Patterns of natural mortality in stream-living brown trout (Salmo trutta)

JAVIER LOBÓN-CERVIÁ*, PHAEDRA BUDY† AND ERIK MORTENSEN1
*Department of Evolutionary Ecology, National Museum of Natural Sciences (CSIC), Madrid, Spain
†Department of Watershed Sciences, Utah State University, Logan, UT, U.S.A. and U.S. Geological Survey, Utah Cooperative Fish and Wildlife Research Unit, Intermountain Center for River Rehabilitation and Restoration, Utah State University, Logan, UT, U.S.A.

SUMMARY

1. We tested the hypothesis that lifetime mortality patterns and their corresponding rates and causal factors differ among populations of stream-living salmonids. To this end, we examined the lifetime mortality patterns of several successive cohorts of two stream-living brown trout (Salmo trutta) populations in Spain and Denmark.

2. In the southern population, we observed a consistent two-phase pattern, in which mortality was negligible during the first half of the lifetime and severe during the rest of the lifetime. In contrast, the northern population demonstrated a three-phase pattern with an earlier phase varying from negligible to severe, followed by a second stage of weak mortality, and lastly by a third life stage of severe mortality.

3. Despite substantial differences in the mortality patterns between the two populations, the combined effect of recruitment (as a proxy of the density-dependent processes occurring during the lifetime) and mean body mass (as a proxy of growth experienced by individuals in a given cohort) explained c. 89% of the total lifetime mortality rates across cohorts and populations.

4. A comparison with other published data on populations of stream-living brown trout within its native range highlighted lifetime mortality patterns of one, two, three and four phases, but also suggested that common patterns may occur in populations that experience similar individual growth and population density.

Keywords: density, growth, mortality rates, recruitment, stream-living salmonids

Introduction

The elucidation of mortality patterns across the lifetime and their corresponding rates and their causal factors is central in fish ecology research and critical for the effective design of management and conservation strategies. Across the lifetime, a wide array of factors may cause mortality including intrinsic factors such as lethal alleles in genotypes (Wootton, 1990), constraints in body size and temperature on metabolism (Pepin, 1991; McCoy & Gillooly, 2008) and age, sex and reproduction (Gunderson & Dygert, 1988; Hutchings, 1994). Extrinsic factors are also influential and may include the availability of space and food, parasites, predation, diseases and harsh environmental conditions such as extremes of temperature, discharge, oxygen depletion, winter conditions (Hurst, 2007) and climatic changes (Biró, Post & Booth, 2007). Moreover, both intrinsic and extrinsic factors may act in combination with fishing-induced mortality in exploited populations.

However, identifying mortality patterns in the wild and their causal factors has proved difficult for both marine and freshwater fish populations. Such difficulties have led to the development of a variety of predictive models through theoretical approaches involving metabolic (Brown et al., 2004) and size spectrum theories (Peterson & Wrobleski, 1984; Kerr & Dickie, 2001), mathematical inferences (Wang, 1999) and empirical models relating mortality rates with other life history traits (Beverton &
Stream-living salmonids exhibit an intriguing degree of variability in individual growth and population densities across ranges of environmental or climatic regions within their distributional ranges (Lobo´n-Cervia´, 2007a). Moreover, observational (Millner, Wyatt & Scott, 1993; Lobón-Cervia´, 2007b) and experimental studies (Heggenes & Børstrom, 1991) have demonstrated that habitat quality at the very small geographical scale of a stream or even of a stream reach may have profound effects on population density, suggesting that mortality patterns and their causal factors may differ widely within and among populations, within the species distributional range.

In this study, we tested the hypothesis that mortality patterns and their causal factors differ among populations of stream-living salmonids. To this end, we examined patterns of lifetime mortality over successive cohorts in two populations of stream-living brown trout, *Salmo trutta* L., that represent opposite extremes of individual growth and population density (Lobo´n-Cervia´, 2007a), as well as in life history modes exhibited by brown trout throughout its natural distributional range (Cucherousset et al., 2005). Moreover, these two populations inhabit streams located near the opposing extremes of temperature regimes and streams typology that occurs within the European geographical and climatic ranges. Population one in Rio Chaballos (henceforth RIOCHAB) is a typical V-shaped stream flowing through the rugged, mountainous landscape of the Cantabrian corridor of north-western Spain and is a tributary of the Rio Esva (Asturias). Two study sites of Rio Chaballos were located some 800 m apart and were similar in length (75 m long), area (240–260 m²), average width (4–5 m) and average depth (20–30 cm). In these, stream brown trout are strictly resident and complete their entire life-cycle including spawning, within small stream reaches (Lobón-Cervía´, 2007b).

**Stream temperature regimes**

Daily water temperatures were recorded in the two streams during the study years (Mortensen, 1985; Lobón-Cervia´ & Rincón, 1998) and are summarised here as mean monthly temperatures with maximum and minimum ranges (Fig. 1). For any given month, year-to-year variation in water temperature was remarkably greater in the southern stream, where mean winter temperatures remained >7 °C during most of the study years, with a minimum at 3–4 °C observed in only a few, exceptionally cold winters and up to 12 °C in several years. In August, the warmest month, temperatures attained mean values around 18–19 °C, with a maximum mean of 22 °C. This regime differs substantially from the northern stream, where the year-to-year variation in the mean monthly temperatures varied markedly less; winter temperatures were typically 2–4 °C below the southern stream, and the warmest mean temperatures in the summer seldom attained a mean of 13 °C (Fig. 1).
similar to those in this study. BISBA brown trout are also sedentary until smolting and downstream migration that essentially occurs at > age-2 (Mortensen, 1985 and personal communication). Consequently, in the two populations, the decline in survivor density over time reflects mortality ‘sensu strictu’ except during the oldest life stage (i.e. $Z_{ab}$ see below) of BISBA brown trout that includes both mortality and emigration.

Both RIOCHAB and BISBA populations were composed of age-0 to age-3 individuals with slightly longer lifespan in BISBA (c. 1200 days) than in RIOHAB (c. 1000 days). Only complete cohorts quantified from recruitment to the time of complete disappearance of individuals from the study sites were analysed. In total, this study encompasses 14 cohorts (1974–1987) from BISBA and 14 cohorts (1986–1999) and 12 cohorts (1988–1999) from site 1 and site 2 of RIOCHAB, respectively. Unfortunately, the 1997 cohort at site 2 experienced too low recruitment for mortality rates to be estimated; hence, this cohort was excluded from further analyses.

For the purposes of this study, we used recruitment ($R_c$, ind. m$^{-2}$) as an index of density-dependent processes that may occur across the lifetime (Lobón-Cerviá, 2009), and this was estimated as the number of individuals commencing a cohort, that is the number of juveniles quantified in the first sample of a given cohort when these youngest juveniles were 30 days old in BISBA and 60 days old in RIOCHAB. Mean body weight ($W_M$, g) was used as a proxy of the growth experienced by the individuals of a given cohort during the entire lifetime and was estimated as the mean weight averaged across all individual weights recorded across all samples of that cohort. Thus, these body weights were the mean of c. 15 samples in RIOCHAB and c. 28 samples in BISBA.

Functional relationships highlighted in this study were depicted using the following linear and nonlinear relationships in the following forms:

**Linear:** $Y = a + bX$  \(\text{Model 1}\)

**Power:** $Y = aX^b$  \(\text{Model 2}\)

**Two-phase:** $Y = a_1 \pm b_1 X(X<k_1) \pm a_2 \pm b_2 X(X \geq k_1)$  \(\text{Model 3}\)

and three-phase regressions:

$Y = a_1 \pm b_1 X(X<k_1) \pm a_2 \pm b_2 X(k_2 \geq X \geq k_1) \pm a_3 \pm b_3 X(X \geq k_2)$  \(\text{Model 4}\)

Note that Models 3 and 4 have two restrictions for continuity: a first restriction at $a_1 + b_1 k_1 = a_2 + b_2 k_1$ for Model 3 and a second restriction at $a_3 + b_3 k_2 = a_4 + b_4 k_2$ for Model 4. In all these models, $a, a_1, a_2$ and $a_3; b, b_1, b_2$

---

**Data collection and analysis**

The three-pass depletion method with electro-fishing was used to quantify long-term trends in brown trout size and density (Lobón-Cerviá, 1991). Monthly censuses were conducted until the total disappearance of the 1974–1988 cohorts in BISBA and every second month for the 1986–1999 cohorts at site 1 and 1988–1999 cohorts at site 2 in RIOCHAB (Lobón-Cerviá, 2007b). Thus, the number of individuals in a given cohort was quantified 13–17 times in RIOCHAB and 22–33 times in BISBA. During the earliest years of study, scales from every single individual were collected for age determination; in later years, the age of individuals was clearly detectable based solely on the length-frequency distributions and we only collected scales to verify the age of a few individuals. We assigned a birth date as a fixed date of emergence. Actually the time of emergence varied slightly from year-to-year with some 10–15 days above or below the fixed dates. However, we considered that time interval not to affect our analysis given that the lifespan was around 1000–1200 days in the two populations. We then assigned the age of individuals of a given cohort as the number of days after emergence or birth date. Long-term tagging procedures over the years 1988–1998 (J. Lobón-Cerviá, unpublished) highlighted that RIOCHAB brown trout are strictly sedentary, completing their life cycles within stream sections of a size...
and $b_3$ are constants whereas $k_1$ and $k_2$ represent the thresholds or critical break points upon which the response variable changes direction as a function of the predictive variable.

Selected sets of models were used to fit a given data set. The Akaike information criterion (AIC, Burnham & Anderson, 1998) was used to select the best model among models to fit a given data set. In general, when comparing models, the one with lower AIC score is the most likely to be the correct. However, the absolute differences between AICc values (also known as Akaike weights) provide an estimate of the probability that a model is correct. A difference in AICc scores between two models of 0 indicates that the two models have an equal 50% probability of being correct; a difference of 2 indicates a 73% probability and differences from 5 to 10 indicate 90 to 100% probability that a model is correct (Motulsky & Christopoulos, 2004). All models were fitted by least-squared, quasi-Newton algorithms available in Statistica 7.0.

More specifically, we compared linear versus two-phase regressions (i.e. Models 1 and 3) for RIOCHAB and linear versus two-phase versus three-phase regressions (i.e. Models 1, 3 and 4) for BISBA to fit log$_{10}$-transformed survivor density as a function of time (days after emergence) to identify: (1) life stages (i) herein defined as the non-mortality life stage ends abruptly and shifts to a mortality stage in which the log$_{10}$-transformed density of survivors $(Z_i, \text{day}^{-1})$ is expressed as the addition of the slopes of the corresponding regressions (with the sign changed), whereas total lifetime mortality rate of a given cohort $(Z_T, \text{day}^{-1})$ is expressed as the addition of the $Z_i$ values over the (i) successive life stages that characterise a given cohort. When the total lifetime mortality rate $Z_T$ was used as dependent variable, indivisible ‘0s’ were first transformed by setting $Z_T = -100^*Z_T$.

**Results**

*Recruitment and body weights*

Recruitment, growth and the corresponding mean body weights differed substantially among cohorts within populations and by several fold between the two populations. In the northern BISBA, the number of recruits attained values as high as 15.8 ind. m$^{-2}$ (1988 cohort); weight-at-age averaged across cohorts attained 10.1 g, 49.2 g and 66.9 g at first, second and third birth date, respectively, and the mean body weights ranged from 12.8 g (1974 cohort) to 30 g (1979 cohort). In contrast, in the southern RIOCHAB, the maximum recruitment never exceeded 1.2 m$^{-2}$ (1987 cohort at site 1), weights-at-age were double than those of BISBA brown trout with 24.5 g, 82.7 g and 170 g at first, second and third birth date, respectively, and the mean body weights ranged from 36.7 g (1988 cohort) to 78.0 g (1999 cohort) at site 1.

**Assessment of mortality**

Graphical analysis of the relationship between the log$_{10}$-transformed density of survivors (ind. m$^{-2}$) as a function of time (days after emergence) highlighted distinctly nonlinear declines in all cohorts in addition to marked differences in the occurrence and intensity of mortality across the lifetime, for both study populations (Figs 2 & 3).

In RIOCHAB, the decline in the log-transformed density of survivors over time was strongly consistent among cohorts in the two study sites. A comparison between linear and two-phase regressions highlighted that all probabilities (i.e. Akaike weights) supported the selection of two-phase regressions (Table 1). An exception was the 1986 cohort where evidence for a linear regression was overwhelming ($P_L > 99.9\%$; Table 1). Two-phase regressions fitted to each single cohort were all highly significant and explained a substantial portion of the variance (64.5–96.8\%; Table 1). For all cohorts, the slope of the first stage was flat and non-significant, and the null hypothesis of slope $= 0$ could not be rejected for any cohort at the two sites. Thus, the RIOCHAB pattern of mortality was characterised by two distinct life stages: (i) an earlier life stage in which the log$_{10}$-transformed density of survivors remained nearly constant for a prolonged time period and (ii) a dramatic shift to an increased mortality that persisted until the complete disappearance of each cohort. Based on these results, we assumed negligible mortality from recruitment to approximately half of the cohort’s lifetime. After an average of $c. 460$ days after emergence, the non-mortality life stage ends abruptly and shifts to a second life stage of severe and constant mortality. We observed only one exception to this pattern, the 1986 cohort at site 1, for which constant mortality appeared to occur across the entire lifetime (Fig. 2a). Moreover, lifetime mortality ($Z_T$) did not differ significantly between the two study sites ($F_{1,23} = 0.63, P = 0.44$) and across cohorts, averaged $Z_T = 0.0025 \text{ day}^{-1}$ (range 0.0001–0.0048 day$^{-1}$).

In contrast to RIOCHAB, in the northern BISBA population, graphical analysis of the relationship between
the log_{10}-transformed density of survivors (ind. m^{-2}) as a function of time (days after emergence), highlighted that mortality occurred across the entire lifetime (Fig. 3). However, consistent with RIOCHAB, we did observe distinctly nonlinear trajectories of mortality associated with different life stages. Apparently, a first, early life stage of short duration and severe mortality was followed by a second, prolonged period of weaker mortality, which was followed by yet a third period of severe mortality. The Akaike weights indicated the superiority of three-phase regressions for practically all cohorts. However, at least in the 1978 and 1982 cohorts, the evidence was comparatively weaker (Table 2), suggesting a similar validity for the two models. For consistency, however, we applied three-phase linear regressions to every single cohort. These fits were all highly significant and explained most of the variance (93.6–98.9%; Table 2).

Nevertheless, the slopes of the first life stage in the cohorts of 1978, 1979, 1982, 1983 and 1986, and of the second life stage in the cohorts of 1977 and 1980, were non-significant (Table 2). The null hypothesis of slope = 0 could not be rejected, indicating that no or negligible mortality occurred during the first life stage of those six cohorts and during the second life stage of two cohorts (out of 15).

Thus, the pattern of mortality in the northern BISBA was characterised by the occurrence of three life stages of different temporal duration and mortality rates. A shorter, earlier life stage lasting, on the average, 160 days after emergence is characterised by variability in the mortality rates with a predominance of severe mortality in highly recruited cohorts relative to a few weakly recruited cohorts with mortality c. zero. In this earlier life stage, the average cohort mortality was $Z_1 = 0.0033$ day$^{-1}$. The

![Fig. 2](image-url)
second life stage of lower mortality attained a mean of $Z_2 = 0.0011$ day$^{-1}$, and lasted some 512 days (672 days after emergence), and also included two cohorts with no mortality. A third life stage, characterised by severe mortality, lasted until the complete disappearance of the cohort, with a mean mortality rate of $Z_3 = 0.0031$. 

Table 1. Mortality rates ($Z_1$ and $Z_2$) as the slopes (with the sign changed) of two successive life stages highlighted by fitting two-phase regressions to log$_{10}$-transformed survivors density versus time (days after emergence) for the cohorts 1986–1999 of site 1 and 1988–1999 of site 2 of RIOCHAB brown trout

<table>
<thead>
<tr>
<th>Cohort</th>
<th>$A$</th>
<th>$Z_1$</th>
<th>$K$</th>
<th>$Z_2$</th>
<th>$R^2$</th>
<th>$P_{\text{TWO}}$</th>
<th>$P_L$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>86</td>
<td>0.025</td>
<td>0.0027*</td>
<td></td>
<td>0.0027*</td>
<td>95.9</td>
<td>0.09</td>
<td>99.1</td>
</tr>
<tr>
<td>87</td>
<td>0.035</td>
<td>0.0013NS</td>
<td></td>
<td>0.0038</td>
<td>96.3</td>
<td>67.8</td>
<td>32.2</td>
</tr>
<tr>
<td>88</td>
<td>-0.006</td>
<td>0.0001NS</td>
<td>517</td>
<td>0.0037</td>
<td>95.0</td>
<td>99.9</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>89</td>
<td>0.018</td>
<td>0.0006NS</td>
<td>283</td>
<td>0.0035</td>
<td>90.8</td>
<td>97.2</td>
<td>2.8</td>
</tr>
<tr>
<td>90</td>
<td>-1.159</td>
<td>0.0008NS</td>
<td>499</td>
<td>0.0020</td>
<td>76.9</td>
<td>77.3</td>
<td>22.7</td>
</tr>
<tr>
<td>91</td>
<td>-0.522</td>
<td>0.0008NS</td>
<td>373</td>
<td>0.0025</td>
<td>82.5</td>
<td>93.1</td>
<td>6.9</td>
</tr>
<tr>
<td>92</td>
<td>-0.299</td>
<td>0.0011NS</td>
<td>367</td>
<td>0.0021</td>
<td>96.0</td>
<td>92.3</td>
<td>7.7</td>
</tr>
<tr>
<td>93</td>
<td>-0.791</td>
<td>0.0006NS</td>
<td>477</td>
<td>0.0030</td>
<td>72.4</td>
<td>91.5</td>
<td>8.5</td>
</tr>
<tr>
<td>94</td>
<td>-1.329</td>
<td>0.0000NS</td>
<td>320</td>
<td>0.0010</td>
<td>81.4</td>
<td>88.4</td>
<td>11.6</td>
</tr>
<tr>
<td>95</td>
<td>-1.223</td>
<td>0.0000NS</td>
<td>450</td>
<td>0.0014</td>
<td>67.1</td>
<td>83.8</td>
<td>16.2</td>
</tr>
<tr>
<td>96</td>
<td>-0.952</td>
<td>0.0007NS</td>
<td>475</td>
<td>0.0018</td>
<td>64.5</td>
<td>69.8</td>
<td>30.2</td>
</tr>
<tr>
<td>97</td>
<td>-0.614</td>
<td>0.0002NS</td>
<td>543</td>
<td>0.0024</td>
<td>89.7</td>
<td>89.1</td>
<td>9.9</td>
</tr>
<tr>
<td>98</td>
<td>-0.402</td>
<td>0.0007NS</td>
<td>490</td>
<td>0.0026</td>
<td>96.4</td>
<td>94.1</td>
<td>5.9</td>
</tr>
<tr>
<td>99</td>
<td>-0.779</td>
<td>0.0004NS</td>
<td>491</td>
<td>0.0034</td>
<td>96.6</td>
<td>85.8</td>
<td>14.2</td>
</tr>
<tr>
<td>Site 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>88</td>
<td>0.000</td>
<td>0.0003NS</td>
<td>469</td>
<td>0.0031</td>
<td>96.5</td>
<td>99.9</td>
<td>0.1</td>
</tr>
<tr>
<td>89</td>
<td>-0.159</td>
<td>0.0008NS</td>
<td>472</td>
<td>0.0033</td>
<td>95.5</td>
<td>97.5</td>
<td>2.5</td>
</tr>
<tr>
<td>90</td>
<td>-0.771</td>
<td>0.0002NS</td>
<td>466</td>
<td>0.0034</td>
<td>89.5</td>
<td>77.4</td>
<td>22.6</td>
</tr>
<tr>
<td>91</td>
<td>-0.273</td>
<td>0.0009NS</td>
<td>372</td>
<td>0.0022</td>
<td>89.3</td>
<td>95.2</td>
<td>4.8</td>
</tr>
<tr>
<td>92</td>
<td>-0.519</td>
<td>0.0005NS</td>
<td>382</td>
<td>0.0018</td>
<td>86.9</td>
<td>93.4</td>
<td>6.6</td>
</tr>
<tr>
<td>93</td>
<td>-0.833</td>
<td>0.0002NS</td>
<td>481</td>
<td>0.0020</td>
<td>85.6</td>
<td>97.0</td>
<td>3.0</td>
</tr>
<tr>
<td>94</td>
<td>-0.709</td>
<td>0.0006NS</td>
<td>382</td>
<td>0.0019</td>
<td>80.6</td>
<td>99.9</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>95</td>
<td>-0.792</td>
<td>0.0003NS</td>
<td>452</td>
<td>0.0019</td>
<td>85.7</td>
<td>89.6</td>
<td>10.4</td>
</tr>
<tr>
<td>96</td>
<td>-0.389</td>
<td>0.0007NS</td>
<td>479</td>
<td>0.0021</td>
<td>96.8</td>
<td>99.6</td>
<td>0.4</td>
</tr>
<tr>
<td>98</td>
<td>-0.675</td>
<td>0.0009NS</td>
<td>368</td>
<td>0.0019</td>
<td>88.7</td>
<td>97.4</td>
<td>2.6</td>
</tr>
<tr>
<td>99</td>
<td>-1.196</td>
<td>0.0001NS</td>
<td>473</td>
<td>0.0024</td>
<td>89.6</td>
<td>92.7</td>
<td>7.3</td>
</tr>
</tbody>
</table>
Patterns of mortality in stream brown trout

Table 2 Mortality rates ($Z_1$, $Z_2$, and $Z_3$) as the slopes (with the sign changed) of three successive life stages highlighted by fitting three-phase regressions to log$_{10}$-transformed survivors’ density (ind. m$^{-2}$) versus time (days after emergence) for the 1974–1987 cohorts of BISBA brown trout

<table>
<thead>
<tr>
<th>Cohort</th>
<th>$A$</th>
<th>$Z_1$</th>
<th>$Z_2$</th>
<th>$K_1$</th>
<th>$Z_3$</th>
<th>$R^2$</th>
<th>$P_{\text{THREE}}$</th>
<th>$P_{\text{TWO}}$</th>
<th>$P_L$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1974</td>
<td>1.079</td>
<td>0.0075</td>
<td>96</td>
<td>0.0014</td>
<td>781</td>
<td>0.0044</td>
<td>98.3</td>
<td>99.9</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>1975</td>
<td>0.629</td>
<td>0.0034</td>
<td>120</td>
<td>0.0011</td>
<td>516</td>
<td>0.0032</td>
<td>97.9</td>
<td>77.0</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>1976</td>
<td>0.277</td>
<td>0.0026</td>
<td>257</td>
<td>0.0008</td>
<td>650</td>
<td>0.0027</td>
<td>97.8</td>
<td>59.2</td>
<td>29.4</td>
</tr>
<tr>
<td>1977</td>
<td>0.243</td>
<td>0.0024</td>
<td>150</td>
<td>0.0004NS</td>
<td>564</td>
<td>0.0025</td>
<td>96.3</td>
<td>49.4</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>1978</td>
<td>0.145</td>
<td>0.001NS</td>
<td>184</td>
<td>0.0008</td>
<td>504</td>
<td>0.0015</td>
<td>93.6</td>
<td>61.8</td>
<td>38.2</td>
</tr>
<tr>
<td>1979</td>
<td>-0.003</td>
<td>0.0007NS</td>
<td>71</td>
<td>0.0013</td>
<td>723</td>
<td>0.0018</td>
<td>96.8</td>
<td>99.9</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>1980</td>
<td>0.072</td>
<td>0.0025</td>
<td>237</td>
<td>0.0001NS</td>
<td>464</td>
<td>0.0020</td>
<td>97.7</td>
<td>99.8</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>1981</td>
<td>0.576</td>
<td>0.0037</td>
<td>198</td>
<td>0.0014</td>
<td>896</td>
<td>0.0036</td>
<td>96.0</td>
<td>99.6</td>
<td>0.04</td>
</tr>
<tr>
<td>1982</td>
<td>-0.002</td>
<td>0.0021NS</td>
<td>225</td>
<td>0.0012</td>
<td>907</td>
<td>0.0042</td>
<td>97.9</td>
<td>53.0</td>
<td>47.0</td>
</tr>
<tr>
<td>1983</td>
<td>0.672</td>
<td>0.0034NS</td>
<td>69</td>
<td>0.0012</td>
<td>675</td>
<td>0.0031</td>
<td>97.6</td>
<td>99.8</td>
<td>0.01</td>
</tr>
<tr>
<td>1984</td>
<td>0.808</td>
<td>0.0035</td>
<td>150</td>
<td>0.0014</td>
<td>600</td>
<td>0.0025</td>
<td>96.8</td>
<td>58.1</td>
<td>25.1</td>
</tr>
<tr>
<td>1985</td>
<td>0.529</td>
<td>0.0018</td>
<td>250</td>
<td>0.0010</td>
<td>780</td>
<td>0.0040</td>
<td>96.8</td>
<td>99.8</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>1986</td>
<td>0.492</td>
<td>0.0028NS</td>
<td>115</td>
<td>0.0012</td>
<td>456</td>
<td>0.0031</td>
<td>97.7</td>
<td>65.0</td>
<td>35.1</td>
</tr>
<tr>
<td>1987</td>
<td>1.168</td>
<td>0.0073</td>
<td>114</td>
<td>0.0017</td>
<td>646</td>
<td>0.0035</td>
<td>96.5</td>
<td>98.8</td>
<td>0.1</td>
</tr>
</tbody>
</table>

$K_1$ and $K_2$ are the temporal duration of each life stage (days after emergence). $A$ is the intercept and $R^2$, the variance explained. All slopes significant in, at least, $P < 0.01$ except those indicated with NS (i.e., non-significant). The probabilities (in %) or Akaike’s weights to select the correct model among three-phase ($P_{\text{THREE}}$), two-phase ($P_{\text{TWO}}$) and linear ($P_L$) regressions.

Moreover, the mortality rates differed significantly ($F_{2,42} = 12.9$, $P < 0.001$) among the three life stages with the rates of earliest life stage being significantly ($F_{1,28} = 16.2$, $P < 0.001$) greater than those of the second life stage, but not significantly different ($F_{1,28} = 0.20$, $P = 0.66$) than the rates of the third life stage. We further explored whether mortality rates co-varied among life stages, in other words whether or not a particularly high or low mortality rate in an earlier life stage is associated with a high or low mortality in a later life stage. Based on correlation analysis, the relationship between $Z_1$ and $Z_2$ was significant ($P = 0.04$) but only explained ($R^2$) 29.2% of the variance. The correlation between $Z_1$ and $Z_3$ was not significant ($P = 0.09$, $R^2 = 0.21$), and nor was the correlation between $Z_2$ and $Z_3$ ($P = 0.13$, $R^2 = 0.16$). These results indicated that mortality rates are generally independent among life stages.

Overall, the lifetime mortality rates in the high-density BISBA population were several fold greater (total lifetime mortality averaged across cohorts $Z_T = 0.0075$ day$^{-1}$) than in the southern, low-density population (total lifetime mortality averaged across cohorts $Z_T = 0.0025$ day$^{-1}$).

Major differences in overall mortality patterns and rates between these two populations are depicted in Fig. 4 by a composite survivorship (averaged across cohorts) curve for BISBA, as compared to RIOCHAB.

Relationships between recruitment, body mass and mortality rates

For each single population, total cohort-specific mortality rates ($Z_T$) decreased with increased body mass, and fits of negative power regressions (>90% probability to be better than linear regressions) were highly significant in both populations. In BISBA, the slope was steeply negative ($B = -1.23$) and significant ($P = 0.001$), explaining 76.2% of the variance. In contrast, in RIOCHAB, the slope was also negative but much shallower ($B = -0.87$) and was significant ($P < 0.01$), but explained only 36% of the variance. Notably, neither the lower-than-unity slope of RIOCHAB nor the higher-than-unity slope of BISBA was significantly different from unity ($B = -1$) ($F_{1,13} = 0.26$, $P = 0.61$ and $F_{1,13} = 1.20$, $P = 0.29$ for RIOCHAB and BISBA, respectively) and, as a consequence, the hypothesis that the populations do not differ from each other could not be rejected.

When the data from both populations were pooled, the decline in mortality rates as a function of body weight depicted a smooth and highly significant ($P < 0.001$) power function across the wide range of body masses we observed (Fig. 5) and explains a substantial 89% of the variance. The new slope for the pooled data set, $B = -1.05$, was not significantly different from unity ($B = -1$) ($F_{1,38} = 0.53$, $P = 0.47$). Consequently, the relationship of body mass-dependent mortality rates (Fig. 5) may be simply reduced to:

$$Z_T = 16.1/W_M$$

In contrast to body mass, recruitment exerted a positive effect on mortality rates. For each single population, mortality rate increased as a function of recruitment, and

© 2011 Blackwell Publishing Ltd, *Freshwater Biology, 57*, 575–588
power models (in the two instances >98% probability to be better than linear regressions) were highly significant, explaining substantial amounts of variance: \( R^2 = 80.9\% \) (\( P < 0.001 \)) for BISBA and \( R^2 = 37.0\% \) (\( P < 0.002 \)) for RIOCHAB. An ANCOVA for the \( \log_{10} \)-transformed data revealed highly significant differences between the two power models (>95% probability to be better than a negative power regression) were highly significant, explaining substantial amounts of variance: \( R^2 = 80.9\% \) (\( P < 0.001 \)) for BISBA and \( R^2 = 37.0\% \) (\( P < 0.002 \)) for RIOCHAB. An ANCOVA for the \( \log_{10} \)-transformed data revealed highly significant differences between the two slopes (\( F_{1,37} = 39.8, P = 0.02 \)). Nonetheless, when the data were pooled, mortality again demonstrated a smooth continuous trajectory (Fig. 6) of increase with recruitment across the whole range of recruitment values. This power model was also highly significant (\( P < 0.001 \)) and explained 89.1% of the variance:

\[
Z_T = 0.427Rc^{0.394}
\]

We further explored whether body mass was related to recruitment. In both populations, body mass declined linearly with increased recruitment; both linear regressions were significant: \( R^2 = 0.49 \) (\( P < 0.001 \)) for RIOCHAB and \( R^2 = 0.46 \) (\( P < 0.001 \)) for BISBA. An ANCOVA revealed that the slopes of the two populations differed significantly (\( F_{1,37} = 24.9, P < 0.001 \)). Once again, when data were pooled (Fig. 7), the resulting relationship highlighted a consistent smooth decline of body mass with increased recruitment over the range of recruitment values we observed. In this case, however, two different slopes were evident: a markedly steeper slope at low recruitment followed by a shallow decline at high recruitment (Fig. 7). This relationship was best described (>95% probability to be better than a negative power regression) by a two-phase regression of the form:

\[
W_M = 67.6 - 29.4Rc \times (Rc \leq 1.62) + 21.0 - 0.57Rc \times (Rc > 1.62)
\]
This two-phase regression demonstrated a distinct phase shift at 1.62 ind. m$^{-2}$ and significantly explained a substantial amount ($R^2 = 88.1\%$) of the variation in body mass.

**Discussion**

In this study, we highlighted long-term patterns of natural mortality between two substantially different populations of stream-dwelling brown trout: a resident, low-density population with fast growth and an adfluvial, high-density population with slow growth. The two populations inhabit two streams located 1900 km apart and are near the opposing extremes of temperature regimes that typify the north–south climatic clines of the European brown trout distribution, namely, a warm-water stream in north-western Spain (RIOCHAB) and a cooler stream in Denmark (BISBA). Essentially, the life stages in which mortality occurred were consistent across cohorts within populations, life stage-specific mortality rates varied widely among cohorts and differed markedly between populations.

In the southern RIOCHAB, mortality was negligible (with only one exception) during the first half of the lifetime. This life stage then ends abruptly to give rise to a second life stage of severe and constant mortality over time, until the total disappearance of the cohorts. In contrast, most cohorts in the northern BISBA population experienced extremely high recruitment levels and severe mortality occurred during the first life stage with the exception of a few weakly recruited cohorts in which mortality was negligible. Neither the lower mortality rates in the second life stage nor the third life stage that includes both mortality and emigration appeared to be related to the earlier mortality experienced during previous life stages (uncorrelated or weakly correlated across life stages).

These results are consistent with the hypothesis that patterns of mortality, and life stages subject to mortality, are population-specific and that mortality rates vary widely among cohorts, within and among populations. Further support for this hypothesis is revealed by a comparison with other populations reported in the literature. Based on a long-term assessment of several sites of the Shelligan Burn (Scotland), Egglishaw & Shackley (1977) reported a composite four-phase mortality pattern. In this population, mortality occurred during the whole lifetime but with variable intensity. For example, mortality rates during the first summer of life (June to August) were lower than those during the following winter (September to December) after which chronic mortality persisted with similar rates during the rest of the lifetime. Mann, Blackburn & Beaumont (1989) assessed several cohorts of the Tadnoll Brook population, a chalk stream of the southern U.K., where mortality also occurred during the whole lifetime. Nevertheless, visual inspection of the patterns depicted in their Fig. 3 highlighted a two-phase pattern with an earlier phase of lower mortality that extended over age-0 and age-1 individuals followed by a second phase of markedly higher mortality rates. Elliott
(1993), in a comparison between the two-first years of life of a sea-migratory and a resident population in two nearby streams of the Lake District (U.K.), reported two-phase relationships with an earlier life stage commencing in the alevin stage with severe mortality followed by a weakly and constant mortality life stage until the end of the second year of life. Finally, Lobón-Cerviá (2007b) described identical mortality patterns for brown trout in other sites downstream Rio Chaballos and other nearby streams within the Rio Esva drainage. All these patterns were characterised as well by two life stages with an earlier life stage with no mortality followed by a second stage of severe mortality.

Based on this comparison, we recognise four distinctly shaped lifetime mortality patterns: (i) a unique instance of constant mortality across the lifetime recorded in one cohort of the RIOCHAB population; (ii) two-phase patterns with an earlier life stage of negligible mortality followed by a second life stage of severe mortality, as firmly demonstrated by our own data; (iii) a three-phase pattern with an earlier life stage of variable mortality ranging from weak to severe, followed by a second phase of weak mortality and followed by a third phase of severe mortality; and (iv) a four-phase pattern with variable mortality rates across the lifetime as described by Egglishaw & Shackley (1977).

However, although we observed a variety of different mortality patterns, our comparison also suggested that similar mortality patterns may occur in populations subject to similar environmental conditions and/or in populations where brown trout exhibit similar individual growth and population densities. For example, the two-phase pattern that typifies the RIOCHAB population matches exactly the patterns elucidated for other sites downstream Rio Chaballos and other nearby populations subject to similar environmental conditions within the Rio Esva drainage in north-western Spain (Lobón-Cerviá, 2007b). Moreover, this two-phase pattern is most similar to that described by Mann et al. (1989) for the British Tadnoll Brook (U.K.), where brown trout showed comparable growth, recruitment and density to RIOCHAB. At the opposite extreme of growth and density, the patterns of mortality in the BISBA population are most similar to those reported by Elliott (1985, 1993) for the high-density population of the slow-growing population of Black Brows Beck (U.K.). This population is also characterised by an earlier juvenile stage of severe mortality that only differs in the length of the temporal duration from the BISBA by a c.30 days (i.e. c. 70 days after emergence, Elliott, 1993, versus BISBA >100 days after emergence, this study). In these two populations, this juvenile life stage of severe mortality is followed by a second life stage of markedly weaker mortality.

When we look both within and among populations, it is somewhat surprising that among the numerous causes of mortality (see Introduction), we isolated the mean body weight as a proxy of the growth experienced by individuals during the lifetime, and the initial number of recruits as a proxy of the density-dependent processes occurring during the lifetime (Lobón-Cerviá, 2009). Both recruitment and mean body mass explained c. 89% of all the variation in the total lifetime mortality rates observed across cohorts and populations.

Recruitment levels differed substantially between the two studied populations. Although a review of recruitment levels reported for stream-living brown trout in the literature is beyond the scope of this study, maximum levels of recruitment around 1.5–2.0 ind. m⁻² are most commonly reported across populations, whereas levels as high as those in this study (>15.0 ind. m⁻²) have only been reported for the U.K. population of Black Brows Beck (Elliott, 1985, 1993). Plausibly, such profound differences may be associated, at least in part, with the V-shaped versus U-shaped stream channels. Both the BISBA (Denmark) and Black Brows Beck (U.K.) are U-shaped streams of glacial origin that may sustain high levels of recruitment and hence high mortality rates during an early life stage. In contrast, the vast majority of studies on brown trout have been performed on V-shaped streams in mountainous landscape that, for the most, are considered the most typical brown trout habitat throughout its natural distribution, and in these streams, maximum recruitment is typically <1.5–2.0 ind. m⁻².

The hypothesis that mortality rates should scale body size (length or weight) has been recurrently explored across fish species and habitats with some generalities emerging, although the underlying mechanisms are poorly understood. For example, Lorenzen (1996) examined relationships between body weight and annual mortality across fish species and habitats, and highlighted a negative power relationship with a scaling factor = -0.29 across natural ecosystems. Other estimates inferred from different empirical and theoretical approaches report scaling factors in the range -0.24 to -0.37 (Peterson & Wroblewski, 1984; McGurk, 1986; Brown et al., 2004; McCoy & Gillooly, 2008), and a recently developed model relating annual mortality and body length for marine fish species highlighted a scaling factor = -1.6 (Gislasson et al., 2010). Unfortunately, comparisons with our results are hindered by different
approaches of estimating body mass and mortality rates; in our trout populations, the relationship between total lifetime mortality rates and body mass was simply
\[ Z_T = 16.1/W_{mT}. \]

Competitive interactions underlying density-dependent mortality are well documented not only in stream salmonids (Elliott, 1989) but also in other freshwater (Wootton & Smith, 2000) and marine fishes (Myers & Cadigan, 1995). In our stream-living brown trout populations, the relationship of mortality rates with body mass and recruitment implies that individuals of slow-growing cohorts and highly recruited cohorts are associated with higher rates of mortality. Previous studies on the self-thinning (i.e. density-body mass) intra-cohort relationships of these two populations highlighted two-phase patterns quite similar to the mortality pattern highlighted in this study: an early phase with low or negligible slope continues until a threshold size is reached (10.2 g in BISBA and 30–40 g in RIOCHAB) upon which severe declines of density per mass unit increment occurs until the total disappearance of the cohorts (Rincón & Lobón-Cerviá, 2002; Lobón-Cerviá & Mortensen, 2006). These concurrent patterns strongly suggest that, in the two populations, individuals essentially die because they grow in a spatially limited habitat. During the first half of the lifetime, smaller, growing individuals are below the carrying capacity. The amount of habitat suitable for these smaller individuals is sufficient and as a consequence, no mortality occurs during this first life stage. A threshold size is achieved when individuals attain the carrying capacity and the amount of habitat suitable for those, larger individuals is limited. Upon this threshold size, the effect of size (i.e. body mass) and density concur to enhance a second life stage in which severe mortality continues until the total disappearance of the cohorts. Interestingly, the operation of density(recruitment) dependence on growth induces smaller individuals that may thus occupy more abundant habitat and also has the advantage of delaying the occupation of even more limited habitat suitable for larger individuals.

Attempts to elucidate causes of mortality in fish populations have suggested different factors that are unlikely to operate in our brown trout populations. The notion that seasonal environments are prone to cause differential mortality rates across seasons, and more specifically that winter conditions may reduce density through ecological and physiological processes or even function as a critical period for survival, has long been recognised. As such, there is an increasing interest in determining specific winter conditions that cause mortality (Post & Evans, 1989) and in developing a better understanding of how those conditions may operate on the ability of fish to survive harsh winters (Hurst, 2007). The patterns elucidated in this study are characterised by life stage-specific mortalities differing in intensity and temporal duration, but these patterns do not match ‘seasons’ or ‘years’. Thus, our results reject the hypothesis that the season ‘per se’ affects mortality, even the cooler winters experienced by the northern BISBA population. This finding is consistent with Carlson et al. (2008), who reported over-winter mortality rates of magnitudes similar to other seasons for brown trout in cool Norwegian streams as well as with Huusko et al. (2007) who suggested that overwinter mortality is related to specific habitat characteristics and/or to the stream ice regime.

At the opposite extreme, warm summer stream temperatures, which are most common in southern European streams, are deemed unfavourable or even lethal for salmonids. In the populations studied herein, the summer ‘per se’ had no obvious effect on mortality while the year-to-year variation in summer stream temperature appeared unrelated to the among-cohort variation in mortality. Moreover, during the study years water temperatures were documented exceeding 22 °C in July and August (see Lobón-Cerviá & Rincón, 1998 for detailed temperature records), but in no case did these temperatures prove to have negative effects or even cause detectable mortalities.

Mortality associated with reproductive costs has also been suggested to occur in stream salmonids (Hutchings, 1994) and marine fish species (Myers & Doyle, 1983). If reproduction actually induces mortality, we would expect to observe a shift in the pattern of mortality soon after reproduction. However, in the resident RIOCHAB population where all individuals spawn when they are 20 months old (Lobón-Cerviá et al., 1997), we observed no evidence for this hypothesis; the decline in survival density remained constant before, during and after reproduction until the total disappearance of individuals in all cohorts and sites offering no evidence of a reproductive-induced mortality.

As mentioned earlier, mortality rates are foundational components of population dynamics, and estimation errors associated with difficulties inherent in the quantification of mortality in the wild may significantly limit fish population assessments (Mertz & Myers, 1997). In this context, the life stage-dependent mortality rates elucidated for our brown trout populations suggest that annual or age-specific mortalities most commonly reported in the literature (e.g. Chen & Watanabe, 1989) may actually include (or exclude) life stages of different mortality rates and as such represent ‘statistical’ rather
than ‘biological’ populations (Mann et al., 1989), and consequently may not reflect the true mortality processes underlying their population dynamics. This problem highlights the importance of long-term studies and, as emphasised by Elliott (1990), the need for more detailed studies focused on frequent population censuses over replicate habitats that permit the detection of life stage-specific mortality rates. Unfortunately, these studies are still rare even for the most common short-living fish populations in which the quantification of full life cycles is greatly facilitated.

The fishery literature includes plenty of models to predict mortality rates based on life history traits (Hoening, 1983; Quinn & Deriso, 1999 and references in the introduction), which are mostly used in the design of fishery management of marine fish populations. Our study adds to the literature simple empirical models relating body mass and recruitment with mortality rates for brown trout populations located at the extremes of growth and density throughout the species distributional range. Further validations of these simple models across additional populations would facilitate short cuts to predicting mortality rates that could then be incorporated into robust fishery and conservation models. In addition, these mortality patterns may be useful as reference points for exploited (fished) populations and/or to document human-induced population changes including the potential effects of global change.

Acknowledgments

This work was supported, in part, by the U.S. Geological Survey Utah, Cooperative Fish and Wildlife Research Unit. The Rio Chaballos data set was collected as part of long-term monitoring of the Rio Esva fish populations. Bisballe Baeck data set was collected by the late Dr. E. Mortensen while he served as a senior researcher for the National Agency of Environmental Protection (Denmark). This study arose from a collaborative action between the National Museum of Natural Sciences (CSIC, Spain) and the Utah State University (U.S.A.). Comments by Dr. Th. Jenkins, Dr. A. Vollestad and several anonymous reviewers contributed to improve the MS substantially. Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References


(Manuscript accepted 23 November 2011)