

# Seasonal mortality and the effect of body size: a review and an empirical test using individual data on brown trout

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## Summary

1. For organisms inhabiting strongly seasonal environments, over-winter mortality is thought to be severe and size-dependent, with larger individuals presumed to survive at a higher rate than smaller conspecifics. Despite the intuitive appeal and prevalence of these ideas in the literature, few studies have formally tested these hypotheses.

2. We here tested the support for these two hypotheses in stream-dwelling salmonids. In particular, we combined an empirical study in which we tracked the fate of individually-marked brown trout across multiple seasons and multiple years with a literature review in which we compiled the results of all previous pertinent research in stream-dwelling salmonids.

3. We report that over-winter mortality does not consistently exceed mortality during other seasons. This result emerged from both our own research as well as our review of previous research focusing on whether winter survival is lower than survival during other seasons.

4. We also report that bigger is not always better in terms of survival. Indeed, bigger is often worse. Again, this result emerged from both our own empirical work as well as the compilation of previous research focusing on the relationship between size and survival.

5. We suggest that these results are not entirely unexpected because self-sustaining populations are presumably adapted to the predictable seasonal variation in environmental conditions that they experience.

**Key-words:** MARK, over-winter, seasonal variation, selection analysis, survival

## Introduction

For organisms inhabiting strongly seasonal environments, winter is often considered to be a stressful period (e.g. Myrseth & Østbye 1995; Berg & Bremset 1998; Finstad, Næsje & Forseth 2004a). Indeed, winter survival rates can be low (e.g. Mitro & Zale 2002) but also variable (e.g. Pistorius, Follestad & Taylor 2006). This variability can drive population dynamics in vertebrates including mammals (e.g. Soay sheep: Clutton-Brock *et al.* 1991; roe deer: Gaillard *et al.* 1993; red deer: Albon *et al.* 2000), birds (e.g. willow tit: Lahti *et al.* 1998), and fishes (Needham, Moffett & Slater 1945). For this reason, winter is generally considered to be a harsh period that regulates population size. On the other hand, harsh environmental conditions can occur in other seasons as well (e.g. drought

conditions during the summer) and survival rates during other seasons can also be low (e.g. Schaub & Vaterlaus-Schlegel 2001). Whether winter mortality rates typically exceed those during other seasons has yet to be critically evaluated.

Moreover, over-winter mortality is often assumed to be size-dependent, with the smallest individuals experiencing reduced survival relative to larger conspecifics (a point also noted in a recent review by Hurst 2007). Both energy reserves and metabolic rate scale with body size such that larger individuals generally have higher energy reserves but lower metabolism (e.g. Shuter & Post 1990; Schultz & Conover 1999). This suggests that smaller individuals should be less likely to survive a period of starvation. Indeed, previous empirical work has demonstrated that large individuals sometimes have a survival advantage during the winter (e.g. mammals (Rödel *et al.* 2004; Korslund & Steen 2006), fishes (reviewed in Sogard 1997) and invertebrates (Smith 2002)). However, other research has demonstrated that smaller is sometimes better (e.g. Hendry, Letcher & Gries 2003). The

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results, therefore, appear to be mixed. We took the approach of asking, within a system, whether large individuals consistently survive the winter (and the summer) at higher rates than do smaller individuals.

#### STREAM-DWELLING SALMONIDS

Stream-dwelling salmonids represent an excellent system in which to test for evidence of seasonal variation in survival as well as the importance of size to survival for a number of reasons. First, stream-dwelling salmonids reside in seasonal environments and so experience a wide range of environmental conditions (e.g. Elliott 1994; Quinn 2005) – some of which are known to affect survival. For instance, winter survival rates can be low (e.g. as low as 15% for age-0 brown trout (*Salmo trutta* L.), Needham *et al.* 1945; recently reviewed in Huusko *et al.* 2007). Limited winter habitat (Whalen, Parrish & Mather 1999), collapse of overhanging snow banks (Needham *et al.* 1945), and the depletion of lipid stores (e.g. Berg & Bremset 1998; Finstad *et al.* 2004a) have all been implicated as factors contributing to this over-winter mortality. And yet summer survival rates can also be low (e.g. Elliott, Hurley & Elliott 1997) due to shrinking habitat availability, anoxia, elevated water temperatures and drought (e.g. Elliott *et al.* 1997; Elliott 2000; Hakala & Hartman 2004).

Second, stream-resident salmonids exhibit considerable intra-cohort variation in body size (e.g. Elliott 1994), suggesting substantial substrate for selection to act on. This variation can arise and be maintained by a number of factors including (i) variation in breeding and emergence timing, (ii) variation in individual growth rates, and (iii) variation in life histories (e.g. mature or not, migrate to a new environment or not). Differential mortality has been assessed both at the population level (i.e. among year comparisons of winter survival vs. average pre-winter body size) and at the individual level (i.e. comparing the body size of individuals that survive the winter vs. those that do not). The latter is preferable to the former because the former does not conclusively demonstrate that individuals that were relatively small within a year were less likely to survive.

Third, stream-dwelling salmonids are highly territorial (e.g. Kalleberg 1958), which facilitates the repeated sampling of individual fish. Individual-based data combined with multiple recapture events per year facilitate the estimation of (i) seasonal survival rates using Cormack-Jolly-Seber models, which account for variation in recapture probabilities, and (ii) the relationship between initial body size and survival through some episode of selection (e.g. winter, summer) using formal analyses of selection (e.g. Lande & Arnold 1983; Brodie, Moore & Janzen 1995), which enable comparisons of the strength of selection among studies.

Despite the intuitive appeal that survival is reduced in winter relative to other seasons and that mortality is size-dependent, few studies have formally tested these hypotheses. Herein we investigate these hypotheses by studying a stream-dwelling population of brown trout. We first estimated trout survival rates in a single stream across multiple seasons (summer,

winter), for multiple cohorts, and for multiple age-classes using the program MARK (White & Burnham 1999). This allowed us to ask whether summer survival consistently exceeded winter survival for different cohorts and different age-classes. We then estimated the strength of size-dependent survival in both the summer and winter, again for multiple cohorts and multiple age-classes using formal selection analyses (Lande & Arnold 1983; Janzen & Stern 1998). This allowed us to ask whether selection consistently favoured large individuals across seasons and across years that differed in abiotic (flow, temperature) and biotic (trout density) conditions. Finally, we reviewed the literature on stream-dwelling salmonids to determine the strength of support for the above hypotheses.

## Materials and methods

### STUDY SITE

Brown trout were sampled from a small forest stream in southeastern Norway (Bellbekken; see Fig. 1 in Olsen & Vøllestad 2001a) during the period 2002–2006. Twenty-five contiguous stream sections were used as permanent study sites, spanning in total 1504 m of the downstream part of the stream (average section length = 60.2 m). Our study site started at a waterfall (station 1 below the waterfall, stations 2–25 above the waterfall), which prevents upstream migration under most conditions. Below the waterfall the stream enters the larger river Julussa. Long term tagging studies indicate that some individuals from Bellbekken migrate downstream, but no tagged individuals have ever been registered to move upstream past the waterfall (Olsen and Vøllestad, unpublished data). Recent population genetic studies have shown that the Bellbekken and Julussa trout are genetically differentiated with relatively high  $F_{ST}$  values ( $F_{ST} = 0.0216–0.0522$ ; Taugbøl 2008). Mean width of the stream channel was 4.46 m with a mean depth of 21 cm during low summer flow conditions. Because the Bellbekken is such a small stream it is seldom, possibly never, visited by anglers (E.M. Olsen and L.A. Vøllestad, personal observation.) suggesting that mortality is natural and not due to angling.

With the exception of 2003, when the data logger was lost, water temperature during the summer was recorded daily throughout the growth season using data loggers. Daily measurements of air temperature were accessed from a nearby weather station (at Rena) through the Norwegian Meteorological Institute. At the monthly scale, summer water and air temperatures are highly correlated ( $r^2 = 0.86$ ), allowing us to estimate mean monthly water temperature data for 2003 using the mean air temperature recorded at Rena. During winter, the stream is covered with ice, and water temperature is approximately 0 °C (E.M. Olsen, personal observation). Daily measurements of water flow were not available for Bellbekken, but flow measured in the nearby river Fura, which drains the same type of area, contains the same type of bedrock and vegetation, and receives the same amount of rainfall was used as a proxy for daily variation in water flow. These data were made available by the Norwegian Water Management Authority.

### DATA COLLECTION

The trout population was sampled with a backpack electrofishing apparatus during early summer (June) and autumn (late September to early October). Ice prevented electrofishing during the winter. All sites were normally sampled within 4–5 days. During some sampling occasions, sampling had to be interrupted due to heavy rain and

**Table 1.** Estimated total number and SE of brown trout (age-0 fish excluded) in the Bellbekken during 2002–2006

Year	Capture season	<i>N</i>	SE
2002	Autumn	895	24
2003	Spring	904	63
2003	Autumn	786	53
2004	Spring	1413	20
2004	Autumn	1033	22
2005	Spring	1255	35
2005	Autumn	1171	29
2006	Spring	1004	27
2006	Autumn	1079	31

increasing water flow. Sampling was then resumed when the water level had receded. Sampling was always performed when conditions for sampling were good (i.e. low water flow, stable weather conditions). Brown trout density (excluding age-0 fish) at each site and sampling occasion was estimated using the Zippin three-pass removal method (White *et al.* 1982; Bohlin *et al.* 1989). Estimated total population number for all sites pooled for the different sampling periods varied between 895–1413 individuals (age-0 excluded) (Table 1). In the following statistical analyses, we used mean seasonal density (numbers on total stream area) as a covariate.

Passive integrated transponders (PIT-tags, Prentice, Flagg & McCutcheon 1990) were used to individually mark all brown trout larger than 50 mm. The tags were normally inserted within the body cavity of the fish, but some of the larger individuals received the PIT-tag intra-muscularly. During a part of the study, some of the smaller fish were individually tagged by injection of a coloured elastomer material just under the skin (Olsen & Vøllestad 2001b). Irrespective of tagging method, trout were anaesthetized prior to tagging with benzocaine and fork length was measured (to the nearest millimetre). At first capture, a sample of scales was removed for age determination. A total of 3280 brown trout were successfully tagged and released in Bellbekken. Out of these, 1684 individuals were recaptured at least once within the study area with the tag intact.

#### ANALYSES OF APPARENT SURVIVAL AND RECAPTURE PROBABILITIES

To test the hypothesis that survival varied among seasons, we estimated survival from our live capture–recapture data on brown trout using the Program MARK (White & Burnham 1999). The main advantage of this approach is that survival and recapture probabilities are estimated separately. This means that survival will not be biased by, for instance, weather conditions during sampling affecting the number of fish caught. In short, the fate of each tagged fish was described with a capture history (Lebreton *et al.* 1992), and capture history matrices were then used as input files for the program MARK (White & Burnham 1999). MARK provides maximum likelihood estimates of apparent survival,  $\phi$ , and recapture probability,  $p$ , where  $\phi$  represents the combined probability that a fish survives from capture occasion  $i$  to capture occasion  $i + 1$  and is available for recapture at capture occasion  $i + 1$ . Fish leaving the study site on a permanent basis will not be available for recapture and will therefore appear to have died, hence the term *apparent* survival. Note that in this study, we estimated monthly survival from seasonal capture occasions (early summer and autumn), rather than simply annual survival from annual samples. Winter intervals between capture

**Table 2.** Data sets for modelling of age-specific survival and recapture probabilities in program MARK. Each age-specific data set was composed from individuals tagged at that age plus individuals captured and tagged at an earlier age and then recaptured again at the age of interest. For instance, modelling survival at age-1 was based on a total of 1501 fish captured and tagged at age-1 plus 29 individuals originally tagged as age-0 fish and then recaptured at age-1

Data sets	Sample size components based on age at tagging					Total
	Age-0	Age-1	Age-2	Age-3	Age-4	
Age-0	116					116
Age-1	29	1501				1530
Age-2	21	684	927			1632
Age-3	13	251	386	531		1181
Age-4	0	63	169	167	168	567

occasions lasted 8–9 months while summer intervals lasted 3–4 months. Our winter intervals covered part of the spring and autumn seasons due to difficult sampling conditions (i.e. flooding) that are frequent during these times of the year. In the program MARK, the length of each time interval is used as an exponent of the survival estimate for the corresponding interval, so that survival estimates are comparable even if the intersample time intervals vary in length.

Our main goal was to test for effects of body size on survival, either as directional selection (linear effect) or as stabilizing selection (quadratic effect). Therefore, body lengths and squared body lengths were included as individual covariates in the capture history matrices. Prior to analyses, the data for both traits were variance standardized, that is, the data were standardized to a mean of zero and a SD of unity for each data set by subtracting the mean value and dividing by the SD. For two reasons, we estimated survival separately for each age-group: first, body size at age is likely to be more informative than body size alone because age might also influence survival, for example, through reproduction. Second, the MARK software will only allow one value of an individual covariate, such as body size, to be included for each capture history (that is, for each fish). Our capture–recapture data, however, often contained information on length at succeeding ages for a given fish. This information would be lost in a simple analysis on the total data set, containing all age groups. In order to keep as much information on body size as possible, we therefore constructed five separate data sets for fish captured and released at age-0 up to age-4, respectively. Fish that were tagged and subsequently recaptured at older ages were included as new capture histories in all relevant data sets, with a new value for body size. For instance, if a fish was first captured at age-1 and then recaptured at age-3, it would be included in the age-1 data set with two observations and then in the age-3 data set with one observation. Total sample sizes are presented in Table 2.

For each of the five data sets, a global model containing an interaction effect between time and age on survival ( $\phi_{\text{age} \times \text{time}}$ ) was used for goodness-of-fit testing and as a starting point for model selection. Survival was estimated independently for the age when length was measured while subsequent ages were pooled. The reason for choosing this approach is that we wanted to examine the effect of body length on survival during the time period immediately following length-measurement and release, when the body length that was measured would be most informative. In summary, the construction of five smaller age-based data sets from the total material (as described

above) allowed us to make full use of the information we had on body length of recaptured fish. Next, the construction of age-based models in MARK allowed us to estimate the effect of size on survival for the specific season following length-measurement and release. Capture probability was modelled with full time dependence but no age structure ( $P_{\text{time}}$ ). The goodness-of-fit of the global models was evaluated using the median c-hat method (with 10 levels of c-hat and 10 replicate points at each level) available in MARK. Model selection was based on the AIC corrected for small sample bias (Hurvich & Tsai 1989) and the estimated level (c-hat) of overdispersion (Burnham & Anderson 1998).

The model selection involved three main steps, which were run independently for each of the five data sets: First, we tested whether time dependence in survival could be simplified with an additive model ( $\phi_{\text{age+time}}$ ), or a model with time dependence at the age of first capture ( $\text{age}_i$ ) but constant survival of older fish ( $\text{age}_i, \phi_{\text{time}}$ ), this last model highlighting the main focus of estimating survival at the age where body length was measured. Second, we tested for effects of body length (length) on survival at  $\text{age}_i$  (linear effect:  $\text{age}_i, \phi_{\text{time+length}}$ , quadratic effect:  $\text{age}_i, \phi_{\text{time+length}^2}$ ). Third, we tested whether time dependence in survival could be simplified to a seasonal effect where winter survival differs from summer survival ( $\text{age}_i, \phi_{\text{wint}}$ ), or as a function of environmental covariates. Two environmental covariates were tested: the minimum daily water flow (minwater) during each survival period and the population density (popdens) measured at the start of each survival interval. We hypothesized that low water level and/or high population density would have negative effects on survival. Minimum water flow was used rather than mean water flow because the lowest water level will form gradually over a longer period as the stream dries up, indicating the most extreme conditions that the trout will have experienced. We also tested for an interaction effect of minwater and popdens on survival ( $\text{age}_i, \phi_{\text{minwater} \times \text{popdens}}$ ), as well as additive effects of the two environmental covariates ( $\text{age}_i, \phi_{\text{minwater+popdens}}$ ).

#### DATA SETS FOR ESTIMATING SELECTION

Each combination of starting sample and age-class comprised one data set. For most starting samples, we estimated selection acting on four age-classes (age-1 to age-4). However, during the fall sampling of 2002, there were too few age-4 individuals to perform a meaningful analysis of selection. Additionally, during the fall sampling of 2003 and 2004, age-0 fish were large enough to tag and thus we estimated selection acting on this additional age-class during these two intervals only. The data collected in 2006 were used for recapture information only. The combination of seven starting samples and multiple age-classes yielded 29 data sets for estimating selection.

#### ESTIMATING SELECTION

To test the hypothesis that survival was size-dependent, we used formal approaches for estimating selection acting on trout body length (Lande & Arnold 1983; Brodie *et al.* 1995; Janzen & Stern 1998). Specifically, we performed two sets of logistic regressions of relative fitness on variance standardized body length for each combination of starting sample and age-class (i.e. for each data set). For a given data set, individuals that were caught in the next sample or any sample thereafter (i.e. individuals that survived) were assigned an absolute fitness of unity. Individuals that were never recaptured again were assumed dead and assigned an absolute fitness of zero. For each data set, relative fitness was then calculated as absolute fitness

(0 or 1) divided by the average absolute fitness for all individuals in that data set. For each data set, we standardized body length and squared body length to a mean of zero and a SD of unity (mean and SD determined for each data set). We then estimated directional and quadratic selection via two sets of regressions. In the first set, we regressed relative fitness against standardized body length to estimate logistic selection differentials, which represent the total strength of selection acting on body length. In the second set, we added squared values for body length to the first set of regressions to estimate quadratic (nonlinear) selection differentials. Coefficients from these latter regressions are often interpreted as representing stabilizing selection (when negative) or disruptive selection (when positive).

We also performed univariate cubic splines (nonparametric regressions) to visualize the form of selection acting on each data set (Schluter 1988). Following Sinclair, Swain & Hanson (2002) and Carlson *et al.* (2007), we generated these splines within the program R (GAM function), wherein the smoothing parameter is selected by generalized cross-validation. To facilitate interpretation of these splines, we used raw (unstandardized) length data combined with absolute fitness (0 or 1).

## Results

### RECAPTURE PROBABILITIES AND APPARENT SURVIVAL

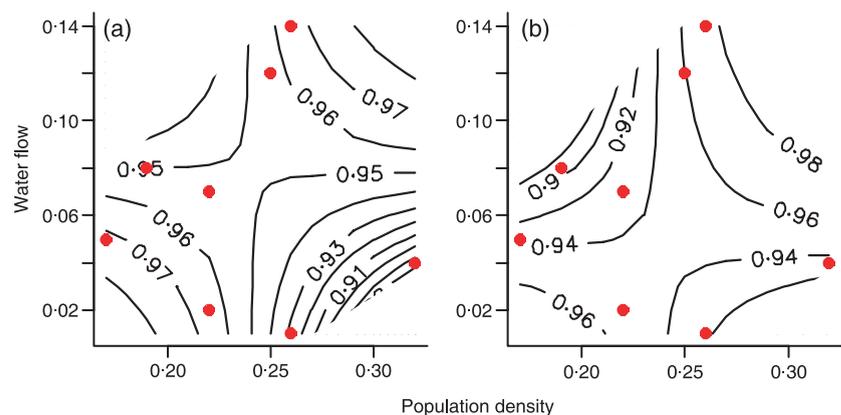
The median c-hat goodness-of-fit tests indicated that the global model ( $\phi_{\text{age} \times \text{time}}, P_{\text{time}}$ ) fit the data adequately (Table 3; c-hat < 2 for all age classes). Accordingly, this model was used as a starting point for analysing the data on brown trout survival. For all age classes, model selection results favoured more constrained models as compared to the global starting model (Table 3; models 1, 6, 10, 18 and 21). In general, the data did not support a consistent seasonal effect on survival. The seasonal effect was not retained in any of the most parsimonious models (Table 3; models 1, 6, 10, 18 and 21). At age-2 and age-3 years, however, there was support for simplifying full time-dependence in survival with an interaction effect between time-specific minimum water flow and brown trout population density (models 10 and 18, respectively, Table 3). The interaction effect suggests that at low water levels, an increase in population density was associated with a decrease in survival probability (Fig. 1). At intermediate water levels, a change in population density had little or no effect on survival (Fig. 1). At higher water levels, the data on population density was too sparse to draw any conclusions.

There was support for a small but significant negative linear effect of body size on survival at age 2, 3 and 4 years (Table 3;  $\text{age}_2 \beta_{\text{length}} = -0.0063$  (SE = 0.0030), model 10;  $\text{age}_3 \beta_{\text{length}} = -0.01669$  (SE = 0.0046), model 18;  $\text{age}_4 \beta_{\text{length}} = -0.01934$  (SE = 0.0083), model 21). At younger ages, the models containing a length-effect received less support but suggested a weak, positive linear effect of body size on survival at age-1 year (Table 3;  $\text{age}_1 \beta_{\text{length}} = 0.0047$  (SE = 0.0037), model 7).

Monthly survival probabilities (across all age groups) ranged from 0.85 to 0.98 (Table 4), corresponding to a yearly survival between 0.14 and 0.79. Capture probabilities (across all age groups) ranged from 0.28 to 0.68 (Table 5).

**Table 3.** Model selection for estimating brown trout survival ( $\phi$ ), showing the number of estimated parameters ( $k$ ), the deviance, the AIC score and the weight of evidence in favour of a particular model ( $w_i$ ) (Burnham & Anderson 1998). Only models with  $w_i > 0.01$  are presented. A general differentiation in survival between age at first capture and later ages is denoted  $\phi_{age}$ . Survival effects modelled specifically at age of first capture ( $age_i$ ) are denoted  $age_i\phi$ . These constrained models all had constant survival at later ages. Time dependence in survival is denoted  $\phi_{time}$ . An effect of minimum water flow on survival is abbreviated minwater; population density, popdens; body length, length; body length squared, length2; winter vs. summer, wisu. Capture probability was estimated independently for each sampling occasion and without age structure ( $P_{time}$ ). Bolded text indicates the model receiving the most support with each data set

Model number	Model structure	$k$	Deviance	AIC	$w_i$
Age-0 data set, c-hat = 1.91					
1	$\phi_{age}$	<b>10</b>	<b>212.4</b>	<b>233.7</b>	<b>0.75</b>
2	$age_0\phi_{minwater \times popdens}$	12	211.6	237.5	0.11
3	$age_0\phi_{minwater+popdens}$	12	212.2	238.0	0.09
4	$age_0\phi_{time}$	13	211.6	239.8	0.04
5	$age_0\phi_{time+length}$	14	211.6	242.1	0.01
Age-1 data set, c-hat = 1.28					
6	$age_1\phi_{time}$	<b>16</b>	<b>5067.5</b>	<b>5099.7</b>	<b>0.50</b>
7	$age_1\phi_{time+length}$	17	5066.2	5100.4	0.35
8	$age_1\phi_{time+length2}$	18	5066.2	5102.4	0.13
9	$\phi_{age \times time}$	21	5064.5	5106.8	0.01
Age-2 data set, c-hat = 1.39					
10	$age_2\phi_{minwater \times popdens+length}$	<b>13</b>	<b>4361.0</b>	<b>4387.2</b>	<b>0.44</b>
11	$Age_2\phi_{wisu}$	11	4367.0	4389.1	0.17
12	$age_2\phi_{time+length}$	18	4353.0	4389.2	0.16
13	$age_2\phi_{time}$	17	4355.9	4390.2	0.10
14	$age_2\phi_{time+length2}$	19	4353.0	4391.2	0.06
15	$age_2\phi_{popdens+length}$	12	4368.0	4392.1	0.04
16	$age_2\phi_{minwater+popdens+length}$	13	4368.0	4394.1	0.01
17	$\phi_{age+time}$	16	4362.1	4394.3	0.01
Age-3 data set, c-hat = 1.40					
18	$age_3\phi_{minwater \times popdens+length}$	<b>13</b>	<b>2619.9</b>	<b>2646.1</b>	<b>0.76</b>
19	$age_3\phi_{time+length}$	18	2612.9	2649.3	0.16
20	$age_3\phi_{time+length2}$	19	2612.6	2651.1	0.06
Age-4 data set, c-hat = 1.35					
21	$age_4\phi_{length}$	<b>10</b>	<b>1204.6</b>	<b>1224.8</b>	<b>0.36</b>
22	$age_4\phi_{minwater+length}$	11	1204.0	1226.3	0.17
23	$\phi_{age}$	9	1208.5	1226.7	0.14
24	$age_4\phi_{popdens+length}$	11	1204.5	1226.9	0.13
25	$age_4\phi_{minwater \times popdens+length}$	12	1203.7	1228.1	0.07
26	$age_4\phi_{minwater+popdens+length}$	12	1204.0	1228.3	0.06
27	$age_4\phi_{wisu}$	10	1208.5	1228.7	0.05



**Fig. 1.** Effects of brown trout population density and minimum stream water flow on brown trout monthly apparent survival probabilities at age-2 (a) and age-3 years (b). Circles mark observed combinations of population density and minimum water flow.

SELECTION

Directional selection varied among seasons and, in all but one case, among age-classes within a season. Despite this

variation, several patterns emerged. First, directional selection tended to favour relatively small individuals because 17 of 29 directional coefficients were negative (Table 6). This result was confirmed by cubic spline plots (Fig. 2). Second, directional

Season	Apparent survival probability ( $\phi$ )				
	Age-0 Model 1	Age-1 Model 6	Age-2 Model 10	Age-3 Model 18	Age-4 Model 21
Winter 2002	0.91 (0.02)	0.97 (0.01)	0.95 (0.01)	0.89 (0.01)	0.92 (0.01)
Summer 2003	*	0.98 (0.02)	0.97 (0.01)	0.93 (0.01)	0.92 (0.01)
Winter 2003	0.91 (0.02)	0.97 (0.01)	0.95 (0.01)	0.93 (0.01)	0.92 (0.01)
Summer 2004	*	0.91 (0.02)	0.89 (0.02)	0.93 (0.02)	0.92 (0.01)
Winter 2004	0.91 (0.02)	0.98 (0.01)	0.97 (0.01)	0.95 (0.01)	0.92 (0.01)
Summer 2005	*	0.85 (0.02)	0.93 (0.01)	0.92 (0.02)	0.92 (0.01)
Winter 2005	0.91 (0.02)	0.96 (0.01)	0.96 (0.01)	0.96 (0.01)	0.92 (0.01)
Summer 2006	*	0.96 (0.00)	0.97 (0.01)	0.98 (0.01)	0.92 (0.01)

\*Summer survival could not be estimated for age-0 brown trout because these fish were too small to be tagged during the capture occasions in spring.

Season	Capture probability ( $P$ )				
	Age-0 Model 1	Age-1 Model 6	Age-2 Model 10	Age-3 Model 18	Age-4 Model 21
Spring 2003	0.48 (0.49)	0.46 (0.08)	0.49 (0.06)	0.58 (0.08)	0.66 (–)*
Autumn 2003	0.48 (0.49)	0.29 (0.04)	0.36 (0.04)	0.43 (0.05)	0.56 (0.07)
Spring 2004	0.28 (0.11)	0.60 (0.04)	0.57 (0.05)	0.65 (0.06)	0.59 (0.08)
Autumn 2004	0.43 (0.14)	0.41 (0.03)	0.58 (0.03)	0.61 (0.05)	0.64 (0.06)
Spring 2005	0.43 (0.13)	0.52 (0.03)	0.52 (0.03)	0.56 (0.05)	0.57 (0.07)
Autumn 2005	0.30 (0.12)	0.46 (0.03)	0.56 (0.03)	0.63 (0.04)	0.68 (0.06)
Spring 2006	0.58 (0.18)	0.46 (0.03)	0.48 (0.04)	0.50 (0.05)	0.61 (0.08)
Autumn 2006	0.47 (0.19)	0.49 (0.04)	0.53 (0.04)	0.53 (0.04)	0.68 (0.06)

\*SE not estimable.

**Table 6.** Directional (logistic) and quadratic (nonlinear) selection acting on body length in Bellbekken brown trout. Coefficients (SE in parentheses) are presented for each year/season/age-class combination. Probability: \* $P < 0.05$ , bolded entries indicate the coefficients that were significant after Bonferroni corrections for multiple tests (corrections applied within each age-class)

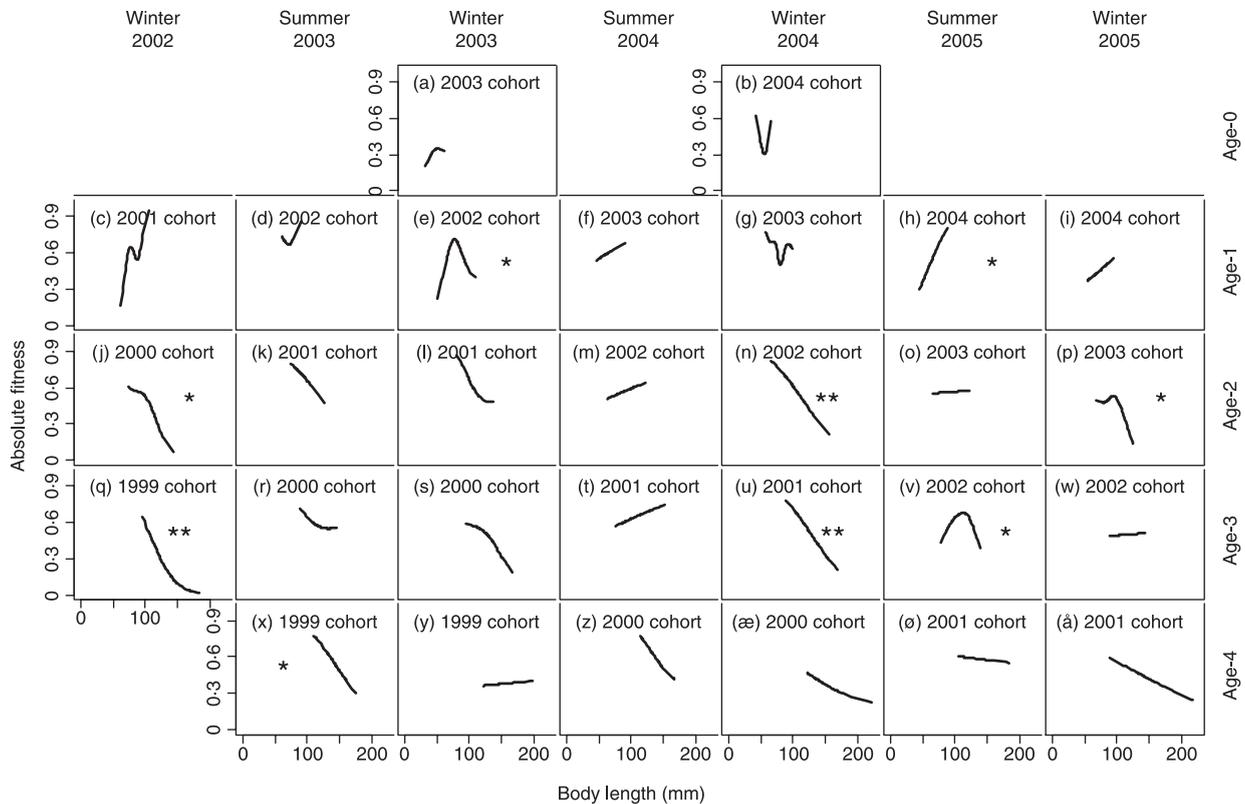
Season	Selection coefficients				
	Age-0	Age-1	Age-2	Age-3	Age-4
Directional coefficients					
Winter 2002		0.23 (0.23)	–0.35 (0.14)*	<b>–0.76 (0.18)*</b>	
Summer 2003		0 (0.2)	–0.24 (0.22)	–0.13 (0.17)	–0.41 (0.2)*
Winter 2003		0.12 (0.24)	–0.03 (0.14)	–0.37 (0.26)	–0.34 (0.22)
Summer 2004			0.07 (0.11)	0.08 (0.1)	–0.37 (0.22)
Winter 2004		–0.07 (0.39)	–0.21 (0.12)	<b>–0.38 (0.12)*</b>	<b>–0.59 (0.21)*</b>
Summer 2005			0.32 (0.12)*	0.01 (0.11)	0.01 (0.14)
Winter 2005			0.14 (0.11)	–0.16 (0.12)	0.02 (0.14)
Quadratic coefficients					
Winter 2002		–0.99 (3.15)	–3.57 (2.24)	–3.47 (3.3)	
Summer 2003		6.86 (6.13)	4.08 (3.8)	4.14 (2.94)	3.59 (3.21)
Winter 2003		–5.17 (3.99)	–4.14 (1.78)*	5.96 (4.05)	–4.95 (3.46)
Summer 2004			–0.71 (1)	0.58 (1.3)	–0.37 (2.13)
Winter 2004		10.9 (7.85)	2.36 (1.84)	–0.71 (1.22)	1.49 (2.57)
Summer 2005			–0.02 (1.24)	0.76 (1.39)	–4.61 (2.15)*
Winter 2005			1.2 (1.52)	–3.64 (1.78)*	1.71 (2.2)

selection tended to be weak (6 of 29 coefficients were significant at  $\alpha = 0.05$ , 3 were significant after Bonferroni corrections for multiple tests; Table 6). Third, of the six significant coefficients, five were negative (Table 6) suggesting that smaller

individuals were favoured. Fourth, four of the six significant coefficients were confined to two seasons (winter 2002, winter 2004). Finally, during the winter of 2004, selection favoured relatively short fish for all five age-classes for which selection

**Table 4.** Age-specific monthly survival probabilities ( $\phi$ ) of brown trout in southeastern Norway, estimated from the top-ranked model for each age-class (model numbers provided in Table 2). The 'winter' season is from autumn in year<sub>*i*</sub> to spring in year<sub>*i+1*</sub>. The 'summer' season is from spring in year<sub>*i*</sub> to autumn in year<sub>*i*</sub>. Estimates were generated at the mean body length and the observed value of water flow and population density, when these covariates were included in the top-ranked model. SE is given in parenthesis

**Table 5.** Estimated capture probabilities ( $P$ ) of brown trout in south eastern Norway. Estimates were generated from the top-ranked models from each data set (model numbers provided in Table 2), where, for example, 'Age-2' refers to capture probability of fish that are 2 years old or older, in the data set having 2 year old fish as the youngest age group included. SE is given in parenthesis



**Fig. 2.** Relationship between trout body length and apparent survival (0 = never recaptured and assumed dead; 1 = recaptured at a future sample/survived focal interval). Each plot represents a season/age-class combination. Season information is provided along the top row of the plot and age-class information is provided along the right column of the plot. Those splines associated with significant size effects from the formal selection analyses are indicated with an asterisk, where \* indicates  $P < 0.05$  and \*\* indicates that the coefficient was significant after Bonferroni corrections for multiple tests (applied within each age class; see also Table 6).

was estimated (age-0 to age-4) as revealed by negative directional coefficients in all cases. Cubic spline plots confirmed this result for fish greater than age-2 (Fig. 2n,u,æ) but suggested a more complicated pattern for age-0 and age-1 fish. In particular, the splines suggested that selection was disruptive for the age-0 (Fig. 2b) and age-1 fish (Fig. 2g) with the shortest and longest individuals surviving at a higher rate than intermediate-sized fish.

Quadratic selection was generally weak (significant at  $\alpha = 0.05$  in 3 of 29 intervals, none of which were significant after Bonferroni corrections for multiple tests; Table 6) and stabilizing selection (negative quadratic coefficients) was no more likely than disruptive selection (positive quadratic coefficients) (Table 6). The three cases of significant quadratic selection were all associated with negative coefficients (i.e. evidence of stabilizing selection). This result was confirmed by the cubic spline plots, which revealed stabilizing selection for three season-age combinations: winter 2003/age-1 fish (Fig. 2e), winter 2005/age-2 fish (Fig. 2p), and summer 2005/age-3 fish (Fig. 2v). The cubic spline plots also confirmed that linear selection was more common than nonlinear selection across ages, seasons, and years (Fig. 2).

## Discussion

This study yielded several results. First, monthly survival during the winter did not exceed monthly survival during the summer as revealed by relatively little support for models containing a season effect (Table 3). Second, abiotic (minimum water flow) and biotic (trout density) factors were important at some ages (age-2 and age-3), that is, a model including these factors together with their interaction (models 10 (age-2) and 18 (age-3), Table 3) received more support than the full time-dependence in survival model (models 12 (age-2) and 19 (age-3), Table 3). The presence of an interaction revealed that at low water levels, an increase in population density was associated with a reduction in survival (Fig. 1) and that at high trout densities an increase in flow was associated with an increase in survival. Third, the importance of body length to survival varied as a function of age (weak positive linear effect of size for age-1, model 7, Table 3; negative linear effect of size for age-2 through age-4, models 10, 18 and 21, respectively, Table 3). Fourth, formal selection analyses relating body size to survival through the summer and winter supported the above conclusions – directional selection was generally weak

and often favoured relatively small individuals (Table 6). Finally, nonlinear selection was largely absent as quadratic selection coefficients rarely differed from zero (Table 6). Cubic spline visualizations of the form of selection further suggest that nonlinear selection was less common than linear selection acting on Bellbekken brown trout. Taken together, these results suggest that survival is not always reduced in the winter nor do large trout consistently survive at a higher rate.

#### SEASON-DEPENDENT SURVIVAL

We here investigated whether survival rates varied by season (winter vs. summer) across multiple years and, in each year, by age. Despite the range of ages and years (i.e. conditions) considered, we found no evidence that survival rates varied by season (Table 3). Additionally, we approached this same question by compiling the results from previously published studies on stream-dwelling salmonids that compared winter survival to survival rates during other seasons. This body of research is exceedingly small – only eight studies have compared whether survival rates in winter differ from other seasons (see Table S1 in Supplementary Material). Some of these studies present data for multiple species (Carlson & Letcher 2003), age classes (Elliott 1981, 1993; Letcher, Gries & Juanes 2002; Carlson & Letcher 2003; Carlson *et al.* present study), or populations (Elliott 1993; Lund, Olsen & Vøllestad 2003) resulting in 16 comparisons of seasonal survival rates. This body of research demonstrates that winter survival does not consistently fall below survival rates during other seasons (see Supplementary Table S1). For instance, four comparisons suggest no difference between winter and summer survival rates (Elliott 1993; Lund *et al.* 2003; Carlson *et al.* present study), five comparisons found that survival rates were lower during winter than during other seasons (Letcher *et al.* 2002; Mitro & Zale 2002; Lund *et al.* 2003), and seven comparisons found that survival rates were lowest during seasons other than the winter (Egglshaw & Shackley 1977; Elliott 1993; Olsen & Vøllestad 2001a; Carlson & Letcher 2003). We therefore conclude that winter mortality cannot be assumed to be more severe than mortality during other seasons.

The most plausible explanation for the above results is that organisms inhabiting seasonal environments are adapted to the annual environmental regime. Prior to winter, for instance, stream-dwelling salmonids will increase their lipid content (e.g. Berg & Bremset 1998) and these lipid reserves help fuel metabolism through the winter period. Moreover, diet and energetic studies suggest that stream-dwelling salmonids continue to feed during the winter (Cunjak 1988; Heggenes *et al.* 1993; Finstad *et al.* 2004b) and so do not rely entirely on stored energy to avoid starvation. Additionally, populations distributed along latitudinal gradients are locally adapted to winter severity. For example, when raised in a common environment simulating winter conditions, a northern population of Atlantic salmon (*Salmo salar* L.) had higher mass-specific growth rates, energy intake, and growth efficiency relative to two southern populations (Finstad *et al.* 2004a). Moreover, northern populations are more adapted for conditions

under the ice (Finstad & Forseth 2006). In addition to the aforementioned physiological adaptations, stream resident salmonids also display a variety of behavioural adaptations to minimize the probability of encountering unfavourable physical conditions. For instance, stream-dwelling salmonids switch from a diurnal towards a nocturnal activity pattern as winter approaches (e.g. Bremset 2000). Moreover, during winter, juvenile Atlantic salmon hide beneath rocks, where water velocities approach zero, to minimize energy expenditure (Cunjak 1988). Stream resident brook trout (*Salvelinus fontinalis* Mitchell) and brown trout also show a strong preference for positions beneath cover during the winter (Cunjak & Power 1986).

Finally, we suggest that over-wintering under the ice might not be that dangerous. For instance, predation from avian and mammalian predators is likely reduced once streams become ice-covered. Additionally, the near-freezing water temperature of ice-covered streams leads to reduced metabolic demands overall. For these reasons, stream salmonid populations at lower latitudes or altitudes (i.e. locations where ice cover is insignificant) may be at a distinct disadvantage because (i) they are susceptible to predation by endothermic predators and (ii) metabolic demands are elevated due to the elevated water temperatures. To the extent that this is true, a severe winter might have a greater impact on low latitude/altitude populations, which are less adapted to ice cover conditions (e.g. Finstad & Forseth 2006), than on high latitude/altitude populations.

#### SIZE-DEPENDENT SURVIVAL

In addition to estimating survival rates, we also tested whether survival was a function of body size. Across four winters (2002–2005) and three summers (2003–2005), and across five age-classes (age-0 to age-4), we found that selection on trout body size was typically weak (only 6 of 29 directional coefficients significant at  $\alpha = 0.05$  level, Table 6). Moreover, selection often favoured relatively small individuals as 17 of 29 directional coefficients were negative (Table 6). These results support the notion that selection should be weak in self-sustaining (i.e. adapted) populations. However, these results do not support the hypothesis that larger body size confers a survival advantage – neither during the winter nor during the summer. We also note that the percent of negative directional coefficients increased with age (Table 6), which suggests that we may also be detecting a cost of reproduction (e.g. Hutchings *et al.* 1999). The mean age at maturity for brown trout in Bellbekken is 3.1 years for males and 3.5 years for females (Olsen & Vøllestad 2005), suggesting that a large proportion of the age-3 and age-4 trout sampled during autumn would be spawning during that season. In general, survival is reduced after spawning (Hutchings *et al.* 1999) and, moreover, larger fish within an age class generally reach maturity earlier than smaller individuals of the same age class (Olsen & Vøllestad 2005).

To assess the generality of our results, we compiled the results of previous studies in nature examining the size-dependence

of mortality in stream-dwelling salmonids (see Supplementary Table S2). The review contains information on 13 studies many of which examined the size-dependence of mortality across multiple time periods (Hunt 1969; Quinn & Peterson 1996; Einum & Fleming 2000; Good *et al.* 2001; Hendry *et al.* 2003; Carlson, Hendry & Letcher 2004; Letcher *et al.* 2005; Carlson *et al.* present study), ages (Hendry *et al.* 2003; Carlson *et al.* 2004; Carlson *et al.* present study), species (Meyer & Griffith 1997), or populations (Lund *et al.* 2003; Johnston, Bergeron & Dodson 2005) yielding a total of 74 estimates of the strength of size-dependent mortality. The results of this review provide support that bigger is not always better. Some studies argued that bigger-is-better after finding a positive relationship between mean pre-winter body size and winter survival rates (Hunt 1969) but this approach does not reveal whether the smallest individuals were most likely to die *within a given year*. After restricting our focus to the subset of studies testing whether survival was related to an individual's body size (i.e. excluding Hunt 1969), some results suggest that bigger was generally better (Smith & Griffith 1994; Einum & Fleming 1999), that bigger was generally worse (Carlson *et al.* 2004; Carlson *et al.* present study), or that survival was not a function of size (Lund *et al.* 2003). Often, the results varied among years (Quinn & Peterson 1996; Good *et al.* 2001; Hendry *et al.* 2003; Letcher *et al.* 2005), among sites (Meyer & Griffith 1997; Johnston *et al.* 2005), or among ages (Einum & Fleming 2000; Letcher *et al.* 2005). We conclude, therefore, that bigger cannot be assumed to be better for stream-dwelling salmonids.

The above results are perhaps not surprising given that adapted populations should not regularly experience strong episodes of selection. Indeed, selection tends to be weak in wild populations (Kingsolver *et al.* 2001). One explanation for our results, therefore, is that large body size is only favoured when environmental conditions are extreme (e.g. harsh winter, flood, drought, etc.). Indeed, Good *et al.* (2001) found that larger Atlantic salmon survived the summer at a higher rate than smaller salmon during a drought year but *smaller* salmon survived at a higher rate during a flood year. These results suggest stressful environmental conditions do indeed drive strong episodes of selection but that the direction of selection is not consistent (see also Grant & Grant 2002; Seamons, Bentzen & Quinn 2007). A second explanation for our results is that getting big is costly (Arendt 1997; Blanckenhorn 2000). Indeed, numerous recent studies have pointed out the costs associated with fast growth including increased susceptibility to predation (e.g. Billerbeck, Lankford & Conover 2001; Munch & Conover 2003) and reduced swimming performance (e.g. Lankford, Billerbeck & Conover 2001). Taken together, these results suggest that getting big can be dangerous and that being big may not confer a survival advantage.

#### NON-RANDOM OVER-WINTER MORTALITY

In the present study, we have focused on whether over-winter mortality is higher for smaller stream-dwelling salmonids and have concluded that the results vary both among and within

systems. However, in some other fish species, there does appear to be higher over-winter mortality of smaller fish (e.g. Schultz, Conover & Ehtisham 1998). Why is non-random over-winter mortality seen in some fish species but not in others? One possibility is that life span plays a role. For instance, in annual fishes or fishes that rarely live for a full year, fish need to either be born early enough in the year (e.g. Reznick *et al.* 2006) or to grow rapidly enough to attain a sufficient size and sufficient energy reserves to survive the winter (e.g. Reznick & Braun 1987; Schultz *et al.* 1998). Stream-dwelling salmonids are iteroparous and long-lived (e.g. Bellbekken brown trout can live up to 9 years and spawn at least during three consecutive seasons) and, consequently, size becomes confounded with reproductive investment as the fish grow/age. In Bellbekken brown trout, we found that smaller fish were more likely to survive than larger fish (Table 6, Fig. 2) but large older fish are more likely to be mature (brown trout mature as early as age-2 in the Bellbekken). One possible explanation for our empirical results, therefore, is that larger fish are paying a cost of reproduction that the smaller fish are not.

#### SUMMARY

We here tested the long-standing hypotheses that (i) winter mortality is generally high relative to the other seasons and (ii) that large body size confers a survival advantage. We employed multiple approaches to test these hypotheses including a field study tracking the fates of individual fish across multiple seasons and multiple years as well as a literature review. We found little empirical support for the aforementioned hypotheses – including from our own field study and from other studies, which included a range of study systems and species (see Supplementary Tables S1 and S2). We suggest that these results are not surprising when considering that self-sustaining populations are presumably adapted to the predictable conditions they experience. For instance, organisms inhabiting seasonal environments should develop adaptations to cope with seasonal changes in their environment – and they do (e.g. Cunjak 1988; Bremset 2000; Finstad *et al.* 2004a; Finstad & Forseth 2006). Moreover, self-sustaining populations should not regularly experience strong episodes of selection – and they do not (e.g. Kingsolver *et al.* 2001). We conclude that the empirical support in favour of the winter-is-worse and bigger-is-better hypotheses is equivocal at best and encourage future research that tests the conditions under which these assumptions hold true in natural populations.

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## Supplementary material

The following supplementary material is available for this article:

**Table S1** A comparison of apparent survival rates among seasons for stream-dwelling salmonids.

**Table S2** Evidence of size-selective mortality acting on stream-dwelling salmonids.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2745.2008.01416.x>

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