Using simulated escape events to assess the annual numbers and destinies of escaped farmed Atlantic salmon of different life stages from farms sites in Norway

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To improve assessments of the environmental risks of aquaculture, a series of simulated escapes of farmed Atlantic salmon (*Salmo salar* L.) from seawater netpens were performed. Individually tagged post-smolts and adult Atlantic salmon were released from various locations at different times of the year. Post-smolts that escaped during their first summer were capable of rapid migration towards the open sea. A small fraction returned to spawn and were recaptured after 1–3 years at sea (0.4%, range 0.0–1.1%). A total of 13% of the post-smolts that escaped during autumn were reported in nearby fisheries during subsequent months, partly because they had grown large enough to be caught in the gillnets used, but more importantly because migratory behaviour diminished towards the end of the year. The mean recapture rate of adult salmon was high after releases in fjords (7–33%), lower after coastal releases (4–7%), and zero on the outer coast. Most of these recaptures were immature fish recaptured in sea relatively close to the release site during their first months post-release. Recaptures of adult escapees after 1–2 years in the wild were very rare (0.09%), probably because of their low survival. A Monte Carlo method was developed to estimate the annual numbers of escapees from Norwegian fish farms based on reported catches of escaped farmed salmon in the sea and in rivers and the recapture probabilities reported here. The model provides a tool to estimate numbers of escapees independently from the reported numbers. Importantly, our analysis suggests that the total numbers of post-smolt and adult escapees have been two- to fourfold as high as the numbers reported to the authorities by fish farmers, depending on whether the incomplete sea fishery statistics are compensated for.

Keywords: environmental risks, escapements, farmed Atlantic salmon, fish farms, recapture.

Introduction

Atlantic salmon (*Salmo salar* L.) farming has become a major industry, with a worldwide production of 1.4 million t in 2010 (FAO, 2012). More than 65% of this volume comes from fish farms in Norway, which also hosts a large proportion of the wild river populations of Atlantic salmon. It has become evident that the fish-farming industry has an environmental dark side, which may be reflected in a decline in natural populations (Ford and Myers, 2008). Two negative impacts that have raised concern (Anon., 2009) are the spread of diseases and parasites such as the salmon louse, which may reduce the survival of young wild salmon migrating from rivers to the sea (Krkošek *et al.*, 2012; Skilbrei *et al.*, 2013; Vollset *et al.*, 2014) and the escapes of farmed fish. Escaped farmed Atlantic salmon enter rivers wherever salmon sea cage farming occurs, in both Europe and North America (Milner and Evans, 2003; Walker *et al.*, 2006; Fiske *et al.*, 2006; Morris *et al.*, 2008; Green *et al.*, 2012) and are capable of spawning in the wild (Lura and Sægrov, 1991; Poole *et al.*, 2000). In the natural range of wild Atlantic salmon, hybridization between escaped farmed and wild Atlantic salmon populations may result (Crozier, 1993; Clifford *et al.*, 1998; Glover *et al.*, 2012; 2013). This is believed to reduce the viability of the wild salmon populations (Fleming *et al.*, 2000; McGinnity *et al.*, 2003).

Farmed young Atlantic salmon are reared in hatcheries in freshwater until the smolt stage, when they are transferred to seapens in seawater. Fish farmers have an obligation to, and usually do, report escapement incidents from netpens (Jensen *et al.*, 2010), which include escapes of all stages from post-smolts to large adult salmon. The reported numbers of escaped salmon in Norway have ranged between 112 700 and 921 000 fish year^{-1} between 2001 and 2011 (Norwegian Directorate of Fisheries; http://www.fiskeridir.no). However, there have been suggestions that a significant proportion of escapes are not reported (Skilbrei and Wennevik, 2006; Glover *et al.*, 2008; Glover, 2010; Skilbrei and Jørgensen, 2010). Claims have been made in the public debate that the actual number of escapes is much higher than reported, but to date, no formal assessments of this assertion have been undertaken.

Assessment of the environmental risks of escaped farmed fish is essential to enable the identification of measures to reduce or mitigate the risk of mixing between escaped farmed and wild Atlantic salmon (Taranger *et al.*, 2011). Some key questions are: (i) how many escaped farmed salmon can be recaptured, (ii) how far and how rapidly do they disperse from the escape site, (iii) do they home to the vicinity of the escape site when they become sexually mature, and (iv) how many enter rivers to spawn? The answers to these questions probably depend on a number of factors, for example, the locality of the fish farm relative to local fisheries, coastal currents, and proximity to fjords (where applicable) and Atlantic salmon river populations. Localities for fish farms range from small to large fjords, sheltered regions of the coast, to the extreme coast at the edge of the open sea.

Biological factors such as life stage and size of fish at escape are also important determinants of dispersal and post-escape behaviour. If a fish escapes as a smolt or post-smolt during spring or summer (when the wild smolts migrate), it must first learn to feed on natural prey and avoid predators during migration to feeding grounds in the open sea, and remain there for at least a year before reaching sexual maturity and returning to spawn in freshwater. Hatchery-reared juveniles released into the wild usually suffer high initial mortality [reviews by Svåsand *et al.* (1998) and Jonsson and Jonsson (2006)]; compared to wild smolts, only a small proportion manage to fulfill the cycle from smolt to adulthood. The situation is different for large salmon that escape from netpens. Their size limits the number of potential predators, but it is not known whether fish escaping outside of natural migration periods are close to sexual maturity and will show migratory behaviour to feeding areas in the open sea. Post-escape behaviour may, therefore, be under the influence of a number of internal and external factors, including size, life stage, and season (Hansen and Jonsson, 1989; Skilbrei, 2010a), sexual maturity status, and environmental conditions in the fish farm (Skilbrei *et al.*, 2014).

Detailed information about the survival and behaviour of escaped farmed Atlantic salmon is important for the management of salmon populations and the farming industry. In this paper, a series of simulated escape incidents with farmed Atlantic salmon performed by the Institute of

Marine Research (IMR) from 2005 to 2010 were summarized. The aim of this paper is twofold: (i) study the post-escape behaviour, spread, and recapture of Atlantic salmon post-smolts and adults released from different sites on the Norwegian coast; and (ii) by combining the information thus obtained with a new Monte Carlo simulation method, assess the issue of unreported escapes by comparing the predicted numbers of escaped farmed salmon with the actual reports from Norwegian fish farms.

Material and methods

Tagging and release of fish

Released fish were tagged with T-bar Anchor tags (Hallprint, Hindmarsh Valley, South Australia; Table 1). We have chosen to use the terms "post-smolts" for 1-year old spring smolts that were released from netpens in seawater at some time between spring and early autumn, "large post-smolts" for post-smolts released during autumn that had not reached 0.9 kg in mean body weight, and "adults" for groups above 0.9 kg, irrespective of whether they were sexually mature. "Out-of-season post-smolts" are smolts that have been transferred to marine netpens during autumn (see description below). The letters HI (Norwegian acronym for the Institute of Marine Research; IMR), IMR's Internet address (www.imr.no), and postal code were printed on the T-bar tags, together with an individual alphanumeric code. The following three types of experiments were performed:

1. Recapture in four bagnets in Altafjord, tagging, and immediate rerelease of recently escaped adult Atlantic salmon. It was assumed that the fish came from the escape of 90 000 adult salmon from a commercial fish farm in the fjord on 3 June 2005 (Release site 1; Figure 1). Tagging started 6 June, with 96% of fish tagged and released by the end of June.
2. Tagging and release of farmed Atlantic salmon from netpens. Post-smolt and adult salmon were released from nine commercial fish farms located along the Norwegian coast in 2005 and 2006 (release sites 2–5, 7, and 8; Figure 1). For release sites 7 and 8 (Figure 1), releases from adjacent farms are treated as one release site.

   To establish a time-series, post-smolts were tagged and released from the Matre Research Station in the small fjord Masfjord every year from 2005 to 2010 (release site 6). Masfjord is a 24-km long narrow fjord that enters a larger, more open fjord system on the west coast of Norway. Large post-smolts were included in 2007 and 2008 (see Table 1). One-half of the fish were treated against salmon lice prior to release. The treatment affected survival only marginally, so this effect is not discussed in this report.

   Smaller groups of fish were also tagged with acoustic tags to study post-escape behaviour in a small fjord (Masfjord, site 6) and a large fjord (Hardangerfjord, site 7). Hardangerfjord is more than 150 km long and hosts a large Atlantic salmon aquaculture industry (Skilbrei and Wennevik, 2006). Telemetry experiments were incorporated in all the five releases from Matre Research Station in 2008 (Skilbrei, 2010a). In Hardangerfjord, five separate groups of acoustically tagged adults were released in 2005 and 2006 (Skilbrei *et al.*, 2010), and fish with transmitters were included in the large releases in the fjord in autumn 2006 (Skilbrei and Jørgensen, 2010). The recapture data of acoustically tagged fish were included in the tagging/recapture data (Table 1). In addition, the recapture rates of fish that were tagged with both tags or with T-bar tag only were used to compare report rates of high (NOK 600) and low reward tags (NOK

100) (Skilbrei and Jørgensen 2010).

3. Releases of out-of-season post-smolts. Zero-age, out-of-season smolts were reared indoors at Matre Research Station. The photoperiod was manipulated by using a long–short–long daylength treatment to synchronize and stimulate smoltification (Berge *et al.*, 1995; Duston and Saunders, 1995). A reduction to 12 h of daylight is supposed to signal winter (Skilbrei *et al.*, 1997), and this photoperiod was used for 6 weeks beginning in July and followed by 6–8 weeks of continuous light before the smolts, silver in colour, were transferred to outdoor netpens in seawater under short natural daylength in September–October. They were released from netpens from September to December (Table 1; Skilbrei, 2013).

Estimation of numbers of escaped farmed Atlantic salmon

The numbers of escaped salmon recaptured in rivers and on the coast can be expressed in terms of recapture probabilities (p) and the numbers of escaped salmon ($N^{escaped}$):

$$N_{sea} = p_{postsmolt\to sea}N_{postsmolt}^{escaped} + p_{adult\to sea}N_{adult}^{escaped}$$
$$N_{river} = p_{postsmolt\to river}N_{postsmolt}^{escaped} + p_{adult\to river}N_{adult}^{escaped} \quad (1)$$

Based on the results reported in this paper, recapture probabilities are known parameters, albeit with some uncertainty. The numbers of escaped salmon caught in rivers and on the coast have been estimated by Anon. (2013) and data provided by Statistics Norway (www.ssb.no). Because a system of two linear equations with two unknowns ($N_{postsmolt}^{escaped}$ and $N_{adult}^{escaped}$) is solvable, equation (1) provides a method for estimating the numbers of escaped salmon in a way that is independent from reported numbers of escaped salmon.

An important complication is that neither the recapture probabilities nor the numbers of caught escaped salmon can be known precisely. Therefore, a simulation approach was adopted where the distributions of the input parameters were first specified; subsequently, input values were randomly drawn from these distributions and equation (1) was used to calculate point estimates for the numbers of escapees; the second step was repeated a large number of times (100 000). The parameterization of the model is presented in Table 2. The recapture probabilities were adjusted to account for the likelihood of underestimation, due to fishers not reporting marked salmon (p^{rep}), either because the tag was lost or because they choose not to report them. The maximum for the probability of recapture of adult escapees in the sea ($p_{adult\to sea}$) (0.1) is lower than the estimate derived from the experimental releases in fjords (0.06–0.33), but higher when compared to coastal release data (0.0–0.05). Most of the experimental releases were in fjords were recapture is high compared with coastal areas (see Results for details), and probably also compared to many other fjords. Therefore, the estimate was lowered to reflect the fact that many fish farms are located at the coast and in areas with low fishing effort.

The parameters in Table 2 represent the basic scenario that was regarded *a priori* as the most plausible. On the basis of scrutiny of the corresponding predictions, the simulations for three alternative scenarios were rerun:

1. Constraining the proportion of (spring) post-smolt escapees among salmon caught in rivers to the interval 10…50%. We consider that both very high and very low proportions of post-smolt escapees are unlikely; one study estimated the proportion to be 30% (unpublished), but we must assume that a range of values is possible.

2. Multiplying all marine captures eightfold (i.e., $N_{sea} \rightarrow 8N_{sea}$). Because the official statistics do not cover many important types of gear, marine catches are underreported (see Discussion). The chosen factor is our best estimate based on the data in Figure 5a, but it is not based on rigorous calculations. Because of the uncertainty regarding the degree of underrepresentation in marine captures, additional simulations were run for a range of underrepresentation levels (see Supplementary materials, Figure S1).
3. The combination of the aforementioned scenarios. Other parameters and assumptions were left unchanged in these additional runs.

For certain combinations of input parameters, the predicted numbers of escaped salmon can be negative. This indicates that the combination of input parameters is biologically infeasible and was, therefore, discarded. For the default parameters and assumptions, this happened for 21% of the replicates.

Recapture of tagged fish

On the basis of information provided by fishers who returned fish tags (fisher's name, size of fish, date and location of catch, and fishing gear), the recapture data were classified into the following categories according to fishery:

1. Official sea fishery (Sea): A traditional fishery with bagnets and salmon gillnets operating during 1–3 summer months and targeting the spawning migration of wild salmon. Reporting the catch is mandatory. The incidence of escaped farmed salmon in this fishery has been calculated and is used as the estimate of the catch of escaped farmed salmon in the sea (Anon., 2013).
2. Autumn fishery for escape farmed salmon (Autumn): A floating gillnet fishery for escaped salmon during autumn and early winter that is opened in specific regions (Skilbrei and Wennevik, 2006). A fisher who wants to participate is supposed to report to the county governor's office before the start of the fishery and also report the catch. The catch reports are not included in the official sea fishery statistics, but are available separately (www.ssb.no).
3. Autumn?: Salmon recaptured in gillnets during the autumn fishery for escaped salmon, where it is not known if the fisher officially participated in the autumn fishery. The numbers of fishers in this category reporting tags are much higher than the numbers of fishers officially participating in the autumn fishery, so it was assumed that the majority of these recaptures were not reported elsewhere.
4. Gillnets: The sum of salmon recaptured in gillnets during autumn by fishers who had not registered for the autumn fishery, fish captured in areas not covered by the autumn fishery, in other types of gillnets (bottomset, trammelnets), and at other times of the year.
5. Rod: Salmon caught by angling or trolling.
6. Unknown: Fishing method or gear was not reported by the fisher who returned the tag.

Results

Recaptures and spread of released fish

Post-smolts and adults released from sites 1–5, and adults from site 8, were recaptured relatively close to their release sites, most within a radius of 150 km (Figure 1). However, the recaptures of 1–3-sea-winter (SW) Atlantic salmon released as post-smolts from sites 6 and 8 in western Norway were more dispersed (Figures 1, 2). Although 49% of the total catch of the site 6 releases was recaptured in the inner part of the Masfjord in the vicinity of release site 6, the rest were spread in the sea and rivers from the southern tip of Norway to northern Norway. In total, 59% of the catch of adult fish stemming from site 6 post-smolt releases was angled in rivers or in the freshwater outlet of the hydroelectric power plant close to the release site.

The recaptures rate of 1–3 SW Atlantic salmon of the post-smolts released from site 6 varied considerably within and between release years, from close to zero to slightly above 1% (Figure 3). The fish released in five successive releases from May to early August 2005 generally performed much better at sea than the 2006–2010 releases. The sea age of the homing Atlantic salmon differed between release years, as the relative proportion of grilse was very low following the 2007–2008 releases (Figure 4). The reported recapture of 1–3 SW Atlantic salmon from the releases of post-smolts from release sites 2–5, 7, and 8 in 2005 ranged from zero to 0.9% (Table 1).

Few of the large post-smolts released from release site 6 during autumn were recaptured as grilse and multisea winter salmon (<0.2%, Figure 3). Much higher proportions were captured during the first weeks and months after release (12–15%; Table 1), mostly within the fjord (358 of 361 reported recaptures). No large post-smolts were recaptured shortly after release from site 3, but two individuals returned as adults (0.4%, Table 1).

Recapture rates depended on the release site. When adult fish were released on the outermost coastline, none were reported as recaptured. Recaptures increased to 4–7% for coastal releases and were highest in fjords (ranging from 7 to 33% among the fjords, Table 3). The recapture rate ranged from 7 to 43% in the Hardangerfjord (site 7; Table 1). On average, 0.16% (range 0–1.8%, Table 1) of the released adults was recaptured in rivers, usually during the first three months after release.

Most adult fish were recaptured during the first 1–1.5 months post-release (number of days until 90% of the catch taken is shown in Table 1) within the fjord of release. The exceptions were two releases from release site 6 (Masfjord) during autumn 2008, when a large proportion of released fish remained close to the netpens at the release site until late winter, feeding on surplus food pellets (Olsen and Skilbrei, 2010). From 94 to 100% of the adult fish that were released from netpens in fjord sites (site 6 Masfjord and site 7 Hardangerfjord) and were reported recaptured within a few months were taken within the same fjord [1227 of 1231 recaptures of adults released in Masfjord in 2008, 32 of 34 recaptures from Hardangerfjord in 2005; 42 of 45 recaptures of acoustically tagged fish in Hardangerfjord 2005–2006 and (Skilbrei *et al.*, 2010), and 310 of 321 recaptures from releases in autumn 2006 (Skilbrei and Jørgensen, 2010)]. In Altafjord, 86% of the escapees captured and released from bagnets were recaptured within the fjord (n = 53) and in the Alta River (n = 4) during 2006.

Only seven of 8023 Atlantic salmon (0.09%) released as adults were reported recaptured 1–2 years later (Table 3). None of these were recaptured far from the release site. Three adults released from site 1 were recaptured the next summer (Figure 1), two adults were caught in the vicinity of site 5 the following year (Figure 1), one adult released on 25 September 2006 was recaptured one year later a few kilometers from site 7, and one adult released on 17 September 2008 was angled 1 km from site 6 two years later.

Escaped post-smolts appeared to have a much higher chance of prolonged survival and of reaching sexual maturity in the wild than escaped adult fish. The mean recapture rate of 1–3 SW salmon was 0.39% for post-smolt releases, while only 0.09% of the released adults survived one year or longer (Table 4). A total of 22% of the adults were reported to have been recaptured during the first few months after release.

The recapture of out-of-season post-smolts was very low, only one individual of almost 23 000 fish released during three successive years [Tables 1 and 4, Skilbrei (2013)].

Fishing gears and reporting of catch of recaptures in the sea

A relatively small proportion (~10%) of the total tag recaptures in the sea originated from fisheries where the catch is supposed to be reported to the authorities (the “Sea” and “Autumn” fisheries). Salmon released as post-smolts were more frequently caught in the traditional fishery for spawning migrating wild salmon (42%) when they returned from open sea as 1–3 SW salmon (Figure 5).

Estimates of the number escaped farmed Atlantic salmon

Based on the estimated numbers of escaped farmed salmon in rivers and on the coast in 2005–2011, the Monte Carlo simulations under the basic scenario (see Methods) suggest that about 1 million salmon escape annually (Figure 6). The median estimate is just under 1 million, and 90% of the estimates fall between about 0.5 and 2.3 million. Constraining the proportion of post-smolts among the river-caught escapees results in a reduction in the estimated numbers of escaped salmon; the median estimate is reduced to about 0.7 million escapees. A much larger proportion of input parameter combinations leads to biologically infeasible results; about 85% compared to 21% under the basic scenario. Assuming that marine catches are underreported eightfold (based on the data presented in Figure 5a), the estimated number of escapees rises to a median value of about 1.5 million. The proportion of discarded replicates is about 88%. The higher the assumed degree of underreporting, the larger the estimated total number of escapees, but the increase is much less than strict proportionality would suggest. Each 100% increase in marine catches increases the total estimate by about 83 000 individuals (see Supplementary material, Figure S1). Combining an increased marine catch with a constrained proportion of postsmolt catches does not appreciably change the estimated total numbers of escapees (Figure 6), but the proportion of discarded replicates is further increased to 93%.

Under the basic scenario, the model suggests that most salmon escape as post-smolts (Figure 7). Constraining the proportion of post-smolts among the river-caught escapees shifts the composition of escapees to roughly equal proportions of young escapees and adults. This involves larger numbers of adult escapees and lower numbers of postsmolt escapees compared to the basic scenario. The assumption of larger marine catches leads to a dominance of adults among the escapees, and this tendency is further strengthened by constraining the post-smolt catch proportions.

Identifying parameter combinations that lead to biologically impossible results can provide information about plausible values of the input parameters. Under the basic scenario, few replicates are discarded, and deviations from randomness are minor, both with respect to reported catches vs. recapture probabilities (see Supplementary material, Figure S2) and to pairwise comparisons among recapture probabilities (see Supplementary material, Figure S3). Under the alternative scenarios, a much higher proportion of replicates lead to biologically impossible results, and clear deviations from randomness emerge. When the proportion of post-smolts among the river-caught escapees is constrained, the replicates retained are characterized by somewhat higher coastal catches than in the input data. A correlation between coastal catches and the recapture probability of adult escapees in the sea emerges; under this scenario, below-average coastal catches are incompatible with the higher end of the assumed recapture probability. The lowest values of the probability of recapture of adult escapees in rivers are also unlikely (see Supplementary material, Figure S2). A positive correlation between the recapture probabilities of adult escapees in rivers and in the sea also emerges; a high recapture probability of adult escapees in the sea is only feasible in combination with a high recapture probability of adult escapees in rivers (see Supplementary material, Figure S3).

A rather different picture emerges when marine catches are increased, irrespective of whether the proportions of post-smolts in the river catches are constrained (see Supplementary material, Figures S2 and S3). There is a strong bias against medium-to-high probabilities of recapture of adult escapees in rivers and against low-recapture probabilities of adult escapees in the sea. It is also noteworthy that the replicates that give feasible results are characterized by below-mean marine catches (see Supplementary material, Figure S2). Thus, high marine catches only appear to be possible given a high probability of recapture of adult escapees in the sea.

Compared with the mean annual reported number of escaped salmon of almost 413 000 individuals (Table 5), our estimate is two- to fourfold higher, depending whether we compensate for the incomplete sea fishery statistics. The discrepancy between the reported and estimated escape numbers is particularly large for the escapement of spring smolts and post-smolts, which stands for less than 4 % of the reported escapees (Table 5).

Discussion

This paper, which summarizes what is by far the largest dataset to date on experimental releases to the wild of farmed Atlantic salmon, has shown that life stage at the time of escape has a profound influence on the survival, dispersal, and potential recapture of the escapees on both short and long time-scales. For the first time, rigorous estimates of the numbers of Atlantic salmon that have escaped from salmon farms are presented, taking the life stage of escapees into account.

Smolts and post-smolts that escape during spring or summer migrate rapidly to the open sea and may return as 1–3 SW salmon. Our recapture rates were low, usually less than 1%, which is in accordance with the expectation that cultured smolts have a poor marine survival rate (reviewed by Jonsson and Jonsson, 2006). Furthermore, the recapture rate and age at sea differed between release years, probably because of fluctuations in the marine ecosystem (ICES, 2010; Friedland and Todd, 2012) that also influenced the marine performance of several wild Atlantic salmon stocks in the region (Skilbrei *et al.*, 2013). The chance of autumn escapees surviving to maturity appeared to be lower, possibly coinciding with a reduction in the migratory behaviour of large post-smolts during autumn (Skilbrei, 2010a) and increased recaptures of fish with a low or absent migratory drive in the vicinity of the release site [site 6 in 2007 and 2008 (Olsen and Skilbrei, 2010)].

Out-of-season smolts make up more than 40% of smolt production in Norway. When these fish escape, they may migrate rapidly even if they escape during autumn (Skilbrei, 2013). However, their survival in the sea appears to be very poor, and out-of-season smolts and post-smolts that escape during their first autumn in sea are thought to pose a less serious threat to wild Atlantic salmon populations than escapes of spring smolts and post-smolts (Skilbrei, 2013). No data on survival into adulthood of out-of season smolts released after the smolt stage have been reported. However, out-of-season smolts placed in sea cages in autumn and experimentally released the following May migrated rapidly towards the open sea (Skilbrei *et al.*, 2014).

Most of the recaptured 1–3 SW Atlantic salmon that were released as post-smolts were reported as recaptured in the release area. At some level, imprinting (Johnstone *et al.*, 2011; Putman *et al.*, 2013) occurs in escaped post-smolts during their outward migration. However, the recapture of post-smolts released at site 6 from a large geographic area suggests that the imprinting and/or homing mechanisms were weaker than those of wild smolts, which are generally believed to have a straying rate of less than 10% (Stabell, 1984). This is in accordance with comparisons between experimental releases of wild and cultured smolts in a stream in western Norway (Jonsson *et al.*, 2003) and sea-ranching experiments in the area (Skilbrei and Holm, 1998). The coastal current moves very close to the coast of western Norway. It is believed that current systems directly influence the dispersal of adult escapees (Hansen, 2006; Hansen and Youngson, 2010) and may also play a role in imprinting and/or navigation from the open sea back to freshwater or to different release sites. There are few data on the homing ability of adult escapees. The present observation that all seven recaptures of released adults that survived at least one year at sea were recaptured in the vicinity of the release site, some within only a few kilometers, may indicate homing behaviour. Besides, transplantation experiments with adult escaped farmed salmon document a tendency on the part of escaped farmed salmon to return to a specific river system at spawning time (Whoriskey and Carr, 2001).

A significant proportion of adult Atlantic salmon released in fjords were recaptured, most during the first couple of months. Significantly higher recapture rates of the more highly rewarded acoustic transmitters than of fish that were only tagged with T-bar anchor tags in the Hardangerfjord basin (ratio 3:2; Skilbrei and Jørgensen, 2010) suggest that the actual catch may have been >50% after some of the releases, similar to the high recapture rates following the release of large farmed Atlantic salmon tagged with acoustic transmitters in Altafjord (Chittenden *et al.*, 2011). The high fishing mortalities are consistent with behavioural studies in fjords showing that released fish moved around in Sunndalsfjorden/Tingvollfjorden (Solem *et al.*, 2013); Hardangerfjord (Skilbrei *et al.*, 2010), Masfjord (Olsen and Skilbrei, 2010; Skilbrei, 2010a) and Altafjord (Chittenden *et al.*, 2011) close to the surface for weeks or months.

The recapture rates of adult Atlantic salmon were lower on the coast and zero on the outermost coast. The fish probably disperse more rapidly in more open systems than in fjords. Moreover, fishing effort is probably lower on the outer coastline, compared, for example, with the Hardangerfjord basin, where there are many recreational fishers (Skilbrei and Jørgensen, 2010), or in the Altafjord, where a bagnet fishery operates throughout summer (Chittenden *et al.*, 2011). A reduced chance of recapture after escape from exposed localities than from partly enclosed fjords has been proposed as one of the reasons for the lack of clear evidence of a greater prevalence of escapes in the Atlantic salmon catch in the years immediately following reported escape events in Scotland (Green *et al.*, 2012).

Our experimentally escaped adult Atlantic salmon rarely survived for a year or longer in the wild. Only 0.07% of released adults were reported to have been recaptured after one year, and 0.01% after two years. This was surprising given the energy status of cultured fish of this size, which might have been expected to keep them alive for a long period of time. However, our results are in agreement with earlier releases of adult salmon from Norwegian and Scottish fish farms (Hansen, 2006; Hansen and Youngson, 2010). High fishing mortality during the first months after fjord releases significantly reduced the numbers of tagged fish, which by itself will have lowered the probability of long-term survival. It is likely that the adult escapees experienced high natural mortality, but the present study was not designed to assign a cause of death. Hansen (2006) suggested that adults escaping in late autumn are transported with the currents to cold Arctic waters, where they do not survive the winter. Mortality during the second year in the sea (from 1 to 2 SW salmon) has been estimated to be as high as 65% in sea-ranching experiments (Jonasson *et al.*, 1994), so a large proportion probably die of natural causes, e.g. predation by seals (Whoriskey *et al.*, 2006). Escaped Atlantic salmon have been found on the feeding grounds in the Norwegian Sea and appear to feed on a variety of natural prey (Jacobsen and Hansen, 2001), but it is still not known to what extent adult escapees manage to switch to natural prey, or how this ability influences their long-term survival in the wild. Farmed rainbow trout *(Oncorhynchus mykiss)* that escape close to the smolt stage appear to switch more easily to natural food items than larger fish that try to feed on a variety of ingestible items at the surface (Rikardsen and Sandring, 2006; Skilbrei, 2012). Analysis of the stomach contents of escaped Atlantic salmon captured in coastal areas has shown that 60–96% of the fish had empty stomachs (Hislop and Webb, 1992; Soto *et al.*, 2001; Morton and Volpe, 2002; Abrantes *et al.*, 2011), and fatty acid profiling has indicated that adult escapees failed to switch to natural prey (Olsen and Skilbrei, 2010; Abrantes *et al.*, 2011).

The low long-term survival rates of adult escapees lead us to conclude that they have a better chance of entering rivers if they mature sexually during the same year they escape. The physiological maturity of the fish at the time of escape is influenced by earlier environmental conditions, production regime, and hereditary factors (Hansen *et al.*, 1992; Gjerde *et al.*, 1994; Taranger *et al.*, 2010). The hormonal and physiological maturation process is initiated several months before the gonads enlarge, and the fish develop external and other characteristics of maturity (review by Taranger *et al.*, 2010), so an escapee that is immature according to the quality classification in the aquaculture industry may well be fully mature later in the same year. We have not found good documentation of the expected incidence of sexual maturity in Norwegian farmed salmon during the second autumn in the sea, but a range of 0–11 % has been observed in experimental groups (G. L. Taranger, pers. comm.). Adult escapees may enter nearby rivers within days of being released (Heggberget *et al.*, 1993). Escaped farmed Atlantic salmon often enter rivers during autumn (Gausen and Moen, 1991; Fiske *et al.*, 2006), and these can be identified in rivers based on morphological indicators such as rounded and eroded tail and fins (Lund *et al.*, 1991; Walker *et al.*, 2006; Erkinaro *et al.*, 2009), which fits with the expectation that many will have escaped relatively recently from netpens. Continued farming through adulthood greatly increases environmentally induced phenotypic divergences between farmed and wild salmon (Fleming *et al.*, 1994; Solberg *et al.*, 2013).

We have developed a novel approach to estimate numbers of escaped farmed salmon, revealing a large discrepancy between the official statistics in the period 2005–2011 and the estimates presented here. However, the magnitude of the discrepancy remains uncertain. There are two main sources of uncertainty. The official Norwegian statistics for catches of escaped farmed salmon are incomplete, particularly for the marine catches (see below). The predictions naturally depend on the degree of underreporting, but they are not very sensitive. For eightfold underreporting (700%), predicted total escapees increase by about 57% (Figure 6; see Supplementary material, Figure S1). This relatively modest sensitivity is partly explained by the increase in the proportion of discarded replicates, in effect compensating for the increase in marine catches by shifting mean recapture probabilities (see Supplementary material, Figures S2 and S3). This reflects the other source of uncertainty: recapture probabilities. This uncertainty stems not only from normal observation uncertainty, but also from the underlying heterogeneity in recapture probabilities, that is, variability in the context in which fish escape (exact timing and location of the escape as well as the life stage of escaping fish). For these reasons, we see the main value of the new method in providing a complementary way to assess the quality of the existing framework for monitoring salmon escapements, rather than providing an accurate assessment of escapements.

Our data suggest that the official Norwegian statistics for catches of escaped farmed salmon in the sea are very incomplete, mostly because most of the escapees are caught by anglers or gillnetted by recreational fishers who are not obliged to report the catch. Contributing to this are the restriction of the official sea fishery to mid-summer, that most of the escapees are reported to have escaped during the winter half-year (77% from 2006–2012; http://www.fiskeridir.no), and the fact that the report rate from the autumn fishery targeting escaped farmed salmon is unknown, but possibly low. Furthermore, recapture campaigns are mobilized after large escaped events, but the recaptures are not summarized in official statistics. For these reasons, the discrepancy between official figures and the actual catch will be large for weakly migratory adult salmon that escape during autumn and lower for smolt and post-smolt escapees, as their spawning migration coincides with the traditional fishery for wild salmon.

Estimates of the total numbers of escapees based on official fishery statistics are, therefore, surely too low. The alternative estimate, based on eightfold increase in sea catches, may, on the other hand, be too high if fishing effort in the two main fjord systems studied in this study is higher than the average fishing pressure along the coast. We assume that the most probable estimate would lie between the two estimates ,but closer to the latter. In either case, our estimates of the total number of escapees from 2005 to 2011 are well above the official statistics, suggesting that a high proportion of farmed Atlantic salmon that escape are not reported by the fish farmers. It is not very likely that major escape incidents, e.g. when floating structures break up during storms or ships collide with fish farms, go unreported. In addition to some relatively large unreported escape events (Glover *et al*., 2008; Glover, 2010), we suggest that smaller unnoticed or unreported escapes (so called "trickle escapes") make up a significant proportion of escapes not included in the official statistics. This is in accordance with experiences with salmonid farming in Chile (Sepúlveda *et al*., 2013), and with observations showing that escaped farmed salmon appear to stem from multiple sources (Skilbrei and Wennevik, 2006; Zhang *et al*., 2013).

Very few reports on smolt and post-smolt escapes have been filed (~4% of total escape reports), so the gap between reported and estimated escape numbers is largest for young fish. Escapes of smolts and post-smolts have been identified as an environmental hazard by Norwegian authorities, partly because salmon released as smolts that have survived for longer periods in the wild are reported to compete more effectively on the spawning grounds than recently escaped salmon (Fleming *et al*., 1996, 1997). In order to minimize the risks, national regulations regarding operational procedures in aquaculture came into force in Norway in 2008, among them being the obligation to implement a risk analysis of handling and transporting smolts, and to ensure that the mesh size used in netpens for post-smolts is correctly adapted to the size of the fish they contain (e.g. Regulation 2008-06-17 No. 822). The few reports of smolt and post-smolt escapes also contrast with the monitoring of wild and escaped salmon in Norwegian rivers using scale analysis, which has demonstrated that the fish are a mix of young (smolts and post-smolts) and adult escapees (Sægrov and Urdal, 2006). Recently, fatty acid profiling has been improved to provide reliable data on salmon dietary history (Olsen *et al*., 2013). The method is being applied to monitor the escape history of escaped farmed salmon in rivers. Preliminary results show that ~30% had escaped as smolts and post-smolts (unpublished data). Both the fish farmers and the Directorate of Fisheries have a high focus on fish escapees, and measures to prevent smolt escapes and technical failures (www.fiskeridir.no) are already implemented. In cases of unknown escapes, DNA tracing are used with success (e.g. Glover, 2012). Our study simulated actual escapes in 2005–2011, and the new measures implemented might have improved the unnoticed escapes of smolts. However, our study has documented that even more effort has to be put into preventing fish from escaping.

In principle, our modelling approach could also be used to estimate yearly numbers of escapees. This would require allocating captures to the year of escape (not necessarily the same as the year of capture, see Figure 4). Another important challenge is in the uncertainty of recapture probabilities. Our estimates represent aggregates, covering a range of different situations. In a certain year, a few escape events may dominate, and the recapture estimates used here might not be representative. Estimation at the annual level might, therefore, lead to larger biases in the results than estimation over longer time-scales where this uncertainty is partly averaged out. Nevertheless, the new method can provide a useful way for interpreting annual recapture statistics.

Life stage, physiological status, and time and site of escape have clear implications for the probabilities of recapture in different fisheries in the sea and freshwater, as well as for the timing and probability of sexually mature escapees entering rivers. For example, escaped smolts and post-smolts do not recruit to the traditional sea and river fisheries before they reach maturity after one or more years in the wild. In contrast, escapes of immature adults during autumn may result in high recapture rates in the sea shortly after the escape, especially if there is a local fishery designed to catch them, but with relatively few mature adults migrating into rivers. Because of this complexity, neither the sea nor the river fishery will mirror the size or age distribution of the annual Norwegian salmon farming industry cohort of escaped farmed salmon at the time of escape. Since it is generally accepted that escaped farmed salmon represent a significant threat to the genetic integrity of wild populations (Naylor *et al.*, 2005; Fergusson *et al.*, 2007; Glover *et al.*, 2013), we suggest that more detailed monitoring of the escape history of the farmed salmon that enter rivers should be implemented. Improved knowledge of the origin of these fish, especially with respect to their age and size at escape, could provide authorities and the aquaculture industry a better basis in which to develop more effective strategies to mitigate the problems caused by escaped farmed salmon.

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Table 1. Release/recapture data. Number (*n*) and mean weight (s.d.) at release, date of release of post-smolt, large (L.) post-smolt, out-of-season-post-smolts, and adult fish. The number of days from release to recapture of 90% of the recaptures of postsmolt and adult fish are also shown. Recaptures are split into fish that were caught during the following months (0+), or recaptured after 1, 2, or 3 years (1SW, 2SW and 3SW salmon), and also into recaptures in rivers (R) or in sea (S). References to papers describing post-release behaviour or showing parts of the data are listed.

Site no.	Fish stage	*n*	Weight (kg)	Release date	90% catch	Recapture (*n*) 0+ R	0+ S	1SW R	1SW S	2SW R	2SW S	3SW R	3SW S	All *n*	All %	Reference
1	Adult	850	2.82 (1.02)	14.06.2005	46	4	53	1	2					60	7.06	
2	Post-smolt	1 000	0.20 (0.03)	21.06.2005							1			1	0.10	
2	Adult	502	1.17 (0.17)	09.11.2005											0.00	
3	Post-smolt	1 000	0.09 (0.02)	22.06.2005					5		3		1	9	0.90	
3	L. post-smolt	495	0.58 (0.10)	11.10.2005					1		1			2	0.40	
3	Adult	301	2.94 (0.43)	21.06.2006											0.00	
4	Post-smolt	1 000	0.21 (0.09)	12.07.2005					2		2		2	6	0.60	
4	Adult	300	2.00 (0.43)	28.06.2006	17	2	15							17	5.67	
5	Post-smolt	627	0.09 (0.02)	17.06.2005			1							1	0.16	
5	Adult	350	1.80 (0.32)	27.06.2006	26	1	13		2					16	4.57	
6	Post-smolt	1 936	0.05 (0.01)	27.05.2005				1	2		2		1	6	0.31	Skilbrei (2010b)
6	Post-smolt	2 002		10.06.2005				2	7	1	6		3	19	0.95	Skilbrei (2010b)
6	Post-smolt	1 978	0.07 (0.02)	24.06.2005				4	8		3	1	3	19	0.96	Skilbrei (2010b)
6	Post-smolt	2 000		08.07.2005				1	10	1	4		3	19	0.95	Skilbrei (2010b)
6	Post-smolt	2 000	0.09 (0.02)	22.07.2005				1	13		3		4	21	1.05	Skilbrei (2010b)
6	Post-smolt	1 999		05.08.2005			2	1	7	1	4	1	3	19	0.95	Skilbrei (2010b)
6	Post-smolt	5 041	0.22 (0.09)	29.05.2006		1		1	3	3	7		2	17	0.34	
6	Post-smolt	5 074	0.22 (0.09)	29.05.2006					1	1	6			8	0.16	
6	Post-smolt	4 000	0.08 (0.01)	01.06.2007						3	2	1	4	10	0.25	Skilbrei (2013)
6	Post-smolt	4 000	0.08 (0.01)	05.06.2007							1	1		2	0.05	Skilbrei (2013)
6	Post-smolt	3 637	0.11 (0.03)	03.07.2007					3		1		3	7	0.19	Skilbrei (2013)
6	Post-smolt	3 391	0.19 (0.03)	03.08.2007			16						3	19	0.56	
6	L. post-smolt	3 034	0.43 (0.09)	05.10.2007	38	2	354				1	2	2	361	11.90	
6	Post-smolt	3 700	0.16 (0.03)	16.05.2008								2		2	0.05	Skilbrei (2010a, 2013)
6	Post-smolt	2 000	0.24 (0.07)	26.06.2008			3			1	4	1	2	11	0.55	Skilbrei (2010a, 2013)
6	L. post-smolt	2 000	0.51 (0.19)	14.08.2008	81		290				2		2	294	14.70	Skilbrei (2010a); Olsen and Skilbrei (2010)
6	Adult	2 000	0.95 (0.27)	17.09.2008	39		700				1			701	35.05	Skilbrei (2010a); Olsen and Skilbrei (2010)
6	Adult	1 780	1.56 (0.42)	27.10.2008	151		532							530	29.78	Skilbrei (2010a); Olsen and Skilbrei (2010)
6	Post-smolt	3 997	0.14 (0.05)	15.05.2009				2	3	1	3	2		11	0.28	Skilbrei (2013)
6	Post-smolt	3 999	0.15 (0.05)	18.06.2009						1				1	0.03	Skilbrei (2013)
6	Post-smolt	3 991	0.16 (0.05)	21.05.2010				11	10	3	2			26	0.65	
6	Post-smolt	3 800	0.16 (0.06)	29.06.2010				5	10	1	3		1	20	0.53	
6	Out-of season	3 989	0.10 (0.02)	25.10.2007								1		1	0.03	Skilbrei (2013)
6	Out-of season	4 260	0.15 (0.03)	03.12.2007											0.00	Skilbrei (2013)
6	Out-of season	3 997	0.06(0.006)	24.09.2008											0.00	Skilbrei (2013)
6	Out-of season	2 992	0.11 (0.02)	4.11.2008											0.00	Skilbrei (2013)

6	Out-of season	1 790	0.22 (0.03)	17.12.2008										0.00	Skilbrei (2013)
6	Out-of season	5 945	0.10 (0.01)	7.11.2009										0.00	Skilbrei (2013)
7	Post-smolt	1 000	0.19 (0.04)	08.06.2005										0.00	
7	Adult	496	0.96 (0.25)	13.10.2005	31	1	33						34	6.85	
7	Adult	468	5.45 (1.35)	25.09.2006	27	1	199		1				201	42.95	Skilbrei and Jørgensen (2010)
7	Adult	515	1.56 (0.48)	27.09.2006	27		188						188	36.50	Skilbrei and Jørgensen (2010)
7	Adult	132	2.8 – 4.3	2005 - 06	47		50						50	37.88	Skilbrei *et al.* (2009), Skilbrei *et al*. (2010)
8	Post-smolt	1 000	0.12 (0.03)	14.06.2005				1			3		4	0.40	
8	Adult	280	2.72 (0.78)	05.07.2006	46	5	14						19	6.79	

Table 2. Parameterization of equation (1) for the Monte Carlo simulations.

Variable	Explanation	Distribution or value	Source
N_{sea} N_{river}	Estimated catch in 2005–2011 in the sea and in rivers	lognormal $(\mu = 24039, \sigma = 11535)$ lognormal $(\mu = 5529, \sigma = 892)$	Anon. (2013), Figure 4.4; Statistics Norway
$p_{postsmolt \to sea}$ $p_{adult \to sea}$ $p_{postsmolt \to river}$ $p_{adult \to river}$	Recapture probabilities of post-smolts and adults in the sea and in rivers	$\text{uniform}(0.001, 0.005)/p^{rep}$ $\text{uniform}(0.01, 0.010)/p^{rep}$ $\text{uniform}(0.001, 0.005)/p^{rep}$ $\text{uniform}(0.001, 0.010)/p^{rep}$	This paper This paper This paper This paper
p^{rep}	Probability of marked salmon not being reported	$(1 - p^{mark\ lost})(1 - p^{unreported}) = (1 - 0.1)(1 - 0.33) = 0.603$	Skilbrei and Jørgensen (2010)

Table 3. Classification of percentage recapture rate (*n*) of released adult salmon according to the geographical location of the release sites (on outer coast, coast, or in fjord).

Site	Locality type	Released (*n*)	0+ % Sea	River	Total	1–2SW %
2	Outer coast	502	0	0	0	0
3	Outer coast	302	0	0	0	0
4	Coast	300	5.00 (15)	0.67 (2)	5.67	0
5	Coast	350	3.71 (13)	0.29 (1)	4.00	0.57 (2)
8	Coast	280	5.00 (14)	1.79 (5)	5.79	0
1	Altafjord	850	6.24 (53)	0.47 (4)	6.71	0.35 (3)
6	Hardangerfjord	1 659	32.54 (1 230)	0	32.54	0.06 (1)
7	Masfjord	3 780	30.20 (504)	0.18 (1)	32.38	0.03 (1)
Total		8 023	22.8 (1 829)	0.16 (13)	22.96	0.09 (7)

Table 4. Overview of the results where release groups are sorted into size groups (out-of-season smolts, spring post-smolts, large post-smolts, and adult fish). The time of recapture is given by the number of years post-release.

Released (*n*)	Size (kg)	Type	Recapture rate % (*n*)				
			0+	1SW	2SW	3SW	1–3SW
22 973	<0.23	Out-of-season	0.00	0.00	0.00	0.004 (1)	0.004%
64 172	<0.23	Spring post-smolts	0.04 (23)	0.18 (114)	0.12 (78)	0.07 (45)	0.36%
5 529	≈0.50	Large post-smolts	11.68 (646)	0.02 (1)	0.07 (4)	0.11 (6)	0.20%
8 023	>0.90	Adult	22.95 (1 841)	0.07 (6)	0.01 (1)	0 (0)	0.09%

Table 5. Numbers of escaped farmed salmon based on reports to the Directorate of Fisheries 2005–2011 (Source: http://www.fiskeridir.no). The 2006–2011 data are classified into the assumed lifestage according to date and mean size at escape where pre-smolts <0.012, 0.02 kg < smolts and post-smolts <0.3, 0.35 kg <large post-smolts <0.6, 0.02 kg <autumn (out-of-season) smolts and post-smolts <0.2, 0.4 kg <large autumn post-smolts <0.6 kg, and adult >0.6 kg. Smolts and post-smolts escaped during spring and summer, large post-smolts and autumn smolts during autumn, whereas autumn post-smolts escaped during spring.

Year	Presmolts	Smolts and post-smolts	Large post-smolts	Out-of-season smolts and post-smolts	Large out-of-season post-smolts	Adults	Unknown size	Total
2005							717 000	717 000
2006		5	1 192	45 801		868 557	2 000	917 555
2007	36 000	8 757		500	30 000	197 378		272 635
2008	890	2 300		37 500		72 038		112 728
2009	840	5 732	70	1 440	81 074	105 885		195 041
2010	25 782	66 200		5 052		209 748		306 782
2011	500		114 134	17 002		235 606	2	367 244
Total *n*	64 012	82 994	115 396	107 295	111 074	1 689 212	719 002	2 888 985
Yearly mean	10 669	13 832	19 233	17 883	18 512	28 153		412 712
% of total	2.95	3.82	5.31	4.94	5.11	78.15		100

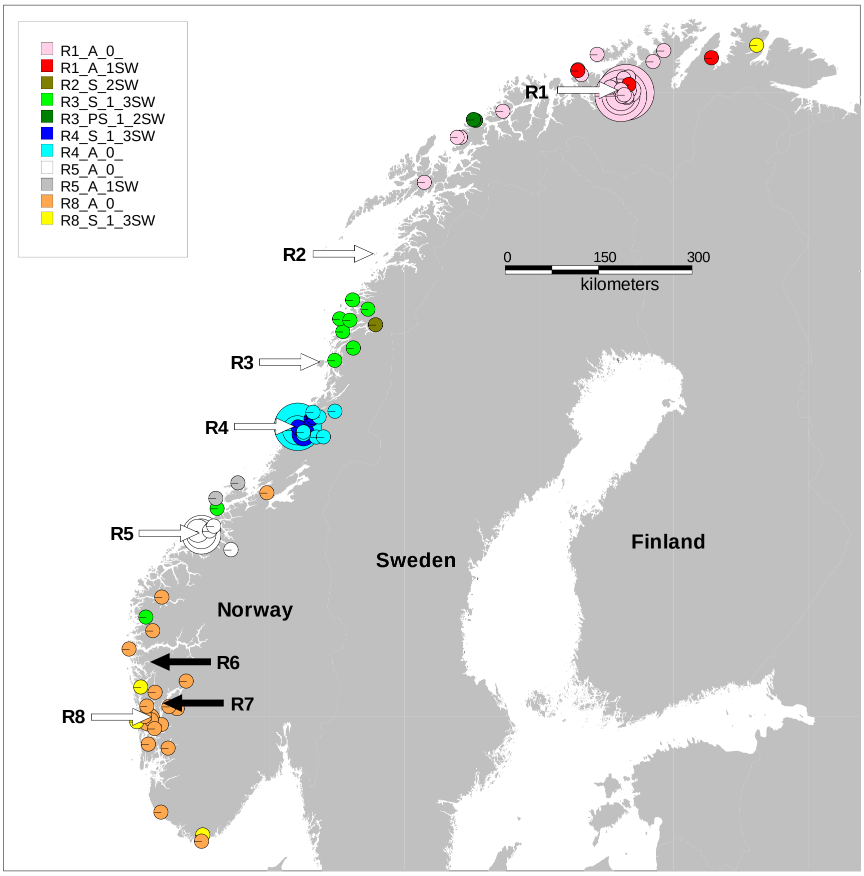

Figure 1. Recaptures of adult salmon from releases of post-smolts and adult at release sites R1, R2, R3, R4, R5, and R8 (white arrows). Sizes of pies vary according to the number of fish recaptured, from 1 to 10. Location of release sites R6 and R7 are also shown (black arrows).

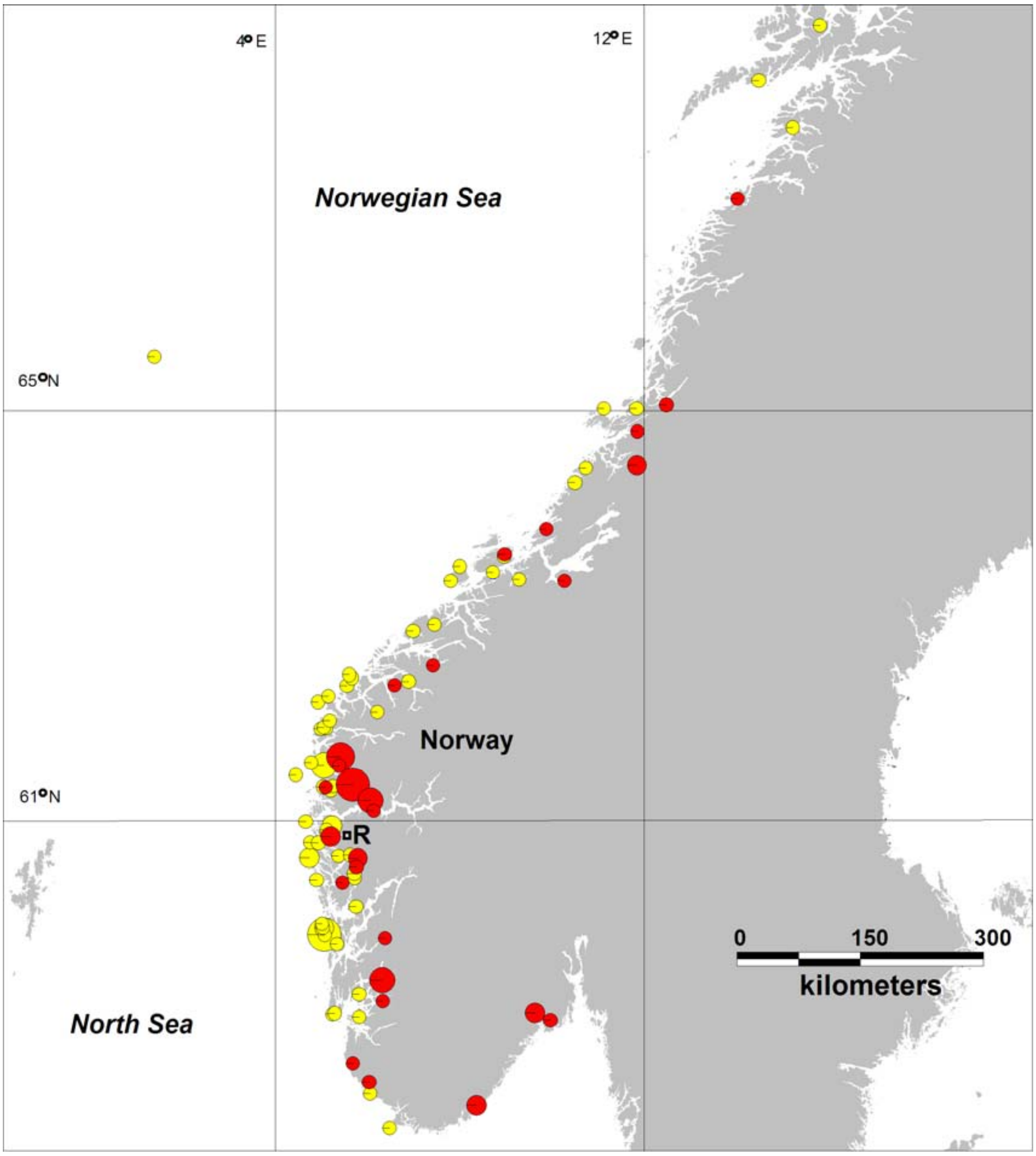

Figure 2. Recaptures of 1–3SW salmon during 2006–2013 in sea (yellow pies) and freshwater (red pies) after releases of post-smolts at Site 6 (R) from 2005 to 2010. Fish recaptured in sea and rivers in the vicinity of the release site (<6 km distance; 49% of total catch) are not included in the figure. Sizes of pies vary according to the number of fish recaptured, from 1 to 5 individuals.

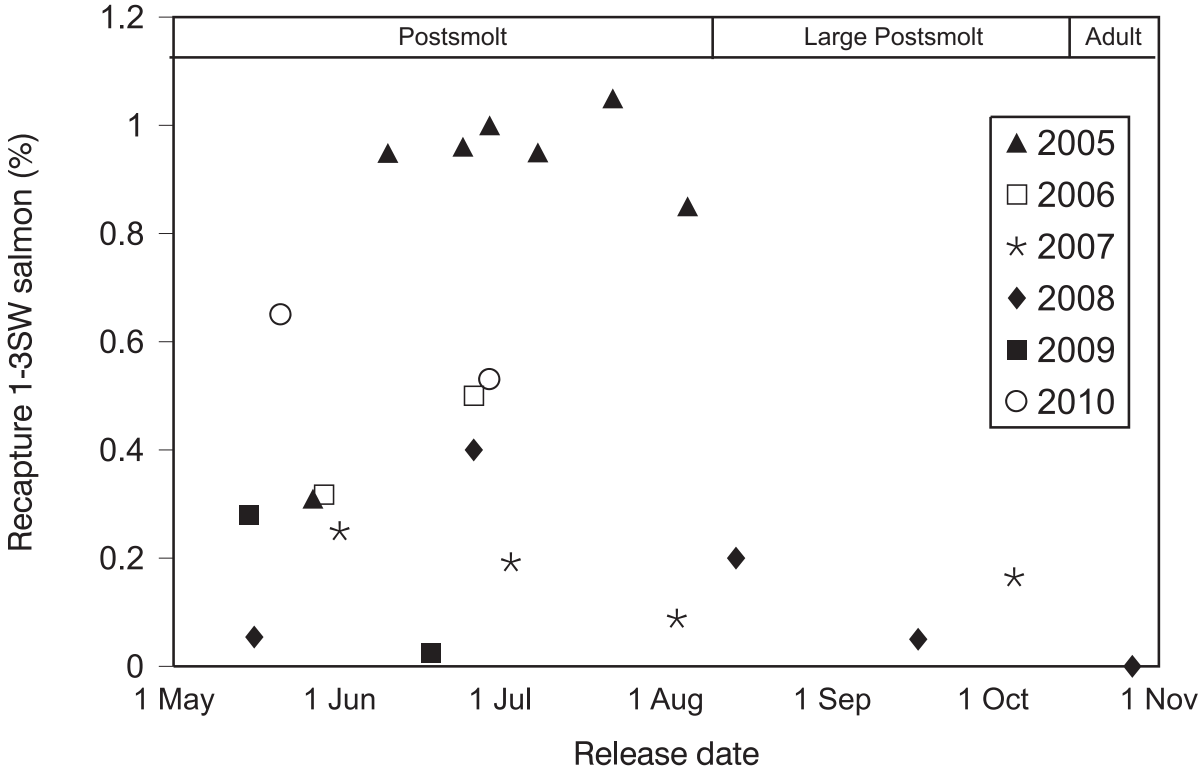

Figure 3. Recapture rates of 1–3 SW salmon recaptured during 2006–2012 released as post-smolts or adults at Site 6 on various dates from 2005 to 2010.

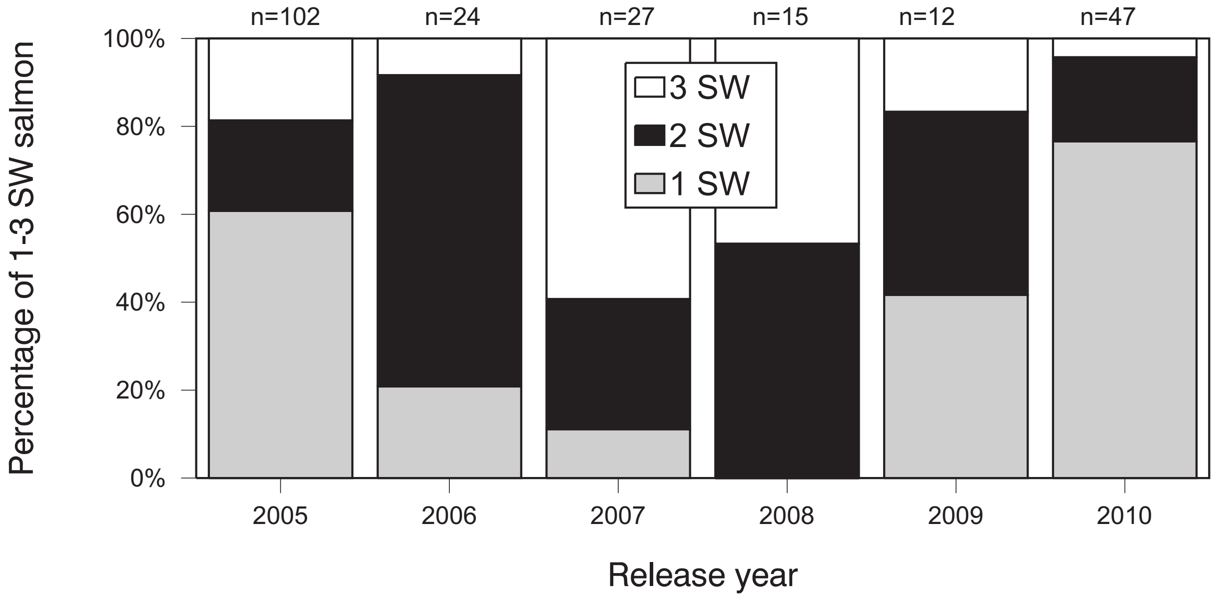

Figure 4. Percentages of 1–3SW salmon among the recaptures of the post-smolts released from Site 6 during 2005–2010. Numbers of fish are given above the bars.

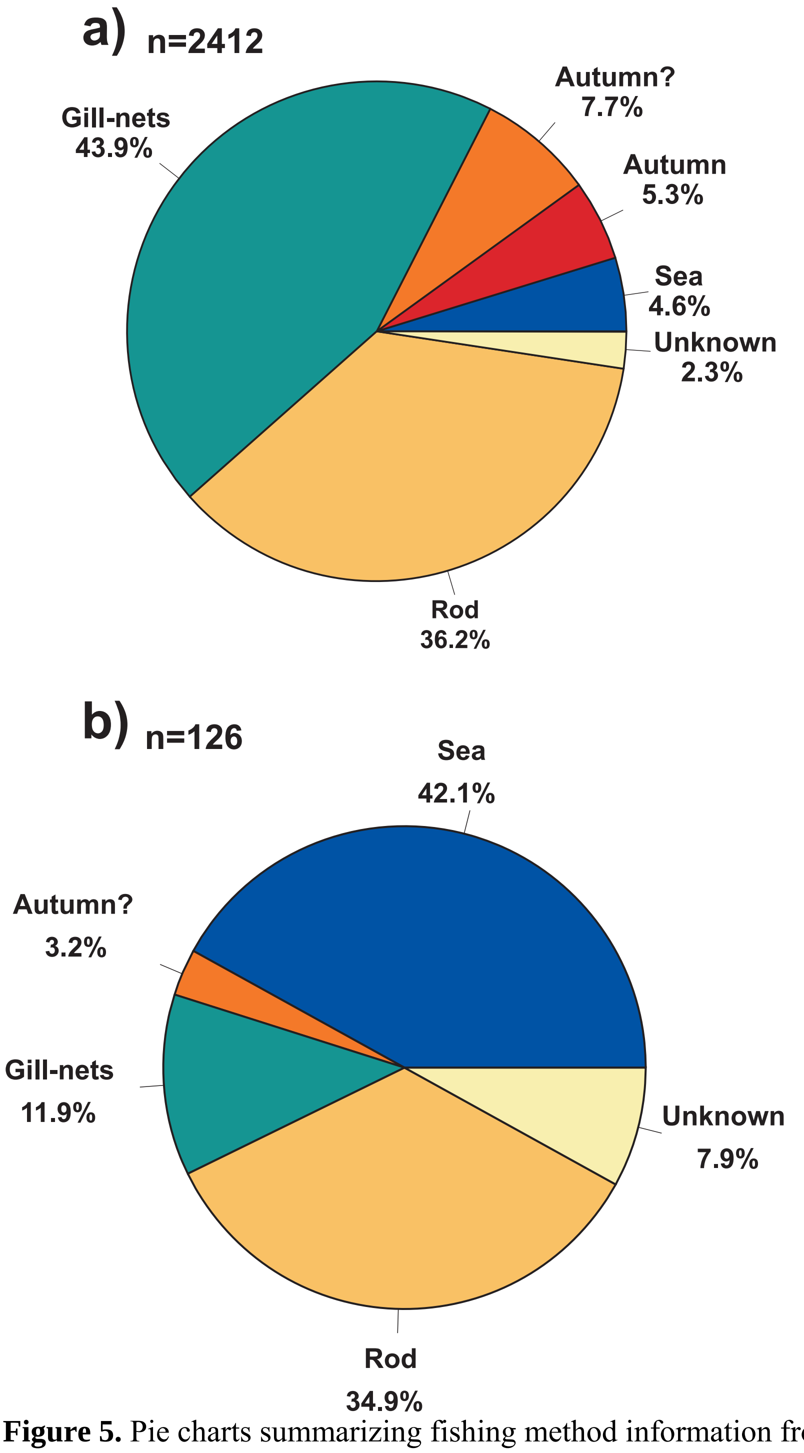

Figure 5. Pie charts summarizing fishing method information from fishers reporting recapture of tagged salmon in sea where (a) shows all recaptures in sea and (b) only includes the catch of 1–3 sea-winter salmon released as post-smolts. "Sea" is traditional sea fishery for wild salmon during summer, "Autumn" is fishery targeting escaped farmed salmon, "Rod" is angling and trolling, and "Gillnets" is gillnetted fish not included in the other categories. See text for more detailed descriptions of the categories.

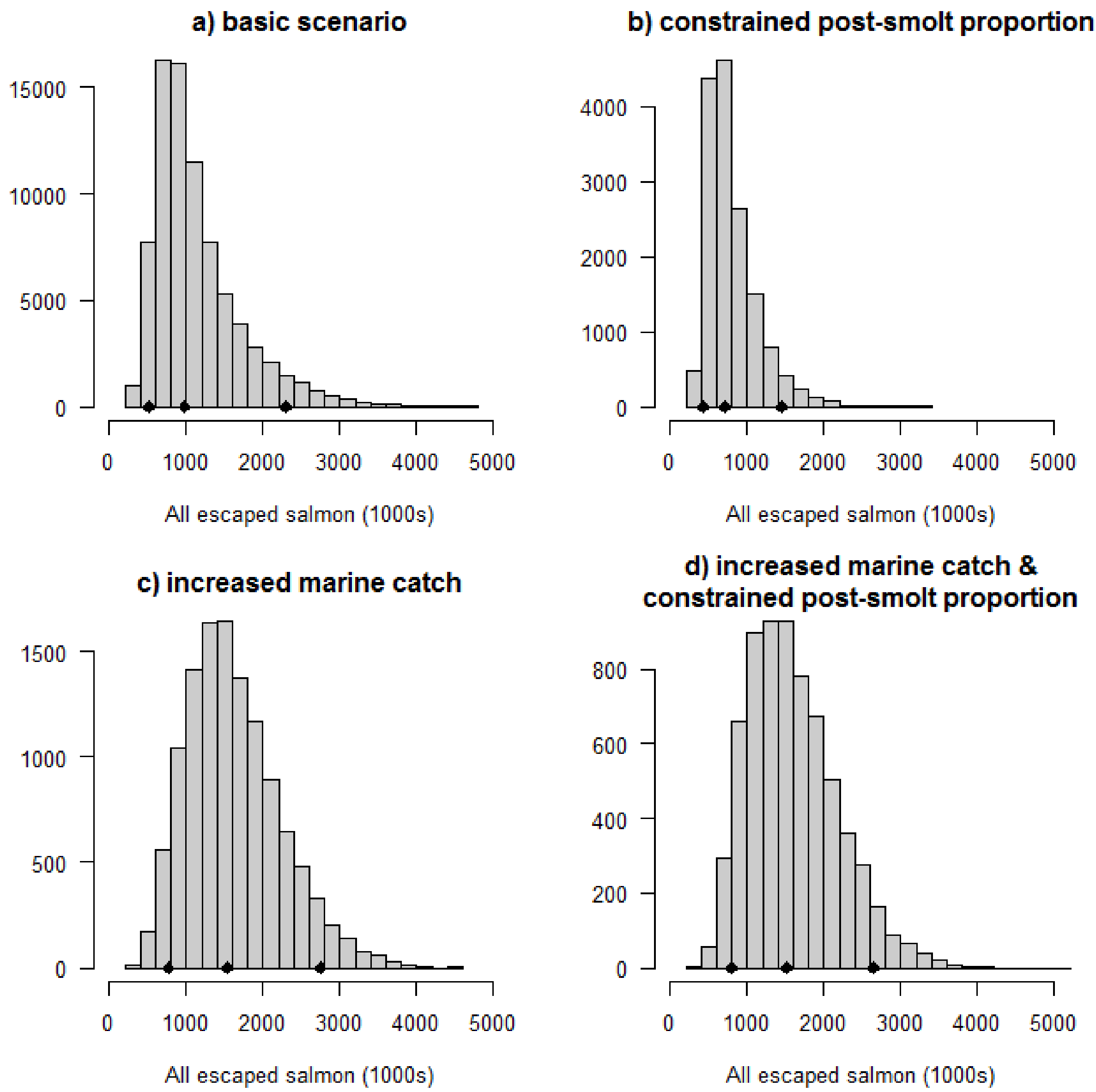

Figure 6. Estimated numbers for annually escaped farmed salmon (spring post-smolts and adults) based on the estimated numbers captured of escaped farmed salmon in rivers and sea in 2005–2011 and recapture probabilities. Histograms illustrate uncertainty in the estimates caused by uncertainty in reported catches and recapture probabilities. Diamonds on the x-axis correspond to 5, 50, and 95 percentiles. See text for the explanation of the scenarios.

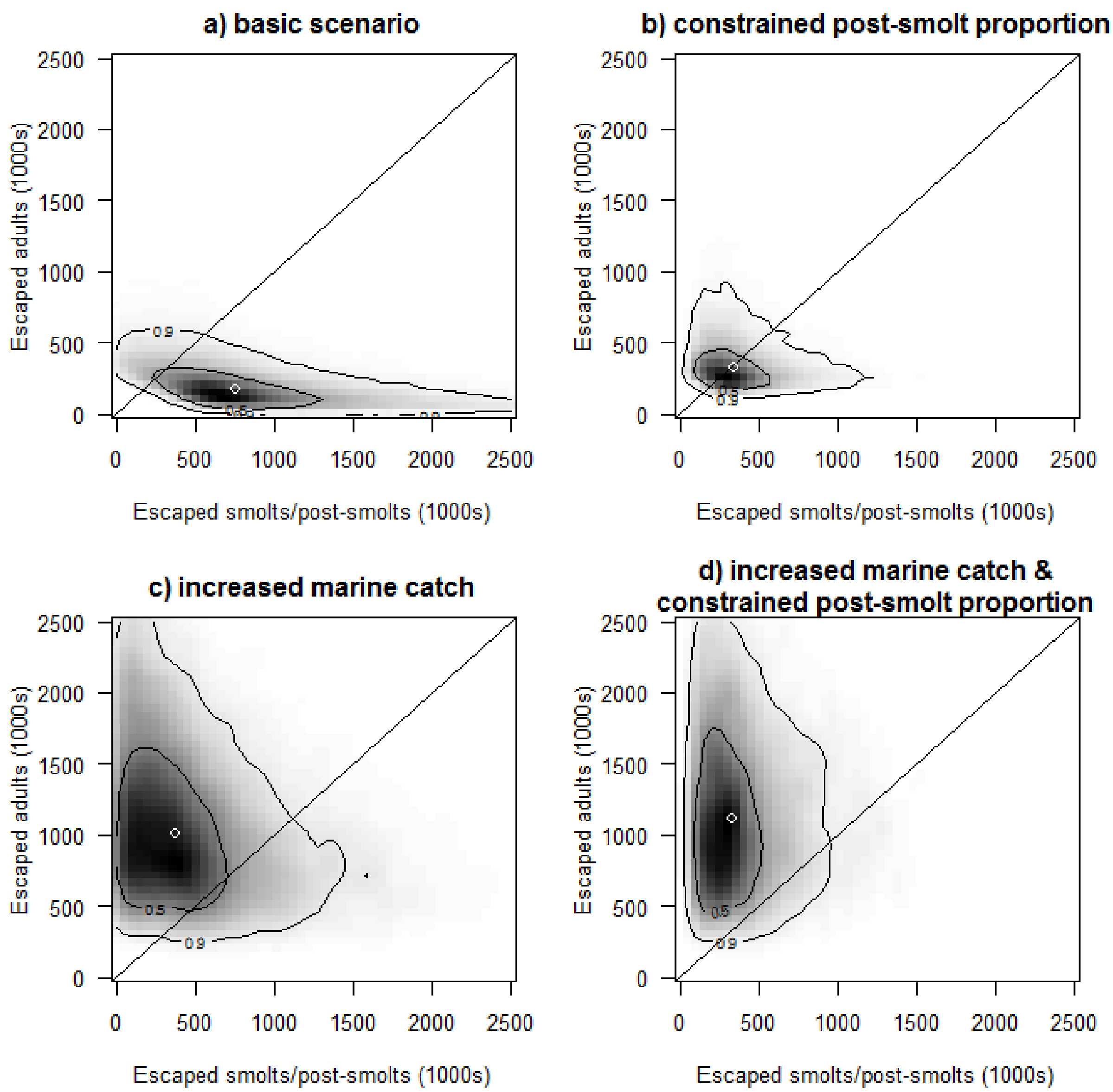

Figure 7. Two-dimensional density distributions for salmon escaped as post-smolts and adults. White circles indicate the median estimated, and contour lines encircle 50 and 90% of replicates. Diagonal corresponds to equal numbers of post-smolt and adult escapees.

Supplementary material

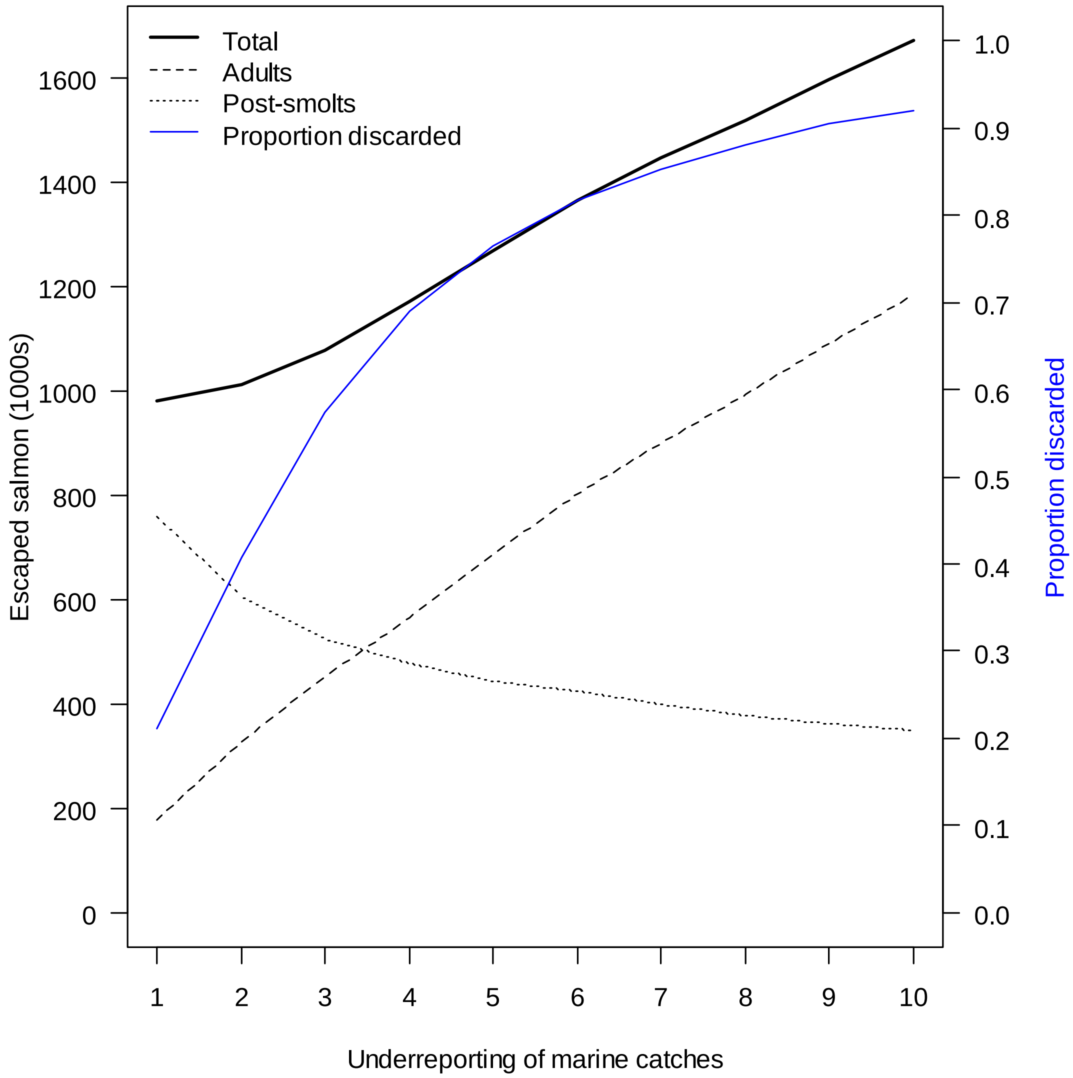

Figure S1. Sensitivity of the results on the degree of underreporting of marine catches. The more serious the underreporting, the higher the predicted total numbers of escapees. This increase is due to increased numbers of adult escapees, whereas post-smolt escapees are declining. Increasing underreporting also leads to a higher proportion of replicates yielding biologically impossible results. The average slope of the curve for total numbers is about 83 000. In the main text, underreporting factors 1 (= no underreporting) and 8 were used.

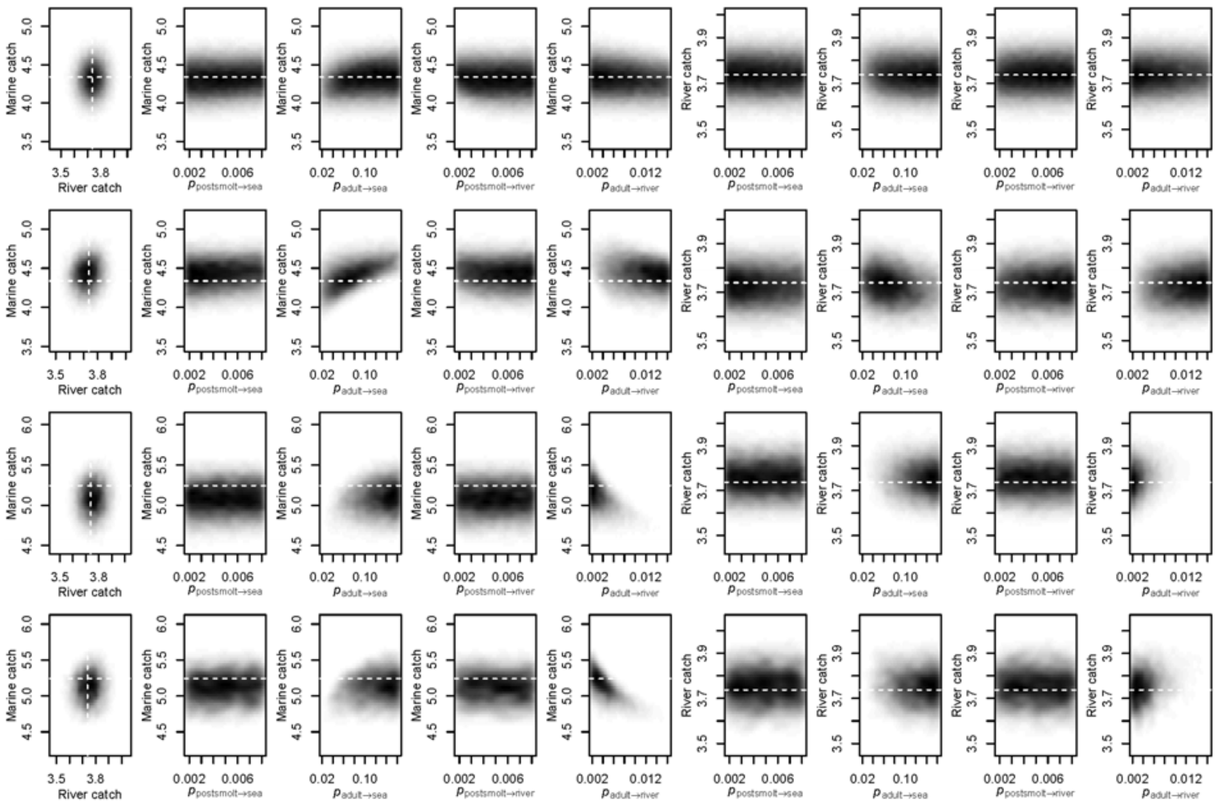

Figure S2. Two-dimensional probability density distributions of catches and recapture probabilities in replicates that give biologically meaningful results. Rows correspond to the four scenarios (basic scenario, constrained post-smolt proportions in river catches, increased marine catch, and the combination of the latter two). Catches in the input data follow a log-normal distribution; white dashed lines indicate the mean catch. Catches are plotted log-transformed (base 10). Recapture probabilities in the input data are uniformly distributed. Deviations from the original distributions indicate that certain parameter combinations are prone to produce biologically impossible predictions.

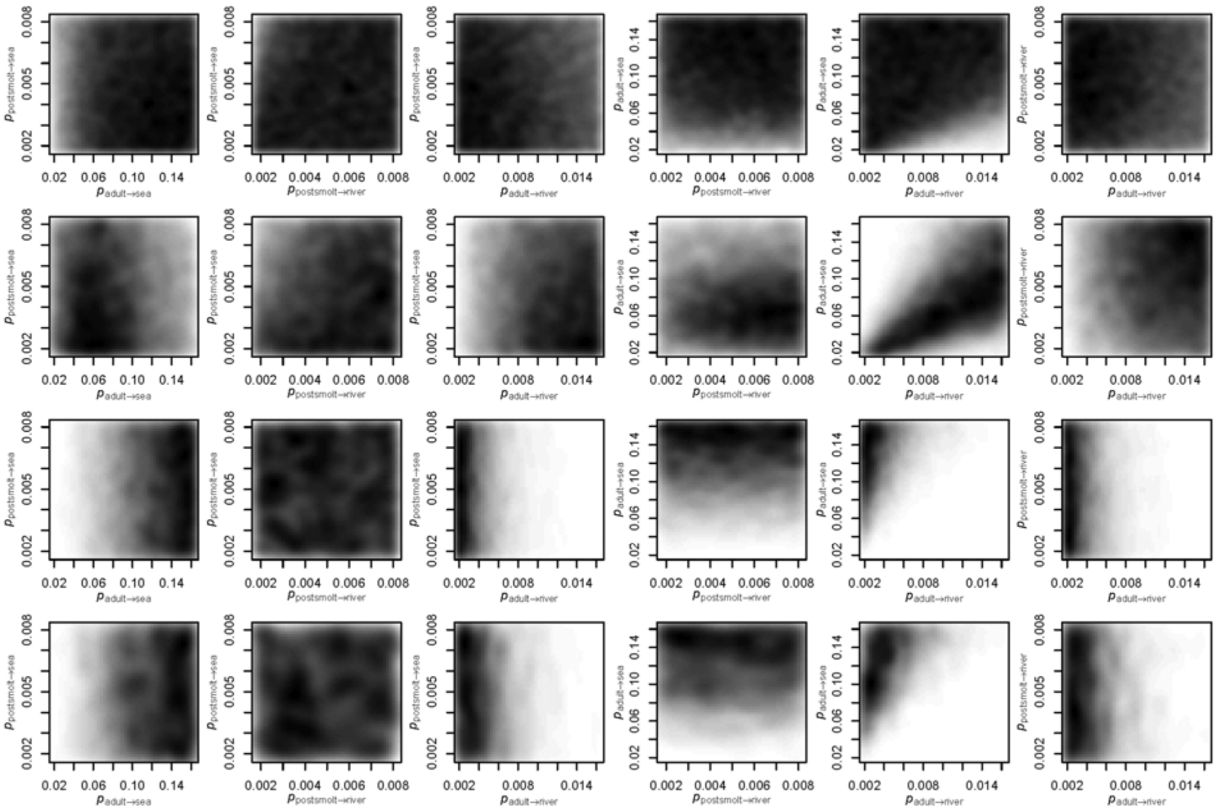

Figure S3. Two-dimensional probability density distributions of recapture probabilities in replicates that give biologically meaningful results. Rows correspond to the four scenarios (basic scenario, constrained post-smolt proportions in river catches, increased marine catch, and the combination of the latter two). Input data are uniformly distributed within the displayed rectangles. Non-uniform density distributions indicate that certain parameter combinations are prone to produce biologically impossible predictions.