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First-year survival of brown trout in three Norwegian streams

E. Lund, E. M. Olsen and L. A. Vøllestad*

Division of Zoology, Department of Biology, University of Oslo, P. O. Box 1050 Blindern, N-0316 Oslo, Norway

Monthly survival rates during the first year of life were estimated for the 1999 cohort of stream-resident brown trout *Salmo trutta* in three Norwegian streams, using capture-mark-recapture methods and the Cormack–Jolly–Seber model. It was hypothesized that reduced survival would occur during the winter. For one of the study populations, the data did support seasonal variation in survival, with monthly survival rates being lower during winter than during summer (0.65 *v.* 0.99). For the remaining two populations, there was no evidence for seasonal variations in monthly survival rates, but monthly survival rates were significantly different (0.87 *v.* 0.99). No evidence was found for size-dependent winter survival. Some marked individuals emigrated from the study sites, suggesting that survival rates were underestimated and that different survival rates among populations were partly due to different emigration rates. Net immigration of brown trout was evident at all three study sites.

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Key words: 0+ brown trout; capture-mark-recapture; density; season; survival.

INTRODUCTION

Survival during early life stages is important for the dynamics of fish populations (Wootton, 1990; Elliott, 1994). In temperate regions, the winter season is often considered as a period of severe conditions and high mortality for stream-dwelling salmonids. The low temperatures affect fish physiology, *e.g.* by reducing digestive and swimming abilities (Rimmer *et al.*, 1985; Elliott, 1994). Furthermore, low water levels and formation of ice may decrease the availability of fish habitats. If suitable shelters are in short supply (Armstrong & Griffiths, 2001), density-dependent survival during winter may be expected. Further, floods, droughts and ice break-ups may cause serious disturbances, perhaps leading to increased mortality or movement of individuals (Needham & Jones, 1959; Seegrist & Gard, 1972; Cunjak *et al.*, 1998; Whalen *et al.*, 1999).

In juveniles of Atlantic salmon *Salmo salar* L. and brown trout *Salmo trutta* L., individual energy content decreases during winter (Gardiner & Geddes, 1980; Berg & Bremset, 1998). Metcalfe & Thorpe (1992) suggested that the decrease in energy content is caused by increased feeding costs in winter. Feeding involves the obvious benefit of acquiring energy, but also incurs costs from using energy on catching and handling

*Author to whom correspondence should be addressed. Tel.: +47 22854640; fax: +47 22854605; email: avollest@bio.uio.no

the food and being exposed to predators. Therefore, there may be a trade-off between active feeding and passive starving in energetically favourable positions characterized by low water velocity and cover against predators. If the low water temperatures in winter reduce the swimming ability of salmonids (Rimmer *et al.*, 1985), the increased cost of catching food and being exposed to predators may be larger than the benefit of acquiring energy from the food. Thus, the fish will seek cover more often at cold than at warm temperatures (Cunjak & Power, 1986; Huntingford *et al.*, 1988; Valdimarsson & Metcalfe, 1998). In Atlantic salmon, appetite increases and feeding is resumed when energy levels drop below some threshold, where the critical value reflects the minimum expected energy demands until spring (Metcalfe & Thorpe, 1992; Bull *et al.*, 1996). The strategy of seeking cover during winter may be beneficial in minimizing energy expenditure and reducing mortality from predation. The poor energy status of individuals may lower their survival probability by reducing their ability to handle the severe winter conditions.

Berg & Bremset (1998) suggested that the loss of energy during winter has especially serious consequences for the smaller individuals. The 'big is better' hypothesis states that, generally, the larger individuals have the benefit of being better at avoiding predators, better at resisting starvation and better at tolerating physical extremes (Sogard, 1997). In salmonids, some reports support size-dependent survival during the first winter (Lindroth, 1965; Hunt, 1969; Smith & Griffith, 1994; Meyer & Griffith, 1997) whereas others have not (Hendry *et al.*, in press).

In studies on early survival of salmonid fishes, survival estimates are often based on changes in the cohort density during a given time period (Allen, 1951; Le Cren, 1973; Egglishaw & Shackley, 1977; Elliott, 1984; Crisp, 1993; Crisp & Beaumont, 1995). The estimates of cohort density are obtained by repeated sampling (*e.g.* by nets or electrofishing) in a defined area. It is often assumed that movement of individuals is restricted, so that changes in density are due to mortality, not migration (Gowan *et al.*, 1994). If this assumption is violated, however, migrating individuals will alter the density of the cohort and bias the survival estimates (Riley *et al.*, 1992; Bridcut & Giller, 1993; Gowan & Fausch, 1996). By following individually marked fish through time (Lebreton *et al.*, 1992), survival rates can be estimated without using information on changes in cohort density. Emigration of marked individuals will still lead to biased survival estimates, but immigration of unmarked individuals will not influence the estimated survival rates.

In this study, capture-mark-recapture (CMR) methodology (Lebreton *et al.*, 1992) was used to estimate the first-year survival in three populations of stream-resident brown trout in south-east Norway. Because of the effect of low water temperature on brown trout energy budgets and the potential effects of water level changes and ice formation on brown trout habitat, winter survival was expected to be lower than summer survival. Potential effects of variation in body size on survival were also tested.

MATERIALS AND METHODS

STUDY AREA

The investigation was carried out in three streams, Gjesa, Ulvåa and Søre Osa (hereafter Osa), located within *c.* 15 km in south-east Norway (Olsen & Vøllestad, 2001*a*). The altitude

of the area is between 240 and 360 m a.s.l. One site in each stream was selected for sampling of 0+ year brown trout. In Gjesa, the smallest stream, the study site had a mean width of 3·2 m (range = 2·0–4·7 m), mean depth of 11·9 cm (0–57 cm) and a wetted area of 353 m^2. The site started where the stream entered the larger stream, Julussa, and consisted of a 186 m stretch of riffles, interspaced with a few pools. Upstream of the site, brown trout were present for c. 500 m. Ulvåa was larger [mean width of the site was 9·6 m (8·3–10·3 m), mean depth was 28·4 cm (0–52 cm)], consisting mainly of riffles and glides. The wetted area was 513 m^2, at a length of 54 m. Upstream of the site, brown trout were present for several km without there being any specific barriers to migration. Downstream from the site, brown trout can move unimpeded for c. 150 m before reaching a large waterfall that probably functions as a barrier to upstream migration. Downstream passage is possible, and two marked brown trout have been recaptured in Osa, downstream of the waterfall (Olsen & Vøllestad, 2001a). Osa was the largest stream, often >30 m in width. It was not possible to sample the whole width of the stream, as the middle part was too deep. The site in Osa had a mean width of 15·3 m (11·0–20·0 m) and a mean depth of 31·0 cm (0–75 cm). The wetted area was 563 m^2, at a length of 40 m. Brown trout can move for several hundred metres in each direction before reaching dams that stop upstream, but not downstream, migration. No migration of brown trout among the three sites was possible.

The brown trout in these three streams are resident, showing no evidence for extensive migrations. The brown trout is small sized, rarely reaching sizes >20 cm fork length (L_F) and ages >7 years (Olsen & Vøllestad, 2001a). Minnow *Phoxinus phoxinus* (L.) were common in Osa, but sporadic in the two other sites. Small individuals of perch *Perca fluviatilis* L. were sporadically found in all three streams. Gjesa was the only stream with Alpine bullhead *Cottus poecilopus* Heckel and an occasional, small (0+ year) pike *Esox lucius* L. Ducks *Mergus* sp. and herons *Ardea cinerea* L. were observed in Osa. Mink *Mustela vison* Schreber was observed in Gjesa and Osa, and it was probably common at all three sites.

ABIOTIC FACTORS

Water temperature was measured every second hour, except in the period October 1999 to June 2000. Due to device malfunction, temperature data for Osa in 1999 were not available. Mean daily water temperature followed the same pattern through summer and autumn in the three streams. Water temperatures were mainly <15° C (Fig. 1). Water level was estimated
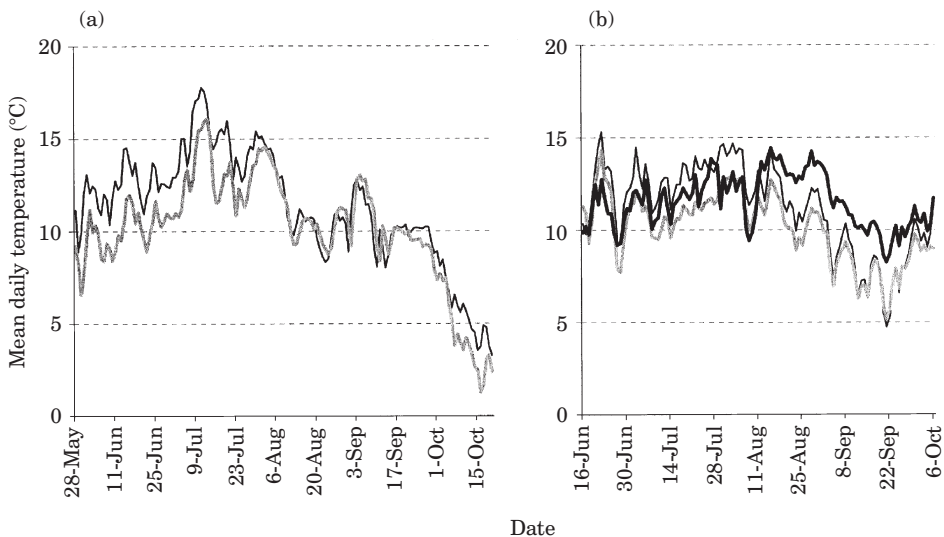

FIG. 1. Mean daily water temperatures in (a) 1999 and (b) 2000 in three Norwegian streams, Gjesa (——), Ulvåa (——) and Osa (——).
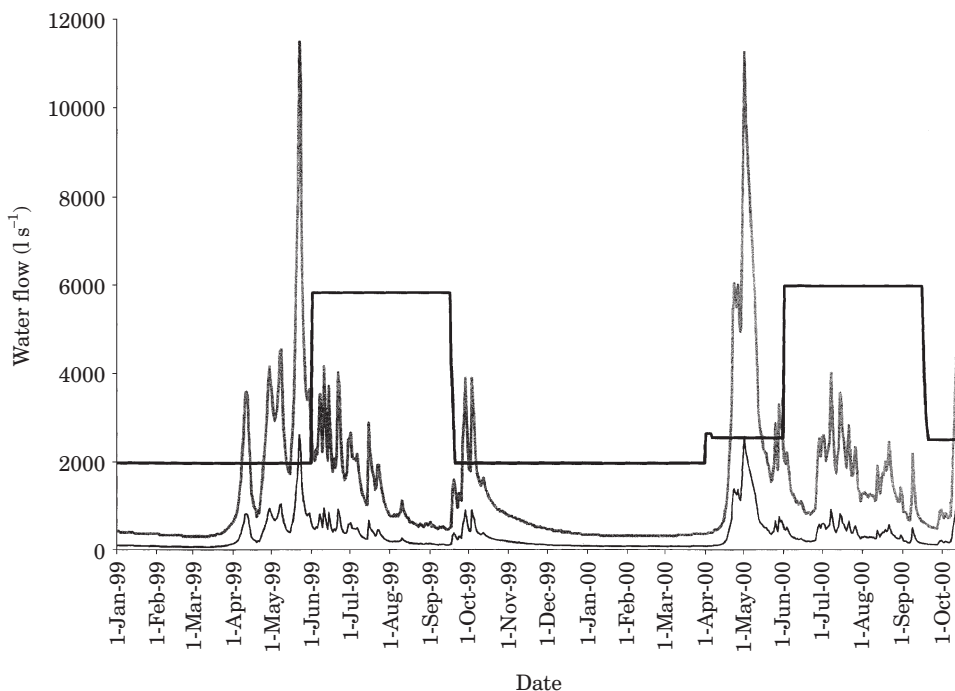
FIG. 2. Water flow during 1999–2000 in three Norwegian streams Gjesa (—), Ulvåa (—) and Osa (—). Osa is regulated by a reservoir upstream of the capture site.

in two ways: (1) by a visual assessment on each capture occasion, and (2) from data supplied by the Norwegian Water Resources and Energy Directorate (NVE) (Fig. 2). The visual assessment categorized water level as low, medium or high. The NVE values for Gjesa and Ulvåa were based on daily recordings ($1 s^{-1}$) at a nearby metering station, and they were scaled to describe the flow of water in the two streams. These estimates therefore only gave indirect estimates of the flow in these two streams, as flow patterns may have differed among subcatchments within the same area. The estimates, however, gave a good indication of the long-term variability in flow among seasons. The visual estimates were used when modelling recapture rate (influenced by instant rates of change in water flow) and the NVE values when modelling survival rate (influenced by high or low flow levels over time). In Gjesa and Ulvåa, the water flow increased in April to May and in September to October Water flow was measured directly in Osa. Because of regulation for hydropower production, Osa had no spring or autumn flow peaks. Osa had two relatively constant flow levels, the highest being in summer.

CAPTURE AND MARKING

Brown trout belonging to the 1999 cohort were captured by systematic electrofishing using a backpack apparatus (Bohlin *et al.*, 1989). At each site, three to six upstream passes were made during a capture occasion. The first captures were made in August 1999 (capture occasion 1). Subsequent capture occasions in September and November 1999, and in June, August and October 2000 made up a total of six capture occasions and five survival intervals. Survival intervals' represent the time between capture occasions, *i.e.* survival interval 1 was the period between capture occasions 1 and 2. Sampling was not performed on the same day at the three sites, but this difference was small compared to the length of the survival intervals. Therefore, the length of survival intervals was set equal among sites. Ice and high water flows made it impossible to sample at these sites between November 1999 and June 2000.
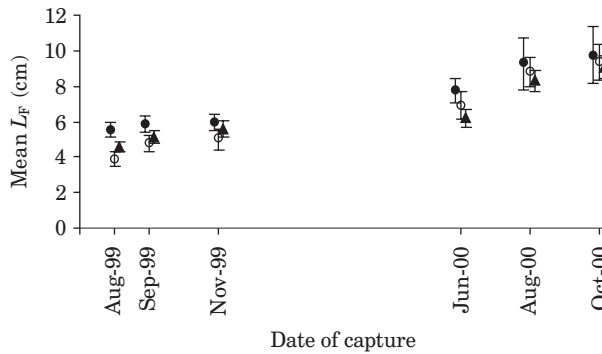
FIG. 3. Mean ± S.D. fork length of the 1999 cohort of brown trout at each capture occasion in three Norwegian streams, Gjesa (●), Ulvåa (○) and Osa (▲).

After each pass during a capture occasion, the captured fish were anaesthetized with benzocaine and L_F was measured to the nearest mm. In all three populations, the main increase in L_F was during survival intervals 3 and 4, *i.e.* from November to August (Fig. 3). The brown trout in Gjesa were largest at all capture occasions. The brown trout were marked by subcutaneous injections of coloured elastomer at different anatomical locations. Each fish received two marks in areas near the fins. Four different colours were used, giving each brown trout unique, externally visible, internal marks. Experiments have demonstrated that this method does not affect the growth rate or the survival rate of marked 0+ year brown trout in the laboratory, and that mark loss is low (Olsen & Vøllestad, 2001b). Scale samples were collected when marking 1+ year brown trout of the 1999 cohort (in 2000). After the final pass of each capture occasion, all brown trout were released randomly within the site.

In Gjesa and Osa, marking was performed on capture occasions 1, 2 and 3, leaving only recapturing for occasions 4, 5 and 6. In Ulvåa, all unmarked brown trout were marked at all capture occasions (due to further studies on this cohort). At capture occasions 1, 2 and 3, recognizing 0+ year brown trout was easy, because of a distinct difference in body size compared to other age classes. At capture occasions 4, 5 and 6, the size difference between 1+ and >1+ year was not as distinct, and age was determined from scale samples (Jonsson, 1976). The total number of marked brown trout was 604: 134 in Gjesa, 397 in Ulvåa and 73 in Osa. The number of marked individuals recaptured once or more than once was 74 (55%) in Gjesa, 110 (28%) in Ulvåa and 50 (68%) in Osa.

SURVIVAL ANALYSIS

A capture history was constructed for each marked brown trout (Lebreton *et al.*, 1992). Capture history matrices were used as input files for the computer programme MARK (White & Burnham, 1999). MARK computes maximum likelihood estimates of ϕ, the apparent survival probability, and p, the recapture probability. Apparent survival represents the combined probability that an animal survives from capture occasion i to capture occasion $i+1$ and that it has not emigrated. Animals that emigrate permanently from the study area will appear to have died (White & Burnham, 1999). Temporary emigration, where the fish is not seen during one or more capture occasions before again being recaptured, does not affect apparent survival probability, only recapture probability.

The Cormack–Jolly–Seber (CJS) model was used as a starting point for the survival analyses. This model allows both survival and recapture probabilities to vary with time for a single group of animals (Lebreton *et al.*, 1992). The fit of the CJS model to the data was tested separately for each study site, using goodness-of-fit (GOF) tests in the programme RELEASE (Burnham *et al.*, 1987). A significant GOF test indicates lack of fit. Then, MARK was used to compare different candidate models and to estimate apparent survival and recapture probabilities. All study sites were now included in one single analysis. This

TABLE I. Notation of possible effects on survival rate and recapture rate

Notation	Effect on survival rate (ϕ) or recapture rate (p)
.	constant: all rates constant
t	time: ϕ, different for all survival intervals; p, different for all capture occasions
g	group: rate different among populations
s	season: winter from September to June
n	season: winter from November to June
1	season: survival rates equal between summers
2	season: survival rates different between summers
constant	constant: ϕ constant for given populations
G, U, O	populations: Gjesa, Ulvåa, Osa
w	water level: visual observations (low, medium, high), p varies with w[*]
W	water level: NVE[†] values ($1\,s^{-1}$), ϕ vary with W[*]
c	temperature (°C): both rates vary with temperature[*]
e	fishing effort (number of passes): p varies with fishing effort[*]
×	interaction, *e.g.* between population and time ($g \cdot t$)
+	additive effect, *e.g.* of population and time ($g + t$)

[*]To optimize parameter estimation, covariates were scaled to have a mean in the interval [0, 1].
[†]Values obtained from the Norwegian Water Resources and Energy Directorate.

approach was justified since all sites were sampled within the same field sessions. An extended CJS model, with an interaction effect between study site and time, denoted $\phi(g \cdot t)p(g \cdot t)$ (Table I), had the maximum parameterization and served as the global starting model. All further models applied to the data were special cases of this model, *e.g.* by constraining the full time variation to produce seasonal and constant models or by incorporating other factors than time.

Seasonal models varied according to how winter was defined. Winter was either defined as the period from September to June (survival intervals 2 and 3) or defined as the period from November to June (survival interval 3). When defining winter as the September to June period, survival interval 5 partly corresponded to the defined winter season, but was treated as summer. In seasonal models, survival rates were either equal or different between summers. Models with seasonal effect on survival in only one or two populations were also tested. In this study, ϕ denoted monthly apparent survival, where 1 month was defined as 30 days.

Model selection was based on the corrected Akaike information criterion, AIC_C (Hurvich & Tsai, 1989), where models with the lowest AIC_C value represent the best compromise between bias (including too few parameters) and lack of precision (including too many parameters; Burnham & Anderson, 1998). The model with the lowest AIC_C value will therefore have more support, but models within 1–2 AIC_C units of the best model also have substantial support and should receive consideration in making inferences (Burnham & Anderson, 1998). Normalized Akaike weights were used to assess the relative probability of each model being closest to the unknown reality that generated the data, in the set of candidate models (Burnham & Anderson, 1998).

When selecting models, the model component for recapture rate (p) was selected first, by running models differing only in this component. The component for survival rate (ϕ) was not altered and consisted of the interaction between population and time, *i.e.* the global model for survival. After selecting the best model for recapture rate, the same process was performed on the component for survival rate, this time keeping the selected model for recapture rate fixed and testing different models for survival rate.

The hypothesis of individual body length having an effect on winter survival was tested (one-way ANOVA) by comparing the mean L_F of 0+ year brown trout marked in

September 1999. If survival was size-dependent, it was expected that the mean size in September was larger for brown trout recaptured during summer 2000 than for those that were never recaptured after the winter.

POPULATION DENSITY AND MIGRATIONS

To allow comparison of survival rates based on population densities and survival rates based on CMR, population densities were estimated. The density of the 1999 brown trout cohort, as well as for all brown trout age classes >0+ years (excluding 0+ years), at the three sites was estimated at each capture occasion using the removal method in the computer programme CAPTURE (White *et al.*, 1982). A generalized model (model M_{bh}) was used, allowing differing capture probabilities among samplings (Otis *et al.*, 1978). On each capture occasion, three to six removal passes were performed in 2–6 h.

Emigration from the sites was studied by sampling brown trout in areas outside the sites in Gjesa and Ulvåa on capture occasion 5. In Gjesa, one 150 m section upstream of the site was sampled. Downstream of the site, Gjesa runs into Julussa, which was considered unsuitable for efficient sampling. In Ulvåa, sampling was performed 150 m up- and downstream of the site. Only one pass was done when sampling outside of the sites. All brown trout captured outside of the sites were released at the same place as they were captured. Osa was not sampled outside of the site. Immigration of unmarked brown trout to the study sites was evaluated by inspecting the ratio between the number of marked recaptures and the total number of captures (marked + unmarked) of the 1999 cohort, at each capture occasion.

RESULTS

SURVIVAL ANALYSIS

For all study sites, the CJS model fitted the data adequately (Gjesa: $\chi^2 = 0.625$, d.f. $= 7$, $P = 0.999$; Ulvåa: $\chi^2 = 0.353$, d.f. $= 10$, $P = 1.000$; Osa: $\chi^2 = 3.979$, d.f. $= 7$, $P = 0.782$). The first part of the model selection procedure was to find the model that best explained variation in recapture rate. The hypothesis of constant recapture rate had little statistical support (Table II). The best model, $p(g \times w)$, had water level at each capture occasions as a covariate. The interaction term indicated that the effect of water level was different among populations. Models $p(g + t)$ and $p(g \times w)$ were close in AIC_c values. Model $p(g \times w)$, however, had 1·35 times the support of model $p(g + t)$, and was selected as the best model for recapture rate. The estimated recapture rates varied between 0·13 and 0·76 (Fig. 4). On capture occasion 3 (November 1999), recapture rates were low at all sites. In both Gjesa and Ulvåa, this low recapture rate coincided with high flows. In Osa, recapture rates were generally low. The highest recapture rates were estimated in Gjesa at capture occasions 2 and 6 (September 1999 and October 2000).

By combining the recapture model $p(g \times w)$ with various models for survival rate, the model selection was completed (Table III). Models with constant survival rates at all sites and without any population effect scored high AIC_c values, suggesting that survival rates differed in time and among populations. Seasonal models had low AIC_c values when defining winter as the period from September to June (*i.e. s*-models). When modelling seasonal effect for one or two sites (constant survival rates at the other sites), two models, in which survival rates were constant in Gjesa (both models) and Osa (one model), scored the lowest AIC_c values overall. The difference in AIC_c between these two models was 2·04. The model with constant survival in both Gjesa and Osa had 2·8 times as much

TABLE II. Selection of the best model for recapture rate. $AIC = -2\ln(Likelihood) + 2K$, where K is the number of parameters. AIC_c is corrected for small sample size. ΔAIC_c is the difference in AIC_c between the current model and the model with the lowest AIC_c. AIC_c weight is the relative support of individual models. Number of estimated parameters in the model equals no. para. The deviance is the difference between $-2\ln(Likelihood)$ of the current model and $-2\ln(Likelihood)$ of the saturated model, where the saturated model is defined as the model with number of parameters equal to the sample size

Model		AIC_c	ΔAIC_c	AIC_c weight	No. para	Deviance
$\phi(g \times t)$	$p(g \times w)$	1358·0	0·00	0·442	15	127·2
$\phi(g \times t)$	$p(g + t)$	1358·6	0·60	0·328	18	121·6
$\phi(g \times t)$	$p(g \times w + e)$	1359·8	1·82	0·178	17	124·9
$\phi(g \times t)$	$p(g \times t)$	1363·5	5·49	0·028	23	116·0
$\phi(g \times t)$	$p(t)$	1365·0	7·01	0·013	16	132·2
$\phi(g \times t)$	$p(g + c)$	1366·5	8·55	0·006	13	139·9
$\phi(g \times t)$	$p(g + e)$	1370·2	12·26	0·001	12	145·7
$\phi(g \times t)$	$p(g \times c)$	1371·7	13·75	0·0	16	138·9
$\phi(g \times t)$	$p(g + w)$	1372·2	14·19	0·0	14	143·5
$\phi(g \times t)$	$p(g \times e)$	1372·2	14·27	0·0	16	139·4
$\phi(g \times t)$	$p(g)$	1372·7	14·74	0·0	11	150·2
$\phi(g \times t)$	$p(e)$	1381·1	23·18	0·0	13	154·5
$\phi(g \times t)$	$p(w + e)$	1381·9	23·90	0·0	14	153·2
$\phi(g \times t)$	$p(c)$	1384·3	26·30	0·0	13	157·7
$\phi(g \times t)$	$p(w)$	1388·6	30·62	0·0	13	162·0
$\phi(g \times t)$	$p(.)$	1390·6	32·67	0·0	12	166·1

support in terms of AIC_c weight as the model with constant survival in Gjesa only. Thus, the model $\phi(g + s1)G + O$ constant $p(g \times w)$ was selected as the best, indicating a seasonal effect on survival in Ulvåa and constant survival rates in Gjesa and Osa.
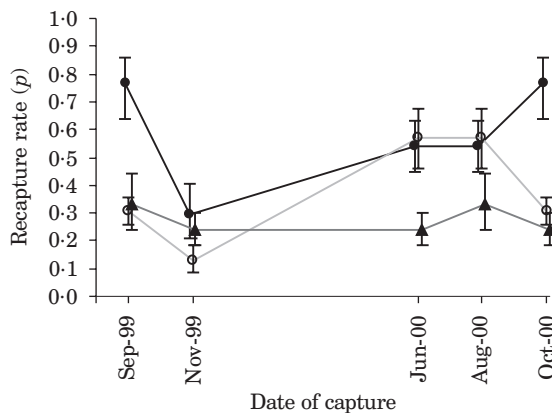

FIG. 4. Estimated recapture rates (p) ($\pm 95\%$ CI) of brown trout of the 1999 cohort under the selected model $p(g \times w)$ in three Norwegian streams Gjesa (●), Ulvåa (○) and Osa (▲). Recapture rate at capture occasion 1 is not estimable, due to the lack of previous capture occasions.

TABLE III. Selection of the best model for survival rate. AIC $= -2\ln(Likelihood) + 2K$. AIC_c is corrected for small sample size. ΔAIC_c is the difference in AIC_c between the current model and the model with the lowest AIC_c. AIC_c weight is the relative support of individual models. Number of estimated parameters in the model equals no. para. The deviance is the difference between $-2\ln(Likelihood)$ of the current model and $-2\ln(Likelihood)$ of the saturated model, where the saturated model is defined as the model with number of parameters equal to the sample size

Model		AIC_c	ΔAIC_c	AIC_c weight	No. para	Deviance
$\phi(g+s1)G+O\ constant$	$p(g \times w)$	1353·6	0·00	0·474	8	137·3
$\phi(g+s1)G\ constant$	$p(g \times w)$	1355·6	2·04	0·171	9	137·3
$\phi(g \times s2)$	$p(g \times w)$	1357·2	3·59	0·079	12	132·7
$\phi(g \times s1)$	$p(g \times w)$	1357·3	3·71	0·074	10	136·9
$\phi(g+s2)G\ constant$	$p(g \times w)$	1357·6	3·97	0·065	10	137·2
$\phi(g+s2)G+O\ constant$	$p(g \times w)$	1357·6	3·98	0·065	10	137·2
$\phi(g \times t)$	$p(g \times w)$	1358·0	4·36	0·054	15	127·2
$\phi(g+s1)$	$p(g \times w)$	1362·7	9·06	0·005	9	144·3
$\phi(g+s1)O\ constant$	$p(g \times w)$	1362·7	9·06	0·005	9	144·3
$\phi(g \times n2)$	$p(g \times w)$	1364·5	10·88	0·002	12	140·0
$\phi(g+s2)$	$p(g \times w)$	1364·7	11·08	0·002	10	144·3
$\phi(g+s2)O\ constant$	$p(g \times w)$	1364·7	11·09	0·002	10	144·3
$\phi(g \times n1)$	$p(g \times w)$	1366·7	13·05	0·001	10	146·2
$\phi(g+t)$	$p(g \times w)$	1366·9	13·31	0·001	12	142·4
$\phi(g \times c)$	$p(g \times w)$	1367·2	13·57	0·001	11	144·7
$\phi(g+c)$	$p(g \times w)$	1369·8	16·22	0·0	9	151·5
$\phi(g+n1)$	$p(g \times w)$	1372·2	18·62	0·0	9	153·9
$\phi(g+n2)$	$p(g \times w)$	1374·1	20·51	0·0	11	151·6
$\phi(g \times W)$	$p(g \times w)$	1385·6	32·04	0·0	11	163·2
$\phi(g+W)$	$p(g \times w)$	1386·2	32·59	0·0	10	165·8
$\phi(g+s2)G+U\ constant$	$p(g \times w)$	1395·4	41·76	0·0	9	177·0
$\phi(g+s1)G+U\ constant$	$p(g \times w)$	1398·2	44·59	0·0	9	179·8
$\phi(g)$	$p(g \times w)$	1398·2	44·59	0·0	9	179·8
$\phi(g+s2)U\ constant$	$p(g \times w)$	1398·6	44·98	0·0	10	178·2
$\phi(g+s1)U\ constant$	$p(g \times w)$	1399·9	46·26	0·0	10	179·4
$\phi(g+s1)U+O\ constant$	$p(g \times w)$	1399·9	46·26	0·0	10	179·4
$\phi(g+s2)U+O\ constant$	$p(g \times w)$	1400·6	47·03	0·0	11	178·2
$\phi(W)$	$p(g \times w)$	1492·8	139·16	0·0	8	276·4
$\phi(t)$	$p(g \times w)$	1516·9	163·25	0·0	11	294·4
$\phi(c)$	$p(g \times w)$	1525·4	171·85	0·0	8	309·1
$\phi(.)$	$p(g \times w)$	1541·2	187·62	0·0	7	326·9

Using the selected model, monthly survival rates during the winter season (September 1999 to June 2000) were highest in the Osa population (0·99; 0·99–0·99, 95% CI), lower in Gjesa (0·87; 0·84–0·89) and lowest in Ulvåa (0·65; 0·59–0·70). The monthly survival rate in Ulvåa during the summer seasons was estimated to 0·99 (0·99–1·00). Based on the monthly estimates, the probability of surviving the entire winter in Gjesa, Ulvåa and Osa was 0·29, 0·02 and 0·91, respectively.

There was no significant difference in mean L_F between individuals recaptured and individuals not recaptured after the winter season (Table IV). Thus, the

TABLE IV. Testing (one-way ANOVA) the difference in mean fork length (in September 1999) of individuals recaptured and individuals not recaptured after winter (September 1999 to June 2000)

Population	Group	n	Mean $\pm$ 95% CI L_F (cm)	F	P
Gjesa	Recaptured	18	$5 \cdot 86 \pm 0 \cdot 20$	$0 \cdot 093$	$0 \cdot 761$
	Not recaptured	64	$5 \cdot 83 \pm 0 \cdot 11$		
Osa	Recaptured	24	$5 \cdot 14 \pm 0 \cdot 15$	$0 \cdot 465$	$0 \cdot 496$
	Not recaptured	15	$5 \cdot 22 \pm 0 \cdot 18$		

probability of surviving the winter (and being recaptured afterwards) seemed independent of the body size in September. In Ulvåa, the number of recaptures after winter was too low to test for the difference between the two groups.

POPULATION DENSITY AND MIGRATIONS

In August 1999, there were considerable differences among sites in 0+ year brown trout density (Table V). Although the CI for the estimates in Ulvåa were wide, Ulvåa seemed to be the high-density site. The August density in Ulvåa was more than three times the density in Gjesa, and more than 25 times the density in Osa. This situation changed during the next 12–14 months. The density of 0+ year brown trout in Ulvåa declined sharply during the first 3 months, and the cohort continued to decline through the winter. By October 2000, the density of the 1999 cohort in Ulvåa was reduced to <8% of its density in August 1999. In Gjesa & Osa the 1999 cohorts increased in density during the period from August 1999 to August 2000.

The density of >0+ year brown trout varied among sites (Table V). The density was generally low in Ulvåa during the whole period (<10 individuals $100 \, m^{-2}$) and significantly higher in both Osa and Gjesa. The density of larger fish was especially low in November 1999.

In Ulvåa, eight marked individuals were recaptured outside of the study site at capture occasion 5 (August 2000), indicating some emigration from the site. Most recaptures (seven) were made downstream of the study site. There were 27 recaptures inside the study site. No marked brown trout were recaptured outside of the study site in Gjesa.

The ratio between the number of marked brown trout recaptured and the total number of brown trout captured (marked + unmarked) at each capture occasion differed among sites and with time (Fig. 5). In Osa, immigration of unmarked individuals seemed more intense during summer 2000, in Ulvåa it seemed to occur during winter, whereas in Gjesa immigration occurred during winter and spring.

DISCUSSION

Survival rate of 0+ year brown trout varied strongly among streams. In two out of three streams, no evidence for seasonal variation in survival was found, indicating that winter is not necessarily the time of high mortality in 0+ year brown trout. Further, no evidence for size-dependent mortality during winter was found. In all

TABLE V. Estimated population density (individuals 100 m^{-2}; 95% CI in parentheses) of brown trout from three Norwegian streams. Densities are given separately for the 1999 cohort, and for all brown trout aged ≥1 year combined

Date	Gjesa		Ulvåa		Osa	
	0+ years (1999 cohort)	≥1 years	0+ years (1999 cohort)	≥1 years	0+ years (1999 cohort)	≥1 years
May 1999*		13·0 (10·5–18·7)		6·0 (5·3–10·9)		42·5 (23·8–124)
June 1999*		14·7 (13·0–23·2)		4·5 (4·5–6·0)		24·0 (19·2–48·1)
August 1999	18·9 (18·4–22·4)	21·3 (21·0–23·8)	66·1 (38·8–220)	9·6 (9·2–12·1)	2·5 (2·5–4·6)	21·0 (20·1–23·8)
September 1999	25·8 (24·1–34·0)	25·2 (24·7–27·8)	32·8 (32·4–34·5)	5·9 (5·9–7·4)	8·2 (7·3–12·1)	25·4 (25·4–27·2)
November 1999	16·7 (15·6–22·1)	4·8 (5·4–8·5)	16·8 (14·8–23·4)	2·0 (2·0–2·0)	7·6 (5·8–18·8)	15·1 (14·6–17·4)
June 2000	31·2 (26·9–43·9)	33·1 (29·2–45·0)	8·2 (8·2–8·2)	11·9 (11·9–13·3)	9·6 (8·9–13·3)	28·2 (26·8–32·0)
August 2000	39·4 (38·0–43·3)	43·9 (42·5–47·9)	10·9 (10·2–14·4)	15·6 (13·2–20·1)	16·3 (15·3–19·7)	23·8 (22·7–26·6)
October 2000	38·8 (37·7–42·2)	41·9 (40·8–45·3)	6·2 (5·1–7·0)	9·2 (9·2–10·7)	17·8 (16·5–22·0)	25·6 (24·3–28·8)

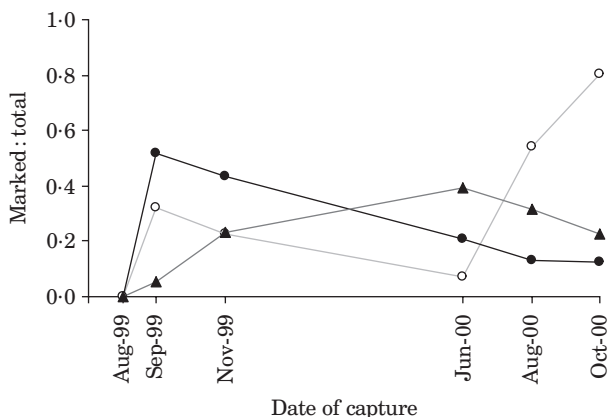*No individuals of the 1999 cohort were captured before August 1999.

FIG. 5. The observed ratio between the number of marked captures and the total number of captures
(marked + unmarked) of the 1999 cohort of brown trout, at each capture occasion in three Norwegian
streams Gjesa (●), Ulvåa (○) and Osa (▲).

streams, movement of 0+ year brown trout was observed. The data suggest that at
two of the study sites used, Gjesa and Osa, immigration was higher than emigra-
tion and mortality. At the last site, Ulvåa, mortality or emigration was clearly
higher than immigration.

SEASONAL VARIATION IN SURVIVAL

At two of the three study sites, there was no evidence for seasonal variation in
monthly survival rates, whereas in the third population, Ulvåa, monthly survival
rates were significantly lower during winter than during summer (0·65 *v.* 0·99).

The low winter survival in Ulvåa may have been caused by intraspecific compe-
tition for winter habitats. Juvenile brown trout change habitat during autumn and
winter, and the spatial niche seems to be narrower in winter than in summer
(Mäki-Petäys *et al.*, 1997, 2000; Heggenes *et al.*, 1999). The preferred winter habitat
is characterized by low water velocity and submerged overhead cover (Cunjak &
Power, 1986, 1987a). Young brown trout choose habitat with lower water velocity
than older brown trout, and they prefer to seek cover in interstitial crevices of cob-
ble substratum, often along the riverbank (Griffith & Smith, 1993; Mäki-Petäys
et al., 1997). Low water level and possible accumulation of ice may decrease the
number of available and suitable habitats of young brown trout (Cunjak *et al.*,
1998; Whalen *et al.*, 1999). Thus, the combination of a narrow spatial niche and a
reduction in available habitat may lead to intraspecific competition for habitat
among young brown trout during winter (Chapman, 1966; Gregory & Griffith,
1996; Solazzi *et al.*, 2000; Armstrong & Griffiths, 2001).

The relatively constant water level in Osa may have contributed to the constant
survival rates in Osa by preventing drought and maintaining the number of avail-
able habitats of 0+ year brown trout during winter. Gjesa, the other stream with
constant survival rates, however, is not regulated. If the naturally reduced water
levels during winter implied a seasonal effect on survival, this would have been
demonstrated in Gjesa, as well as in Ulvåa. Probably the physical characteristics
of each site determine to what extent reduced water level affects survival.

The defined winter season included periods of peak flood, both in autumn and in spring. Although previous studies have shown that mainly the alevin stage experience decreasing densities during such events (Jensen & Johnsen, 1999; Cattanéo *et al.*, 2002), peak floods may have caused displacement and mortality of 0+ year brown trout during winter in the present study. Variation among the sites in stream gradients and in access to hydraulic shelters for 0+ year brown trout may have led to different apparent survival among the studied populations. No data on these factors were obtained.

The model selection procedure favoured seasonal models that defined winter as the period from September to June, rather than from November to June. Although the seasonal effect was revealed only in Ulvåa, the fact that seasonal models had more support when the low-survival period in winter included the period of the major temperature decline (Fig. 1) supports the metabolic deficit hypothesis of Cunjak & Power (1987*b*). This hypothesis suggests that, although brown trout feed all winter, they suffer a metabolic deficit during acclimation to rapidly declining water temperatures in late autumn and early winter. The assimilated energy is not sufficient to cover the cost of acclimation. This hypothesis was supported by studies on first-winter survival in rainbow trout *Oncorhynchus mykiss* (Walbaum), where mortality mainly occurred in early winter (Smith & Griffith, 1994; Meyer & Griffith, 1997). The constant survival rates in Gjesa and Osa indicate that the metabolic deficit during acclimation is not always detrimental, and that survival rates may remain constant during the rest of the winter. Furthermore, the constant survival rates suggested that the reduced energy content of brown trout during winter (Gardiner & Geddes, 1980; Berg & Bremset, 1998) does not necessarily imply an increased mortality (Olsen & Vøllestad, 2001*a*).

MIGRATIONS

The recapture of marked 0+ year brown trout outside the study site (mostly downstream) in Ulvåa indicated some emigration. Number of recaptures inside the study site was only 3·4 times higher than outside. This suggests that emigration of marked individuals from the study sites was likely. The demonstrated emigration of marked brown trout in Ulvåa, suggests that survival rates were underestimated. Furthermore, population differences in apparent survival could be a result of different emigration rates rather than survival rates. In Ulvåa, the apparently low survival may be due to large movements of brown trout rather than high mortality. In three Canadian streams, Cunjak & Randall (1993) found low site-fidelity of juvenile Atlantic salmon during winter. Unstable winter conditions were suggested to cause in-stream movements by young Atlantic salmon. Variation in site-fidelity among streams was suggested to be a consequence of different availability of winter habitats among streams. The same mechanism may be acting in the present study. If no suitable winter habitat is available at the study site in Ulvåa, the brown trout may move elsewhere during winter. If this hypothesis holds, investigations of other parts of Ulvåa might have revealed high survival and increasing population densities, as demonstrated in Gjesa and Osa. Sampling below and above the site in Ulvåa, however, gave no indication that density of the 1999 cohort was significantly higher at these sites during 2000.

For some marked individuals, several capture occasions occurred before they were recaptured, suggesting either temporary emigration or low recapture rates. In Osa, the combination of low recapture rates and high survival rates may indicate temporary emigration. When temporary emigrants are recaptured, the survival rate of previous survival intervals increases. The study site in Osa did not cover the entire width of the stream, allowing fish to move in and out of the site in three directions and making temporary emigration likely. The high estimated survival rate of brown trout in Osa suggested that permanent emigration from the study site was low.

In Gjesa and Osa, the increases in density of the 1999 cohort with time indicate considerable immigration to the sites. This was further supported by the marked : total ratios, which indicate immigration in Ulvåa as well. In Ulvåa, immigration coincided with a decrease in the population density, suggesting that mortality rate (emigration included) was higher than the rate of immigration. At one study site, Cunjak & Randall (1993) observed increasing population densities during spring (after a decline in density during winter), suggesting that the site served as rearing habitat during summer. The increasing densities in Gjesa and Osa may indicate that these sites function as rearing habitats for 0+ year brown trout. For the site in Ulvåa, the opposite situation may occur, with declining density as juveniles move to their rearing sites.

The results from this study indicate that there exists sites functioning as either sources or sinks for young brown trout in small streams. The study sites used here were relatively large (353–563 m^2), but still could not 'capture' this variation adequately. If such movements are common, leading to temporal and spatial variation in density, the choice of methods for estimating survival is important. The use of temporal variation in cohort density will clearly not be a useful method without increasing the scale of the study (Cattanéo *et al.*, 2002). CMR methods are still useful, but the sites used should be selected to capture the variation in immigration and emigration that seems to exists among sites. Otherwise, it will be difficult to separate the effects of mortality and permanent emigration.

VARIATION IN SURVIVAL AMONG POPULATIONS

There was considerable variation in survival among populations. During winter, rates of monthly survival in Gjesa, Ulvåa and Osa were 0·87, 0·65 and 0·99, respectively. When calculating the total probability of surviving the winter, the difference among sites became increasingly distinct (0·29, 0·02 and 0·91 in Gjesa, Ulvåa and Osa, respectively).

The observed first-year survival rates of brown trout in Gjesa and Osa are in agreement with earlier estimates. Monthly survival of 0+ year brown trout has been reported to vary between 0·90 and 0·94 (Le Cren, 1973; Mortensen, 1977*a*, *b*). In the Shelligan Burn, Egglishaw & Shackley, 1977 found monthly survival rates of 0+ and 1+ year brown trout of 0·79 from September to December in the first year, and 0·89 from January to September in the second year. From age 5 months onwards, mean survival rates of brown trout varied between 0·86 and 0·98 in Cow Green streams (Crisp, 1993), and between 0·90 and 0·96 in the Afon Cwm (Crisp & Beaumont, 1995).

On the first capture occasion (August 1999), population density differed considerably among the study sites. Ulvåa had the highest density of 0+ year brown trout.

If first-year survival of brown trout is density-dependent (Crisp, 1993; Crisp & Beaumont, 1995; Nordwall *et al.*, 2001), this may explain the higher mortality in Ulvåa. Furthermore, a decreasing density in Ulvåa during winter may have reduced density-dependent mortality and led to high survival rates during summer 2000. Conflicting with this explanation, is the high survival in Ulvåa during the interval August to September 1999, when density was high. Possibly, density-dependent mortality was most important during winter, inducing the seasonal effect on survival observed in Ulvåa. It is probable that intercohort, rather than intracohort competition is the most important density-dependent factor (Nordwall *et al.*, 2001). If so, survival would be expected to be highest in Ulvåa, the site with the lowest total density of brown trout older than 0+ years. This was not the case. The density of >0+ year brown trout in Osa was more than twice that in Ulvåa.

In Gjesa, the presence of Alpine bullhead may reduce the survival of 0+ year brown trout and contribute to the differing survival among populations, as this species is absent in Ulvåa & Osa. Olsen & Vøllestad (2001*a*) demonstrated that survival rates of brown trout (age class >0+ years) probably were lower in sympatry with Alpine bullhead than in allopatry, suggesting interspecific competition in sympatric populations.

SIZE-DEPENDENT SURVIVAL

In Gjesa and Osa, no difference was found between the September 1999 mean body size of brown trout recaptured after the winter and those not recaptured, *i.e.* the 'big is better' hypothesis was not supported (Sogard, 1997). Meyer & Griffith (1997) demonstrated size-dependent survival in rainbow trout and brook trout *Salvelinus fontinalis* (Mitchill), but the effect of size on first-winter survival was suggested to be more likely when winter conditions were severe. Thus, lack of indications of size-dependent survival may be due to moderate conditions during the winter 1999–2000. On the other hand, Sogard (1997) suggested that size-dependent survival is more likely when conditions are moderate, because mortality is high in all size classes when conditions are extreme. The high mortality in Ulvåa during the winter would thus suggest extreme conditions and no size-dependent survival. Sogard (1997) also stated that size-dependent survival requires relatively high mortality rates. At low mortality, non-random survival will not be detectable. Possibly, the mortality in Gjesa and Osa was too low to observe size-dependent survival, or size-dependent mortality will only take effect in years when the brown trout do not reach some minimum size for survival.

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