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Estimates of survival of stream-dwelling brown trout using mark-recaptures

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Estimated monthly apparent survival of stream-dwelling brown trout *Salmo trutta* in south-east Norway was higher in winter than in summer, and lower in Alpine bullhead *Cottus poecilopus* sites than in allopatric sites. Apparent survival denotes true survival \times local site fidelity. Emigration may also explain differences in apparent survival. All brown trout included in this study were at least 1 year old.

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Key words: brown trout; mark-recapture; Alpine bullhead; survival; summer; winter.

INTRODUCTION

To estimate survival probabilities in the wild, and to detect how key environmental factors cause survival to vary spatially and temporally, is of importance in ecology. Yet survival can be a difficult process to quantify in natural populations (McCallum, 2000). Mark-recapture studies may hold the most promise for estimating natural mortality in fish stocks (Vetter, 1988).

The present study employs mark-recapture techniques to estimate survival of stream-dwelling brown trout *Salmo trutta* L. in a natural experimental setting (Diamond, 1986) where waterfalls block the upstream dispersal of fish within streams. Below the waterfalls brown trout lives in sympatry with the Alpine bullhead *Cottus poecilopus* Heckel. Above the waterfalls brown trout lives in allopatry. Cottids have limited capabilities of upstream movement (Mason & Machidori, 1976; Utzinger *et al.*, 1998). Brown trout probably colonized the upstream habitats before the isostatic uplift of landmasses following the last ice age made them inaccessible. Alternatively, man has carried it upstream at a later point of time. Freshwater cottids frequently form dense populations (Mann, 1971; Karlström, 1977) and may compete with young salmonids for food and space (Andreasson, 1971; Gaudin & Caillere, 1990; Gabler & Amundsen, 1999). Therefore, brown trout survival was predicted to be lower in the sympatric areas, as compared to the allopatric areas. It was also predicted that brown trout survival would be higher during the summer than during the winter, when north-temperature fishes may experience a substantial depletion of energy reserves (Dutil, 1986; Cunjak, 1988; Hutchings *et al.*, 1999).

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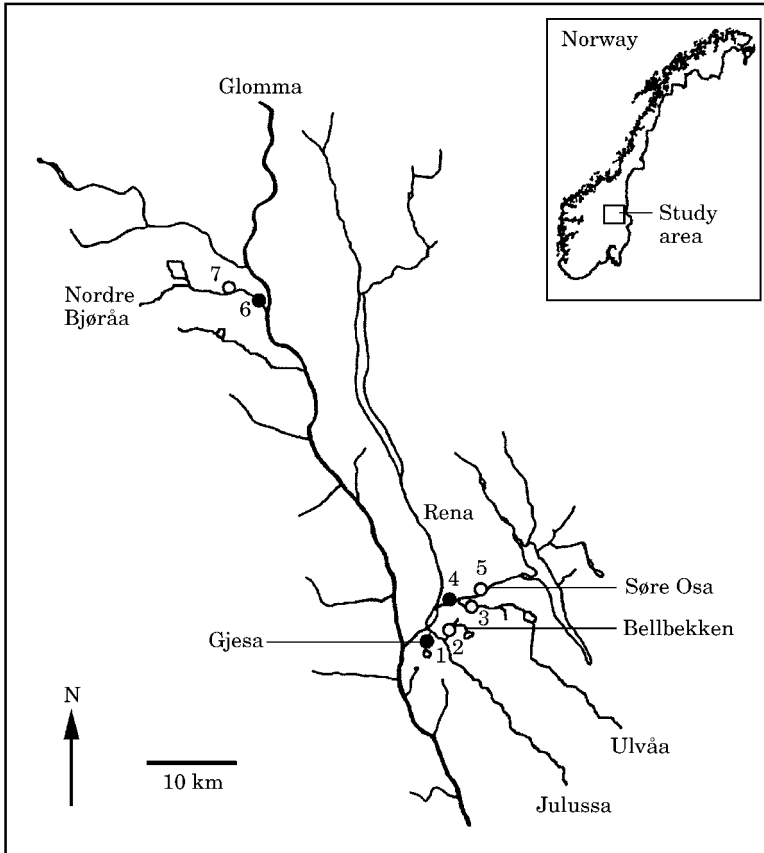


FIG. 1. The study sites in south-east Norway where the Alpine bullhead is either present (●) or absent (○): Gjesa (1), Bellbekken (2), Ulvåa (3), lower site in Søre Osa (4), upper site in Søre Osa (5), lower site in Nordre Bjøråa (6) and upper site in Nordre Bjøråa (7).

MATERIALS AND METHODS

STUDY POPULATIONS

Brown trout were sampled from forest streams in south-east Norway (Fig. 1). All study sites were located within a range of 70 km and 240–420 m above sea level. In the streams Nordre Bjøråa and Søre Osa (hereafter Bjøråa and Osa), brown trout was sampled both above and below a major waterfall. These waterfalls define the upper boundary of the Alpine bullhead populations. In addition, brown trout were sampled from the streams Gjesa, Ulvåa and Bellbekken. The Alpine bullhead is absent from Ulvåa and Bellbekken due to waterfalls at the outlets, while it is present in Gjesa.

SAMPLING PROCEDURE, ESTIMATION OF POPULATION DENSITIES

The populations were sampled with a backpack electrofishing apparatus during 1997–1999, between early May and late September (early November in 1999). Ice excluded fishing during the winter. Specific stream sections were used as permanent study sites. At a given sampling occasion, each site was fished systematically from the downstream to the upstream limit several times (the removal method; White *et al.*, 1982; Bohlin *et al.*, 1989). The lower site in Bjøråa was only fished once or twice, due to the large area that had to be covered (Table I). The other sites were covered with three passes. In 1999, the effort was often increased to four, five or six passes. A total of 13

TABLE I. Environmental parameters at the study sites. Area was adjusted for the percentage of substratum not submerged in water. The substratum type was classified according to a modified Wentworth scale (Hegggenes, 1988a), using categories from sand (size group 4) up to large boulders (size group 11)

Study site	Length (m)	Transects	Mean width (m) [range]	Mean depth (cm) [range]	Area (m ²)	Mean substratum size [range]	Mean % bottom vegetation	Mean % canopy
Gjesa	186.0	32	3.2 [2.0-4.7]	11.9 [0-57]	353	8.2 [7-11]	3	15
Bellbekken	167.5	29	4.0 [2.8-8.6]	13.2 [0-36]	509	8.3 [4-11]	9	37
Ulvåa	54.0	10	9.6 [8.3-10.3]	28.4 [0-52]	513	9.5 [8-11]	25	5
Osa lower	63.0	10	10.8 [4.0-16.0] ^a	37.4 [0-82]	653	9.8 [7-11]	20	5
Osa upper	40.0	9	15.3 [11.0-20.0] ^a	31.0 [0-75]	563	9.9 [7-11]	11	5
Bjøråa lower	660.0	8 (67) ^b	8.3 [4.6-13.3]	20.3 [0-78]	3117	10.2 [7-11]	26	19
Bjøråa upper	145.0	15	8.1 [6.1-11.5]	24.8 [0-83]	799	10.2 [7-11]	59	27

^aTotal width of this stream was 20-40 m.

^bFor most of the transects (number in parentheses), only stream width was recorded.

TABLE II. Number of brown trout tagged at the seven study sites, and the number of brown trout recaptured at least once within the study areas with the tag intact

Study site	Alpine bullhead	Tagged	Recaptured
Gjesa	Present	179	96
Bellbekken	Absent	248	127
Ulvåa	Absent	179	98
Osa lower	Present	87	23
Osa upper	Absent	576	265
Bjøråa lower	Present	380	107
Bjøråa upper	Absent	357	96
		2006	812

capture sessions were conducted, four in 1997, four in 1998 and five in 1999. Each session lasted 4–6 days. The time span between each session was usually 5–6 weeks. The two Bjøråa sites could not be fished at the first and third occasion in 1997, and the first occasion in 1998, when heavy flooding made this stream inaccessible. The populations in Gjesa and Bellbekken were not sampled until the third occasion in 1997. Brown trout and Alpine bullhead population densities were estimated with a generalized removal model (model M_{bh} ; Otis *et al.*, 1978) in programme CAPTURE (White *et al.*, 1982). Age 0 year fish were not included in the density estimates.

TAGGING PROCEDURE

Passive integrated transponders were used (PIT-tags; Prentice *et al.*, 1990) to individually mark the brown trout. 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 the last field season some of the smaller fish were individually tagged by injection of a coloured elastomer material just under the skin (Olsen & Vøllestad, 2001). Before tagging, the brown trout was anaesthetized with benzocaine, weighed (to the nearest 0.1 g), and fork length (L_F) measured (to the nearest mm). If captured for the first time, a sample of scales was removed for age determination (Devries & Frie, 1996). A total of 17 brown trout was accidentally killed by electroshock on first capture and one brown trout was killed during a recapture event. Seven brown trout died from lack of oxygen when temporarily stored in a bucket of water, and four died during the tagging procedure. A total of 2006 brown trout was successfully tagged and released at the study sites. Out of these, 812 individuals were recaptured at least once within the study areas with the tag intact (Table II). All tagged brown trout included in this study was at least 1 year old.

ANALYSIS OF SURVIVAL AND RECAPTURE PROBABILITIES

A capture history was constructed for each tagged brown trout, representing the fate of the individual through the study (Lebreton *et al.*, 1992). Capture history matrices were used as input files for the computer software 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 is available for recapture at capture occasion $i+1$. Animals that emigrate permanently from the study area will appear to have died (White & Burnham, 1999).

The Cormack–Jolly–Seber (CJS) model was used as a starting point for the 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 was tested separately for each study site, using goodness-of-fit (GOF) tests in programme RELEASE (Burnham *et al.*, 1987). A significant GOF test indicates lack of fit. Programme 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 approach was justified since all sites were sampled within the same field sessions. This way, the successive survival intervals will cover more or less the same time periods for all brown trout populations in the study. An extended CJS model, with an interaction effect between study site and time, had the maximum parameterization and served as the global starting model. All further models applied to the data were special cases of this model, for example models where apparent survival probabilities were constrained to be constant over time or recapture probabilities to be constant between sites. In this study ϕ will denote monthly apparent survival, where 1 month is defined as 30 days.

Model selection was based on the corrected Akaike Information Criterion, AIC_C (Hurvich & Tsai, 1989). The model with the lowest AIC_C value represents 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 most 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). In addition, Likelihood Ratio (LR) tests between nested models were used for hypothesis testing (Lebreton *et al.*, 1992). A significant difference between a null model (reduced) and an alternative model (more general) indicates that the null model fits less well, i.e. that the extra parameters included in the alternative model contribute significant to variation in the data. The alternative model should then be preferred over the null model.

HABITAT CLASSIFICATION

Several habitat variables were quantified at each study site, partly for descriptive purposes and partly to model capture probabilities as a function of habitat (Table I). A measuring tape was stretched across the stream at regular intervals. Each transect was divided into 50 cm long sections, and at the middle of each section depth to the nearest cm was measured. For each section as a whole a visual classification was made of: (1) the dominant substratum type, (2) the percentage of substratum not submerged in water (dry substratum), and (3) the percentage of the substratum covered with vegetation (mosses and green algae). Total width was recorded for each transect. The percentage of each transect covered by the canopy was visually classified. The habitat classification was only performed once at each location, when the water level was relatively low. At each site and occasion the water level was quantified as low, normal or high. This covariate was used in combination with an estimate of fishing effort (number of passes) in an attempt to simplify full time variation in recapture probabilities.

BIAS ON SURVIVAL ESTIMATES

True survival will be underestimated by tag loss and permanent emigration. Tag loss was estimated by removing the adipose fin of all tagged trout. In the autumn of 1998 and 1999, areas 50–300 m above and below the regular study sites were sampled to gain a qualitative impression of emigration. Each area was normally covered with three passes.

OTHER SPECIES

Brown trout and Alpine bullhead were the two most abundant fish species in the streams, although the minnow *Phoxinus phoxinus* L. was relatively common at the two Osa sites and occasionally captured at the two Bjøråa sites and in Gjesa. Perch *Perca fluviatilis* L. were found sporadically in Osa, Ulvåa and Gjesa. Pike *Esox lucius* L. is a potential predator on brown trout, and a few small individuals were captured at the lower site in Bjøråa and in Gjesa. It was suspected that these individuals had migrated up from downstream habitats, and that the pike had only a minor influence on the brown trout in the study areas. Of other possible predators, ducks *Mergus* sp. and herons *Ardea cinerea* L. were spotted at the two Osa sites, while mink *Mustela vison* Schreber was observed on the banks of Gjesa and Osa. Anglers use all streams except perhaps Gjesa.

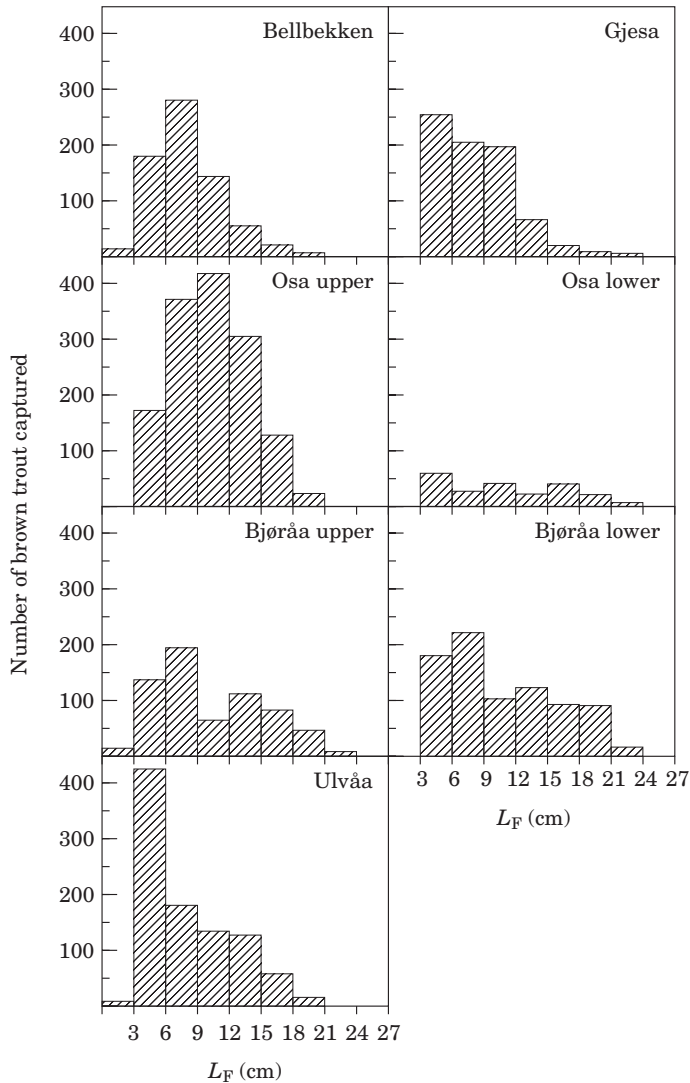


FIG. 2. Brown trout length distribution at the seven study sites, based on the total number of catches in 1997–1999. At the lower site in Bjøråa two larger individuals (32 and 37 cm) were captured but are not shown in the figure.

RESULTS

LENGTH AND AGE DISTRIBUTIONS, POPULATION DENSITIES

Most brown trout individuals were <20 cm (Fig. 2), and none were older than 7 years (Fig. 3). The age distributions varied substantially between years (Fig. 3). Brown trout population density was highest at the upper site in Osa, more intermediate in Gjesa, Bellbekken, Ulvåa and the upper site in Bjøråa, and low at the lower sites in Osa and Bjøråa (Fig. 4). In the summer of 1998, Alpine bullhead density was estimated as 4.68 (95% CI 4.27–5.74) individuals per 100 m² at the lower site in Bjøråa, 10.57 (10.11–12.40) at the lower site in Osa, and 15.3 (11.61–54.11) in Gjesa.

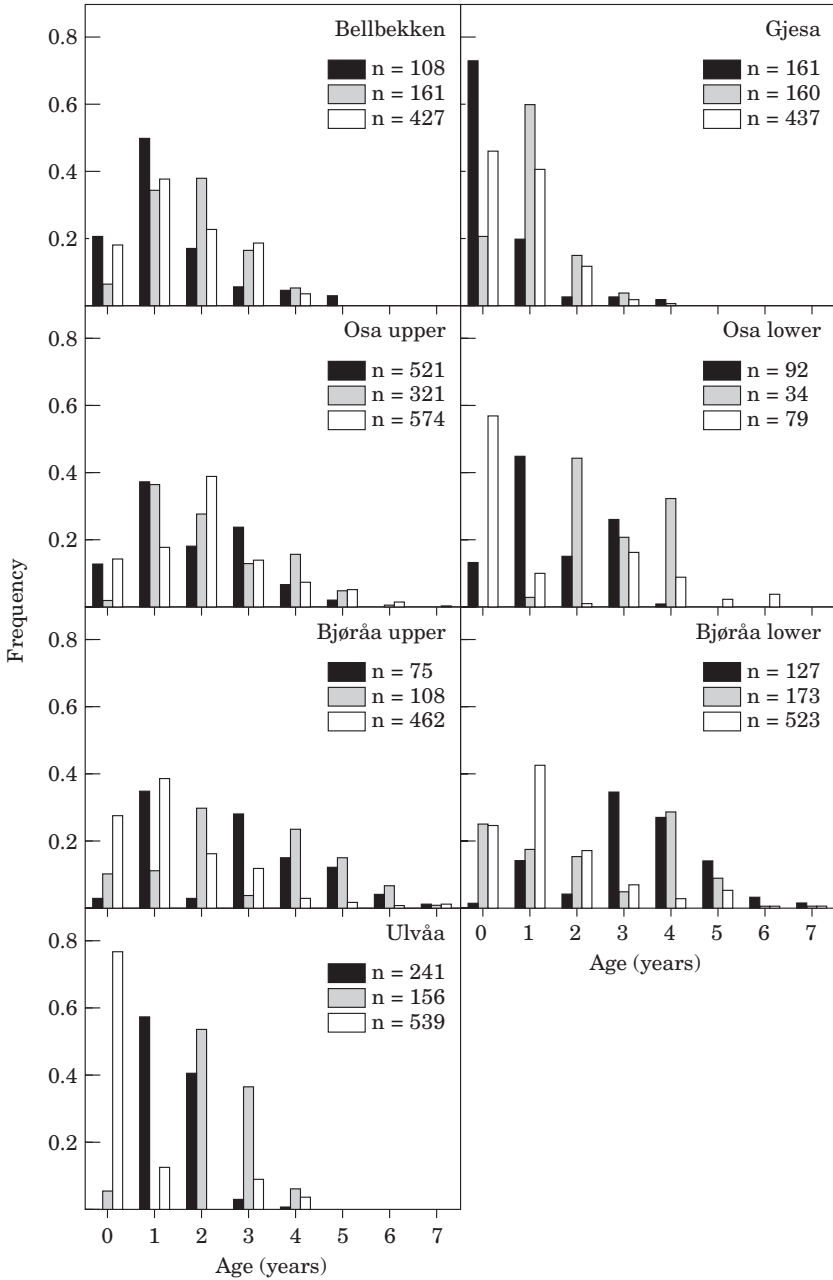


FIG. 3. Brown trout age distribution at the seven study sites, based on the total number of catches each year. ■, 1997; □, 1998; □, 1999.

ANALYSIS OF SURVIVAL AND RECAPTURE PROBABILITIES

For all study sites except the lower site in Osa, the CJS model fitted the data adequately (Table III). The data set from the lower site in Osa was sparse (Table II), and a general GOF test could not be computed. This site was excluded from the survival analysis. A starting model with an interaction effect between study

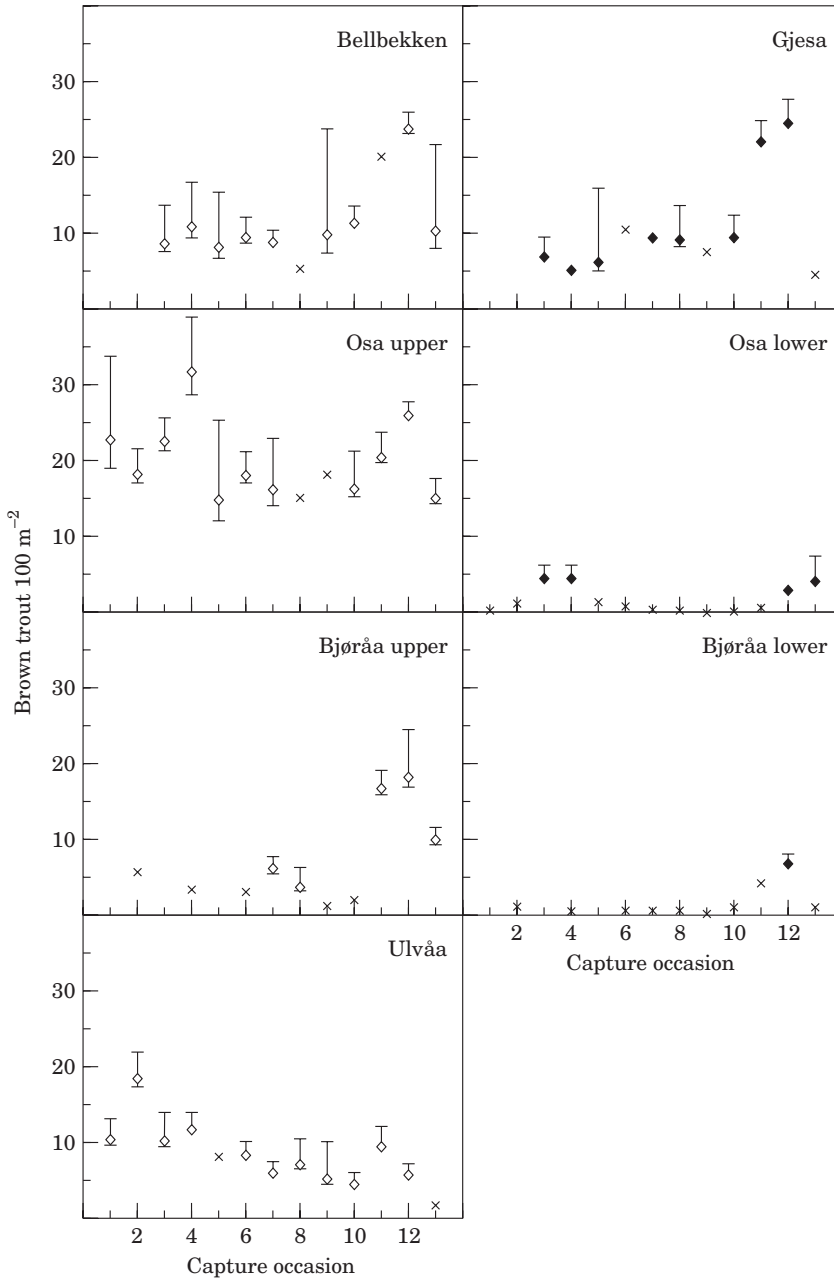


FIG. 4. Estimated brown trout population densities ($\pm 95\%$ CI) in allopatry (\circ) or sympatry with the Alpine bullhead (\bullet) during 1997 (capture occasion 1–4), 1998 (capture occasion 5–8), and 1999 (capture occasion 9–13). When estimates could not be computed due to sparse data or insufficient population depletion between the electrofishing passes, the number of captured individuals 100 m^{-2} is given (x). At capture occasion 12, a part of the population was removed from the study site in Gjesa and the lower site in Bjøråa. Age 0 year brown trout are not included in the estimates.

TABLE III. Goodness-of-fit tests for site specific models with full time variation in both survival and recapture probabilities (Cormack–Jolly–Seber models)

Study site	χ^2	d.f.	<i>P</i>
Gjesa	21.15	24	0.63
Bellbekken	16.05	27	0.95
Ulvåa	27.75	36	0.84
Osa upper	45.16	51	0.70
Bjøråa lower	15.10	18	0.66
Bjøråa upper	11.54	20	0.93

site and time for both survival and recapture probabilities was accepted for the remaining six sites. From this global model, recapture probability was modelled first, while allowing survival probability to vary both between study sites and in time. The model with the lowest AIC_C was then used to model the survival probabilities (McCallum, 2000).

In the best model of recapture probabilities, the site effect was retained while time variation was simplified with the covariates water level and fishing effort (Tables IV and V). The best model of survival probabilities had an additive effect of site, where the sites were grouped according to Alpine bullhead presence or absence, and season (Table IV). This seasonal effect represents a simplification of full time variation where each year is divided in two periods: (1) the field season from early summer to autumn (named ‘summer’), and (2) the winter season, covering the time period between two successive field seasons. Survival was constrained to be constant between the three summer seasons, and also between the two winter seasons. The model without the Alpine bullhead parameter, emphasizing only a difference between summer and winter survival, also had some support (Table IV). The model with a full time effect instead of a season effect, the model with separate estimates for each study site instead of just presence or absence of Alpine bullhead, and the model with separate survival estimates for each summer and winter received less support (Table IV). In terms of Akaike weights, the best model (Table IV) had a relative support of 0.44, while the second best model had a relative support of 0.15. The results from the hypothesis testing were in line with the ranking based on information criteria. *LR* tests indicated that the Alpine bullhead variable contributed significantly to variation in the data (Table VI). Furthermore, results indicated that grouping the sites according to the presence or absence of the Alpine bullhead should be preferred to full site variation in survival (Table VI), and that a model with simple seasonal variation in survival (summer different from winter) should be preferred to more complex models with either separate estimates for each summer and winter or full time variation in survival (Table VI).

Using the most parsimonious model for inference, monthly brown trout survival probability was lower during summer than during winter, and was also lower in the Alpine bullhead sites than in the allopatric sites (Fig. 5). The

TABLE IV. Model selection for estimating apparent survival (ϕ) and recapture (p) probabilities of brown trout in six adjacent sites in south-east Norway. For each candidate model, the AIC_C value, the number of parameters (np), and the deviance (DEV) is given. Recapture probabilities were modelled first, and the best model (bold type) used to model survival. Model notation is explained in Table V

Survival (ϕ)	Recapture (p)	AIC_C	np	DEV
<i>I Global model</i>				
$\phi_{site \times t}$	$p_{site \times t}$	6300.1	110	1698.3
<i>II Modelling recapture</i>				
$\phi_{site \times t}$	$P_{(site \times w)+e}$	6296.3	61	1798.5
$\phi_{site \times t}$	P_{site+t}	6332.8	72	1811.9
$\phi_{site \times t}$	$P_{(site \times w)+e}^*$	6342.1	53	1860.9
$\phi_{site \times t}$	P_{site}	6379.6	54	1896.4
$\phi_{site \times t}$	p_t	6403.6	61	1905.8
$\phi_{site \times t}$	$p.$	6463.5	49	1990.7
<i>III Modelling survival</i>				
$\phi_{bull+season2}$	$P_{(site \times w)+e}$	6280.1	16	1874.7
$\phi_{season2}$	$P_{(site \times w)+e}$	6282.3	15	1878.9
ϕ_{bull+t}	$P_{(site \times w)+e}$	6283.2	25	1859.6
$\phi_{site+season2}$	$P_{(site \times w)+e}$	6283.3	20	1869.9
$\phi_{bull+season1}$	$P_{(site \times w)+e}$	6283.6	19	1872.2
ϕ_t	$P_{(site \times w)+e}$	6284.1	24	1862.5
$\phi_{season1}$	$P_{(site \times w)+e}$	6285.1	18	1875.7
ϕ_{site+t}	$P_{(site \times w)+e}$	6285.8	29	1854.0
$\phi_{site+season1}$	$P_{(site \times w)+e}$	6286.3	23	1866.8
ϕ_{bull}	$P_{(site \times w)+e}$	6292.6	15	1889.2
$\phi.$	$P_{(site \times w)+e}$	6294.7	14	1893.4
ϕ_{site}	$P_{(site \times w)+e}$	6295.9	19	1884.4

*Models where the covariate stream width was replaced with either stream depth, bottom substratum, bottom vegetation or canopy cover all had higher AIC_C values.

recapture probabilities were normally between 0.25 and 0.50, although during some floods events the estimates were below 0.1 and during summer droughts they were as high as 0.75.

BIAS ON SURVIVAL PROBABILITIES

A total of 31 brown trout was recaptured outside of their site of tagging. Two individuals originally tagged in Ulvåa were recaptured at the lower site in Osa; these were the only observations of movement between sites. One individual tagged in Gjesa was recaptured in the stream Julussa (Fig. 1). An extra data set was constructed to investigate the effect of observed emigration on survival probabilities. The 31 emigrants were now coded as 'recaptured but not released' at their last regular capture within the study area (Johannesen & Ims, 1996). Using the best model from the first analysis (Table IV), the survival estimates did not increase by more than 1.4%.

Tag loss was estimated to be 2.0% (17 out of 860 recaptures). A few of them were probably by spawned females, but some were also smaller, juvenile individuals. Tag loss occurred at all study sites. These fish were re-tagged and released.

TABLE V. Explanation and notation of models used in the model selection procedure for estimating apparent survival (ϕ) and recapture (p) probabilities of brown trout in six adjacent sites in south-east Norway

Model notation		Biological meaning
Survival	Recapture	
$\phi_{site \times t}$	$p_{site \times t}$	Interaction effect between study site and time
ϕ_{site+t}	p_{site+t}	Additive effects of study site and time
ϕ_{site}	p_{site}	Effect of study site
ϕ_t	p_t	Effect of time
$\phi.$	$p.$	Constant
	$p_{(site \times w)+e}$	Interaction effect between study site and water level, additive effect of fishing effort
	$p_{(site \times w)+e}$	Interaction effects between stream width and water level, additive effect of fishing effort*
$\phi_{site+season1}$		Additive effects of study site and season, with separate estimates for each summer and winter
$\phi_{season1}$		Effect of season, with separate estimates for each summer and winter
$\phi_{site+season2}$		Additive effects of study site and season, with pooled estimates for summer and winter respectively
ϕ_{s2}		Effect of season, with pooled summer and winter estimates
ϕ_{bull}		Effect of Alpine bullhead presence or absence
ϕ_{bull+t}		Additive effects of Alpine bullhead presence or absence and time
$\phi_{bull+season1}$		Additive effects of Alpine bullhead presence or absence and season, with separate estimates for each summer and winter
$\phi_{bull+season2}$		Additive effects of Alpine bullhead presence or absence and season (pooled)

*The fit of models where the covariate stream width was replaced with either stream depth, bottom substratum, bottom vegetation or canopy cover was also examined.

TABLE VI. Likelihood ratio test results between the best model from the AIC_C model selection procedure and the next four models on the list (Table IV)

Test	Alternative model	Null model	χ^2	d.f.	P
1	$\phi_{bull+season2}$	$\phi_{season2}$	4.19	1	0.041
2	ϕ_{bull+t}	$\phi_{bull+season2}$	15.16	9	0.087
3	$\phi_{site+season2}$	$\phi_{bull+season2}$	4.86	4	0.30
4	$\phi_{bull+season1}$	$\phi_{bull+season2}$	2.58	3	0.46

DISCUSSION

MODEL SELECTION AND INFERENCE

Inference was based on the model with additive effects of Alpine bullhead and season on brown trout survival probability, as all other candidate models had

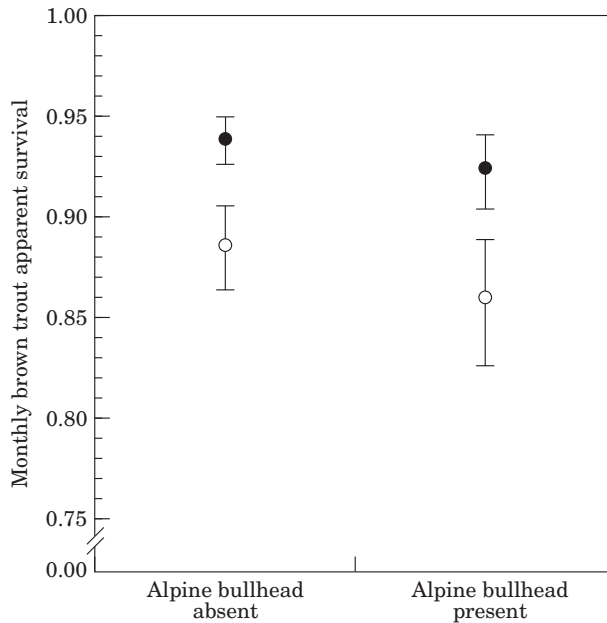


FIG. 5. Estimates of monthly brown trout apparent survival probabilities \pm 95% CI during summer (○) and winter (●) at sites with ($n=2$) and without ($n=4$) sympatric populations of the Alpine bullhead under model $\phi_{bull+season2}, P_{(site \times w)+e}$ (Table V).

AIC_C values more than two units above this model. Hypothesis testing supported this decision. However, the top model had an Akaike weight of only 0.44. This weight suggests that the model is not convincingly best if other replicate data sets were available. The results must therefore be interpreted with care.

Age-effects were not included in the candidate models. Most of the brown trout (85%) were tagged at age 1–3 years, and the estimates probably best reflect survival for this life-stage. If the data had contained major age-effects on survival, this should have produced a poor fit of the global model (Lebreton *et al.*, 1992).

SEASONAL VARIATION IN SURVIVAL

In this study, there was no evidence for a winter bottleneck in brown trout survival. On the contrary, the estimates of monthly survival probabilities were higher during winter than during summer. In general, stream-living salmonids suffer high annual mortality rates (Alexander, 1979), and may utilize a substantial part of their energy stores during winter (Cunjak, 1988; Berg & Bremset, 1998; Hutchings *et al.*, 1999). However, brown trout often feed throughout the year (Cunjak & Power, 1987; Bremset, 2000), switching from a predominantly diurnal towards a nocturnal activity pattern at the onset of winter (Heggenes *et al.*, 1993; Bremset, 2000). Concealment during daytime might lower the risk of predation from mink, herons and mergansers. An ice-cover can also offer protection against terrestrial predators. Angling is not permitted during the spawning season and is not possible in the winter due to the ice-cover. Summer droughts may have a negative effect on salmonid populations (Elliott *et al.*,

1997), although this was probably not important in the present study. The summer of 1999 was very dry compared to 1998, but there was no evidence of major differences in survival between these 2 years. Emigration could be more prominent in the summer, causing an apparent drop in survival.

THE BROWN TROUT–ALPINE BULLHEAD INTERACTION

This study suggests that brown trout survival is slightly lower in sites where it is found in sympatry with the Alpine bullhead than in neighbouring allopatric populations. Moreover, brown trout population densities in Bjøråa and Osa were lower in the sympatric downstream sites than in the allopatric upstream sites. Although confounding factors are a problem in natural experiments, the results indicate interspecific competition between brown trout and Alpine bullhead. Within Bjøråa and Osa, the habitat classification suggested only small differences in water depth, substratum type, underwater vegetation, and canopy cover. Furthermore, temperatures will probably not differ due to the small geographic distance between these sites. Adult cottids may prey on brown trout fry in a period after the fry emerge from the river gravel early in the summer (Andreasson, 1980). This can explain low brown trout population densities in sympatric areas. It cannot explain, however, why the mortality of older brown trout should be higher in sympatry. Cottids may reduce the number of drifting prey available to salmonids by cropping benthic invertebrates (Brocksen *et al.*, 1968; Dahl, 1998), but brown trout from the sympatric sites in Osa and Bjøråa grew faster than brown trout from the allopatric sites in these streams (Olsen, 2000). A simple situation in which interspecific competition for food reduces trout survival seems unlikely.

Both brown trout and cottids use the shelter provided by rocks and logs (Antonelli *et al.*, 1972; Mills & Mann, 1983; Bachmann, 1984; Heggenes, 1988b). Brown trout may experience interspecific competition for such favourable positions (Fausch & White, 1981). In sympatry with other species, including cottids, brown trout may spend more time in areas with less shelter and therefore a higher risk of predation from terrestrial animals (Glova, 1987; Näslund *et al.*, 1998). Both mink and mergansers were sighted in the study areas, and can sometimes have a significant impact on salmonid populations (Alexander, 1979; Wood, 1987; Heggenes & Borgstrøm, 1988).

Emigration could be more prominent in the sympatric areas, causing an apparent drop in survival. Given the small number of observations (only two sympatric and four allopatric sites included in the survival analysis), concern could be raised that there is a greater risk of yielding spurious results.

BIAS ON SURVIVAL PROBABILITIES

Due to tag loss and emigration, true survival was underestimated. The bias caused by the 31 recaptured emigrants was not large, but these individuals represent an unknown fraction of those that emigrated. The large number of marked brown trout never recaptured after first release leaves open the possibility that many fish permanently left the study areas. There can be substantial movement in populations of stream-dwelling trout species (Gowan *et al.*, 1994; Gowan & Fauch, 1996a,b), although several studies also suggest a high degree of local site fidelity (Bachman, 1984; Hesthagen, 1988; Carlsson *et al.*, 1999).

Between-stream movements may occur, as brown trout inhabiting complex systems sometimes use smaller streams as nursery habitats (Jonsson, 1989). In the present study, there was no indication of any spawning migration from the larger rivers. The brown trout in these systems grow to a relatively large size (>30 cm) before sexual maturation (A. Linløkken, pers. comm.), and would have been easy to identify among the small-sized mature individuals at the study sites. Many of the brown trout tagged as juveniles in 1997 reached maturity in 1998 and 1999, while repeatedly captured within the study sites.

A 2% rate of tag-loss could lead to bias of some importance. However, as tag loss occurred among brown trout from all study sites, it is unlikely that the ranking of the candidate models was affected.

In conclusion, this study indicates both seasonal- and between-population variation in brown trout survival within a restricted geographical area. The winter is often considered a critical period for stream-resident fishes in northern habitats, but the present study show that this need not always be the case, as the estimated monthly apparent survival probabilities were higher during the winter than during the summer. The estimated apparent brown trout survival probabilities were lower in sites with sympatric Alpine bullhead than in allopatric populations, suggesting that biotic interactions could lead to reduced survival for stream-dwelling brown trout.

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