



Patterns of intraspecific variability in the response to caloric restriction



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ARTICLE INFO

Article history:

Received 23 July 2013

Received in revised form 10 December 2013

Accepted 12 December 2013

Available online 31 December 2013

Section Editor: T.E. Johnson

Keywords:

Caloric restriction

Evolution of aging

Rotifer

Resource allocation

Trade-off

Intermittent fasting

ABSTRACT

Caloric restriction (CR) is cited as the most robust means of increasing lifespan across a range of taxa, yet there is a high degree of variability in the response to CR, both within and between species. To examine the intraspecific evolutionary conservation of lifespan extension by CR, we tested the effects of chronic caloric restriction (CCR) at multiple food levels and of intermittent fasting (IF) in twelve isolates from the *Brachionus plicatilis* species complex of monogonont rotifers. While CCR generally increased or did not change lifespan and total fecundity, IF caused increased, unchanged, or decreased lifespan, depending upon the isolate, and decreased total fecundity in all but one isolate. Lifespan under ad libitum (AL) feeding varied among isolates and predicted the lifespan response to CR: longer-lived isolates under AL were less likely to have a significant increase in lifespan under CCR and were more likely to have a significantly shortened lifespan under IF. Lifespan under AL conditions and the response to CR were not correlated with hydroperiodicity of native habitat or with time in culture. Lack of trade-off between lifespan and fecundity under CCR, and differences in lifespan and fecundity under CCR and IF, even when average food intake was similar, suggest that longevity changes are not always directly determined by energy intake and that CCR and IF regimens extend lifespan through diverse genetic mechanisms.

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1. Introduction

Caloric restriction (CR) is frequently cited as the most reliable means of extending lifespan across diverse taxa and is frequently employed as a means to investigate the mechanisms of aging. Studies of CR in non-human model systems, with the goal of applying the results to better understand aging in humans, assume a common selective pressure as the origin of the CR response, yet the universality of this pressure is uncertain. A prevailing hypothesis is that the extension of lifespan due to CR is an evolutionary adaptation to low nutrient conditions, delaying senescence to increase the chance of reproducing when food again becomes available (Harrison and Archer, 1988). According to the life history theory, the timing and duration of key events in an organism's life—including development, age of maturity and first reproduction, parental investment, and senescence—are shaped by natural selection to maximize the number of viable offspring (Fisher, 1958; Stearns, 1989). In a natural extension of the life history theory, the disposable soma theory posits that in the face of limiting resources there is a trade-off between reproduction and maintenance of the adult body; plasticity in life history allows the optimal investment in somatic maintenance and reproduction with changes in the environment (Holliday, 1989; Kirkwood, 1977; Kirkwood, 2002). These theories predict that

organisms experiencing high extrinsic mortality would not evolve the capacity to extend lifespan or alter reproduction in response to environmental changes, and that CR would have the greatest effect on species with short reproductive lifespan and little effect on long-lived species like humans (Harrison and Archer, 1988; Phelan and Rose, 2005). Phelan and Austad (1989) pointed out that reproductive senescence, the end of the reproductive period, may not be relevant to evolution in natural systems if post-reproductive individuals are rare in the wild, but mounting evidence suggests that senescence is common in natural populations (Nussey et al., 2013). Over the years, resource allocation theories have been augmented by aspects of the hormesis hypothesis: the idea that stressors activate repair mechanisms, providing widespread repair and protection and possibly even increasing lifespan. Food limitation may be a stressor in itself, or increased food searching behavior due to CR could expose an organism to increased stressors, so upregulating stress-defense mechanisms would increase the chance of survival and secondarily extend lifespan (Masoro, 2007; Masoro and Austad, 1996; Phelan and Austad, 1989).

The more that CR is studied the more variability is found in its effect on lifespan, both within and among species. For example, wild mice under CR do not extend lifespan as strongly as laboratory mice, suggesting that laboratory conditions select for the CR effect, that there is genetic variability in the ability to respond to CR in wild populations that is not seen in inbred lines, or that the wild mice were simply not restricted at the correct level to see an effect (Harper et al. 2006). In a survey of 40 laboratory mouse strains, CR had no significant effect on the majority of strains, extended female lifespan in about one fifth of strains, and

Abbreviations: CR, caloric restriction; CCR, chronic caloric restriction; IF, intermittent fasting; AL, ad libitum.

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decreased female lifespan in about a quarter of strains; there was no correlation between lifespan under ad libitum (AL) and CR food conditions (Liao et al., 2010).

Different modes of imposing CR lead to variable results in the delay of age-related diseases, increased longevity, and changes in fecundity (Anson et al., 2003; Anson et al., 2005; Cleary and Grossmann, 2011; Dogan et al., 2011; Greer and Brunet, 2009; Gribble and Mark Welch, 2013). Recent studies suggest that long-lived primates subjected to CR may have increased lifespan and/or delayed onset of age related diseases in some but not all cases, differences that may be due to variation in the CR regimen (Mattison et al., 2012). Distinct genetic mechanisms have been associated with different CR regimens and species, highlighting the possible lack of a single selective pressure that gave rise to CR-mediated lifespan extension (Greer and Brunet, 2009; Kenyon, 2010). Additionally, expected trade-offs between fecundity and lifespan are not always seen either in long or short-lived animals (Gribble and Mark Welch, 2013; Johnston et al., 2006; Kirk, 2001; Sawada and Enesco, 1984). Exploring this variability in the CR response provides another means of probing the mechanisms and origins of aging.

In this study we investigated the effects of chronic caloric restriction (CCR) and intermittent fasting (IF) on the lifespan and fecundity of 12 isolates from the *Brachionus plicatilis* species group of monogonont rotifers. Rotifers have long been used for aging research and currently are being revived as a relevant model for phenotypic and molecular genetic research on aging. Studies on an array of rotifer species demonstrated that some increase, while others decrease, lifespan in response to CR (Fanestil et al., 1965; Gribble and Mark Welch, 2013; Kaneko et al., 2010; Kirk, 2001; Meadows and Barrows, 1971; Stelzer, 2001; Weithoff, 2007).

Rotifers are microscopic, aquatic, basally-branching triploblasts, with a number of advantages as an animal system for the study of aging (Austad, 2009). Their small size and ease of culturing allows testing of multiple treatments with a high degree of replication. As facultatively sexual animals, monogonont rotifers generally reproduce asexually, with a diploid female producing diploid eggs by mitosis. These eggs hatch into asexual (amictic) females, giving rise to a clonal population. In response to a quorum sensing mechanism, sexual (mictic) females are produced that generate haploid eggs through meiosis. If unfertilized, these haploid eggs hatch into males that can fertilize other haploid gametes to produce diploid, diapausing eggs. Males do not feed, so studies of CR are conducted on females.

The cultures used in this study were isolated from brackish ponds from around the world that varied in hydroperiodicity (the duration a wetland is covered by water) from ephemerally to permanently hydrated (Table 1, see table for hydroperiodicity definitions from Brock et al., 2003). All isolates belong to the *B. plicatilis* cryptic species complex, made up of at least 13 morphologically similar but genetically

distinct groups (Gómez et al., 2002; Mills et al., 2007) that have been the focus of several recent aging studies (Gribble and Mark Welch, 2013; Kaneko et al., 2010; Oo et al., 2010; Snell et al., 2012). Ten of the 12 isolates used in this study were from a single clade (Clade A) within the species complex and are able to interbreed, suggesting any differences in CR have evolved recently (Gribble and Mark Welch, 2012; Snell, 1989; Snell and Hawkinson, 1983; Suatoni et al., 2006). The other two isolates, *Brachionus* sp. Tiscar and *Brachionus* sp. Towerinninesis, are members of a different clade (Clade B) and cannot interbreed with the other isolates in this study (Gribble and Mark Welch, 2012; Mills et al., 2007; Suatoni et al., 2006).

The goal of this study was to explore the degree of conservation in the response to CR among closely related rotifer species and to determine if differences might be predictably related to environmental conditions including habitat stability or time in culture. Examination of variability in the lifespan and fecundity responses of closely related rotifer species derived from different environments provides a comparative system of “natural mutants” with which to investigate possible trade-offs between lifespan and reproduction and the universality of CR-mediated lifespan extension.

2. Materials and methods

Culturing and experimental conditions followed Gribble and Mark Welch (2013) and are described briefly below.

2.1. Cultures

The chlorophyte *Tetraselmis suecica* was maintained in 2 L flasks of bubbled 15 ppt artificial seawater (ASW) f/2 medium (Guillard, 1975) and was used as food for rotifer cultures. Both rotifer and algae cultures were kept at 21 °C on a 12:12 h light:dark cycle. Cultures of *T. suecica* used for CR studies were maintained in semi-continuous log phase growth by daily removal of approximately 20% of the culture and replacement with f/2 medium. Maternal *Brachionus* spp. females were maintained in ad libitum (AL) food conditions for at least one week prior to experiments to prevent known maternal effects of CR on offspring (Kaneko et al., 2010). Origins of isolates and species designations are given in Table 1. Data for the *B. manjavacas* RUS isolate were previously published (Gribble and Mark Welch, 2013).

2.2. Experimental conditions

In this study, we conducted life table experiments to examine the effects of different food concentrations on lifespan and reproduction of 12 isolates from the *B. plicatilis* cryptic species complex. Amictic eggs were removed from mature amictic females by vortexing, isolated by micropipette, and allowed to hatch for 5 h. Neonates were

Table 1

Species designation, culture origin, habitat type, and time in culture for 12 isolates from the *Brachionus plicatilis* species complex. Hydroperiodicity of native habitat is designated by E, ephemeral (fills for a few days after unpredictable rainfall); S, seasonal (alternately wet and dry every year, according to season); SP, semi-permanent (usually holds some water but occasionally dries); P, permanent (always holds water). Definitions from Brock et al. (2003).

Isolate	Species	Origin	Habitat	Years in culture
BmanL5	<i>B. manjavacas</i>	Manjavacas (Cuenca), Spain	SP	14
BmanMAN	<i>B. manjavacas</i>	Manjavacas (Cuenca), Spain	SP	2
BmanRUS	<i>B. manjavacas</i>	Azov Sea, Russia	SP	30
MNCHU008	<i>B. plicatilis</i> Austria	Chuluutiin Tsagaan Nuur, Mongolia	E	6
Bp HOS	<i>B. plicatilis</i> sensu stricto	El Hondo Sur lagoon, Spain	SP	2
BpL1	<i>B. plicatilis</i> sensu stricto	Torreblanca Sur (Castellon), Spain	S	10
BpL3	<i>B. plicatilis</i> sensu stricto	Torreblanca Sur (Castellon), Spain	S	10
BpSAL	<i>B. plicatilis</i> sensu stricto	Salobrejo Pond, Spain	SP	2
CGAL6	<i>B. plicatilis</i> sensu stricto	Clot de Galvany (Alicante), Spain	SP	14
USGET006	<i>B. plicatilis</i> sensu stricto	Eel Culture Pond, Mie Province, Japan	P	40
JPNAG023	<i>B. sp.</i> Tiscar	?	?	?
AUYEN020	<i>B. sp.</i> Towerinninesis	Yenyenning Lakes, Australia	SP	5

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