

Salmon Tracking (SALT) 2020



Rapport APN-61274

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1 Sammendrag

Abstrakt

Forskningsprosjektet SalmonTracking 2020 (SALT2020) ble etablert i 2017 xmed formål å forbedre kunnskapsnivået om de ville ressursene av laks og sjørøret i området fra Karmøy til Stad tette kunnskapshull knyttet til Trafikklysordningen.

SalmonTracking 2020 har observert vandringsmønstre og bestandsutvikling til vill laks og sjørøret gjennom bruk av bl.a. kameraer, datachip og radiomerking, antenner i vassdrag, registreringsbøyer i fjord- og kystmiljø og bruk av el-fiske.

Prosjektet har lagt vekt på å avklare når laksen og sjørøreten vandrer ut av/inn i elvene, hvor den svømmer, hvor fort og dypt den svømmer. Herunder bl.a. å måle andelen tilbakevandrende laks og sjørøret.

Forskningen viser at villaksen går ut av fjorden på et tidspunkt der det er mindre lus enn det overvåkingen med bl.a. trål etter villsmolt har vist. Dette kan tyde på at lus har en annen påvirkning på den ville laksesmolten enn det en til i dag har ment.

Forsøkene med akustiske merker (radiomerker) har også vist at vassdrag med innsjøer og en øvre/nedre elvestrekning, har avvikende utvandringstidspunkt med opptil 2-3 uker.

De foreløpige funnene kan tyde på at *trafikklyssystemet* har hatt et for dårlig fundament. De nye forskningsresultatene kan bidra til å styrke dette.

Abstract

The research project SalmonTracking 2020 (SALT2020) was established in 2017, and aims to improve the level of knowledge about the wild resources of salmon and sea trout in the area from Karmøy to Stad. At the same time, the purpose is to close knowledge gaps related to the Traffic Light System currently used to control salmon farming production along the Norwegian coast.

SalmonTracking 2020 observes migration patterns and population development of wild salmon and sea trout through the use of cameras, computer chips and radiolabelling, antennas in watercourses, registration buoys in the fjord and coastal environment and the use of e-fishing.

The project focuses on clarifying when the salmon and sea trout migrate out of/into the rivers, where they swim, how fast and deep they swim, including measuring the proportion of migratory salmon and sea trout.

The project findings show that wild salmon leave the fjord at a time when there are less lice than the monitoring of wild smolt has shown. This may indicate that lice have a different influence on the wild salmon smolt than previously assumed.

The experiments with acoustic marks (radiotags) have also shown that watercourses with lakes and an upper/lower stretch of river have deviant emigration times by up to 2-3 weeks.

The preliminary findings may indicate that the *Norwegian Traffic Light System* has had too poor scientific foundation. The new research results may contribute to strengthening this.

Prosjektleder

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Kvalitetskontroll

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De vitenskapelige arbeidene tilknyttet arbeidspakkene i prosjektet er skrevet på engelsk (for publisering i peer-review journaler). Denne sluttrapporten er derfor i store deler på engelsk.

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2 Bakgrunn

Ideen bak SalmonTracking 2020 er å få fram ny og konkret viten om vill laksefisk og sjøørret i Produksjonsområde 3 (PO3), koordinere denne, se på mulighetene til å bygge en modell for overvåking og publisere funnene i en mer helhetlige sammenheng.

Høsten 2016 startet havbruksaktørene i dagens produksjonsområde 3 (PO3) et aktivt arbeid langs to hovedlinjer:

1. Hvordan styrke fiskehelsesituasjonen i PO3.
2. Hvordan øke kunnskapsnivået om vill laks og sjøørret i PO3.

PO3 Kunnskapsinkubator ble valgt som felles plattform for satsingen der alle næringsaktørene deltok. Det ble valgt et eget styre og arbeidet ble igangsatt.

I juni 2018 ble næringsaktørene i PO3 enige om felles ambisjoner knyttet til ovennevnte Punkt 1 og som bl.a. omhandler smitteveier, lus, svinn, strømmodellering mv. Ambisjonene bygde videre på et godt samarbeidsklima aktørene har bygget opp seg imellom gjennom flere år.

I arbeidet med å øke kunnskapsnivået om vill laks og sjøørret ble flere forskningsinstitusjoner og enkeltforskere allerede vinteren 2017 kontaktet for konkrete råd og innspill.

Arbeidet som ble igangsatt, hadde sitt utgangspunkt i de beskrivelser og den usikkerhet som ble trukket fram av «*Eksperutvalget*» og «*Styringsgruppen*» om kunnskapsgrunnlaget for det nye «*Trafikklyssystemet*». Vår hensikt er i første omgang å framskaffe mest mulig konkret kunnskap om bestandene av laks og sjøørret, og på denne bakgrunn få en bedre plattform for å vurdere mer målrettede tiltak for å styrke bestandene av vill laks og sjøørret i vårt produksjonsområde. Herunder også å skape et kunnskapsgrunnlag for senere, presise evalueringer av effekter av tiltak.

Utover i 2017 ble planene konkretisert for hvordan faktisk øke kunnskapen om vill laks og sjøørret i PO3. Planen fulgte tre hovedlinjer:

Bestandsutvikling

Hvordan få bedre kunnskap om bestandene av laks og sjøørret i utvalgte elver i produksjonsområdet. Herunder, hvordan få et klarere bilde av hvilken fisk det er som svømmer inn og ut av elvene, og således vurdere bestandsutvikling på årsklassenivå, lusebildet, innslaget av oppdrettsfisk på avveie mv.

Vandringsmønstre

Hvordan få bedre kunnskap om bevegelsesmønstret til vill laks og sjøørret i produksjonsområdet. Når svømmer laksen og sjøørreten ut av elvene, hvor svømmer den, hvor fort svømmer den, hvem er det som svømmer ut/hvem kommer tilbake/hvor kommer de tilbake, hvor oppholder fisken seg om vinteren mm. Herunder bl.a. å måle andelen tilbakevandrende laks og sjøørret.

Prematur tilbakevandring

Hvor mange sjøørreter avslutter sjøoppholdet sitt for tidlig. Er det forskjell i omfanget av denne atferden mellom geografiske områder?

Hver av hovedlinjene inneholder flere delprosjekt/-element som til sammen gir et styrket helhetsbilde i kunnskapen om vill laksefisk.

Tiltaket ble samlet vurdert til å ha en helhet som best dekket flere av de hull som *Styringsgruppen* og *Ekspertgruppen* i *Trafikklyssystemet* hadde beskrevet i sine rapporter. De er også målrettet, praktisk og kunnskapsintensive. Prosjektet fikk navnet *SalmonTracking 2020*, og følgende metoder ble lagt til grunn:

Akustisk merking

Merking av laks og sjøørret i elv og med akustiske merker for å registrere når fisken vandrer, oppholdstid i fjord/kystområde, fart, dybde, overlevelse etc. Utsett av ca. 150 radiobøyer i elve- og fjordsystemene i PO3.

PIT- merking

Merking av laks og sjøørret med «Pit-tag» for å registrere vandring inn og ut av elver. Merket har «uendelig» levetid og påvirker fisken i liten grad. Måle parametere er oppholdstid i sjøen, vandringstidspunkt, overlevelse over et helt livsløp. Utplassering av antenner i flere vassdrag i tillegg til håndholdte skannere for «stikkprøver».

Videoovervåking

Plassering av kamera i utvalgte elver i Produksjonsområdet for overvåking av bestandene av laks og sjøørret, årsklassefordeling, vandringstidspunkter mm.

El-fiske Registrere andelen prematur tilbakevandret sjøørret til elvemunninger, andelen lus pr fisk og beregne lusepåslag + remerkning av fisk med Pit-tag for senere registrering av overlevelse og vandring mm.

Innledende prosjektfase ble satt til 3 år, med mulighet for forlengelse.

Følgende institusjoner ble engasjert til å forestå det kommende forskningsarbeidet;

- NMBU/UiN/SINTEF/Inaq AS – til å gjennomføre studier knyttet til vandringstid/-hastighet/-mønster ved bruk av akustiske merker.
- Rådgivende Biologer AS – til å gjennomføre studier knyttet til vandringsmønstre, tilbakevandring, feilvandring, overlevelse samt registrering av prematur tilbakevandret sjøørret.
- Skandinavisk Naturovervåking AS – til å gjennomføre studier knyttet til bestandsutvikling fordelt på årsklasser, lusepåslag/-skader mv.

Følgende vassdrag inngår i dag i prosjektet;

Eidfjordvassdraget, Granvinsvassdraget, Mundheimselva, Tørvikvassdraget, Uskedalselva, Omvikedalselva (Storeelv) og Oselva. Selve overvåkingen av prematur tilbakevandret sjøørret skjer i ca. 16 elver totalt i PO3. Prosjektet koordineres med andre tiltak i samme område.

Arbeidet ble offisielt igangsatt 1. januar 2018, men allerede i 2017 ble to vassdrag i PO3 overvåket m.o.t. bestandsutvikling. Resultatene har kommet overraskende på alle involverte og omgivelsene da rapportene fra Granvinselva og Mundheimselva dokumenterte at bestands-situasjonen var betraktelig bedre enn det som har vært beskrevet i tidligere rapporter og i media. Det har gjort oss trygge på at *SalmonTracking 2020* vil tilføre og utvide kunnskapsgrunnlaget for vill laksefisk i PO3. Dette danner grunnlag for gjennomføring av tiltak som kan iverksettes, og videre evalueres.

Kvalitetssikring

Prosjektbeskrivelse og plan er kvalitetssikret i henhold til interne rutiner hos Akvaplan-niva og gjennom FHF's rutiner for gjennomgang av faglig og næringsmessige relevans.

3 Problemstilling og formål

Hovedmålet med prosjektet har vært å utvikle og beskrive en helhetlig modell for overvåking av de ville ressursene av laks og sjørøret i et produksjonsområderegime. Delmålene har vært:

Delmål DP1: Sette sammen delrapportene fra forskningen i PO3/PO4 i en helhet, og publisere disse nasjonalt/internasjonalt.

Delmål DP2: Gjennom det opparbeidede materialet, se på mulighet for å utvikle en helhetlig overvåkingsmodell knyttet til produksjonsområdene.

Delmål DP3: Sammenligne bestanden av sjørøret og villaks fra elvene i PO3 med tilsvarende elver/områder nasjonalt.

SalmonTracking 2020 prosjektet har observert vandringsmønstre og bestandsutvikling til vill laks og sjørøret gjennom bruk av bl.a. kameraer, datachip og radiomerking, antenner i vassdrag, registreringsbøyer i fjord- og kystmiljø og bruk av el-fiske.

Prosjektet har hatt til hensikt å avklare når laksen og sjørøret vandrer ut av/inn i elvene, hvor den svømmer, hvor fort og dypt den svømmer mm. Herunder bl.a. å måle andelen tilbakevandrende laks og sjørøret

Hvor mange og i hvilke vassdrag kommer sjørøret for tidlig tilbake, og er det områder som peker seg ut/ikke peker seg ut når det gjelder lakselusindusert prematur tilbakevandring.

Prosjektet registrerer nå bestandsutviklingen og vandringsmønstre i 10 elver i PO3 og PO4, de registrerer prematur tilbakevandring i ca. 40 elver og man overvåker både villaks og sjørøret.

Leveranser

1. Åpent oppstartsmøte med prosjektgruppe og referansegruppe (juni 2019)
2. Populærvitenskapelig artikkel/presentasjon av SALT2020 (juli 2020)
3. Presentasjon på AqKva 2019 - 2021 (januar hvert år).
4. Vitenskapelig publikasjon fra DP1 (status villaks og sjørøret i PO3) (juni 2019)
5. Presentasjon på FHF møte/seminar (2019 - 2021)
6. Vitenskapelig publikasjon fra DP3 (bestandssammenligning av villaks og sjørøret i PO3 og andre områder) (april 2020)
7. Populærvitenskapelig artikkel (hovedfunn DP1) (august 2020)
8. Vitenskapelig publikasjon fra DP2 (utvikling av helhetlig overvåkingsmodell i en PO) (juni 2021)
9. Åpent avslutningsmøte med prosjektgruppe, styringsgruppe og oppdrettere i PO3 (juni 2021)
10. Populærvitenskapelig artikkel – hovedfunn DP1-3 (august 2021)
11. Faglig og administrativ sluttrapport (høst 2021).

4 Prosjektgjennomføring

De første rapportene under SalmonTracking 2020-paraplyen kom i løpet av våren 2019. Da starter arbeidet med å se den innsamlede informasjonen i disse i sammenheng.

Arbeidet i prosjektet ble delt inn i følgende tre arbeidspakker:

Delprosjekt 1. Sammenstille delrapportene fra forskningen i PO3/PO4 i en helhet, og publisere disse nasjonalt/internasjonalt

Hensikten med DP1 er å få fram helhetlig kunnskap om ressursene av vill laks og sjørørret i et produksjonsområde basert på konkrete registreringer/konkret forskning.

FoU-aktiviteter; gjennomføring og metode

De ulike delprosjektene i SalmonTracking 2020 medfølges av årlige delrapporter. I DP1 skal vi gå inn og trekke ut data som kan settes sammen i en helhetlig rapport med mål om publisering.

Delprosjekt 2. Utvikle en helhetlig overvåkingsmodell knyttet til produksjonsområdene

Hensikten med DP2 er å se på mulighetene for å skape en større forutsigbarhet i hvordan et produksjonsområde kan overvåkes, og slik skape større forutsigbarhet for næringsaktørene i et PO.

FoU-aktiviteter; gjennomføring og metode

Prosjektgruppen vil gå inn i forskningen fra elvene Granvin, Uskedal og Mundheim og se på hvordan det er mulig å utvikle en helhetlig, mer faktabasert overvåkingsmodell fra elv til kyst, basert på ulike typer merking av fisk samt bestandsovervåking.

Delprosjekt 3. Sammenligne bestanden av sjørørret og villaks fra elvene i PO3 med tilsvarende elver/områder nasjonalt

Hensikten med DP3 er å sammenligne bestandsutvikling for laks og sjørørret i ulike sammenlignbare geografiske områder i Norge.

Aktiviteter; Gjennomføring og metode

I DP3 måles bestandsutviklingen ved bruk av data fra drivtelling, fangst og videoovervåking. Målet er å beregne totalt innsig av laks og sjørørret til et fjordsystem og sammenligne dette med et sammenlignbart fjordsystem. Ulike menneskeskapt påvirkninger i de ulike fjordsystemene klassifiseres og variasjon i bestandsutviklingen testes mot variasjon i påvirkning.

5 Oppnådde resultater, diskusjon og konklusjon

Delprosjekt 1. Sammenstille delrapportene fra forskningen i PO3/PO4 i en helhet, og publisere disse nasjonalt/internasjonalt

FoU-aktiviteter; gjennomføring og metode

Study 1. Synchrony and multimodality in the timing of Atlantic salmon smolt migration

Abstract

The timing of the smolt migration of Atlantic salmon (*Salmo salar*) is a phenological trait important to the management of this species. In regions that are heavily impacted by aquaculture, understanding when and how smolts migrate to the sea is crucial to understanding how salmon populations will be affected by the elevated salmon lice concentrations produced by salmon farms. Here, acoustic telemetry was used to monitor the fjord migration of post-smolts from four rivers across two fjord systems in western Norway. Smolts began their migration throughout the month of May in all populations. Within-population, the timing of migration was multimodal with peaks in migration determined by the timing of spring floods. As a result, migrations were synchronized across populations with similar hydrology. There was little indication that the timing of migration had an impact on survival from the river mouth to the outer fjord. However, populations located deeper within the fjord experienced lower survival rates and had higher variance in fjord residency times. Explicit consideration of the multimodality inherent to the timing of smolt migration may improve estimates of salmon lice-induced mortality

Results

Overall, 70 % of tagged individuals were subsequently detected as migrators (Table 1). Three individuals were removed from all analyses, as the true fate of these individuals was difficult to ascertain due to the number of unreliable detections.

Fjord Entry Date

Median and 25 % quantiles of fjord entry dates were largely similar between rivers and years, differing up to 6 days (Table 1). However, quantiles belie the shapes of these distributions. Smolts from all four rivers displayed multimodality in the distribution of fjord entry dates, and these modes largely occurred at the same time across rivers (Figure 2).

1 *Table 1: Sample sizes and quantiles of fjord entry dates and arrival dates in the outer fjord for each river year.*

River Year	# Tagged	# Migrated	Proportion Migrated	Quantiles of Fjord Entry Dates			# of Migrants Detected in Zone D	Proportion of Migrants Detected in Zone D	Quantiles of Arrival to Outer Fjord		
				25 %	50 %	75 %			25 %	50 %	75 %
Granvin 2018	86	66	0.77	2018-05-06	2018-05-12	2018-05-24	25	0.38	2018-05-17	2018-05-22	2018-05-27
Eio 2018	74	57	0.77	2018-05-10	2018-05-17	2018-05-30	13	0.23	2018-05-22	2018-05-22	2018-06-01
Eid 2018	66	59	0.89	2018-05-06	2018-05-10	2018-05-25	31	0.53	2018-05-08	2018-05-12	2018-05-14
Stryn 2018	33	19	0.58	2018-05-08	2018-05-16	2018-05-29	6	0.32	2018-05-21	2018-06-06	2018-06-15
Stryn 2017	118	71	0.60	2017-05-06	2017-05-16	2017-05-17	27	0.38	2017-05-12	2017-05-16	2017-05-23
Total:	378	272	0.72				102	0.38			

Fitting normal distributions to fjord entry dates revealed that two normal distributions most efficiently explained both Eio and Eid fjord entry dates, while four normal distributions were most supported by the BIC selection procedure for Granvin fjord entry dates. For the data from Stryn, four and five normal distributions were most supported by the data from 2017 and 2018, respectively (Figure 2, see also Figure S1).

Both Eio and Eid displayed one initial narrow distribution, with a broader distribution afterwards. Granvin displayed three narrow distributions, with a broad distribution between the second and third narrow distributions. Stryn displayed a similar pattern in both 2017 and 2018, with two narrow distributions with broader distributions around them.

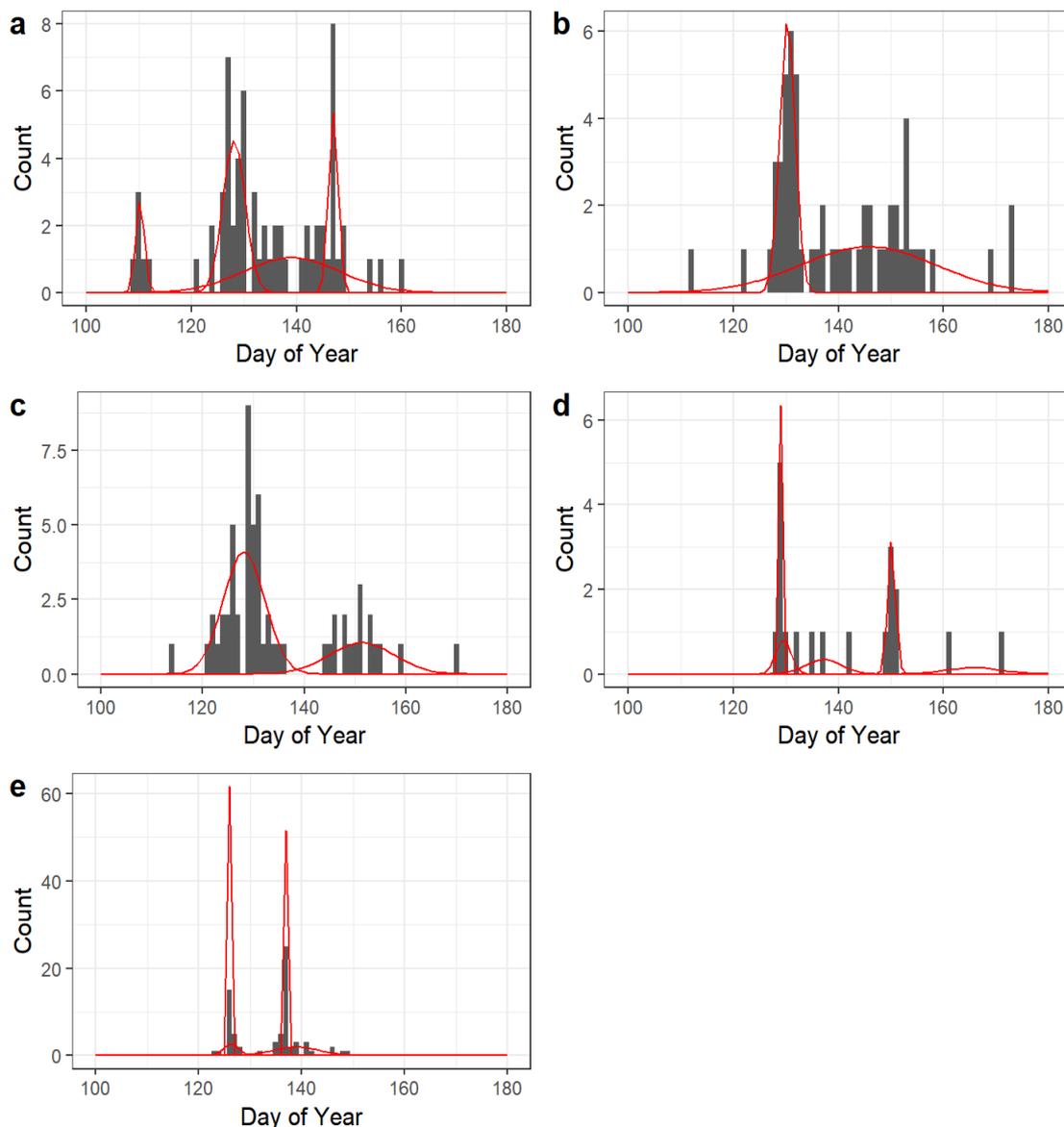


Figure 2: Histograms of fjord entry dates for each river year, along with results of Gaussian clustering of these fjord entry dates. Plots represent Granvin 2018 (a), Eio 2018 (b), Eid 2018 (c), Stryn 2018 (d), and Stryn 2017 (e). Clusters are scaled according to the number of individuals assigned to that cluster.

The first major peak occurred around day of year 125-130 in all rivers, corresponding to May 6th – May 11th, though Granvin had a smaller peak in migration around day of year 110 (April

21st). The second major peak was much more variable in its timing and occurred anywhere between 135 to 150 days into the year.

Environmental Correlates of Migration

The first major peak in migration seemed to coincide with a peak in discharge in all four rivers (Figure 3).

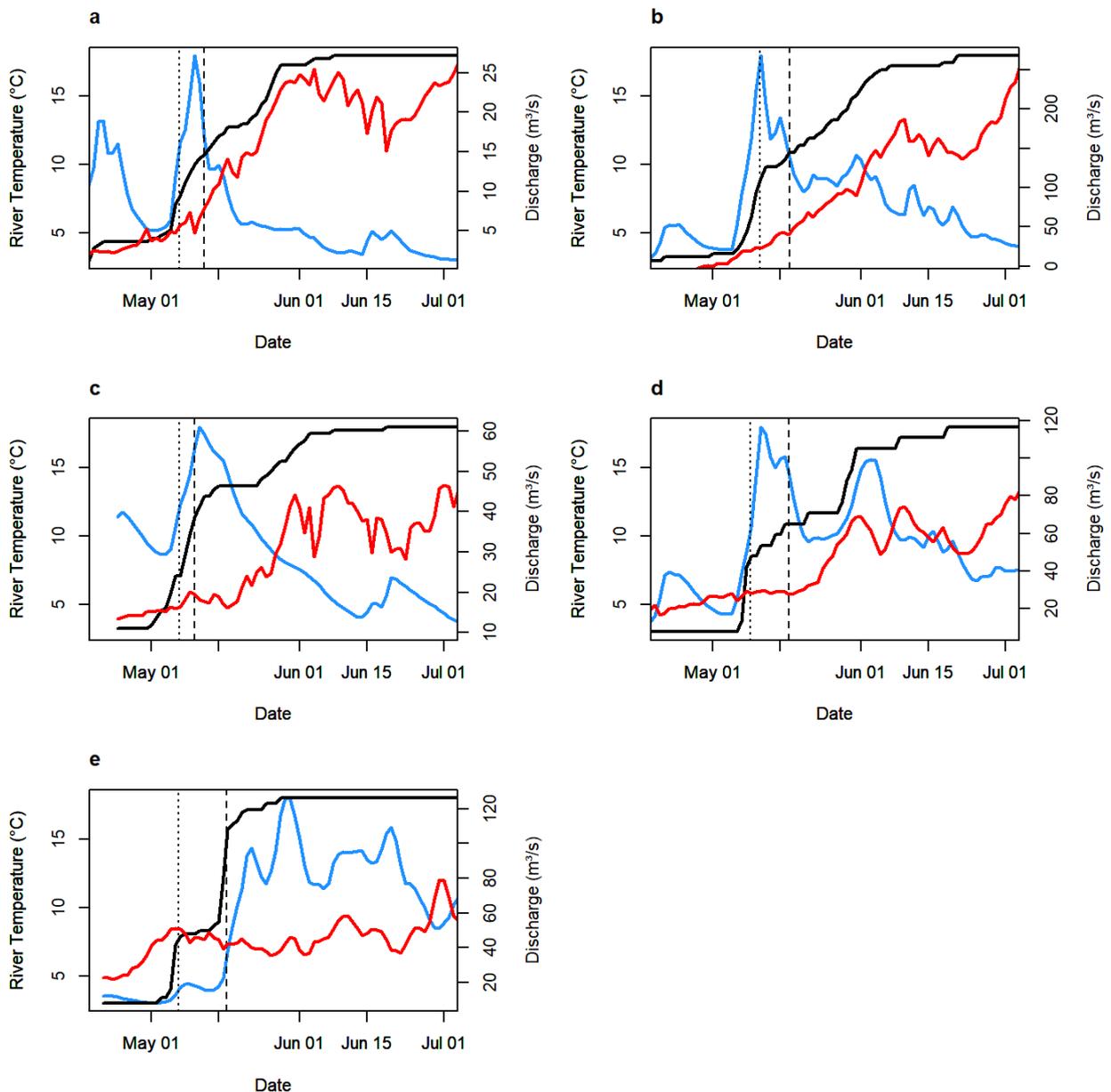


Figure 3: Mean daily water discharge (blue), mean daily temperature (red), and cumulative migration curve (black) through the migration period for (a) Granvin 2018, (b) Eio 2018, (c) Eid 2018, (d) Stryn 2018, and (e) Stryn 2017. 25 % and 50 % migration dates are shown as dotted and dashed lines, respectively.

Generalized linear mixed modelling fitted to fjord entry dates revealed that the most supported model included the effects of temperature, discharge, day-to-day change in discharge, and an interaction term between discharge and change in discharge. This model also included a random effect of river year, such that the intercept was allowed to vary between river years, but not slopes. Substantial collinearity ($r_p = 0.803$) between temperature and day of year necessitated

fitting these variables in separate models. The model with the effect of temperature rather than day of year had the lowest AIC ($\Delta AIC = 6.62$).

The estimates/predictions of this model indicate that migration probability is initially only high when the discharge is low and the day-to-day change in discharge is positive. However, as the temperature increases through the season, the migration probability increases under all river conditions, but especially for cases where the discharge is high and the day-to-day change in discharge is negative (Figure 4).

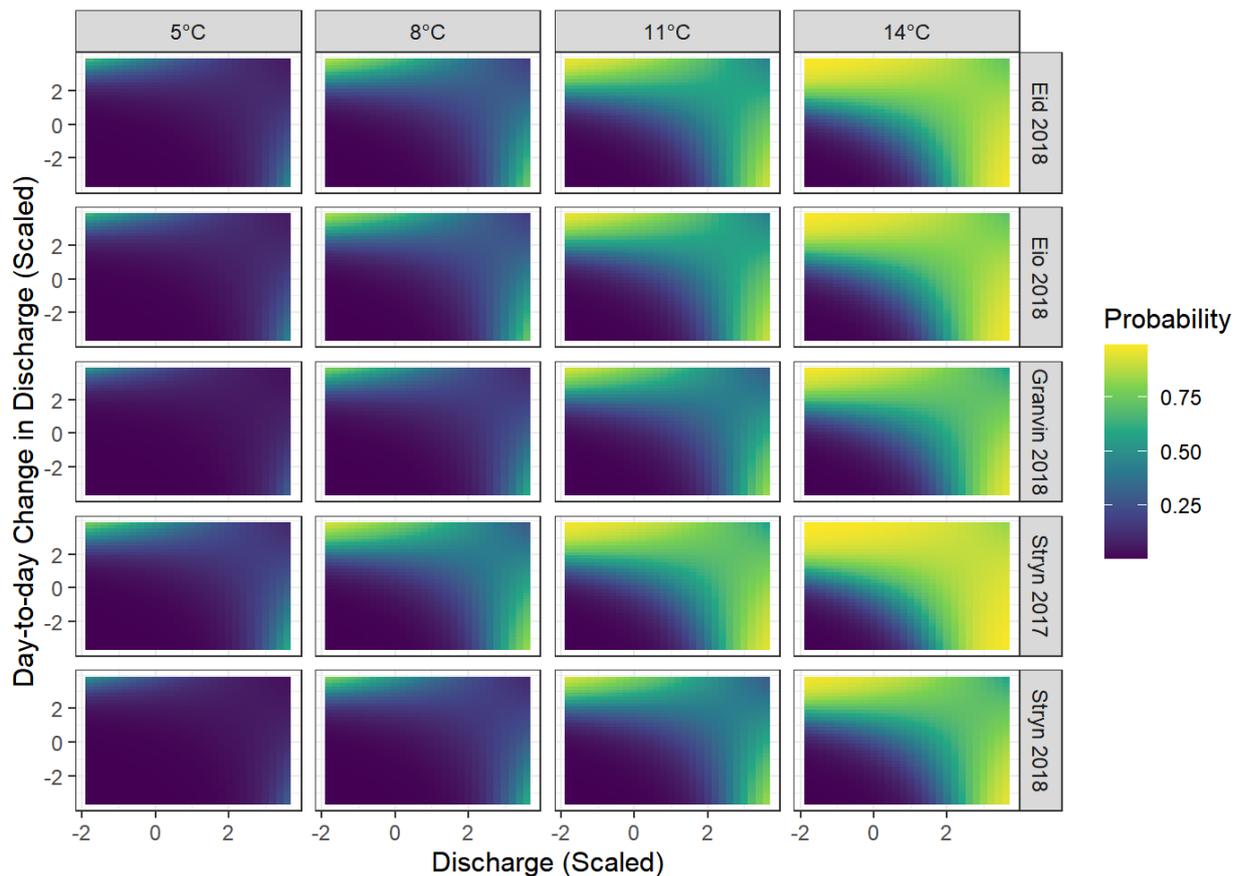


Figure 4: Migration probability predictions from best model of migration triggers. Yellow indicates a high probability of migration and blue indicates a low probability of migration given a set of river conditions.

Migration

The majority of smolt from all rivers moved through the fjord in a very directional manner (Figure 5).

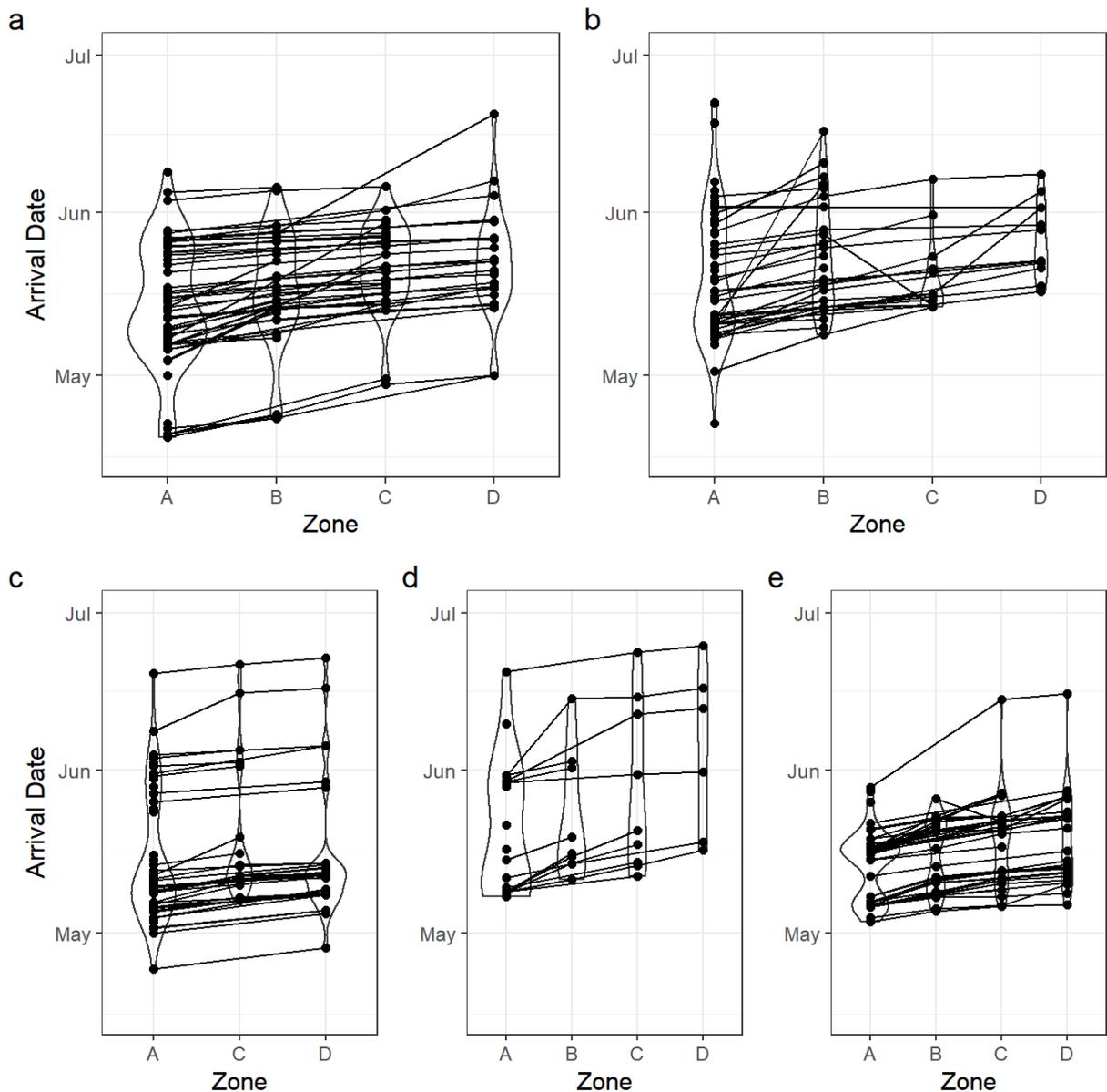


Figure 5: Arrival dates in each zone of the fjord for all migrators from Granvin 2018 (a), Eio 2018 (b), Eid 2018 (c), Stryn 2018 (d), and Stryn 2017 (e). Each line represents an individual fish.

As a result, the amount of time it takes for smolts to reach the outer fjord is largely in concordance with the distance that each smolt must travel (Figure 6). However, there is substantial variation between individuals such that smolts originating from the same river may differ in their arrival times by up to 21 days. This between-individual variation increases as the distance between the river mouth and the outer fjord increases, such that the coefficient of variation increases from 0.40 in the smolts originating from the outermost river of Eid to 0.60 in smolts from the innermost river of Eio.

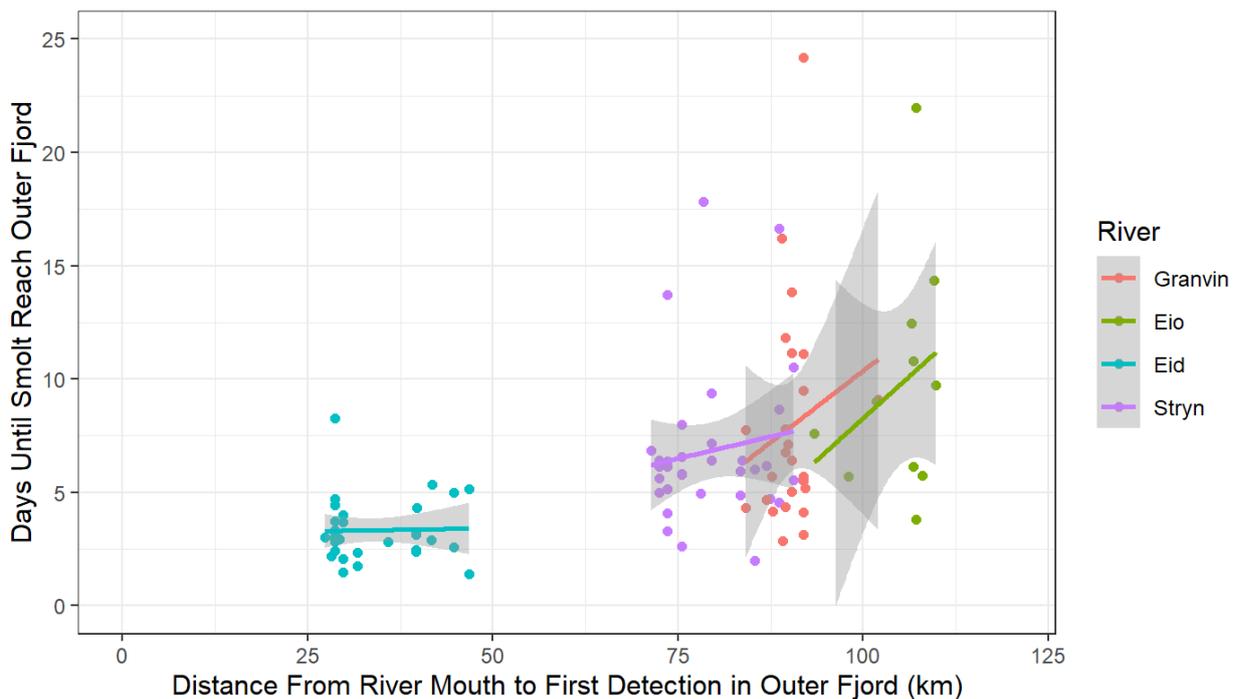


Figure 6: Travel time in days between the river mouth and the outer fjord as a function of the distance between the river mouth and the location of the first detection in the outer fjord for each individual, where the outer fjord is represented by zone D. Colored lines represent the results of river-specific linear regressions along with associated 95 % confidence intervals.

Survival Analysis

The most supported model for detection probability allowed detection probability to vary among fjord zones. With data from Granvin and Eio, the most supported model for survival probability allowed survival probability to vary among zones and rivers, though models also including the effects of fjord entry date, sun position at fjord entry, and/or smolt length were not significantly worse ($\Delta AIC_c < 2$). With only data from Eid, the best model included only the effect of smolt length, though the model that also allowed survival rates to differ between zones was not significantly worse ($\Delta AIC_c < 2$). Using both years of data from Stryn, the best model had a constant probability of survival through the fjord, though models including the effects of length and/or zone were not significantly worse ($\Delta AIC_c < 2$) (Table S2).

Probability of detection in the first zone was at or near 1 in all models. This indicates that nearly all smolt are detected in or near the mouth of the river. Throughout the rest of both fjords, probability of detection varied from 0.42 to 0.82 (Table S3).

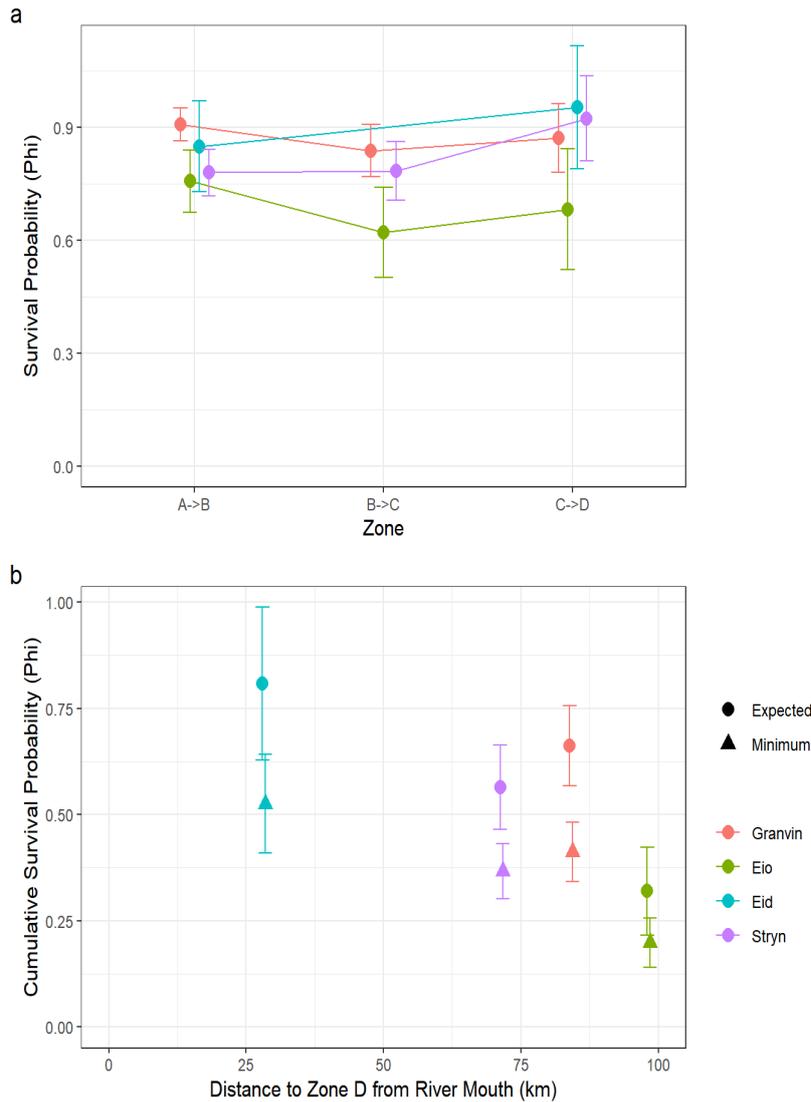


Figure 7: a) Estimated probability of survival between each zone of the fjord for all rivers. Error bars represent standard error of estimates. Survival probabilities in the last transition are expected survival probabilities based on a best guess of the probability of detection equal to 0.65. b) Minimum and expected cumulative survival probabilities for the entire fjord migration for each river as a function of the distance from the river mouth to the last zone. Error bars represent standard error of estimates.

Smolt originating from Eio consistently experienced lower survival rates throughout the fjord (Figure 7a), but by assessing overlap of confidence intervals there were no significant differences between populations in any zone, nor were there significant differences between zones. However, cumulative survival rates through the fjord indicated that longer fjord migrations lead to lower cumulative fjord survival (Figure 7b, Table S4).

The proportion of individuals that were positively identified as having died within receiver range served as a check on survival rates as survival rates cannot exceed one minus this proportion. Only the expected survival rate for migrators from Eid came close to this proportion (Table S4).

Discussion

In all four study rivers, smolts began their migration between late April and early June with clear multimodal distributions across all river years. Though the median migration time differed by up to five days, the timing of the first major cluster of migration differed only by two days among rivers in 2018 (see Supplementary Materials). Spring floods occurred at roughly the same time in all rivers in 2018, and modelling showed that both discharge and the relative change in discharge were important correlates of migration, while temperature seemed more important later in the season. Estimated fjord survival rates ranged between 32 % and 81 % among rivers, with no clear survival bottlenecks within the fjord.

Migration times were consistent with previous research showing that salmon smolts from this area of Norway predominantly migrate in May^{1,29}. However, median migration dates were on average 10.8 days earlier than those used to estimate salmon lice induced mortality per population⁴⁶. More years of data would be necessary to determine whether this difference is consistent.

Multimodality in smolt migration timing has been observed in many other systems (e.g. ^{3,24,29,47-49}) However, the mechanisms behind this multimodality and its ecological consequences are rarely discussed (though see Freshwater et al. (2019)⁵⁰). Given that variability in migration timing may now have greater fitness consequences than in the past due to greater salmon lice concentrations later in the season¹⁶, this variability warrants investigation.

We show here that the timing of the observed modes in migration timing in these populations seems to be primarily influenced by the timing of river spring floods, though temperature seems more important as the season progresses. The importance of water discharge and temperature in triggering migration has been observed many times elsewhere^{3,21,23-25,49,51}. Here, the degree to which river conditions control the phenology of migration timing is the likely cause of the observed synchronization among rivers with similar hydrological properties. As all of the studied rivers are primarily fed by snowmelt throughout the migration period, the same regional weather systems can lead to a near simultaneous upswing in snowmelt and subsequent discharge in each river.

However, this does not in and of itself explain how individual smolts decide during which river discharge peak to migrate in. Three non-mutually exclusive hypotheses could explain this: 1) smolts differ in a set of environmental thresholds that must be crossed for migration to trigger, 2) smolts differ in their level of preparedness for seawater entry through time, and 3) multimodality may represent a compromise between a bet hedging strategy and a synchronization strategy.

A threshold model has been proposed to explain the phenomenon of partial migration⁵², and a similar model could explain the variability we see here. Here, smolt would require one or more environmental variables to cross some threshold before they initiate their migration. This threshold could then differ among individuals due to genetic variation or phenotypic plasticity. Here, we see that in each river year, the second peak in river discharge is both steeper and taller than the first (Figure 3), leaving open the possibility that fish that migrated on the first peak had a lower discharge threshold. Exploring this hypothesis would likely require an experiment designed to measure the thresholds for individual fish, using an artificial experimental river or a flume where discharge, temperature, and photoperiod could be manipulated. However, the ecological relevance of such designs is debatable.

Physiological preparedness for seawater entry is a prerequisite for smolt migration^{18,53,54}. However, the physiological smolt window, i.e. the window of time when the salmon are physiologically prepared for migration, and the environmental smolt window, i.e. the window of time in which salmon could be triggered to begin the migration, may or may not be fully overlapping periods of time. The timing of these windows seem to be determined by different environmental and/or endogenous cues, where the parr-smolt transformation is primarily determined by photoperiod and temperature^{11,18,55,56}. Given that temperature and photoperiod regimens can vary widely between salmon rivers, there must be between-population variation in the way these regulate smoltification, which may explain documented between-population variance in migration timing⁵⁷. However, within-population variation in the timing of the smolt transformation has not been properly investigated⁵⁷. Skilbrei et al. (2010)⁴⁸ found consistent differences in migration timing between 1+ hatchery smolts, 2+ hatchery smolts, and wild smolts, indicating that experienced environment likely influences the timing of the physiological smolt window.

In any case, both the physiological smolt window and the environmental smolt window are evolved traits that allow smolts to arrive at their feeding areas at the optimal time. However, there is an inherent difficulty in determining the optimal migration time given the conditions within the river, as the conditions that determine the optimality are distant in both space and time. If migration triggers are unreliable predictors of the optimal migration time, we would expect fish to hedge their bets through stochastic reaction norms⁵⁸. Simultaneously, migrating synchronously can reduce a smolt's individual risk of predation through a predator swamping effect⁵⁹. Migrating in discrete batches may represent a compromise between the two evolutionary pressures for bet hedging and synchronization. However, theoretical modelling would be necessary to evaluate whether such a compromise would be evolutionarily stable.

Additionally, common garden experiments show that farmed and farmed-wild intraspecies hybrid smolts differ from wild smolts in their migration timing²⁹, such that genetic introgression from domesticated salmon will likely increase within-population variation in migration timing. As all of the studied populations have experienced some degree of introgression⁶⁰, this may explain some portion of the observed within-population variation. Further work is needed to establish whether within-population variation in the physiological smolt window exists and to what degree genetic variation can influence both the physiological smolt window and how smolts react to migration triggers.

Expected cumulative survival rates through the fjord ranged between 32 % and 81 %. This is in line with previous results showing survival through the early marine migration to range between 29 % and 92 % across a variety of rivers¹². Smolt length seemed to have a positive effect on fjord survival, especially for smolts originating from Eid. To date, evidence for the hypothesized relationship between smolt length and marine survival has been equivocal in wild salmon^{61,62}. Perhaps the most compelling evidence has been provided by⁶³, which used state-space models to show a relationship between smolt length and adult return rates for smolts originating from the River Frome. One likely mechanism for this relationship is that increased smolt length reduces the likelihood of predation by gape-limited predators⁶⁴. As post-smolts are believed to be under the greatest risk of predation while they migrate⁶⁴, it is not unexpected that a relationship between smolt length and survival would manifest itself in the fjord migration.

There was little support that migration timing had an effect on fjord survival as no candidate models including the effect of fjord entry date proved significantly better than other models, though nor were they significantly worse in the candidate models for smolts from Granvin and Eio. Similarly, there were no apparent benefits of synchronized migration as candidate models that included the effect of the maximum posterior probability of belonging to a narrow cluster proved to be significantly worse in all three datasets. However, there are three things that are important to consider here.

First, low sample sizes precluded our ability to test overly complex models. Given that Cormack-Jolly-Seber models simultaneously estimate both survival and detection rates within each zone, the number of parameters to estimate quickly grows large.

Second, it is important to stress that the mortality estimated here likely comes before any salmon lice-induced mortality. Salmon post-smolts are unlikely to be infected by salmon lice until they reach the outer fjord where the salmon lice concentrations are highest⁶⁵. Additionally, there will likely be a time lag between salmon lice infection and any resulting mortality. As a result, smolts will likely be outside of our receiver network before any salmon lice-induced mortality can occur. This means that variation in migration timing will probably have a greater effect on return rates than fjord survival, especially in years where salmon lice densities are high¹⁶.

Third, benefits of synchronized migration should mostly manifest themselves during river migration where smolt are confined to relatively small spaces that can be exploited by opportunistic predators. Given that the observed estuarine residence times are negligible (see Supplementary Materials) and that the length of the rivers are short, synchronized migration may not present a significant benefit for migrating smolts in these populations. Also, as the analysis only used smolt that could be positively identified as migrators, estimated mortality rates do not include mortality in the river. Further, there is some evidence that migrating salmon only school when migrating during the day⁶⁶. As the majority of the smolt in this study began their migration during relative darkness (Figures S2, S3), the predator swamping strategy may not be necessary.

Likewise, there were no significant differences in survival rates between different sections of the fjord or between rivers. However, cumulative survival through the fjord clearly show that populations that are situated deeper in the fjord experienced lower survival rates. This effect likely explains some portion of the effect of river location on salmon density observed by Vollset et al. (2014)⁶⁷.

We observed that smolts originating from Eio consistently experienced lower mortality rates than smolts originating from Granvin in each zone of the fjord, despite that only zone A is different for these two populations. In other words, the 20 extra kilometers that post-smolt from Eio needed to traverse in zone A seemed to have a carryover effect into the other zones, leading to reduced survival throughout the fjord. This indicates that exhaustion represents a significant cause of death, though this result could be partially explained by delays between predation and gastric expulsion of the tag leading to apparent smolt movement between zones⁶⁸.

Similarly, mean travel times to the outer fjord increased when populations were situated deeper within the fjord. However, within-population variation in travel times also increased such that fjord residency times for individuals from the innermost river varied by up to three weeks. Such large within-population differences in travel time through the fjord have been observed previously⁶⁹ and it is worth investigating the underlying causes of this variation as it may lead to large differences in an individual's risk of infection by salmon lice. This effect likely plays some part in the observation that post-smolts caught in trawls of the outer fjord in the latter part of the season are primarily coming from the inner fjord⁷⁰.

In conclusion, we found that explicit consideration of the multimodality of migration timing improved our understanding of both within- and between-population variation of this trait. Future research should focus efforts on understanding within-population variation and not only between-population variation, as understanding this will be paramount to understanding how populations will react to changing fjord conditions. Especially, an investigation of the degree to which genetic variation structures this trait will be necessary to understand the capacity salmon have to evolve this trait.

Study 2. Population status of wild salmonids in an aquacultural area: a case study from the Hardangerfjord, Western Norway

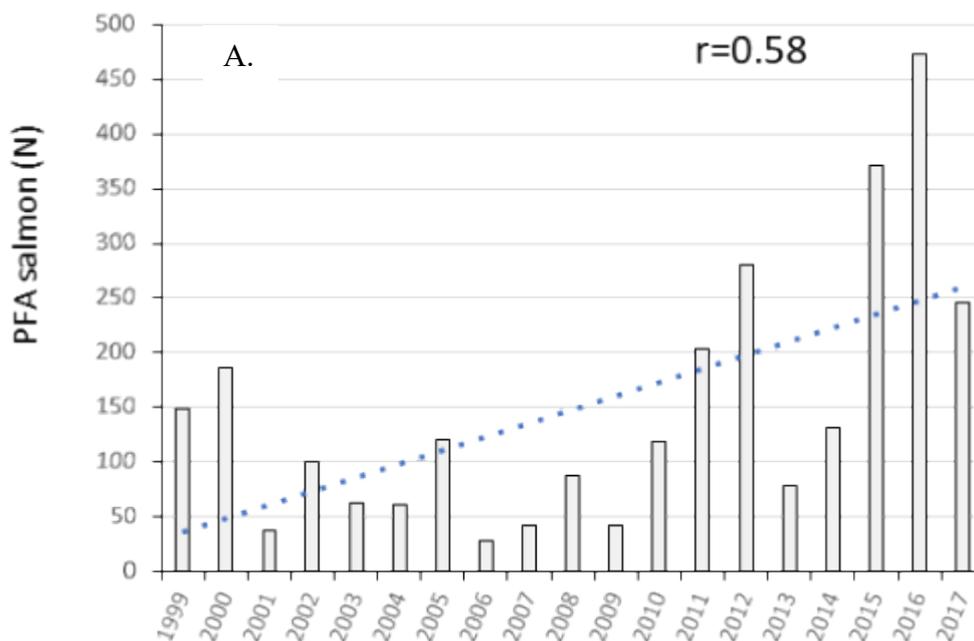
ABSTRACT

The rivers that drain into the Hardangerfjord were historically known to have numerous populations of both sea trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*). After a decline in catches during the last decades many of the rivers have been closed for fishing. In this study we use snorkelling observations from seven rivers in the Hardangerfjord combined with data from recreational fisheries catch statistics from 1999 to 2017 to estimate the pre-fishery abundance (PFA) in the period to describe the current situation and analyse the patterns of density of wild salmon and sea trout in the area. Overall, both salmon and sea trout population were found to be increasing in the study area in the period studied. Present data show that 7 out of 7 of the salmon populations and 4 out of 7 sea trout populations studied are increasing indicating good natural growth of both species in the studied rivers in the Hardangerfjord system.

Results

Eidfjordvassdraget

Pre-fisheries abundance (PFA) of Atlantic salmon and sea trout has been studied in Eidfjordvassdraget during 1999-2017 and 2001-2017, respectively (Fig. 2). During this period the PFA of both salmon and mature sea trout has increased significantly ($r = 0.58$ and 0.70 , respectively, $p < 0.01$). The PFA studies in Eidsfjordvassdraget do not include immature trout or salmon that are not at their spawning places once the snorkelling is done. It follows that the numbers found are minimums number for the populations of both species in the river, but as same type of investigation is done every year it should not lead to bias or wrong estimation of the population development.



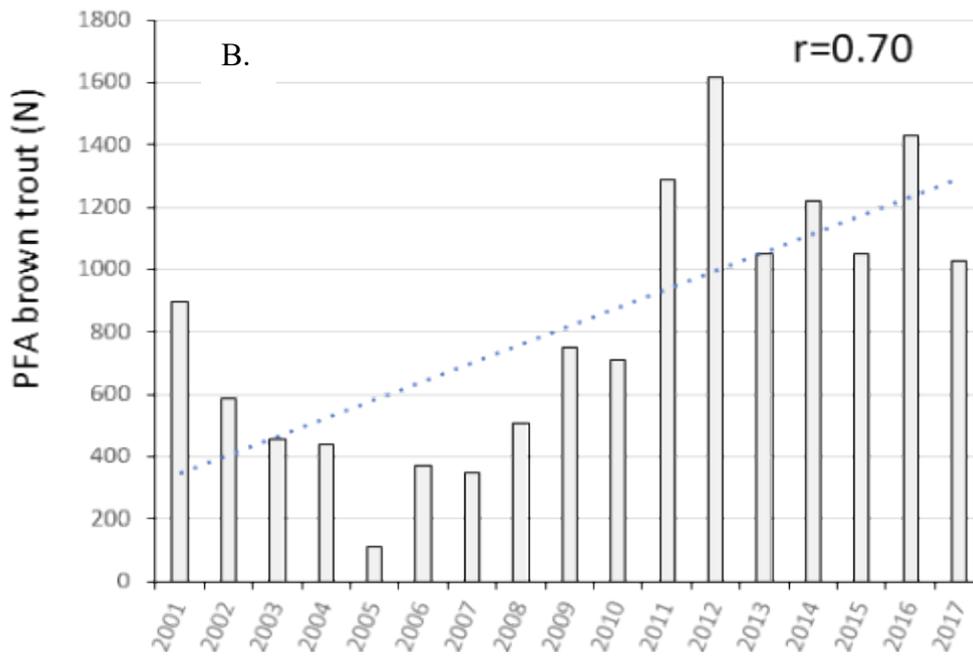


Figure 2. Pre-fisheries abundance (PFA) of Atlantic salmon (A) and anadromous sea trout (B) in the Eidfjordvassdraget during 1999-2017 (salmon) and 2001-2017 (sea trout). Dotted line indicates correlation (r) between PFA and study period (year).

Granvinsvassdraget

PFA of salmon increased in Granvinsvassdraget in the period 2004-2017 (Fig. 3A, $r = 0.41$ $p < 0.05$), whereas number of mature sea trout in the river was stable during the same period (Fig. 3B, $r = 0.04$, $p > 0.45$). Similar to Eidfjordvassdraget the numbers found do not include immature trout or salmon that are not at their spawning places once the snorkelling is done so the numbers should be considered as minimums number for the river population. This river has been investigated with video surveillance in 2014-18 and those data indicate that the sea trout population in Granvin is increasing (Lamberg et al. 2018)

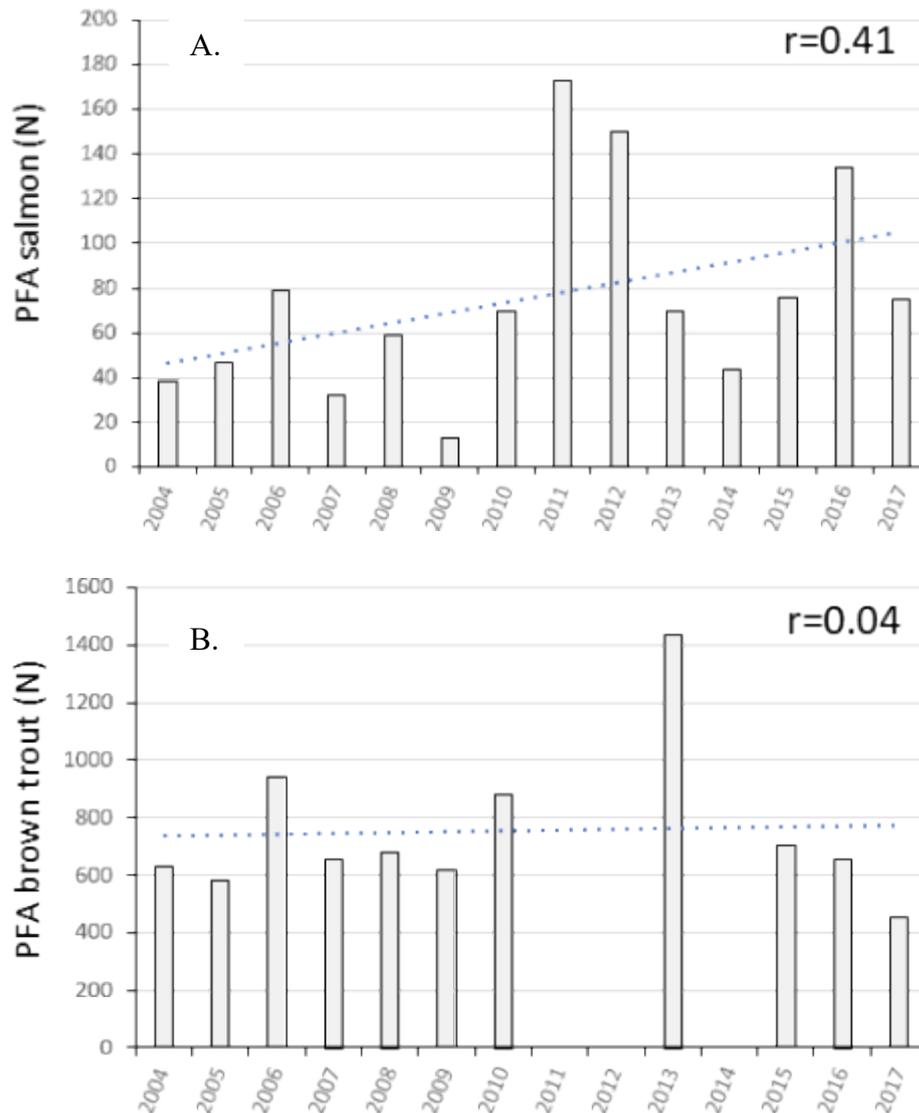


Figure 3. Pre-fisheries abundance (PFA) of Atlantic salmon (A) and anadromous sea trout (B) in the Granvinsvassdraget during 2004-2017. Dotted line indicates correlation (r) between PFA and study period (year).

Kinso

PFA has been monitored for both species in the Kinso river during 2004-2017 and population size of both species was found to increase (Fig. 4, $r = 0.28$ for both species, $p < 0.05$).

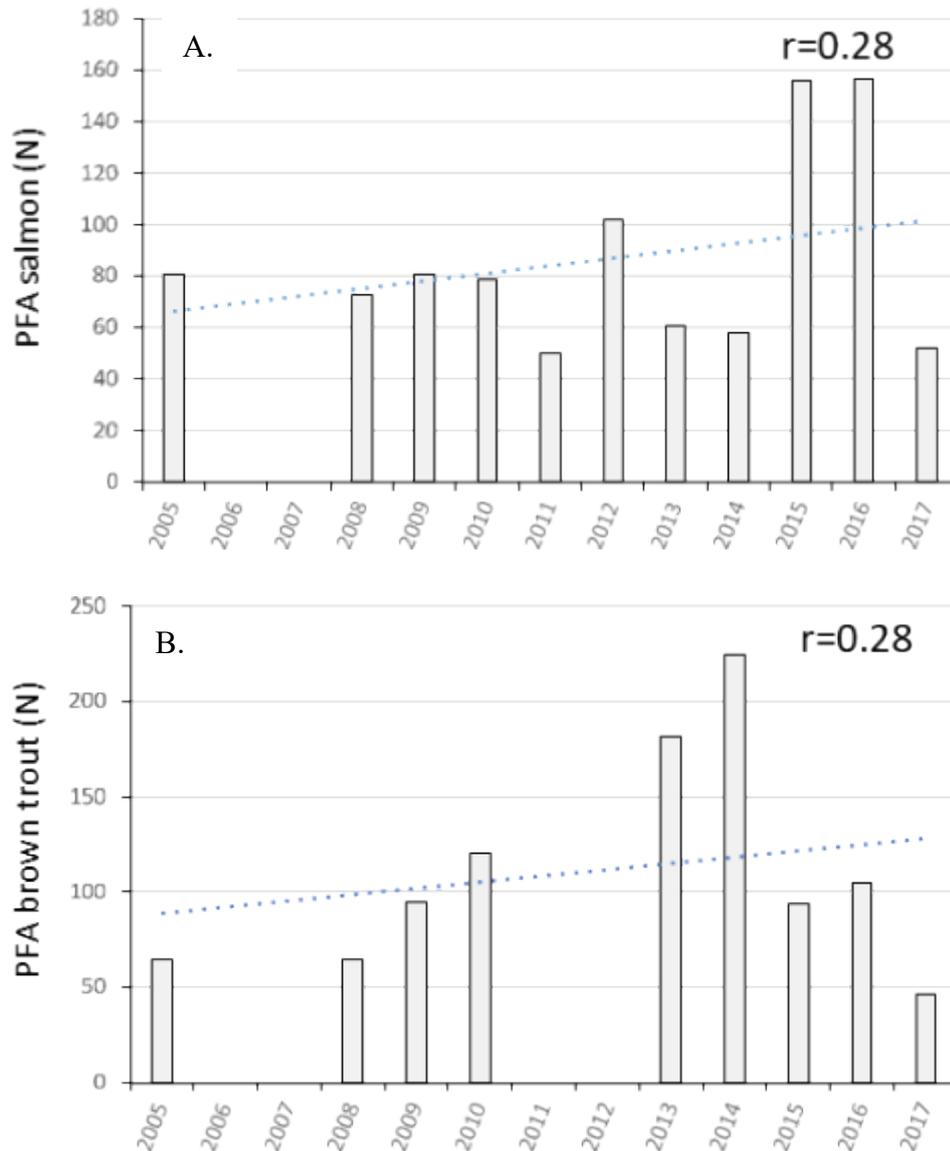


Figure 4. Pre-fisheries abundance (PFA) of Atlantic salmon (A) and anadromous sea trout (B) in the Kinso river during 2005-2017. Dotted line indicates correlation (r) between PFA and study period (year).

Rosendal rivers

PFA has been monitored for both species in the Rosendal rivers during 2004-2017 and PFA of both species was found to increase (Fig. 5, $r = 0.30$ and 0.35 , respectively, $p < 0.05$).

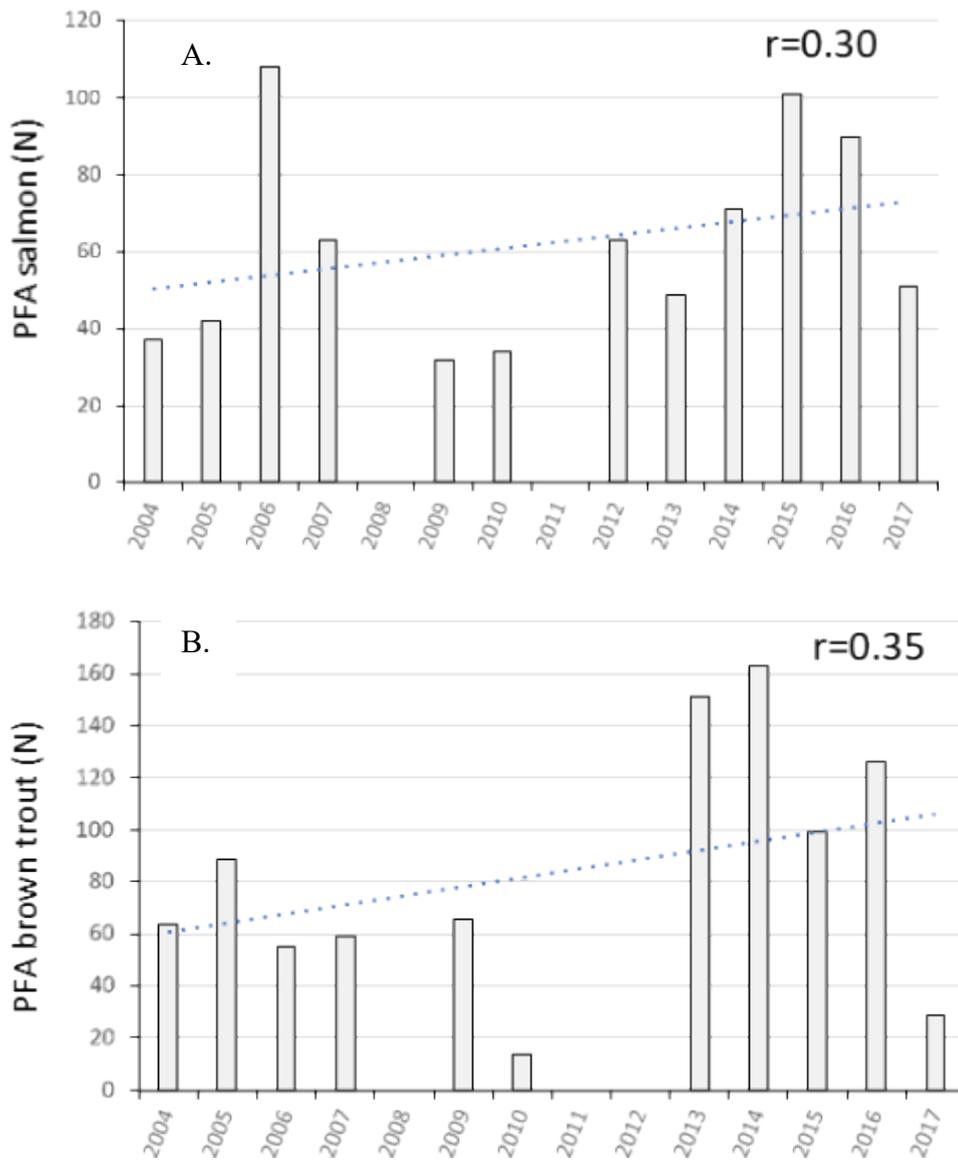


Figure 5. Pre-fisheries abundance (PFA) of Atlantic salmon (A) and anadromous sea trout (B) in the Rosendal rivers during 2004-2017. Dotted line indicates correlation (r) between PFA and study period (year).

Omvikelva

PFA has been monitored for both species in the Omvikelva river during 2004-2017. PFA of salmon has increased (Fig. 6A, $r = 0.87$, $p < 0.001$), whereas PFA of sea trout has decreased in the same period (Fig. 6B, $r = -0.58$, $p < 0.01$).

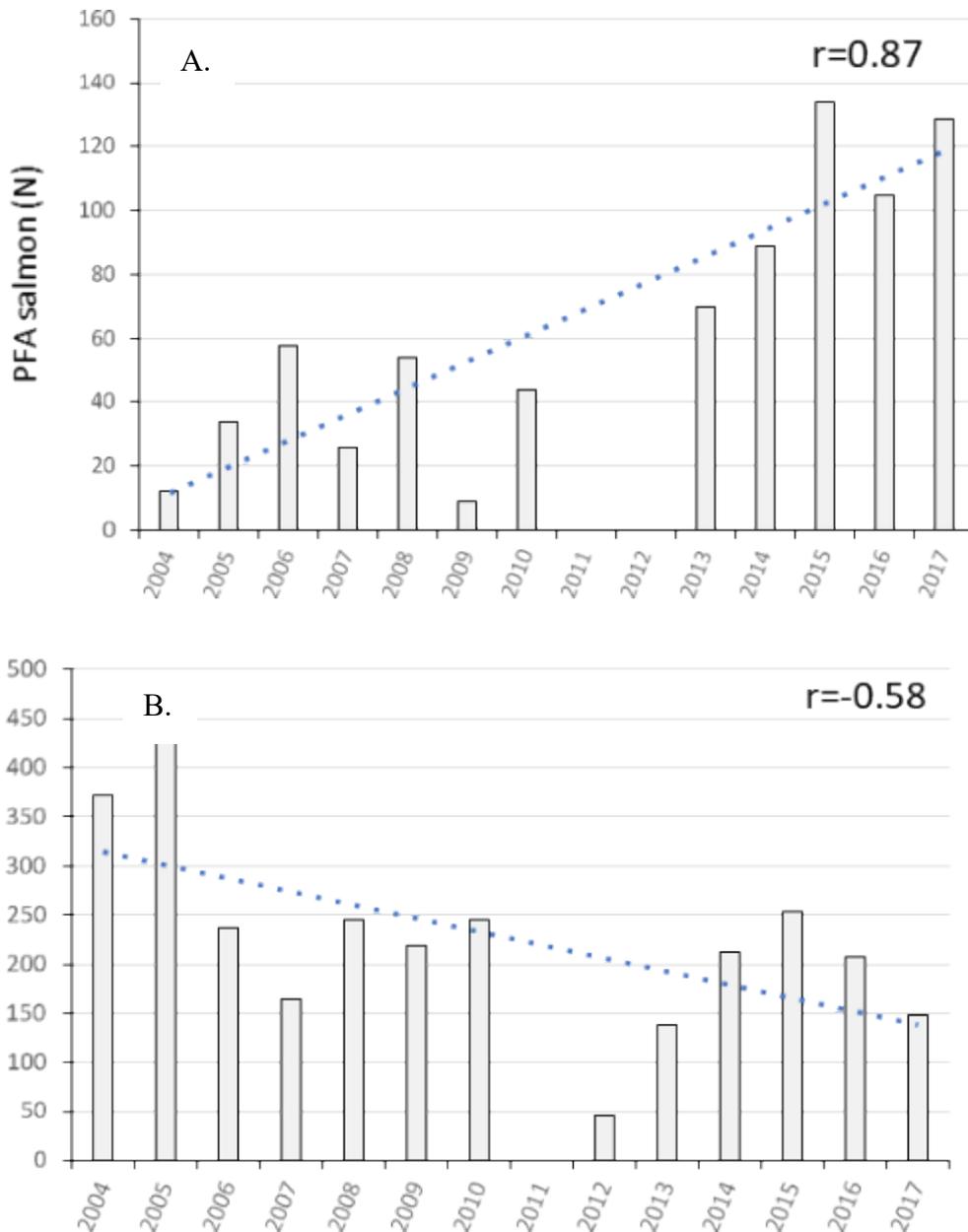


Figure 6. Pre-fisheries abundance (PFA) of Atlantic salmon (A) and anadromous sea trout (B) in the Omvik river during 2004-2017. Dotted line indicates correlation (r) between PFA and study period (year).

Uskedalselva

PFA has been monitored for both species in the Uskedalselva river during 2006-2017. PFA of salmon has increased (Fig. 7A, $r = 0.64$, $p < 0.001$), whereas PFA of sea trout has been stable in the same period (Fig. 7B, $r = -0.12$, $p > 0.05$).

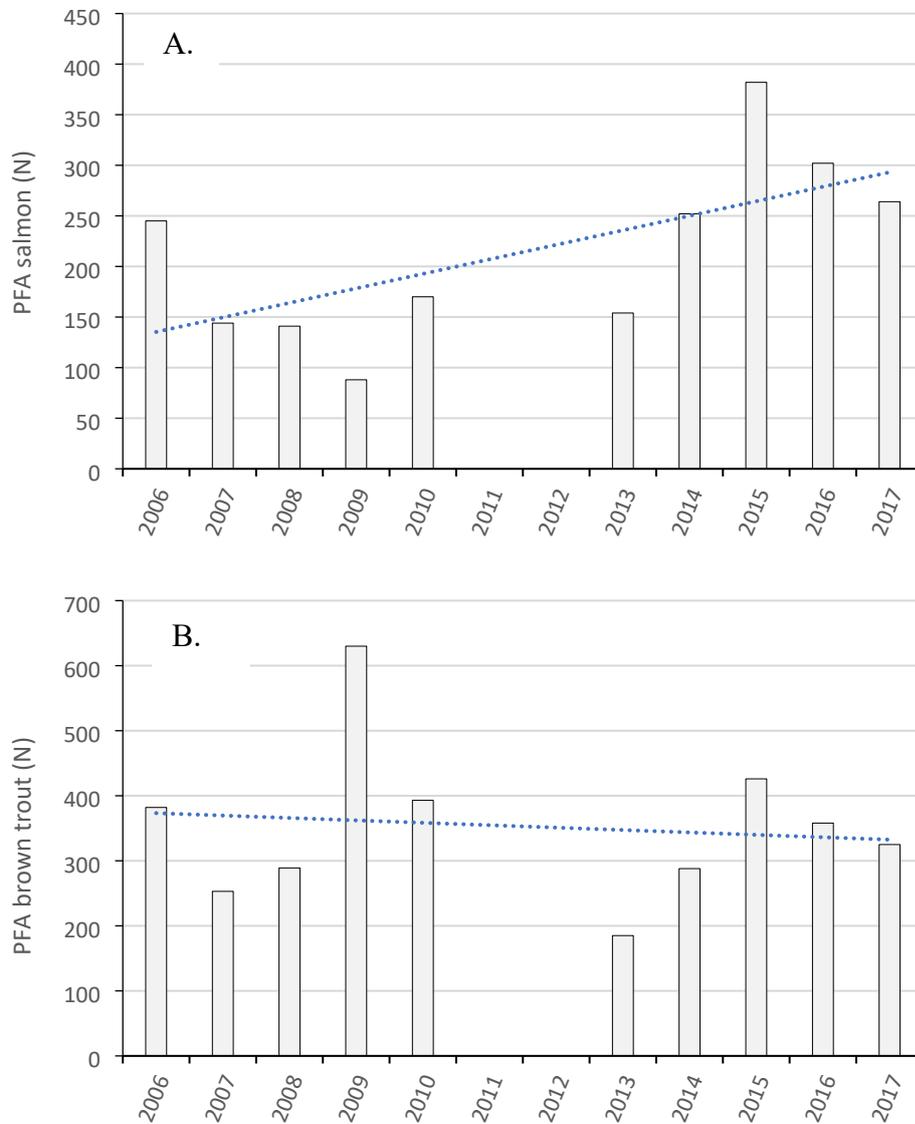


Figure 7. Pre-fisheries abundance (PFA) of Atlantic salmon (A) and anadromous sea trout (B) in the Uskedalselva during 2006-2017. Dotted line indicates correlation (r) between PFA and study period (year).

Etnevasdraget

PFA in the Etnevasdraget has been monitored for salmon between 2004-2017 for sea trout during 2006-2017 (Fig. 8). PFA of salmon has increased (Fig. 8A, $r = 0.49$, $p < 0.01$), whereas PFA of sea trout has been more variable same period (Fig. 8B, $r = 0.21$, $p > 0.05$). It should be noted that the PFA estimation for sea trout is a minimum estimate similar to those in Eidfjord and Granvin as they do not include immature fish or mature fish with resting year (i.e. not spawning).

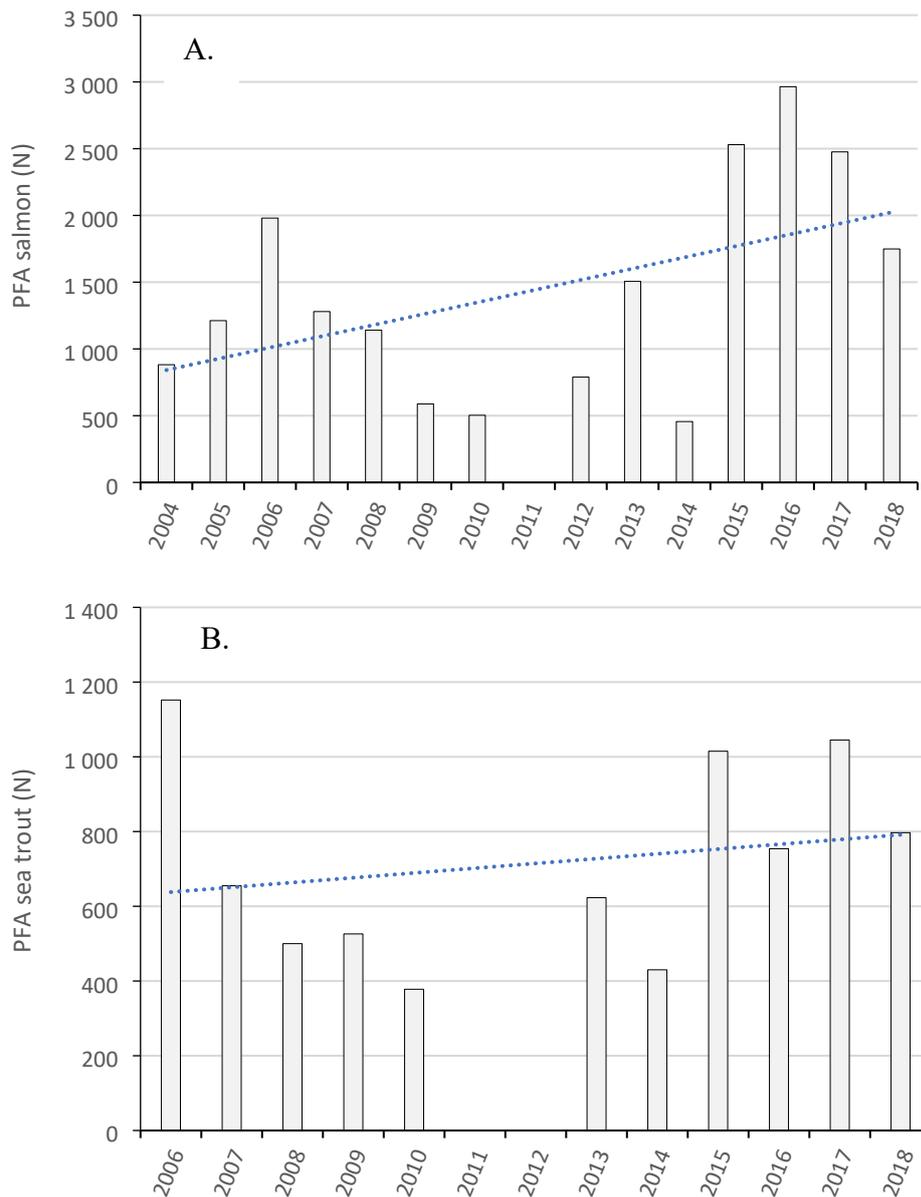


Figure 8. Pre-fisheries abundance (PFA) of Atlantic salmon (A) and anadromous sea trout (B) in the Etnevasdraget during 2004-2017. Dotted line indicates correlation (r) between PFA and study period (year).

Overall situation of Atlantic salmon population in the studied rivers

In the seven river systems in the Hardanger fjord system included in this study PFA data exist from 2009 to 2017 and overall the PFA in these rivers has increased from around 1000 individuals in 2009-10 to around 4000 individuals in 2015-2017 (Fig. 9). In 2016 the total recreational fishery for salmon in whole of Hardanger fjord system was 1466 individuals (Statistics Norway (SSB), <https://www.ssb.no/statbank>). No salmon were caught in the sea in 2016. In the same year the PFA (snorkelling + recreational fishery) for the studied seven rivers was 4267 individuals (Fig. 9).

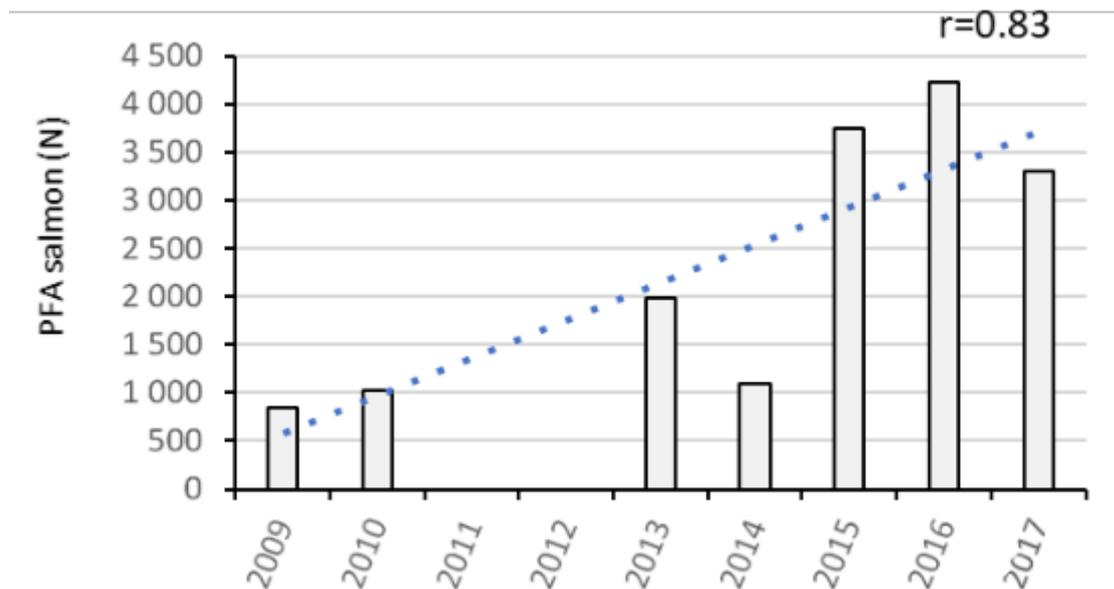


Figure 9. Combined pre-fisheries abundance (PFA) of Atlantic salmon from the seven studied river system in the Hardanger basin in 2009-2017. Dotted line indicates correlation (r) between PFA and study period (year).

Discussion

Earlier reports (Otterå et al. 2004; Skaala 2014a-c) have described the situation for the wild salmonid populations in the Hardangerfjord as critical and that escaped farmed salmon and salmon lice were responsible for an important part of the problem. Although management authorities and salmon farmers have introduced a number of measures to reduce the infection pressure of salmon lice on wild fish, infection levels continued to be high and appeared to be closely associated with the localization and biomass of farmed salmon (Taranger et al. 2011; Skaala et al. 2014c). With the decline in many of the anadromous sea trout and Atlantic salmon populations in these rivers, interest in angling activity also appears to have declined, with a corresponding bias in catch statistics (Skaala et al. 2014c). From about 2000, restrictions in river angling and sea fishing for anadromous fish have been gradually introduced in this area to reduce mortality and protect spawning populations. Since 2004, spawning populations have been assessed in the rivers by divers from Uni Research (Skaala et al. 2010; Vollset et al. 2014). In most river systems in the region, numbers of wild spawning salmon have been low, and estimated egg deposits have been below 2-4 eggs/m², i.e. below the recommended density for sustainable recruitment (Jonsson et al. 1998; Skaala et al. 2014c). The exception is River

Etneelva, which still has a stable spawning population of sufficient size to support recreational angling (Skaala et al. 2014c). Overall present study does not support the previous findings (Otterå et al. 2004; Skaala et al. 2014a-c) of declining salmon stock status in Hardangerfjord as there was an increase in salmon population size between 1999-2017 in all seven river systems studied. This is in line with the larger study of Skoglund et al. (2019) covering 56 river systems in Western Norway. They found a general increase in pre-fishery abundance (PFA) for salmon in the period 2011-2018 compared to the period of 2004-2010. The populations of anadromous brown trout showed larger local and regional differences compared to salmon (Skoglund et al. 2019). The hypothesized that this was due to improved conditions for growth and survival in the sea in the 2011-2018 period. It was noted that historical PFA data for this area was lacking making comparison back in time difficult. Data from recreational fisheries of salmon in the area from 1960-90 indicates larger population sizes than found in this and the study of Skoglund et al. (2019), but this is difficult to validate. The ongoing program of monitoring regional PFA for both salmon and anadromous sea trout (Skoglund et al. 2019) is a good method to follow population development in this area which is a key prerequisite for successful conservation management of these species in the fjord system.

Vollset et al. (2014) hypothesized that some of the variance in density of salmon and sea trout in the Hardangerfjord basin can be explained by the location of the river in the fjord, with fish from rivers with a longer fjord exposure having a lower density. Their results suggest that there is an inverse log-linear relationship between the density of salmon each year in the period 2004-2011 and the migration distances from river to open sea. It was pointed out that catch statistics are available for some of the inner rivers, but most of these data are, with few exceptions, of poor quality due to inadequate reporting (Vollset et al. 2014). It is therefore difficult to analyse whether the populations in the inner parts of the fjord have had a divergent trend in population size compared to the outer fjord systems. It follows that comparison of historical data is almost impossible, making validation of their conclusion difficult by comparing their data with older data. However, comparison with present PFA data from 1999-2017 do not support their hypothesis as longer fjord exposure was not correlated with lower population density. In the present study the highest numbers of salmon and anadromous sea trout were found for the rivers with the longest fjord exposure (Eidsvikvassdraget and Granvikvassdraget). The underlying causation factor suggested by Vollset et al. (2014) was that extended fjord exposure lead to longer exposure of the fish to sea lice. Jansen et al. (2012) demonstrated that there was correlation between sea lice on individual salmon farms and local biomass density in the surrounding farms. Severe infections of salmon lice on wild salmonids in the Hardangerfjord have earlier been found to coincide with high infection rates at salmon farms (Bjørn et al. 2011). The contrast between the findings of Vollset et al. (2014) and present data might be linked to lower lice infestations in the latter part of the period investigated i.e. > 2011. In the Hardangerfjord system coordinated delousing during the smolt run in spring have been implemented since 2010 (with a limit of < 0.3 lice or 0.1 female lice per salmon) and there are indication that the lice situation in the fjord system has improved (Malkenes 2020). This in turn may lead to improved growing conditions for the wild salmonids in the fjord system which may help to explain the contrasting findings of Vollset et al. (2014) and present data.

In the marine phase, salmon farming has a major impact on wild anadromous populations, particularly through infection by the salmon louse (Skaala et al. 2014c). The impact level

depends on several factors, such as the density of salmon farms, water temperature, migration routes and duration of migration in the fjord. Heuch et al. (2009) studied possible explanatory factors associated with lice infections on salmon farms in the Hardanger fjord between 2004 and 2006. Salinity, mean fish weight and treatment type were all shown to be significantly positively correlated with mean abundance of adult female lice. The two innermost zones had the lowest lice mean abundances, whereas the outermost zones, consistently had more lice. However, the marine migration of anadromous sea trout is restricted to the fjord basin where the fish may remain for several months before returning to freshwater (Klemetsen et al. 2003). This means that anadromous sea trout may be more severely affected than Atlantic salmon by the parasite. Data from 2004-2009 (Heuch et al. 2009; Finstad 2010) indicated high level of lice infection on salmon smolts and anadromous sea trout whereas later reports have indicated an improved lice situation in the Hardanger fjord system (Malkenes 2020). If the anadromous sea trout can be seen as a proxy for the severity of the lice situation (Klemetsen et al. 2013) in the fjord system then one would expect an increased population growth given that the lice situation is improving. Present data show that 6 out of 7 anadromous sea trout populations studied are increasing or stable indicating good natural growth of the populations studied which may indicate improved lice situation in the fjord system as a whole.

In the present study we found slight increasing (Eidsfjord, Kinso, Rosendal, Etne), stable (Granvin, Uskedal) or decreasing (Omvik) sea trout stocks. Overall, the population size of sea trout from these 7 river systems is increasing the study period (2001-2017) which is partly in contrast to some earlier findings. The study of Skurdal et al. (2001) found that the annual catches of anadromous trout in the Granvin population, the supposedly largest population in the system, had decreased from approximately 1000 individuals in 1975 to approximately 100 individuals in 2001 following the expansion of salmon farming (Skurdal et al. 2001). In the present study the Granvin sea trout population varies between 450 to 1400 individuals i.e. much higher than the estimates of Skurdal et al. (2001). Annual catches in the Etne population have historically been less than in the Granvin River, that is < 1000 individuals, but this population remains of considerable size (Hansen et al. 2007; present study). Of the seven systems studied the largest populations of sea trout was found in Eidsfjord, Granvin and Etne all of which had stable or increasing population sizes. Hansen et al. (2007) studied possible gene flow between sea trout population in Hardanger and found asymmetric gene flow from the largest populations to the smaller populations. It follows that it is important to maintain large population size in river systems with the largest sea trout populations and that future population recoveries will be mediated primarily by the remaining large population (Hansen et al. 2007). This underlines the importance of the stable or increasing populations in Eidsfjord, Granvin and Etne found in the present study which may help to explain the overall increasing population size of sea trout in the Hardanger system found in the present study. Possible gene flow from larger to smaller populations has also been reported for brook trout (*Salvelinus fontinalis*) in Quebec, Canada (Fraser et al. 2004). As a follow up of the data presented in this study, we have used video surveillance between 2017-2020 to study the population size of six rivers in the Hardanger system with one river previously not studied (Mundheimselva). This river is in the heart of the aquaculture production area in Hardanger surrounded by 8 salmon farms in a 10 km radius. In spite of this, it was found that the Mundheimselva had one of the largest densities of mature sea trout in 2017 (61 ind./hectare, Lamberg and Kvitvær 2018) much higher than found other rivers

in the Hardanger system in 2017 (22 ind./hectare, Skoglund et al. 2018). Mundheimselva is a small river with insufficient water volume to sustain overwintering of salmon and anadromous sea trout compared to e.g. the Granvinvassdraget (Lamberg et al. 2018), so it is only possible to monitor the mature individuals within the population. It is still unknown where the immature individuals from this river can be found during winter. Tagging and tracking should be used to solve this problem as this will also help us to understand how sea lice affects the fish during its life cycle.

In conclusion the present study shows that both salmon and anadromous sea trout populations were found to be increasing in the study area in the period studied. Present data show that 7 out of 7 of the salmon populations and 4 out of 7 anadromous sea trout populations studied are increasing indicating good natural growth of the populations.

Delprosjekt 2. Utvikle en helhetlig overvåkingsmodell knyttet til produksjonsområdene

FoU-aktiviteter; gjennomføring og metode

Study 1. Evaluation and comparison of three methods for estimating Atlantic salmon smolt (*Salmo salar*) outmigration timing¹

Introduction

Migration of juvenile salmonids from freshwater to marine environments for increased feeding/growth opportunities, but with high mortality risk, is a common life-history strategy. In Atlantic salmon it is present as a fixed trait in most populations. Migration entails preadaptation of hypoosmoregulatory capacity (smoltification) and a subsequent movement to open ocean feeding areas in the North Atlantic ocean (Gilbey et al., 2021). Reduced population sizes of Atlantic salmon may in part be explained by reduced survival in the marine phase of the life-cycle (Thorstad et al., 2021). Timing of migration is of obvious importance for survival and growth in this highly seasonal environment, and the phenology of smolt (freshwater) and post-smolt (marine) migration in salmonids has been studied for decades. The general pattern in Atlantic salmon smolt is spring migration coordinated by increased daylength and initiated as response to a temperature increase/threshold (refs) and/or increased water discharge (refs). Individuals having reached size (10-16 cm) and body energy thresholds during the previous growth season leaves their lotic environment during a period of 6-8 weeks. There are exceptions to this generalized pattern, such as autumn migration and prolonged migration windows (ref). With clear genetic structuring between regions and populations in Atlantic salmon (Bourret et al. 2013), local adaptation in migration timing seems highly likely, and has to some degree been documented between (Birnie-Gauvin et al. 2018) and within populations (Miettinen et al. 2021). The relatively recently occurring anthropogenic impact of increased sea-lice (*Lepeophtheirus salmonis*) infection pressure from coastal salmonid aquaculture (e.g. Hvidsten et al, 2007; Dempster et al., 2021) is migration timing-dependent (Bøhn et al. 2020). The observed and modelled (Asplin et al. 2011) production and dispersal of sea-lice eggs from aquaculture, as well as time required for development into infectious life-stages (Asplin et al. 2011) generally causes a sharp increases in infection pressure as spring progresses (Johnsen et al. 2020). However, within-year variation in both sea lice production at the aquaculture sites and variation in hydrological conditions may affect timing and magnitude of this pattern (Sandvik et al. 2020). The use of predictive models in management/conservation efforts in Norway requires realistic input on wild smolt/post-smolt migration in time and space (Sandvik et al. 2016). Subsequent regulatory measures towards the aquaculture producers rely in part on migration timing estimates and assumptions of migration patterns (Vollset et al. 2018). A data resolution of one-week intervals is currently used in the impact assessments. The median date of migration for each specific salmon population is either estimated from actual data from each river, or (in most cases) based on estimates from other rivers in the region if river-specific data is lacking. Both the accuracy and precision of this approach may be called into question. When incorporated into predictive models that ultimately derive an estimate on sea-lice induced mortality for each wild salmon population, a “virtual post smolt model” using an equal number of daily migrants from each river for 40 consecutive days centered around estimated median migration date has been used. This approach has been further developed using skewed migration patterns (Johnsen

¹ Dette er foreløpig draft utgave av fag-felle manuskript med det målet å lage en helhetlig overvåkingsmodell for en PO (her PO3).

et al. 2020), but hitherto not included data obtained directly from monitoring smolt migration in the rivers. The reliance on median and percentile estimates of outmigration may be a less than ideal approach, given the multimodality of migration documented for a number of populations (Urke et al., 2013a; 2013b; 2014 Bjerck et al., 2021). Accurately estimating the timing and pattern of the migration of Atlantic salmon smolt from their natal rivers to the adjacent coastal areas has therefore become an issue of increased focus.

Several methods are available to monitor when smolts are leaving freshwater. Permanent traps are used as monitoring tool in select rivers with the generation of time-series data (Imsa, Talvik, Burrishole). Permanent traps are located either in smaller rivers where such structures are more easily maintained, or as part of hydropower dam infrastructure (Stjørdalselva mm). Rotary screw traps are a monitoring tool used in both large and smaller rivers (e. g. Storelva, Driva). Such traps capture a portion of migrating smolts and estimates of timing and magnitude of the smolt run can be made. However, the sensitivity to water discharge and avoidance of the traps during favorable light conditions may influence these estimates. Apart from temporary or permanent physical traps, several tagging methods are available. Also, camera technology is currently being used in many monitoring programs. Choice of method(s) may influence the timing estimates substantially, as recently reported for Norwegian rivers by Vollset et al. (2021). However, the same methods are never applied simultaneously in the same rivers in the Vollset et al. (2021) dataset, leaving some uncertainty as to whether the reported differences are due to differences between rivers and years rather than methodological. To further elucidate this issue, we compared 3 of the available methods (Acoustic telemetry (AT), Passive Integrated Transponder telemetry (PIT) and camera transect registrations (CAM) at two rivers in Western Norway for 2 consecutive years (2019-2020) during spring smolt migration (April-July). The analysis aims to inform possible methodological biases and their influence on the resulting estimates, as well as offer some insights into the pros and cons of choice of method. Finally, we discuss the use and usefulness of obtained data in model applications to further the knowledge-based management of Atlantic salmon populations.

Materials and methods (NB. Work in progress)

Study area

The Bjørnafjord and Hardangerfjord systems in Western Norway are some of the most intensified production regions for salmonid aquaculture in Norway, and they are extensively studied to elucidate effects on wild salmon. Two rivers located in the area, with differing distance to open ocean and differing climatic/hydrological profiles were chosen in this study.

The river Granvin is located in the inner part of Hardangerfjord and drains into Granvinsfjorden, an arm of inner Hardangerfjord. The watershed is primarily mountainous; the 25th percentile of elevation of this watershed is 461 m above sea level. The river is Xkm long between a 4.1 km² lake and the outlet into the fjord.

The river Os is drains into the outer parts of Bjørnafjord, at roughly the same latitude as the river Granvin, but much closer to the sea. This watershed is primarily comprised of farmland and low-lying hills. Due to its proximity to the open sea and lower elevations, runoff is more important than the snowmelt for the dynamics of this river.

Methods

Acoustic telemetry: Coded sound signal (kHz range) emitted by tag typically intraperitoneally in salmon smolts (e.g: xxxx). Depending on tag type, a coded ID signal alone, or in combination with sensor data such as temperature and depth, is transmitted at regular intervals and recorded if within deployed receiver range. Acoustic telemetry is typically used for the benefits of functionality in both freshwater and marine environments, and enables data collection from large portions of the coastal migration. Detection range and probability is dependent on receiver

array but is typically high in geographically restricted estuarine environment. In a turbulent river environment, detection range is more restricted and.

Specifically, for this study, pre-smolts were collected by electrofishing in early/mid-April, tagged and returned to the river to enable natural migration progression. Individuals were deemed probable smolts by size and physical appearance (silvering of body, darkening of fin margins) and tagged using XX, XX, XX tags supplied by ThelmaBiotelAS. Detailed description of tagging procedure can be found in Bjerck et al, 2021). Animal ethics permits (XXX, XXX) detailed size limits for tagging with the different tag types. Migration time was estimated as the first detection in the estuary after the last detection in freshwater.

Downsides: smolt size and number, representativity. Catching and handling of fish, including tag size. Mostly focused on the latter

PIT:

Description of methodology used in these river-years for PIT method.

CAM:

Description of methodology used in these river-years for camera method.

Results (NB. Work in progress)

Table 1: Overview of the numbers of fish tagged and/or recorded as migrators for each method, river, and year, along with the quantiles of migration timing.

River	Year	Method	N Tagged	N Recorded	25 %	50 %	75 %
Granvin	2019	AT	50	32	24-04	08-05	20-05
		PIT	378	32	19-05	20-05	24-05
		CAM	NA	171	17-05	20-05	22-05
	2020	AT	56	37	24-04	20-05	23-05
		PIT	856	31	26-04	02-05	22-05
		CAM	NA	142	09-05	22-05	27-05
Os	2019	AT	106	86	24-04	28-04	27-05
		PIT	1997	118	24-04	02-05	07-05
		CAM	NA	1557	24-04	29-04	01-05
	2020	AT	60	51	16-04	29-04	07-05
		PIT	1050	128	08-05	12-05	24-05
		CAM	NA	1116	02-05	06-05	10-05

Table 2: Discussion on pros and cons of each method

	AT	PIT	CAM
Sample size			
Detection probability			
Species recognition			
Night vs day			
Down-time/failure			
Capture & handling fish			

Analysis 1:

Test for significant differences between each method within each river-year using non-parametric tests, though this tells us little about how or why these methods may be different.

Analysis 2:

With acoustic and PIT data, we will use a generalized linear mixed model to test the effects of temperature, day of year, water discharge, and daily change in discharge on the number of smolt that migrated on a given day with a given number of smolt that could have migrated on that day. Maybe others have opinions on how best to measure change in discharge, but the difference between that day's discharge and the previous day's discharge seems to be the easiest and the most intuitive.

With camera data, we don't know how many smolt could have migrated on a given day, so we might have to model it a bit differently, but the basics will be the same.

Analysis 3: Multimodality

This uses a clustering algorithm from the R package `mixsmsn` to estimate the number of overlapping distributions you would need to best explain the shape of the migration distribution. This can also estimate the size and shape for these distributions. We can then check for statistical differences between these distributions across methods. This will tell us whether the different methods are capturing the same 'peaks' in migration.

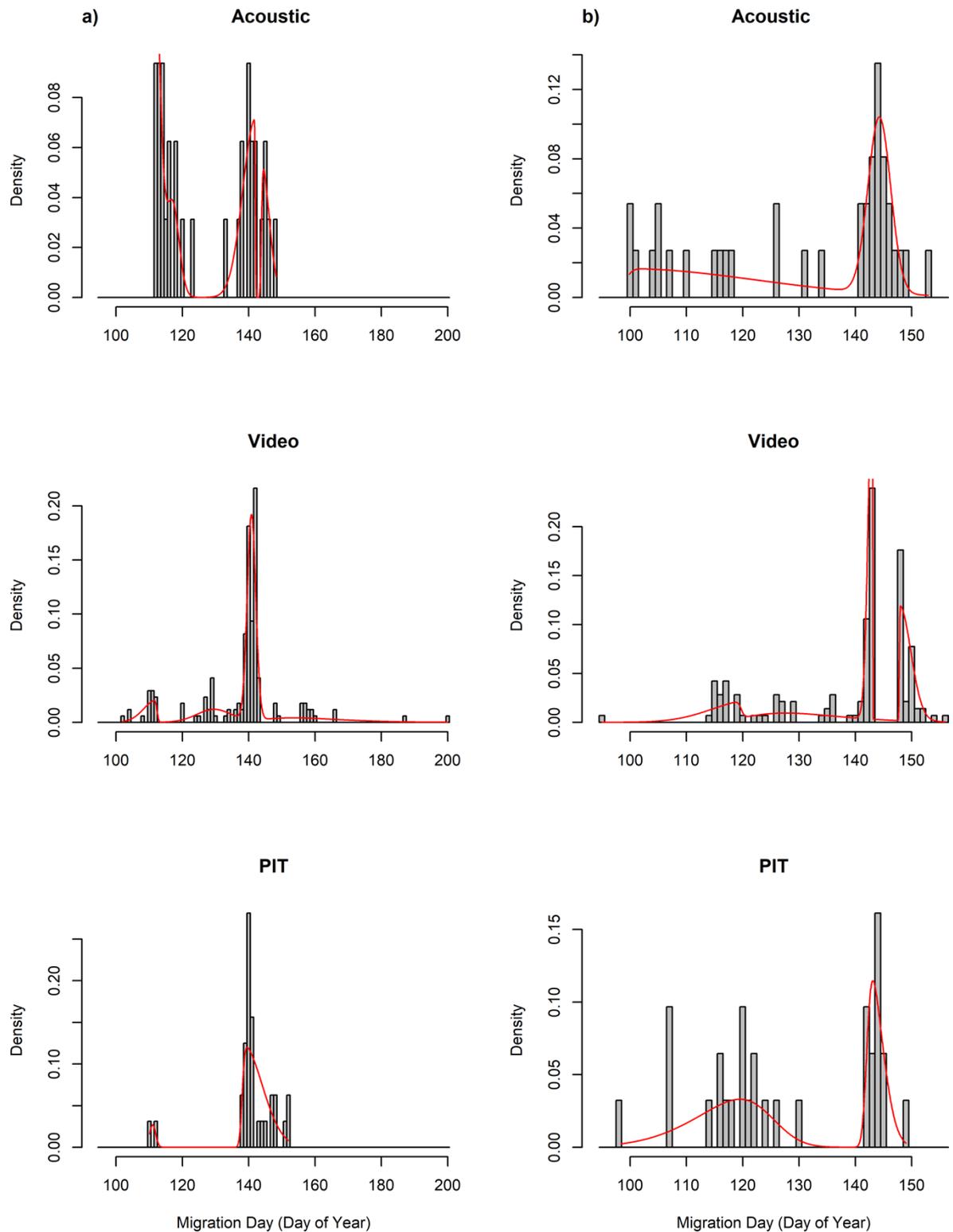


Figure 1: Histograms of migration dates, along with red line showing clustering results for each method in the river Granvin. Column a) and b) show migration dates for 2019 and 2020, respectively.

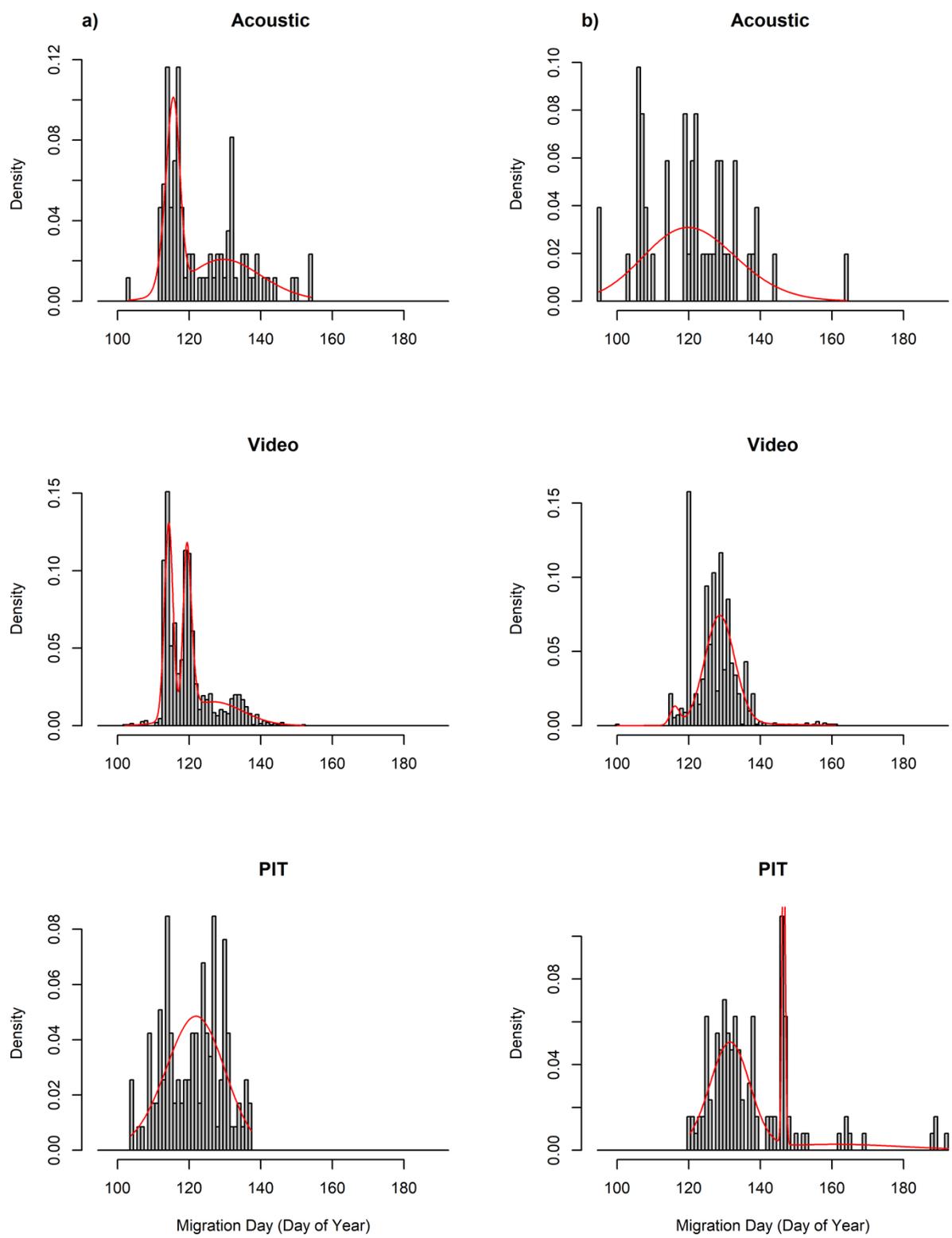


Figure 2: Histograms of migration dates for each method, along with red line showing clustering results, in the river Os. Column a) and b) show migration dates for 2019 and 2020, respectively.

Analysis 4: Sensitivity to Environment

We will look for differences in the number of fish detections relative to environmental conditions such as time of day and water discharge, e.g. Figure 4. Do some methods only detect fish under certain conditions? We will discuss whether this may be due to biological reasons or methodological reasons.

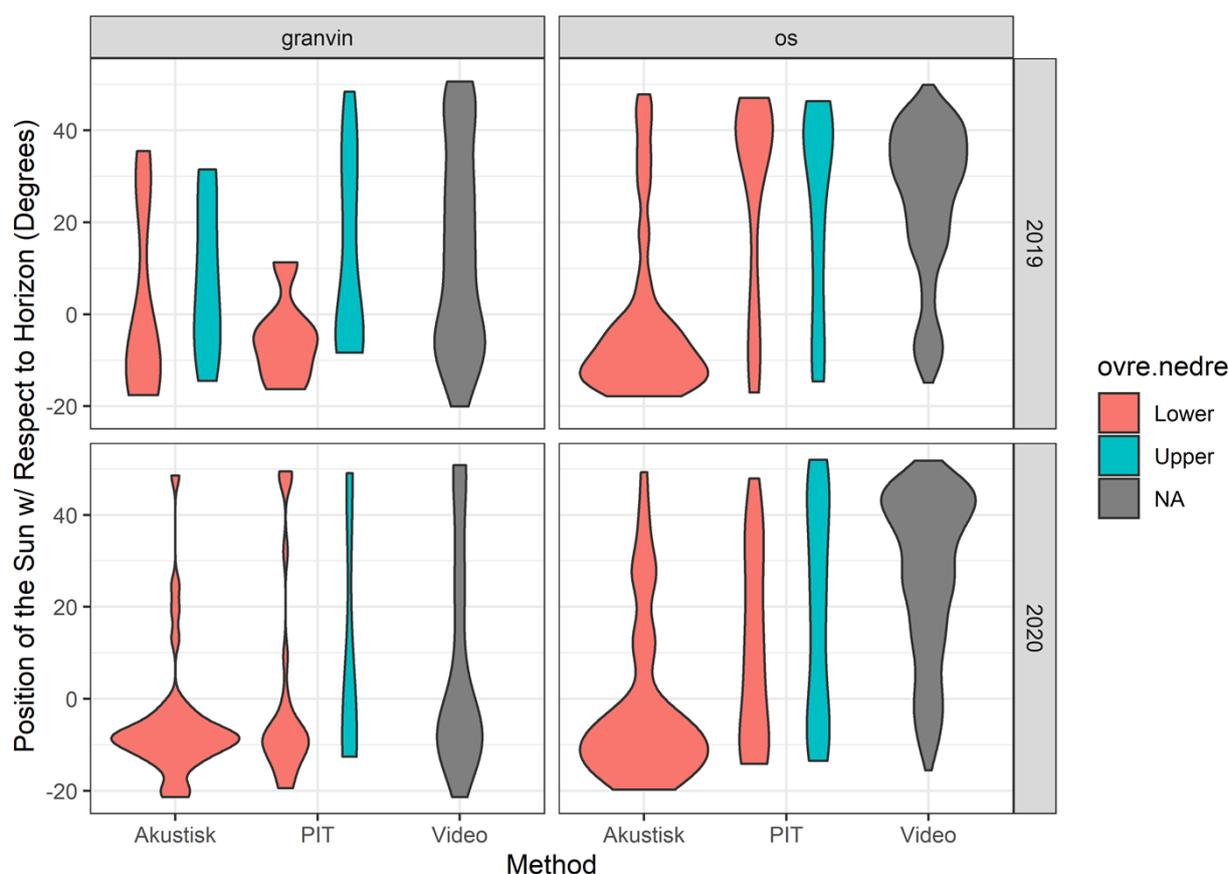


Figure 3. Violin plots showing the position of the sun with respect to the horizon in degrees at recorded migration times for each method, year, and river. Violins are colored red for those smolt captured and released in the lower portion of the watershed, and blue for those from the upper portion of the watershed.

Discussion

We compared 3 methods used in parallel in two rivers for two consecutive migration seasons (2019 and 2020). Pre smolts tagged with PIT and Acoustic Telemetry tags, and camera transects close to river mouth was compared. Results show rather large deviations in some river years when the current model input parameter 25th or 50th date of migration for each population was compared, while the results were virtually similar in other instances. None of the methods consistently produced migration data approaching a normal distribution over time that would lend itself to an accurate description by using the aforementioned percentiles, nor do the data support using a fixed 10-day interval between 25% and 50% migration, as variation here was substantial. We therefore recommend abandoning this approach in rivers with sufficient monitoring data in favour of using more realistic migration scenarios in future risk assessments.

Delprosjekt 3. Sammenligne bestanden av sjøørret og villaks fra elvene i PO3 med tilsvarende elver/områder nasjonalt

Aktiviteter; Gjennomføring og metode

I DP3 skal vi måle bestandsutviklingen ved bruk av data fra drivtelling, fangst og videoovervåking. Målet er å beregne totalt innsig av laks og sjøørret til et fjordsystem og sammenligne dette med et sammenlignbart fjordsystem. Ulike menneskeskapte påvirkninger i de ulike fjordsystemene klassifiseres og variasjon i bestandsutviklingen skal testes mot variasjon i påvirkning.

Study 1. Using merged pre-fisheries abundance as a parameter evaluating status of Atlantic salmon and sea trout populations: a Norwegian case study

ABSTRACT: Methods used to monitor variation in population sizes in both Atlantic salmon and sea trout have been widely used in Norway the last 20 years. However, a national management regime where population data is used, is only established for one of the two species, the Atlantic salmon. One prerequisite for using this “one species” model is that there is negligible intraspecific competition between salmon and trout in the rivers. This may be an oversimplification of the real situation. The pre fisheries abundance (PFA) monitored with underwater video systems will in most rivers include, both salmon and sea trout. In the present study we estimated a total PFA for rivers or groups of rivers in eight small regions in Norway in 2019. The total size of each river system measured by abiotic factors like river area, river length, annual mean water flow and size of precipitation field, and one biotic factor, smolt age, was used to standardize PFA data across regions. A comparison shows that total PFA of salmon and trout are varying among regions where the highest estimated PFA was four times higher than the lowest. Compared to the traditional one species approach the merged PFA data show a different population status in the eight regions. The difference in the two approaches was mainly linked to variation in sea trout populations. Merging data from salmon and trout populations in defined regions, may draw a more relevant picture of population status as a means to evaluate anthropogenic impact.

1. RESULTS

3.1. Comparing salmon spawning target in the eight river regions in 2019

According to the estimated region merged spawning target for Atlantic salmon the total weight of female spawners corrected for river areas varied between the eight river regions. The highest value was found for region 5, Orkla and the lowest for region 7 (Fig. 2). In 2019 the recorded biomass of females in the spawning populations that year measured in proportion (%) of spawning target (conservation limit = 100 %) in the eight regions was highest in region 1, 2 and 6 and lowest in region 5 (Fig. 3).

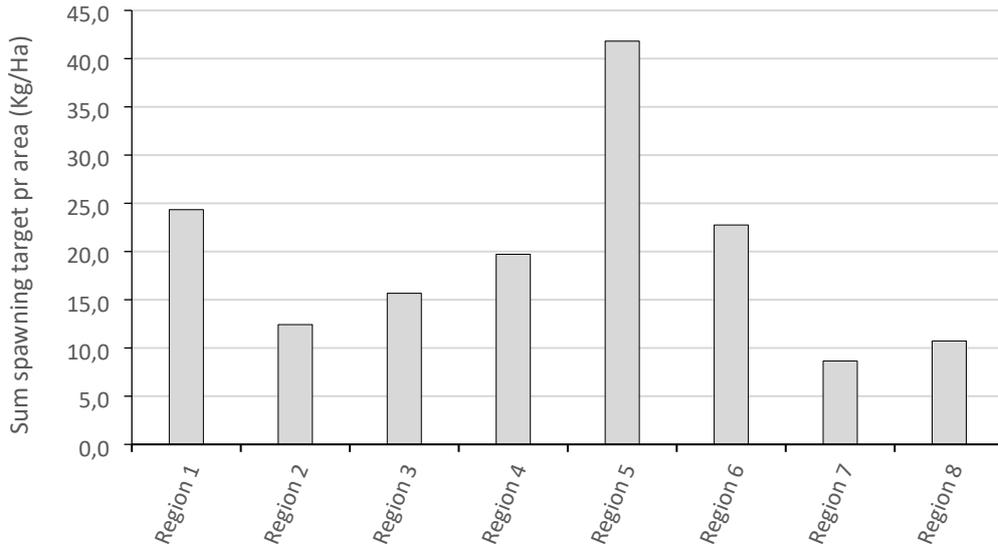


Fig. 2. Spawning target (ST) (modelled conservation limit) summed for all rivers in each of eight studied regions. The ST is corrected for total river smolt production area.

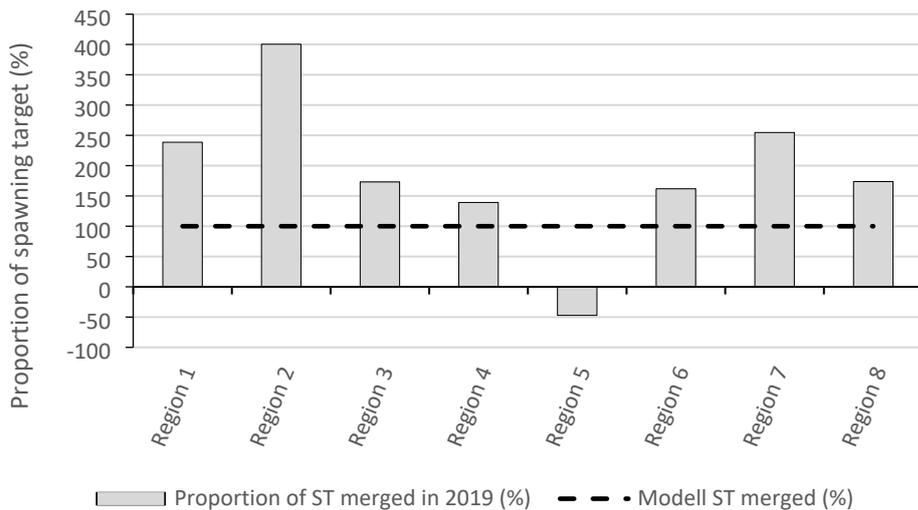


Fig. 3. Estimated total biomass of spawning females merged for all rivers in each of the eight regions in 2019 expressed as proportion (%) of modelled spawning target (ST = 100 %). (data from annual report 2020: Norwegian Scientific Advisory Committee for Atlantic Salmon).

3.2 Comparing total PFA in eight geographical regions in 2019

Total PFA for each of the eight river regions were estimated and controlled for merged river area and smolt age. The comparison of the eight regions shows a varying number of salmon and trout entering the coast outside the rivers in 2019 (Fig. 4). Three of the river regions, regions 1, 3 and 6 have a total PFA that is from two to four times higher than in the other regions.

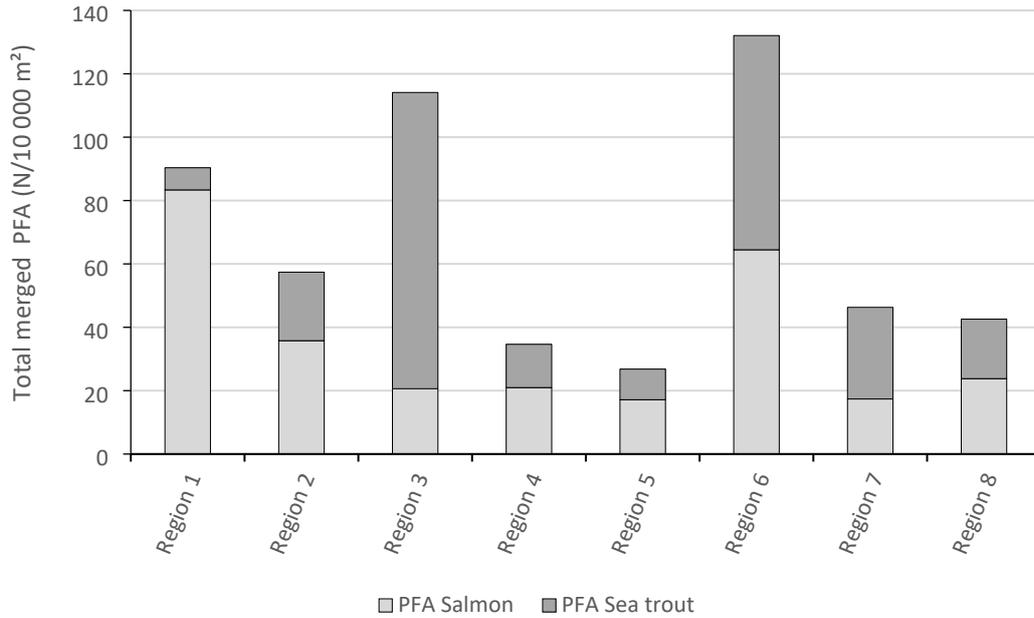


Fig. 4. Total PFA corrected for river area and smolt age merging data on Atlantic salmon and sea trout in the eight studied regions in 2019.

3.3 Comparing the ST- and the PFA-approach in 2019

Comparing the ranks of the eight regions for the ST-approach and the PFA-approach in 2019 show that one region is given the same rank (river region 1). In some regions the PFA-approach give higher ranks (region 3, 6 and 8). In the other regions the PFA-approach results in lower rank than the ST-approach (region 2, 4, 5, and 7) (Fig. 5).

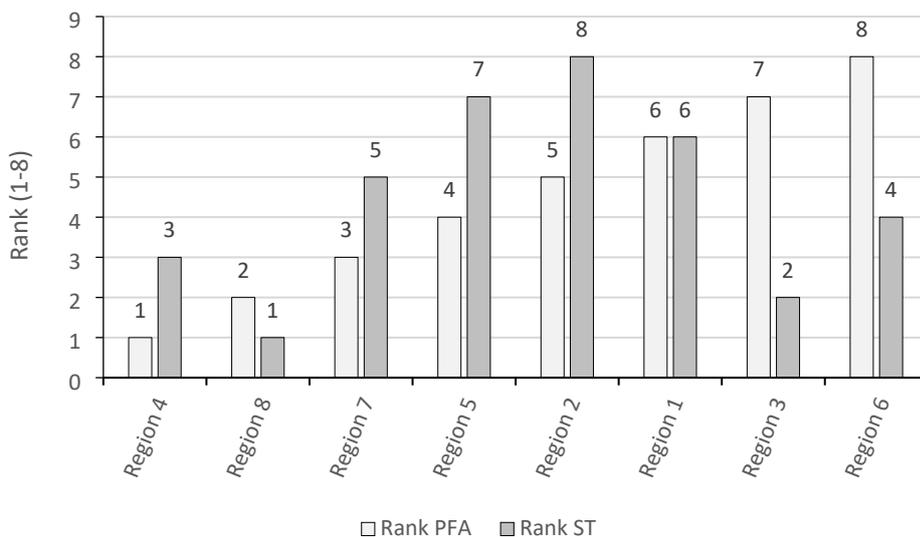


Fig 5. The ranking of the eight regions from 1 (lowest) to 8 (highest total biomass of spawning females/highest number of fish in PFA)

3.3 Average smolt age

The average smolt age registered in the eight studied regions varied from 2.3 to 4.1 years (Table 2). It was not possible to find data on smolt age for both salmon and trout in all rivers. Where data from both species were available, smolt age seemed to be the same for salmon and trout in most cases, but not always. Smolt age will also vary over time within rivers but there is a general increase in smolt age with latitude due to lower temperatures going from south to north (Fig. 6).

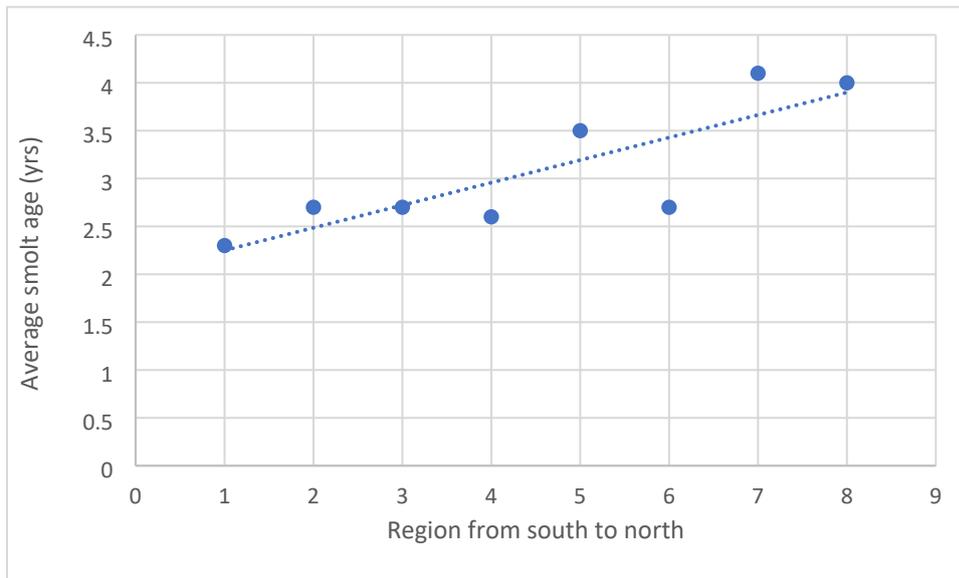


Fig. 6. Average smolt age in the eight studied river regions.

3. DISCUSSION

The goal of this study was to test a way of measuring how anthropogenic factors in general, affect Atlantic salmon and sea trout. This was done through monitoring population sizes by using video counts of individuals entering rivers (river PFA) or snorkelling counts on the spawning grounds. Together with catch reports both from the sea and from the rivers it was possible to estimate a total PFA controlled for total river smolt production area and smolt age in one single, or several rivers merged, draining out into a defined part of a fjord. The test was performed on 2019 PFA data in eight such regions or parts of fjords. The use of methods aiming at total counts of individuals in populations remove, to a greater extent, the problem of large confidence intervals linked to methods using sampling (e.g. catch statistics). However, the ambition of counting all individuals in populations by means of methods relying on visual identification, also introduces some potential uncertainty (e.g. Stien et al. 2017). The use of a total PFA as a parameter is still partly dependent on some uncertainty of catch statistics but now only linked the one-sided effect from unreported catches and not the two-sided uncertainty of the confidence intervals combined with the unreported catch as earlier.

The test show that the total 2019 PFA of the eight selected fjord regions with corresponding rivers, was varying more than four times from the region with the lowest estimated total PFA to the region with the highest. This large variation indicates that some anthropogenic factor is

affecting the populations. The expected result would to a greater extent similar PFA-values in the eight studied regions due to a standardisation of smolt production area and smolt age.

There was a difference in the ranks of the eight regions between using the ST-approach and the PFA-approach. This is probably due to the introduction of sea trout in the numbers. Since 2009 the state of many of the over 400 salmon populations in Norwegian rivers have been evaluated by use of the concept spawning target (Forseth et al. 2013). Theoretical models made for eight different populations/rivers have been used as benchmark for a varying number of the more than 400 Norwegian salmon rivers each year (Anon 2020). Theoretical models often simplify the real world and real ecosystems. That is also the case with the spawning target model. One such simplification is that there is no input data in the salmon model concerning the size of the sea trout population in the same river. It is suspected that there is density dependent competition between salmon and trout (Pulg et al. 2019), especially in all the stages from swim up to the smolt stage (Einum 2005; Jonsson & Jonsson 2011). If the salmon spawning target model does not involve population data on trout, it only tells a part of the story. That is why our study test the use of both species in a combined total PFA. A region where both species thrive may be a sign of less anthropogenic effects on the fish, compared to regions where the populations are small when controlled for total river area. Since we do not know if there is a constant number balance between the two species is, a better approach may be to merge the two data sets.

In regions/fjords made up of many small rivers that are located close to each other, there is a question if there are unique salmon and trout populations in each river or if there is a greater extent of mix (Hindar et al. 2004; Hansen et al. 2007). Both video surveillance projects (Lamberg & Kvitvær 2018; Lamberg et al. 2018a, b) and snorkelling projects (Skoglund et al. 2019) especially in region three in our study, show that there is a relatively high proportion of adipose fin clipped fish in many rivers where no such tagging method is used. This indicates that there are both trout and salmon entering rivers where they have not grown up to smolt stage. These are fish from “foreign” rivers that are possible to detect with our visual methods. The ones that are not tagged are not singled out in the same way, a fact that indicate that there is mix of fish from several “populations” in many of the small rivers. In several of the 27 rivers of this study, the water course contains one or more lakes or large water volumes where sea trout, both immature and mature, may stay over winter. In our study we have chosen to merge data from several rivers within a region, since there is probably a large proportion of the sea trout that will spawn in a different river from the waters where it stays over winter. A sea trout migration between rivers has been indicated in several studies (Klemetsen et al. 2003, Degerman et al. 2012; Lamberg & Gjertsen 2017).

In the last years, commercial Atlantic salmon sea fisheries activity has been reduced on both sides of the Atlantic (Limburg & Waldman 2009) including Norway (Anon 2020). In general, relatively few trout end up in sea catches (Arnekleiv et al. 2014). The recreational fishing for salmon and trout in the sea, however, has increased in the same period. Since the catch from this activity is not reported, there are no good documentation of the increase. In this kind of fishing, learning techniques from others can change the success rate. The introduction of social media, discussion groups and video sharing apps on internet (e.g. Facebook from 2006 and YouTube in 2005) have probably increased the interest for salmon and trout sea recreational fishing and the skills of the individual practitioner. An increasing part of the total number of

salmon and sea trout removed in the fjords and on the coast and not reported will result in a lower measured total PFA. Obtaining an exact total salmon and trout PFA for rivers or aggregations of rivers (merged numbers), could be a method for evaluating the overall situation for the two species. Since the Norwegian national farmed salmon production regulation system (“Traffic light system”, Vollset et al. 2017; Myksvoll et al. 2018) reports the state for each of 13 regions, a verification of status of wild anadromous fish in each of these regions could work as a verification tool for the theoretical models. Bringing in the sea trout in the models can be an important step to measure the effect of sea lice since the trout spends more time in the fjords, than the salmon.

Methods for monitoring variation in population size through estimation of pre fisheries abundancy for both Atlantic salmon and sea trout have been widely used in Norway, especially the last 20 years (Skoglund et al. 2018, 2019; Anon 2020). The use of traps covering whole river cross sections, snorkelling and underwater video surveillance have improved data on PFA compared to earlier years where sampling methods were more common. Of these sampling methods, catch reports and statistics, were dominating. Sampling data will be inherently imprecise due to often small sampling sizes and lack of required random sampling procedure (Løland et al. 2016). To be able to use catch data to estimate total population sizes, knowing the catch rate was prerequisite. However, the catch rate varies between rivers and years and will be influenced by, among other factors, fishing conditions, fishing rules, and river morphology. Another problem with catch statistics the last 20 years, is that an increasing number of rivers have been closed for recreational fishing (Langset & Staldvik 2011), so there are no catch reports available to estimate population size. The introduction of methods which aim at counting all individuals in a population, or more correctly, all the individuals returning to a river each year, has improved the data on population development for both Atlantic salmon and sea trout Svenning et al. (2016). A more precise description of these methods is that they aim at counting all individuals above a certain age and life history stage.

In small rivers where salmon and trout are not able to stay over winter, due to small water volumes in the cold part of the year, the fish often show a “hit and run” strategy (Lamberg & Kvitvær 2016). They will enter the small river when water levels are sufficient in the time frame of spawning and after spawning, return to sea water or another river for winter stay. The use of snorkelling method may give underestimates of PFA in such small rivers and in water courses with lakes. Especially that holds for sea trout where large parts of the individuals are either immature or having a resting year from spawning. Both groups will when a lake is available, stay in a large water volume where it is not possible to perform a snorkelling count. Even if data on variation in population size can be relevant for evaluating impact from anthropogenic factors in general there remains a question of how to define a population. Measuring PFA involves catch data from the sea, a catch that involves mixed populations. In addition, the fish entering the rivers are also in many cases a mix of populations. One way of bypass this obstacle is to merge data from several populations in an area and treat them as one as done in the present study.

4. CONCLUSION

In this study, using PFA estimates from 2019, it is suggested that the merged PFA may be a more relevant parameter to separate the effects of different anthropogenic factors, and especially the effects of sea lice. The study also points out what parameters should be monitored in the future to make the model more robust. In addition to video surveillance and snorkelling, measuring PFA depend on correct catch statistics. Correct statistics may be achievable in the rivers, but presently not from the sea. Increasing unregistered trolling catches from the coast and the fjords for both anadromous species the last years will disturb the FPA estimates. The ambition of monitoring whole ecosystems is at present probably unrealistic but an introduction of a reporting system for all catch of Atlantic salmon and sea trout in sea water will improve the possibilities of measuring other anthropogenic factors that affects these two species.

6 Hovedfunn

- Forskningen i SALT2020 indikerer at laksen svømmer ut 2-3 uker tidligere enn det modellene brukt i trafikklysordningen (TLS) legger til grunn.
- Registreringene i SALT2020 viser at laksen oppholder seg 8-10 dager i fjorden, mens TLS har satt 26 dager for Hordaland og Sogn og Fjordane.
- Forsøkene med akustiske merker (radiomerker) hos laks- og sjøørretsmolt har vist at vassdrag med innsjøer og en øvre/nedre elvestrekning, har avvikende utvandringstidspunkt med opptil 2-3 uker.
- Funnt fra forsøk med PIT-merker indikerer at sjøørreten vandrer mellom ulike elver, at den går opp og avluser seg, svømmer videre i fjorden, og så hjem igjen til opprinnelig elv.

7 Leveranser

All forskning som utføres i prosjektet skal kunne publiseres, og iht. FHF sin norm for bl.a. sluttrapportering. Følgende konkrete leveranser følger av prosjektet og er blitt levert i prosjekttiden.

1. Åpent oppstartsmøte med prosjektgruppe og referansegruppe (juni 2019)
2. Populærvitenskapelig artikkel/presentasjon av SALT2020 (juli 2020)
3. Presentasjon på AqKva 2019 - 2021 (januar hvert år).
4. Vitenskapelig publikasjon fra DP1 (status villaks og sjørret i PO3) (juni 2019)
5. Presentasjon på FHF møte/seminar (2019 - 2021)
6. Vitenskapelig publikasjon fra DP3 (bestandssammenligning av villaks og sjørret i PO3 og andre områder) (april 2020)
7. Populærvitenskapelig artikkel (hovedfunn DP1) (august 2020)
8. Vitenskapelig publikasjon fra DP2 (utvikling av helhetlig overvåkingsmodell i en PO) (juni 2021)
9. Åpent avslutningsmøte med prosjektgruppe, styringsgruppe og oppdrettere i PO3 (juni 2021)
10. Populærvitenskapelig artikkel – hovedfunn DP1-3 (august 2021)
11. Faglig og administrativ sluttrapport (høst 2021)

Vedlegg 1. Arbeidspakke 1. Synchrony and multimodality in the timing of Atlantic salmon smolt migration in two Norwegian fjords

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Synchrony and multimodality in the timing of Atlantic salmon smolt migration in two Norwegian fjords

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The timing of the smolt migration of Atlantic salmon (*Salmo salar*) is a phenological trait increasingly important to the fitness of this species. Understanding when and how smolts migrate to the sea is crucial to understanding how salmon populations will be affected by both climate change and the elevated salmon lice concentrations produced by salmon farms. Here, acoustic telemetry was used to monitor the fjord migration of wild post-smolts from four rivers across two fjord systems in western Norway. Smolts began their migration throughout the month of May in all populations. Within-population, the timing of migration was multimodal with peaks in migration determined by the timing of spring floods. As a result, migrations were synchronized across populations with similar hydrology. There was little indication that the timing of migration had an impact on survival from the river mouth to the outer fjord. However, populations with longer fjord migrations experienced lower survival rates and had higher variance in fjord residency times. Explicit consideration of the multimodality inherent to the timing of smolt migration in these populations may help predict when smolts are in the fjord, as these modes seem predictable from available environmental data.

Juvenile Atlantic salmon (*Salmo salar*), known as smolts, migrate to the sea from their natal rivers as a part of their natural life cycle. Throughout the range of this species, this migration occurs mostly during spring and early summer when smolts are 1–6 years old and at a size of 12–25 cm^{1,2}. However, the timing of migration within each population is highly variable, both within and between years^{3,4}. In addition, climate change and the rise of aquaculture are significantly altering the fitness consequences of this variation which may have profound consequences for the overall health of these populations. As a result, understanding between- and within-population variation in migration timing, and the factors that structure this variation, has become more important than ever.

Return rates to the river indicate that an optimal migration time exists⁵. There seems to be a consistent positive effect of high sea surface temperatures during outmigration on return rates across Norwegian populations, likely due to increased prey availability^{6–8}. However, smolts arriving in the sea too late may run the risk of missing out on optimally sized prey items⁹. As such, smolts face the fundamental problem of needing to determine the optimal time to migrate using conditions within freshwater when the conditions that determine this optimality are in the ocean, far away in space and time. As there is no guarantee that the freshwater environment and the marine environment will change in tandem, this potential for phenological match-mismatch will likely grow as the climate changes^{1,10,11}.

Smolts migrating from the river to the open sea generally experience substantial mortality rates, primarily because of predation, but also because of the physiological and metabolic challenge of migrating long distances to drastically different environments^{12,13}. Adding to this, the post-smolt migration period is the period in the salmon lifecycle where it is the most susceptible to salmon lice (*Lepeophtheirus salmonis*) infestation¹³. Net-pen production of salmonids has vastly increased the number of available hosts for parasitic salmon lice, consequently increasing the numbers of these ectoparasites in the waters surrounding fish farms^{14,15}. As most fish farms are located in the coastal archipelago between the mouth of the fjord and the open sea, post smolts must necessarily risk infestation to complete their migration. However, modelling and monitoring of salmon lice abundance

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Vedlegg 2. Arbeidspakke 1. Manuskript til peer-review vitenskapelig artikkel

Det understrekes at manuskriptet ikke kan kopieres, refereres, eller på annen måte brukes før etter at dette er publisert som forfatterevaluert (per-reviewed). Manuskriptet sendes til behandling i en vitenskapelig journal høsten 2021.

Population status of wild salmonids in an aquacultural area: a case study from the Hardangerfjord, Western Norway

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KEYWORDS

Atlantic salmon; sea trout; salmon farming; population status; Hardanger

ABSTRACT

The rivers that drain into the Hardangerfjord were historically known to have numerous populations of both sea trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*). After a decline in catches during the last decades many of the rivers have been closed for fishing. In this study we use snorkelling observations from seven rivers in the Hardangerfjord combined with data from recreational fisheries catch statistics from 1999 to 2017 to estimate the pre-fishery abundance (PFA) in the period to describe the current situation and analyse the patterns of density of wild salmon and sea trout in the area. Overall, both salmon and sea trout population were found to be increasing in the study area in the period studied. Present data show that 7 out of 7 of the salmon populations and 4 out of 7 sea trout populations studied are increasing indicating good natural growth of both species in the studied rivers in the Hardangerfjord system.

Introduction

Fjords are unique coastal landscape structures that require enhanced basic and applied biological research (Brattegard et al. 2011; Skaala et al. 2014a). In Norway, efforts have recently been made to study selected fjord systems more effectively and integratively (Skaala et al. 2014a-c). The Hardangerfjord is approximately 180 km long and 2–10 km wide, and is the second largest fjord in Norway (Skaala et al. 2014a). The sill depth is about 170 m, and the fjord has several deep basins with a maximum depth of 850 m. Several large rivers run into the fjord and in the side fjords the surface water is permanently brackish. The rich populations of fish and shellfish have provided food and work since the times of the first recorded settlement, about 8000 years ago (Skaala et al. 2014a). The Hardangerfjord region provides good opportunities for industrial activities based on both the tributary freshwater systems and the main fjord. Consequently, the fjord basin may be affected by a number of local anthropogenic activities, such as agriculture, aquaculture, fisheries, hydroelectric power production, pollution from households and industry, and also through more indirect mechanisms such as climate change (Skaala et al. 2014a). Because the Hardangerfjord system consists of a number of large and small fjord arms and has several connections to the open sea, the current pattern is relatively complicated with large spatial and temporal variability. A detailed description of the fjord physics (currents, temperature, and salinity) can be found in Asplin et al. (2014) and Johnsen et al. (2014). Aquaculture of Atlantic salmon (*Salmo salar* Linnaeus, 1758) is an important industry in the Hardangerfjord system and at present it is one of the fjords with the highest density of salmon farms in the world (Skaala et al. 2014a) with an estimated production of approximately 110,000 metric tonnes with around 150 production sites in the whole area (Even Søfteland, PO3 kunnskapsinkubator, Bergen, pers. comm.).

Anadromous brown trout / sea trout (*Salmo trutta* Linnaeus, 1758) and Atlantic salmon migrate between freshwater and marine environments. To survive and thrive, their habitats must meet a number of physical, chemical and biological requirements (Verspoor et al. 2007).

Changes in both the freshwater environment (Borgström and Aas 2000; Rosseland 2000) and the marine environment, either due to natural causes or human activities (Ford and Myers 2008; Gargan et al. 2012), may affect salmonid populations. The impact on wild salmonid populations as a result of human activities has received significant attention over recent decades, and impact factors are well documented (Skaala et al. 2014c). Atlantic salmon has been in a long-term decline, both in terms of the number of populations and in terms of reduced productivity both in freshwater and the marine environment (Hindar et al. 2011; Fortseth et al. 2013). A number of anthropogenic factors are responsible for the decline, such as loss of connectivity due to construction of dams, hydropower facilities, habitat alternations or destruction, pollution, overexploitation and the more recent effects of salmon farming (such as genetic introgression and increased parasite loads). The problem of genetic introgression may have been previously overestimated as a recent study of 20 Norwegian rivers has demonstrated that there is only a moderate correlation between the observed frequency of escapees and introgression of farmed salmon (Glover et al., 2013). Since the early 1990s, farming of Atlantic salmon and rainbow trout (*Oncorhynchus mykiss*) has intensified, leading to establishment of net-pens distributed throughout the fjord. Concurrently wild Atlantic salmon and brown trout populations have declined in the Hardanger fjord system (Skaala et al. 2014a-c) as well as in other parts of Norway (Taranger et al. 2015).

In 2010 the Norwegian Directorate of Fisheries in close cooperation with the Directorate for Nature Management, the Norwegian Food Safety Authority and the Hordaland County Governor called for an assessment of the anadromous populations in the Hardangerfjord and suggestions for immediate mitigation efforts that could reduce pressure on the populations (Skaala et al. 2010, 2014c). In 2009, the Ministry presented its ‘Strategy for an Environmentally Sustainable Norwegian Aquaculture Industry’ (Taranger et al. 2011, 2015). Five areas in which salmon farming has the potential to negatively affect the environment were stressed: genetic introgression with wild fish, pollution, transmission of diseases including salmon lice to wild populations, allocation of aquatic habitat to fish farming, and the problem of obtaining adequate feed resources from an already heavily exploited marine ecosystem. Two of the goals in this strategic plan are of particular relevance for wild populations of anadromous fish:

- fish farming should not contribute to permanent genetic changes in wild fish populations; and
- diseases in farmed fish must not be allowed to reduce the size of wild fish populations.

To improve the population situation for salmon and sea trout in the Hardanger fjord system Skaala et al. (2014c) suggested a seven-step conservation plan which further highlighted:

- reduction of infection pressure from salmon lice (*Lepeophtheirus salmonis*); and
- monitoring the size of spawning populations.

In order to reduce the infection pressure from salmon lice aquaculture farmers in the Hardanger area have enforced a strict lice controlling regime which have resulted in improved salmon lice situation in the fjord system (Malkenes 2020). Whether this has led to population

growth for salmon and sea trout in the fjord system is at present unknown. By combining data from snorkelling and catch in seven river systems distributed in all parts of the Hardanger fjord system it may be possible to achieve an overview over the population development in the different river systems during the period from 1999-2017. Accordingly, the objective of the study was to investigate the possible consequences of salmon farming on the status of wild populations of Atlantic salmon and brown trout in the Hardanger fjord system by analysing population data from 1999-2017 in seven selected river in the fjord system and comparing with available historical data.

Materials and methods

Study area

This study is based on data from seven rivers draining into the Hardangerfjord, on the west coast of Norway (Figure 1). All seven rivers originate in alpine regions and descend down a steep gradient to a slower-running and anadromous lower part. Even though the habitat conditions vary, all rivers can be considered as functioning reproduction areas for salmon and sea trout. Four of the seven rivers have been regulated for hydropower use. The main regulation effects are caused by changes in water discharge (hydropower plants in side-channels or bypass tubes) leading to reduced water discharge, reduced wetted area and an altered temperature regime. Glaciers are present in three of the seven watersheds, indicating lower summer water temperatures, higher altitude of the drainage area and larger water discharge during summer.

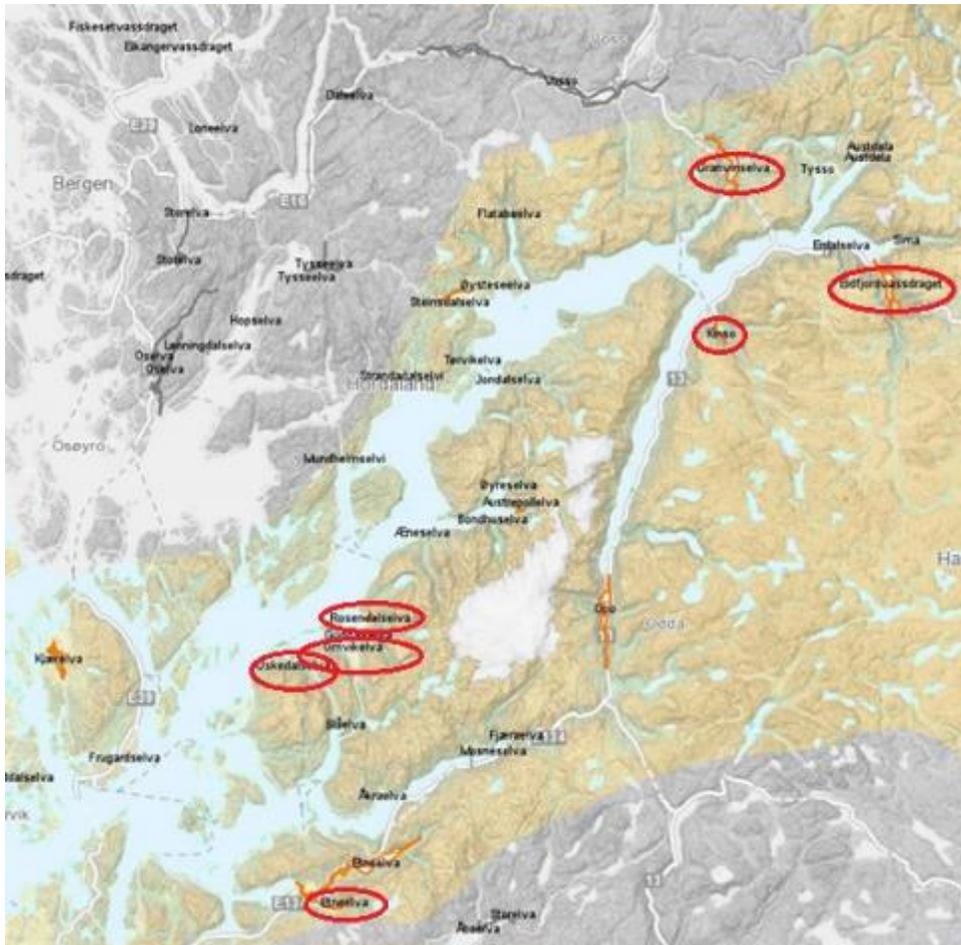


Figure 1. Map of the Hardangerfjord basin, with location of rivers with Atlantic salmon and sea trout studied indicated with red circles.

Snorkelling

The drift snorkelling observations were conducted similar to those described earlier by Orell et al. (2011) and Vollset et al. (2014). In short, the snorkelling teams consist of divers equipped with a dry suit, diving mask, snorkel and neoprene gloves. The snorkelers drift in parallel and make frequent stops to discuss the observations. One team leader notes the exact position of the observations on a waterproof map. In order to avoid double-counting, the count only includes fish that pass the observer in the upstream direction or fish that are holding their position and thereby passed by the diver. Standardization among rivers is obtained by only using trained personnel for snorkelling and by adjusting the numbers of divers to the size and width of the river, i.e. varying from one to three divers in each team.

Snorkelling in Hardanger was conducted annually from 1999 to 2017 during low discharge periods from mid-September to mid-November (Skoglund et al. 2019). This period was chosen to encounter the spawning population, as both sea trout and salmon spawn in autumn (Jonsson and Jonsson 2011). In addition, this represents the time after recreational fishing. Within this period, the date varied between rivers and years according to changing ambient

conditions. The presented in the present study are part of larger regional study in the same period (Skoglund et al. 2019).

Catch data

Data on catch was achieved from recreational fishing for both species in all the studied rivers during the study period.

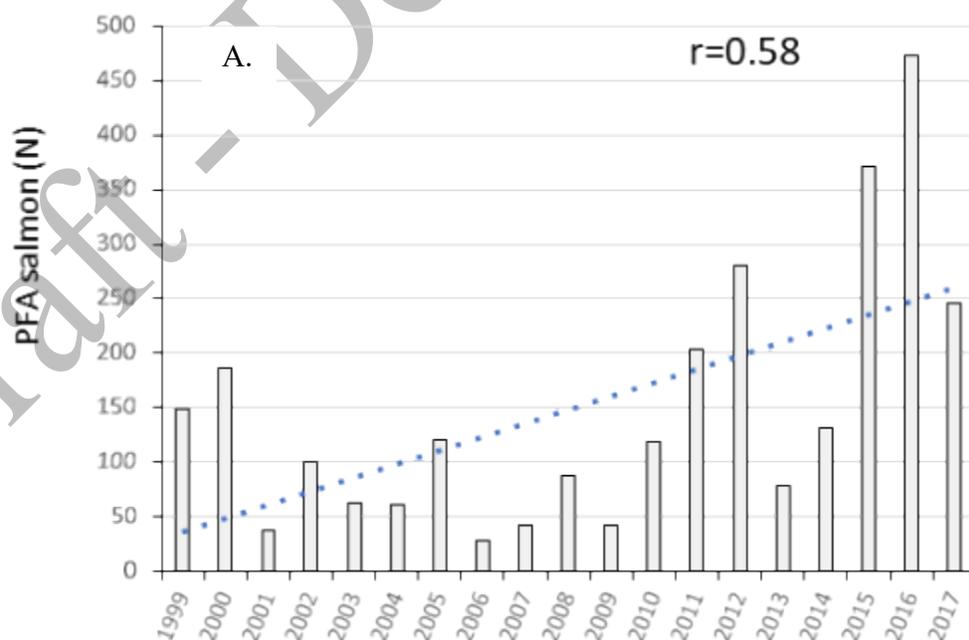
Statistical analysis

All statistical analyses were conducted using Statistica™ 12.0 software. A Kolmogorov-Smirnov test (Zar, 1984) was used to assess for normality of distributions. The homogeneity of variances was tested using the Levene's F test (Zar, 1984). The relationship between pre-fisheries abundance and time (year) was tested using a linear regression (Zar, 1984). A significance level (α) of 0.05 was used if not stated otherwise.

Results

Eidfjordvassdraget

Pre-fisheries abundance (PFA) of Atlantic salmon and sea trout has been studied in Eidfjordvassdraget during 1999-2017 and 2001-2017, respectively (Fig. 2). During this period the PFA of both salmon and mature sea trout has increased significantly ($r = 0.58$ and 0.70 , respectively, $p < 0.01$). The PFA studies in Eidsfjordvassdraget do not include immature trout or salmon that are not at their spawning places once the snorkelling is done. It follows that the numbers found are minimums number for the populations of both species in the river, but as same type of investigation is done every year it should not lead to bias or wrong estimation of the population development.



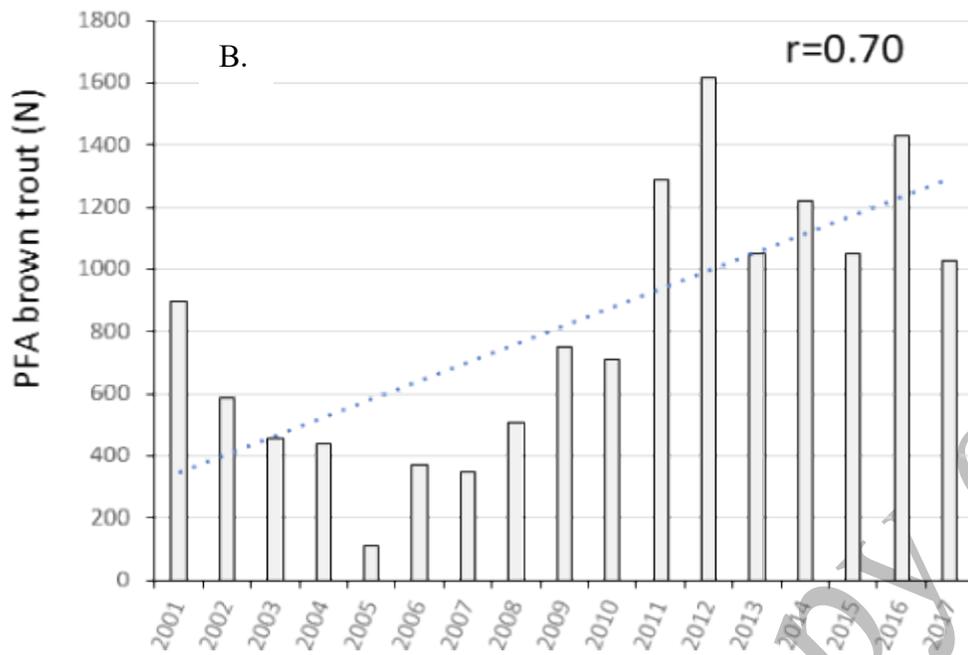


Figure 2. Pre-fisheries abundance (PFA) of Atlantic salmon (A) and sea trout (B) in the Eidfjordvassdraget during 1999-2017 (salmon) and 2001-2017 (brown trout). Dotted line indicates correlation (r) between PFA and study period (year).

Granvinsvassdraget

PFA of salmon increased in Granvinsvassdraget in the period 2004-2017 (Fig. 3A, $r = 0.41$ $p < 0.05$), whereas number of mature sea trout in the river was stable during the same period (Fig. 3B, $r = 0.04$, $p > 0.45$). Similar to Eidfjordvassdraget the numbers found do not include immature trout or salmon that are not at their spawning places once the snorkelling is done so the numbers should be considered as minimums number for the river population. This river has been investigated with video surveillance in 2014-18 and those data indicate that the sea trout population in Granvin is increasing (Lamberg et al. 2018)

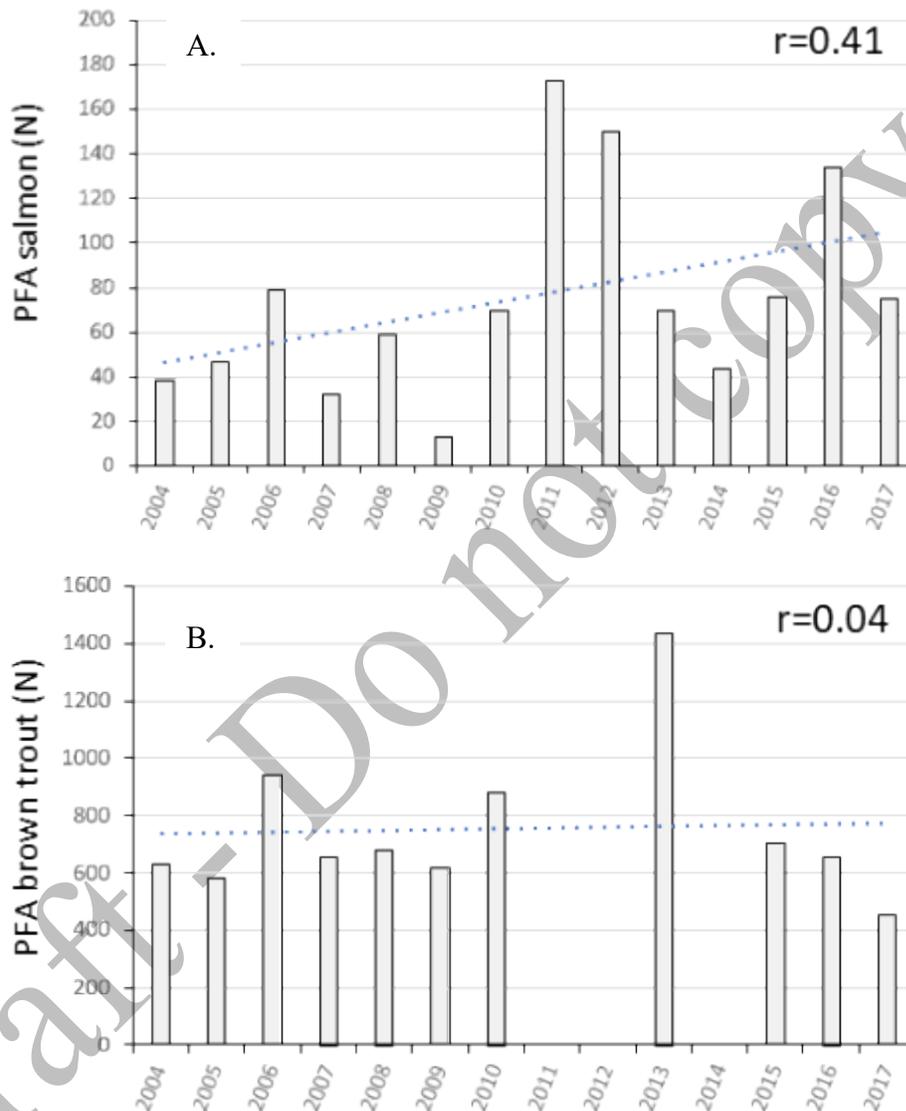


Figure 3. Pre-fisheries abundance (PFA) of Atlantic salmon (A) and sea trout (B) in the Granvinsvassdraget during 2004-2017. Dotted line indicates correlation (r) between PFA and study period (year).

Kinso

PFA has been monitored for both species in the Kinso river during 2004-2017 and population size of both species was found to increase (Fig. 4, $r = 0.28$ for both species, $p < 0.05$).

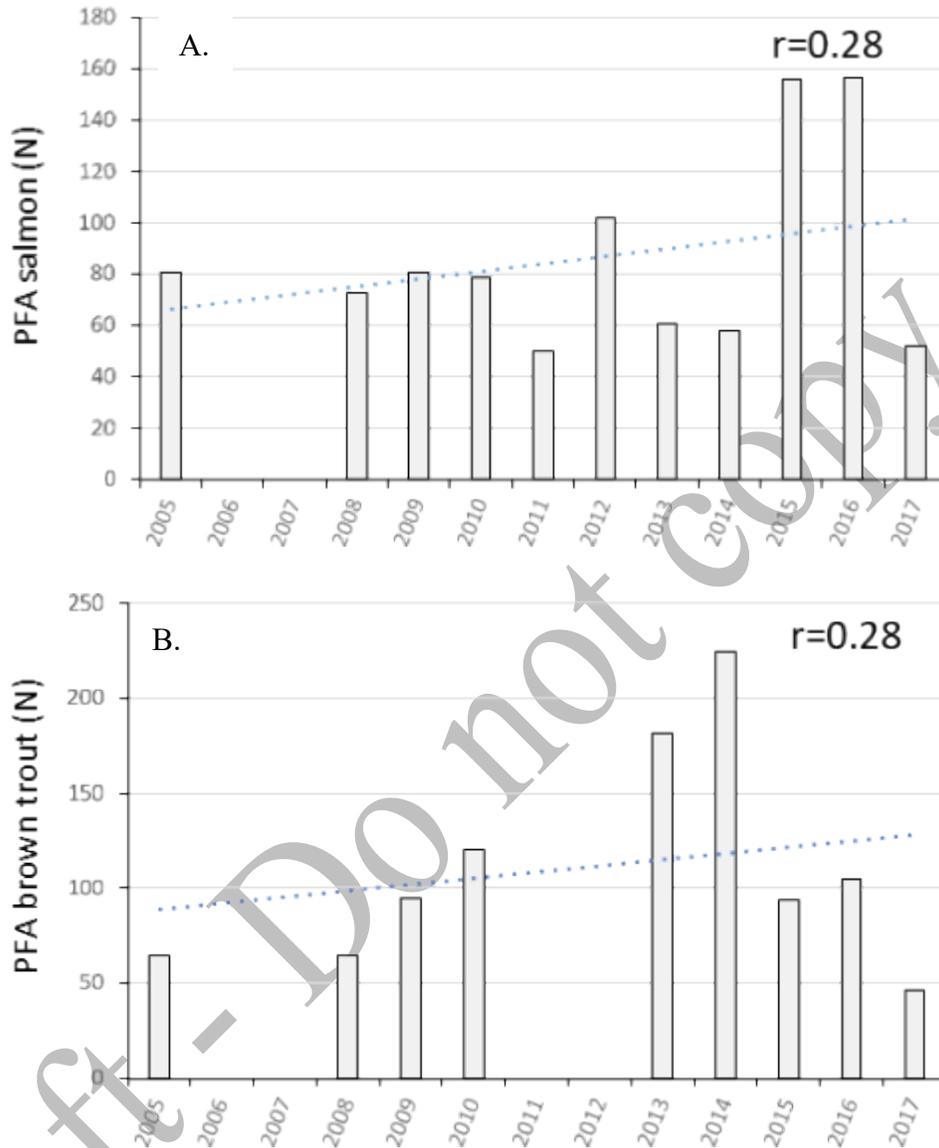


Figure 4. Pre-fisheries abundance (PFA) of Atlantic salmon (A) and sea trout (B) in the Kinso river during 2005-2017. Dotted line indicates correlation (r) between PFA and study period (year).

Rosendal rivers

PFA has been monitored for both species in the Rosendal rivers during 2004-2017 and PFA of both species was found to increase (Fig. 5, $r = 0.30$ and 0.35 , respectively, $p < 0.05$).

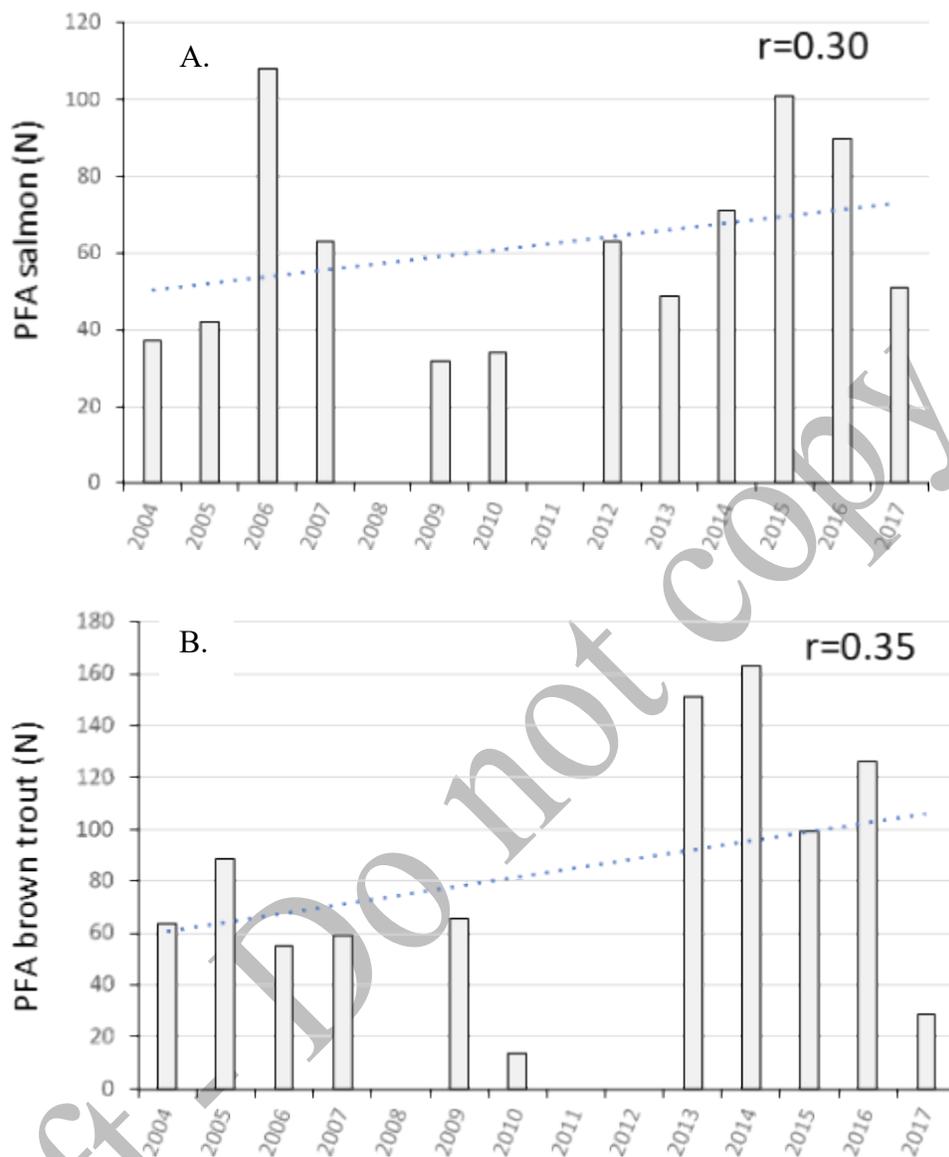


Figure 5. Pre-fisheries abundance (PFA) of Atlantic salmon (A) and sea trout (B) in the Rosendal rivers during 2004-2017. Dotted line indicates correlation (r) between PFA and study period (year).

Omvikelva

PFA has been monitored for both species in the Omvikelva river during 2004-2017. PFA of salmon has increased (Fig. 6A, $r = 0.87$, $p < 0.001$), whereas PFA of sea trout has decreased in the same period (Fig. 6B, $r = -0.58$, $p < 0.01$).

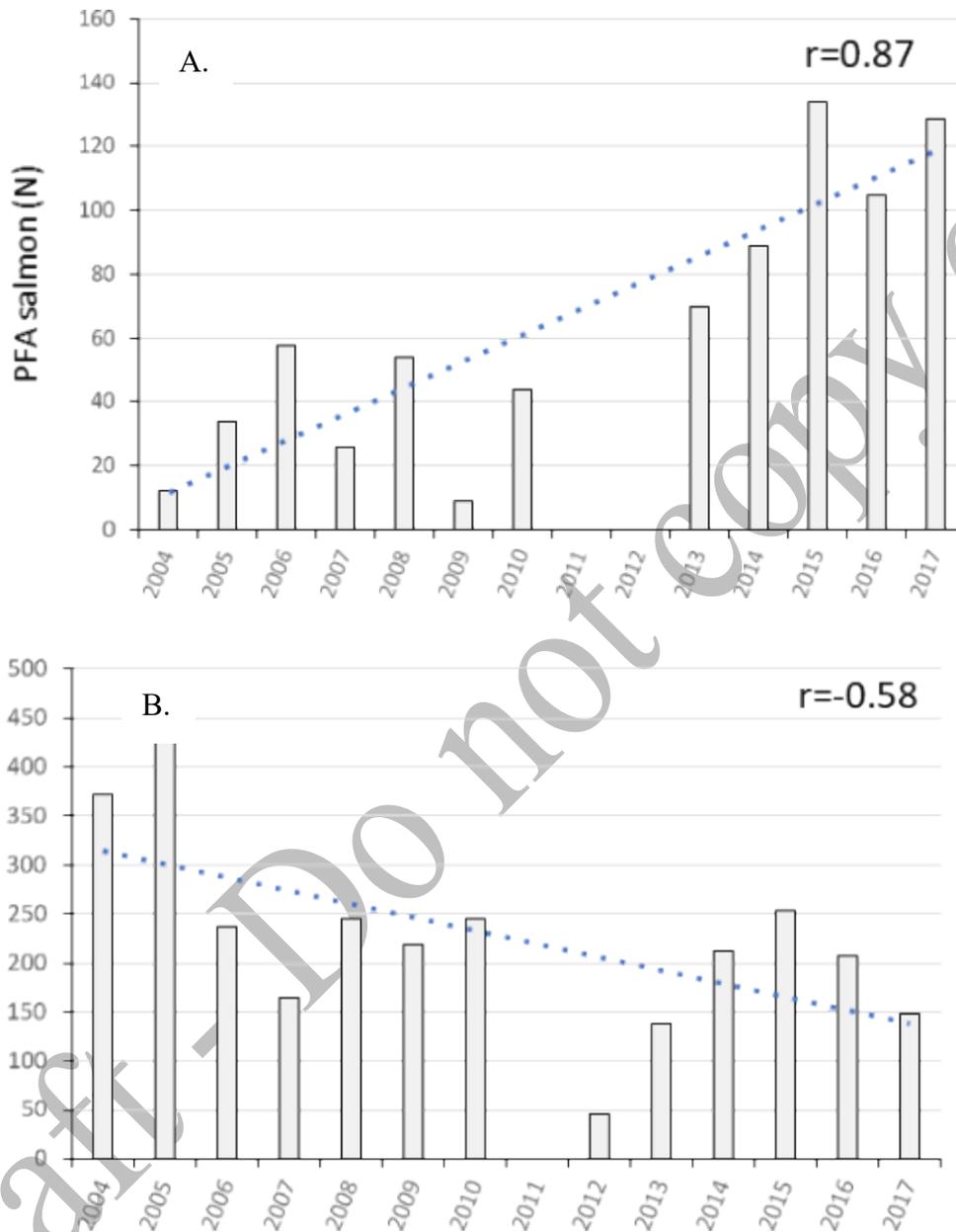


Figure 6. Pre-fisheries abundance (PFA) of Atlantic salmon (A) and sea trout (B) in the Omvik river during 2004-2017. Dotted line indicates correlation (r) between PFA and study period (year).

Uskedalselva

PFA has been monitored for both species in the Uskedalselva river during 2006-2017. PFA of salmon has increased (Fig. 7A, $r = 0.64$, $p < 0.001$), whereas PFA of sea trout has been stable in the same period (Fig. 7B, $r = -0.12$, $p > 0.05$).

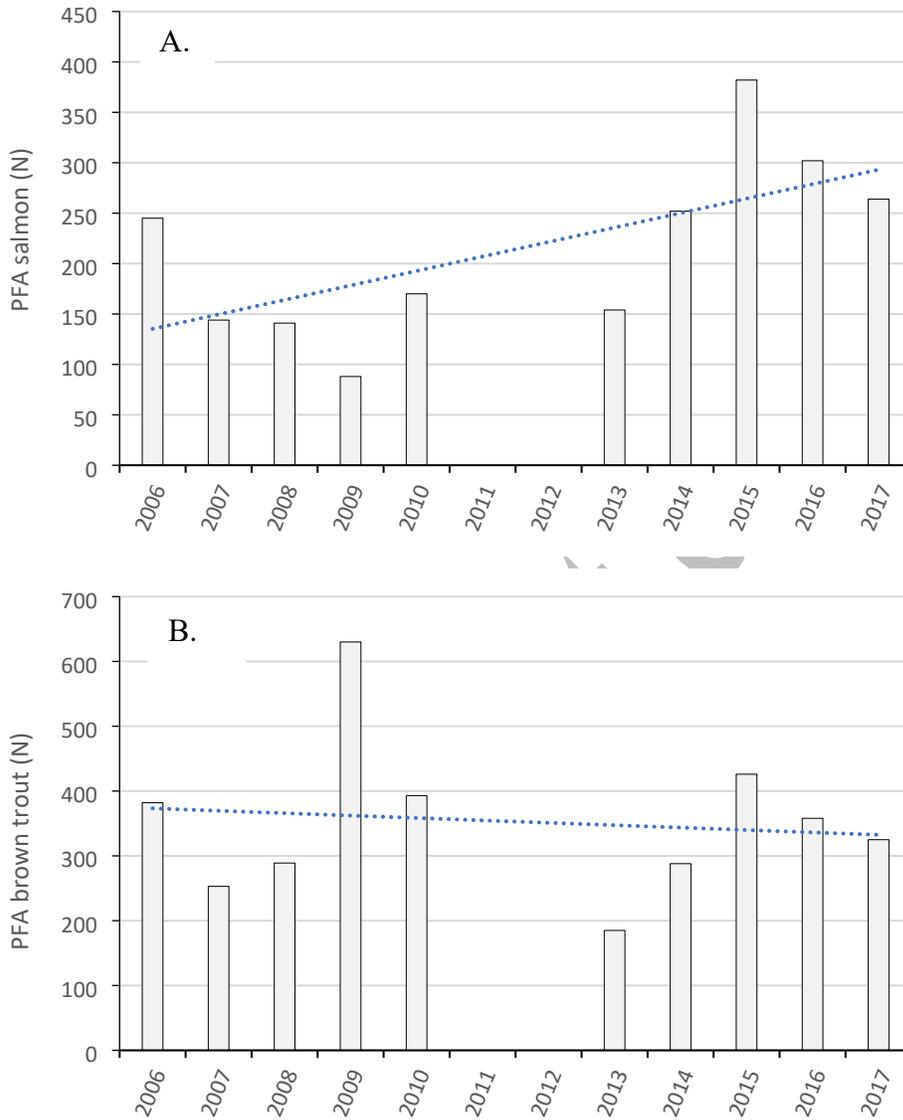


Figure 7. Pre-fisheries abundance (PFA) of Atlantic salmon (A) and sea trout (B) in the Uskedalselva during 2006-2017. Dotted line indicates correlation (r) between PFA and study period (year).

Etnevasdraget

PFA in the Etnevasdraget has been monitored for salmon between 2004-2017 for sea trout during 2006-2017 (Fig. 8). PFA of salmon has increased (Fig. 8A, $r = 0.49$, $p < 0.01$), whereas PFA of sea trout has been more variable same period (Fig. 8B, $r = 0.21$, $p > 0.05$). It should be noted that the PFA estimation for sea trout is a minimum estimate similar to those in Eidfjord and Granvin as they do not include immature fish or mature fish with resting year (i.e. not spawning).

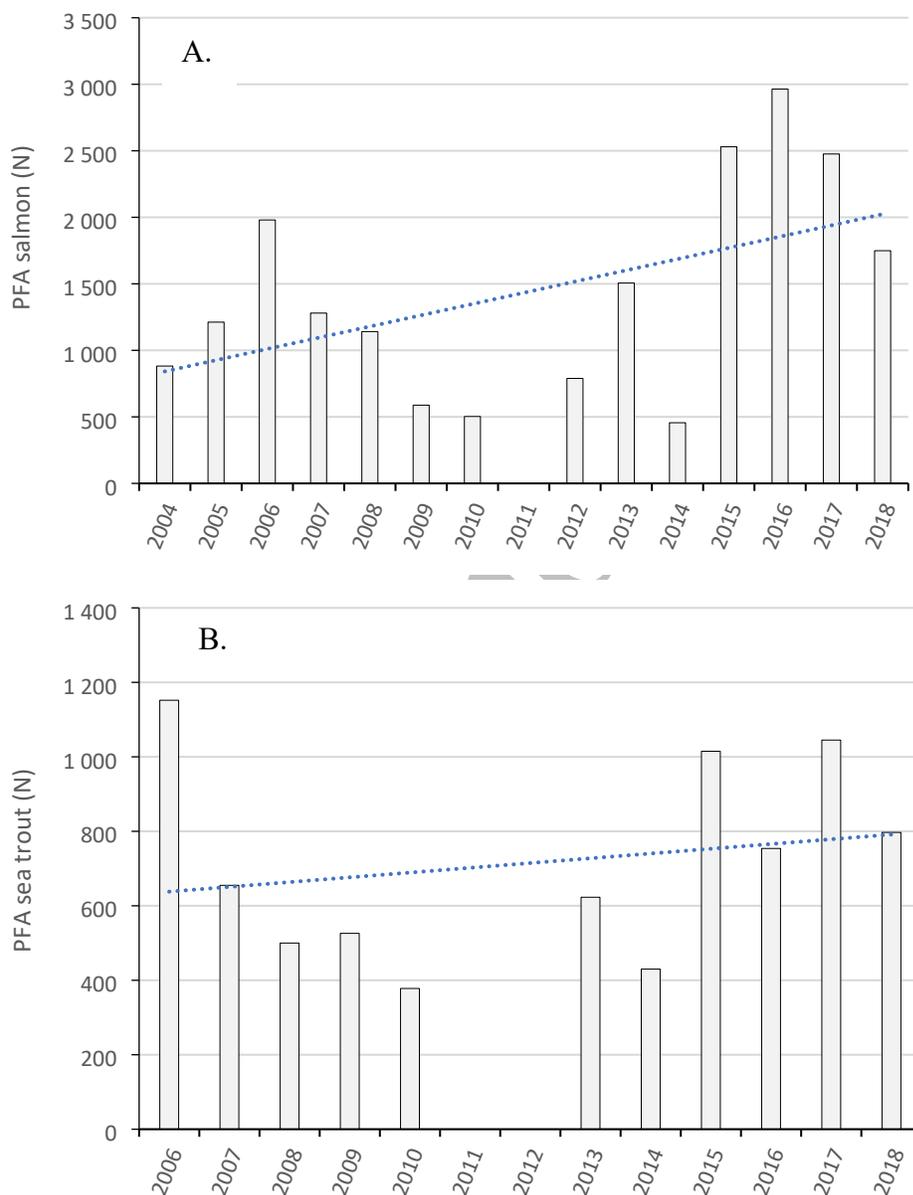


Figure 8. Pre-fisheries abundance (PFA) of Atlantic salmon (A) and sea trout (B) in the Etnevasdraget during 2004-2017. Dotted line indicates correlation (r) between PFA and study period (year).

Overall situation of Atlantic salmon population in the studied rivers

In the seven river systems in the Hardanger fjord system included in this study PFA data exist from 2009 to 2017 and overall the PFA in these rivers has increased from around 1000 individuals in 2009-10 to around 4000 individuals in 2015-2017 (Fig. 9). In 2016 the total recreational fishery for salmon in whole of Hardanger fjord system was 1466 individuals (Statistics Norway (SSB), <https://www.ssb.no/statbank>). No salmon were caught in the sea in 2016. In the same year the PFA (snorkelling + recreational fishery) for the studied seven rivers was 4267 individuals (Fig. 9).

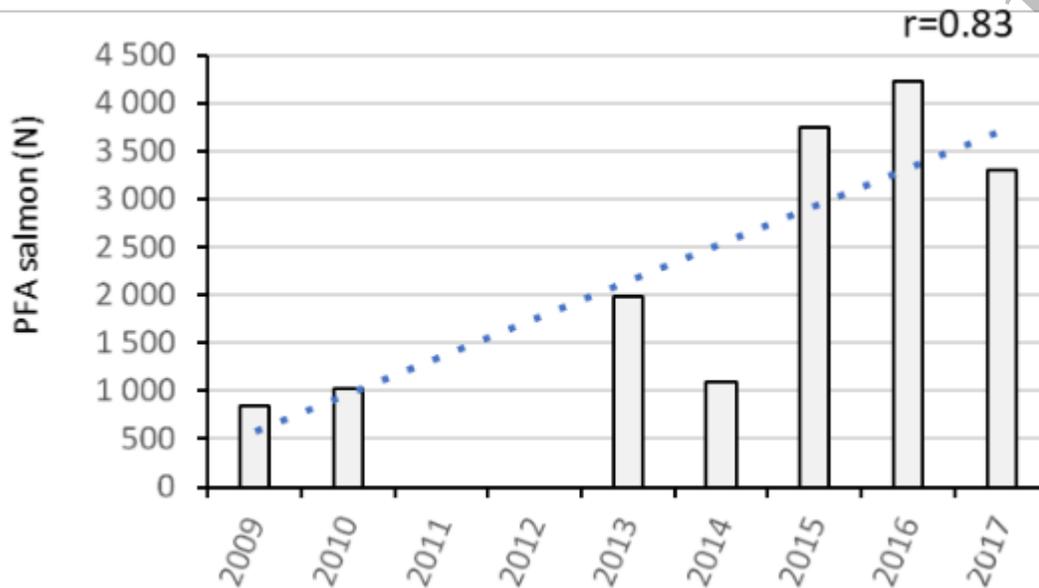


Figure 9. Combined pre-fisheries abundance (PFA) of Atlantic salmon from the seven studied river system in the Hardanger basin in 2009-2017. Dotted line indicates correlation (r) between PFA and study period (year).

Discussion

Earlier reports (Otterå et al. 2004; Skaala 2014a-c) have described the situation for the wild salmonid populations in the Hardangerfjord as critical and that escaped farmed salmon and salmon lice were responsible for an important part of the problem. Although management authorities and salmon farmers have introduced a number of measures to reduce the infection pressure of salmon lice on wild fish, infection levels continued to be high and appeared to be closely associated with the localization and biomass of farmed salmon (Taranger et al. 2011; Skaala et al. 2014c). With the decline in many of the sea trout and Atlantic salmon populations in these rivers, interest in angling activity also appears to have declined, with a corresponding bias in catch statistics (Skaala et al. 2014c). From about 2000, restrictions in river angling and sea fishing for anadromous fish have been gradually introduced in this area to reduce mortality and protect spawning populations. Since 2004, spawning populations have been assessed in

the rivers by divers from Uni Research (Skaala et al. 2010; Vollset et al. 2014). In most river systems in the region, numbers of wild spawning salmon have been low, and estimated egg deposits have been below 2-4 eggs/m², i.e. below the recommended density for sustainable recruitment (Jonsson et al. 1998; Skaala et al. 2014c). The exception is River Etneelva, which still has a stable spawning population of sufficient size to support recreational angling (Skaala et al. 2014c). Overall present study does not support the previous findings (Otterå et al. 2004; Skaala et al. 2014a-c) of declining salmon stock status in Hardangerfjord as there was an increase in salmon population size between 1999-2017 in all seven river systems studied. This is in line with the larger study of Skoglund et al. (2019) covering 56 river systems in Western Norway. They found a general increase in pre-fishery abundance (PFA) for salmon in the period 2011-2018 compared to the period of 2004-2010. The populations of sea trout showed larger local and regional differences compared to salmon (Skoglund et al. 2019). The hypothesised that this was due to improved conditions for growth and survival in the sea in the 2011-2018 period. It was noted that historical PFA data for this area was lacking making comparison back in time difficult. Data from recreational fisheries of salmon in the area from 1960-90 indicates larger population sizes than found in this and the study of Skoglund et al. (2019), but this is difficult to validate. The ongoing program of monitoring regional PFA for both salmon and sea trout (Skoglund et al. 2019) is a good method to follow population development in this area which is a key prerequisite for successful conservation management of these species in the fjord system.

Vollset et al. (2014) hypothesized that some of the variance in density of salmon and sea trout in the Hardangerfjord basin can be explained by the location of the river in the fjord, with fish from rivers with a longer fjord exposure having a lower density. Their results suggest that there is an inverse log-linear relationship between the density of salmon each year in the period 2004-2011 and the migration distances from river to open sea. It was pointed out that catch statistics are available for some of the inner rivers, but most of these data are, with few exceptions, of poor quality due to inadequate reporting (Vollset et al. 2014). It is therefore difficult to analyse whether the populations in the inner parts of the fjord have had a divergent trend in population size compared to the outer fjord systems. It follows that comparison of historical data is almost impossible, making validation of their conclusion difficult by comparing their data with older data. However, comparison with present PFA data from 1999-2017 do not support their hypothesis as longer fjord exposure was not correlated with lower population density. In the present study the highest numbers of salmon and sea trout were found for the rivers with the longest fjord exposure (Eidsvikvassdraget and Granvikvassdraget). The underlying causation factor suggested by Vollset et al. (2014) was that extended fjord exposure lead to longer exposure of the fish to sea lice. Jansen et al. (2012) demonstrated that there was correlation between sea lice on individual salmon farms and local biomass density in the surrounding farms. Severe infections of salmon lice on wild salmonids in the Hardangerfjord have earlier been found to coincide with high infection rates at salmon farms (Bjørn et al. 2011). The contrast between the findings of Vollset et al. (2014) and present data might be linked to lower lice infestations in the latter part of the period investigated i.e.

> 2011. In the Hardangerfjord system coordinated delousing during the smolt run in spring have been implemented since 2010 (with a limit of < 0.3 lice or 0.1 female lice per salmon) and there are indication that the lice situation in the fjord system has improved (Malkenes 2020). This in turn may lead to improved growing conditions for the wild salmonids in the fjord system which may help to explain the contrasting findings of Vollset et al. (2014) and present data.

In the marine phase, salmon farming has a major impact on wild anadromous populations, particularly through infection by the salmon louse (Skaala et al. 2014c). The impact level depends on several factors, such as the density of salmon farms, water temperature, migration routes and duration of migration in the fjord. Heuch et al. (2009) studied possible explanatory factors associated with lice infections on salmon farms in the Hardanger fjord between 2004 and 2006. Salinity, mean fish weight and treatment type were all shown to be significantly positively correlated with mean abundance of adult female lice. The two innermost zones had the lowest lice mean abundances, whereas the outermost zones, consistently had more lice. However, the marine migration of sea trout is restricted to the fjord basin where the fish may remain for several months before returning to freshwater (Klemetsen et al. 2003). This means that sea trout may be more severely affected than Atlantic salmon by the parasite. Data from 2004-2009 (Heuch et al. 2009; Finstad 2010) indicated high level of lice infection on salmon smolts and sea trout whereas later reports have indicated an improved lice situation in the Hardanger fjord system (Malkenes 2020). If the sea trout can be seen as a proxy for the severity of the lice situation (Klemetsen et al. 2013) in the fjord system then one would expect an increased population growth given that the lice situation is improving. Present data show that 6 out of 7 sea trout populations studied are increasing or stable indicating good natural growth of the populations studied which may indicate improved lice situation in the fjord system as a whole.

In the present study we found slight increasing (Eidsfjord, Kinso, Rosendal, Etne), stable (Granvin, Uskedal) or decreasing (Omvik) brown trout stocks. Overall, the population size of brown trout from these 7 river systems is increasing the study period (2001-2017) which is partly in contrast to some earlier findings. The study of Skurdal et al. (2001) found that the annual catches of anadromous trout in the Granvin population, the supposedly largest population in the system, had decreased from approximately 1000 individuals in 1975 to approximately 100 individuals in 2001 following the expansion of salmon farming (Skurdal et al. 2001). In the present study the Granvin brown trout population varies between 450 to 1400 individuals i.e. much higher than the estimates of Skurdal et al. (2001). Annual catches in the Etne population have historically been less than in the Granvin River, that is < 1000 individuals, but this population remains of considerable size (Hansen et al. 2007; present study). Of the seven systems studied the largest populations of brown trout was found in Eidsfjord, Granvin and Etne all of which had stable or increasing population sizes. Hansen et al. (2007) studied possible gene flow between brown trout population in Hardanger and found asymmetric gene flow from the largest populations to the smaller populations. It follows that it is important to maintain large population size in river systems with the largest brown trout

populations and that future population recoveries will be mediated primarily by the remaining large population (Hansen et al. 2007). This underlines the importance of the stable or increasing populations in Eidsfjord, Granvin and Etne found in the present study which may help to explain the overall increasing population size of brown trout in the Hardanger system found in the present study. Possible gene flow from larger to smaller populations has also been reported for brook trout (*Salvelinus fontinalis*) in Quebec, Canada (Fraser et al. 2004). As a follow up of the data presented in this study, we have used video surveillance between 2017-2020 to study the population size of six rivers in the Hardanger system with one river previously not studied (Mundheimselva). This river is in the heart of the aquaculture production area in Hardanger surrounded by 8 salmon farms in a 10 km radius. In spite of this, it was found that the Mundheimselva had one of the largest densities of mature brown trout in 2017 (61 ind./hectare, Lamberg and Kvitvær 2018) much higher than found other rivers in the Hardanger system in 2017 (22 ind./hectare, Skoglund et al. 2018). Mundheimselva is a small river with insufficient water volume to sustain overwintering of salmon and anadromous sea trout compared to e.g. the Granvinvassdraget (Lamberg et al. 2018), so it only possible to monitor the mature individuals within the population. It is still unknown where the immature individuals from this river can be found during winter. Tagging and tracking should be used to solve this problem as this will also help us to understand how sea lice effects the fish during its live cycle.

In conclusion the present study shows that both salmon and sea trout population were found to be increasing in the study area in the period studied. Present data show that 7 out of 7 of the salmon populations and 4 out of 7 sea trout populations studied are increasing indicating good natural growth of the populations.

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References

- Asplin L, Johnsen IA, Sandvik AD, Albretsen J, Sundfjord V, Aure J, Boxaspen KK, et al. 2014. Dispersion of salmon lice in the Hardangerfjord. *Marine Biology Research* 10:216–25.
- Bjørn PA, Nilsen R, Serra Llinares RM, Asplin L, Boxaspen K, Finstad B, et al. 2011. Sluttrapport til Mattilsynet over lakselusinfeksjonen på vill laksefisk langs norskekysten i 2011. Rapport fra Havforskningen 19(2011). Bergen: Institute of Marine Research. 33 pp. (in Norwegian).
- Borgstrøm R, Aas P. 2000. Miljøendringer, Vassdragsreguleringer. In: Borgstrøm R, Hansen LP, editors. *Fisk i ferskvann; Et samspill mellom bestander, miljø og forvaltning*. Oslo: Landbruksforlaget, p 216–29. (in Norwegian)
- Finstad B. 2010. The Hardanger Salmon Lice Project – Final Report, 33 pp. <https://www.fhf.no/prosjekter/prosjektbasen/552352/>
- Fortseth T, Fiske P, Barlaup B, Gjøsæter H, Hindar K, Diserud OH. 2013. Reference point based management of Norwegian Atlantic salmon populations. *Environmental Conservation* 40:356–66.
- Ford JS, Myers RA. 2008. A global assessment of salmon aquaculture impacts on wild salmonids. *PLOS Biology* 6:411–17. 10.1371/journal.pbio.0060033
- Fraser DJ, Lippé C, Bernatchez L. 2004. Consequences of unequal population size, asymmetric gene flow, and sex-biased dispersal on population structure in brook charr (*Salvelinus fontinalis*). *Molecular Ecology* 13:67–80.
- Gargan PG, Forde G, Hazon N, Russell DJF, Todd CD. 2012. Evidence for sea lice-induced marine mortality of Atlantic salmon (*Salmo salar*) in western Ireland from experimental releases of ranched smolts treated with emamectin benzoate. *Canadian Journal of Fisheries and Aquatic Sciences* 69:343–53. 10.1139/f2011-155
- Glover KA, Pertoldi C, Besnier F, Wennevik V, Kent M, Skaala Ø. 2013. Atlantic salmon populations invaded by farmed escapees: quantifying genetic introgression with a Bayesian approach and SNPs. *BMC Genetics*, 14: 4.
- Hansen MM, Skaala Ø, Jensen LF, Bekkevold D, Mensberg KLD. 2007. Gene flow, effective population size and selection at major histocompatibility complex genes: brown trout in the Hardanger Fjord, Norway. *Molecular Ecology* 16:1413–25.
- Heuch PA, Olsen RS, Malkenes R, Revie CW, Gettinby G, Baillie M, Lees F, Finstad B. 2009. Temporal and spatial variations in lice numbers on salmon farms in the Hardanger fjord 2004–06. *Journal of Fish Diseases* 32:89–100.
- Hindar K, Hutchings JA, Diserud O, Fiske P. 2011. Stock, recruitment and exploitation. In: *Atlantic Salmon Ecology*, ed. Ø. Aas, S. Einum, A. Klemetsen & J. Skurdal, pp. 299–332. Oxford, UK: Blackwell Publishing Ltd.
- Jansen PA, Kristoffersen AB, Viljugrein H, Jimenez D, Aldrin M, Stien A. 2012. Sea lice as a density-dependent constraint to salmonid farming. *Proceedings of the Royal Society* 279:2330–38.
- Johnsen IA, Fiksen Ø, Sandvik AD, Asplin L. 2014. Vertical salmon lice behavior as a response to environmental conditions and its influence on regional dispersion in a fjord system. *Aquaculture Environment Interactions* 5:127–141.
- Jonsson B, Jonsson N, Hansen LP. 1998. The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon *Salmo salar*. *Journal of Animal Ecology* 67:751–62.
- Jonsson B, Jonsson N. 2011. *Ecology of Atlantic Salmon and Brown Trout – Habitat as a Template for Life Histories*. New York: Springer. 708 pages.
- Lamberg A, Kvitvær T. 2018. Videoovervåking av laks og sjørret i Mundheimselva i 2017. SNA report 14/2018, 68 pp. (in Norwegian).
- Lamberg A, Strand R, Kanstad-Hanssen Ø. 2018. Videoovervåking av laks og sjørret i Granvinsvassdraget i 2017. SNA-rapport 05/2018, 62 pp. (in Norwegian).
- Malkenes RH. 2020. Lakselus og fiskehelse. FHF sea lice conference, 21–22 January, Trondheim, Norway (<https://www.fhf.no/arrangementer/arrangementer/lusekonferansen-2020/>).

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- Orell P, Erkinaro J, Karppinen P. 2011. Accuracy of snorkelling counts in assessing spawning stock of Atlantic salmon, *Salmo salar*, verified by radio-tagging and underwater video monitoring. *Fisheries Management and Ecology* 18:392-99.
- Otterå H, Skilbrei O, Skaala Ø, Boxaspen K, Aure J, Taranger GL, et al. 2004. Hardangerfjorden, produksjon av laksefisk og effekter på de ville bestandene av laksefisk. *Fisken og Havet* 3/2004. 36 pages. (in Norwegian)
- Rosseland BO. 2000. Forsuring av vassdrag: effekter og tiltak. In: Borgstrøm R, Hansen LP *Fisk i ferskvann: Et samspill mellom bestander, miljø og forvaltning*. Oslo: Landbruksforlaget, p 230–46. (in Norwegian)
- Skaala Ø, Johnsen GH, Barlaup BT. 2010. Prioriterte strakstiltak for sikring av ville bestander av laksefisk i Hardangerfjordbassenget i påvente av langsiktige forvaltningstiltak. Rapport fra Havforskningen nr. 10. Bergen: Institute of Marine Research. 37 pp. (in Norwegian)
- Skaala Ø, Sjøtun K, Dahl E, Husa V, Bjørge A, Uiblein F. 2014a. Interactions between salmon farming and the ecosystem: Lessons from the Hardangerfjord, western Norway. *Marine Biology Research* 10:199–202.
- Skaala Ø, Kålås S, Borgstrøm R. 2014b. Evidence of salmon lice-induced mortality of anadromous brown trout (*Salmo trutta*) in the Hardangerfjord, Norway. *Marine Biology Research* 10:279–88.
- Skaala Ø, Johnsen GH, Lo H, Borgstrøm R, Wennevik V, Hansen MM, et al. 2014c. A conservation plan for Atlantic salmon (*Salmo salar*) and anadromous brown trout (*Salmo trutta*) in a region with intensive industrial use of aquatic habitats, the Hardangerfjord, western Norway. *Marine Biology Research* 10:308–22.
- Skoglund H, Wiers T, Normann ES, Barlaup B, Lehman GB, Landro Y, et al. 2018. Gytefisktelling av laks og sjøaure og uttak av rømt oppdrettslaks i elver på Vestlandet høsten 2017. LFI-report nr 310:33 pp. (in Norwegian).
- Skoglund H, Vollset KW, Barlaup B, Lennox R. 2019. Gytefisktelling av laks og sjøaure på Vestlandet – status og utvikling i perioden 2004-2018 (Estimation of spawning population of Atlantic salmon and sea trout in Western Norway – status and development in the period 2004-2018). NORCE report nr. 357, Bergen, Norway, 44 pp. (in Norwegian).
- Skurdal J, Hansen LP, Skaala Ø, Sægrov H, Lura H. 2001. Elvevis vurdering av bestandsstatus og årsaker til bestandsutviklingen av laks i Hordaland og Sogn og Fjordane. Direktoratet for Naturforvaltning. Utredning 2001–2, 40pp. (in Norwegian.)
- Taranger GL, Boxaspen KK, Abdullah SM, Svåsand T, editors. 2011. Risk assessment and environmental impact of Norwegian aquaculture. Extracts from *Fisken og havet* særnummer 3-2010. 97 pages.
- Taranger GL, Karlsen Ø, Bannister RJ, Glover KA, Husa V, Karlsbakk E, et al. 2015. Risk assessment of the environmental impact of Norwegian Atlantic salmon farming. *ICES Journal of Marine Science* 72:997-1021.
- Verspoor E, García de Leániz C, McGinnity P. 2007. Genetics and habitat management. In: Verspoor E, Stradmeyer L, Nielsen JL *The Atlantic Salmon. Genetics, Conservation and Management*. Oxford: Blackwell Publishing, pp. 399–424.
- Vollset KW, Skoglund H, Pulg U, Wiers T, Gabrielsen SE, Lehmann GB, et al. 2014. Spatial and temporal patterns in abundance of sea trout, Atlantic salmon and escaped farmed salmon in the Hardangerfjord: Is location within a fjord important for river abundance? *Marine Biology Research* 10:268-78.

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Using merged pre-fisheries abundance as a parameter evaluating status of Atlantic salmon and sea trout populations: a Norwegian case study

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RUNNING TITLE: Using PFA to evaluate salmon and trout population status

ABSTRACT: Methods used to monitor variation in population sizes in both Atlantic salmon and sea trout have been widely used in Norway the last 20 years. However, a national management regime where population data is used, is only established for one of the two species, the Atlantic salmon. One prerequisite for using this “one species” model is that there is negligible intraspecific competition between salmon and trout in the rivers. This may be an oversimplification of the real situation. The pre fisheries abundance (PFA) monitored with underwater video systems will in most rivers include, both salmon and sea trout. In the present study we estimated a total PFA for rivers or groups of rivers in eight small regions in Norway in 2019. The total size of each river system measured by abiotic factors like river area, river length, annual mean water flow and size of precipitation field, and one biotic factor, smolt age, was used to standardize PFA data across regions. A comparison shows that total PFA of salmon and trout are varying among regions where the highest estimated PFA was four times higher than the lowest. Compared to the traditional one species approach the merged PFA data show a different population status in the eight regions. The difference in the two approaches was mainly linked to variation in sea trout populations. Merging data from salmon and trout populations in defined regions, may draw a more relevant picture of population status as a means to evaluate anthropogenic impact.

KEY WORDS: Atlantic salmon · Sea trout · Salmon farming · Population status · Anthropogenic effects

2. INTRODUCTION

Anadromous brown trout / sea trout (*Salmo trutta* L.) and Atlantic salmon (*Salmo salar* L.) migrate between freshwater and marine environments. To survive, thrive and reproduce, their habitats must meet several physical, chemical, and biological requirements (Verspoor et al. 2007). Changes in both the freshwater environment (Borgstrøm & Aas 2000; Rosseland 2000) and the marine environment, either due to natural causes or human activities (Ford & Myers 2008; Gargan et al. 2012), may affect salmonid populations. The impact on wild salmonid populations because of human activities has received significant attention over recent decades, and several impact factors are documented (e.g. Skaala et al. 2014a-b; Forseth et al. 2017). Atlantic salmon has, throughout its distribution area, been in a general decline, in terms of reduced productivity both in freshwater and the marine environment (Hindar et al. 2011; Forseth et al. 2013, 2017). Several anthropogenic factors are probably responsible for the decline, such as loss of connectivity due to construction of dams, hydropower facilities, habitat degradation, pollution, overexploitation, and the more recent effects of salmon farming (such as genetic introgression and increased parasite loads). Since the early 1990s, farming of Atlantic salmon has intensified, leading to establishment of net-pens distributed throughout the Norwegian fjords and coast. Concurrently wild Atlantic salmon and brown trout populations experienced a general decline from the late 1980 according to catch statistics in

Norway (Anon 2020).

However, from 2007 to 2019 the estimated pre fisheries abundancy (PFA) and spawning populations measured mainly through catch statistic shows increasing Atlantic salmon populations (Anon 2020). The situation for the trout is still unclear. In the marine phase, salmon farming has an impact on both wild anadromous populations, particularly through infection by the salmon louse (Krkošek et al. 2006; Skaala et al. 2014b; Kristoffersen et al. 2018). The impact level depends on several factors, such as the density of salmon farms, water temperature, migration routes and duration of migration in the fjord. If the sea trout can be seen as a proxy for the severity of the lice situation (Klemetsen et al. 2013) in the fjord system, then one would expect an increased population growth given that the lice situation is improving. Measuring population size variation is therefore important. The most useful population measure is not necessarily the number of spawning fish, but rather the PFA. Through the whole period of 30 years there has been a variation in number of caught anadromous salmonids from year to year. In the same period limitations on catch have been introduced. The active use of spawning target as a management tool for Atlantic salmon was stepped up from 2009 (Forseth et al. 2013). It has always been a challenge using catch statistics as a measurement of spawning populations size, since catch rate and fishing intensity many times are unknown variables. On the other hand, the increasing use of video surveillance, traps and snorkelling counts used to estimate both PFA and spawning populations have increased the precision in the estimates. A comparing of population status between periods is, therefore, not straight forward. There is also a variation in population development between regions in Norway. Using estimates of PFA and spawning populations to measure anthropogenic factors affecting wild fish to be able to solve problems and introduce measures to create effective management strategies, is therefore challenging. Atlantic salmon and trout populations are affected by variation in many anthropogenic and natural factors (Klemetsen et al. 2003; Thorstad et al. 2007). In the last years increasing focus has been on effects of salmon farming activity on the populations of wild salmon and trout. Ideally the most important natural and anthropogenetic factors influencing population size should be controlled for to single out the effect of farming activity.

Another challenge is how to define a population. In the spawning target model, presently used in managing Atlantic salmon populations in Norway, one important assumption in this model is that a population is specific for one river. However, surveillance data show that this is not always correct (Lamberg et al. 2018a, b). Atlantic salmon individuals starting their life in one river can, after sea sojourn and maturation, spawn in a different river. Especially may this hold for individuals growing up to smolt stage in small rivers (Skaala et al. 2010; Gjerde et al. 2021). This phenomenon is even more pronounced in sea trout (Davidsen et al. 2018, Lamberg 2020). Negative effects from increased levels of sea lice from salmon farming activity, potentially affect hosts in whole fjord systems and thus both salmon and trout from several “populations” at the same time. Considering today's unclear definition of the concept “population” we suggest in this study to merge population data from several rivers within a region as a better way of describing wild population development in that area. The regions we

define are smaller than the 13 regions (production regions) that are used as management entities in the national “traffic light scheme” for farmed salmon production capacity.

Finally, there is a question of what a sustainable population size is? If mitigations can lead to increasing populations (Thorstad et al. 2007), how is it possible to define that we have reached acceptable levels? For Atlantic salmon, the Norwegian government have decided to use spawning target (number of spawned eggs per area riverbed) as one parameter (Forseth et al. 2013). Genetic integrity is another and harvesting potential is a third. One problem with spawning population size is that Atlantic salmon and sea trout are living in the same or overlapping areas (Klemetsen et al. 2003). There is an unknown component of competition between the two species, which is not directly considered in the spawning target models. Physical environmental factors can also favour one or the other of the two, and these factors may vary over time. To bypass this obstacle, we suggest merging data from the two species and measure total production as one number. The third factor to consider when trying to establish what is a “sufficient number” of returning salmon and trout to a river, is that both species and especially trout, have a relatively high age at maturity (Jonsson & Jonsson 2011), both have few large eggs and show to some extent parental care by protecting eggs by burying them in the river gravel. They also often reproduce in more than one season. Such species, when not harvested and not affected by other anthropogenic factors will probably grow to a population size at far higher levels than that experienced in Norway the last century, where practically no population in Norway has not been affected by harvesting (e.g. Forseth et al. 2017). By use of data from underwater video surveillance systems monitoring river PFA, snorkelling surveys of spawning populations and catch statistics in 27 rivers located to eight different small coastal regions in Norway in 2019, we have compared the total salmon and trout merged PFA among regions. This is suggested as a first step to establish a method for measuring effects of anthropogenic factors in general, and to salmon farming activity in the fjords in special.

3. MATERIALS AND METHODS

2.1. Study area

Population data were collected from 27 rivers distributed in 8 river regions (Table 1 and Fig. 1). The data was collected using either underwater video systems or snorkelling surveys (Table 1). The eight regions were chosen primarily because population data exist from rivers in the regions. Secondly, the regions should be approximately the same size in terms of anadromous fish production area, length, combined length of rivers (river stretch accessible to anadromous fish, Table 2) and comparable combined mean water discharge (Table 2). The combined river area accessible to anadromous fish (Table 2), precipitation area (Table 2), theoretical spawning target for Atlantic salmon was also used to compare the regions.

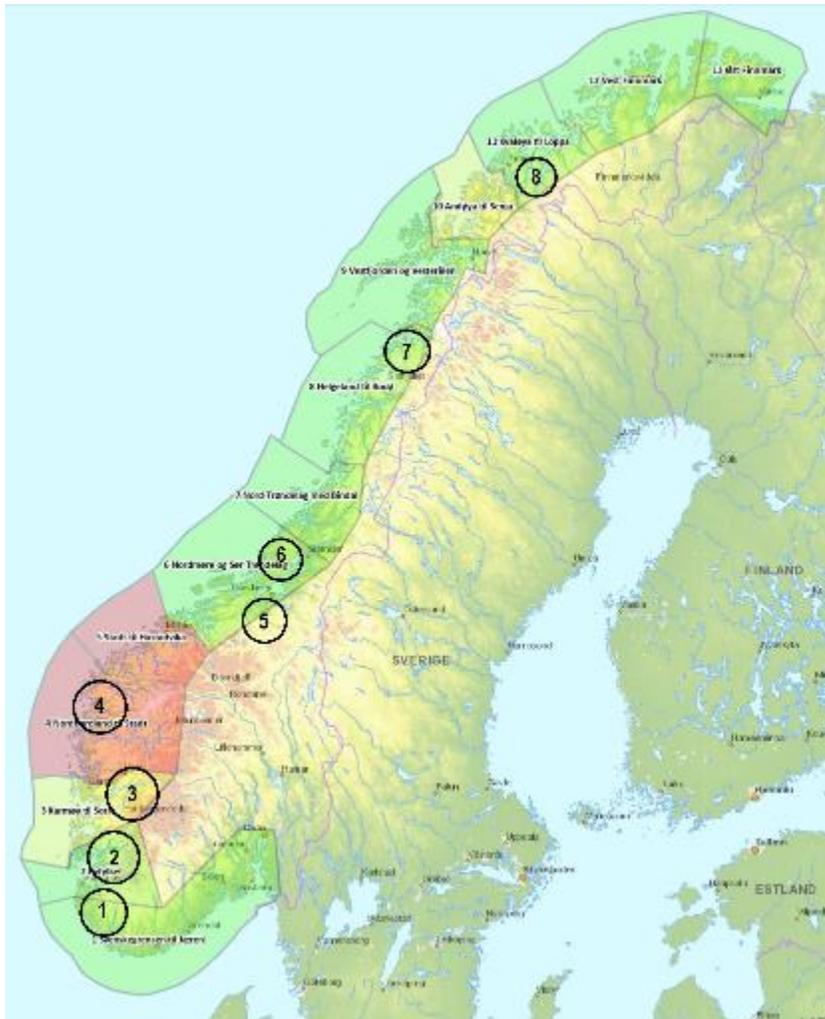


Fig. 1. The eight smaller river regions (black circles 1 – 8) studied in the present study. The 13 larger production zones established for regulating farmed salmon production in Norway (Myksvoll et al. 2018) are denoted with a small numbers and names,

Table 1. The methods used for measuring population size in river in each of the 27 rivers in the eight regions

Regio n	River	Method	Number of lakes	Winter habitat sea trout
1	Bjerkreimselva	Video in two fish ladders	6	yes
2	Frafjordelva	Snorkelling	1	yes
2	Dirdalselva	Snorkelling		
2	Espedalselva	Snorkelling	2	yes
2	Forsandåna	Snorkelling		
2	Årdalselva	Snorkelling	1	yes
2	Hålandselva	Snorkelling		
2	Vikedalselva	Snorkelling		
2	Rødneelva (Sandeid)	Snorkelling		
3	Eidfjordvassdraget	Snorkelling	1	yes
3	Etneelva	Snorkelling/Trap	1	yes
3	Granvinsvassdraget	Snorkelling/Video	1	yes
3	Jondalselva	Snorkelling		
3	Kinso	Snorkelling		
3	Omvikelva	Snorkelling/Video		
3	Rosendalselvene	Snorkelling		
3	Sima	Snorkelling		
3	Steinsdalelva	Snorkelling	1 (estuary)	
3	Uskedalselva	Snorkelling		
4	Nausta	Video in fish ladder/Snorkelling		
4	Gaula (Sunnfjord)	Video in fish ladder		
5	Orkla	Video/Snorkelling		yes
6	Stordalselva	Video	1	yes
6	Norddalselva	Video		yes
7	Saltdalselva	Snorkelling	1	yes
7	Beiarelva	Snorkelling		yes
8	Målselva	Video in fish ladder/Snorkelling		yes

Table 2. Hydrogeographic information an average smolt age of the eight studied regions of the present study

Regio n	River length (km) accessible to anadromous fish	Annual mean water discharge (m ³ /s)	River area (m ²) accessible to anadromous fish	Precipitation field (km ²)	Smolt age (years)
1	52.0	54	1.774.413	703	2.3
2	56.8	108	2.602.491	1253	2.7
3	74.0	131	1.542.336	1722	2.7

4	26.4	76	1.833.010	908	2.6
5	88.0	67	4.522.770	3051	3.5
6	36.8	17	1.724.595	374	2.7
7	101.2	100	4.728.820	2396	4.1
8	112.2	171	5.000.000	3015	4.0

2.2 Physical river data

The lengths of rivers accessible to anadromous species were measured both from satellite photo www.norgebilder.no and for some rivers, data is published earlier (Hindar et al. 2007; Vollset et al. 2014). The corresponding area was found in several sources. For the Hardangerfjord area (region 3) areas were found in Hindar et. al. (2007), Skoglund et al. (2008) and Hellen et al. (2013). In addition, the area of Orkla and Bjerkreimsvassdraget were measured from www.norgebilder.no. Precipitation field and mean water flow was found on www.nevina.nve.no.

2.3. Average smolt age

To control region data for differences in smolt age, it was assumed that yearly mortality of salmon and trout parr older than two years was 50 % (Hindar et. al. 2007). The deviation from smolt age of 2 years was calculated by the difference between observed average smolt age (ASA) minus 2 years was used as correction factor on PFA data (PFA*correction factor + PFA). It was assumed that trout and salmon smolts had the same average age in each river.

2.4 Salmon populations spawning target

Data on spawning target (conservation limit) for each of the 27 salmon populations in this study were obtained from model estimates performed by the Norwegian Scientific Advisory Committee for Atlantic Salmon (Anon 2020).

2.5 Estimating PFA

The total PFA for salmon and sea trout in the regions is a sum of fish caught in the fjord outside the rivers and river PFA. Catch data from the sea fisheries was found at www.ssb.no. Since catch data from gill nets contains a mix of fish from different rivers in a region, it is difficult to define how large part of total PFA from a specific river or region is caught in the sea fisheries. For our eight river regions we used estimated data developed by the Norwegian Scientific Advisory Committee for Atlantic Salmon (Anon 2020). In these estimates number of Atlantic salmon in the sea fisheries are calculated as proportion of the spawning population estimated in each river the same year.

River PFA is the number of both species ascending the river in a season. This number can be monitored by a combination of snorkelling counts in the spawning season and the river catch (killed fish) that same year or by video surveillance close to the mouth of the river in the sea.

2.5.1 Snorkelling

The drift snorkelling observations were conducted like those described earlier by Orell et al. (2011), Vollset et al. (2014) and Svenning et al. (2016). In short, the snorkelling teams consist of divers equipped with a wet suit, diving mask, snorkel, fins and neoprene gloves. The snorkelers drift in parallel and make frequent stops to discuss the observations. Each person in the team notes the number of fish and position of the observations with reference to a waterproof map. To avoid double-counting, the count only includes fish that pass the observer in the upstream direction or fish that are holding their position and thereby passed by the diver. Standardization among rivers is obtained by only using trained personnel for snorkelling and by adjusting the numbers of divers to the size and width of the river, i.e. varying from one to three divers in each team.

Snorkelling is conducted during low discharge periods from mid-September to mid-November. This period is chosen to encounter the spawning population, as both sea trout and salmon spawn in autumn (Jonsson & Jonsson 2011). In addition, this represents the time after recreational fishing and the count therefore represents the real spawning population. Within this period, the date varied between rivers and years according to changing ambient conditions. The data in the present study are part of larger regional studies (Kanstad-Hansen et al. 2019; Skoglund et al. 2019; Holte et al. 2020).

2.5.2 River catch data

Data on river catch was achieved from recreational fishing for both species in all the studied rivers during the study period. The data is extracted from www.fangstrapp.no, www.ssb.no, www.scanatura.no and local river administrations (Orkla and Målselv).

2.5.3 Underwater video surveillance

Underwater video surveillance is a method first tested in 1995 but with increased use from 2005 to 2020. The basic principle differs between rivers and size of cross sections from the small narrow, fish ladders, to open river cross sections more than 40 meters wide. Enough cameras are used to cover all possible parts of the water volume on the specific location, where fish can pass within the camera sector. For further description of method see Svenning et al. (2016).

4. RESULTS

3.1. Comparing salmon spawning target in the eight river regions in 2019

According to the estimated region merged spawning target for Atlantic salmon the total weight of female spawners corrected for river areas varied between the eight river regions. The highest value was found for region 5, Orkla and the lowest for region 7 (Fig. 2). In 2019 the recorded biomass of females in the spawning populations that year measured in proportion (%) of spawning target (conservation limit = 100 %) in the eight regions was highest in region 1, 2 and 6 and lowest in region 5 (Fig. 3).

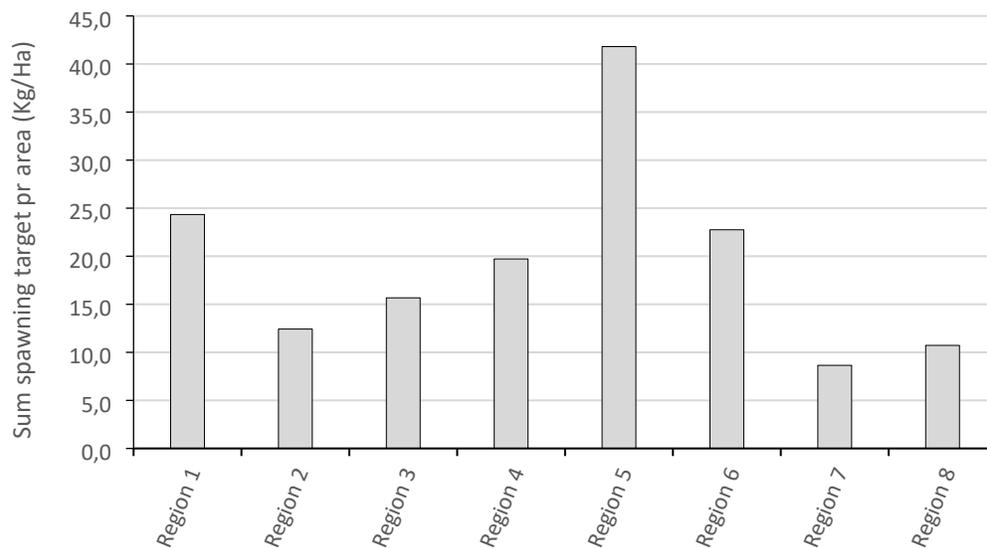


Fig. 2. Spawning target (ST) (modelled conservation limit) summed for all rivers in each of eight studied regions. The ST is corrected for total river smolt production area.

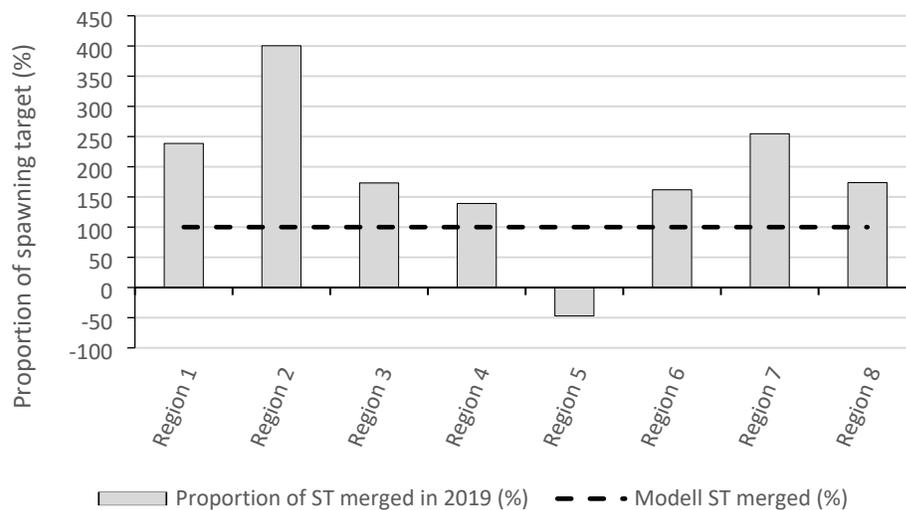


Fig. 3. Estimated total biomass of spawning females merged for all rivers in each of the eight regions in 2019 expressed as proportion (%) of modelled spawning target (ST = 100 %). (data from annual report 2020: Norwegian Scientific Advisory Committee for Atlantic Salmon).

3.4 Comparing total PFA in eight geographical regions in 2019

Total PFA for each of the eight river regions were estimated and controlled for merged river area and smolt age. The comparison of the eight regions shows a varying number of salmon and trout entering the coast outside the rivers in 2019 (Fig. 4). Three of the river regions, regions 1, 3 and 6 have a total PFA that is from two to four times higher than in the other regions.

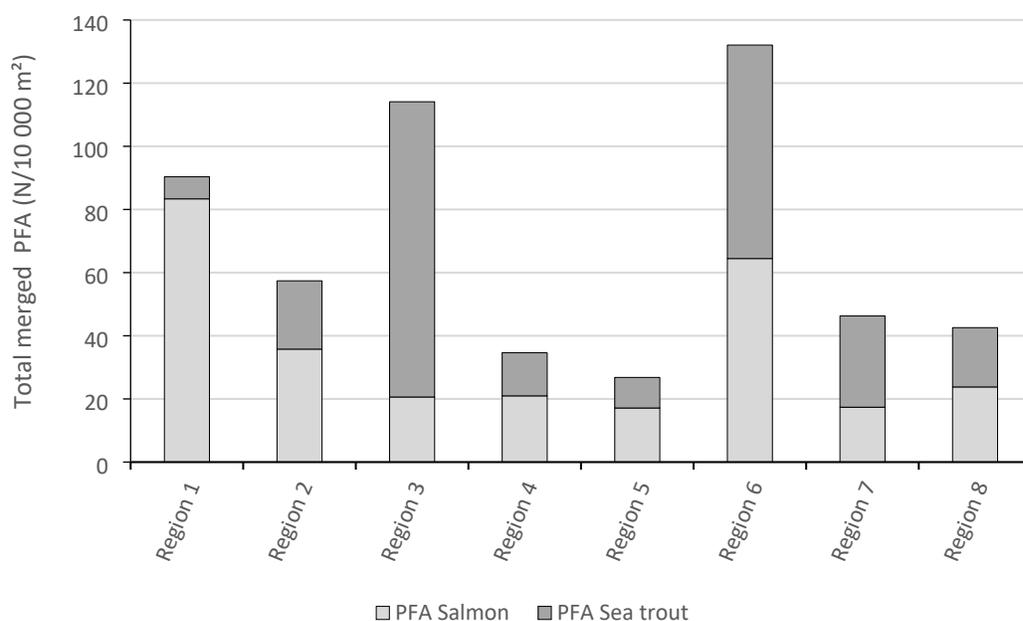


Fig. 4. Total PFA corrected for river area and smolt age merging data on Atlantic salmon and sea trout in the eight studied regions in 2019.

3.3 Comparing the ST- and the PFA-approach in 2019

Comparing the ranks of the eight regions for the ST-approach and the PFA-approach in 2019 show that one region is given the same rank (river region 1). In some regions the PFA-approach give higher ranks (region 3, 6 and 8). In the other regions the PFA-approach results in lower rank than the ST-approach (region 2, 4, 5, and 7) (Fig. 5).

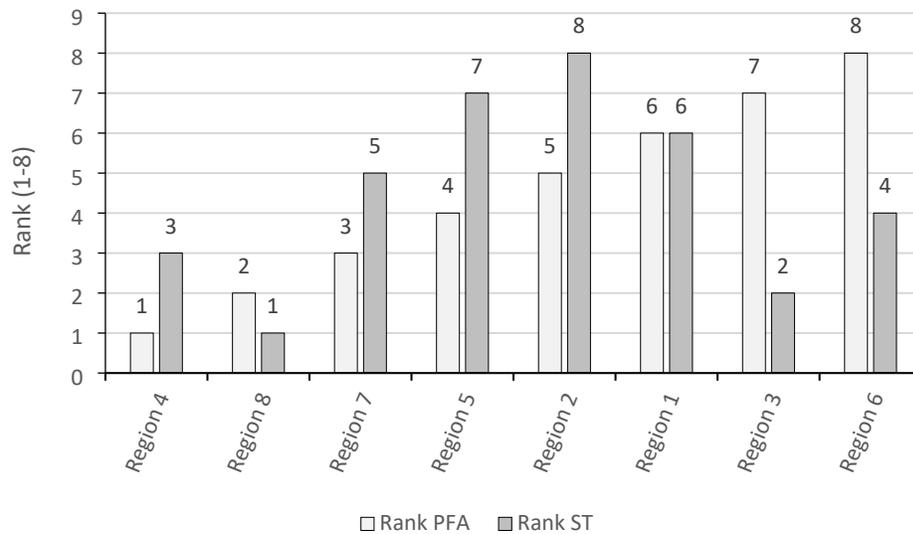


Fig 5. The ranking of the eight regions from 1 (lowest) to 8 (highest total biomass of spawning females/highest number of fish in PFA)

3.5 Average smolt age

The average smolt age registered in the eight studied regions varied from 2.3 to 4.1 years (Table 2). It was not possible to find data on smolt age for both salmon and trout in all rivers. Where data from both species were available, smolt age seemed to be the same for salmon and trout in most cases, but not always. Smolt age will also vary over time within rivers but there is a general increase in smolt age with latitude due to lower temperatures going from south to north (Fig. 6).

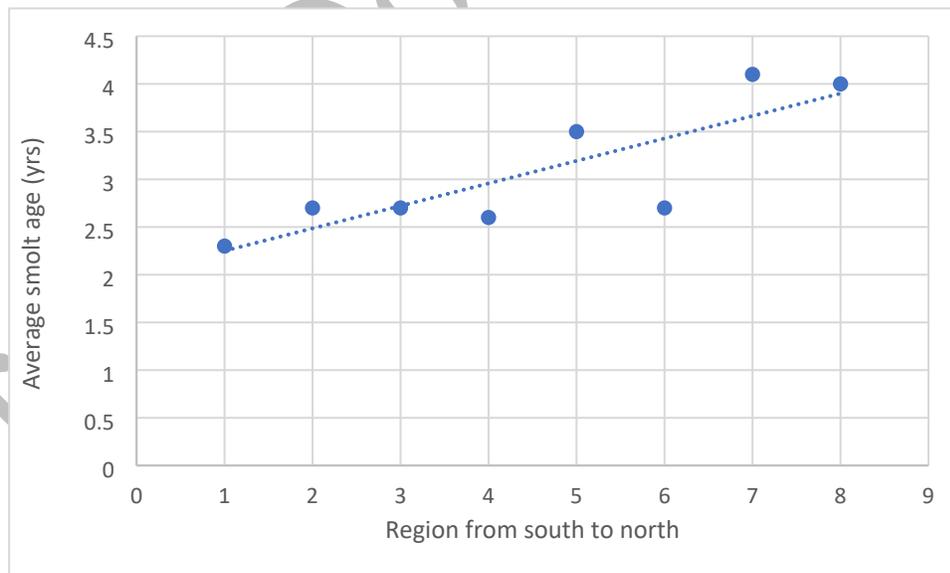


Fig. 6. Average smolt age in the eight studied river regions.

5. DISCUSSION

The goal of this study was to test a way of measuring how anthropogenic factors in general, affect Atlantic salmon and sea trout. This was done through monitoring population sizes by using video counts of individuals entering rivers (river PFA) or snorkelling counts on the spawning grounds. Together with catch reports both from the sea and from the rivers it was possible to estimate a total PFA controlled for total river smolt production area and smolt age in one single, or several rivers merged, draining out into a defined part of a fjord. The test was performed on 2019 PFA data in eight such regions or parts of fjords. The use of methods aiming at total counts of individuals in populations remove, to a greater extent, the problem of large confidence intervals linked to methods using sampling (e.g. catch statistics). However, the ambition of counting all individuals in populations by means of methods relying on visual identification, also introduces some potential uncertainty (e.g. Stien et al. 2017). The use of a total PFA as a parameter is still partly dependent on some uncertainty of catch statistics but now only linked the one-sided effect from unreported catches and not the two-sided uncertainty of the confidence intervals combined with the unreported catch as earlier.

The test show that the total 2019 PFA of the eight selected fjord regions with corresponding rivers, was varying more than four times from the region with the lowest estimated total PFA to the region with the highest. This large variation indicates that some anthropogenic factor is affecting the populations. The expected result would to a greater extent similar PFA-values in the eight studied regions due to a standardisation of smolt production area and smolt age.

There was a difference in the ranks of the eight regions between using the ST-approach and the PFA-approach. This is probably due to the introduction of sea trout in the numbers. Since 2009 the state of many of the over 400 salmon populations in Norwegian rivers have been evaluated by use of the concept spawning target (Forseth et al. 2013). Theoretical models made for eight different populations/rivers have been used as benchmark for a varying number of the more than 400 Norwegian salmon rivers each year (Anon 2020). Theoretical models often simplify the real world and real ecosystems. That is also the case with the spawning target model. One such simplification is that there is no input data in the salmon model concerning the size of the sea trout population in the same river. It is suspected that there is density dependent competition between salmon and trout (Pulg et al. 2019), especially in all the stages from swim up to the smolt stage (Einum 2005; Jonsson & Jonsson 2011). If the salmon spawning target model does not involve population data on trout, it only tells a part of the story. That is why our study test the use of both species in a combined total PFA. A region where both species thrive may be a sign of less anthropogenic effects on the fish, compared to regions where the populations are small when controlled for total river area. Since we do not know if there is a constant number balance between the two species is, a better approach may be to merge the two data sets.

In regions/fjords made up of many small rivers that are located close to each other, there is a question if there are unique salmon and trout populations in each river or if there is a greater

extent of mix (Hindar et al. 2004; Hansen et al. 2007). Both video surveillance projects (Lamberg & Kvitvær 2018; Lamberg et al. 2018a, b) and snorkelling projects (Skoglund et al. 2019) especially in region three in our study, show that there is a relatively high proportion of adipose fin clipped fish in many rivers where no such tagging method is used. This indicates that there are both trout and salmon entering rivers where they have not grown up to smolt stage. These are fish from “foreign” rivers that are possible to detect with our visual methods. The ones that are not tagged are not singled out in the same way, a fact that indicate that there is mix of fish from several “populations” in many of the small rivers. In several of the 27 rivers of this study, the water course contains one or more lakes or large water volumes where sea trout, both immature and mature, may stay over winter. In our study we have chosen to merge data from several rivers within a region, since there is probably a large proportion of the sea trout that will spawn in a different river from the waters where it stays over winter. A sea trout migration between rivers has been indicated in several studies (Klemetsen et al. 2003, Degerman et al. 2012; Lamberg & Gjertsen 2017).

In the last years, commercial Atlantic salmon sea fisheries activity has been reduced on both sides of the Atlantic (Limburg & Waldman 2009) including Norway (Anon 2020). In general, relatively few trout end up in sea catches (Arnekleiv et al. 2014). The recreational fishing for salmon and trout in the sea, however, has increased in the same period. Since the catch from this activity is not reported, there are no good documentation of the increase. In this kind of fishing, learning techniques from others can change the success rate. The introduction of social media, discussion groups and video sharing apps on internet (e.g. Facebook from 2006 and YouTube in 2005) have probably increased the interest for salmon and trout sea recreational fishing and the skills of the individual practitioner. An increasing part of the total number of salmon and sea trout removed in the fjords and on the coast and not reported will result in a lower measured total PFA. Obtaining an exact total salmon and trout PFA for rivers or aggregations of rivers (merged numbers), could be a method for evaluating the overall situation for the two species. Since the Norwegian national farmed salmon production regulation system (“Traffic light system”, Vollset et al. 2017; Myksvoll et al. 2018) reports the state for each of 13 regions, a verification of status of wild anadromous fish in each of these regions could work as a verification tool for the theoretical models. Bringing in the sea trout in the models can be an important step to measure the effect of sea lice since the trout spends more time in the fjords, than the salmon.

Methods for monitoring variation in population size through estimation of pre fisheries abundancy for both Atlantic salmon and sea trout have been widely used in Norway, especially the last 20 years (Skoglund et al. 2018, 2019; Anon 2020). The use of traps covering whole river cross sections, snorkelling and underwater video surveillance have improved data on PFA compared to earlier years where sampling methods were more common. Of these sampling methods, catch reports and statistics, were dominating. Sampling data will be inherently imprecise due to often small sampling sizes and lack of required random sampling procedure (Løland et al. 2016). To be able to use catch data to estimate total population sizes, knowing the catch rate was prerequisite. However, the catch rate varies between rivers and

years and will be influenced by, among other factors, fishing conditions, fishing rules, and river morphology. Another problem with catch statistics the last 20 years, is that an increasing number of rivers have been closed for recreational fishing (Langset & Staldvik 2011), so there are no catch reports available to estimate population size. The introduction of methods which aim at counting all individuals in a population, or more correctly, all the individuals returning to a river each year, has improved the data on population development for both Atlantic salmon and sea trout Svenning et al. (2016). A more precise description of these methods is that they aim at counting all individuals above a certain age and life history stage.

In small rivers where salmon and trout are not able to stay over winter, due to small water volumes in the cold part of the year, the fish often show a “hit and run” strategy (Lamberg & Kvitvær 2016). They will enter the small river when water levels are sufficient in the time frame of spawning and after spawning, return to sea water or another river for winter stay. The use of snorkelling method may give underestimates of PFA in such small rivers and in water courses with lakes. Especially that holds for sea trout where large parts of the individuals are either immature or having a resting year from spawning. Both groups will when a lake is available, stay in a large water volume where it is not possible to perform a snorkelling count. Even if data on variation in population size can be relevant for evaluating impact from anthropogenic factors in general there remains a question of how to define a population. Measuring PFA involves catch data from the sea, a catch that involves mixed populations. In addition, the fish entering the rivers are also in many cases a mix of populations. One way of bypass this obstacle is to merge data from several populations in an area and treat them as one as done in the present study.

6. CONCLUSION

In this study, using PFA estimates from 2019, it is suggested that the merged PFA may be a more relevant parameter to separate the effects of different anthropogenic factors, and especially the effects of sea lice. The study also points out what parameters should be monitored in the future to make the model more robust. In addition to video surveillance and snorkelling, measuring PFA depend on correct catch statistics. Correct statistics may be achievable in the rivers, but presently not from the sea. Increasing unregistered trolling catches from the coast and the fjords for both anadromous species the last years will disturb the PFA estimates. The ambition of monitoring whole ecosystems is at present probably unrealistic but an introduction of a reporting system for all catch of Atlantic salmon and sea trout in sea water will improve the possibilities of measuring other anthropogenic factors that affects these two species.

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LITTERATURE CITED

- Anon (2020) Status of wild Atlantic salmon in Norway 2020. Vitenskapelig råd for lakseforvaltning, 147 pp (in Norwegian with summary in English), <https://www.vitenskapsradet.no/>
- Arnekleiv JV, Kjørstad G, Rønning L, Davidsen JG, Sjørnsen AD (2014) Studies on freshwater biology in the river Stjørdalsvassdraget in 2009-2013. – NTNU Vitenskapsmuseet naturhistorisk rapport 2014-3: 1-82
- Borgstrøm R, Aas P (2000) Miljøendringer, Vassdragsreguleringer. In: Borgstrøm R, Hansen LP (eds) Fisk i ferskvann; Et samspill mellom bestander, miljø og forvaltning. Oslo: Landbruksforlaget, p 216–29. (in Norwegian)
- Davidsen JG, Eldøy SH, Sjørnsen AD, Rønning L and others (2018) Marine migrations and area use of brown trout in Tosenfjorden, Bindal municipality – NTNU Vitenskapsmuseet naturhistorisk rapport 2018-8, 84 pp (in Norwegian with abstract in English)
- Degerman E, Leonardsson K, Lundqvist H (2012) Coastal migrations, temporary use of neighbouring rivers, and growth of sea trout (*Salmo trutta*) from nine northern Baltic Sea rivers. ICES J Mar Sci 69:971-980
- Einum S (2005) Salmonid population dynamics: stability under weak density dependence? Oikos 110:630–633.
- Ford JS, Myers RA (2008) A global assessment of salmon aquaculture impacts on wild salmonids. PLOS Biology 6:411–17. 10.1371/journal.pbio.0060033
- Forseth T, Fiske P, Barlaup B, Gjøsæter J and others (2013) Reference point based management of Norwegian Atlantic salmon populations. Env Cons 40:356–366
- Forseth T, Barlaup BT, Finstad B, Fiske P and others (2017) The major threats to Atlantic salmon in Norway. ICES J Mar Sci 74:1496-1513
- Gargan PG, Forde G, Hazon N, Russell DJF, Todd CD (2012) Evidence for sea lice-induced marine mortality of Atlantic salmon (*Salmo salar*) in western Ireland from experimental releases of ranched smolts treated with emamectin benzoate. Can J Fish Aquat Sci 69:343–53. 10.1139/f2011-155
- Gjerde B, Celeste J, Luqman M, Hindar K and others (2021) Genetisk variasjon og genetiske markører for motstandskraft mot *Gyrodactylus salaris* hos laks i infiserte vassdrag. NOFIMA rapport 18/2021, ISBN 978-82-8296-648-1, 55 pp. (in Norwegian with abstract in English).
- Hansen MM, Skaala O, Jensen LF, Bekkevold, D, Mensberg KLD (2007) Gene flow, effective population size and selection at major histocompatibility complex genes: brown trout in the Hardanger Fjord, Norway. Molec Ecol 16:1413-1425
- Hellen BA, Kambestad M, Johnsen GH (2013) Habitatkartlegging og forslag til tiltak for sjøaure i utvalgte vassdrag ved Hardangerfjorden. Rådgivende biologer as Rapport nr. 1781:251 pp, (in Norwegian).
- Hindar K, Tufto J, Sættlem LM, Balstad T (2004) Conservation of genetic variation in harvested salmon populations. ICES J Mar Sci 61:1389-1397
- Hindar K, Diserud O, Fiske P, Forseth T and others (2007). Gytebestandsmål for laksebestander i Norge. NINA Rapport 226:78 pp. (in Norwegian)
- Hindar K, Hutchings JA, Diserud O, Fiske P (2011) Stock, recruitment and exploitation. In: Aas Ø, Einum S, Klemetsen A, Skurdal J (eds) Atlantic Salmon Ecology. Blackwell Publishing, Oxford, p 299-332
- Holte E, Skoglund H, Solem Ø, Kanstad-Hansen Ø and others (2020) Overvåking av gytebestander av laks og sjørret i Norge, 2019. NINA Rapport 1849:226 pp. (in Norwegian).
- Jonsson B, Jonsson N (2011) Ecology of Atlantic Salmon and Brown Trout. Habitat as a Template for Life Histories. Springer, New York, 708 p
- Kanstad-Hansen Ø, Gjertsen V, Bentsen V, Lamberg A (2019) Oppvandring av sjøvandrende laksefisk i fisketrappa i Målselvfossen i 2019. Ferskvannsbilogen Rapport 2019-08:20 pp. (in Norwegian).
- Klemetsen A, Amundsen PA, Dempson JB, Jonsson B and others (2003) Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): A review of aspects of their life histories. Ecol Fresh Fish 12:1–59

-
- Kristoffersen AB, Qviller L, Helgesen KO, Vollset KW, Viljugrein H, Jansen PA (2018) Quantitative risk assessment of salmon louse-induced mortality of seaward-migrating post-smolt Atlantic salmon. *Epidemics* 23: 19–33
- Krkošek M, Lewis MA, Volpe JP, Morton A (2006) Fishfarms and sea lice infestations of wild juvenile salmon in the Broughton Archipelago — a rebuttal to Brooks (2005). *Rev Fish Sci* 14: 1–11
- Lamberg A (2020) Bestandsovervåking av laks og sjøørret i Granvinsvassdraget i 2019. SNA report 11/2020, 71 pp. ISBN: 978-82-8341-050-1 (in Norwegian)
- Lamberg A, Gjertsen V (2017) Videoovervåking av sjøørret og laks i Stordalselva 2011-2016. SNA report 01/2017, 36 pp. (in Norwegian).
- Lamberg A, Kvitvær T (2018) Videoovervåking av laks og sjøørret i Mundheimselva i 2017. SNA report 14/2018, 68 pp. (in Norwegian).
- Lamberg A, Strand R, Kanstad-Hanssen Ø (2018a) Videoovervåking av laks og sjøørret i Granvinsvassdraget i 2017. SNA-rapport 05/2018, 62 pp. (in Norwegian).
- Lamberg A, Bjørnbet S, Berdal M, Gjertsen V and others (2018b) Videoovervåking av laks og sjøørret i Orkla i årene 2013 til 2017. SNA-rapport 11/2018, 69 pp. (in Norwegian).
- Langset M, Staldvik F (2011) Utvikling i offentlige reguleringer av laksefiske i sjø og vassdrag 1850 – 2010-med hovedvekt på fisketid. KLV - notat nr 5 2011 nr. 5-2011 (in Norwegian).
- Limburg KE, Waldman JR (2009) Dramatic Declines in North Atlantic Diadromous Fishes. *Bioscience* 59:955-965.
- Løland A, Omholt SW, Lamberg A, Kristensen T and others (2016). Metodevurdering for registrering av rømt oppdrettslaks. NTNU Rapport ISBN 978-82-998249-3-4:44 s. (in Norwegian).
- Myksvoll MS, Sandvik AD, Albretsen J, Asplin L and others (2018) Evaluation of a national operational salmon lice monitoring system—from physics to fish. *PLoS One* 13: e0201338
- Orell P, Erkinaro J, Karppinen P (2011) Accuracy of snorkelling counts in assessing spawning stock of Atlantic salmon, *Salmo salar*, verified by radio-tagging and underwater video monitoring. *Fish Managm Ecol* 18:392-399
- Pulg U, Vollset KW, Lennox RJ (2019) Linking habitat to density-dependent population regulation: How spawning gravel availability affects abundance of juvenile salmonids (*Salmo trutta* and *Salmo salar*) in small streams. *Hydrobiologia* 841:13-29
- Rosseland BO (2000) Forsuring av vassdrag: effekter og tiltak. In: Borgstrøm R, Hansen LP Fisk i ferskvann: Et samspill mellom bestander, miljø og forvaltning. Oslo: Landbruksforlaget, p 230–46. (in Norwegian)
- Skaala Ø, Sjøtun K, Dahl E, Husa V and others (2014a) Interactions between salmon farming and the ecosystem: Lessons from the Hardangerfjord, western Norway. *Mar Biol Res* 10:199–202
- Skaala Ø, Johnsen GH, Barlaup B (2010) Prioriterte strakstiltak for sikring av ville bestander av laksefisk i Hardangerfjordbassenget i påvente av langsiktige forvaltningstiltak. Report fra Havforskningen. Institute of Marine Research, Bergen, 10/2018, 39 pp
- Skaala Ø, Johnsen GH, Lo H, Borgstrøm R and others (2014b) A conservation plan for Atlantic salmon (*Salmo salar*) and anadromous brown trout (*Salmo trutta*) in a region with intensive industrial use of aquatic habitats, the Hardangerfjord, western Norway. *Mar Biol Res* 10:308–322
- Skoglund H, Wiers T, Normann ES, Barlaup B and others (2018) Gytefisktelling av laks og sjøaure og uttak av rømt oppdrettslaks i elver på Vestlandet høsten 2017. LFI-report nr 310:33 pp. (in Norwegian).
- Skoglund H, Vollset KW, Barlaup B, Lennox R (2019) Gytefisktelling av laks og sjøaure på Vestlandet – status og utvikling i perioden 2004-2018 (Estimation of spawning population of Atlantic salmon and sea trout in Western Norway – status and development in the period 2004-2018). NORCE report nr. 357, Bergen, Norway, 44 pp. (in Norwegian).
- Stien LH, Nilsson, J, Bui S, Fosseidengen JE and others (2017) Consistent melanophore spot patterns allow long-term individual recognition of Atlantic salmon *Salmo salar*. *J Fish Biol* 91:1699-1712
- Svenning MA, Lamberg A, Dempson B, Strand R and others (2016) Incidence and timing of wild and escaped farmed Atlantic salmon (*Salmo salar*) in Norwegian rivers inferred from video surveillance monitoring. *Ecol Freshw Fish* 26:360-370

-
- Thorstad EB, Økland F, Aarestrup K, Heggberget TG (2007) Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human impacts. *Rev Fish Biol Fish* 18:345-371
- Verspoor E, García de Leániz C, McGinnity P (2007) Genetics and habitat management. In: Verspoor E, Stradmeyer L, Nielsen JL (eds) *The Atlantic Salmon. Genetics, Conservation and Management*. Oxford: Blackwell Publishing, p 399–424
- Vollset KW, Skoglund H, Pulg U, Wiers T and othes (2014) Spatial and temporal patterns in abundance of sea trout, Atlantic salmon and escaped farmed salmon in the Hardangerfjord: Is location within a fjord important for river abundance? *Mar Biol Res* 10:268-278
- Vollset KW, Dohoo I, Karlsen Ø, Halttunen E and others (2017) Disentangling the role of sea lice on the marine survival of Atlantic salmon. *ICES J Mar Sci* 75: 50–60

