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Temporal variation in lake-run brown trout (*Salmo trutta*) mixed-stock fishery catches in a large Fennoscandian lake

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Understanding the relative contributions of potential source populations to fishery catches is vital for proper management of harvested fish stocks. Little is known about the temporal variation in commercially important brown trout (*Salmo trutta*) catch in large boreal lakes. We estimated contributions of 34 putative source populations to the brown trout catch in two lakes, Inarijärvi and adjacent Paadarjärvi (northern Finland) during 2006–2011. Genetic stock identification indicated that there is considerable temporal variation in the catch proportions in Inarijärvi and they are mainly associated with different contributions of the tributaries of the Ivalojoki and Juutuanjoki. In Paadarjärvi, catch proportions were relatively constant during the sampling period. Our study demonstrated the importance of temporal sampling when estimating catch proportions for management purposes.

Introduction

Large boreal lakes in the northern hemisphere are important for the local community as they provide natural resources for commercial and recreational purposes (Toivonen *et al*. 2004, Lehtonen *et al*. 2008). Inarijärvi, located in northern Finland, is one of the largest lakes (approx. 1042 km^2) in Fennoscandia. The main tributaries are the Ivalojoki and the Juutuanjoki, and Inarijärvi is connected to the Barents Sea via the Juutuanjoki. There are several commercially important fish species inhabiting Inarijärvi such as vendace (*Coregonus albula*), arctic charr (*Salvelinus alpinus*) and whitefish (*Coregonus lavaretus*). Approximately 30–50 tonnes of brown trout is fished every year and thus it plays an important role in both local recreational and commercial fisheries (Swatdipong *et al*. 2010, 2013). Knowledge about the ecology and genetics of the fish stocks is an important part of the sustainable use of these valuable natural resources. One important aspect in proper management is the understanding how different source populations contribute to the catch (Begg *et al*. 1999, Palsbøll *et al*. 2007). Many salmonid populations are endangered due to overfishing and, hence, the knowledge of catch composition helps to identify issues

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important for conservation planning (Schwartz *et al*. 2007). For example, heavy fishing pressure on small populations could lead to local extirpation of economically important stocks.

Several studies have highlighted the importance of temporal variation in allele frequencies when inferring micro evolutionary patterns (Waples 1989, Waples 1990). Empirical studies have shown that allele frequencies may vary both spatially and temporally due to fluctuations in effective population sizes or patterns of gene flow (Potvin & Bernatchez 2001). For example, Atlantic salmon (*Salmo salar*) and brown trout studies have documented either variable or constant allele frequencies between temporal population samples (Vähä *et al*. 2008, Lehtonen *et al*. 2008, Ozerov *et al*. 2013). On a more practical scale, knowledge of temporal variation in fishery sample composition is important for estimating annual variation in the contribution of the source populations (Koljonen 2006). Understanding temporal patterns in catch composition is not only important for management planning but also for understanding the biology of the study species. In Atlantic salmon inhabiting the Baltic Sea for example, catch proportions have been shown to vary annually, which has been suggested to reflect differences in migration patterns and smolt production levels (Koljonen 2006).

Genetic stock identification (GSI) has been the workhorse for the estimation of catch proportions for several decades (Begg & Waldman 1999, Manel *et al*. 2005, Anderson *et al*. 2008). In the GSI approach, the fishery samples are assigned to the putative source populations based on their molecular marker e.g. microsatellite genotype information. The GSI approach involves estimating the probability of the baseline population allele frequencies producing the genotype in question in the fishery sample (Koljonen *et al*. 2005, Anderson *et al*. 2008). In practice, GSI is most efficient with a thorough sampling of the putative source populations as well as a large fishery sample. The resolution of GSI improves with increasing number of alleles, higher heterozygosity as well as the degree of population differentiation among the baseline populations (Anderson *et al*. 2008).

Earlier GSI analyses of the Inarijärvi brown trout indicated the importance of the main tributaries (the Juutuanjoki and Ivalojoki) as contributors to the fishery. However, the sampling period of the earlier work spanned just a few years and therefore the catch proportions were assessed in a single sample (Swatdipong *et al*. 2013). Thus, the level of temporal variation in the fishery sample remains poorly understood in Inarijärvi. In order to understand temporal variation in the Inarijärvi and the adjacent Paadarjärvi brown trout catch, we assessed the catch proportions in fishery samples from three periods between 2006 and 2011. We conducted GSI of fishery samples to a baseline consisting of 33 populations and analyzed the data both at regional and genetic grouping levels. We showed that there is considerable temporal variation in the annual fishery sample composition mainly associated with variation in the contribution of the two main rivers of the Inarijärvi system. The importance of this temporal variation is discussed in the context of lake-run brown trout biology and stock management.

Material and methods

Samples and genotyping

The data set consisted of earlier published data (Swatdipong *et al*. 2013) supplemented with four new baseline populations (Rep, Tol, Tuo and Sal) as well as 108 new individuals which were added to some of the existing baseline populations (Table 1 and Fig. 1). In addition, new fishery samples (n = 391) collected in 2010 and 2011 from Inarijärvi and Paadarjärvi were added. Altogether, the data set contained 33 baseline populations (n = 1163) and 1052 fishery samples from the period 2006–2011. Individuals originating from stocking were identified by their alizarin-red stained otoliths or coded wire tags and were excluded from the analyses. To assess the level of temporal variation in the fishery samples from the main basin of Inarijärvi, separate analyses were conducted for samples collected in four different periods: 2006–2007 (n = 133), 2008 (n = 389), 2010 (n = 245) and 2011 (n = 85). In the Paadarjärvi, two periods were assessed separately: 2006 + 2008 (n = 139) and 2010–2011 (n = 61). DNA extraction and microsatellite

genotyping protocols followed those described in (Swatdipong *et al*. 2010, 2013) with slight modifications. In order to verify consistent genotyping calls between years, 33 of the formerly genotyped samples were re-genotyped along the new samples from 2010–2011. Twelve microsatellite loci were successfully genotyped.

Statistical analyses

Standard population genetic parameters (HW equilibrium, allelic richness, expected and observed heterozygosity, H_E and H_O, respectively) were estimated as implemented in the R package *Hierfstat* (Goudet 2005). The degree of genetic differentiation among the baseline samples was estimated with F_{ST} according to Weir and Cockerham (1984). Population genetic structure among the baseline populations was estimated with a Bayesian clustering algorithm as implemented in the software Baps 6.0 (Corander *et al*. 2008). The number of genetic clusters was treated as an unknown parameter and the number of clusters was estimated by optimizing HW equilibrium and linkage disequilibrium in the genetic samples. The 'clustering of groups of individuals' option was used and the upper bound for the number populations was set to 5, 10, 15, 20, 25, 30, 35 and 40. The partition

Table 1. Details of the baseline population sampling (N: northern, E: eastern, W: western, S: southern) and population genetic parameters. Numbers in parenthesis indicate the sample size used in Swatdipong *et al.* (2013). A_R = allelic richness (8 diploid individuals), H_E = expected heterozygosity, F_{IS} = deviation from the Hardy-Weinberg equilibrium.

Sampling site	Popul. code	Coordinates	Sampling year	*n*	A_R	H_E	F_{IS}
Surnujoki, N	Sur	69°16′43.48′N, 28°45′39.98′′E	2005	33 (15)	4.09	0.65	–0.02
Tsiuttajoki, N	Tsi	69°12′35.29′N, 27°46′2.09′′E	2002–2008, 2013	55 (53)	3.50	0.56	–0.02
Niipijoki, N	Nii	69°6′4.37′′N, 27°32′30.39′′E	2008, 2013	18 (15)	3.09	0.54	–0.04
Naamajoki, N	Naa	69°2′32.23′′N, 28°31′54.11′′E	2008	18	3.03	0.49	–0.01
Nellimjoki, E	Nel	68°49′26.16′′N, 28°36′41.00′′E	2008	15	4.01	0.64	–0.08
Kontosjoki, E	Kon	68°41′31.09′′N, 28°33′10.56′′E	2009, 2013	21 (13)	3.72	0.61	–0.24
Kielajoki, W	Kie	69°17′9.83′′N, 26°36′2.75′′E	2008	21	4.01	0.63	–0.11
Kaamajoki, W	Kaa	69° 3′59.59′′N, 27°4′45.79′′E	2008	22	4.71	0.69	0.00
Kettukoski, W	Ket	68°55′8.14′′N, 26°44′48.69′′E	2008	23	4.12	0.60	0.00
Vaskojoki, W	Vas	68°54′54.65′′N, 26°39′41.39′′E	2006	43	4.16	0.63	0.03
Kurtojoki, W	Kur	68°59′4.83′′N, 25°56′38.31′′E	2008	11	3.86	0.65	–0.07
Lankojoki, W	Lan	68°50′15.39′′N, 26°21′27.75′′E	2008	28	3.96	0.57	0.02
Ahvenjoki, W	Ahv	68°42′11.85′′N, 26°25′2.98′′E	2009	19	4.24	0.65	0.08
Menesjoki upper, W	MeU	68°39′34.48′′N, 26°18′31.99′′E	2008	21	4.47	0.67	0.00
Menesjoki lower, W	MeL	68°47′45.66′′N, 26°25′29.38′′E	2007	16	4.76	0.64	0.00
Juutuanjoki, W	Juu	68°54′23.74′′N, 26°59′55.37′′E	2004	82	3.77	0.59	0.01
Tuohijoki, W	Tuo	68°40′ 26.95′′N, 26° 17′25.01′′E	2013	18	4.38	0.66	0.08
Nukkumajoki, W	Nuk	68°52′50.56′′N, 27° 4′34.37′′E	2008	19	4.29	0.66	–0.02
Repojoki, W	Rep	68°27′ 23.07′′N, 25° 32′1.49′′E	2013	64	4.52	0.66	0.06
Tolosjoki, W	Tol	68°28′ 26.05′′N, 27° 16′ 28.56′′E	2013	33	4.45	0.65	0.03
Sallijoki, W	Sal	68°27′ 31.59′′N, 25° 55′ 43.54′′E	2013	26	4.23	0.65	0.03
Ivalojoki–Alakoski, S	IvaAP	68°35′9.65′′N, 27°20′43.09′′E	2008	24	4.92	0.70	–0.03
Sotajoki, S	Sot	68°30′25.83′′N, 26°50′11.99′′E	2008, 2013	34 (21)	4.41	0.65	0.05
Appisjoki, S	App	68°31′22.96′′N, 26°36′34.54′′E	2007, 2013	46 (29)	4.27	0.66	–0.04
Kyläjoki, S	Kyl	68°26′23.06′′N, 26°32′24.49′′E	2008, 2013	43 (33)	4.17	0.66	–0.05
Taimenjoki, S	Tai	68°25′41.66′′N, 26°21′47.18′′E	2007, 2013	38 (29)	4.75	0.71	–0.04
Rullajoki, S	Rul	68°22′58.01′′N, 26°23′21.84′′E	2008, 2103	39 (30)	4.58	0.68	0.06
Karvajoki, S	Kar	68°27′49.07′′N, 26° 5′18.62′′E	2007, 2013	42 (31)	4.08	0.64	–0.01
Ivalojoki, S	Iva	68°22′18.61′′N, 25°55′32.19′′E	2004, 2008, 2013	74 (66)	4.19	0.65	0.02
Ivalojoki–Joupinniva, S	IvaJH	68°20′13.55′′N, 25°42′53.46′′E	2008	25	3.75	0.62	0.00
Lismajoki, S	Lis	68°21′15.56′′N, 25°30′52.75′′E	2008	32	3.2	0.56	0.05
Naskamajoki, S	Nas	68°20′30.60′′N, 25°26′9.50′′E	2008	22	3.07	0.53	0.00
Upper Naskamajoki, S	IvaN	68°20′41.94′′N, 25°25′43.25′′E	2008	18	3.32	0.54	0.10

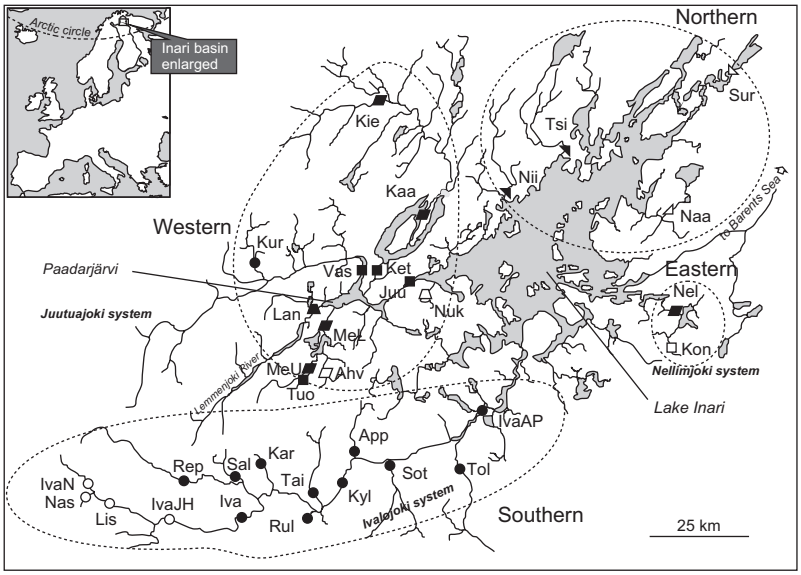

Fig. 1. Sampling locations of the baseline populations and main river systems in the Inarijärvi area. Dashed lines indicate the groupings used for estimating regional catch proportions (northern, eastern, southern and western). Population symbols indicate the different genetic clusters found in the Bayesian clustering analysis.

having the highest probability was considered as the most likely population structure.

Genetic stock identification was carried out using two approaches. First, the fishery samples were assigned to their putative source populations using the maximum likelihood method implemented in the program Oncor (*see* http://www.montana.edu/kalinowski/Software/ONCOR.htm) as was used earlier (Swatdipong *et al*. 2013). Briefly, this method estimates a probability of a given baseline population producing genotype of an individual in the fishery sample. Confidence intervals for assignments were estimated with 10 000 bootstrap replicates. Second, the Bayesian method implemented in the program cBayes (Neaves *et al*. 2005) was used for the genetic stock identification. One of the potential benefits of this method in comparison to the maximum likelihood method (Oncor) is that the allele frequencies are updated with the information in the mixture sample during the analysis. This may help to estimate allele frequencies more reliably in the baseline populations with small sample sizes given that they are present in the mixture sample. Simulation studies have shown that in some empirical data sets the Bayesian method might be more accurate than the maximum likelihood (Koljonen *et al*. 2005, Griffiths *et al*. 2010). The Bayesian estimation of stock proportions involved 10 000 steps, a burn-in period of 9000 steps and eight independent chains resulting altogether in 8000 samples from the posterior distribution. Convergence was assessed with Gelman and Rubin shrink factors. Previous research indicated that the assignment to the level of single populations had considerable uncertainty in Inarijärvi, with the 95% confidence intervals often including zero. The assignments were however confident at the regional level (Swatdipong *et al*. 2013). Therefore, assignments were conducted at a regional scale and on the genetic clusters identified by the Bayesian clustering method to avoid possible bias in the genetic stock proportions. The classification of the baseline populations at the regional scale (northern, eastern, southern and western) was based on the geographical origin of the populations and on practical management purposes.

Results

Basic population genetic parameters

Altogether three genotyping inconsistencies were found among the 33 control samples. These errors were located in different loci and two of them involved shift in one repeat unit and one was an allele dropout case. The error rate was thus 0.75% (3 error/396 repeat genotypes).

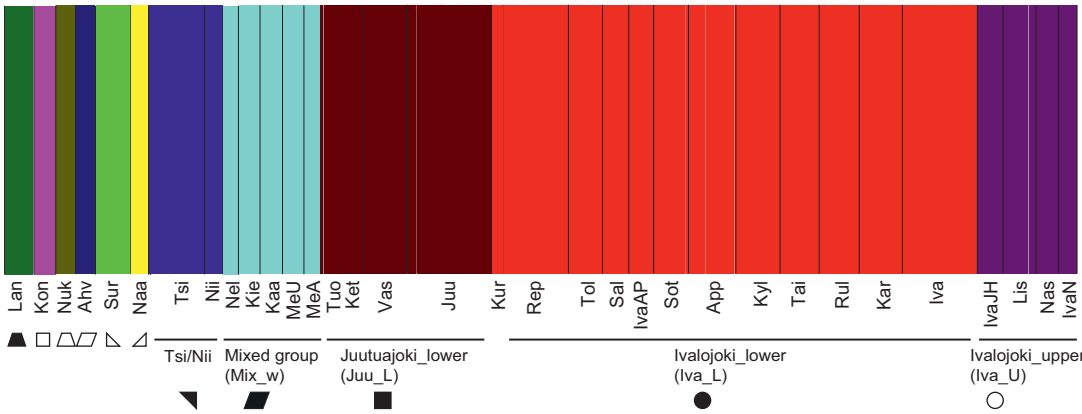

Fig. 2. The result of the Bayesian clustering of the baseline populations. Colors indicate the genetic groups found among the baseline populations. Symbols denote the genetic clusters; for their geographical locations *see* Fig. 1. Lan, Kon, Nuk, Ahv, Sur and Naa were identified as single populations in the clustering analysis.

Overall, the error rate was low and probably had little effect on the assignment probabilities.

Mean allelic richness across loci was 5.52 and varied from 2.0 (Str60inra) to 7.29 (Ssa407) for a sample size of eight individuals (Table 1). The mean heterozygosity across loci was 0.63 and varied from 0.43 (Str60inra) to 0.83 (Ssa407) (Table 1). There were no significant deviations from the HW equilibrium at the locus or population levels after the Bonferroni correction at the 0.05 significance level (Tables 1 and 2). The baseline populations exhibited a relatively high degree of genetic differentiation (F_{ST} = 0.098, 95%CI = 0.084–0.113) (*see* Appendix 1). The Bayesian clustering algorithm found the highest likelihood for eleven genetic groups among the baseline populations (Fig. 2). Most of the genetic clusters comprised geographically adjacent populations but in some cases remote populations were clustered together. For example, the Tuohijoki clustered together with the Juutuanjoki, the Kettujoki and the Vaskojoki rather than the geographically more adjacent Menesjoki populations. In a similar fashion, populations originating from the western and eastern Inarijärvi tributaries formed another group with little geographical affinity. The largest group (Iva_L) comprised 12 populations located in the lower parts of the Ivalojoki. The populations located in the upper parts (Iva_U) of the Ivalojoki formed a distinct group from the lower Ivalojoki populations. All remaining genetic clusters, except Tsi/Nii, were single populations located mostly in the upper river catchments (Fig. 1).

Estimation of stock proportions

In Inarijärvi, there was considerable temporal variation in the catch especially between samples from 2006–2007 and 2008 as compared with the samples from 2010 and 2011 at the regional scale detected both with maximum likelihood (Figs. 3a–d and 4a–d) and Bayesian (Figs. 3e–h and 4e–h) methods (Appendix 2).

Table 2. Locus-level population genetic indices. A_R = allelic richness (8 diploid individuals), H_E = expected heterozygosity, F_{IS} = deviation from the Hardy-Weinberg equilibrium, F_{ST} = population differentiation.

Locus	A_R	H_E	F_{IS}	F_{ST}
Ssosl438	3.41	0.46	0.00	0.12
Ssosl311	6.45	0.74	0.08	0.08
Str15inraP	3.08	0.61	–0.04	0.07
Str543inraP	6.00	0.74	0.02	0.10
OneU9	3.52	0.56	–0.01	0.09
Strutta58P	6.13	0.76	–0.04	0.12
Str60inra	2.00	0.43	–0.03	0.15
Str73inra	2.98	0.56	–0.02	0.14
Ssosl417	4.88	0.72	0.00	0.11
Str85inraP	4.12	0.50	0.01	0.08
Bs131	4.39	0.62	–0.06	0.11
Ssa407	7.29	0.83	0.02	0.08
Mean	5.52	0.63	0.00	0.10

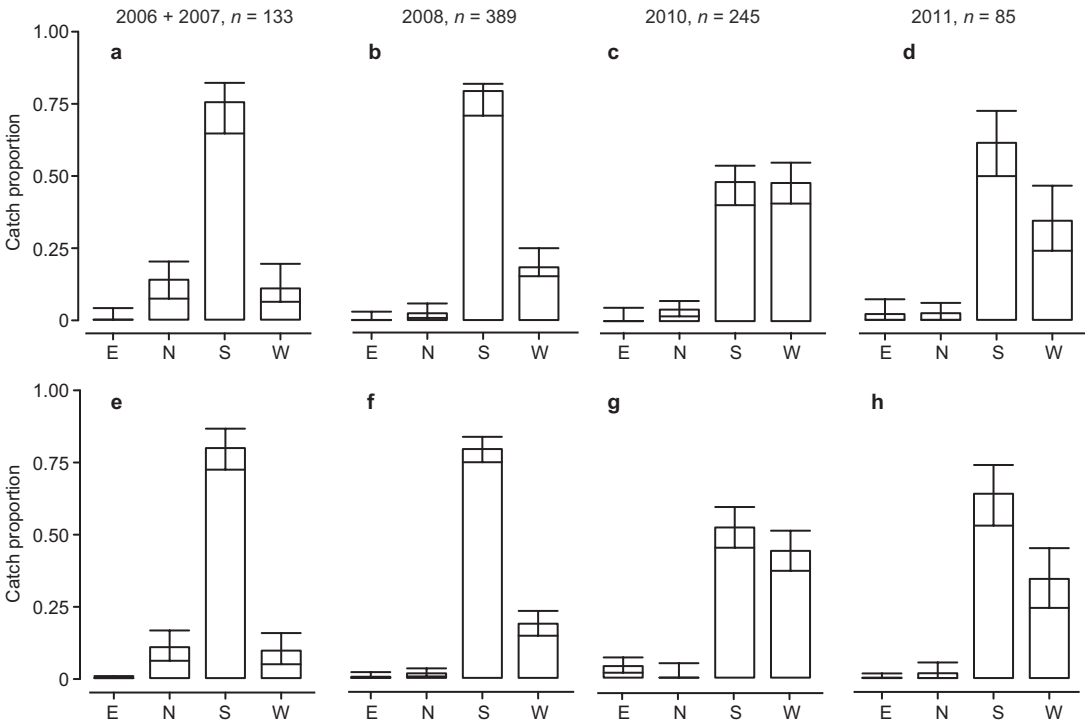

Fig. 3. Results of genetic stock identification in the Inarijärvi main basin at the regional level: (**a**–**d**) GSI results based on the maximum likelihood method (Oncor), and (**e**–**h**) GSI results based on the Bayesian method (cBayes). E = eastern, N = northern, S = southern, W = western.

This variation was mainly associated with variable contributions of the southern and western groups whereas the eastern and northern groups contributed relatively little throughout the sampling period. The contribution of the southern group was higher during 2006–2008 as compared with that during 2010–2011. The highest contributions of the southern group were found in 2006 + 2007 and 2008, 75% (95%CI = 62%–82%) and 79% (71%–82%), respectively. In contrast, the southern group contribution varied from 48% (40%–54%) to 61% (50%–72%) in 2010 and 2011. The contribution of the western group followed the opposite pattern being the highest in 2010 (48%, 41%–55%) and 2011 (34%, 24%–46%). In 2006 + 2007, the western group contribution was 11% (6%–19%) and in 2008 18% (15%–25%). The contribution from the northern group was relatively high in 2006 + 2007 (14%, 7%–20%) but in other years less than 4%. The eastern group contribution was insignificant throughout the sampling period, i.e. 95%CIs always included zero.

At the genetic-group level, the major contributions to the Inarijärvi catch came from lower parts of the Ivalojoki and the Juutuanjoki (Fig. 4e–h, *see* also Fig. 1 and Appendix 3). Other genetic groups generally contributed less than 5% to the annual catch, an exception being Tsi/Nii, which contributed 11% (5%–17%) in 2006 + 2007. Variation in the lower parts of the Ivalojoki and the Juutuanjoki were consistent with the regional assignments such that the contribution of the Ivalojoki was highest in 2006 + 2007 (75%, 62%–81%) and 2008 (80%, 70%–82%). Lower parts of the Juutuanjoki contributed 10% (5%–17%) in 2006 + 2007 and 17% (13%–22%) in 2008. In 2010 and 2011, the Juutuanjoki proportions were considerably higher [44% (36%–51%) and 34 (21%–44%), respectively] and the Ivalojoki proportions lower [48% (40%–54%) and 60% (49%–72%), respectively].

The Paadarjärvi catch proportions were relatively constant across the years but the catch proportions followed the same patterns as in Inarijärvi at the regional and genetic cluster levels.

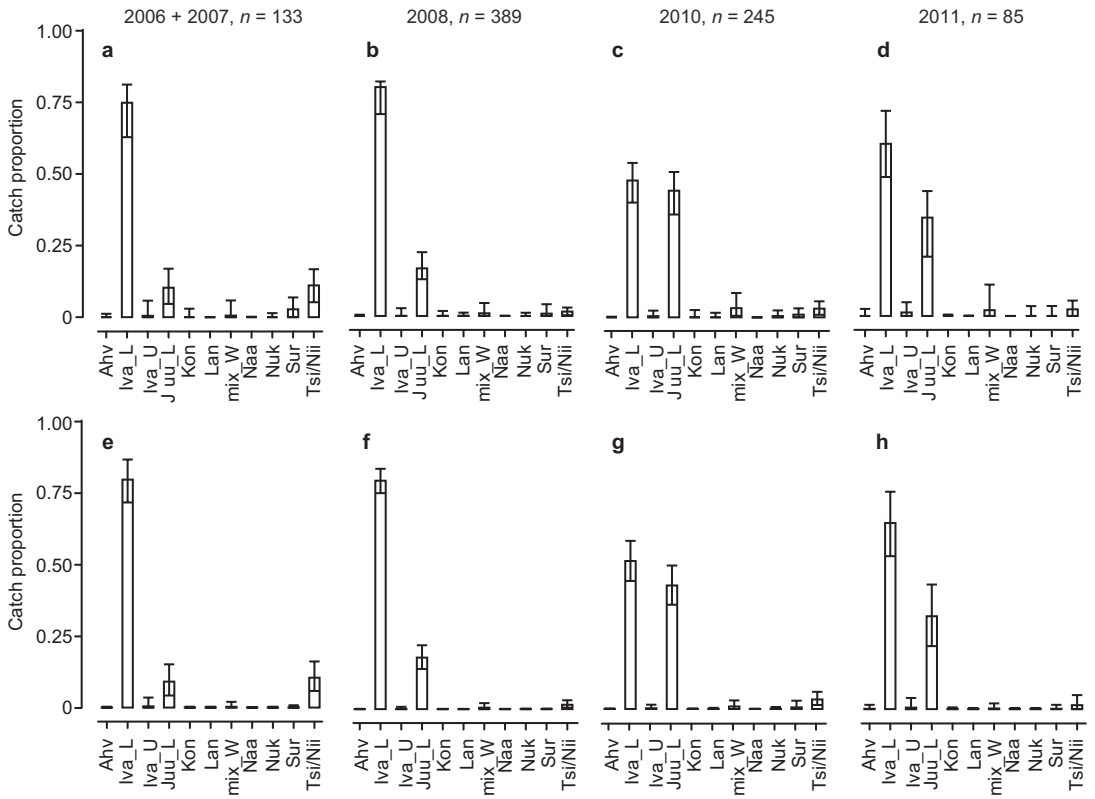

Fig. 4. Results of genetic stock identification in Inarijärvi main basin at the genetic cluster level: (**a–d**) GSI results based on the maximum likelihood method (Oncor), and (**e–h**) GSI results based on the Bayesian method (cBayes).

The western group contributed 86% (65%–94%) in 2006 + 2008 and, 80% (60%–91%) in 2010 + 2011. The proportion of the southern group in 2006 + 2008 was 10% (4%–27%) and in 2010 + 2011, 20% (9%–40%), whereas the eastern and northern groups had insignificant contributions (Fig. 5a–d and Appendix 4). The lower part of the Juutuanjoki contributed 37%–47% during both sampling periods while the lower Ivalojoki 30%–34% (Fig. 6a–d and Appendix 5). The mixed group, consisting of populations from the western and eastern parts of Inarijärvi contributed 14%–26% to the Paadarjärvi catch while contributions of the other groups were insignificant (Fig. 6a–d). In order to estimate contributions from the rivers flowing to Paadarjärvi, the baseline populations were ordered according to the geographical origin. This analysis indicated that the Menesjoki contributed little to the Paadarjärvi catch and the main contributor was the lower Juutuanjoki group.

The Bayesian estimates of the stock proportions were concordant with the maximum likelihood estimates both at the regional and genetic cluster levels (Figs. 3a–d *vs*. 3e–h and 4a–d *vs*. 4e–h; Appendices 1–4). Only the Paadarjärvi assignments differed somewhat from those of the maximum likelihood estimates such that the confidence intervals were wider and in many cases included zero. The Bayesian estimates also indicated a higher contribution of the western populations in 2010 + 2011 (mean 96%, 95% posterior probability 87%–100%) in the Paadarjärvi catch.

Discussion

Our study demonstrates that brown trout catch proportions can vary temporally in a large Fennoscandian lake across a six-year period. There were some similarities between the periods. For

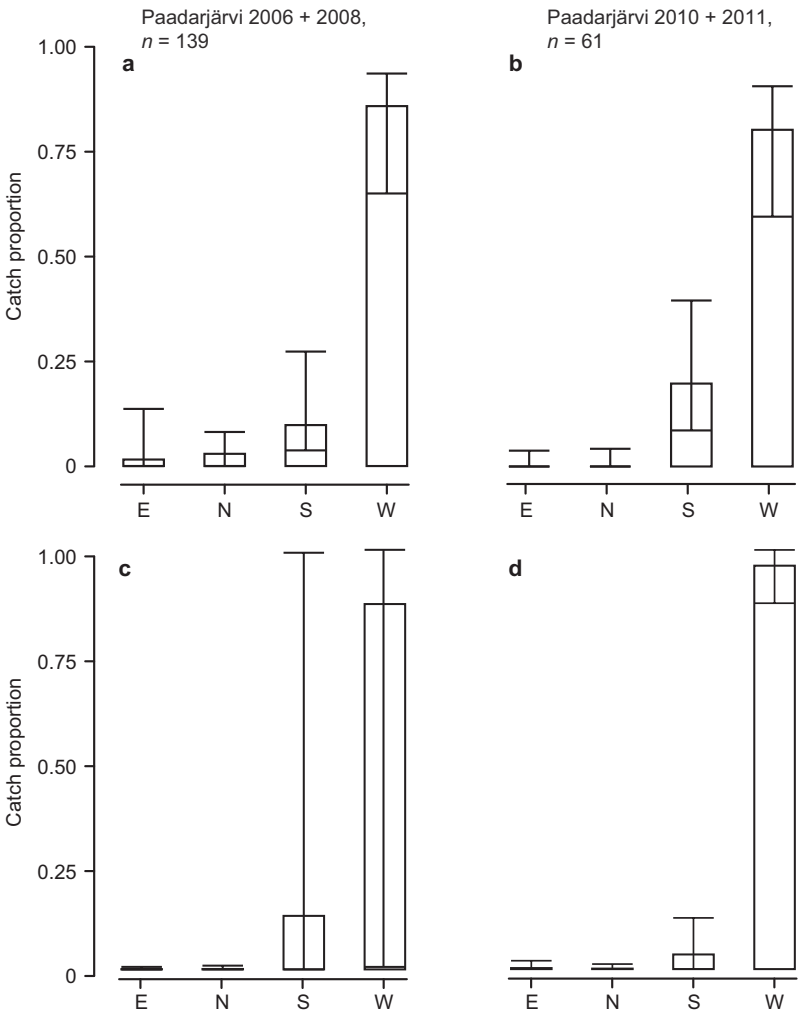

Fig. 5. Results of the genetic stock identification in Paadarjärvi at the regional level: (**a** and **b**) GSI results based on the maximum likelihood method (Oncor), and (**c** and **d**) GSI results based on the Bayesian method (cBayes). E = eastern, N = northern, S = southern, W = western.

example, two main tributaries in the Inarijärvi basin were consistently major contributors to the brown trout catch, but their contributions varied during the sampling period. The upper reaches of the river catchments, the eastern and northern populations seem to contribute only little to the overall catch. On the other hand, the catch proportions remained relatively constant in Paadarjärvi.

Important issues in genetic stock identification include the precision and accuracy of the estimation of catch proportions (Anderson *et al*. 2008). Several lines of evidence suggest that the estimates reported here are relatively robust at the regional and the genetic cluster levels. First, the estimates of the Bayesian and maximum likelihood methods are generally in concordance. This indicates that the estimation of catch proportions is robust for methods with different assumptions. Earlier studies have shown that the Bayesian method is generally more accurate in some empirical data sets but some studies have shown that both methods gave similar results (Koljonen *et al*. 2005, Griffiths *et al*. 2010). Small sample size or missing baseline populations have been shown to affect the accuracy and precision of the individual assignments and estimation of stock proportions (Anderson *et al*. 2008). An effort was made for this study to increase the number of baseline populations as well to increase the sample size. However, due to logistical difficulties the sample size of some baseline populations remained low but this might not have affected the results. Earlier simulations on these same

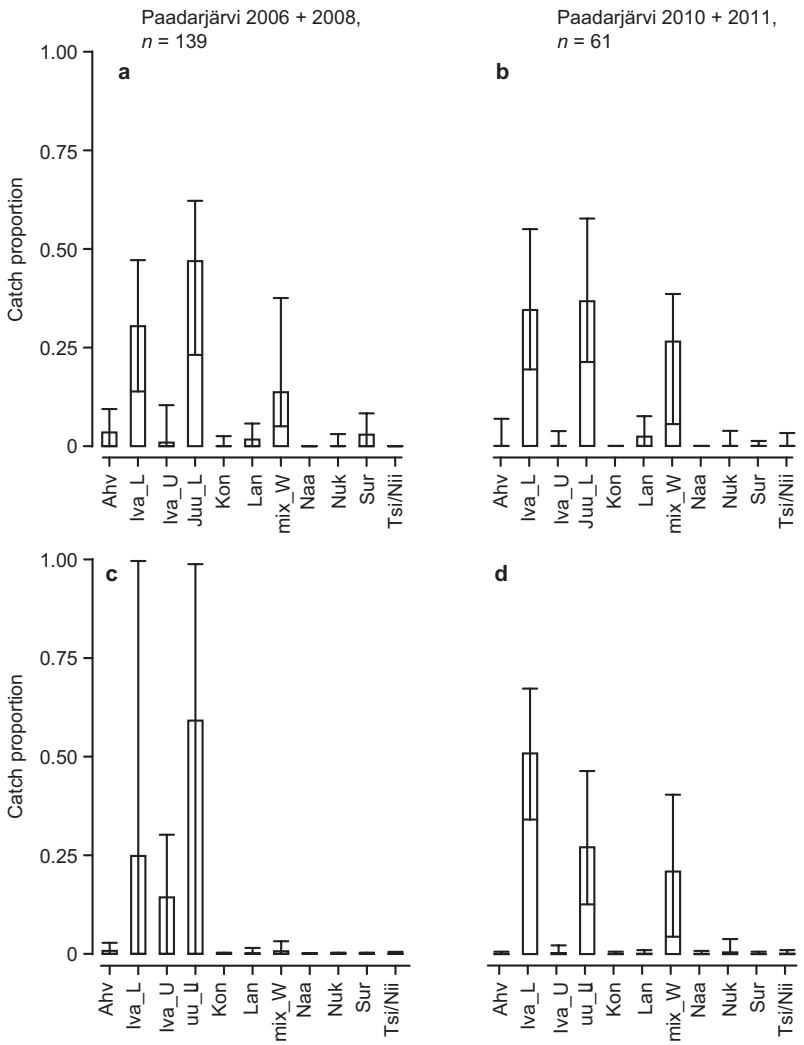

Fig. 6. Results of the genetic stock identification in Paadarjärvi at the genetic cluster level: (**a** and **b**) GSI results based on the maximum likelihood method (Oncor), and (**c** and **d**) GSI results based on the Bayesian method (cBayes).

populations had shown that small sample size or missing baseline populations had only a small effect on the estimated stock proportions (Swatdipong *et al*. 2013). We sampled on average 31 individuals (range 11–82) for each population which should generally be sufficient to estimate population allele frequencies in most cases (Hale *et al*. 2012). However, the number of individuals needed depends on the particular application and larger sample sizes are needed for accurate mixed stock analyses especially for closely related populations. Further, the assignments were conducted at regional and genetic cluster levels, each of which has higher sample sizes than the individual populations. It is possible that there are missing baseline populations in the data set given the numerous tributaries in Inarijärvi but ecological data support the view that the collection includes the main brown trout breeding areas (Swatdipong *et al*. 2010, 2013). Simulation studies have shown that the level of baseline population differentiation affects the accuracy of the estimation of stock proportions. The higher the genetic differentiation among the baseline populations, the more reliable estimates of stock proportions can be expected. The population differentiation (F_{ST}) among the baseline populations in this study was ~0.1, which may have facilitated stock proportion estimation. However, the resolution can be improved by increasing the number polymorphic loci in case of small differentiation among baseline populations (Anderson *et al*. 2008). Finally, some of the

baseline populations comprised samples collected in different years and thus temporal variation in allele frequencies might affect the genetic stock identification results. Earlier work has shown that the temporal differences in allele frequencies are relatively small ($F_{ST} < 0.05$) among the Inarijärvi baseline populations (Swatdipong *et al*. 2013). Therefore, it is unlikely that temporal variation in baseline populations had a large effect on genetic stock identifications.

The Inarijärvi brown trout had been under extensive supplementary stocking during the past decades. While we aimed to exclude all hatchery-origin individuals from the fishery samples, it is still possible that some stocked fish were present. This is because the identification of stocked individuals is not 100% accurate as coded wire tags can be lost after release of stocked trout back into the wild. This leaves open the possibility that a small proportion of hatchery fish could remain unrecognized and hence be present in the fishery samples. However, when a large proportion of hatchery-origin fish were included in the analysis the results of genetic stock identifications remained relatively unaffected (data not shown). It is also possible that the baseline populations can include some hatchery-origin fish. For example, the Nellimjoki population (Nel) clustered together with distantly located western populations. This pattern might be explained by the release of stocked trout from a nearby hatchery, which might have affected the genetic composition of the Nellimjoki population (Swatdipong *et al*. 2010).

What could explain the temporal variation in catch proportions? One possibility is that it might be due to non-random distribution of the catch samples because the fishing effort was not standardized between years. In order to test this, we divided fishery samples according to the management sampling areas defined by the Natural Resources Institute Finland and tested if there were differences in the spatial distribution of the catch samples between years. Non-random distribution seems unlikely as there were no statistically significant differences in the spatial distribution of the catch samples (Kolmogorov-Smirnov test: $D = 0.101$, $p = 0.83$). However, we cannot completely rule out other factors such as seasonal variation in fishing effort affecting the distribution of fishery catches. The contribution of the Ivalojoki stock decreased substantially whereas the Juutuanjoki contribution increased during the sampling period. Several abiotic and biotic factors have been shown to affect migration patterns in brown trout as well as in other salmonid fishes. Temperature requirements of brown trout have been shown to be variable depending on the life stage and thus might affect the timing of feeding migrations from the river to the lake (Elliott and Elliott 2010). Prey item abundance or migrations can affect vertical migrations of whitefish (*Coregonus lavaretus*) in a subarctic lake (Kahilainen *et al*. 2004). There might be also annual variation in the number of offspring produced in each river system and thus the relative contributions may vary accordingly. However, the ultimate cause of stock proportion variation in Inarijärvi is yet to be determined.

In contrast, the stock proportions in Paadarjärvi were relatively constant during the sampling period. It appears that the Juutuanjoki fish use Paadarjärvi as feeding area but also a considerable number migrate to the main basin of Inarijärvi. On the other hand, smaller rivers flowing to Paadarjärvi (e.g. the Menesjoki) contributed little to the Paadarjärvi catch. The sample size of the Paadarjärvi catch was relatively small, which might explain the large posterior probability intervals of the Bayesian mixed stock estimates. Therefore, larger sample sizes would be needed to confirm the patterns observed in the Paadarjärvi catch.

Genetic stock identification studies — especially involving temporal sampling — were rarely conducted in fish species inhabiting large, northern-hemisphere lakes. Thus, direct comparisons with other studies are difficult. In Atlantic salmon, the results of mixed stock analyses have been variable with respect to temporal variation. In the Baltic Sea, the salmon catch had considerable spatio-temporal variation (Koljonen *et al*. 2005, Koljonen 2006). Also the proportions of individuals with wild or hatchery origin in Atlantic salmon fisheries catches have been found to vary over time in the Baltic Sea (Koljonen 2006, Koljonen *et al*. 2014). On the other hand, population-specific migration behavior patterns of one-sea-winter fish have been found to be constant over period of four years in the Tenojoki

located in northern Finland (Vähä *et al*. 2008, 2011). This may suggest that temporal variation in stock proportions could be commonplace in salmonids and thus highlights the importance of temporal sampling as a component of source population contribution estimation.

Our study indicates that the main contributors to the Inarijärvi catch are consistently the trout stocks originating from the lower parts of the Ivalojoki and the Juutuanjoki. This is slightly surprising given the large number of potential spawning rivers in the Inarijärvi region. The northern group contributed about 10% in 2006 but the proportion decreased to ~2% (with the 95% confidence interval including zero) later in the sampling period. The eastern group had non-significant contribution throughout the sampling period. The small contribution of the eastern and northern populations might reflect the true pattern but the baseline population coverage in the above-mentioned regions was low and future sampling efforts should concentrate on these regions to confirm the observed pattern. The upper reaches of most river catchments around the entire lake also contributed insignificantly, which may indicate that brown trout from those locations are resident and do not migrate to the Inarijärvi main basin or alternatively the low production in these tributaries.

Overall, our results highlight the importance of temporal sampling in estimating catch proportions. We also show that lower parts of the Juutuanjoki and the Ivalojoki play an important role as spawning areas and therefore have a high priority for conservation. Nevertheless, the other brown trout populations in the Inarijärvi area contribute to the overall genetic diversity in brown trout and should not be neglected in conservation planning. The overall genetic diversity and life-history variation in a given ecosystem are vital for productivity and thus for ecosystem services (Schindler *et al*. 2010). The long term patterns in catch proportions and their relation to brown trout biology described here are interesting starting points for future studies.

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Appendix 1. F_{ST} distance matrix the genetic relationships among the Inarijärvi brown trout baseline populations. Population codes are given in Table 1.

	Tsi	Nii	Naa	Nel	Kon	Kie	Kaa	Ket	Vas	Kur	Lan	Ahv	MeU	MeuL	Juu	Tuo	Nuk	Rep	Tol	Sal	IvaAP	Sot	App	Kyl	Tai	Rul	Kar	Iva	IvaJH	Lis	Nas	IvaN
Sur	0.081	0.080	0.178	0.096	0.143	0.140	0.092	0.122	0.104	0.110	0.175	0.113	0.095	0.092	0.143	0.106	0.103	0.093	0.085	0.113	0.075	0.102	0.087	0.099	0.090	0.067	0.113	0.109	0.115	0.163	0.167	0.161
Tsi		0.053	0.177	0.111	0.170	0.172	0.130	0.122	0.107	0.162	0.191	0.171	0.126	0.153	0.135	0.132	0.142	0.151	0.157	0.186	0.130	0.178	0.138	0.161	0.144	0.118	0.170	0.164	0.154	0.193	0.227	0.193
Nii			0.157	0.108	0.173	0.145	0.118	0.142	0.104	0.155	0.155	0.153	0.112	0.126	0.144	0.119	0.149	0.106	0.089	0.157	0.091	0.127	0.098	0.126	0.105	0.094	0.140	0.122	0.143	0.182	0.221	0.174
Naa				0.228	0.272	0.249	0.223	0.228	0.180	0.195	0.257	0.257	0.228	0.256	0.231	0.219	0.236	0.191	0.218	0.218	0.183	0.208	0.169	0.193	0.186	0.168	0.217	0.177	0.201	0.249	0.308	0.219
Nel					0.122	0.082	0.051	0.098	0.074	0.106	0.135	0.115	0.072	0.093	0.092	0.080	0.083	0.088	0.100	0.133	0.072	0.099	0.080	0.098	0.071	0.073	0.112	0.104	0.105	0.125	0.179	0.151
Kon						0.132	0.112	0.103	0.103	0.180	0.166	0.181	0.112	0.128	0.095	0.098	0.095	0.151	0.160	0.200	0.129	0.174	0.154	0.145	0.108	0.109	0.179	0.158	0.176	0.206	0.245	0.224
Kie							0.026	0.117	0.098	0.104	0.085	0.099	0.066	0.083	0.110	0.080	0.092	0.073	0.080	0.115	0.077	0.079	0.079	0.075	0.063	0.066	0.091	0.089	0.116	0.154	0.201	0.156
Kaa								0.065	0.055	0.065	0.087	0.069	0.021	0.059	0.062	0.031	0.063	0.058	0.066	0.086	0.043	0.064	0.065	0.065	0.047	0.051	0.074	0.078	0.084	0.133	0.156	0.131
Ket									0.010	0.080	0.136	0.133	0.039	0.104	0.016	0.020	0.108	0.120	0.141	0.140	0.081	0.125	0.129	0.135	0.089	0.088	0.144	0.129	0.115	0.195	0.202	0.188
Vas										0.056	0.126	0.106	0.031	0.096	0.028	0.009	0.100	0.085	0.104	0.105	0.052	0.086	0.096	0.102	0.058	0.073	0.111	0.100	0.096	0.161	0.180	0.152
Kur											0.154	0.098	0.060	0.110	0.110	0.044	0.113	0.044	0.066	0.071	0.043	0.052	0.070	0.084	0.051	0.045	0.064	0.071	0.056	0.130	0.146	0.129
Lan												0.162	0.107	0.093	0.126	0.137	0.099	0.096	0.118	0.154	0.106	0.116	0.101	0.101	0.084	0.095	0.139	0.097	0.128	0.149	0.196	0.157
Ahv													0.048	0.090	0.160	0.087	0.124	0.077	0.090	0.089	0.062	0.065	0.092	0.096	0.084	0.083	0.101	0.100	0.122	0.163	0.195	0.158
MeU														0.051	0.054	0.001	0.077	0.063	0.070	0.077	0.038	0.067	0.086	0.089	0.056	0.059	0.089	0.090	0.095	0.147	0.161	0.149
MeuL															0.126	0.088	0.063	0.055	0.064	0.079	0.060	0.061	0.056	0.069	0.063	0.048	0.091	0.075	0.085	0.133	0.145	0.126
Juu																0.035	0.110	0.137	0.151	0.179	0.105	0.149	0.146	0.148	0.103	0.111	0.166	0.147	0.152	0.207	0.233	0.213
Tuo																	0.088	0.079	0.083	0.099	0.043	0.081	0.104	0.110	0.062	0.070	0.106	0.107	0.100	0.166	0.177	0.166
Nuk																		0.080	0.098	0.103	0.077	0.103	0.084	0.082	0.065	0.056	0.097	0.094	0.103	0.126	0.152	0.147
Rep																			0.013	0.023	0.019	0.011	0.012	0.017	0.013	0.017	0.014	0.013	0.049	0.077	0.099	0.085
Tol																				0.054	0.028	0.035	0.040	0.049	0.038	0.042	0.049	0.049	0.083	0.114	0.129	0.129
Sal																					0.034	0.029	0.038	0.038	0.029	0.033	0.026	0.033	0.077	0.132	0.143	0.125
IvaAP																						0.018	0.025	0.029	0.015	0.023	0.032	0.024	0.040	0.078	0.100	0.075
Sot																							0.027	0.029	0.022	0.035	0.034	0.020	0.047	0.087	0.101	0.079
App																								0.009	0.021	0.016	0.025	0.012	0.036	0.059	0.099	0.049
Kyl																									0.010	0.015	0.015	0.007	0.048	0.072	0.106	0.070
Tai																										0.008	0.022	0.018	0.047	0.084	0.109	0.089
Rul																											0.017	0.016	0.040	0.081	0.109	0.087
Kar																												0.019	0.050	0.088	0.101	0.094
Iva																													0.045	0.066	0.098	0.069
IvaJH																														0.028	0.038	0.015
Lis																															0.041	0.016
Nas																																0.068

Appendix 2. The estimated catch proportions and their 95% confidence intervals in Inarijärvi at the regional level.

Group	2006 + 2007		2008		2010		2011	
	Oncor	cBayes	Oncor	cBayes	Oncor	cBayes	Oncor	cBayes
Southern	0.75 (0.65–0.82)	0.80 (0.72–0.86)	0.79 (0.71–0.82)	0.79 (0.75–0.84)	0.48 (0.40–0.54)	0.52 (0.45–0.59)	0.61 (0.50–0.72)	0.64 (0.53–0.74)
Western	0.11 (0.06–0.19)	0.10 (0.05–0.16)	0.18 (0.15–0.25)	0.19 (0.15–0.23)	0.48 (0.41–0.55)	0.44 (0.37–0.51)	0.34 (0.24–0.46)	0.34 (0.24–0.45)
Northern	0.14 (0.07–0.20)	0.11 (0.06–0.17)	0.02 (0.01–0.06)	0.02 (0.01–0.03)	0.04 (0.02–0.07)	0.00 (0.00–0.05)	0.02 (0.00–0.06)	0.02 (0.00–0.05)
Eastern	0.00 (0.00–0.04)	0.00 (0.00–0.00)	0.00 (0.00–0.03)	0.00 (0.00–0.02)	0.00 (0.00–0.05)	0.04 (0.02–0.07)	0.02 (0.00–0.07)	0.00 (0.00–0.02)

Appendix 3. The estimated catch proportions and their 95% confidence intervals in Inarijärvi at the genetic cluster level.

Group	2006 + 2007		2008		2010		2011	
	Oncor	cBayes	Oncor	cBayes	Oncor	cBayes	Oncor	cBayes
Iva_L	0.75 (0.62–0.81)	0.80 (0.72–0.87)	0.80 (0.70–0.82)	0.80 (0.75–0.84)	0.48 (0.40–0.54)	0.52 (0.45–0.59)	0.60 (0.49–0.72)	0.65 (0.53–0.76)
Ahv	0.00 (0.00–0.12)	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–0.03)	0.00 (0.00–0.02)
Sur	0.03 (0.00–0.07)	0.00 (0.00–0.00)	0.00 (0.00–0.04)	0.00 (0.00–0.00)	0.01 (0.00–0.03)	0.01 (0.00–0.03)	0.00 (0.00–0.04)	0.00 (0.00–0.02)
Tsi/Nii	0.11 (0.05–0.17)	0.10 (0.06–0.16)	0.02 (0.00–0.03)	0.02 (0.00–0.03)	0.03 (0.01–0.06)	0.03 (0.01–0.06)	0.02 (0.00–0.05)	0.01 (0.00–0.05)
Naa	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–0.00)
Kon	0.00 (0.00–0.03)	0.00 (0.00–00.0)	0.00 (0.00–0.02)	0.00 (0.00–0.00)	0.00 (0.00–0.03)	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–0.00)
mix_W	0.00 (0.00–0.06)	0.00 (0.00–0.02)	0.00 (0.00–0.05)	0.00 (0.00–0.02)	0.03 (0.01–0.08)	0.01 (0.00–0.03)	0.02 (0.00–0.11)	0.00 (0.00–0.02)
Juu_L	0.10 (0.05–0.17)	0.09 (0.04–0.15)	0.17 (0.13–0.22)	0.18 (0.14–0.22)	0.44 (0.36–0.51)	0.43 (0.36–0.50)	0.34 (0.21–0.44)	0.32 (0.22–0.43)
Lan	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–0.01)	0.00 (0.00–0.00)	0.00 (0.00–0.01)	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–0.00)
Nuk	0.00 (0.00–0.14)	0.00 (0.00–0.00)	0.00 (0.00–0.01)	0.00 (0.00–0.00)	0.00 (0.00–0.02)	0.00 (0.00–0.00)	0.00 (0.00–0.03)	0.00 (0.00–0.00)
Iva_U	0.00 (0.00–0.06)	0.00 (0.00–0.04)	0.00 (0.00–0.03)	0.00 (0.00–0.00)	0.00 (0.00–0.02)	0.00 (0.00–0.01)	0.01 (0.00–0.05)	0.00 (0.00–0.04)

Appendix 4. The estimated catch proportions and their 95% confidence intervals in Paadarjärvi at the regional level.

Group	2006 + 2008		2010 + 2011	
	Oncor	cBayes	Oncor	cBayes
Southern	0.10 (0.04–0.27)	0.13 (0.00–1.00)	0.20 (0.09–0.40)	0.04 (0.00–0.12)
Western	0.86 (0.65–0.94)	0.87 (0.01–1.00)	0.80 (0.60–0.91)	0.96 (0.87–1.00)
Northern	0.03 (0.00–0.08)	0.00 (0.00–0.01)	0.00 (0.00–0.05)	0.00 (0.00–0.01)
Eastern	0.02 (0.00–0.14)	0.00 (0.00–0.00)	0.00 (0.00–0.05)	0.00 (0.00–0.02)

Appendix 5. The estimated catch proportions and their 95% confidence intervals in Paadarjärvi at the genetic cluster level.

Group	2006 + 2008		2010 + 2011	
	Oncor	cBayes	Oncor	cBayes
Iva_L	0.30 (0.14–0.48)	0.23 (0.00–1.00)	0.34 (0.19–0.55)	0.51 (0.34–0.67)
Ahv	0.03 (0.00–0.09)	0.00 (0.00–0.03)	0.00 (0.00–0.07)	0.00 (0.00–0.01)
Sur	0.03 (0.00–0.08)	0.00 (0.00–0.00)	0.00 (0.00–0.01)	0.00 (0.00–0.02)
Tsi/Nii	0.00 (0.00–0.00)	0.00 (0.00–0.01)	0.00 (0.00–0.03)	0.00 (0.00–0.02)
Naa	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–0.00)
Kon	0.00 (0.00–0.03)	0.00 (0.00–0.00)	0.00 (0.00–0.03)	0.00 (0.00–0.00)
mix_W	0.14 (0.05–0.38)	0.00 (0.00–0.03)	0.26 (0.06–0.39)	0.21 (0.04–0.40)
Juu_L	0.47 (0.23–0.62)	0.59 (0.00–0.99)	0.37 (0.21–0.58)	0.27 (0.13–0.46)
Lan	0.02 (0.00–0.06)	0.00 (0.00–0.02)	0.02 (0.00–0.08)	0.00 (0.00–0.01)
Nuk	0.00 (0.00–0.03)	0.00 (0.00–0.00)	0.00 (0.00–0.04)	0.00 (0.00–0.04)
Iva_U	0.00 (0.00–0.10)	0.14 (0.00–0.30)	0.00 (0.00–0.04)	0.00 (0.00–0.02)