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1 **Population-level variation in senescence suggests an important role for temperature in an**  
2 **endangered mollusc**

3  
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20  
21 **Short title:** Thermal scaling of senescence in a long-lived mollusc

22 **Abstract**

23 Age-related declines in survival and function (senescence) were thought not to exist in wild  
24 populations as organisms, and particularly in invertebrates, do not live long enough. While, recent  
25 evidence has demonstrated that senescence is both common and measurable even in wild  
26 populations under field conditions, there are still organisms that are thought to exhibit “negligible  
27 senescence”. We explore variation in rates and patterns of senescence in the biogerontological  
28 model organism *Margaritifera margaritifera* across five populations, which differ in their age  
29 profile. In particular, we tested the theory of negligible senescence using time-at-death records for  
30 1091 specimens of *M. margaritifera*. There is clear evidence of senescence in all populations, as  
31 indicated by an increase in mortality with age, but the nature of the relationship varies subtly  
32 between populations. We find strong evidence of a mortality plateau at later ages in some  
33 populations but this is unequivocally absent from others. We then demonstrate that the temporal  
34 scaling of the rates of senescence between five populations of *M. margaritifera* can be explained by  
35 the variation in the thermal environment of the population. Hence climate change may pose a threat  
36 to the demography of this long-lived, endangered species, and a greater understanding of the  
37 relationship between river temperature and population structure will be essential to secure the  
38 species against global temperature increases. Our findings demonstrate that useful insights can be  
39 drawn from a non-invasive monitoring method to derive demographic data, and we suggest a wide-  
40 scale application of this method to monitor populations across the whole latitudinal (and, hence,  
41 thermal) range of the species.

42

43 **Keywords:** ageing, conservation, freshwater, *Margaritifera margaritifera*, mortality.

## 44 **Introduction**

45 It has long been suggested that senescence does not occur in the wild due to high extrinsic rates of  
46 mortality, although a wealth of recent studies have firmly refuted that assumption (Nussey *et al.*  
47 2013). Such studies have covered a wide and growing range of both invertebrates and vertebrates,  
48 reinforcing the theory that senescence is a ubiquitous phenomenon that manifests in all organisms.  
49 This is perhaps unsurprising given that some species are capable of reducing their extrinsic  
50 mortality through large body size, armoured carapaces, or escape behaviour such as flight  
51 (Kirkwood & Austad 2000). Examples have been described of particular taxa that are thought to  
52 exhibit “negligible senescence” – i.e. senescence that is so slow as to be difficult to quantify if it is  
53 present at all. These taxa tend to exhibit unusual forms of multicellularity such as the clonal *Hydra*  
54 (Martínez 1998), or a capacity to “reverse development” through reversion to the juvenile stage  
55 following cellular damage in other Cnidaria (Piraino *et al.* 2004). Less controversial examples of  
56 negligible senescence include deep ocean species such as the bivalve *Arctica islandica*, which has  
57 been recorded at ages of around 507 years at the time of capture (Butler *et al.* 2013) and which has  
58 been put to extensive use as a monitoring proxy for global environmental change. The longevity of  
59 *A. islandica* has been attributed to peculiarities in its metabolism, such as a reduced level of reactive  
60 oxygen species production (Munro *et al.* 2013), although there is evidence that *A. islandica* is also  
61 robust to a wide range of stressors (Ungvari *et al.* 2013). A growing body of biogerontological  
62 research on bivalve molluscs has demonstrated that longevity is positively (but weakly) associated  
63 with body size, and negatively (and strongly) associated with growth rates (Ridgway, Richardson &  
64 Austad 2011). This group has been identified as a new model of ageing, with a range of active  
65 research questions from genomics to ecosystems (Abele, Brey & Philipp 2009).

66  
67 While the marine *A. islandica* holds the record for the longest metazoan lifespan, its freshwater  
68 counterpart is the pearl mussel, *Margaritifera margaritifera* (Linnaeus, 1758). *M. margaritifera*,  
69 classified as Critically Endangered (CR) in Europe by the IUCN (Cuttelod, Seddon & Neubert

70 2011), is found across western Europe from the Iberian Peninsula to Scandinavia and in northwest  
71 Russia (Lopes-Lima *et al.* in press). The presence of *M. margaritifera* on lists of conservation  
72 concern may stem from its long pre-reproductive maturation, which may be as little as 7 years in  
73 the Iberian Peninsula but takes 10-15 years in the UK and likely much longer in colder climates,  
74 and its reliance on salmonid hosts during larval development and dispersal (Skinner, Young &  
75 Hastie 2003, Lopes-Lima *et al.* in press). Moving north along the latitudinal gradient from the  
76 Iberian Peninsula to Russia, *M. margaritifera* reaches greater ages and greater sizes, although age,  
77 size, and fecundity are correlated across populations suggesting that this is the product of  
78 phenotypic plasticity rather than adaptive change (Bauer 1992). River temperature has been  
79 suggested to correlate positively with the percentage of gravid *M. margaritifera* in a population,  
80 although these observations are complicated by variations in the timing of glochidia release  
81 (Österling 2015). It has been suggested that this species is able to increase its metabolic rate by up  
82 to 130x in order to repair wounds (Ziuganov *et al.* 2000), although the data are based on a very  
83 small sample size. If this extreme wound repair phenomenon occurs, it appears that it is insufficient  
84 to stave-off senescence as populations of *M. margaritifera* have been show to exhibit increased  
85 mortality at later ages (i.e. "actuarial senescence"; Popov & Ostrovsky 2011). However, no  
86 evidence has yet been presented of reproductive senescence in the species (Bauer 1987). It is also  
87 well known that the activity of antioxidant enzymes (e.g. catalase, superoxide dismutase) declines  
88 during aging in a wide array of animals, including humans (Martin & Grotewiel 2006). However,  
89 catalase and superoxide dismutase activities do not decline with age in *M. margaritifera* adults (14-  
90 44 years; Fernández, San Miguel & Fernández-Briera 2009).

91  
92 In addition to the *presence* of senescence, the conservation of long-lived species relies on a firm  
93 understanding of the shape of age-related mortality curves. In particular, differentiating between  
94 rapid declines in survival prior to reproductive maturity and mortality plateaus that occur in some  
95 species at later ages will provide much-needed parameterization of population models to predict the

96 long term viability of this species across its range. Furthermore, the temporal scaling of senescence  
97 could have substantial implications for species that have evolved life histories optimised for slow  
98 environments, especially if the scaling was related to a changing environmental variable such as  
99 temperature. The identification of intraspecific variation in senescence can be used to explore the  
100 mechanisms underlying age-related mortality in nature (Austad 1996). In this study, we analyse  
101 senescence patterns in five populations of *M. margaritifera*: four populations from Galicia in  
102 northern Spain and one population from Russia. We first test for the presence of senescence and  
103 then explore the scaling of different senescence rates in relation to the thermal environment of the  
104 populations.

105

## 106 **Methods**

### 107 *Field sampling*

108 The study material comprises 1091 empty shells of the freshwater pearl mussel (*Margaritifera*  
109 *margaritifera*, Linnaeus 1758). Sampled Spanish populations (n= 964) for longevity were located in  
110 Galicia (43° N) in north-western Spain (these populations lie at the southern edge of the species  
111 European range). Shells have been collected since 2007 using a random search method at four river  
112 sites within Galicia: Eo (n=450), Masma (n=323), Tea (n=107) and Ulla (n=84). The field methods  
113 have been described elsewhere (Lois *et al.* 2014, San Miguel *et al.* 2004). The mollusc species  
114 involved in this study is listed as Endangered in Galicia (CATGEA 2007). To remove shells (empty  
115 shells or shell fragments) requires permission for any disturbances on living organisms, and  
116 collecting was always carried out under the supervision of forest rangers from the autonomous  
117 government (Xunta de Galicia, Spain). Data were supplemented by shell age-at-death from a fifth  
118 population located in Peypia Stream in Leningrad Oblast (ca. 60°N, 31°E; n=127; Popov &  
119 Ostrovsky 2011).

120

### 121 *Shell ageing*

122 Ageing for specimens was done by counting annual rings for each individual according to  
123 Hendelberg (1961). To render these annuli clearly visible, shells were placed in a 5% solution of  
124 KOH at 50° C to carefully remove the periostracum. The yearly periodicity of deep annuli on the  
125 shells of *M. margaritifera* has been explained in detail and validated by several authors (Neves &  
126 Moyer 1988, Ziuganov et al. 2000, Ziuganov *et al.* 1994, Bauer 1992, San Miguel et al. 2004).

127

### 128 *Comparison of senescence models*

129 A general rule of thumb for sample sizes used in the calculation of survivorship curves is that  
130 population sizes should be greater than the reciprocal of the mortality risk for the period of interest  
131 (Curtsinger, Gavrilova, & Gavrilov, 2006). For instance, our populations have 50% mortality times  
132 of between 20 and 40 years, giving annual mortality rates of 1/40 and 1/80 and minimum  
133 recommended sample sizes of 40-80 individuals which is met by all of our samples. We  
134 acknowledged that the number of older individuals in all populations is considerably smaller and as  
135 a result our confidence concerning patterns of senescence at later ages is reduced.

136

137 Age-at-death data for the 1091 shells were collated and analysed for six common models of  
138 senescence, including a null model of no senescence (summarized in Table 1). Models were fitted  
139 using the SurvCurv website (Ziehm & Thornton, 2013). This tool allows the calculation of the fit of  
140 a variety of models through time-at-death data, with a comparison of model fit using Akaike's  
141 information criterion (AIC). We first analysed all the populations pooled to obtain a species-level  
142 description of the shape of the survivorship curve. We then calculated separate model comparisons  
143 for each of the constituent populations to investigate geographical variation in patterns of  
144 senescence.

145

### 146 *Temporal scaling in senescence*

147 In addition to testing for differences in the patterns of senescence in the raw mortality curves, we  
148 tested for the presence of temporal scaling of senescence between populations using the methods of  
149 Stroustrup et al. (2016). Briefly, we applied Buckley-James accelerated failure time models to  
150 account for differences in the duration of senescence curves between groups of individuals, then  
151 evaluated differences between the scaled curves using Kolmogorov-Smirnov tests. Finally, it is of  
152 interest to identify the proximate factors underlying the temporal scaling of senescence, and so we  
153 directed our attention to the thermal environment of the rivers in which the populations were found.  
154 Daily river temperature data were available for all of the four Galician rivers from 29/09/2012 to  
155 20/07/2014. Stream temperatures were not available for the Leningrad Oblast site, so we used data  
156 from the ART-Russia river temperature study site at 63.82°N, 38.47°E (approximately 500km from  
157 Peypia), as an exemplar of a boreal Russian lotic water body for which temperature data were  
158 available at 10 day intervals from 05/01/2000 to 25/12/2003 (Lammers, Pundsack & Shiklomanov  
159 2007). We calculated mean temperatures ( $\pm$ SE) of the water bodies across the available data to  
160 provide representative measures of the general thermal differences between rivers. While this  
161 thermal variable is a rather simplistic representation of the thermal environments of the five  
162 populations, the particular characteristics of the thermal niche that impact on survival and  
163 metabolism of *M. margaritifera* are unknown. The mean value provides a relative measure of  
164 energy availability between the five sites. We provide temperature time series in Figure S1 to  
165 illustrate the variation in detail.

166

## 167 **Results**

168 Age structures were very different for the five populations. While the maximum age in Leningrad  
169 Oblast was 95 years, the maximum age in Tea was only 27 years. Full age structure data are given in  
170 Table 2. The results of the analysis demonstrate unequivocal ageing across all populations, with the  
171 Exponential (no senescence) model being ranked last with  $\Delta$ AIC>100 in all populations. Taken as a  
172 single sample pooled across all populations, the results suggest that there is a levelling-off of the



173 mortality in older individuals as indicated by the logistic and logistic-Makeham models being  
174 selected as best-fit models in Table 3. However, when individual populations are analysed it is clear  
175 that there are a range of different best-fit models that imply different processes influencing survival  
176 (see Figure 1 for variation in the shape and rate of senescence). Leningrad Oblast (Figure 1A) and  
177 Masma (Figure 1B) populations both have best-fit models based around the logistic relationship  
178 (logistic or logistic-Makeham), suggesting that these population experience an exponential increase  
179 in mortality that plateaus at later ages. Where present, the Makeham correction adds an additional  
180 age-independent mortality probability.

181

182 While not the best-fit models, both the Tea (Figure 1D) and Ulla (Figure 1E) populations also show  
183 some support for the logistic models, which are within  $\Delta AIC < 10$  of the top model in both cases. It  
184 is likely that the small sample size ( $n=84$ ) is responsible for the lack of clear best-fit model in the  
185 case of Ulla. However, the best-fit models are Gompertz and Gompertz-Makeham, both of which  
186 imply the same exponential increase in mortality as the logistic models but without the plateau at  
187 later ages.

188

189 Of interest are the comparisons between the Eo population (Figure 1C) and the other four groups of  
190 animals. Eo has the largest sample size for specimens ( $n=450$ ) and so we can be most confident  
191 about the model comparison in this site. However, the Eo population also appears to support a  
192 Weibull model of ageing that vastly out-performs the other models ( $\Delta AIC \geq 21$  in all other cases).

193 The Weibull model implies a sub-exponential rate of increase in mortality with age and the absence  
194 of a plateau at later ages. The presence of the Weibull model as the top model in the Tea population  
195 suggests that this may not be a phenomenon isolated to Eo.

196

197 After rescaling, there were no significant differences in the pattern of senescence between any pair  
198 of populations ( $p > 0.7$  in all cases, Table S1), suggesting that the rescaled senescence curves were

199 quantitatively similar (Fig 2B). The mean annual temperature at each river or stream site shows a  
200 very strong correlation ( $r=0.908$ ,  $p=0.033$ ) with the coefficients of temporal scaling in the  
201 senescence curves for each population (Figure 3), suggesting that the variation in rates of  
202 senescence is linked to the thermal environment.

203

## 204 **Discussion**

205 The concept of “negligible senescence” is controversial and examples of “immortal” species are  
206 frequently special cases or equivocal while senescence is the norm (Nussey et al. 2013). However,  
207 there is strong evidence presented here that *M. margaritifera* at least exhibits a mortality plateau at  
208 later ages in some populations that may constitute negligible late-life senescence even though  
209 mortality rates increase with age over most of the lifespan. Despite the mortality plateau being well  
210 supported in the dataset consisting of five pooled populations, it is clear that this is not a species-  
211 wide phenomenon, as some individual populations show no evidence of such a plateau. Of  
212 particular interest is the potential role of temperature in determining the temporal scaling of  
213 senescence, which may contribute in important ways to both the physiology and demography of this  
214 species. It is known that temperature exerts a strong influence on *M. margaritifera* growth (Schöne  
215 et al. 2004), and the nature of that individual-level thermal response allows inferences concerning  
216 past climate (Schöne 2008). However, the majority of temperature experiments that have  
217 investigated *M. margaritifera* growth or survival have not used experimental manipulations of river  
218 temperature or large-scale comparisons across biomes, but have relied instead on seasonal or local,  
219 between-stream thermal differences (Denic et al. 2015, Taubert, Gum & Geist 2013). Below we  
220 discuss the implications of these different senescence trajectories and the implications of climate  
221 change for the conservation of the species.

222

223 The conservation of long-lived animals requires an understanding of the species’ demography,  
224 involving both mortality and reproductive rates and how those are impacted by the age-structure of

225 populations. Typically, individuals within a population exhibit a short pre-reproductive period  
226 followed by an increase in reproductive capacity to a point at which senescence occurs. In parallel,  
227 initial (juvenile) mortality may be very high, followed by a decline in mortality rates with age as the  
228 animal grows, and finally an age-related increase in mortality during actuarial senescence. Actuarial  
229 senescence has been suggested to play a key role in increasing extinction risk and rates (Robert *et*  
230 *al.* 2015), and understanding what drives senescence may help conserve long-lived animals  
231 (Hayward *et al.* 2014). As a result, the missing data on age-related demographic processes for long-  
232 lived groups such as sea birds (Lewison *et al.* 2012) or turtles (Heppell, Crowder & Crouse 1996)  
233 represent a substantial priority for future research.

234  
235 It has been suggested that *M. margaritifera*, which likely lives at least as long as elephants, sea  
236 birds, turtles, and other long-lived vertebrates (Philipp & Abele 2010), experiences negligible  
237 actuarial or reproductive senescence after the age of 20 (Bauer 1987), and that the species therefore  
238 represents a rare example of negligible senescence in a non-clonal metazoan. Our results support  
239 the conclusion that negligible senescence occurs in some populations after a certain age, but we  
240 provide clear evidence of inter-population variation in this pattern. For instance, while individuals  
241 >20 years old may be largely safe from natural enemies (Bauer 1987), the majority of animals in the  
242 Tea population (Figure 1D) are already dead by that age. The significance of these results lie in  
243 their relationship to the temporal scaling of senescence. The evolution of suites of “slow” life  
244 history traits, such as long pre-reproductive periods and slow growth, is of benefit in environments  
245 with low extrinsic mortality but also in environments of low intrinsic mortality. The negative  
246 correlation between temporal scaling and environmental temperature provide the first direct  
247 evidence that there may be a direct demographic consequence of temperature variation on *M.*  
248 *margaritifera* populations. Some experimental studies have looked at the developmental and  
249 metamorphosis success of unionid mussels and have shown that both high and low temperatures  
250 reduce survival (Taeubert, El-Nobi & Geist 2014). However, while such experiments are highly

251 tractable within *M. margaritifera* due to the number of rearing facilities in operation, studying the  
252 consequences of temperature on adult senescence would require an extensive, long-term experiment  
253 with collaboration across the network of conservation agencies currently working on the species.  
254 With average global river temperatures predicted to increase by 0.8-1.6°C (van Vliet *et al.* 2013)  
255 and far higher rates in the cold, boreal latitudes that currently harbour substantial populations of *M.*  
256 *margaritifera*, climate change may pose a considerable risk to the species. In addition to current  
257 “head start” breeding programmes, current research suggests two other potential mitigation  
258 measures. First, genetic variation between breeding stocks in responses to environmental variation  
259 suggests that one mitigation measure may be to transplant southern populations into cooler northern  
260 sites (Denic *et al.* 2015). Meanwhile river thermal environments could be preserved through the  
261 maintenance or enhancement of riparian vegetation which shades and cools water and also holds  
262 back sediment (Palmer *et al.* 2009).

263

264 These results, derived from an animal that has benefitted from several large conservation projects,  
265 provide valuable insights into the practical use of demographic patterns in conservation. In addition  
266 to simply incorporating patterns of actuarial and reproductive senescence into population dynamics  
267 models, it is possible to compare across populations to evaluate the current status of populations  
268 based on the relative contributions of age-related and extrinsic mortality pressures. The  
269 demographic snapshot afforded by the random collection of shells represents a stable history of the  
270 population that is readily accessible to researchers. However, analogous records could be found by  
271 estimating age at capture in living animals (Zajitschek *et al.* 2009, Hastie *et al.* 2000, Eaton & Link  
272 2011, Ailloud *et al.* 2015), and deriving estimates of mortality curves from those age structures.

273 There is also, clearly, a need to collect further data from the species using the “found shells”  
274 approach described here. Such a sampling method has the advantage of being non-destructive and  
275 easily carried out across multiple sites. Prospective sampling sites should include a stratified  
276 random sample of *M. margaritifera* habitats from across Europe with representatives from different

277 thermal regimes. Since thermal data are not available for all rivers, sampling should focus on those  
278 rivers for which temperature data have been collected (preferably for the past 5-10 years to give an  
279 estimate of interannual variability). Such field sampling could be coupled to field and laboratory  
280 experiments on local populations that monitor filtration and metabolic responses to variations in  
281 river temperature (e.g. Hartmann *et al.* 2016). Indeed, two key areas for study would be the UK  
282 (Hastie *et al.* 2000) and Sweden (Österling, Arvidsson & Greenberg 2010), where substantial  
283 populations of *M. margaritifera* are known to occur. Those other two regions not only bridge the  
284 thermal gap between our Spanish and Russian populations, but also used similar ageing methods to  
285 demonstrate age structures that are intermediate between the long-lived Leningrad Oblast population  
286 and the short-lived Galician populations (maximum age in UK: 26-123yrs; Hastie *et al.*, 2000;  
287 maximum age in Sweden: 80-140yrs; Österling, Arvidsson & Greenberg 2010).

288

289 Contrary to biogeographical theory, peripheral populations that are isolated from one another and  
290 from the causes of decline elsewhere in the range may persist longer than core populations during  
291 range collapse (Lomolino & Channell 1995, Donald & Greenwood 2001). Marginal relict  
292 populations, such as the Iberian populations of *M. margaritifera*, not only represent important  
293 habitats for the conservation of the species as a whole, but also contain genotypes that are either  
294 complementary to or representative of those in core populations (Guo 2012, Eckert, Samis &  
295 Lougheed 2008). The demographic patterns and genetic resources of these populations may  
296 represent valuable tools for the conservation of the species as a whole (San Miguel *et al.* 2004,  
297 Bouza *et al.* 2007). Specifically, it is possible to use mortality models to identify areas where the  
298 long term persistence of reproductive adults is threatened by sources of external mortality. This  
299 information can then be used in conservation programs to focus reintroduction on those areas with  
300 the highest probability of success. These results make clear the importance of biogerontological  
301 research for biodiversity conservation, and the capacity to generate useful insights into problems  
302 and solutions in conservation biology through a refined approach to mortality analysis.

303

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458

459

460 **Tables**

461 Table 1: Models of senescence with mathematical and verbal definitions.

<b>Model</b>	<b>Formula</b>	<b>Interpretation</b>
Exponential	$e^{-a*t}$	Age-independent mortality (i.e. no senescence), survivorship declines exponentially
Weibull	$e^{-(a*t)^b}$	Mortality increases non-exponentially with age
Gompertz	$e^{-\frac{a}{b}*(e^{b*t}-1)}$	Mortality increases exponentially with age
Gompertz-Makeham	$e^{-c*t-\frac{a}{b}*(e^{b*t}-1)}$	Mortality increases exponentially with age, with additional age-independent constant mortality
Logistic	$(1+s*a/b*(e^{b*t}-1))-1/s$	Mortality increases exponentially with age, but slows at older ages
Logistic-Makeham	$e^{-c*t*(1+s+\frac{a}{b}*(e^{b*t}-a))}-1/s$	Mortality increases exponentially with age, but slows at older ages, with additional age-independent constant mortality

462

463 Table 2: Age structures for five populations of *Margaritifera margaritifera* in Russia (Leningrad  
 464 Oblast) and Spain (Masma, Eo, Tea, and Ulla).  
 465

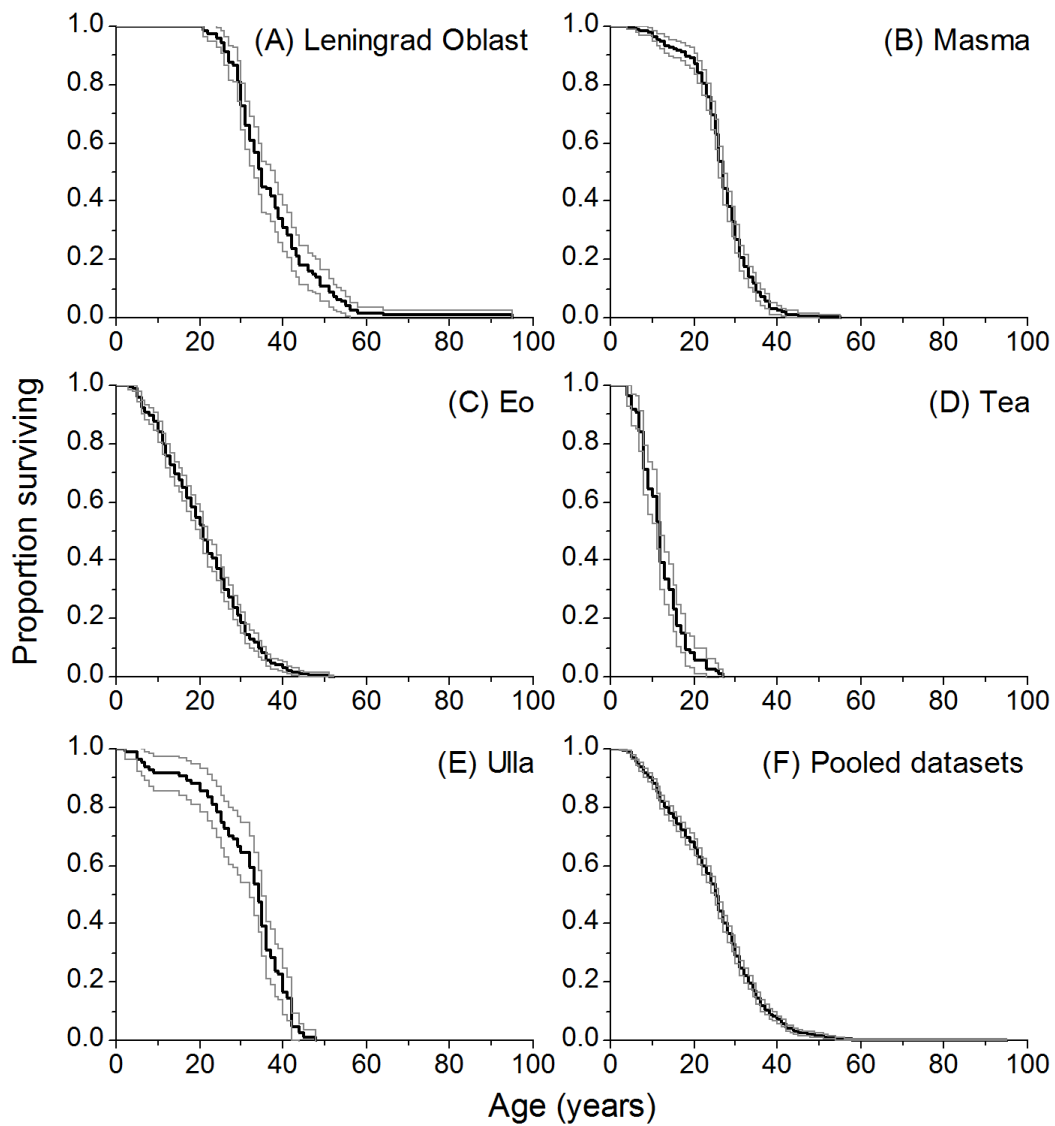
Age class	Leningrad Oblast	Masma	Eo	Tea	Ulla
0-5	0	1	5	4	1
5-10	0	5	51	34	6
10-15	0	18	81	37	0
15-20	0	11	66	23	3
20-25	5	64	79	6	8
25-30	19	117	73	3	10
30-35	38	68	52	0	16
35-40	22	29	25	0	21
40-45	20	6	13	0	17
45-50	9	2	2	0	2
50-55	7	1	3	0	0
55-60	5	1	0	0	0
60-65	1	0	0	0	0
65-70	0	0	0	0	0
70-75	0	0	0	0	0
75-80	0	0	0	0	0
80-85	0	0	0	0	0
85-90	0	0	0	0	0
90-95	0	0	0	0	0
95-100	1	0	0	0	0

466

467 Table 3: Comparison of survivorship models between populations of *Margaritifera margaritifera*  
 468 from Russia (Leningrad Oblast) and four rivers in Spain (Masma, Eo, Tea and Ulla). Values are the  
 469 parameters for the fitting of the different survivorship models and model comparison metrics  
 470 (AIC=Akaike's information criterion;  $w_i$ =Akaike weight). NA=parameter not present in the model.

Population	Model	a	b	c	s	AIC	$\Delta$ AIC	$w_i$
Eo	Weibull	4.20E-02	2.266	NA	NA	3319.7	0.0	1.000
	Logistic	8.44E-03	0.124	NA	0.5382	3340.6	21.0	<0.001
	Logistic-Makeham	8.44E-03	0.124	<0.0001	0.5382	3344.6	25.0	<0.001
	Gompertz	1.34E-02	0.076	NA	NA	3352.8	33.2	<0.001
	Gompertz-Makeham	1.34E-02	0.076	<0.0001	NA	3356.8	37.2	<0.001
	Exponential	4.75E-02	NA	NA	NA	3647.1	327.5	<0.001
Masma	Logistic-Makeham	2.40E-06	0.452	0.0044	2.0000	2165.1	0.0	0.990
	Logistic	3.09E-04	0.243	NA	0.7899	2174.4	9.3	0.010
	Weibull	3.40E-02	4.097	NA	NA	2204.7	39.6	<0.001
	Gompertz	3.01E-03	0.124	NA	NA	2252.8	87.7	<0.001
	Gompertz-Makeham	3.01E-03	0.124	<0.0001	NA	2256.8	91.7	<0.001
	Exponential	3.73E-02	NA	NA	NA	2774.5	609.4	<0.001
Tea	Weibull	7.30E-02	2.589	NA	NA	649.6	0.0	0.872
	Logistic	2.93E-03	0.482	NA	2.0000	653.7	4.1	0.113
	Logistic-Makeham	2.93E-03	0.482	<0.0001	2.0000	657.7	8.1	0.015
	Gompertz	2.11E-02	0.144	NA	NA	672.2	22.6	<0.001
	Gompertz-Makeham	2.11E-02	0.144	<0.0001	NA	676.2	26.6	<0.001
	Exponential	8.23E-02	NA	NA	NA	752.4	102.8	<0.001
Ulla	Gompertz-Makeham	2.57E-04	0.173	0.0054	NA	612.6	0.0	0.692
	Gompertz	1.32E-03	0.129	NA	NA	615.3	2.7	0.183
	Logistic-Makeham	1.72E-04	0.187	0.0058	0.0909	616.5	3.9	0.100
	Logistic	1.32E-03	0.129	NA	0.0000	619.3	6.7	0.025
	Weibull	2.91E-02	3.509	NA	NA	644.7	32.1	<0.001
	Exponential	3.20E-02	NA	NA	NA	750.0	137.4	<0.001
Leningrad Oblast	Logistic	2.61E-05	0.273	NA	2.0000	930.7	0.0	0.881
	Logistic-Makeham	2.61E-05	0.273	<0.0001	2.0000	934.7	4.0	0.119
	Weibull	2.44E-02	3.427	NA	NA	971.9	41.2	<0.001
	Gompertz	5.97E-03	0.056	NA	NA	1036.7	106.0	<0.001
	Gompertz-Makeham	5.97E-03	0.056	<0.0001	NA	1040.7	110.0	<0.001
	Exponential	2.69E-02	NA	NA	NA	1176.4	245.7	<0.001
Pooled sample	Logistic	5.49E-03	0.122	NA	0.5936	8298.2	0.0	0.808
	Logistic-Makeham	5.49E-03	0.122	<0.0001	0.5936	8302.2	4.0	0.109
	Weibull	3.61E-02	2.356	NA	NA	8302.8	4.6	0.083
	Gompertz	1.41E-02	0.056	NA	NA	8474.0	175.8	<0.001
	Gompertz-Makeham	1.41E-02	0.056	<0.0001	NA	8478.0	179.8	<0.001
	Exponential	4.07E-02	NA	NA	NA	9169.9	871.7	<0.001

471



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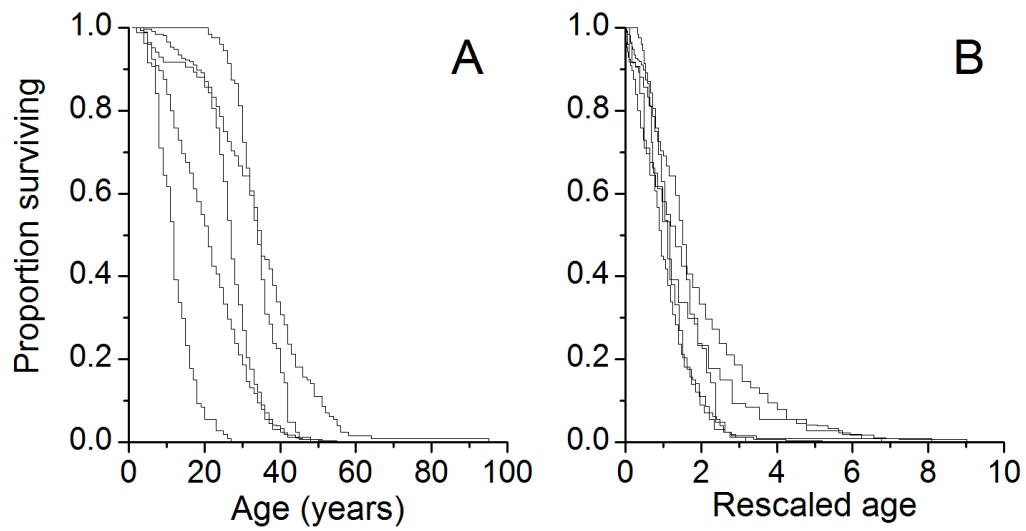
474 Figure 1: Survivorship curves with the best-fit survivorship models (shown in Table 3) from five

475 individual populations of *Margaritifera margaritifera* (A-E) and the species-level survivorship

476 curve from the pooled dataset (F).

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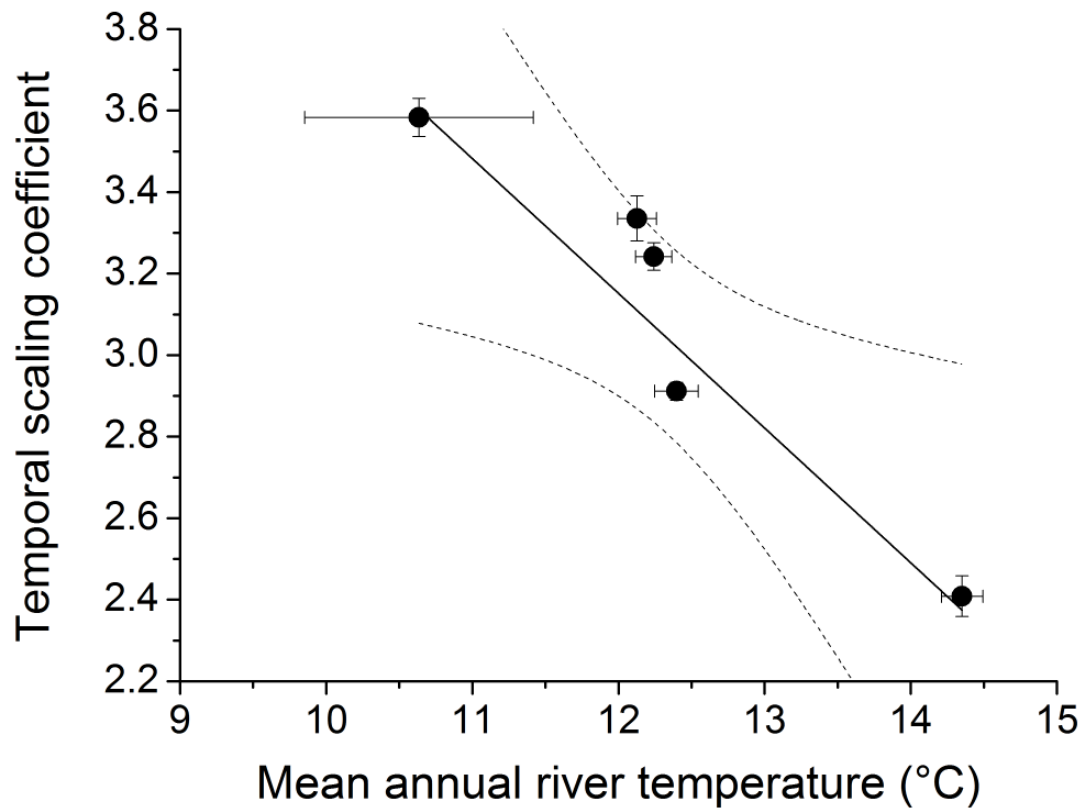




478

479 Figure 2: Mortality curves for five populations of the freshwater pearl mussel, *Margaritifera*  
480 *margaritifera*, showing (A) raw survivorship curves, and (B) survivorship curves following  
481 temporal rescaling.

482



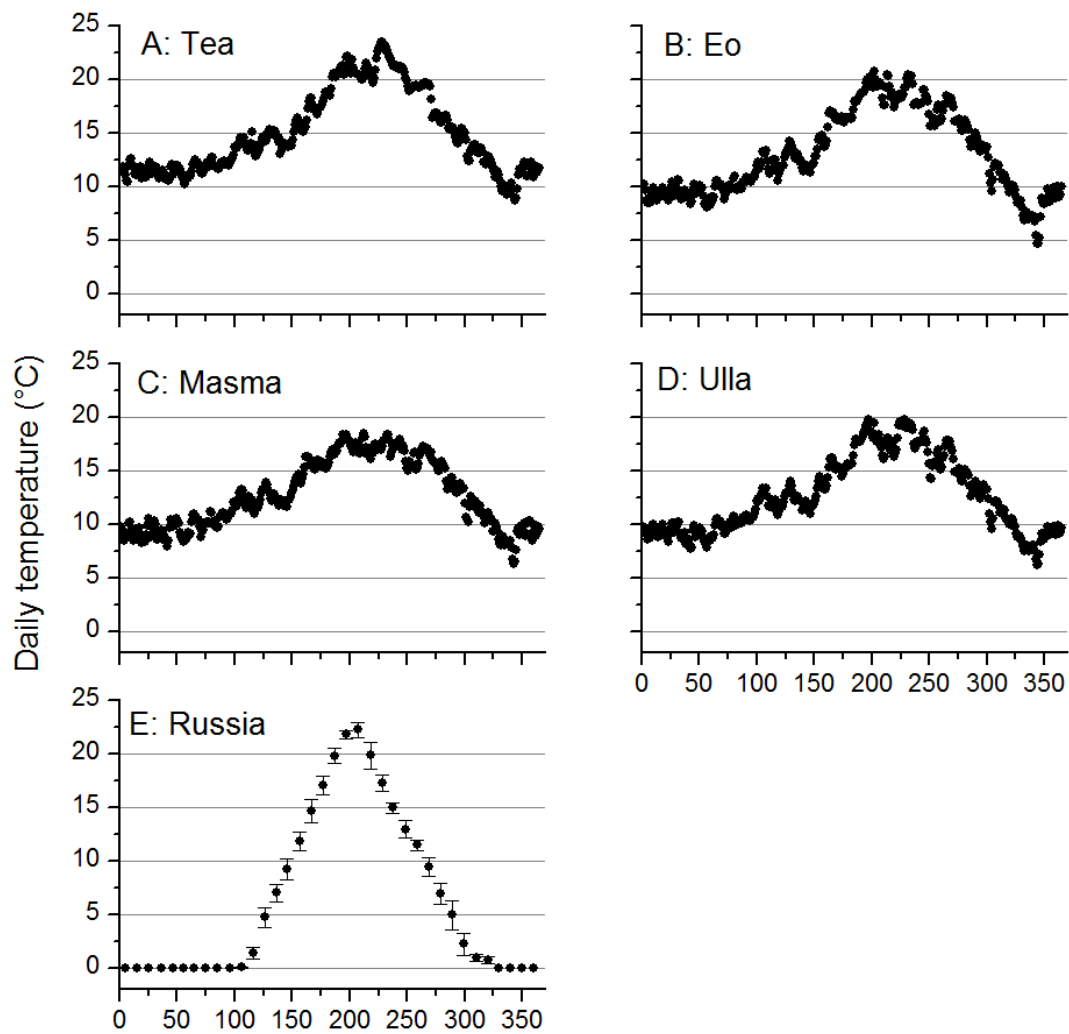
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484 Figure 3: The relationship between the rescaling coefficient and the thermal environment of the

485 population. Error bars are SE. Solid line is a linear regression with dotted lines indicating 95% CI.

486 **Supplementary information**

487 Figure S1: Annual temperature profiles for four Galician streams containing *Margaritifera*  
488 *margaritifera*, and a fifth river dataset to provide a comparison with a boreal lotic water body in  
489 western Russia (see text for details).



490

491 Table S1: Comparison of survivorship curves after temporal rescaling. Values are p-values from  
492 Kolmogorov-Smirnov tests (Stroustrup et al. 2016), where a non-significant p-value indicates no  
493 significant difference between the curves.

	LeningradOblast	Masma	Tea	Ulla
Eo	0.908	0.925	0.975	0.949
LeningradOblast		0.923	0.933	0.744
Masma			0.930	0.812
Tea				0.868

494