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Research article

Influence of harvest restrictions on angler release behaviour and size selection in a recreational fishery

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Fishing regulations such as harvest restrictions are implemented to limit the exploitation of many fish stocks and ensure the sustainability of fisheries. In Norway, inland recreational fisheries are co-managed by the government and by local riparian rights holders, meaning that Atlantic salmon *Salmo salar* harvest restrictions differ somewhat among rivers. Data from Norwegian rivers from 2009 to 2013 were used to test for variation in the proportion of salmon released by anglers and the relative size of salmon harvested and released by anglers in rivers that had varying harvest restrictions in terms of quotas, size restrictions, and/or female harvest restrictions. The proportion of the catch released by anglers was higher in rivers where there were harvest restrictions (proportion released = 0.09–0.24) than in rivers with no such restrictions (proportion released = 0.01). On average, salmon released in rivers with size restrictions larger (average mass difference between harvested and released salmon = −1.25 kg) than those released in rivers without harvest restrictions (difference = 0.60 kg). The proportion of the catch released was larger in rivers with seasonal quotas (0.29) than in rivers with daily (0.07) or collective (i.e. total catch for the river; 0.06) quotas. Rivers with low daily (one salmon per angler per day) or seasonal (<5 salmon per angler per year) quotas had a larger proportion of salmon released (0.23, 0.38, respectively) than rivers with moderate (0.10, 0.21) or high (0.07, 0.16) quotas. High seasonal quotas resulted in larger individuals harvested than released (difference = 1.16 kg), on average, compared to moderate (1.22 kg) and high seasonal quotas (−0.30 kg). We conclude that harvest restrictions influenced the extent to which fish were released and thus the stock composition (i.e. size distribution) escaping the recreational fishery with the potential to spawn.

1. Introduction

Natural resource based recreation and tourism provides significant economic returns through non-exploitative (see Duffus and Dearden, 1990) and consumptive activities such as hunting (Lovelock, 2007) and angling (Ditton et al., 2002; Arlinghaus and Cooke, 2009). Regulating the use of fish and wildlife resources is necessary to balance the economic returns and other socio-economic benefits with the conservation of the local ecosystems and constituent animal populations. Managing natural resources is therefore a combination of managing the resource itself and managing human behaviour, predominantly the users of the resource, in order to ensure long-term sustainability (Clark et al., 2000; Schultz, 2011). In fisheries, regulation of human behaviour requires the implementation of restrictions on angler behaviour in order to moderate the catch and ensure sufficient escapement so that fish stocks can replace themselves and produce a harvestable surplus (Johnson and Martinez, 1995; Cooke and Cowx, 2006; Isermann and Paukert, 2010).

Recreational fisheries are increasingly experiencing over-exploitation associated with high fishing pressure in both freshwater (Post et al., 2002) and marine systems (Coleman et al., 2004). Dedicated and mobile, a group of anglers can effectively deplete

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fisheries resources (Hunt et al., 2011). Catch-and-release is often considered a solution for the problem of over-exploitation of fish in recreational fisheries (Wydoski, 1977; Cooke and Schramm, 2007). This assumption is based on the theory that anglers derive the majority of their satisfaction from the fish capture experience rather than from the harvest and consumption of the fish that they catch. Further, it is assumed that catch-and-release fishing is substitutable for catch-and-keep fishing, although this is not always the case (Ditton and Sutton, 2004; Anderson et al., 2007; Beardmore et al., 2011). Catch-and-release is practiced either voluntarily by anglers or to comply with regulations (i.e. regulatory catch-and-release; Arlinghaus et al., 2007). However, instead of strictly regulating fisheries using catch-and-release, fisheries managers can impose restrictions on harvest for example by implementing quotas, size restrictions, or sex restrictions that limit the proportion of a population that is available to anglers for harvest. Such restrictions provide anglers with a chance to harvest some proportion of their catch while ensuring adequate reproductive potential within the population.

Recreational fishing represents a growing driver of tourism in Scandinavia, particularly in rural regions (Stensland, 2010; Kauppila and Karjalainen, 2012). In Norway, the Atlantic salmon *Salmo salar* fishery is managed by national policies and regulations but also by local regulations developed either by landowners with exclusive rights to fishing on their property or by landowner associations, which represent the interests of a collective of fishing rights holders (Stensland, 2012). There are many restrictions on fisheries including open and closed seasons for fishing. However, there are also regulations on salmon fishing that have local variation, with different restrictions imposed on anglers fishing different rivers. These restrictions generally focus on moderating the harvest of salmon while permitting the retention of some proportion of the catch by recreational anglers. In Norway, these restrictions include quotas, size restrictions, and mandatory female release (Table 1). Regardless of the specific restriction(s) imposed by managers, the objective is consistent, aiming to balance angler satisfaction with sustainability of the fishery in the long-term (Stensland, 2010).

Adult salmon face considerable challenges throughout their migration and are increasingly threatened by habitat alteration and fishery exploitation (Parrish et al., 1998; Thorstad et al., 2008; Otero et al., 2011). Consequently, regulating Atlantic salmon fisheries is a dynamic and difficult task. Effective regulations should reflect management objectives, which are often to maintain spawning populations above conservation limits. Such objectives can be accomplished by increasing the frequency with which fish are released or decreasing the proportion of fish that are captured. Moreover, harvest restrictions might be necessary to protect certain stock components such as large fish that have high fecundity. However, regulatory harvest restrictions can have unintended consequences, particularly when they influence the size of fish that are released such that there is directional selection. Directional selection occurs when certain phenotypes have fitness advantages over others due to intentional (e.g. preferential harvest of large individuals; Allendorf and Hard, 2009) or other (e.g. selective gear type; Kuparinen et al., 2009) mechanisms acting on fisheries. Directional selection is a precursor to fisheries-induced evolution (Kuparinen and Merilä, 2007) and it is therefore important to understand how harvest restrictions influence the size of fish that are released in salmon fisheries. Quantifying how different restrictions function for managing harvest of Atlantic salmon stocks is therefore useful to help regulations meet management objectives. To do so, we analyzed data from Norwegian catch records in Atlantic salmon fisheries with different harvest restrictions including quotas, size restrictions, mandatory female release, and combinations thereof. Specifically, we related the proportion of fish released and the relative size of Atlantic salmon released by anglers to the harvest restrictions implemented in Norwegian rivers from 2009 to 2013.

2. Methods

Salmon catch data were collected from recreational Atlantic salmon fisheries in Norway between 2009 and 2013. To ensure that we had access to comprehensive background data about the fisheries, we analyzed rivers that are assessed by the Norwegian Scientific Advisory Committee for Atlantic Salmon Management. Catch statistics for each of the rivers were provided by Statistics Norway. Detailed reporting by anglers of all individual salmon catches are mandatory in Norway, ensuring that we had accurate catch data. For each river in every year studied, we had data relating to the number of fish harvested and released by anglers as well as the total mass of the salmon harvested and released (which we could divide by the total catch to get the average mass of salmon captured by anglers in all the rivers in every year). Harvest restrictions specified by the local river authority (i.e. landowners association) and fishery management agencies were collected for each year from the local county offices. Although all Atlantic salmon fishing rivers in Norway are managed with regulations such as open and closed seasons, our analysis focused specifically on the implementation of harvest restrictions (Table 1).

Throughout, we addressed two questions about the implementation of harvest restrictions in Norwegian rivers, the first being whether there were differences in terms of the proportion of salmon released and second whether there were differences in the sizes of fish released relative to the sizes of fish harvested. The influence of harvest restrictions on the proportion of salmon released was analyzed with linear mixed effects regression in R (R

Table 1
Harvest restriction types in the Norwegian recreational Atlantic salmon fishery related to quotas and mandatory release of fish. These restrictions are used either singularly or in combination in the different rivers.

Harvest restriction	Description
None	Anglers may harvest whichever fish they choose and there are no quotas[a].
Quota	Anglers may not exceed a personal limit for number of salmon harvested either daily, seasonally, or in combination. Alternatively, a river may have a collective quota for harvest.
Release	Special stipulations that allow the harvest of some fish but require release of others. Examples are rivers open to sea trout (*S. trutta*) fishing where salmon captured as bycatch must be released. In addition, rivers where escaped farmed salmon are common and open to harvest but in which wild salmon must be released.
Female release	Anglers may not harvest female salmon.
Size restriction	Anglers may not harvest salmon exceeding some size limit.
Other	Special stipulations such as in rivers where introduced *Gyrodactylus salaris* parasites exist and anglers are encouraged to harvest fish as part of eradication initiatives.

[a] All rivers have regulations (e.g. seasonal closures, gear restrictions), but this is not covered in this study.

Core Team, 2014). Our initial data set was comprised of proportions of salmon released in each river but due to heteroscedasticity we logit-transformed the response variable using the formula $\ln((y+\varepsilon)/(1-y+\varepsilon))$ where ε was the lowest non-zero proportion of salmon released from any river-year in our data set (0.0018). The logit transformation allowed us to use a Gaussian error distribution and apply a varIdent variance structure (Pinheiro et al., 2014) to account for residual heteroscedasticity, as implemented by the *lme* function in the package nlme (Pinheiro et al., 2014) in R. Tukey-Kramer Honestly Significant Difference (HSD) post-hoc tests were implemented to compare release proportions among harvest restriction types as implemented by *glht* function in the R package multcomp (Hothorn et al., 2008). Second, we used linear mixed effects models to compare size differences among river years with different harvest restriction types. Because only the average mass of fish harvested and released were available for each river, the response variable in the models was the difference in average mass of harvested and released salmon, calculated by subtracting the average mass of salmon harvested in each river-year by the average mass of the salmon released. For this analysis, we excluded rivers in which there were zero salmon released. The anglers that a river attracts can be influenced by the local harvest restrictions, but also by factors such as the location (i.e. proximity to cities and facilities), history/prestige, opinions and culture (i.e. social norms; Stensland and Aas, 2014), and demographics (i.e. number and size of salmon). To account for this, we incorporated river as a random intercept in all models. Heteroscedasticity in the models was corrected by incorporating a varIdent variance structure to the fixed effect based on AIC hypothesis testing of model fit (Pinheiro et al., 2014). Tukey-Kramer HSD tests were implemented for post-hoc pairwise comparisons.

First, we compared the proportion of salmon released and the relative sizes of salmon released among rivers using different harvest restrictions. The restrictions that we assessed were quotas, size restrictions, and mandatory female release. We also assessed rivers that used combinations of these restrictions as well as those that had "other" harvest restrictions (Table 1). Next, we looked more specifically at the types of quotas implemented by fisheries and compared the proportion of salmon released and the relative size of salmon released under daily, seasonal, and collective quotas (Table 1), as well as fisheries using combinations of these quotas. Finally, we compared the proportion of released salmon and the relative sizes of released salmon in fisheries imposing quotas of different strictness, with daily quotas of one salmon considered low, two salmon considered moderate, and 3–5 salmon considered a high quota and seasonal quotas of 0–5, 6–10, and >10 salmon considered low, moderate and high, respectively. All means are presented as ±1 SD.

3. Results

Our data set consists of capture of 564,478 Atlantic salmon recorded in 222 Norwegian rivers between 2009 and 2013. Because we used each river in each year as a single data point, our data set consisted of 996 river-years (not every river was represented in each year of the data set). Most (0.57) of the salmon catch was from large rivers (annual water discharge > 30 $m^3\ s^{-1}$), whereas 0.19 of salmon that were captured were from medium rivers (annual water discharge 10–30 $m^3\ s^{-1}$) and 0.24 of the total catch was from small rivers (annual water discharge < 10 $m^3\ s^{-1}$). Four hundred thirty six river-years reported no salmon released; the catches from these rivers accounted for 0.22 of the total salmon catch in our sample. Small rivers had the smallest proportion of the total salmon catch (0.07) compared to medium (0.16) and large (0.13) rivers. The harvest restriction most frequently implemented in our data set was quotas (0.56 of rivers), whereas the use of size (0.05) or sex (0.01) restrictions was relatively infrequent (Fig. 1). During 2009–2013, the proportion of released salmon increased within our sample from 0.07 in 2009 to 0.15 in 2013 (Fig. 2).

3.1. Differences among harvest restriction types

In river-years without any of the harvest restrictions, the proportion of the captured salmon that was released by anglers was 0.01, whereas in river-years with quotas, the proportion released was 0.09 (Fig. 3a). River-years with a size restriction on harvest had a larger proportion of the catch released (0.16), and river-years with female harvest restrictions had an even larger proportion of salmon released (0.24). River-years with harvest restrictions had significantly more release than river-years with no harvest restrictions (all $t > 6.97$, all $p < 0.01$; Table 2). According to multiple comparisons, the proportion of salmon released in river-years that had harvest restrictions were all significantly different from one another and notably quotas, size restrictions, and female release all differed significantly from one another (Tukey-Kramer HSD: all $z > 4.28$, all $p < 0.01$; Fig. 3a).

In river-years without harvest restrictions, harvested salmon were on average 2.56 ± 0.87 kg whereas released salmon were on average 1.96 ± 1.28 kg; the difference in average mass between harvested and released fish was therefore 0.60 kg in river-years without harvest restrictions. River-years with mandatory female release had a larger average mass difference (0.78 kg) that was not significantly different from the mass difference in river-years without harvest restrictions ($t = 0.38$, $p = 0.71$; Table 2). River-years with quotas (difference = 0.44 kg) also did not have significantly different average mass differences from river-years without harvest restrictions ($t = 0.19$, $p = 0.85$; Table 2). However, river-years with size restrictions (difference = −1.25 kg) had significantly smaller average mass differences than river-years without harvest restrictions ($t = -3.14$, $p < 0.01$; Table 2) or with quotas (Tukey-Kramer HSD pairwise comparison, $z = 4.02$, $p < 0.01$), indicating that this restriction was successful for reducing the size of harvested salmon. However, there was no significant difference in size of salmon released in river-years with size restrictions compared to river-years with female release (Tukey-Kramer HSD $z = -1.67$, $p = 0.78$; Fig. 3b).

3.2. Differences among quota types

In river-years that restricted salmon harvest using quotas, there were differences among river-years based on whether the quota was imposed on daily, seasonal, or collective (for the entire river on a seasonal basis) catches (Fig. 4a). River years with seasonal quotas had the highest proportion of salmon released (0.29), and this proportion was significantly larger than river-years with daily (0.07) and collective (0.06) quotas, which had less frequent release. However, linear mixed effects models indicated that there was no significant difference in the frequency of salmon release in river-years with seasonal quotas compared to river-years with collective (Tukey-Kramer HSD: $z = 0.45$, $p = 0.99$) or daily quotas ($t = 1.46$, $p = 0.15$; Table 3).

There were significant differences in the average mass of released and harvested salmon in river-years with different quota types. In river-years with daily quotas, harvested salmon were on average 2.83 ± 1.21 kg, whereas released salmon were on average 2.96 ± 1.97 kg, a difference of −0.12 kg (Fig. 4b). This was significantly different from the average difference in size of salmon released and harvested in river-years with seasonal (0.32 kg) quotas but not different from river-years with collective (0.82 kg) quotas ($t = 3.58$, $p < 0.01$; $t = 0.56$, $p = 0.58$, respectively; Table 3).

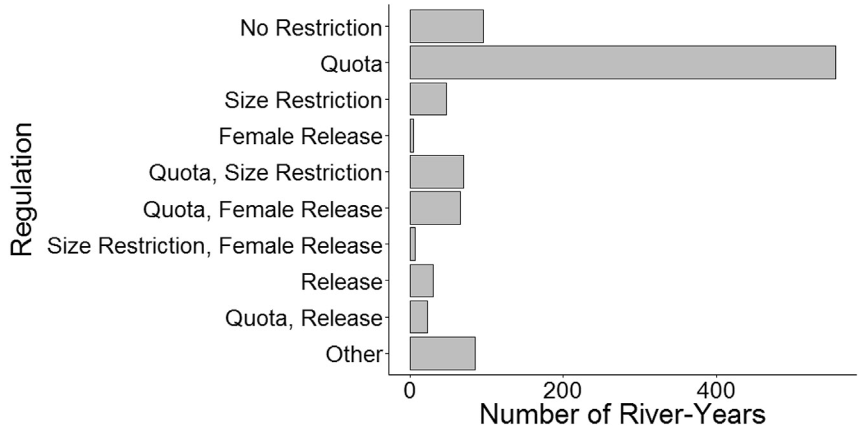

Fig. 1. Harvest restriction types used in the 996 river-years Norwegian Atlantic salmon rivers included in this study during the five-year period 2009–2013. See Table 1 for description of restrictions.

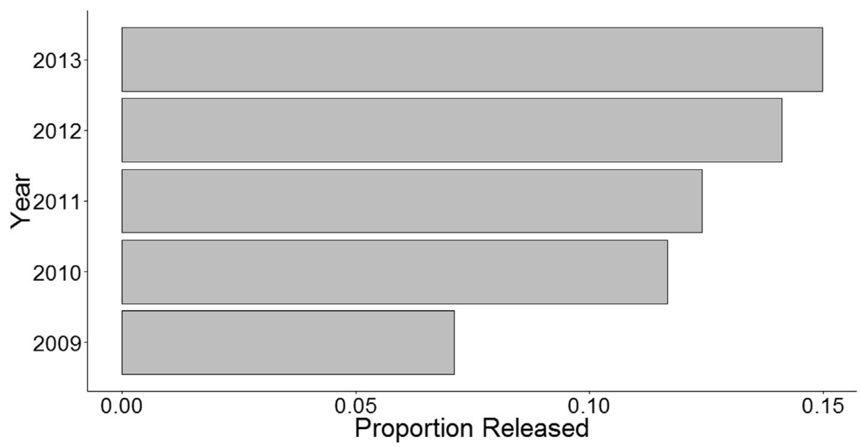

Fig. 2. Proportion of captured Atlantic salmon that was released by recreational anglers in 222 Norwegian rivers during 2009–2013.

3.3. *Differences within daily and seasonal quotas*

The proportion of fish released in river-years that restricted harvest using quotas was different depending on the strictness of the quota (Fig. 5a). River-years with a low daily quota had the highest proportion of captured salmon released (0.23), whereas in river-years with a moderate or high quota, salmon release was less frequent (0.10, 0.07, respectively). The proportion of salmon released was not significantly different between river-years with high or moderately sized daily quotas ($t = 1.18$, $p = 0.24$; Table 4), but river-years with strict daily quotas had higher frequency of salmon released than river years with moderate (Tukey-Kramer HSD: $z = 4.41$, $p < 0.01$) or small daily quotas ($t = 5.03$, $p < 0.01$; Table 4).

In river-years in which daily quotas were low, the average mass of salmon released was 3.69 ± 2.22 kg compared to 3.70 ± 1.61 kg average mass of harvested salmon (difference = 0.00 kg; Fig. 5b). River-years with moderate (difference = −0.01 kg) or high (difference = −0.49 kg) quotas did not have significantly different average size differences between harvested and released salmon ($t = 0.84$, $p = 0.40$; $t = -0.26$, $p = 0.79$; Table 4).

Among river-years where the salmon fishery was managed using seasonal quotas, the proportion of salmon released was relatively small (0.16), compared to instances in which seasonal quotas were low (0.38) or moderate (0.21; Fig. 6a). However, there were no significant differences in the frequency of salmon release for river-years based on the strictness of the seasonal quota (Tukey-Kramer HSD, all $|z| > 0.40$, all $p > 0.48$; Table 5).

In instances when seasonal quotas were high, harvested salmon were on average 2.65 ± 0.32 kg compared to released salmon, which were on average 2.96 ± 0.81 kg (difference = −0.30 kg; Fig. 6b). Similar to river-years with low daily quotas, those with low seasonal quotas had larger fish harvested than released on average (difference = 0.05 kg), which was not significantly different from the average size differences of released and harvested salmon in river-years with high seasonal quotas ($t = -0.01$, $p = 0.99$; Table 5; Fig. 6b). River-years implementing moderate quotas (difference = 0.55 kg) had the largest fish harvested relative to the average size of fish released, a difference that was neither significantly larger than for river-years with high quotas (Tukey-Kramer HSD, $z = 1.17$, $p = 0.47$), nor from those with low quotas ($t = 1.17$, $p = 0.25$; Table 5).

4. Discussion

4.1. *Effect of harvest restrictions*

Irrespective of which harvest restriction was implemented, Atlantic salmon anglers voluntarily released some proportion of their catch because we found that in river-years with no harvest restrictions, there were released fish. However, restrictions increased the proportion of release, which varied in situations with

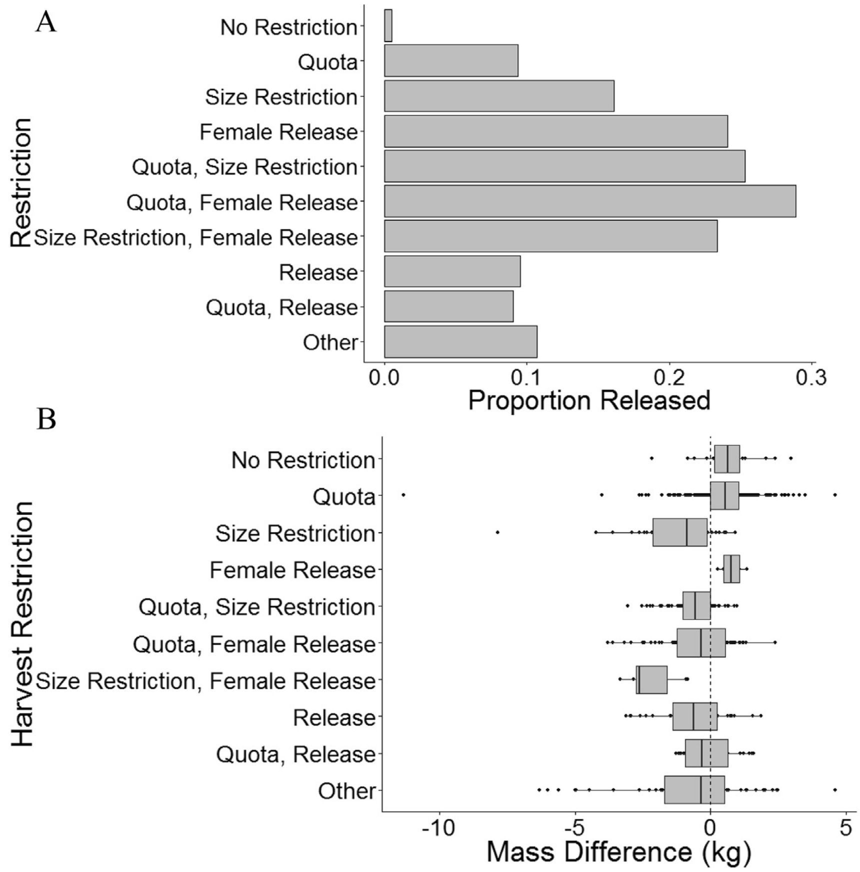

Fig. 3. Fate of Atlantic salmon under different fisheries harvest restrictions in 222 Norwegian rivers during 2009–2013. Panel A shows the proportion of salmon released in fisheries using various restrictions. Panel B shows boxplots of the difference in average mass of salmon harvested compared to the average mass of salmon released under the different restrictions. Boxplots are underlain with individual points representing each river-year to demonstrate the spread of the data. Positive values (i.e. to the right of the dashed line) indicate that on average the harvested salmon were larger than released salmon, whereas negative values (i.e. left of the dashed line) indicate that on average harvested salmon were smaller than released salmon.

Table 2
Mixed effects regression output for the proportion of Atlantic salmon released and relative mass of salmon released in river years regulated with different harvest restrictions. All values are relative to the reference level (no harvest restrictions).

	Proportion released				Mass difference			
	Value ± SE	DF	t-value	p-value	Value ± SE	DF	t-value	p-value
(Intercept)	−5.66 ± 0.21	971.00	−27.42	<0.01	0.34 ± 0.32	389.00	1.06	0.29
Quota	1.25 ± 0.16	971.00	8.03	<0.01	0.06 ± 0.32	389.00	0.19	0.85
Size restriction	2.60 ± 0.33	971.00	7.97	<0.01	−1.56 ± 0.50	389.00	−3.14	0.00
Female release	4.55 ± 0.32	971.00	14.13	<0.01	0.44 ± 1.18	160.00	0.38	0.71
Quota, Size restriction	3.88 ± 0.22	971.00	17.69	<0.01	−0.65 ± 0.38	389.00	−1.72	0.09
Quota, Female release	4.45 ± 0.26	971.00	17.00	<0.01	−0.79 ± 0.37	389.00	−2.13	0.03
Size restriction, Female release	4.48 ± 0.22	971.00	20.59	<0.01	−1.91 ± 0.68	389.00	−2.80	0.01
Release	4.13 ± 0.31	971.00	13.18	<0.01	−1.21 ± 0.48	389.00	−2.54	0.01
Quota, Release	4.42 ± 0.45	971.00	9.85	<0.01	−0.45 ± 0.49	389.00	−0.91	0.36
Other	3.24 ± 0.46	971.00	6.97	<0.01	−0.98 ± 0.51	389.00	−1.93	0.05

different types of restriction. River-years in which no harvest restrictions were implemented had fewer salmon released and larger salmon harvested than released on average. In river-years with harvest restrictions, the proportion of salmon released tended to be higher and the average size difference between harvested and released salmon decreased, indicating that larger salmon were released in settings with restrictions. However, each restriction type had different effects on release in the river-years studied; sometimes, with counterintuitive results. Unsurprisingly, river-years with more restrictions (i.e. second or third order combinations of restriction types; e.g. quotas and size restrictions in combination) had more captured salmon released, because the part of the population open to harvest becomes smaller with more restrictions. However, we mostly focus on the effects of single restrictions in this discussion.

Quotas were the most frequently implemented harvest restriction in this study. River-years with low quotas had the largest proportion of fish released relative to those with moderate or high quotas. The quota strictness had varying effect on the size difference between released and harvested fish (i.e. depending on whether the quota was daily or seasonal). Therefore, the objective of the restriction is important to consider when deciding on a

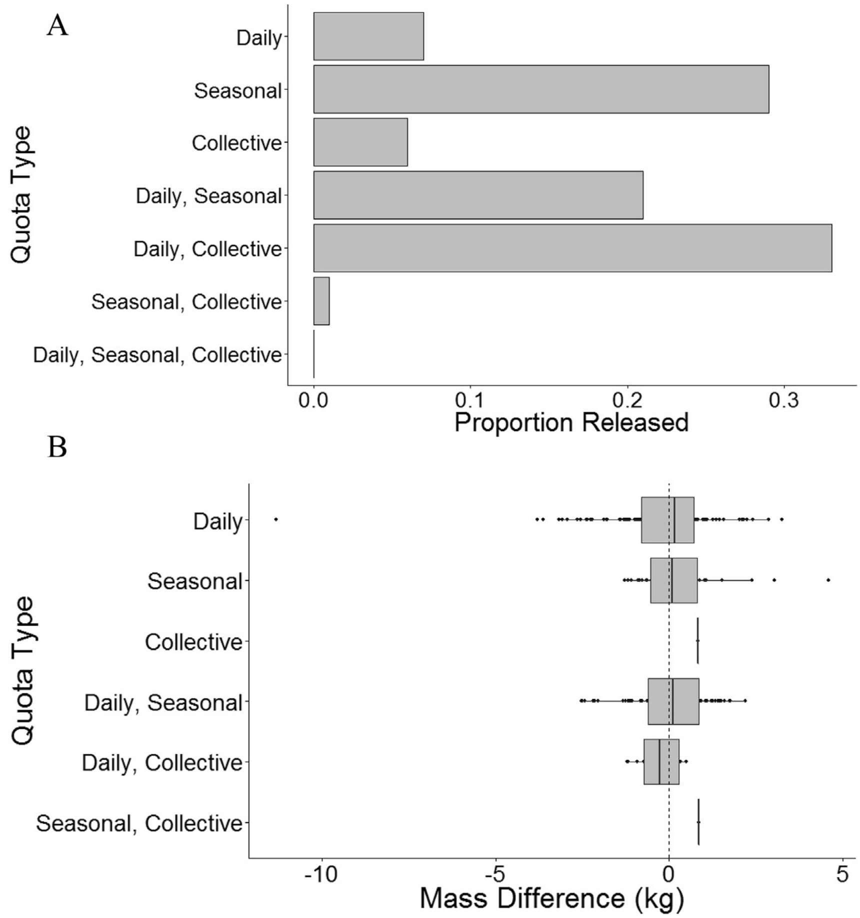

Fig. 4. Proportion and relative mass of released Atlantic salmon in 222 Norwegian rivers during 2009–2013 using different quotas. Panel A shows the proportion of salmon released under the different quotas. Panel B shows boxplots of the average mass of salmon harvested minus the average mass of salmon released. Boxplots are underlain with individual points representing each river-year to demonstrate the spread of the data (253 data points were removed because quota details were unavailable). Positive values (i.e. to the right of the dashed line) indicate that on average the harvested salmon were larger than released salmon whereas negative values (i.e. left of the dashed line) indicate that on average harvested salmon were smaller than released salmon.

Table 3
Mixed effects regression output for the proportion of Atlantic salmon released and relative mass of salmon released in river years regulated with different quotas. All values are relative to the reference level of daily quota. Note that there is no line in mass differences for river-years with daily, seasonal, and collective quotas because after removing river-years with no salmon released there were none in the sample (see Methods).

	Proportion released				Mass difference			
	Value ± SE	DF	t-value	p-value	Value ± SE	DF	t-value	p-value
(Intercept)	−4.40 ± 0.28	659.00	−15.60	0.00	−0.13 ± 0.20	144.00	−0.64	0.53
Seasonal	0.50 ± 0.35	659.00	1.46	0.15	1.23 ± 0.34	144.00	3.58	0.00
Collective	−0.19 ± 1.50	659.00	−0.13	0.90	0.95 ± 1.69	87.00	0.56	0.58
Daily, Seasonal	2.48 ± 0.20	659.00	12.14	0.00	−1.55 ± 1.28	144.00	−1.21	0.23
Daily, Collective	2.42 ± 0.40	659.00	6.11	0.00	−0.18 ± 0.30	144.00	−0.59	0.56
Seasonal, Collective	−1.53 ± 0.64	659.00	−2.39	0.02	1.37 ± 1.29	144.00	1.06	0.29
Daily, Seasonal, collective	−2.36 ± 1.90	659.00	−1.25	0.21				

harvest restriction to impose, for instance whether it is to increase overall release or increase release of large fish. Overall, we found that river-years with quotas did not have a higher proportion of salmon released relative to other restriction types. This is likely because quotas are difficult to attain for salmon anglers given that catch per unit effort is often low (Laughton and Smith, 1993). In settings with high quotas, harvest-oriented anglers would not expect to attain the quota and therefore few salmon would be released.

Restricting female harvest resulted in a high proportion of captured salmon being released by anglers. Given that salmon fecundity is limited by egg availability, female harvest restrictions aim to maximize the productivity of rivers. Male and female salmon have different migration strategies that can lead to different vulnerability to angling. For example, males tend to enter rivers later (Dahl et al., 2004), maintain significantly higher metabolic rates during migration (Lucas, 1994; Altimiras et al., 1996), and survive the migration less frequently (Jonsson et al., 1991). In theory, restricting female harvest should significantly reduce the proportion of salmon eligible to harvest (i.e. by 0.50 assuming equal sex ratios of migratory salmon and equal catch of male and female fish). However, we observed only 0.24 release, potentially

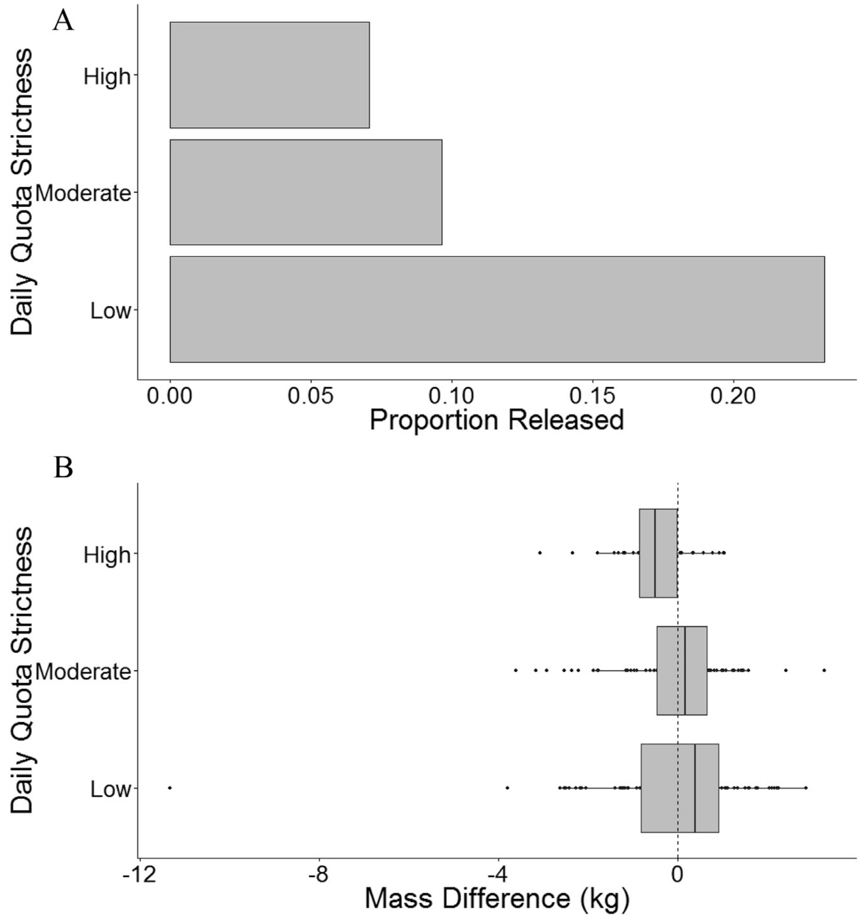

Fig. 5. Proportion and relative mass of released Atlantic salmon in 222 Norwegian rivers during 2009–2013 using daily quotas of varying strictness. Low quotas allow harvest of one salmon per angler per day, whereas moderate quotas allow two and soft quotas permit the daily harvest of three to five salmon per person. Panel A shows the proportion of salmon released under each restriction. Panel B shows the difference between average mass of harvested and released salmon. Boxplots are underlain with individual points representing each river-year to demonstrate the spread of the data. Positive values (i.e. to the right of the dashed line) indicate that on average the harvested salmon were larger than released salmon whereas negative values (i.e. left of the dashed line) indicate that on average harvested salmon were smaller than released salmon.

Table 4
Mixed effects regression output for the proportion of Atlantic salmon released and relative mass of salmon released in river years regulated with daily quotas of varying strictness (see Methods). All values are relative to the reference level of a high daily quota (see Methods).

	Proportion harvested				Mass difference			
	Value ± SE	DF	t-value	p-value	Value ± SE	DF	t-value	p-value
(Intercept)	−4.53 ± 0.30	581.00	−15.22	0.00	−0.28 ± 0.31	124.00	−0.91	0.36
Low daily quota	1.25 ± 0.25	581.00	5.03	0.00	0.10 ± 0.38	124.00	0.26	0.79
Medium daily quota	0.29 ± 0.24	581.00	1.18	0.24	0.36 ± 0.33	124.00	1.11	0.27

attributable to misidentification of females by anglers. Indeed, mature Atlantic salmon are relatively sexually monomorphic until maturation is completed, which generally occurs after weeks to months in freshwater potentially making this a difficult restriction to comply with (Kadri et al., 1997). Although river-years with female release did have a relatively high proportion of salmon released, the average difference in size between released and harvested salmon was smaller than in river-years with size restrictions.

Size restrictions on harvestable fish had the greatest influence on the proportion of captured salmon being released. Many large salmon are females, which generally have higher fecundity than smaller individuals do (Fleming, 1996), and are therefore targeted preferentially by anglers (Fleming, 1998). This means that size restrictions should be effective for conserving individuals with the highest fitness, perhaps even more than sex restrictions would. Moreover, larger individuals may be more susceptible to harvest because they have longer exposure to anglers due to longer river residence (Niemelä et al., 2006). Indeed, Thorley et al. (2007) found that early run salmon in Scotland were recaptured more frequently than were later running salmon, and Pérez et al. (2005) found that early running salmon were preferentially exploited in Spanish recreational fisheries. In river-years without harvest restrictions, anglers generally released small salmon preferentially over large salmon (this study). Given a size restriction, anglers would in theory continue to voluntarily release small salmon, be obligated to release large salmon, and therefore target medium-sized salmon for harvest. This would explain why release was highest when a size restriction was imposed. For the analysis, we pooled all size restrictions into one category, but there are many different limits that can be used on size, and the

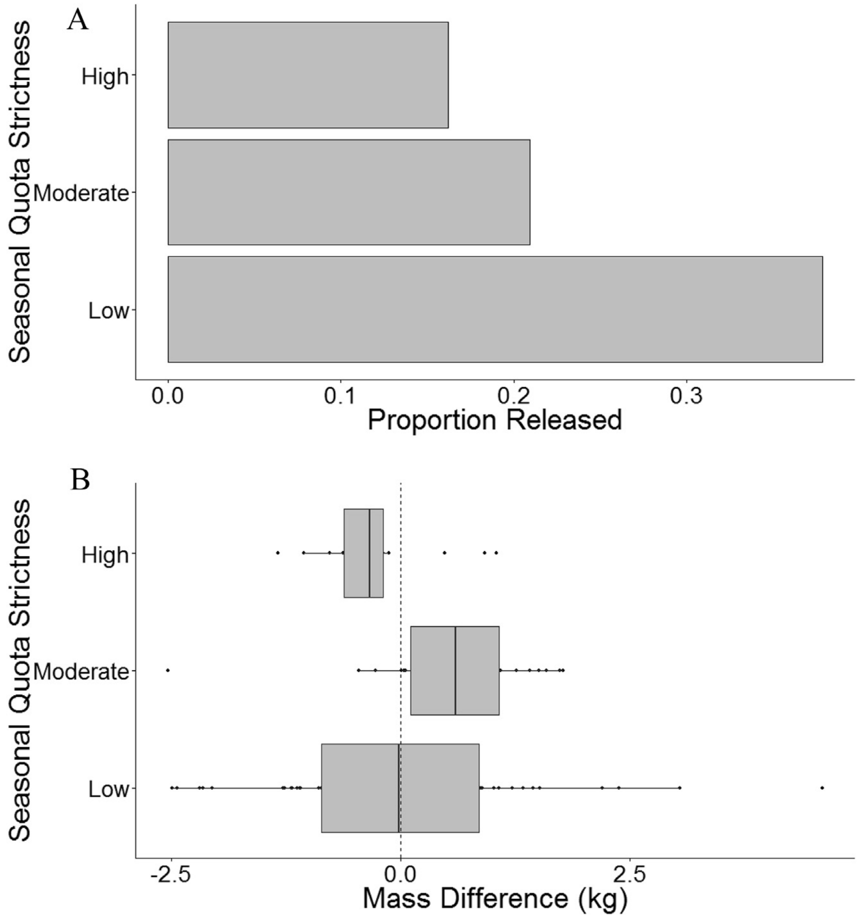

Fig. 6. Proportion and relative mass of released Atlantic salmon in 222 Norwegian rivers during 2009–2013 using seasonal quotas of varying strictness. Low quotas allow harvest of one salmon per angler per day, whereas moderate quotas allow two and soft quotas permit the daily harvest of three to five salmon per person. Panel A shows the proportion of salmon released under each harvest restriction. Panel B shows the difference between average mass of harvested and released salmon. Boxplots are underlain with individual points representing each river-year to demonstrate the spread of the data. Positive values (i.e. to the right of the dashed line) indicate that on average the harvested salmon were larger than released salmon whereas negative values (i.e. left of the dashed line) indicate that on average harvested salmon were smaller than released salmon.

Table 5
Mixed effects regression output for the proportion of Atlantic salmon released and relative mass of salmon released in river years regulated with seasonal quotas of varying strictness (see Methods). All values are relative to the reference level of a high seasonal quota.

	Proportion harvested				Mass difference			
	Value ± SE	DF	t-value	p-value	Value ± SE	DF	t-value	p-value
(Intercept)	−2.29 ± 0.56	185.00	−4.12	<0.01	0.06 ± 0.32	64	0.2	0.85
Low seasonal quota	0.17 ± 0.42	185	0.4	0.69	0.00 ± 0.39	64	0.01	0.99
Moderate seasonal quota	−0.24 ± 0.44	185.00	−0.56	0.58	0.42 ± 0.38	64	1.12	0.27

limit imposed would certainly affect the proportion of fish released.

4.2. Potential drawbacks of harvest restrictions

Instituting regulatory catch-and-release policies appears effective for managing Atlantic salmon fisheries. However, the success of such restrictions is contingent on the survival of fish that are released (Woodward and Griffin, 2003; Coggins et al., 2007). Catch-and-release mortality has been well studied for Atlantic salmon and consistently demonstrated to be low (Whoriskey et al., 2000; Thorstad et al., 2003; Havn et al., 2015; Lennox et al., 2015a). Taken further, catch-and-release can only be effective if surviving fish suffer nominal costs to reproductive success (Wilson et al., 2014), for which there is some evidence in Atlantic salmon (Davidson et al., 1994; Booth et al., 1995; Richard et al., 2013). Nonetheless, efforts to improve post-release survival of fish can potentially be substantial for conservation (Coggins et al., 2007), particularly in rivers where a high percentage of the stock is captured. Therefore, it is important to note that the effectiveness of catch-and-release for salmon depends greatly on angler behaviour. Indeed, salmon mortality can be high under some conditions, particularly when fish are angled for long durations, when air exposure and handling are protracted, or when water temperatures are high (Wilkie et al., 1996, 1997; Dempson et al., 2002; Havn et al., 2015). Anglers participating in recreational fisheries that rely on regulatory catch-and-release must be familiar with best practices for capturing, handling, and releasing fish in optimal condition

(Cooke and Suski, 2005).

Harvest restrictions may drive selection against certain stock components and cause unintended changes to the population (Heino and Godø, 2002). Angling is itself a selective activity that preferentially targets vulnerable components of a stock, while a proportion of the stock is invulnerable or uncatchable (Smith and Taylor, 2014). Ideally, harvest should not create directional selection such that there is potential for long-term phenotypic changes in salmon stocks. However, there is potential for directional selection within salmon fisheries because there are stock components that have higher vulnerability to angling based on size, run timing, and personality traits (Pérez et al., 2005; Consuegra et al., 2005; Thorley et al., 2007). Generally, smaller salmon have higher exploitation rates in Norwegian recreational fisheries (Anonymous, 2009). As a result, directional selection is likely to act against small salmon, particularly if anglers prefer to harvest small salmon. In some salmon fisheries, selective harvest of large fish has driven artificial selection and evolution of traits (e.g. García de Leániz et al., 1992; Consuegra et al., 2005; reviewed in Hard et al., 2008). Avoiding this fisheries-induced evolution should be considered in salmon management and in some cases, restrictions might be needed that match this objective. We found that some restrictions were effective for reducing the harvest of large salmon relative to small salmon, particularly size restrictions.

Associated with size selective harvest is sex-biased harvest. Pérez et al. (2005) found preferential harvest of females in Spanish rivers because of size-selective harvest given that females tended to be larger than males; the opposite can occur when small salmon are preferentially removed. Given that egg number and quality limit population growth, restricting female harvest can be an effective strategy for population management in some scenarios. Although we did not have data regarding the sex of fish released, female harvest restrictions did reduce the size of harvested fish relative to released fish. Because large females have higher fecundity than smaller females, reducing the harvest of the more fecund fish may make it easier to reach spawning targets (usually set as number of eggs per square meter; Forseth et al., 2013). However, releasing only the large females may lead to larger reproductive skew in the population. This may lead to reduced effective population size and increased genetic drift if the population is small (see Serbezov et al., 2012).

4.3. On angler behaviour, motivation, and satisfaction

Harvest restrictions in salmon fisheries have the potential to improve angler experiences in many cases where anglers have catch-oriented, rather than harvest-oriented, fishing objectives. Tagging studies have found that many salmon that are released go on to be recaptured (e.g. Lennox et al., 2015b), which can increase the catch per unit effort in salmon fisheries. When satisfaction is linked to catch rate or total catch of salmon, catch-and-release has the potential to increase angler satisfaction (Richard et al., 2013).

Although we found that type of harvest restriction influenced the release of salmon in recreational fisheries, it is important to consider the human dimension of these restrictions so that the fishery users remain engaged over the long term. Understanding anglers is emerging as an important research priority because angler motivation and satisfaction largely influence their behaviour, compliance, and participation in fisheries (Aas and Kaltenborn, 1995; Aas et al., 2000; Sutton, 2003; Oh et al., 2005; Arlinghaus, 2006). It is increasingly recognized that effective regulations must account for angler preference in order to provide consistently satisfactory angling experiences that will maintain angler interest in local fisheries (Haapasaari et al., 2007). These preferences can vary based on perceptions of conservation or personal outcome objectives (e.g. there are enough fish but they are too small; Aas et al., 2000).

5. Conclusions

Regulations on angler behaviour are an important component of recreational fishery management. Although beyond the scope of this paper, conservation-oriented voluntary angler behaviours are also increasingly important for management (Cooke et al., 2013). In this study, mandatory reporting of salmon catches in Norway provided a unique opportunity to investigate the influence of harvest restrictions on angler release behaviour in a recreational salmon fishery. River-years with mandatory female release had the highest proportion of salmon released, which is intuitive given that about half of the total migratory population should be females and therefore a high proportion of the run should be protected from harvest. Only size restrictions had a significant influence on the size of fish harvested, which increased the size of released salmon relative to harvested salmon. Therefore, we suggest that the harvest restrictions implemented by salmon fishery management in Norway influenced the extent to which fish were released, as well the stock composition (i.e. size distribution) escaping recreational fisheries to spawn. Given that some harvest restrictions had different impacts on angler release behaviour, managers must select restrictions that reflect local conservation objectives for Atlantic salmon. Ultimately, an improved understanding of how angler behaviour responds to various harvest restrictions could contribute to effective fisheries regulation.

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