maintenance or survival by trade-offs between them (Kozłowski, 1992, but see Cox, Lovern, & Calsbeek, 2014). Resource acquisition can reduce the extent of these trade-offs in 'high quality individuals' via buffering temporary resource limitation, but resource acquisition also varies with an individual's life cycle and is more important for resource allocation at early ages (Richardson & Smiseth, 2019; Yearsley et al., 2005).

Age-dependent allocation decisions to reproductive and somatic maintenance functions can be much more complex in clonal or partially clonal species. Resource allocation priorities of clonal animals in certain life stages can differ from what is expected in non-clonal species (Clutton-Brock, 1984; Engen & Saether, 1994; Stearns, 1992) and the integration of clonal growth into life-history models is complicated (Gardner & Mangel, 1999). For instance, resource allocation models of conventional life histories predict an optimal strategy of growing early, then stopping growth and starting reproduction (Cichoń, 1997). However, empirical studies of clonal animals detect a different pattern: clonal reproduction can be more emphasized in early life in individuals with good condition and growth is more important later (Glazier & Calow, 1992). An additional major life-history decision in partially clonal species compared to non-clonal ones is the switch from asexual to sexual reproduction, the timing of which can be flexible and might be triggered only when clonal reproduction is limited by exogenous factors (Burke & Bonduriansky, 2018; Harvell & Grosberg, 1988).

While the reciprocity of asexual and sexual strategies has been relatively well studied in partially clonal organisms, it is still unclear how somatic maintenance co-varies with these age-dependent reproductive allocation decisions. In partially clonal animals, asexual forms often have higher somatic maintenance functions, such as higher regeneration ability (Krois, Cherukuri, Puttagunta, & Neiman, 2013; Saccucci, Denton, Holding, & Gibbs, 2016), increased telomerase activity (Tan et al., 2012), and—possibly as a consequence of these—a lower rate of senescence, such that some of them (e.g. *Hydra* species; Schaible et al., 2015) are potentially immortal (reviewed in Sköld & Obst, 2011, but see Martinez & Levinton, 1992; Sköld, Asplund, Wood, & Bishop, 2011). Despite the exceptional somatic maintenance abilities of clonal animals, these traits are not constant during their lifetime (for instance, telomerase activity [Sköld et al., 2011], regeneration [Meesters & Bak, 1995] or survival [Orive, 1995] decrease with ageing). However, information is scarce about how resource allocation between reproductive modes and regeneration or any other somatic maintenance trait varies with age in clonal or partially clonal organisms. This lack of knowledge hinders understanding senescence in clonal or partially clonal species that often exhibit unconventional, complex senescence patterns such as negligible senescence (constant mortality and fecundity with age) or even negative senescence (decreasing mortality and increasing fecundity with age; Vaupel, Baudisch, Dölling, Roach, & Gampe, 2004).

Here, we studied age-dependent plasticity in both reproductive investment (gametogenesis and asexual reproduction) and somatic maintenance (regeneration capacity and survival rate) in a partially clonal freshwater cnidarian *Hydra oligactis*. Hydra polyps have exceptional regeneration capacity (e.g. whole body regeneration from a piece of tissue as small as 1% of the normal polyp; Shimizu, Sawada, & Sugiyama, 1993) that has captured the imagination of scientists since the 18th century (Trembley, 1744). Regeneration research in hydra has focused on the physiological, developmental and molecular processes underlying this phenomenon (e.g. Bode, 2003; Schaller, 1976; Tardent, 1974) but regeneration as a life-history trait and its age-dependent modulation are less well understood. Regeneration provides obvious advantages via eliminating the negative effects of crucial body part injuries, which is especially important when the probability of repeated injuries is high (Bely & Nyberg, 2010). But as many other traits—like growth or reproduction—regeneration also requires resource investment, thus may impair other life-history traits or vice versa (Henry & Hart, 2005).

Regeneration ability in *H. oligactis* is a highly plastic trait, for example, it is impaired or delayed in sexual individuals (Galliot, Buzgariu, Schenkelaars, & Wenger, 2018; Sebestyén, Barta, & Tökölyi, 2018; Tomczyk et al., 2017). Loss of regeneration in this species may be a consequence of their unique life history within the genus *Hydra*: they switch from asexual reproduction to sexual reproduction during autumn, in order to produce a relatively high number of sexual organs and resting eggs (compared to other *Hydra* species: Schuchert, 2010) then the polyps regularly degenerate and die (Schenkelaars et al., 2017; Tökölyi, Ősz, Sebestyén, & Barta, 2017; Yoshida, Fujisawa, Hwang, Ikeo, & Gojobori, 2006). Post-reproductive senescence is accompanied by drastic changes in cellular composition: the number of interstitial stem cells (ISC) declines while the number of reproductive cells increases, suggesting that ISCs differentiate into reproductive cells (Sebestyén et al., 2018; Tardent, 1974; Yoshida et al., 2006). Importantly, a recent population genetic analysis indicated substantial phenotypic plasticity in reproductive strategies in this species under field conditions (Miklós et al., 2019), but the factors inducing this plasticity are unclear.

We used clonal offsprings of a male and a female *H. oligactis* polyp to examine the role of age-dependent plasticity in life-history traits. We asked whether investment into different reproductive modes and somatic maintenance traits differs if sex is induced in young versus older individuals. We experimentally induced gametogenesis by lowering temperature and measured several aspects of both reproduction and somatic maintenance for eight weeks after induction of gametogenesis in two bud age groups (1 and 4 weeks old): the number of reproductive organs (eggs and testes), start of gametogenesis along with asexual reproduction, head regeneration ability and survival. We also investigated the cellular requirements for these functions: the number of reproductive cells as a measure of sexual investment, and the number of somatic interstitial stem cells as a requirement for somatic maintenance and asexual reproduction.

If fecundity increases and somatic maintenance decreases with age (as general life-history theory suggests), we expect more sexual organs and reproductive cells in older animals, while their regeneration ability, survival and interstitial stem cell number should be reduced. Conversely, it is also possible that both fecundity and somatic maintenance is higher in older individuals because these might have more time to accumulate sufficient resources to sustain both life functions. Asexual reproduction might be prioritized in younger animals in accordance with observations on other partially clonal animals (e.g. Harvell & Grosberg, 1988), although it might show an opposite pattern due to higher condition of adults.

2 | MATERIALS AND METHODS

2.1 | Hydra strains, culture conditions and experimental design

Experimental animals originate from an oxbow lake near Tiszadorogma in Eastern Hungary (47.6712°N, 20.8641°E) and have been kept in the laboratory as culture strains for 1 year prior to the experiments described here. We kept animals individually in 6-well tissue culture plates under standardized conditions in a climate chamber (18°C temperature, 12/12 hr dark/light photoperiod) and ~5 ml standard hydra medium (1.0 mM $CaCl_2$, 0.1 mM $MgCl_2$, 0.03 mM KNO_3, 0.5 mM $NaHCO_3$, 0.08 mM $MgSO_4$; Sebestyén et al., 2018). We fed the hydras with 20 µl freshly hatched *Artemia* spp. nauplii (Tökölyi et al., 2016) two times a week, on the same days. We changed hydra medium on feeding days and on days after feeding (for removing food remains).

We used one male (number of animals (*N*) = 666) and one female strain (*N* = 660) for our experiments, in which freshly detached buds were used 0–4 days after their detachment. Experimental treatment consisted of moving polyps to a wine cooler with even air flow on 7°C and 8 hr light/16 hr dark photoperiod. We conducted this at either of two different time points: 3 days or 24 days after their initiation (Figure 1). Because of the variation in the detachment time, these time intervals resulted in a maximum possible bud age of 7 days (henceforth called '1 week' group) or 28 days ('4 week' group). We used different animals for different types of measurements (head regeneration, cellular composition and survival). We measured both head regeneration and cell number eigth times (weekly for 2 months) after cooling. For logistical reasons, experimental animals were initiated in several distinct batches.

2.2 | Detection of sexual organs and asexual reproduction rate

Hydra oligactis males spread their sperm from several separate testes on their body column, and females produce eggs which detach after maturation (Reisa, 1973). Gametogenesis in both sexes is continuous during the sexual period. We used a stereo microscope to count number of testes on one side of males two times a week and number of detached eggs in females four times a week (each time the medium was exchanged), following temperature change. We measured gametogenesis for 2 months after cooling, since all animals had started their sexual cycle by the end of the second month and repeated sexual cycle has not been reported in this species. We recorded the number of detached buds twice a week on feeding days for 20 weeks after cooling, because asexual reproduction can be repeated several times.

2.3 | Head regeneration measurements

We measured head regeneration in 711 individuals. Each individual was used only once. We decapitated the animals below their mouth at about 15% of body length (containing the mouth tip, tentacles and 10% of the body column). We recorded the initiation of regeneration and coded the presence or absence of emerging tentacles 1 week after decapitation (Sebestyén et al., 2018). Animals were not fed during these measurements and not used for subsequent regeneration or other type of measurements.

2.4 | Cell number measurements

We performed cell number measurements on 187 animals approximately weekly for 2 months after temperature change. Each individual was used only once. We macerated polyps according to standard technique (David, 1973), placed 5 µl of a sample on microscopic slide, which was then examined under 400× magnification in a Euromex iScope phase contrast microscope. We recorded epithelial cell, sperm precursor/nurse cell and interstitial stem cell number (by recording the number of 1, 2, 3–4, 5–8, >8 nests i.e. group of cells) for each sample. Sample measurements were made until we counted at least 100 epithelial cells and cells around them belonging to different cell types (Sebestyén et al., 2018). We used each individual for cell counts measurements only once, meaning that in different time points we collected data from separate individuals.

In males, sperm precursor and non-mature spermatid cells were identified according to the work of Littlefield, Dunne, and Bode (1985). We estimated sperm precursor and non-mature spermatid cell number by counting cell groups, because the large number of cells made exact counting impossible. In females, interstitial cells largely increase their size before reproductive cell formation and give rise to nurse cells (Zihler, 1972), hence in early stages of development reproductive cells are distinguishable from interstitial cells by their increased cytoplasm volume. We counted a cell as a nurse cell if the diameter of its nucleus was at least half-sized compared to the diameter of the cell or smaller. A subset of nurse cells produces gametes while the others are phagocytosed by the oocyte (Alexandrova, Schade, Böttger, & David, 2005),

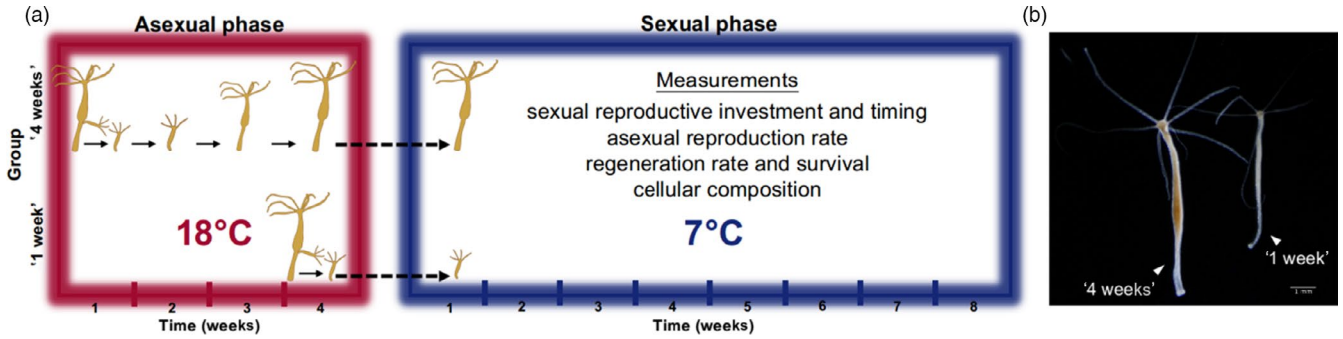

FIGURE 1 Experimental design containing two groups: 1 or 4 weeks old according to their bud age at cooling. Following the temperature change, we measured the number of sexual organs and their first appearance, asexual reproduction rate, head regeneration rate and cellular composition (reproductive and interstitial stem cell number) for 2 months, and survival rate at the end of the fifth month after cooling. Experimental animals were propagated asexually (a). Photos were taken about 1 and 4 weeks old individuals of the female strain kept at 18°C (b)

hence all nurse cells contribute to reproductive investment. We were not able to do histological preparations in females 8 weeks post-cooling because all individuals involved consisted of acellular necrotic tissue.

2.5 | Survival measurements

We kept experimental animals for 5 months and recorded death when animals were fully disintegrated or disappeared. We retained hydras even if they shrank to a very small size. Animals were binary scored as survived or not. Animals were scored as survived if they had intact tentacles, body and foot at the end of the fifth month. Animals were coded as not survived, if they failed to meet these criteria and showed only necrotic tissue. We excluded 12 animals from the analysis due to their accidental loss.

2.6 | Statistical analysis

We used generalized linear mixed models (GLMMs) followed by likelihood ratio tests (LRTs) to test the effects of bud age at cooling variable and time after cooling variable on measured traits. We performed LRTs by comparing the models with bud age at cooling or time after cooling to a null model. To test the interaction between dependent variables, we compared the additive model and the model with interaction as well. We also used LRTs to establish the valid distributions of dependent variables. We fitted time after cooling as a continuous variable and included start date as a random effect to every model, because animals entered into the experiment at different dates may slightly differ from each other. To gain insight to the mechanisms behind the observed patterns, we also fitted our models with time after detachment (i.e. absolute age) and experimental treatment as predictors. This allows us to distinguish ontogenetic effects from age-dependent plasticity.

To analyse cumulative number of asexual buds during the experiment, we used GLMMs with Poisson error distribution since the number of detached buds is a count variable. We performed GLMMs to analyse timing (start day after cooling) and investment (cumulative number of sexual organs) of gametogenesis in groups with different bud age at cooling. We excluded individuals which did not start gametogenesis during the 2 months of measurement. We used Poisson error distribution for these mixed models, except for female gametogenetic investment where the valid distribution was Negative binomial.

For sperm precursor/nurse cell number and male interstitial stem cell number we used zero-inflated models, because our data contained more zero values in some groups than it could be expected by Poisson or Negative binomial distributions. We checked the necessity of zero-inflated models by LRTs and simulated frequencies of zeros of the fitted model (Figure S1). For female interstitial stem cell number, the valid distribution was Negative binomial. Our models contained cell number (sperm precursor or nurse cell, interstitial stem cell) as the dependent variable and bud age at cooling and time after cooling as predictors. We included epithelial cell number as a fixed effect, to normalize to epithelial cell number which was not exactly identical in every sample.

We analysed head regeneration by GLMMs with binomial distribution. Our model contained head regeneration (presence or absence) as dependent variable and bud age at cooling, time after cooling and their interaction as independent variables. For testing the effect of bud age at cooling on survival data, we performed binomial GLMMs followed by LRTs. All analyses were performed in R Statistical Environment version 3.4.4 (R Core Team, 2018) using the GLMMADAPTIVE package (Rizopoulos, 2019).

3 | RESULTS

3.1 | Asexual reproduction rate

Bud age at cooling had a significant effect on overall budding rate in males (LRT = 42.95, degrees of freedom (*df*) = 1, $p < 0.001$, coefficient (*b*) = −0.404, *SE* = 0.061). In females, bud age at cooling was a non-significant effect on bud number ($\chi^2_1 = 2.64$, $p = 0.104$, $b = -0.6 \pm 0.29$), although its trend was similar to males (Figure 2b). As Figure 2 shows, budding rate tended to increase in all groups during the experiment.

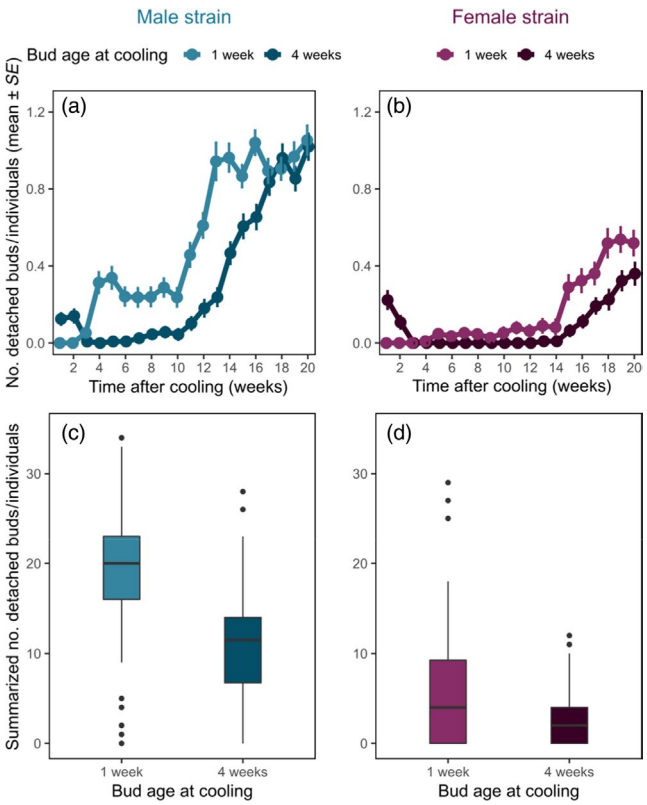

FIGURE 2 Weekly mean numbers of detached buds (a and b) and the overall weekly mean numbers (c and d) in two bud age groups in two stains. Error bars show standard errors (*SE*)

3.2 | Sexual investment and timing

Males in the '4 week' group had significantly more testes ($\chi^2_1 = 22.04$, $p < 0.001$, $b = 0.356 \pm 0.073$) and initiated gametogenesis significantly earlier ($\chi^2_1 = 149.04$, $p < 0.001$, $b = -0.752 \pm 0.06$), than males which were 1 week old at cooling (Figure 3). Females in the '4 week' group had significantly more detached eggs ($\chi^2_1 = 64.76$, $p < 0.001$, $b = 0.538 \pm 0.148$) and more advanced gametogenesis ($\chi^2_1 = 193.32$, $p < 0.001$, $b = -0.225 \pm 0.041$) compared to 1-week-old females at cooling.

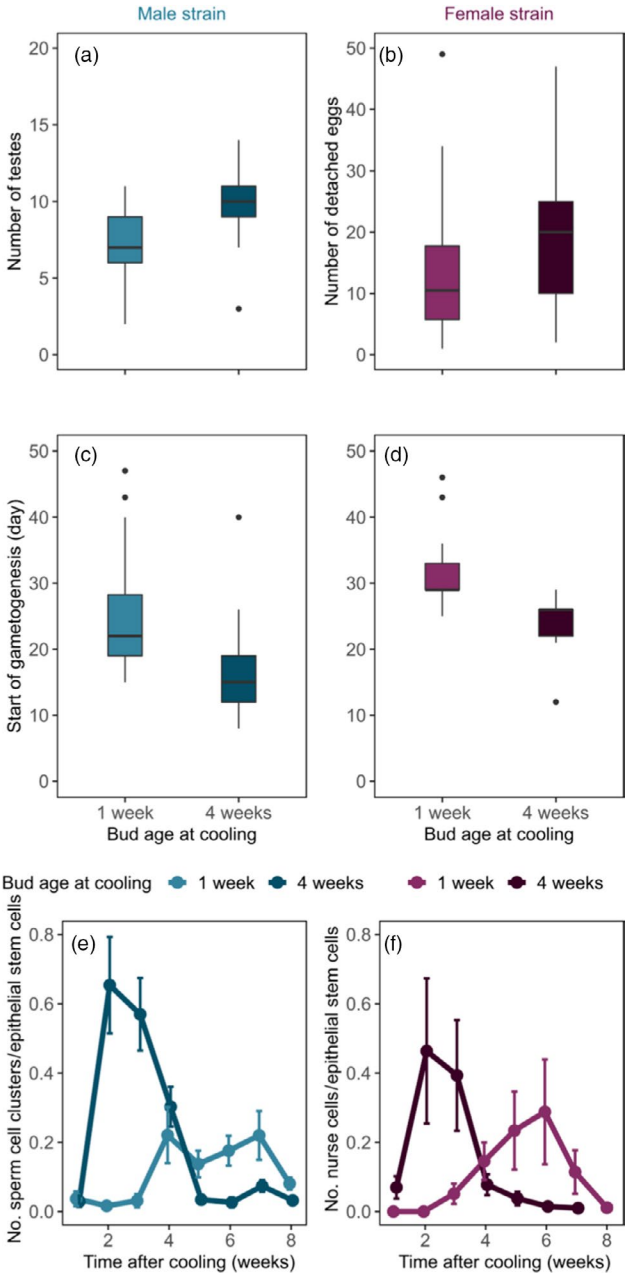

FIGURE 3 Traits related to gametogenesis. The overall number of sexual organs (testes in the male strain (a), detached eggs in the female strain (b)), start day of gametogenesis (male strain (c), female strain (d)). And weekly measurements of reproductive cells (sperm precursor cell clusters or nurse cells, e and f) in the two age groups in two strains

3.3 | Sexual reproductive cell number

In isolation, bud age at cooling had a significant effect on the number of sexual reproductive cells in both sexes (in males: $\chi^2_2 = 9.41$, $p = 0.009$, $b = 0.866 \pm 0.276$, in females: $\chi^2_2 = 7.82$, $df = 2$, $p = 0.02$, $b = -1.286 \pm 0.643$) and time after cooling was also significant (in males: $\chi^2_2 = 34.42$, $p < 0.001$, $b = -0.242 \pm 0.064$, in females: $\chi^2_2 = 19.17$, $p < 0.001$, $b = -0.488 \pm 0.138$). The interaction between these two were significant in males ($\chi^2_2 = 13.15$, $p = 0.001$, $b = -0.435 \pm 0.115$) and marginally significant in females ($\chi^2_2 = 4.75$, $p = 0.093$, $b = -0.671 \pm 0.277$). In both sexes, reproductive cell numbers indicated a delayed start of gametogenesis in animals which were younger at cooling (Figure 3).

3.4 | Initiation of gametogenesis

The proportion of individuals which started gametogenesis during 2 months of measurements was 100% both in 1 week old ($N = 42$) and 4 weeks old ($N = 65$) males, and it was 92.9% in both 1 week old ($N = 56$) and 4 weeks old ($N = 56$) females.

3.5 | Head regeneration

Overall, both older males and females had significantly lower regenerative ability than younger males and females respectively (Figure 4). Bud age at cooling and time after cooling significantly affected head regeneration in both sexes (bud age at cooling:

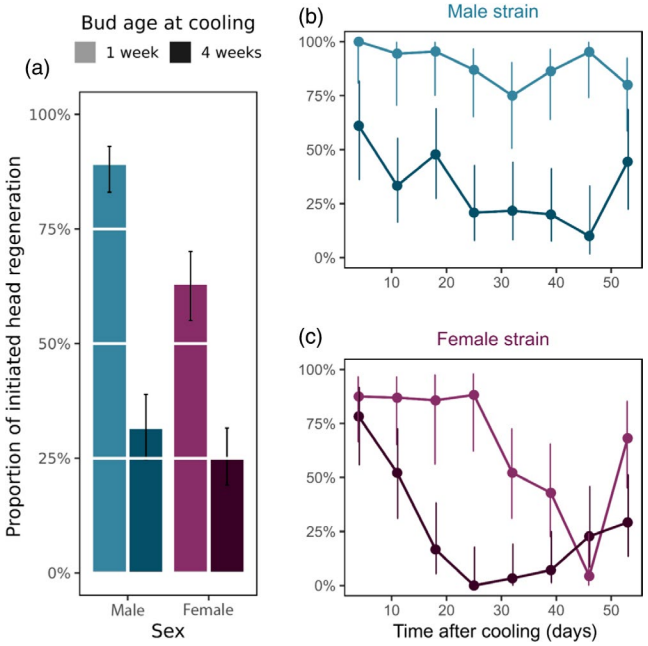

FIGURE 4 Overall initiated head regeneration rate in the two strains (a) and the proportions of weekly measurements in the male strain (b) and the female strain (c). Error bars show 95% confidence intervals

males: $\chi^2_1 = 117.1$, $p < 0.001$, $b = -0.14 \pm 0.015$, females: $\chi^2_1 = 47.12$, $p < 0.001$, $b = -0.085 \pm 0.013$; time after cooling: males: $\chi^2_1 = 5.9$, $p = 0.015$, $b = -0.151 \pm 0.064$, females: $\chi^2_1 = 40.5$, $p < 0.001$, $b = -0.059 \pm 0.01$). The interaction between bud age at cooling and time after cooling had no significant effect on head regeneration in males ($\chi^2_1 = 0.04$, $p = 0.836$, $b = 0.001 \pm 0.007$) or females ($\chi^2_1 = 1.71$, $p = 0.191$, $b = 0.012 \pm 0.009$).

3.6 | Survival

Polyps in the '4 week' group had significantly lower proportion of survived individuals 5 months after cooling in males ($\chi^2_1 = 9.56$, $p = 0.002$, $b = -0.117 \pm 0.051$) and marginally significantly in females ($\chi^2_1 = 3.75$, $p = 0.053$, $b = -0.042 \pm 0.019$, Figure 5).

3.7 | Interstitial stem cell number and bud age

In the case of males, bud age at cooling had significant effects on the number of interstitial stem cells ($\chi^2_1 = 8.24$, $p = 0.004$, $b = -0.73 \pm 0.247$) and time after cooling had a significant effect on male interstitial stem cell number ($\chi^2_1 = 17.65$, $p < 0.001$, $b = -0.201 \pm 0.045$). There was no significant interaction between the effect of bud age at cooling and time after cooling in males ($\chi^2_1 = 0.44$, $p = 0.508$, $b = 0.069 \pm 0.08$).

In females, the effect of bud age at cooling and time after cooling had significant effects independently (bud age at cooling: $\chi^2_1 = 19.72$, $p < 0.001$, $b = -2.647 \pm 0.624$; time after cooling: $\chi^2_1 = 24.43$, $p < 0.001$, $b = -0.415 \pm 0.078$). The interaction between bud age at cooling and time after cooling was significant in the case of females ($\chi^2_1 = 16.9$, $p < 0.001$, $b = -0.598 \pm 0.147$). Interstitial stem cell number of males and females showed a decreasing tendency in both bud age groups during the weeks at cool temperature, as Figure 6 indicates.

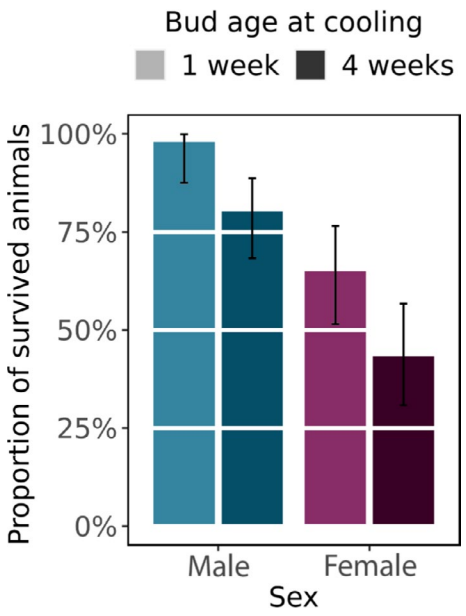

FIGURE 5 Proportion of survived animals following gametogenesis at the end of the fifth month after cooling. Animals were recorded as survived if they had fully intact tentacles, bodies and foot at the end of the experiment. Error bars show 95% confidence intervals

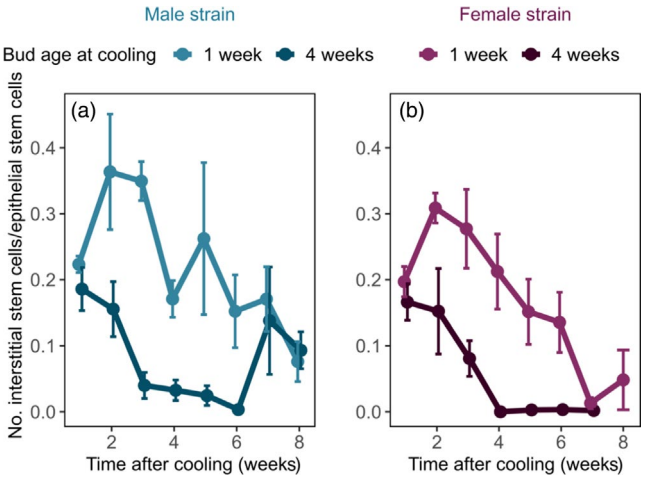

FIGURE 6 Weekly measurements of interstitial stem cells (a and b) in the two bud age groups in two strains

3.8 | Ontogenetic effects versus age-dependent plasticity

Bud numbers calculated by time after detachment rather than time after cooling still showed timing and intensity differences (Figure S2). Reproductive cell numbers, head regeneration in females and interstitial stem cell numbers calculated by time after detachment show that the shift in the temporal dynamics of the two age groups relative to each other was less pronounced, but the effect of age at cooling remained significant (Figures S3–S5).

4 | DISCUSSION

Here, we demonstrated that bud age has an effect on life-history traits in a partially clonal freshwater cnidarian *H. oligactis*. Our results highlight the role of age in phenotypic plasticity and suggest that the relation between reproductive modes and somatic maintenance changes with age. Despite that some clonal or partially clonal species (including *Hydra*) can have exceptional regenerative abilities, high survival rates and negligible or even negative senescence, we found marked age-dependent changes in their reproductive investment and resource allocation decisions in response to experimental induction of sex. Our results suggest that age-dependent reproductive mode strategies are linked to different somatic maintenance. This linkage likely plays a role in evolved senescence patterns (as sexual reproduction is usually paired with decreasing somatic maintenance [Kirkwood

& Rose, 1991] and asexual reproduction can be associated with negligible or negative senescence [Vaupel et al., 2004]); however, our study implies that these patterns might change during an organism's lifetime.

Age or life stage may affect how allocation to reproduction, regeneration, growth or maintenance is prioritized, but there is a difference in this nexus between non-clonal and clonal organisms. In a clonal or partially clonal organism, growth is not just the increase in size of a single somatic unit, but it inheres the production of physically separated clones as well (which can sexually propagate in the future; Harvell & Grosberg, 1988). Asexual reproduction is thought to maintain a population of locally adapted clones (Ayre & Miller, 2004) and less costly than sexual reproduction (Rispe, Pierre, Simon, & Gouyon, 1998). For this reason, asexual reproduction can be advantageous for animals in good conditions and early in their life, since they can rapidly colonize resources for their own genotype, while later they can use more costly sexual reproduction to increase genotypic diversity (Burke & Bonduriansky, 2018).

Our study confirms that sexual reproduction is prioritized later in life in *H. oligactis*. This is in accordance with previous findings in other partially clonal species. For instance, female stick insects that mated in early life (prior to the start of parthenogenetic reproduction) produce fewer eggs, possibly because they were not fully mature at pairing (Burke & Bonduriansky, 2018). Age-dependent sexual maturity is also known in some coral species (Kai & Sakai, 2008), while in *Pelmatohydra robusta* (likely synonymous to *H. oligactis*; Schwentner & Bosch, 2015) a decreased sexual maturation time and increased fecundity with polyp age were reported previously by Noda (1982). Our study also confirms that asexual reproduction in *H. oligactis* is more important at a younger age, paralleling other partially clonal animals where asexual cycles usually forgo sexual cycles (Olive, 2002; e.g. in rotifers: Denekamp et al., 2009, planaria: Castle, 1927 and ascidians: Gasparini et al., 2015). Although these general age-dependent reproductive mode patterns are known, experimental induction of reproductive mode switch in different ages is less frequently investigated but is needed to explicitly assess the costs and benefits of switching to sex.

We also found that these age-dependent reproductive modes are associated with different somatic maintenance costs: young polyps with higher asexual reproduction, delayed and reduced gametogenesis had higher regeneration and survival during our measurements, while the opposite was true for older hydra polyps. In other partially clonal species, high regeneration ability also often associates with asexual reproduction capabilities and higher/increasing survival rate (Mouton, Grudniewska, Glazenburg, Guryev, & Berezikov, 2018; Zattara & Bely, 2016), while the more costly sexual reproduction usually impairs these traits (Harvell & Grosberg, 1988; Henry & Hart, 2005). The negative effect of sexual reproduction is more emphasized when it is usually induced by stress and harsh conditions (Harvell & Grosberg, 1988), thus the response and investment is more urgent and intense (hypothesized in the study species *H. oligactis* as well e.g. Tardent, 1974), although these relations are generally not studied simultaneously with age-dependent changes. Although somatic maintenance traits as regeneration and survival usually do not decline with age in clonal organisms (Tanner, 2001; Yun, 2015), opposite patterns are observed in some cases (e.g. Meesters & Bak, 1995; Orive, 1995; Sköld et al., 2011). This may further suggest that predicting age-related somatic maintenance changes and senescence patterns depend on other life-history parameters of the organism as well (Orive, 1995), like the mode of reproduction. Finally, it is important to mention that we studied age-dependent differences in sex-induced individuals, but our study raises the question whether somatic maintenance changes with age in the asexual stage as well, and if so, how can negligible senescence be maintained with these age-dependent changes.

Beside age, sexual maturity can be also affected by body size, because age might be its predictor and in long-lived partially clonal animals there is often a minimum size for sexual reproduction (Harvell & Grosberg, 1988). Body size might have played a role in our experiment as well, because the importance of growth is known in another hydra species (*H. vulgaris*, in which growth occurs during the first three weeks even in starvation; Levitis & Goldstein, 2013) and the early investment into growth could set back gametogenesis in our study species. Ontogenesis can lead to dynamic changes especially in early life-history stages in clonal or partially clonal organisms (e.g. in corals: Bythell, Brown, & Kirkwood, 2018), and the constant readjustment of energy budget can be a driving mechanism for age-dependent plasticity. Indeed, the age-dependent differences observed in this study might reflect a fixed ontogenetic response. The temporal dynamics of reproductive and interstitial stem cell numbers and regeneration appeared to be shifted by approximately 3 weeks in the '1 week' group relative to the '4 weeks' group (Figures 3, 4 and 6). However, if we take time after detachment (i.e. absolute age) as a predictor to standardize age differences between the experimental groups, age at cooling still influences the traits investigated (Figures S2–S5). Overall, an ontogenetic shift and age-dependent plasticity might both contribute to explain variation in life-history strategies in *H. oligactis*.

On the proximate level, the increasing sexual propensity with age and the higher costs of reproduction in older polyps could be explained by the differentiation patterns of the underlying cell lineages. Reproductive cells in hydra are produced by germline stem cells (a stem cell lineage that is morphologically very similar to multipotent interstitial stem cells but is restricted to gamete production (Nishimiya-Fujisawa & Kobayashi, 2012). Germline stem cells derive from multipotent somatic interstitial stem cells that also give rise to somatic derivatives such as nematocytes, gland cells and nerve cells. Hence, sexual maturation might result in a shift in the differentiation of multipotent interstitial stem cells from somatic to reproductive derivatives. There are some observations indicating that the number of germline stem cells might increase with age after detachment from the asexual parent, at

least in females (Littlefield, 1991). These indicate a preparedness for sexual reproduction in terms of the number of germline stem cells in older age, and it is possible that there are not enough germline stem cells to produce a high number of reproductive cells in 1-week-old polyps. The cost of sexual reproduction could emerge from the reduced availability of limited amount of multipotent interstitial stem cells and their somatic derivatives, which are necessary for asexual reproduction, regeneration and somatic maintenance in general (Nishimiya-Fujisawa & Kobayashi, 2012). Alternatively, the higher costs of reproduction in 4 weeks than 1 week groups might have been caused by a difference in stress susceptibility in response to cold stress (higher susceptibility to cold stress in the younger group). However, in a previous study, we found that resistance to a different stressor (UV-radiation) increases, rather than decreases, with age in this species under a similar age range (Tökölyi et al., 2017). The sex of polyps can make understanding the proximate mechanisms behind the costs of reproduction in *H. oligactis* more complicated, and although we did not compare males and females since each sex was represented by only one clone, some differences between the male and female clones were present.

The presence of age-dependent plasticity in *H. oligactis* could explain some of the variation in life-history strategies observed in natural populations of this species. Sexual reproduction in *H. oligactis* is thought to be a diapausing strategy resulting in resting eggs that can survive winter conditions which the adults cannot survive (Reisa, 1973). However, in natural populations sexual, asexual and non-reproductive polyps regularly co-occur at the same time during autumn (Sebestyén et al., 2018). Some of this variation might be explained by genetic differences, as we have previously found different sexual propensity of clonal lineages derived from the same population, when kept under standard conditions in the laboratory (Tökölyi, Ősz, et al., 2017). However, there is clear evidence for phenotypic plasticity in reproductive modes from population genetics of field-collected individuals (Miklós et al., 2019). Based on the results presented in this study, polyp age could be one of the factors determining this plasticity, such that younger polyps reproduce asexually, while older ones initiate sexual reproduction when temperature drops during autumn. In addition to age, external factors such as food availability (Tökölyi, Kozma, Sebestyén, Miklós, & Barta, 2017) or population density (Bell & Wolfe, 1985) might contribute to variation in reproductive strategies, but the relative role of these factors remains to be elucidated.

The remarkable clonal plasticity observed in *H. oligactis* in this study has implications for reproducibility in laboratory studies involving clonal or partially clonal species. Forms of asexual reproduction (e.g. fragmentation, parthenogenesis or budding) are widespread among several model systems (i.e. planarians of the family *Dugesiidae*, the cladoceran *Daphnia*, rotifers, the starlet sea anemone *Nematostella vectensis* and hydroids of the genus *Hydra* [Hughes, 1989 and references therein]). These organisms are often kept in strain cultures (e.g. planaria, *Daphnia*, rotifers, *N. vectensis* or *Hydra* [Hughes, 1989 and references therein]), implying a mass of asexually propagated animals with varying age. Our study implies that the same environmental effect can induce different resource allocation and reproductive patters at different ages of individual polyps. Therefore, controlling for age in other clonal or partially clonal organisms might reveal similar patterns and certainly enhance the repeatability of studies in other fields.

ACKNOWLEDGEMENTS

This study was supported by NKFIH grant FK 124164. F.S., M.M. and J.T. were supported by the ÚNKP New National Excellence Program of the Hungarian Ministry for Innovation and Technology (ÚNKP-18-3, ÚNKP-19-3 and ÚNKP-19-4). J.T. was supported a János Bolyai Research Scholarship of the Hungarian Academy of Sciences. K.I. was supported by the Hungarian State and the European Union under the EFOP-3.6.1 project.

AUTHORS' CONTRIBUTIONS

F.S., M.M. and J.T. conceived research; F.S., M.M., K.I. and J.T. collected data; F.S. and J.T. analysed data; F.S. and J.T. wrote the manuscript.

DATA AVAILABILITY STATEMENT

Data for this article are archived in Figshare: https://doi.org/10.6084/m9.figshare.8313641.v1 (Sebestyén, Miklós, Iván & Tökölyi, 2019).

ORCID

Flóra Sebestyén https://orcid.org/0000-0001-5310-1647
Jácint Tökölyi https://orcid.org/0000-0002-6908-6493

REFERENCES

Alexandrova, O., Schade, M., Böttger, A., & David, C. N. (2005). Oogenesis in *Hydra*: Nurse cells transfer cytoplasm directly to the growing oocyte. *Developmental Biology*, *281*(1), 91–101. https://doi.org/10.1016/j.ydbio.2005.02.015

Ayre, D., & Miller, K. (2004). Where do clonal coral larvae go? Adult genotypic diversity conflicts with reproductive effort in the brooding coral *Pocillopora damicornis*. *Marine Ecology Progress Series*, *277*, 95–105. https://doi.org/10.3354/meps277095

Bell, G., & Wolfe, L. M. (1985). Sexual and asexual reproduction in a natural population of *Hydra pseudoligactis*. *Canadian Journal of Zoology*, *63*(4), 851–856.

Bely, A. E., & Nyberg, K. G. (2010). Evolution of animal regeneration: Re-emergence of a field. *Trends in Ecology & Evolution*, *25*(3), 161–170. https://doi.org/10.1016/j.tree.2009.08.005

Berube, C. H., Festa-Bianchet, M., & Jorgenson, J. T. (1999). Individual differences, longevity, and reproductive senescence in bighorn ewes. *Ecology*, *80*(8), 2555. https://doi.org/10.2307/177240

Bode, H. R. (2003). Head regeneration in *Hydra*. *Developmental Dynamics*, *226*(2), 225–236. https://doi.org/10.1002/dvdy.10225

Bruno, J. F., & Edmunds, P. J. (1997). Clonal variation for phenotypic plasticity in the coral *Madracis mirabilis*. *Ecology*, *78*(7), 14.

Burke, N. W., & Bonduriansky, R. (2018). The fitness effects of delayed switching to sex in a facultatively asexual insect. *Ecology and Evolution*, *8*(5), 2698–2711. https://doi.org/10.1002/ece3.3895

Bythell, J. C., Brown, B. E., & Kirkwood, T. B. (2018). Do reef corals age? *Biological Reviews*, *93*(2), 1192–1202. https://doi.org/10.1111/brv.12391

Castle, W. A. (1927). The life history of *Planaria velata*. *The Biological Bulletin*, *53*(3), 139–144. https://doi.org/10.2307/1536995

Chen, Q., Sheng, J., Lin, Q., Gao, Y., & Lv, J. (2006). Effect of salinity on reproduction and survival of the copepod *Pseudodiaptomus annandalei* Sewell, 1919. *Aquaculture*, *258*(1–4), 575–582. https://doi.org/10.1016/j.aquaculture.2006.04.032

Chevin, L. M., Lande, R., & Mace, G. M. (2010). Adaptation, plasticity, and extinction in a changing environment: Towards a predictive theory. *PLoS Biology*, *8*(4), e1000357. https://doi.org/10.1371/journal.pbio.1000357

Cichoń, M. (1997). Evolution of longevity through optimal resource allocation. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *264*(1386), 1383–1388. https://doi.org/10.1098/rspb.1997.0192

Cichoń, M. (2001). Diversity of age-specific reproductive rates may result from ageing and optimal resource allocation: Reproductive rates and ageing. *Journal of Evolutionary Biology*, *14*(1), 180–185. https://doi.org/10.1046/j.1420-9101.2001.00243.x

Cichoń, M., & Kozłowski, J. (2000). Ageing and typical survivorship curves result from optimal resource allocation. *Evolutionary Ecology Research*, *2*(7), 857–870.

Clutton-Brock, T. H. (1984). Reproductive effort and terminal investment in iteroparous animals. *The American Naturalist*, *123*(2), 212–229. https://doi.org/10.1086/284198

Cox, R. M., Lovern, M. B., & Calsbeek, R. (2014). Experimentally decoupling reproductive investment from energy storage to test the functional basis of a life-history trade-off. *Journal of Animal Ecology*, *83*(4), 888–898. https://doi.org/10.1111/1365-2656.12228

David, C. N. (1973). A quantitative method for maceration of hydra tissue. *Wilhelm Roux' Archiv Für Entwicklungsmechanik Der Organismen*, *171*(4), 259–268. https://doi.org/10.1007/BF00577724

Denekamp, N. Y., Thorne, M. A., Clark, M. S., Kube, M., Reinhardt, R., & Lubzens, E. (2009). Discovering genes associated with dormancy in the monogonont rotifer *Brachionus plicatilis*. *BMC Genomics*, *10*(1), 108. https://doi.org/10.1186/1471-2164-10-108

Endler, J. A. (1977). *Geographic variation, speciation, and clines* (Vol. 10). Princeton, NJ: Princeton University Press.

Engen, S., & Saether, B. E. (1994). Optimal allocation of resources to growth and reproduction. *Theoretical Population Biology*, *46*(2), 232–248. https://doi.org/10.1006/tpbi.1994.1026

Fischer, B., van Doorn, G. S., Dieckmann, U., & Taborsky, B. (2014). The evolution of age-dependent plasticity. *The American Naturalist*, *183*(1), 108–125. https://doi.org/10.1086/674008

Frost, P. C., Ebert, D., & Smith, V. H. (2008). Bacterial infection changes the elemental composition of *Daphnia magna*. *Journal of Animal Ecology*, *77*(6), 1265–1272. https://doi.org/10.1111/j.1365-2656.2008.01438.x

Galliot, B., Buzgariu, W. C., Schenkelaars, Q., & Wenger, Y. (2018). Non-developmental dimensions of adult regeneration in *Hydra*. *International Journal of Developmental Biology*, *62*(6–8), 373–381. https://doi.org/10.1387/ijdb.180111bg

Gardner, S. N., & Mangel, M. (1999). Modeling investments in seeds, clonal offspring, and translocation in a clonal plant. *Ecology*, *80*(4), 1202–1220. https://doi.org/10.1890/0012-9658(1999)080[1202:MIISCO]2.0.CO;2

Gasparini, F., Manni, L., Cima, F., Zaniolo, G., Burighel, P., Caicci, F., … Ballarin, L. (2015). Sexual and asexual reproduction in the colonial ascidian *Botryllus schlosseri*: Reproduction in a Colonial Ascidian. *Genesis*, *53*(1), 105–120. https://doi.org/10.1002/dvg.22802

Glazier, D. S., & Calow, P. (1992). Energy allocation rules in *Daphnia magna*: Clonal and age differences in the effects of food limitation. *Oecologia*, *90*(4), 540–549. https://doi.org/10.1007/BF01875448

Harvell, C. D., & Grosberg, R. K. (1988). The timing of sexual maturity in clonal animals. *Ecology*, *69*(6), 1855–1864. https://doi.org/10.2307/1941162

Henry, L.-A., & Hart, M. (2005). Regeneration from injury and resource allocation in sponges and corals – A review. *International Review of Hydrobiology*, *90*(2), 125–158. https://doi.org/10.1002/iroh.200410759

Hughes, R. N. (1989). *Functional biology of clonal animals*. London, UK: Chapman and Hall.

Jones, O. R., Scheuerlein, A., Salguero-Gómez, R., Camarda, C. G., Schaible, R., Casper, B. B., … Vaupel, J. W. (2013). Diversity of ageing across the tree of life. *Nature*, *505*(7482), 169–173. https://doi.org/10.1038/nature12789

Kai, S., & Sakai, K. (2008). Effect of colony size and age on resource allocation between growth and reproduction in the corals *Goniastrea aspera* and *Favites chinensis*. *Marine Ecology Progress Series*, *354*, 133–139. https://doi.org/10.3354/meps07216

Kirkwood, T. B. L., & Rose, M. R. (1991). Evolution of senescence: Late survival sacrificed for reproduction. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *332*(1262), 15–24. https://doi.org/10.1098/rstb.1991.0028

Kozłowski, J. (1992). Optimal allocation of resources to growth and reproduction: Implications for age and size at maturity. *Trends in Ecology & Evolution*, *7*(1), 15–19. https://doi.org/10.1016/0169-5347(92)90192-E

Krois, N. R., Cherukuri, A., Puttagunta, N., & Neiman, M. (2013). Higher rate of tissue regeneration in polyploid asexual versus diploid sexual freshwater snails. *Biology Letters*, *9*(4), 20130422. https://doi.org/10.1098/rsbl.2013.0422

Lester, R. T., & Bak, R. P. M. (1985). Effects of environment on regeneration rate of tissue lesions in the reef coral *Montastrea annularis* (Scleractinia). *Marine Ecology Progress Series*, *24*(1/2), 183–185. https://doi.org/10.3354/meps024183

Levitis, D. A., & Goldstein, J. (2013). The consistent, non-destructive measurement of small proteiform aquatic animals, with application to the size and growth of hydra. *Marine and Freshwater Research*, *64*(4), 332. https://doi.org/10.1071/MF12220

Littlefield, C. L. (1991). Cell lineages in *Hydra*: Isolation and characterization of an interstitial stem cell restricted to egg production in *Hydra oligactis*. *Developmental Biology*, *143*(2), 378–388. https://doi.org/10.1016/0012-1606(91)90088-K

Littlefield, C. L., Dunne, J. F., & Bode, H. R. (1985). Spermatogenesis in *Hydra oligactis*: I. Morphological description and characterization using a monoclonal antibody specific for cells of the spermatogenic pathway. *Developmental Biology*, *110*(2), 308–320. https://doi.org/10.1016/0012-1606(85)90090-9

Martin, K. (1995). Patterns and mechanisms for age-dependent reproduction and survival in birds. *American Zoologist*, *35*(4), 340–348. https://doi.org/10.1093/icb/35.4.340

Martinez, D. E., & Levinton, J. S. (1992). Asexual metazoans undergo senescence. *Proceedings of the National Academy of Sciences of the United States of America*, *89*(20), 9920–9923. https://doi.org/10.1073/pnas.89.20.9920

McNamara, J. M., & Houston, A. I. (1996). State-dependent life histories. *Nature*, *380*(6571), 215–221. https://doi.org/10.1038/380215a0

Meesters, E., & Bak, R. (1995). Age-related deterioration of a physiological function in the branching coral *Acropora palmata*. *Marine Ecology Progress Series*, *121*, 203–209. https://doi.org/10.3354/meps121203

Miklós, M., Lackó, L., Sramkó, G., Sebestyén, F., Barta, Z., & Tökölyi, J. (2019). Population genomic structure underlying extremely divergent life-history strategies in hydra. *ResearchGate*. https://doi.org/10.13140/RG.2.2.34448.87044

Mouton, S., Grudniewska, M., Glazenburg, L., Guryev, V., & Berezikov, E. (2018). Resilience to aging in the regeneration-capable flatworm

Macrostomum lignano. *Aging Cell*, *17*(3), e12739. https://doi.org/10.1111/acel.12739

Muko, S., Sakai, K., & Iwasa, Y. (2001). Size distribution dynamics for a marine sessile organism with space-limitation in growth and recruitment: Application to a coral population. *Journal of Animal Ecology*, *70*(4), 579–589. https://doi.org/10.1046/j.1365-2656.2001.00513.x

Nishimiya-Fujisawa, C., & Kobayashi, S. (2012). Germline stem cells and sex determination in *Hydra*. *The International Journal of Developmental Biology*, *56*(6–8), 499–508. https://doi.org/10.1387/ijdb.123509cf

Noda, K. (1982). Sexual differentiation in *Pelmatohydra robusta*. I. Response to a temperature change is dependent on the duration of an asexual period after hatching. *Journal of Experimental Zoology*, *221*(2), 237–243.

Olive, P. J. (2002). Reproduction and life cycles in invertebrates. In John Wiley & Sons, Ltd (Ed.), *Encyclopedia of life sciences* (p. a0003649). Chichester, UK: John Wiley & Sons Ltd. https://doi.org/10.1038/npg.els.0003649

Orive, M. E. (1995). Senescence in organisms with clonal reproduction and complex life histories. *The American Naturalist*, *145*(1), 90–108. https://doi.org/10.1086/285729

R Core Team. (2018). *R: A language and environment for statistical computing*. Retrieved from https://www.R-project.org

Radchuk, V., Turlure, C., & Schtickzelle, N. (2013). Each life stage matters: The importance of assessing the response to climate change over the complete life cycle in butterflies. *Journal of Animal Ecology*, *82*(1), 275–285. https://doi.org/10.1111/j.1365-2656.2012.02029.x

Reisa, J. (1973). Ecology of hydra. In A. Burnett (Ed.), *Biology of hydra* (pp. 59–105). New York, NY and London, UK: Academic Press.

Richardson, J., & Smiseth, P. T. (2019). Effects of variation in resource acquisition during different stages of the life cycle on life-history traits and trade-offs in a burying beetle. *Journal of Evolutionary Biology*, *32*(1), 19–30. https://doi.org/10.1111/jeb.13388

Rispe, C., Pierre, J.-S., Simon, J.-C., & Gouyon, P.-H. (1998). Models of sexual and asexual coexistence in aphids based on constraints. *Journal of Evolutionary Biology*, *11*(6), 685–701. https://doi.org/10.1046/j.1420-9101.1998.11060685.x

Rizopoulos, D. (2019). *Glmmadaptive: Generalized linear mixed models using adaptive gaussian quadrature*. R package version 0.6-0. Retrieved from https://cran.r-project.org/web/packages/GLMMadaptive/index.html

Saccucci, M. J., Denton, R. D., Holding, M. L., & Gibbs, H. L. (2016). Polyploid unisexual salamanders have higher tissue regeneration rates than diploid sexual relatives. *Journal of Zoology*, *300*(2), 77–81. https://doi.org/10.1111/jzo.12339

Schaible, R., Scheuerlein, A., Dańko, M. J., Gampe, J., Martínez, D. E., & Vaupel, J. W. (2015). Constant mortality and fertility over age in *Hydra*. *Proceedings of the National Academy of Sciences of the United States of America*, 201521002. https://doi.org/10.1073/pnas.1521002112

Schaller, H. C. (1976). Action of the head activator as a growth hormone in hydra. *Cell Differentiation*, *5*(1), 1–11. https://doi.org/10.1016/0045-6039(76)90009-9

Schenkelaars, Q., Tomczyk, S., Wenger, Y., Ekundayo, K., Girard, V., Buzgariu, W., … Galliot, B. (2017). *Hydra*, a model system for deciphering the mechanisms of aging and resistance to aging. In J. L. Ram & P. M. Conn (Eds.), *Conn's handbook of models for human aging* (2nd ed., pp. 507–520). Lubbock, TX: Elsevier.

Schröder, T., & Gilbert, J. J. (2004). Transgenerational plasticity for sexual reproduction and diapause in the life cycle of monogonont rotifers: Intraclonal, intraspecific and interspecific variation in the response to crowding. *Functional Ecology*, *18*(3), 458–466. https://doi.org/10.1111/j.0269-8463.2004.00854.x

Schuchert, P. (2010). The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Capitata part 2. *Revue Suisse De Zoologie*, *117*(3), 337–555.

Schwentner, M., & Bosch, T. C. G. (2015). Revisiting the age, evolutionary history and species level diversity of the genus *Hydra* (Cnidaria: Hydrozoa). *Molecular Phylogenetics and Evolution*, *91*, 41–55. https://doi.org/10.1016/j.ympev.2015.05.013

Sebestyén, F., Barta, Z., & Tökölyi, J. (2018). Reproductive mode, stem cells and regeneration in a freshwater cnidarian with postreproductive senescence. *Functional Ecology*, *32*(11), 2497–2508. https://doi.org/10.1111/1365-2435.13189

Sebestyén, F., Miklós, M., Iván, K., & Tökölyi, J. (2019). Data from: Age-dependent plasticity in reproductive investment, regeneration capacity and survival in a partially clonal animal (*Hydra oligactis*). *Figshare*, https://doi.org/10.6084/m9.figshare.8313641.v1

Shimizu, H., Sawada, Y., & Sugiyama, T. (1993). Minimum tissue size required for hydra regeneration. *Developmental Biology*, *155*(2), 287–296. https://doi.org/10.1006/dbio.1993.1028

Sköld, H. N., Asplund, M. E., Wood, C. A., & Bishop, J. D. D. (2011). Telomerase deficiency in a colonial ascidian after prolonged asexual propagation. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, *316B*(4), 276–283. https://doi.org/10.1002/jez.b.21399

Sköld, H. N., & Obst, M. (2011). Potential for clonal animals in longevity and ageing studies. *Biogerontology*, *12*(5), 387–396. https://doi.org/10.1007/s10522-011-9333-8

Stearns, S. C. (1992). *The evolution of life histories* (1st ed.). Oxford, UK; New York, NY: Oxford University Press.

Tan, T. C. J., Rahman, R., Jaber-Hijazi, F., Felix, D. A., Chen, C., Louis, E. J., & Aboobaker, A. (2012). Telomere maintenance and telomerase activity are differentially regulated in asexual and sexual worms. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(11), 4209–4214. https://doi.org/10.1073/pnas.1118885109

Tanner, J. E. (2001). The influence of clonality on demography: Patterns in expected longevity and survivorship. *Ecology*, *82*(7), 1971–1981. https://doi.org/10.1890/0012-9658(2001)082[1971:TIOCOD]2.0.CO;2

Tardent, P. (1974). Gametogenesis in the genus *Hydra*. *American Zoologist*, *14*(2), 447–456. https://doi.org/10.1093/icb/14.2.447

Tökölyi, J., Bradács, F., Hóka, N., Kozma, N., Miklós, M., Mucza, O., … Barta, Z. (2016). Effects of food availability on asexual reproduction and stress tolerance along the fast–slow life history continuum in freshwater hydra (Cnidaria: Hydrozoa). *Hydrobiologia*, *766*(1), 121–133. https://doi.org/10.1007/s10750-015-2449-0

Tökölyi, J., Kozma, B., Sebestyén, F., Miklós, M., & Barta, Z. (2017). Life history traits and previous exposure predict resistance to UV irradiation in the freshwater cnidarian *Hydra oligactis*. *Invertebrate Biology*, *136*(2), 217–227. https://doi.org/10.1111/ivb.12173

Tökölyi, J., Ősz, Z., Sebestyén, F., & Barta, Z. (2017). Resource allocation and post-reproductive degeneration in the freshwater cnidarian *Hydra oligactis* (Pallas, 1766). *Zoology*, *120*, 110–116. https://doi.org/10.1016/j.zool.2016.06.009

Tollrian, R. (1995). Predator-induced morphological defenses: costs, life history shifts, and maternal effects in *Daphnia Pulex*. *Ecology*, *76*(6), 1691–1705. https://doi.org/10.2307/1940703

Tomczyk, S., Schenkelaars, Q., Suknovic, N., Wenger, Y., Ekundayo, K., Buzgariu, W., … Galliot, B. (2017). Deficient autophagy drives aging in *Hydra*. *BioRxiv*, 236638. https://doi.org/10.1101/236638

Trembley, A. (1744). *Mémoires pour servir à l'histoire d'un genre de polypes d'eau douce, à bras en forme de cornes*. Leiden, The Netherlands: Chez Jean & Herman Verbeek.

Vaupel, J. W., Baudisch, A., Dölling, M., Roach, D. A., & Gampe, J. (2004). The case for negative senescence. *Theoretical Population Biology*, *65*(4), 339–351. https://doi.org/10.1016/j.tpb.2003.12.003

West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. Oxford, UK: Oxford University Press.

Yearsley, J. M., Kyriazakis, I., Gordon, I. J., Johnston, S. L., Speakman, J. R., Tolkamp, B. J., & Illius, A. W. (2005). A life history model of somatic damage associated with resource acquisition: Damage protection or prevention? *Journal of Theoretical Biology*, *235*(3), 305–317. https://doi.org/10.1016/j.jtbi.2005.01.009

Yoshida, K., Fujisawa, T., Hwang, J. S., Ikeo, K., & Gojobori, T. (2006). Degeneration after sexual differentiation in hydra and its relevance to the evolution of aging. *Gene*, *385*, 64–70. https://doi.org/10.1016/j.gene.2006.06.031

Yun, M. H. (2015). Changes in regenerative capacity through lifespan. *International Journal of Molecular Sciences*, *16*(10), 25392–25432. https://doi.org/10.3390/ijms161025392

Zattara, E. E., & Bely, A. E. (2016). Phylogenetic distribution of regeneration and asexual reproduction in Annelida: Regeneration is ancestral and fission evolves in regenerative clades. *Invertebrate Biology*, *135*(4), 400–414. https://doi.org/10.1111/ivb.12151

Zihler, J. (1972). Zur Gametogenese und Befruchtungsbiologie von*Hydra*. *Wilhelm Roux' Archiv Für Entwicklungsmechanik Der Organismen*, *169*(3), 239–267. https://doi.org/10.1007/BF00582555

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Sebestyén F, Miklós M, Iván K, Tökölyi J. Age-dependent plasticity in reproductive investment, regeneration capacity and survival in a partially clonal animal (*Hydra oligactis*). *J Anim Ecol*. 2020;89:2246–2257. https://doi.org/10.1111/1365-2656.13287