

Size of wild and hatchery-reared Atlantic salmon populations in the northern Baltic Sea estimated by a stratified mark-recapture method

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We estimated the total size of the Atlantic salmon (*Salmo salar*) population complex (wild and cultured) in the Gulf of Bothnia, northern Baltic Sea, using a stratified mark-recapture method. In 2001 and 2002, 1970 salmon were captured by the commercial trapnet fishery and tagged with external arrow tags. A total of 349 tagged fish was later recaptured among 65 180 salmon screened for tags. Recoveries were gathered by the commercial trapnets and by screening fish entering counting facilities in rivers and broodstock fisheries at the river mouths. In addition, tags were recovered from recreational river catches. Our estimates suggest that the total size of the migrating population in both years was about 230 000 fish. Proportions of wild and cultured salmon differed between the two years. In 2001, the proportion of wild salmon was 37%; the corresponding figure for 2002 was 62%. Based on estimates of wild salmon smolt production and the number of released smolts, the estimated proportion of cultured smolts that survived the feeding migration and returned to the Gulf of Bothnia (2–4%) was approximately 2.5–4.5 times lower than that of wild smolts (9–10%).

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Introduction

The main feeding areas of Baltic salmon (*Salmo salar*; Atlantic salmon in the Baltic Sea is generally called Baltic salmon) are situated in the central and southern parts of the Baltic Main Basin, and only negligible numbers of fish migrate out of the Baltic Sea (Christensen *et al.*, 1994; Karlsson and Karlström, 1994). About 90% of the present natural Baltic salmon production is in the northern part of the Baltic Sea, in the Gulf of Bothnia, where 13 rivers still contain wild salmon populations (Rappe *et al.*, 1999; Romakkaniemi *et al.*, 2003; ICES, 2004). Furthermore, most hatchery-reared salmon smolt releases of the Baltic Sea are carried out in the Gulf of Bothnia to compensate for the lost salmon production in rivers that have been dammed for hydropower production (Rappe *et al.*, 1999; ICES, 2004). Production of hatchery-reared smolts is based

on live broodstock reared from eggs and kept in hatcheries. In addition, substantial numbers of smolts and parr have been released into some rivers in the Gulf of Bothnia to supplement wild production (Romakkaniemi *et al.*, 2003).

Baltic salmon have been heavily exploited during recent decades in offshore and coastal commercial fisheries as well as by riverine recreational fisheries (Rappe *et al.*, 1999; ICES, 2004). Since the mid-1990s, the major wild salmon stocks of the Baltic Sea have been recovering, mainly through the reduction of total allowable catches (TACs) in offshore fisheries and because of strict temporal regulation of the coastal fishery during the spawning migration (Romakkaniemi *et al.*, 2003). Juvenile salmon densities in rivers have increased about tenfold since the mid-1990s, and a marked increase in wild adult salmon numbers has been observed in the catches (Romakkaniemi *et al.*, 2003;

ICES, 2004). In 2003, more than half the salmon caught in the Gulf of the Bothnia were of wild origin (ICES, 2004).

Monitoring and assessing the status of wild Baltic salmon stocks is primarily based on catch records, estimates of juvenile production (electrofishing and smolt trapping), and, in some cases, counts of fish in fish ways and broodstock fisheries. A major challenge for salmon stock assessment is still the estimation of the total size of the Baltic salmon population complex, and the proportion of the different stock components. This information would be of great value for fisheries managers in balancing protection and exploitation of the stocks. In addition, the recent decrease in the survival of cultured salmon (ICES, 2004) calls for better estimates of the exploitable population sizes that enter the Gulf of Bothnia coastal fisheries.

Recently, population (pre-fishery abundance) estimation methods have been developed for Atlantic salmon (Potter *et al.*, 2004). For Baltic salmon, abundance estimates have been obtained by various run-reconstruction models, typically based on Carlin tag returns (Larsson, 1975; ICES, 1988). In recent years, Bayesian methodologies

have been developed for estimating exploitation rates and population sizes for total Baltic salmon abundance (ICES, 2002a; Michielsens, 2003; Michielsens *et al.*, 2006). For the first time, this study attempts to estimate the total size of the salmon population entering the Gulf of Bothnia on their spawning migration, using a full-scale mark-recapture experiment and advanced estimation methods that were specifically developed to estimate population sizes of migrating salmonids (Arnason *et al.*, 1996; Schwarz and Taylor, 1998). In addition, the population estimation allowed marine survival and spawning escapement of wild and cultured salmon to be assessed. A stratified mark-recapture method (Seber, 1982; Arnason *et al.*, 1996) was used to estimate salmon abundance in the Gulf of Bothnia during the spawning migration in 2001 and 2002.

Material and methods

Study area

The Gulf of Bothnia is both the most northern and most isolated part of the Baltic Sea (Figure 1). It can be divided into

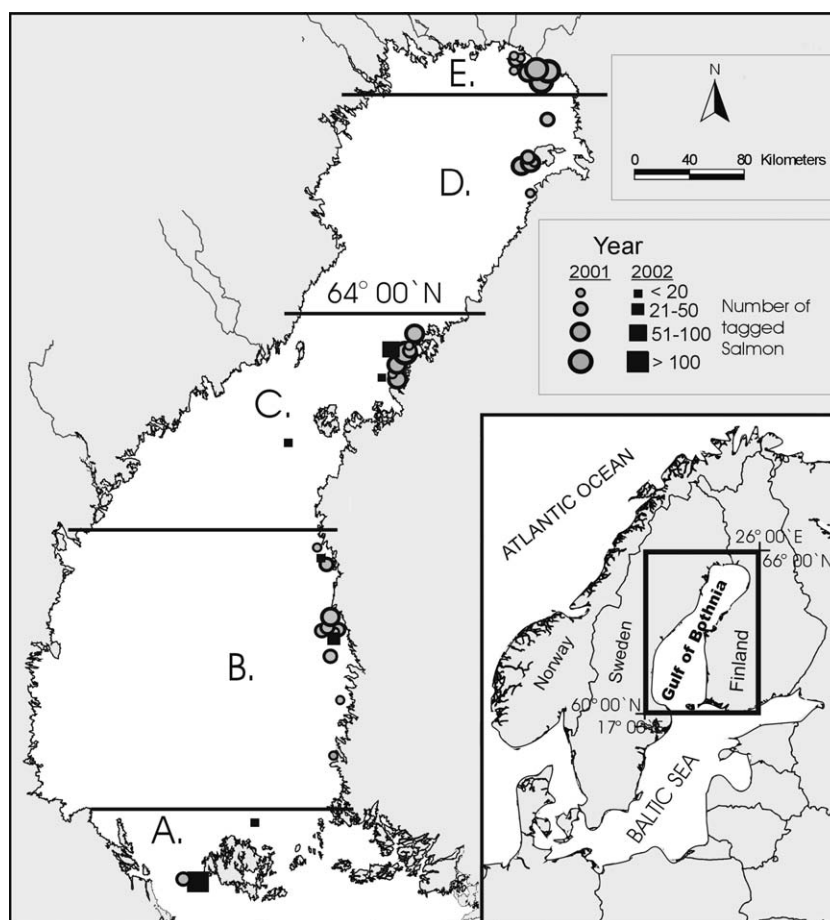


Figure 1. Tagging sites in the Gulf of the Bothnia for five different strata (regions A–E). Locations of different tagging sites in 2001 are indicated by grey circles and in 2002 by black squares.

two separate parts, the Bothnian Sea in the south, and Bothnian Bay in the north. The vast majority of all wild salmon production in the Baltic Sea is in rivers of the Gulf of Bothnia, and some 60% of the cultured Baltic salmon smolts are released annually in the Gulf of Bothnia area (Romakkaniemi *et al.*, 2003; ICES, 2004). The main part of the Gulf is ice-covered for several months of the year, and water temperature is typically low during the open-water period. The Baltic Sea is a brackish water basin, and the salinity in its northern part is especially low (0–4 psu). There is virtually no tide.

Mark-recapture procedure

Mark-recapture data were collected in 2001 and 2002 during the salmon spawning migration in five different strata (A–E; Figure 1) along the coast of the Gulf of Bothnia, by Finnish commercial fishers using 61 and 136 trapnets, respectively. These fishers were part of the research team and were given the right to start fishing earlier than regulations allow.

Salmon were marked with Hallprint arrow tags, which allowed individual recognition. The tag was hitched by a steel-made applicator below the dorsal fin, so that the fluke of the tag was attached to the supporting bones of the dorsal fin. A tag-returning reward of 18€ was offered. Fishers who directly participated in the study were not entitled to the reward, but they were allowed to start fishing salmon and to keep part of their catch before the opening of the legal fishing season.

In all, 2003 salmon, 1364 in 2001 and 639 in 2002, were tagged from mid-May to the end of June, during the main spawning migration of salmon (Table 1), and 349 were later

recaptured in different regions in 2001 and 2002 (Table 1). In 2001, both marking and recapture sites covered the whole Finnish side of the Gulf of Bothnia, whereas in 2002, tagging activity was focused in the southern areas. Most salmon tagging (87% in 2001, 65% in 2002) and catch recording (86% in 2001, 88% in 2002) was carried out by fishers. The rest was taken care of by the staff of the Finnish Game and Fisheries Research Institute (FGFRI). Fishers were trained to tag fish and to make full documentation of their catches. Salmon catch records made by the fishers and FGFRI staff were consistent within each stratum (paired sample *t*-test, sign test; $p > 0.05$). Tagging ceased at the end of July, but monitoring of salmon catches continued by the fishers to the end of the salmon fishing season in late August in both years, constituting 25% of all fish screened for tags in their catch data.

For the at-sea portion of the sample, to estimate population size, we only included tag recoveries from those fishers that were directly involved in the study. Total salmon catches by other coastal fishers were generally not available, so tag recoveries from these catches were excluded. Fish captured in the broodstock fishery or salmon passing fish ladders (Tables 2 and 3) were also screened for tags. This permitted estimation of the proportions of tagged fish in these samples. Recoveries from rivers where salmon catch statistics were available were also included in the analyses.

A total of 28 603 adult salmon was screened in 2001, and 36 577 salmon in 2002. In 2001, the share was equal between Finland and Sweden, whereas in 2002, 69% of the fish were screened in Finland (Table 4). In 2001, the largest proportion (42%) of the screening took place in the

Table 1. Number of salmon tagged by week and stratum (A–E) in 2001 and 2002 in the Gulf of Bothnia (1SW, one-sea-winter salmon; MSW, multi-sea-winter salmon).

Julian week	2001												2002					
	1SW						MSW						1SW		MSW			
	A	B	C	D	E	Total	A	B	C	D	E	Total	A	Total	A	B	C	Total
18								3				3				2		2
19															8	1		9
20		1				1	12	4	3			19	4	4	77	1	3	81
21		5	3			8	13	8	12			33	1	1	53	4	19	76
22		9	8	4	2	23	7	25	57	43	33	165	3	3	27	15	54	96
23		23	25	10	5	63	1	55	140	95	77	368	5	5	54	26	72	152
24		13	21	23	10	67	3	28	67	86	80	264	8	8	85	13	32	130
25			13	9	15	37		3	17	13	31	64	12	12	4	13	11	28
26		6	3	3	33	45		5		8	25	38					25	25
27		8	21	8	56	93				7	13	20					7	7
28			1	1	8	10					3	3						
29				11	18	29					3	3						
30					4	4					1	1						
31			3			3												
Total		65	98	69	151	383	36	131	296	252	266	981	33	33	308	75	223	606

Table 3. Total number of tagged salmon, tag recoveries, and number of screened fish in different strata in 2002. Total numbers of screened and untagged salmon in rivers are based on catch statistics (*), the broodstock fishery connected to fish ladders (**), or the broodstock fishery with a trapnet (***) (after Haikonen *et al.*, 2002, 2003; Juntunen *et al.*, 2003; ICES, 2004; Lars Karlsson and Ingmar Perä, Swedish National Board of Fisheries, unpublished data).

Tagging stratum	Number of fish tagged	Recovery stratum										
		Sea areas					Rivers and adjacent sea areas					
		A	B	C	D	E	Vindelälven**	Ume/Vindelälven*	Luleälven***	Simojki*	Tornionjoki*	Kalixälven*
A	338	0	2	20	3	7	5	1	2	0	7	1
B	77	0	1	6	1	2	0	0	0	0	2	0
C	224	0	0	15	9	10	0	0	0	1	3	2
Total number of fish screened		554	4058	7635	2937	8310	6456	389	1859	200	2669	2064

mortality, non-reporting, or tag misidentification are available.

- (iii) *Equal catchability*: all animals in a given recovery stratum, both tagged and untagged, have the same probability of being captured.
- (iv) All tagged animals released in a given tagging stratum have the same probability of movement to the recovery strata. When the number of tagging strata is smaller than the number of recovery strata, tagged and untagged animals move with the same probability.

In addition, PPE requires that one of the following assumptions is satisfied:

- (i) Recovery probabilities are constant among strata.
- (ii) The ratio of tagged to untagged individuals is constant among all recovery strata.

To overcome the problem presented by having a large number of strata with small or zero values (Tables 1 and 2), certain tagging and recovery strata were either pooled or deleted (see Arnason *et al.*, 1996). Among the advantages of pooling is a reduction in the number of parameters and hence, in general at least, increased precision of population estimates (Arnason *et al.*, 1996). Effects of pooling were examined using SPAS simulations, and tests for

goodness-of-fit confirmed the validity of the following pooling protocol. According to the recovery data, relatively more salmon tagged in the southern strata (A and B) were recovered from the Swedish side of the Gulf of Bothnia than fish tagged in the northern strata (not a single fish from Sweden's southern coast; Tables 2 and 3). In addition, tag recovery rates from the southern strata (A and B) were lower than in the northern strata (C, D, and E) in both years. Moreover, although the feeding migration of Gulf of Bothnia salmon stocks typically extends to the central and southern parts of the Baltic Main Basin, a variable proportion of salmon feed also in the Bothnian Sea (Salminen *et al.*, 1994). Probably because of this, some fish tagged in the southern areas (A and B) were recaptured later in summer in the same areas. Therefore, in 2001, southern (A–B) and northern strata (C–E) were combined into two tagging strata (Table 2). Correspondingly, in 2002, strata A and B were pooled, and C alone formed the second tagging stratum, because no tagging took place in D and E.

Banneheka (1995) showed that it is possible to pool or delete recovery strata without effects to the estimates, as long as there are more recovery strata than tagging strata. Schwarz and Taylor (1998) recommend a stratified method

Table 4. Distribution (%) of screened salmon between Finland and Sweden, trapnet catches of cooperating fishers, and river catches.

Year	Finland					Sweden			
	Coast	Rivers			Total	Rivers			Total
		Broodstock fishery	Catch statistics	River total		Broodstock fishery	Catch statistics	Total	
2001	28	3	15	18	46	42	12	54	100
2002	63	0	6	6	69	23	8	31	100

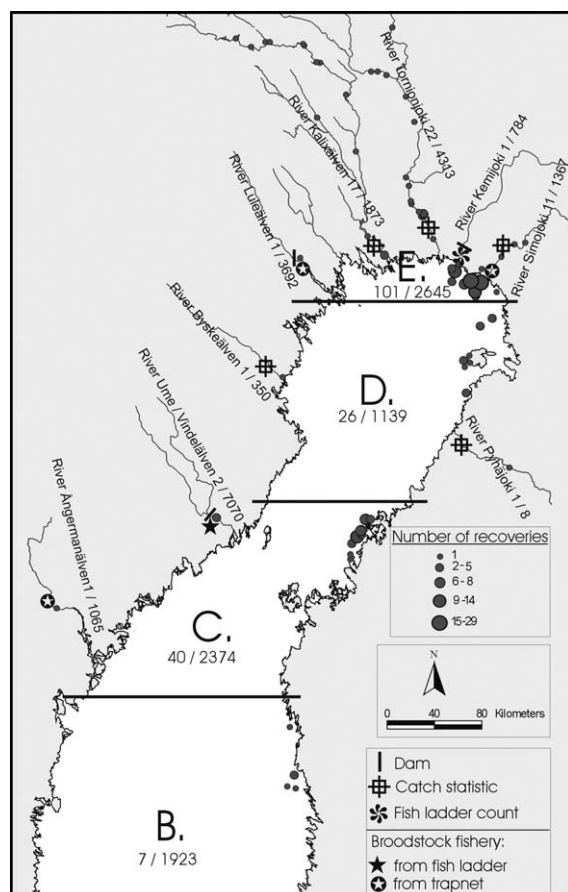


Figure 2. Total numbers of tag recoveries and screened salmon in different sea areas and rivers of the Gulf of Bothnia in 2001. Circles of different sizes indicate the number of recoveries at different sites. Total number of recoveries and screened salmon from trapnets in each stratum are shown below each letter (A–E) for different strata. Corresponding numbers are indicated with river names.

in which a recovery stratum with no recoveries should be deleted rather than pooled with other recovery strata. Therefore, in this study, rivers with catch records but no tag recoveries were omitted. There were also some small rivers which were not sampled, though it is likely that very small proportions of tagged salmon migrated to them (see ICES, 2002a, 2003, 2004; Juntunen *et al.*, 2002, 2003). Therefore, the possible effect of these rivers on the population estimates appears to be negligible.

To ensure sufficient recovery frequencies (minimum 5; Schwarz and Taylor, 1998) across different strata, recovery strata A–C were pooled in both years, resulting in three recovery strata (A–C, D, E; Tables 2 and 3). In both years, the rivers were pooled with their corresponding recovery strata at sea (A–E; Tables 2 and 3; Figures 2 and 3).

After pooling, the size of the population was calculated using the Darroch/Plante maximum likelihood ML estimator, which is included in the SPAS package and is appropriate for this type of data set and assumptions (Arnason *et al.*,

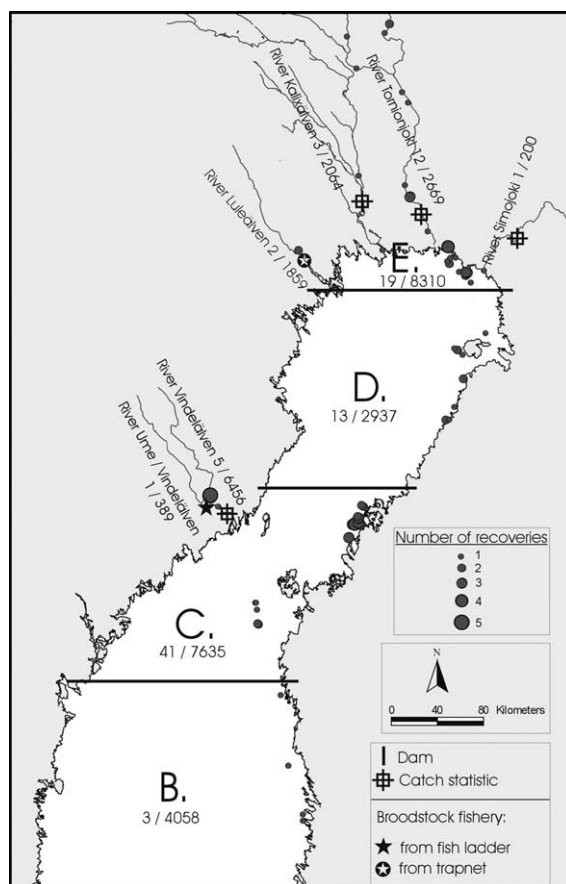


Figure 3. Total numbers of tag recoveries and screened salmon in different sea areas and rivers of the Gulf of Bothnia in 2002. Circles of different sizes indicate the number of recoveries in different sites. Total number of recoveries and screened salmon from trapnets in each stratum are shown below each letter (A–E) for different strata. Corresponding numbers are indicated with river names.

1996). In addition, the pooled Petersen estimator (PPE) was calculated for comparison. Suitability of the ML was studied by G^2 test, and the PPE was evaluated by two χ^2 tests, tests labelled for complete mixing and equal proportions (see Arnason *et al.*, 1996).

Potential tag loss was explored experimentally in a fish farm, using 80 tagged salmon placed in two large tanks, with 40 marked salmon in each. Fish tagging methods used were similar to the tagging methods used at sea. Size of fish varied between 1.0 and 7.0 kg (mean 4.5 kg, s.d. 1.8). Tag retention was observed over a period of three months. The cumulative percentage of tag loss increased linearly towards the final level of 15%. We estimated tag loss for these periods based on interpolation from the cumulative loss curve of the control group in the fish farm, using the average time between tagging and recapture *in situ* for each year. These estimates (ca. 3% for both years) were used in population estimation to correct for tag loss.

We needed also to find a way to characterize the origin of the spawning population. Therefore, we divided the total population into wild and cultured components, based on scale sampling during the main salmon run collected from daily trapnet and driftnet catches from the Finnish sea area between Åland Island and the Swedish coast (Åland Sea; stratum A; Figure 1). These samples were collected both from this study and from other samples collected by the FGFRI. Because the salmon catches from east of Åland, from the archipelago between Åland and the Finnish coast, were negligible (FGFRI commercial fisheries catch data for 1990–2004), it can be assumed that virtually all salmon entering the Gulf of the Bothnia migrate through the Åland Sea. Coupled with this observation, tag recovery patterns indicated that fish distributed themselves throughout the Gulf of Bothnia following tagging (Figure 4). Therefore, we felt justified in using these proportions to characterize hatchery vs. wild origin for our final population estimate. According to the scale data,

37% and 62% of migrating salmon were of wild origin in 2001 ($n = 554$) and 2002 ($n = 736$), respectively.

We were also interested in characterizing the spawning population as country of origin. We lacked genetic data in 2001 to perform this analysis, but for the 2002 population we had stock proportion estimates from the Åland Sea salmon catch samples ($n = 218$), which used micro-satellite DNA analyses to divide the hatchery-reared component into the country of origin. According to this analysis, 57% of the cultured salmon originated from Finnish hatcheries, and the rest from Swedish hatcheries (ICES, 2004). We applied these estimated country-of-origin proportions to the hatchery component of the population estimate to obtain hatchery abundance estimates by country of origin.

Results

The total size of the Gulf of Bothnia salmon migration population in 2001 and 2002 was estimated at ca. 230 000 salmon in both years, using the Darroch/Plante maximum likelihood estimator (Figure 5). In 2001, the estimate was 227 404 salmon (s.e. $\pm 37\,057$); the test of goodness in model fit shows a non-significant test result ($G^2 = 0.01$, 1 d.f., $p = 0.91$), indicating that the use of a Darroch/Plante maximum likelihood estimator was appropriate. In 2002, the estimate was 232 151 salmon (s.e. $\pm 23\,907$; $G^2 = 0.18$, 1 d.f., $p = 0.67$).

Because the χ^2 tests show significant test results for 2001 (complete mixing, $\chi^2 = 6.71$, 1 d.f., $p = 0.01$; equal

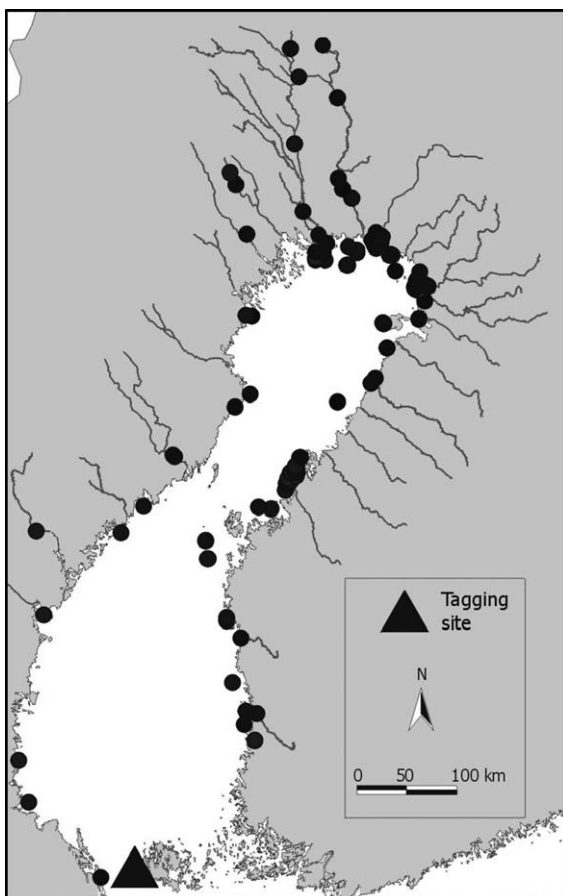


Figure 4. Distribution of tag recoveries (2001 and 2002 combined) from a tagging site west of the Åland islands. Stratum A (the tagging site) is represented by the triangle.

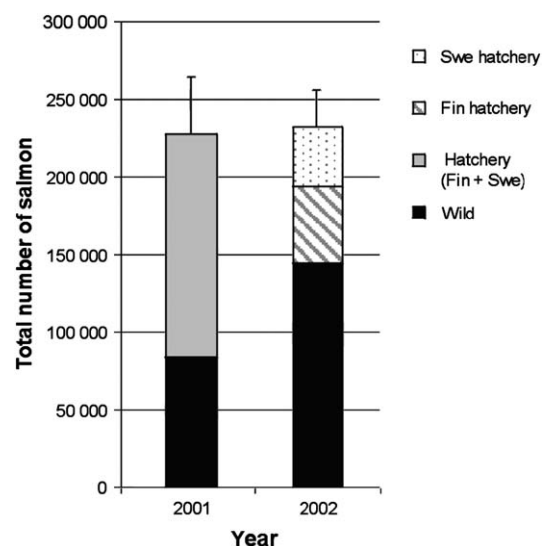


Figure 5. Total population sizes of Atlantic salmon entering the Gulf of the Bothnia in 2001 and 2002 estimated by the Darroch/Plante maximum likelihood estimator. Estimated numbers of wild and hatchery-reared salmon are presented separately. In 2002 cultured salmon are also separated by country of origin (Finland, Fin; or Sweden, Swe). Error bars indicate one standard error of the mean for the overall population estimate.

proportions, $\chi^2 = 79.55$, 2 d.f., $p < 0.01$), the pooled Petersen method was not suitable for analysing the 2001 data. In 2002, test results were not significant (complete mixing, $\chi^2 = 1.31$, 1 d.f., $p = 0.25$; equal proportions, $\chi^2 = 0.33$, 2 d.f., $p = 0.85$), and a pooled Petersen estimate was calculated resulting in 226 401 salmon (s.e. $\pm 20\,260$), with a result similar to the Darroch/Plante maximum likelihood estimate.

In 2001, the estimate of the total number of migrating wild salmon was 84 139 (37%) and that of cultured salmon 143 265. In 2002, the estimated number of wild salmon was 143 934 (62%) and 88 217 for cultured salmon (Figure 5). In 2002, 50 284 (57%) of the cultured salmon originated from Finnish hatcheries, and the remainder (37 933) were from Swedish hatcheries.

Discussion

Our estimates suggest that the total size of the Gulf of Bothnia salmon spawning population was stable between years, ca. 230 000 fish. The ratio of wild to cultured salmon, however, appeared to change markedly, appearing to double between 2001 and 2002. This difference reflects the recent increase in the wild salmon stocks in the Baltic Sea (Romakkaniemi et al., 2003; ICES, 2004). In addition, the change in estimated numbers of wild salmon in this study was in accordance with the increase in wild smolt production for the corresponding smolt cohorts of 1999 and 2000 (ICES, 2004). In the Åland Sea, about 90% of the wild salmon captured in both trapnets and driftnets were 2SW (two-sea-winter) fish in both study years, indicating that the vast majority of the wild salmon in 2001 and 2002 represented the smolt cohorts 1999 and 2000. Trapnets used in the Åland Sea caught fish only in the fish bag (i.e. by trapping, not meshing) with small mesh size (dynema 1 mm, full mesh size 70 mm). Therefore, it is unlikely that this method is selecting specifically for certain size classes. Increased densities of 0+ salmon parr in electrofishing surveys across all large salmon rivers in the Gulf of Bothnia in 2002 and 2003 (ICES, 2004) were reflective of the increased spawning escapement of wild fish between 2001 and 2002 (42%), because most of the cultured salmon do not contribute to natural reproduction in the rivers (Karlsson and Karlström, 1994; Romakkaniemi et al., 2003). Another potential reason for the increasing proportion of wild salmon may have been a decrease in the cultured stock component, despite constant stocking levels. This is consistent with the decreasing trend in cultured salmon survival in the late 1990s and early 2000s (ICES, 2004).

The estimated population size of Swedish cultured salmon in 2002 agrees with earlier estimates of cultured salmon abundance on the Swedish coast of the Gulf of Bothnia. Abundance of cultured salmon was estimated in the estuaries of some Swedish rivers, and these estimates

were related to the total number of smolts released. From the late 1990s to the early 2000s, the relationship developed suggested that 35 000–45 000 cultured salmon were available annually to the fisheries in Swedish rivers and estuaries in the Gulf of Bothnia (ICES, 2002a, b).

Jounela et al. (2006) estimated that the annual spawning run abundance that approached the Finnish coast of the Gulf of Bothnia was 132 000 (s.d. 45 100) and 178 000 (s.d. 44 500) salmon in 2001 and 2002, respectively. These estimates, however, do not represent the entire Gulf of Bothnia, because the fish migrating in the open sea and through the Swedish coastal area were not included. Taking into account the estimated numbers of cultured salmon on the Swedish coast (see above), the total estimate of salmon returning to the Gulf of Bothnia is in accord with the estimates made here. As most of the returning wild salmon originating from the large northern rivers tend to follow the Finnish coastline (Westerberg et al., 1999), the difference between years in the estimates of Jounela et al. (2006) likely reflected the increase in wild salmon populations.

In 2001, the reported total salmon catch from the Gulf of Bothnia in Finland and Sweden was 95 600 salmon; the corresponding figure for 2002 was 98 732 salmon (ICES, 2004). Because no remarkable changes in fishing effort took place between 2001 and 2002 (ICES, 2004), this is further evidence that population sizes were at similar levels in both years.

The wild salmon smolt production in the salmon rivers of the Gulf of Bothnia was about 833 000 smolts (CV 113%) in 1999 and about 1 560 000 smolts (CV 75%) in 2000 (ICES, 2004). In combination with the corresponding wild adult stock size estimates, it appears that 10% and 9% of wild smolts in 2001 and 2002, respectively, survived the feeding migration and returned to the Gulf of Bothnia. During the period 1998–2001, the total number of smolts stocked annually by Finland and Sweden varied between 3.4 and 3.8 million (ICES, 2004). For these same cohorts, it appears that only 4% and 2% of cultured smolts in 2001 and 2002, respectively, survived to return to the Gulf of Bothnia; this translates to between $2.5\times$ and $4.5\times$ lower survival rate than that of wild smolts. Similar estimates have been obtained on the Swedish side of the Gulf of Bothnia, where the survival of cultured salmon has varied between 2.8% and 3.0% in the river Luleälven in recent years. The average return rate during the years 1992–1998 in the River Dalälven was 3.4% (ICES, 2002a). Additionally, our survival estimates are in line with the recent estimates of post-smolt survival and annual mortality of salmon in the Baltic Main Basin (Michielsens et al., 2006).

By comparing our estimated wild and cultured salmon population sizes with the estimated total salmon catch (reported + unreported) in the Gulf of Bothnia (Anon., 1997; ICES, 2002b, 2003, 2004), we can approximately estimate the proportion that escaped all commercial and recreational

fishing. Our estimates suggest that in 2001, 30–42% of the wild salmon migrating population and 23–38% of the cultured salmon population escaped both coastal and river fisheries. In 2002, the corresponding figures were 36–50% for wild salmon and 8–20% for cultured salmon. It should be noted that the estimates of the proportion of wild and cultured salmon in this case are based on salmon catch samples from different fishing areas of the Gulf of Bothnia, not solely on the Åland Sea samples (see above; ICES, 2004; FGFRI, unpublished). By comparison, Swedish studies showed that 37–60% of the cultured salmon entering the estuaries of the Rivers Dalälven and Luleälven escaped fisheries in the late 1990s and early 2000s (ICES, 2002a).

We acknowledge that not necessarily all underlying assumptions of the estimation methods used have been satisfied in this study; this may be especially true for the pooled Petersen method, which includes especially strict assumptions. The assumptions of equal catchability and mixing of tagged and untagged fish across all strata are very difficult to evaluate. Possible failures may be attributable to differences in run timing between salmon of age groups, and between wild and cultured stocks. For example, wild salmon return to the northern Baltic Sea earlier than cultured salmon (Karlsson *et al.*, 1994; McKinnell *et al.*, 1994), and the proportion of small salmon, especially one-sea-winter (1SW) fish, are more pronounced in the later part of the spawning migration (Niva, 2001; FGFRI unpublished data for 2001–2004). It is possible that 1SW salmon pass through the tagging stratum later than the multi-sea-winter salmon and therefore may not have the same probability of being recovered in a river. In the Åland Sea in 2001 and 2002, the proportion of 1SW salmon was only 5% and 4%, respectively. Therefore, we reason that their contribution to the total population was likewise small. The assumptions of closure (see *Material and methods*) are well satisfied in this study, because all fish in the recovery strata were surely present in the tagging strata. Additionally, we contend that there was a non-zero probability that fish tagged in the tagging strata would be recovered in one of the recovery strata (see also Arnason *et al.*, 1996). Sampling of broodstock and rod fisheries in most rivers and estuaries extended rather late in the season (at least until late August), relatively close to the spawning time; this sufficiently satisfied the assumption of closure (Arnason *et al.*, 1996), and also minimized possible bias caused by differences in run timing between salmon of different age groups, and between wild and cultured stocks. In addition, the sampling at sea extended over the entire period of the spawning run from spring to late summer, when coastal catches were close to zero. Using individual arrow tags allowed 100% identification of the tagging stratum for a recovered fish.

Possible biases to the population size estimation caused by tag-induced mortality were apparently very small. The average time from tagging to recovery was 15 days in 2001 and 20 days in 2002. The first dead fish in the tagged

control group at the fish farm was observed as late as 14 days after tagging. Several radio-tagging experiments where Atlantic salmon have been captured and released from coastal trapnets indicate minimum levels of post-tagging survival at 80–99%, although not all undetected fish necessarily died. It is possible that transmitter failure or salmon straying to other rivers could have led to non-detection (Heggberget *et al.*, 1993; Thorstad *et al.*, 1998; Erkinaro *et al.*, 1999; Rivinoja *et al.*, 2001; Jokikokko, 2002). We do not know of any evidence to suggest that seals, or other salmon predators, would target tagged vs. untagged salmon.

Failure in tag reporting does not appear common because broodstock fisheries are operated by employees of research institutes and other professional fishers. The observed proportions of tagged and untagged salmon in catches were equal between fishers, and between the fishers and the research teams of the FGFRI in each stratum, indicating that the non-reporting rate of the fishers involved in this study was most likely very low. In addition, the selected fishers were well informed and motivated to report tags by the promise of detailed information about each tagged salmon that was recovered. A primary motivation for this study was to evaluate the survival of salmon released from a trapnet (Siira *et al.*, in press). Therefore, coastal fishers were aware that a high trapnet-released salmon survival may improve their future prospects for increased harvesting of cultured salmon through a selective fishery (Vander Haegen *et al.*, 2004; Siira *et al.*, in press), where wild fish must be released from trapnets and the fishery targets solely cultured fish. Because temporal closures (delayed openings) of salmon fishing in the Gulf of Bothnia could be either reduced or totally halted if a selective fishery strategy would be introduced, the coastal fishers were highly motivated to return tags. Finally, the reporting motivation of the river fishers was likely increased by the new, highly visible tag design, and especially by the relatively high reward (18€) compared with that for ordinary Carlin tags (5€).

In conclusion, the population size of salmon entering the Gulf of Bothnia has been estimated in the present study for the first time by a full-scale mark-recapture experiment. Despite some uncertainty in meeting the assumptions of the stratified methods employed, our estimates are in accord with corresponding information describing changes in wild salmon production, abundance indices, and estimates of catch, marine survival, and spawning escapement in the Gulf of Bothnia area based on independent data, sampling area, and estimation methodology. The estimates produced in the present study provide fisheries managers with additional information to balance protection of wild salmon with exploitation of cultured salmon. Population estimates of the total number of salmon returning to the Gulf of Bothnia in 2001 and 2002 are also useful reference points for various indices and estimates of wild and cultured salmon in the area.

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