The Low Abundance and High Catchability of Large Piscivorous Ferox Trout (*Salmo trutta*) in Loch Rannoch, Scotland

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Abstract

The Ferox Trout is an ancient member of the Brown Trout (*Salmo trutta*) species complex that may constitute its own species: *Salmo ferox.* Due to their exceptionally large size, Ferox Trout are highly sought after by anglers while their life-history strategy, which includes delayed maturation, multiphasic growth and extended longevity, is of interest to ecological and evolutionary modelers. However, despite their genetic, recreational and theoretical importance, little is known about the typical abundance of Ferox Trout or their vulnerability to angling. To rectify this situation a 16 year mark-recapture study was conducted on Loch Rannoch, which at 19 km^2 is one of the largest lakes in the United Kingdom. A hierarchical Bayesian Jolly-Seber analysis of the data indicates that in 2009 the population of Ferox Trout in Loch Rannoch was approximately 71 individuals. The results also indicate that a single, often unaccompanied, highly-experienced angler was able to catch roughly 8% of the available fish on an annual basis. It is recommended that anglers adopt a precautionary approach and release all trout with a fork length $\geq$ 400 mm caught by trolling in Loch Rannoch.

Introduction

Due to its large size and distinctive appearance the Ferox Trout was originally considered its own species, *Salmo ferox* [15]; an appellation that was lost when all the forms of Brown Trout were lumped into *Salmo trutta.* More recently, Duguid *et al.* [10] have demonstrated that Ferox Trout in Lochs Melvin (Ireland), Awe and Laggan (Scotland) are reproductively isolated and genetically distinct from their sympatric conspecifics and together form a monophyletic grouping. Based on this evidence, Duguid *et al.* [10] argue that the scientific name *S. ferox* should be resurrected.

Ferox Trout are characterized by their large size and extended longevity. The British rod caught record is 14.4 kg (31 lb 12 oz) and the oldest recorded individual was estimated to be 23 $\pm$ 1 years of age based on scale annuli [8].

The consensus view is that Ferox Trout achieve their large size by forgoing spawning until they are big enough to switch to a primarily piscivorous diet at which point they experience an increased growth rate [7, 8, 29]. As top lake predator, they are assumed to subsequently experience high survival and fecundity both of which compensate for the previous lost spawning opportunities [18, 19]. The conditions conducive for producing Ferox Trout have been studied empirically through comparative lake studies [7, 8] and theoretically with ecological models [18, 19] and are thought to include a large (> 1 km^2) oligotrophic lake and an abundant population of Arctic Charr (*Salvelinus alpinus*). The ecological models have even been used to estimate the expected relative abundance of Ferox Trout (on average 6% of the total Brown Trout population). However, there is a lack of robust estimates of the abundance of Ferox Trout or assessments of the potential for angling to impact individual populations. Part of the reason for the paucity of information on Ferox Trout abundance and exploitation is that these large piscivores are rarely caught [10].

In 1994, the first author (AT) - a highly-experienced ferox angler - began tagging and releasing all Ferox Trout captured by himself or his boat companion on Loch Rannoch. He continued this practise for 16 years. The paper uses the resultant dataset to answer two questions: How abundant are Ferox Trout in Loch Rannoch? and What is their catchability? Loch Rannoch was chosen for the study due to its long history of producing large Ferox Trout [7, 8]. Although the current dataset represents a unique opportunity to better understand the life history of this top-level piscivore, the data are nonetheless sparse. Consequently, they are analyzed using Bayesian methods which provide statistically unbiased estimates irrespective of sample size [17, 25].

Methods

Ethics

A collection permit was not required because the fish, which were not classified as protected, were caught by regular angling during the fishing season. Ethical approval was not required because surgical procedures were not performed. The fish handling procedures are described in the Fish Capture and Tagging section.

Field Site

At 19 km^2, Loch Rannoch, which is situated in central Scotland (Fig. 1), is one of the largest lochs in the United Kingdom (Fig. 2). Murray and Pullar [21] provide a description of its physical characteristics. Loch Rannoch, which has a maximum depth of 134 m and a length of 16.7 km, is situated at an altitude of 204 m. It is oligotrophic with a stony shoreline and lies in a setting dominated by mixed relict deciduous and coniferous woodlands with areas of rough grazing and marginal cultivation.

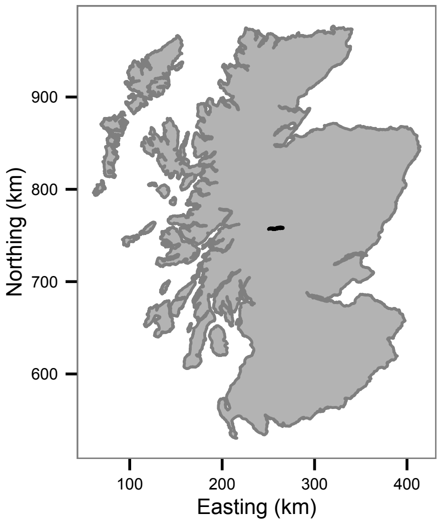

Figure 1: Scotland and the Western Isles. Loch Rannoch is indicated by the black polygon. The coordinates are for the British National Grid OSGB 1936.

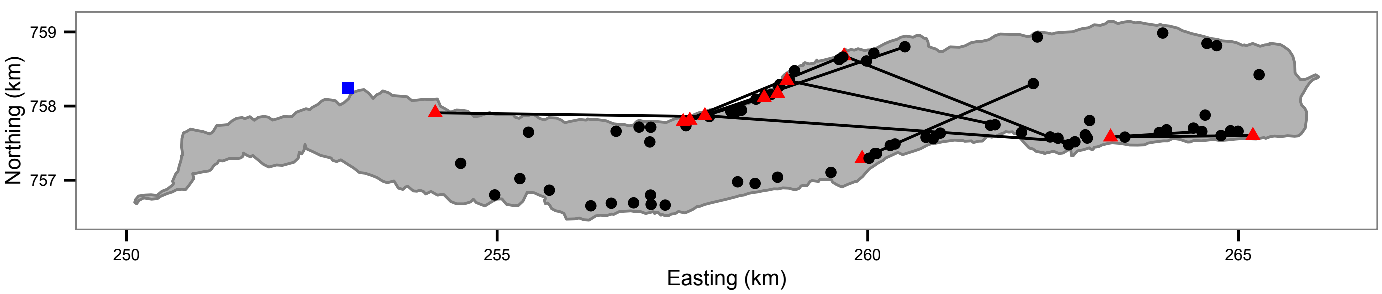

Figure 2: Loch Rannoch. The initial captures of Ferox Trout are indicated by black circles and the inter-annual recaptures by red triangles. Consecutive recaptures of the same individual are linked by black lines. The fish were caught by angling between 1994 and 2009. Rannoch Power Station is indicated by the blue square. The coordinates are for the British National Grid OSGB 1936.

Loch Rannoch is part of the Tummel Valley Hydro Electric generation complex and has been a hydroelectric reservoir since 1928, when Rannoch Power Station began to receive water from Loch Ericht. A low barrage at the eastern end of the Loch limits the change in water level to a maximum of 2.74 m.

As well as Brown and Ferox Trout, the loch contains at least seven other species of fish: Atlantic Salmon (*Salmo salar*), Pike (*Esox lucius*), Perch (*Perca fluviatilis*), Eels (*Anguilla anguilla*), Three-Spined Sticklebacks (*Gasterosteus aculeatus*), Minnows (*Phoxinus phoxinus*) and Arctic Charr.

Ferox85

The Ferox85 group was formed in 1985 to better understand the biology and behavior of Ferox Trout and to facilitate the management of sustainable rod fisheries for this important resource. The informal group consists of approximately 45 members, five of which participated in the study by accompanying AT (also a Ferox85 group member) on one or more occasions. On average they spent 10 days boat angling per year for approximately 10 hours per day while fishing three rods although detailed logs of angling effort were not kept.

Fish Capture and Tagging

Between 1994 and 2009, AT tagged and released all Ferox Trout captured by himself or his boat companion on Loch Rannoch. In the absence of any genetic data, a Ferox Trout was deemed to be any member of the Brown trout species complex with a fork length $\geq$ 400 mm as this is considered to be the upper length threshold for the inferred switch to piscivory [7,8]. All the fish were caught by angling during the fishing season (March 15 to October 6).

The Ferox Trout were angled by trolling mounted dead baits and lures behind a boat at differing depths and speeds [13]. The dead baits (usually Brown Trout or Arctic Charr) were mounted to impart fish-like movement. An echo sounder was used to search the contours of the loch bottom for drop-offs and likely fish holding areas and to ascertain fishing depth. Typically, one entire circuit of the loch's shoreline excluding the shallow west end, which has an area of 3 km^2, was undertaken on each visit.

Hooked fish were played with care and netted directly into a large tank of water before being carefully unhooked. The fish was then transferred into a large fine-mesh keep net (net pen), on the shore closest to the point of capture, where it was allowed to recover before processing. After recovering, the fish was removed from the keep net and placed in a tank containing water and anesthetic (0.05 % aqueous solution of 2-pheoxyethanol). When the fish was sufficiently sedated its fork length and wet mass were obtained. A sample of scales was removed for aging. The adipose fin was then clipped to aid in the identification of recaptures. In addition, all but one fish (63) was externally tagged using a Carlin, dart or anchor tag. The tags included the text "REWARD" and a telephone number for reporting. The reward value which was not printed on the tag was five British pounds. The type of tag used depended on which type was available at the time. After tagging, the fish was returned to the keep net to recover and then released from the shore. The entire procedure typically took less than 30 min. The capture location (Fig. 2) was estimated using a 1:5000 map (National Grid Reference NN600580).

Statistical Analysis

Fish. Two individuals (Fish 53 and 58), which were both recaught once, were excluded from the study because they had a deformed spine and jaw, respectively. After the further exclusion of four intra-annual recaptures, the data set contained information on 80 encounters involving 69 different Ferox Trout (Table 1); 7 of which were recaught in at least one subsequent year.

Table 1: Initial Captures and Subsequent Recaptures of Angled Loch Rannoch Ferox Trout by Year.

Year	Captures	95	96	97	98	99	00	01	02	03	04	05	06	07	08	09
1994	7	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
1995	6		0	0	0	0	0	0	0	0	0	0	0	0	0	0
1996	5			0	0	0	0	0	0	0	0	0	0	0	0	0
1997	2				0	0	0	0	0	0	0	0	0	0	0	0
1998	5					0	0	0	1	0	0	0	1	0	0	0
1999	2						0	0	0	0	0	0	0	0	0	0
2000	12							0	1	1	0	0	0	0	0	0
2001	6								1	0	1	1	0	0	0	0
2002	3									0	0	0	0	0	0	0
2003	4										0	0	0	0	0	0
2004	2											0	0	0	0	0
2005	2												0	1	0	1
2006	1													0	0	0
2007	1														0	0
2008	2															0
2009	9															

Hierarchical Bayesian Model. The abundance, annual survival and probability of (re)capture were estimated from the mark-recapture data using a hierarchical Bayesian Jolly-Seber (JS) model [17]. The model was the superpopulation implementation of Schwarz and Arnason [27] in the form of a state-space model with data augmentation [17]. Based on preliminary analyses the augmented data set was fixed at 69 (genuine and pseudo-) individuals. The zero-inflation of the augmented data set was modeled as an inclusion probability (ψ). Due to the sparsity of data, the annual survival (S) and the probability of (re)capture (p) were assumed to be constant. The only remaining primary parameter was the the probability of an individual recruiting to the population at the start of the first year (ρ_1). The prior probability distributions for ψ, S, p and ρ_1 were all uniform distributions between zero and one. The hierarchical Bayesian JS state-space model made the following assumptions:

1. Every individual in the population had the same constant probability of capture (p).

2. Every individual in the population had the same constant probability of surviving (S).

3. Previously captured individuals were correctly identified.

4. The number of individuals recruiting to the population at the start of each year (B) remained constant.

Parameter Estimates. The posterior distributions of the parameters were estimated using a Monte Carlo Markov Chain (MCMC) algorithm. To guard against non-convergence of the MCMC process, five chains were run, starting at randomly selected initial values. Each chain was run for at least 10^5 iterations with the first half of the chain discarded for burn-in followed by further thinning to leave at least 2000 samples from each chain. Convergence was confirmed by ensuring that the Brooks-Gelman-Rubin convergence diagnostic $\hat{R} \leq 1.05$ for each of the parameters in the model [6, 17]. The reported point estimates are the mean and the 95% credible intervals (CRIs) are the 2.5 and 97.5% quantiles [12].

Model Adequacy. The adequacy of the model was confirmed by posterior predictive checking of the actual versus replicate data where the discrepancy measure was the Freeman-Tukey statistic [17]. The Freeman-Tukey statistic was chosen over the log density [12, 26] because the actual and replicate data were the relatively low number of encounters (captures and recaptures) each year [5].

Software. The analyses were performed using R version 3.2.2 [24], JAGS 3.4.0 [22] and the ranmrdata and ranmr R packages (S1 Software), which were developed specifically for this paper.

Results

Fish. The (re)captured fish varied from 400 to 825 mm in length and from 0.62 to 7.41 kg in mass (Fig. 3). Although two large recaptures appeared to senesce (as evidenced by a decline in mass with increasing length), there was no obvious effect of previous capture on body condition (Fig. 3). Based on scale annuli the youngest fish was 5 years at initial capture while the oldest was 20 years at recapture (Fig. 4). When the scales were not eroded due to resorption the scale ages for recaptures were consistent with the scale ages at initial capture plus the number of years at large. In the case of scale erosion, subsequent ages were based on the scale age at initial capture. Tag loss was only recorded for one of the individuals: fish 21 on its second recapture eight years after it was initially tagged. It was identified from photographs of its melanophore constellations (S1 Photographs), which have been shown to provide a reliable method of individual identification in juvenile Atlantic Salmon [9]. Fish 13 was recaught and retained and fish 45 was recaught and released by non-participatory anglers. Both recaptures were excluded from the dataset.

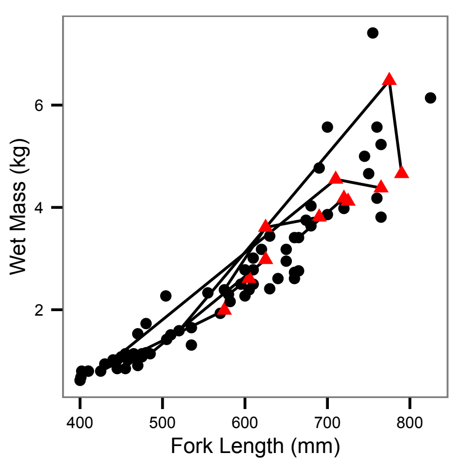

Figure 3: Mass-Length Scatterplot for Ferox Trout Caught by Angling on Loch Rannoch between 1994 and 2009. The initial captures are indicated by black circles and the inter-annual recaptures by red triangles. Consecutive recaptures of the same individual are linked by black lines.

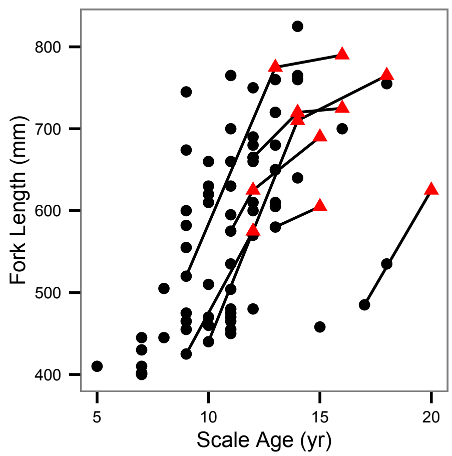

Figure 4: Age-Length Scatterplot for Ferox Trout Caught by Angling on Loch Rannoch between 1994 and 2009. The initial captures are indicated by black circles and the inter-annual recaptures by red triangles. Consecutive recaptures of the same individual are linked by black lines.

Parameter Estimates. The Bayesian JS mark-recapture model estimated the annual survival (S) to be 0.73 (95% CRI 0.57 - 0.89) and the annual probability of capture by the primary author or his companion (p) to be 0.08 (95% CRI 0.03 - 0.16). The inclusion parameter (ψ) was estimated to be 0.43 (95% CRI 0.23 - 0.78) while the probability of recruiting at the start of the first year (ρ_1) was 0.25 (95% CRI 0.13 - 0.42). The number of individuals recruiting to the population annually (B) was 21 individuals (95% CRI 12 - 38). The abundance estimates declined from 111 individuals (95% CRI 38 - 247) in 1994 to 71 individuals (95% CRI 30 - 151) in 2009.

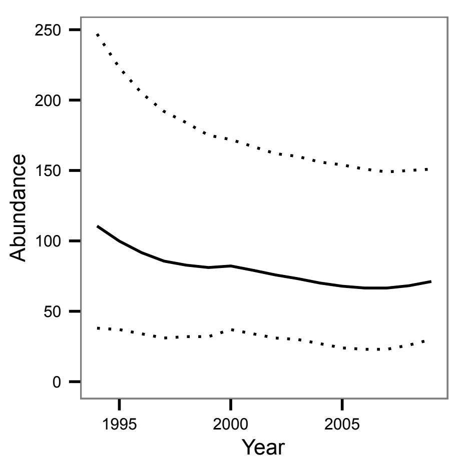

Figure 5: Loch Rannoch Ferox Trout Abundance Estimates by Year. The solid line indicates the point estimate and the dotted lines the 95%credible intervals.

Model Adequacy. The Bayesian p-value on the posterior predictive check was 0.31 which indicates that the distribution of the number of encounters (captures and recaptures) each year was consistent with the assumed constant capture efficiency.

Discussion

Abundance

The JS mark-recapture model estimated that the population of Ferox Trout in Loch Rannoch fell from approximately 111 individuals in 1994 to less than 71 by 2009. Whether or not the abundance estimates are accurate depends in part on the extent to which the assumption of a constant capture probability is met. Although the posterior predictive check confirmed the relative constancy of p through time, individual Ferox Trout may still have differed substantially in their vulnerability to capture by angling. Depending on whether any individual differences were fixed or learnt the abundance values will be over or under-estimates respectively [3, 4]. As is the case for many mark-recapture studies the reliance on a single capture method and the relatively low number of individuals means it is not possible to distinguish between these two possibilities [4].

Taken at face value the most recent abundance estimate corresponds to a density of just 0.037 fish per hectare or 0.044 fish.ha^{-1} if the shallow west end is excluded [11]. For comparison, Johnston et al. [16] estimated that the density of large piscivorous Bull Trout in the 6.5 km Lower Kananaskis Lake, Alberta, was 0.093 fish.ha^{-1} when being overexploited. In response to a zero-harvest regulation, the density of large Bull Trout in Lower Kannaskis Lake increased to over 2.6 fish.ha^{-1} in less than a decade.

Catchability

The results also indicated that, despite the size of the loch, an angler effort (E) of just 0.16 rod-hours.ha^{-1}.yr^{-1} was able to produce an effective exploitation rate ($u = p$) of 0.076. If the catchability coefficient (q) is defined to be the annual instantaneous fishing mortality per unit of effort [2], i.e.,

$$q = \frac{-log(1-u)}{E}$$

then the catchability coefficient is 0.5 rod-hr^{-1}.ha^{-1}.yr^{-1}. Based in part on creel data from Lower Kananaskis Lake, Post et al. [23] considered a q of 0.07 angler-hr^{-1}.ha^{-1}.yr-1 to be representative for large Bull Trout. At least some of the seven-fold difference between the studies could be due to uncertainty: Post et al. [23] also considered a higher q of 0.14 to be representative while the lower CRI for the present study was 0.19. It is also likely that AT's angling experience means that the estimated catchability coefficient is inflated relative to other anglers.

In the absence of creel data for Loch Rannoch, it is not possible to estimate the catchability of Ferox Trout by less experienced anglers. Nonetheless, the exploitation rate by non-Ferox85 group members appears to have been low because despite the offer of a reward only two fish were reported to have been recaught by a member of the public.

The annual interval mortality estimate $(1 - S)$ of 0.27 includes handling and tagging by Ferox85 group members as well as natural mortality and fishing mortality by all other anglers on the loch. As all fish recovered well and were only adipose clipped and marked with a single external tag, it is likely that handling and tagging effects were small.

Furthermore, since the exploitation rate by other anglers on the loch appeared to be low, 27% is probably only a moderate overestimate of the natural mortality rate. For comparison, Johnston et al. [16] estimated the equilibrium natural mortality rate for adult Bull Trout in Lower Kananaskis Lake to be around 27%.

Management and Conservation Implications

A concern for any small salmonid population is that the loss of genetic variation results in loss of adaptive potential or inbreeding depression [28]. Although the levels at which the low genetic variation results in population-level consequences are difficult to predict, the rate at which genetic variation is being lost can be calculated from the effective population size (N_e) [30, 31]. Due to their mating systems and life-histories, the N_e of most salmonid populations is considered to be around 25% of the spawning population size [1, 20]. Thus even if all the adult Ferox Trout in Loch Rannoch spawn in each year then this suggests that the N_e in 2009 was just eight. The low effective population size is concerning because an $N_e \geq 50$ is needed to minimize inbreeding effects and an $N_e \geq 500$ is required to retain long-term adaptive potential [1].

Whether or not the Ferox Trout in Loch Rannoch are at risk of inbreeding depression depends on the extent to which they are reproductively isolated from the other Brown Trout in the loch. If they, like the Ferox Trout in Lochs Melvin, Awe and Laggan, are sufficiently isolated and genetically distinct to be considered a separate species [10] then inbreeding is likely occurring. Alternatively, if the Ferox Trout in Loch Rannoch are simply Brown Trout adopting an alternative life-history strategy, then the effective population size is a function of the total number of Brown Trout spawners and inbreeding is not an issue.

Nonetheless, even if the Ferox Trout in Loch Rannoch are not genetically isolated, a sustained high exploitation rate could result in adaptive change. Mangel and Abrahams' [19] individual-based model predicted that the proportion of the population adopting the ferox life-history strategy is affected by mortality with high size-independent mortality being associated with no or few Ferox Trout. The explanation is straightforward; with increasing mortality the chances of benefiting from delayed maturation diminish. The high catchability suggests that with even small amounts of angler effort, fishing mortality could be strong enough to select against the ferox adaptation [14].

Given the concerns associated with a potentially high exploitation rate on a long-lived, late-maturing population it is recommended that anglers adopt a conservative approach and release all trout longer than 400 mm caught by trolling in Loch Rannoch. There is an urgent need to assess the status of Ferox Trout in other Scottish lochs.

Supporting Information

S1 Software

R Packages. Instructions on how to install the ranmrdata (`http://dx.doi.org/10.5281/zenodo.31948`) and ranmr (`http://dx.doi.org/10.5281/zenodo.31949`) R packages. The packages, which were developed for the current paper, provide the data, allow the results to be easily replicated and the models fitted to other datasets. (MD)

S1 Photographs

Photographs of Fish 21 and 44. The images indicate the consistency of melanophore spot patterns between capture and recapture. (ZIP)

Acknowledgments

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Author Contributions

Conceived and designed the experiments: AT AID. Performed the experiments: AT AID. Analyzed the data: JLT. Wrote the paper: JLT.

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