ARTICLE

Behaviour-mediated alteration of positively size-dependent vulnerability to angling in response to historical fishing pressure in a freshwater salmonid

Jun-ichi Tsuboi, Kentaro Morita, Thomas Klefoth, Shinsuke Endou, and Robert Arlinghaus

Abstract: Positively size-selective vulnerability to fishing is well established in recreational fisheries. Size-selective harvesting can either induce an indirect selection response of behavioural traits that are correlated with size or exert direct selection pressures on behaviours that contribute to vulnerability. In addition, learning to avoid future capture may always happen. Behavioural change caused by fishing may in turn affect the size-selective properties of angling. To test this prediction, field experiments with amago salmon (*Oncorhynchus masou ishikawae*) were conducted. We demonstrated that, as expected, large fish were more vulnerable than smaller individuals in a low fishing pressure (LP) stream and that positively size-selective angling was not (or no longer) present in a high fishing pressure (HP) stream. Moreover, fish in the HP stream were by far less vulnerable to angling with natural bait than fishes in the LP stream. Laboratory studies showed that offspring from HP streams were intrinsically shyer than offspring collected from LP streams. We propose that the increased timidity of individuals inhibiting HP streams disrupted the generally positive relationship among salmon body size and its vulnerability to angling. Fisheries-induced timidity in response to high exploitation rates reduces catchability, affects the size-selective properties of angling, reduces the value of fishery-dependent stock assessments, and potentially affects trophic interactions.

Résumé : La vulnérabilité à la pêche positivement reliée à la taille est un phénomène bien documenté dans les pêches sportives. La pêche avec sélection selon la taille peut soit induire une réaction de sélection indirecte de caractères comportementaux qui sont corrélés à la taille ou exercer des pressions de sélection directes sur des comportements qui accroissent la vulnérabilité. En outre, l'apprentissage de l'évitement de captures futures peut toujours se produire. Les changements comportementaux causés par la pêche peuvent, quant à eux, avoir une incidence sur les propriétés de sélection selon la taille de la pêche. Pour vérifier cette prédiction, des expériences sur le terrain avec des saumons amago (*Oncorhynchus masou ishikawae*) ont été menées. Nous avons démontré que, comme prévu, les grands poissons étaient plus vulnérables que les poissons plus petits dans un cours d'eau caractérisé par une faible pression de pêche (LP) et que la pêche avec sélection positive selon la taille n'était pas (ou plus) présente dans un cours d'eau caractérisé par une forte pression (HP). De plus, les poissons dans le cours d'eau HP étaient beaucoup moins vulnérables à la pêche sportive avec des appâts naturels que les poissons dans le cours d'eau LP. Des études en laboratoire ont démontré que la progéniture provenant des HP était intrinsèquement plus timide que la progéniture prélevée des cours d'eau LP. Nous proposons que la timidité accrue des individus dans les cours d'eau HP perturbe la relation généralement positive entre la taille du corps des saumons et leur vulnérabilité à la pêche sportive. La timidité induite par la pêche en réaction à des taux d'exploitation élevés réduit la capturabilité, influence les propriétés de sélection selon la taille de la pêche, réduit la valeur des évaluations des stocks dépendant de la pêche et pourrait avoir une incidence sur les interactions trophiques. [Traduit par la Rédaction]

Introduction

Recreational fishing can induce evolutionary changes in life history, morphology, physiology, and behaviour in response to excessive and (or) trait-selective exploitation (e.g., Uusi-Heikkilä et al. 2008, 2015; Sutter et al. 2012). Most life-history changes caused by intensive fishing collectively reduce adult body size at age (Jørgensen et al. 2007; Alós et al. 2014). Evolutionary downsizing will in turn affect catch rates because most fishing gears operate positively size-dependently and hence more readily catch the larger size classes of an exploited population. Passively operated fishing gears, such as recreational angling or gill-netting, may not only select on body size and life history (Saura et al. 2010; Arlinghaus et al. 2009; Alós et al. 2014; Evangelista et al. 2015), but also select for activity, exploration, aggression, and other behavioural traits (Heino and Godø 2002; Olsen et al. 2012; Diaz Pauli et al.

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2015; Wilson et al. 2015). Changes in body size and correlated behavioural traits over time in response to intensive fisheries can affect individual reproductive success due to the linear relation of body mass and fecundity characteristic for most temperate fishes (Wootton 1992) and the reduced nest vigilance shown by low vulnerable individuals in species that provide parental care (Sutter et al. 2012). One can also expect intensively angling-exploited fish stocks to not only host smaller growing fishes after maturation (Alós et al. 2014), but also individuals revealing increased levels of timidity due to fisheries-induced behavioural evolution and associated hook-avoidance learning effects in catch-and-release fisheries (Raat 1985; Askey et al. 2006; Alós et al. 2012, 2015; Klefoth et al. 2012, 2013).

In most stream salmonids, dominance hierarchies are common, which are usually size-dependent. Large aggressive fish often become dominant, in turn defending territories, which results in greater foraging rates and growth compared with subdominant individuals (Nakano 1995). Therefore, large dominant salmonids are usually more vulnerable to angling under natural conditions compared with smaller subdominant individuals (Tsuboi and Endou 2008). Moreover, for metabolic reasons absolute food consumption positively correlates with size (Yamamoto et al. 1998), in turn leading to larger fish consuming more than small fish, which also elevates capture probabilities of large compared with small fishes (Brauhn and Kincaid 1982). Finally, the mouth gape of large fish facilitates the take of a larger range of lures and bait types (Arlinghaus et al. 2008*b*), which may further contribute to the greater vulnerability of large fish compared with small fish (Lewin et al. 2006), all other states (e.g., hunger and habitat choice) being equal.

To reach large sizes in highly exploited streams, dominant and bold salmonid individuals need to be able to effectively trade off foraging opportunities and the risk of capture. Boldness, defined as foraging under the risk of predation (Réale et al. 2007), has a genetic basis in salmonids and other fishes (Iguchi et al. 2001; Ariyomo et al. 2013; Dochtermann et al. 2015). Hence, in response to high fishing pressure one would expect freshwater salmonids to become shyer owing to genetic (i.e., fisheries-induced evolution of behavior; Uusi-Heikkilä et al. 2008, 2015) and plastic reasons (i.e., increased hook-avoidance learning; van Poorten and Post 2005; Askey et al. 2006; Klefoth et al. 2012, 2013). When present, increased timidity may decouple the generally present positive relationship of size and vulnerability to fishing across generations (Alós et al. 2015; Januchowski-Hartley et al. 2015). No studies addressing this question exist for wild-living salmonids, but it has been reported that bold and explorative salmonid individuals are preferentially captured by passively operated gill nets and angling gear (Biro and Post 2008; Härkönen et al. 2014).

We tested the vulnerability to angling gear of wild amago salmon (*Oncorhynchus masou ishikawae*) in dependence of their body size and behaviour by comparing individuals inhabiting high angling pressure (HP) and low angling pressure (LP) streams in both natural and laboratory common garden conditions. In the field experiments, we hypothesized that large individuals are more vulnerable than smaller individuals and that fish are particularly hard to catch in a HP stream compared with an LP stream. In associated laboratory experiments, we hypothesized that large fish grow faster and are more vulnerable to angling compared with small fish, but that this effect should be more pronounced in fishes originating from an LP stream. This expectation arose from the idea that the largest fishes of a population that are evolving in a HP stream should be more shy and consequently be less vulnerable to angling compared with similar-sized fish inhabiting an LP stream. Both evolutionary adaptation and learning within the realm of behavioural plasticity may contribute to the very same effect (Alós et al. 2015), but our study was not designed to disentangle among genetic and plastic effects. Instead we aimed at more generally testing the effects of historic fishing pressure on phenotypic expressions and angling vulnerability of a freshwater salmonid using a combined field and laboratory assessment approach.

Table 1. Environmental components of a high fishing pressure (HP) and low fishing pressure (LP) stream.

Stream	Altitude (m)	Stream width (m) (mean ± SD)	No. of litter items left by anglers per hectare (mean, min.–max.)
HP	700	3.73±2.04	33.5, 0–76.9
LP	1160	2.92±1.00	2.7, 0–10.9

Material and methods

Field experiment

To compare the body size-dependent vulnerability to angling between fishes in HP and LP streams, experimental angling was conducted in the Toiwa and Itajiki streams, both belonging to the Fuji River system in central Japan (35°45′N, 138°35′E; Table 1). In both streams, amago salmon is the only resident fish species exhibiting a nonanadromous life history. The Toiwa stream is heavily exploited by anglers because of easy access on paved roads running alongside the stream bank (hereinafter referred to as HP stream). By contrast, the Itajiki stream is located more than 5 km away from the nearest car stop and historically received low fishing pressure (hereinafter referred to as LP stream). Anecdotally, old local anglers interviewed by the first author reported that even in 1950s, it took an hour to reach the HP stream and almost 6 h to reach the LP stream from downtown of the nearest city by bicycle and trekking, underlining the difficult access to the LP stream during the last decades. Corresponding with the historical fishing pressure, during our experimental angling in the years 2008 and 2009, we regularly observed anglers in the HP stream, whereas we met only one angler over a period of 20 days in the LP stream. Moreover, the assumption of historically divergent fishing pressure was supported by the degree of angling-related litter we observed at the stream banks per hectare in the same sections as the ones where we also conducted the angling experiment (Mann–Whitney U test, $p = 0.023$; Table 1). The distance between the two study rivers is about 8.5 km, and both rivers belong to the same catchment and have thus been colonized by same native population of amago salmon until isolation by erosion-control dams in the 1960s (Endou et al. 2006). Angling regulations are identical on both streams (no bag limit and a minimum length limit of 150 mm), and no stocking has been reported for both streams (Tsuboi et al. 2013).

In August 2008 and June 2009, angling experiments were conducted by two to three experimental anglers in three randomly selected sections in each stream, using a 5 m pole (long rod without a reel), a 1 lb line (1 pound = 0.453 kg), and a 0.5 g sinker equipped with a small barbed hook (gape widths of 5.0 mm) to which a stonefly larva was attached as natural bait (Table 2). Fork length and otolith age (from 0 to 4 years old) were measured for each fish caught by angling and also by electrofishing in the first pass (see below). A generalized linear model (GLM) with a binomial distribution of errors was used to compare the relationships between fork length and the vulnerability to angling between the two streams. A generalized additive model (GAM; Zuur et al. 2009) was also used to assess possible nonlinear effects of fork length on angling vulnerability.

Sampling of individuals invulnerable to angling tactics within the river sections was conducted using electrofishing with two passes on the next day of each experimental angling session. These data were also used to assess the population densities. The number of individuals invulnerable to angling in each stream were assessed using the removal method (model M(b), program CAPTURE; White et al. 1978; available from www.mbr-pwrc.usgs.gov/software/index.html; Table 2). Population densities in each stream

Table 2. Summary of amago salmon angling experiments in a high fishing pressure (HP) and low fishing pressure (LP) stream.

Stream	Date of bait angling	Stream length of angling experiment (m)	No. of fish caught by bait angling*	CPUE (individuals·angler-hour^{-1}) (mean, min.–max.)	No. of caught fish by electrofishing: First pass*	No. of caught fish by electrofishing: Second pass	Density of salmon (individuals·m^{-2}) (mean, min.–max.)
HP	8 Aug. 2008	1013	15	0.91, 0.55–1.27	214	121	0.129, 0.087–0.183
	27 June 2009	456	7	0.96, 0.50–1.43	208	70	0.165, 0.134–0.195
LP	7 and 10 Aug. 2008	594	35	2.14, 0.75–4.17	90	45	0.188, 0.110–0.275
	26 June 2009	539	16	2.12, 1.50–3.00	174	52	0.160, 0.158–0.163

*Sampled for anatomy.

just before angling were defined as the sum of the number of individuals angled and the estimated abundance invulnerable to angling divided by the area of study sites. Population densities of the surveyed sections were similar between the two streams (Table 2).

Laboratory growth and behavioural assays

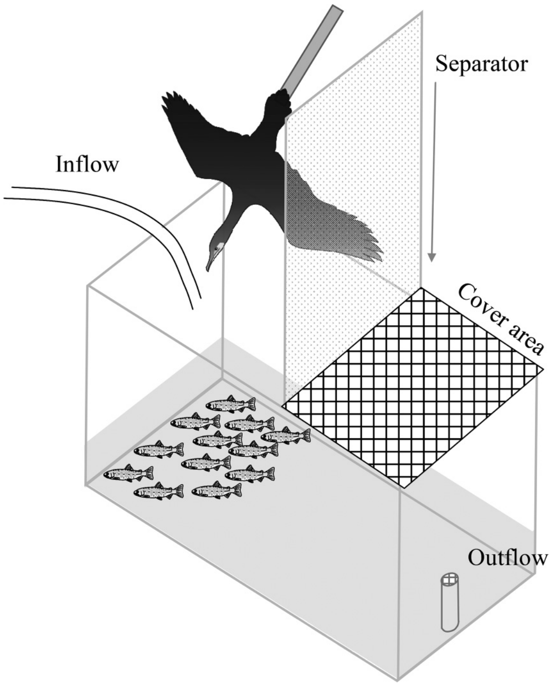
To compare the behavioural characteristics of the LP and HP fish under a common garden, laboratory experiments were conducted using age-0 fish captured at a nonvulnerable fry stage from HP and LP streams. To that end, before the opening of the angling season (1 April 2011), 100 fry of amago salmon were collected using a dip net from the same sections that earlier served as sections for the angling experiment (Table 2; each section about 500 m in stream length) in both the HP and the LP streams on 30 March 2011. We caught fry in all potential habitats and throughout the entire sections. The mean fork length of salmon fry was identical among the streams (HP fish: 30.3 ± 3.2 mm; LP fish: 30.4 ± 2.8 mm; Mann–Whitney *U* test, $p = 0.952$). The fry were probably not exposed to any fishing activity from birth because their habitat (shoreline leaves in low flow) is entirely separated from the habitat anglers access during fishing activities (Nakano 1995). Moreover, sampling took place before the fishing season started.

All fry collected in the wild were reared in two artificial tanks (width × length × depth: 55 cm × 90 cm × 45 cm) separated by stream origin. During culture and subsequent experiments (see below), each tank was fed with spring water (0.2 L·s^{-1}). Each day during the holding period, fish were given a formulated amago salmon diet composed mainly of fish meal, vitamins C, E, and eicosapentaenoic and docosahexaenoic acid ("Rescue A" produced by Scientific Feed Laboratory Co., Ltd., Tokyo) to satiation using automatic feeders.

To assess the growth potential of the two groups, on 11 July 2011 (103 days after capture in the wild), 86 HP fish and 95 LP fish were measured for fork length (mm) and body mass (g) and individually marked using visible implant elastomer tags. During capture and individual marking, there was no significant differences in mortality between the stream origin (HP: 14%; LP: 5%; *G* test, $G = 0.234$; $p = 0.628$). Afterwards, the fish were randomly selected and divided into two replicated groups per strain, and 43 individuals of each replicate were transferred to new tanks ($W \times L \times D$: 32.6 cm × 45.7 cm × 30 cm). During the experimental procedure, fish were fed using the same formulated diet as described above. On 16 August 2011, fork length and body mass were remeasured, and specific growth rates (SGR) were calculated as $100 \times (\ln W_{t2} - \ln W_{t1})/(t2 - t1)$, where W_{t1} and W_{t2} are body mass at times $t1$ and $t2$, respectively. A generalized linear mixed model (GLMM) with a normal distribution of errors was used to compare the relationships between fork length and the SGR between the two strains, using tank replicate as random factor.

Starting the day after growth measurements, juvenile fish from HP and LP streams were subjected to two multiple repeated test series aiming at determining differences in expressions of risk-taking (boldness) and angling vulnerability in the laboratory.

Fig. 1. Schematic representation of the predator display test, using a stuffed cormorant as a model of a risky piscivorous bird.



Predator display test

On 17–19 August 2011, predator display tests were conducted in an experimental tank ($W \times L \times D$: 55 cm × 90 cm × 45 cm) that was partially covered with a black plate ($W \times L$: 55 cm × 30 cm). Five to six HP or LP individuals were jointly netted from the holding tank and transferred to the uncovered area in the experimental tank (Fig. 1). To study how the groups of fish reacted to predation risk, 30 s after the transfer a stuffed cormorant as a model of a natural predator was shown to the fish just above the water surface in the uncovered area. Three seconds after the cormorant's display, a separator among the covered and uncovered area was introduced into the tank to separate the individuals that were hidden under the cover from those that stayed in the uncovered area. After each experiment, fish were transferred back to the holding tank and given the formulated diet to satiation. A total of 96 display tests always involving new combinations of individuals were conducted, and all individuals were tested six times, thus achieving an individual summated hiding score ranging from 0 to 6. A GLMM with a Poisson distribution of errors was used to compare the relationships between fork length and the sensitivity to natural predator between the two strains, using tank replicate as random factor.

Vulnerability to angling gear

On 26–31 August 2011, fishing experiments were conducted using the same fishing gear already used in the natural streams, which involved a 1.5 m pole (without a reel), a 1 lb line, a 0.5 g sinker equipped with a barbed hook (gape widths of 2.0 mm) equipped with a piece of frozen shrimp (about 5 mm total length) as natural bait. Five to six individuals of either the HP or the LP stream fish were randomly netted from the holding tank and transferred to an experiment tank ($W \times L \times D$: 32.6 cm × 45.7 cm × 30 cm) lacking cover. The tank was set up on a table 100 cm above the floor to avoid fish seeing the experimental angler. Fishing time of each trial was 15 min. Captured fish were checked for individual marks and immediately released back into the fishing tank to maintain an equal density. After each experiment, fish were transferred back into the holding tank and given the formulated diet to satiation. A total of 32 fishing experiments were conducted. Each individual was tested twice in a group, and the vulnerability score thus ranged from 0 to a maximum of 2 captures. A GLMM with a Poisson distribution of errors was used to compare the relationships between fork length and the vulnerability to angling between the two strains, using tank replicate as random factor. On 9 September 2011, fork length and body mass were again remeasured to serve as a measure of growth during the experimental phase.

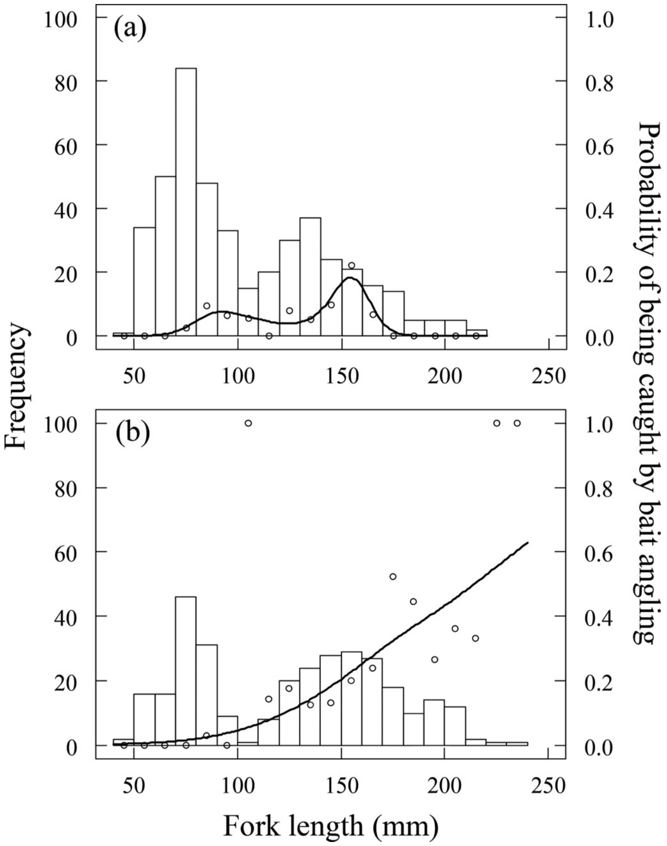
A GLMM with a normal distribution of errors was used to compare the relationships between fork length and the SGR during predator display and angling tests (from 16 August to 9 September 2011) between the two strains, using tank replicate as random factor. A generalized additive mixed model (GAMM; Zuur et al. 2009) was also used to assess possible nonlinear effects of fork length on SGR. SGR of the fishes during behavioural and angling experiments was separately analysed to test for differences in food ingestion rates and growth as a consequence of handling stress to which shy and bold individuals might react differently.

All analyses were conducted using the R package "mgcv" (version 1.7-29). The Akaike information criterion (AIC) was used to identify the best-fitting models.

Results

A total of 73 individual fish were captured by angling for 31 angler-hours, and 974 fish were caught by electrofishing (Table 2). Fork length of these fish ranged from 45 to 236 mm. Amago salmon captured in the HP stream were significantly smaller (HP: 110 ± 42.5 mm; LP: 121 ± 44.5 mm, mean fork length ± SD, $F = 17.64$, $p < 0.001$) and younger (HP: 0.61 ± 0.74; LP: 0.84 ± 0.88, mean years of age ± SD, $F = 19.11$, $p < 0.001$) than those in the LP stream (Fig. 2; also see online supplementary data Fig. S1[1]). Population densities did not differ among the two streams and ranged from 0.087 to 0.275 individuals per square metre (Mann–Whitney U test, $p = 0.602$; Table 2). Despite similar densities, the catch per unit effort (number of fish captured per angler-hour) of bait fishing in the HP stream (0.50–0.93–1.43, min.–mean–max.) was significantly lower than that in the LP stream (0.75–2.13–4.17, min.–mean–max.; Mann–Whitney U test, $p = 0.030$; Table 2). Both fork length and age were within the same range for fish caught by bait angling and electrofishing in the HP stream, but fish caught by angling were larger and older than those caught by electrofishing in the LP stream (Table 3). Fork length, stream, the interactions of fork length and age, and that of fork length and stream were significant factors affecting the vulnerability to bait angling (Table 4). Based on the AIC, a GAM fitted the data on vulnerability to angling better than a GLM (Table 4). The GAM showed that the vulnerability to angling increased with fork length in the LP stream, whereas the vulnerability to angling of fish from the HP stream initially increased with fork length and subsequently decreased with further increases in body size (Fig. 2). The significant interaction of fork length and age indicated that older fish were less vulnerable to angling, even at similar fork lengths (Table 4; Fig. S1[1]).

Fig. 2. Fork length distributions (left-side axis, histograms) and probability of being caught by bait angling (right-side axis, plots and spline curves) on amago salmon in a (*a*) high and (*b*) low fishing pressure stream.



In the laboratory experiments, there was no difference in SGR over a period of 36 days among the two strains before the predator display experiments were conducted (HP: 0.63 ± 0.28; LP: 0.56 ± 0.29, mean ± SD; Table 5). However, in the predator display experiments, the number of times fish were hiding under cover was significantly greater for HP fish (HP: 3.63 ± 1.42; LP: 2.86 ± 1.46 times, mean ± SD; Table 5; Fig. 3), indicating a greater intrinsic timidity of HP fish relative to LP fish. In contrast with the field data reported above for the juvenile and adult fish, under controlled conditions in the laboratory the number of captures of HP and LP fish was not significantly different for juveniles (Table 5). However, during the predator display and angling experiments in the laboratory, the relationship between the SGR assessed over 24 days and fork length was starkly different among the HP and LP fish (Table 5). A GAMM fitted the SGR data better than a GLMM for the period during the predator display and fishing experiments (Table 5). Accordingly, HP fish exhibited significantly lower growth rates than LP fish during the experiments, particularly the larger ones (Fig. 4). We repeated the analysis for fish <95 mm given the small sample sizes presented for the largest fish size classes (see Fig. 4). Even after removing these data, HP fish still showed a significantly lower SGR than LP fish during the predator display and angling experiments (Table 5).

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[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2014-0571.

Table 3. Comparison of fork length (mm) and age (years) (mean ± SD) of amago salmon caught by angling and electrofishing in a high fishing pressure (HP) and low fishing pressure (LP) stream.

			Salmon caught by:			
Stream	Date of bait angling		Angling	Electrofishing	*F*	*p*
HP	8 Aug. 2008	Fork length	115±34	110±42	0.263	0.608
		Age	0.47±0.52	0.53±0.72	0.123	0.726
	27 June 2009	Fork length	128±31	99±35	4.532	0.034
		Age	0.71±0.49	0.48±0.56	1.254	0.264
LP	7 and 10 Aug. 2008	Fork length	164±27	110±40	54.945	<0.001
		Age	1.40±0.60	0.62±0.73	31.484	<0.001
	26 June 2009	Fork length	172±36	124±47	16.512	<0.001
		Age	2.25±0.93	0.90±0.93	30.820	<0.001

Table 4. The best model of a generalized linear model (GLM) and a generalized additive model (GAM) selected by Akaike information criteria (AIC) in a field experiment on the vulnerability to angling of amago salmon in a high and low fishing pressure stream.

Method	Error distribution	AIC	ΔAIC	Independent variable	Coefficient	*p*
GLM	Binomial	395.9	1.7	Stream	1.895	0.024
				Fork length	0.047	<0.001
				Age	2.733	0.011
				Stream × Age	−2.889	<0.001
				Fork length × Age	−0.016	0.007
GAM	Binomial	393.8	3.8	Stream	1.376	0.036
				s(Fork length)*	—	<0.001
				Stream × Age	−2.430	<0.001

Note: The independent variables were stream (high fishing pressure stream = 1, low fishing pressure stream = 0), fork length, age, and their interaction. ΔAIC shows the difference of AIC between the best and full models.

**p* value shows approximate significance of smooth term (*s*).

Table 5. The best model of a generalized linear mixed model (GLMM) and a generalized additive mixed model (GAMM) selected by Akaike information criteria (AIC) for the laboratory behavioural and growth assays on age-0 year amago salmon originating from high and low fishing pressure streams.

Dependent variable	Method	Error distribution	AIC	ΔAIC	Independent variable	Coefficient	*p*
SGR before experiments	GLMM	Normal	48.0	14.9	Fork length	1.895	<0.001
No. of times hiding under cover	GLMM	Poisson	138.1	2.0	Strain	0.247	0.004
					Fork length	0.009	0.002
No. of times caught by bait angling	GLMM	Poisson	118.3	1.6	Fork length	0.032	<0.001
SGR during experiments using full data	GLMM	Normal	−36.2	0.0	Strain	0.705	0.066
					Fork length	0.016	<0.001
					Strain × Fork length	−0.014	<0.001
	GAMM	Normal	−96.8	0.0	Strain	0.643	<0.001
					s(Fork length)*	—	<0.001
					Strain × Fork length	−0.013	<0.001
SGR during experiments using data of <95 mm fish	GLMM	Normal	−74.1	4.7	Strain	−0.262	0.013
					Fork length	0.007	<0.001

Note: The independent variables were strain (originating from high fishing pressure stream = 1, low fishing pressure stream = 0), fork length at the start of each duration, and their interaction. ΔAIC shows the difference of AIC between the best and full models. SGR = specific growth rate.

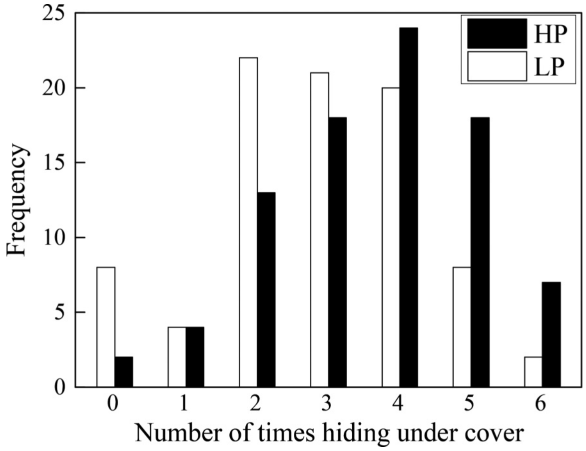
**p* value shows approximate significance of smooth term (*s*).

Discussion

We found large amago salmon to be more vulnerable to angling in an LP stream compared with their smaller conspecifics, while no generally positive size selectivity was present in a HP stream. Moreover, the catch rates of amago salmon were significantly lower in the HP stream, despite similar fish abundances, indicating a substantial reduction of vulnerability to angling, particularly among the large fishes. Such patterns were in agreement with previous research in selected recreationally targeted coastal fish species (Alós et al. 2015). We also provided evidence that fish from the HP stream were shyer and more risk-averse compared with fish from the LP stream, which agreed with laboratory-based harvesting experiments using zebrafish (*Danio rerio*) (Uusi-Heikkilä et al. 2015). Recent studies in brown trout (*Salmo trutta*) and Eurasian perch (*Perca fluviatilis*) found that explorative individuals were preferentially hooked by anglers (Härkönen et al. 2014, 2015). We thus propose that in the HP stream, behaviourally reactive individuals (e.g., active and (or) bold fishes) have been systematically removed from the pool of fishes, leaving behind shyer individuals that are harder to catch.

Given the common garden nature of our experiments using fry that have not been exposed to any angling in the wild, our data may be perceived consistent with an evolutionary response towards increased shyness in response to selective removal of bold fish in the HP stream. However, in the field additional effects of learning to avoid future capture were likely involved, because

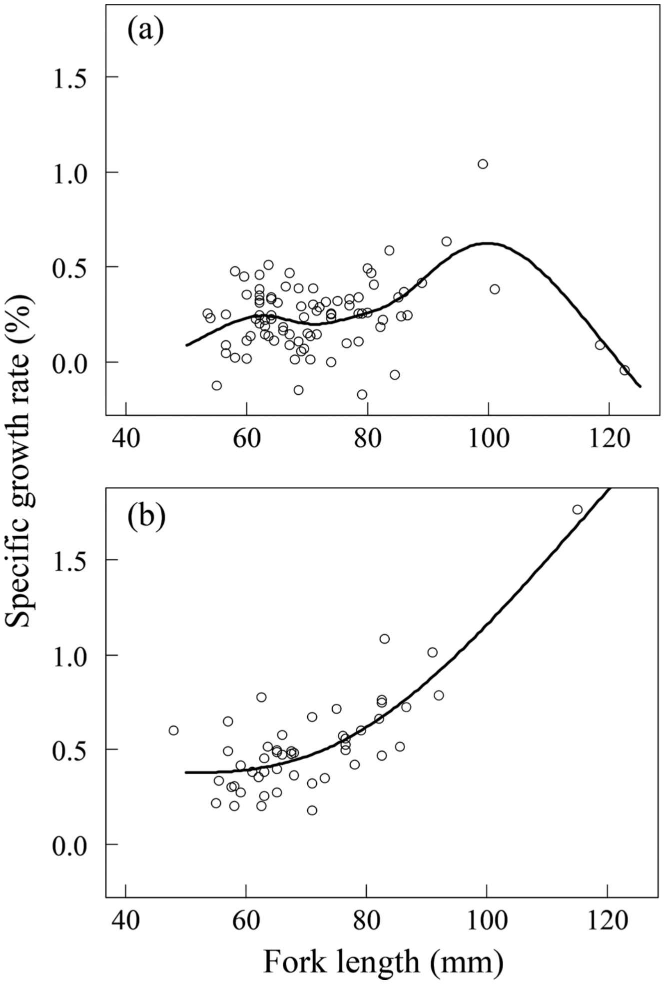
Fig. 3. Frequency distributions of the number of times hiding under cover in the predator display experiments on age-0 year amago salmon originating from a high fishing pressure (HP) and low fishing pressure (LP) stream.



there was no intrinsic difference in angling vulnerability of amago fry under controlled laboratory conditions, and vulnerability in the field decreased further as fish aged, suggesting experiential learning. Indeed, rainbow trout (*O. mykiss*) exposed to catch-and-release angling altered their behaviour and became more wary, in turn substantially reducing catch rates due to hook-avoidance learning (van Poorten and Post 2005; Askey et al. 2006). Moreover, a major limitation of our study is the lack of stream replication, and hence we cannot conclusively relate our study findings to fishing pressure in a cause-and-effect or evolutionary manner. Although spatial proximity and general ecological conditions (including density) were similar among the streams we studied (Tsuboi et al. 2013) with only fishing pressure sticking out as a discriminatory feature, unaccounted ecological factors could have contributed to the study findings. Further research with more streams is needed to confirm the data and the interpretation presented in this paper, but such systems do not exist in our study area. Irrespective of the exact mechanism, any fisheries-induced adaptive response to reduce exposure to fishing gear will not only reduce CPUE and hence angling quality (Arlinghaus 2006; Arlinghaus et al. 2008*a*), but may even obscure the often-reported effect of positive size selectivity of recreational fishing as found here. As a consequence, angler-exploited populations could host large fish that are invulnerable to angling, in turn promoting increasingly dome-shaped selectivity curves that have been repeatedly reported for hook-and-line gear (e.g., O'Farrell and Botsford 2006; Hutchings 2009).

Superficially, the lack of differences of angling vulnerability between the common garden raised fry from HP and LP streams in the laboratory environment may be interpreted as being inconsistent with an evolved response of low vulnerability to fishing. However, an emerging literature is questioning the validity of certain laboratory studies and test areas for revealing complex behaviours and fish personality (Klefoth et al. 2012; Niemelä and Dingemanse 2014), including work in salmonids (Näslund et al. 2015). Similarly, Wilson et al. (2011) failed to find a clear relationship of boldness and vulnerability to angling in a sample of seined bluegill (*Lepomis macrochirus*) when tested in a laboratory environment. The lack of vulnerability differences between HP and LP fish in the laboratory may have been caused by the close proximity to the bait in a tank lacking shelter. By contrast, several studies conducted under seminatural or even natural conditions have now revealed unambiguous relationships of boldness (or correlated traits such as exploration, activity, or choice of risky pelagic habitats) and vulnerability to angling in a range of species (Klefoth et al. 2012, 2013; Matthias et al. 2014; Härkönen et al. 2015; for a theoretical model see also Alós et al. 2012). While we failed to identify vulnerability differences among HP and LP fish in the laboratory, we found age-0 HP fish to avoid the simulated natural predator significantly more frequently than age-0 LP fish, and these fish also grew less under risk of predation under laboratory conditions. Coupled with the field data on differences in vulnerability, we cautiously interpret our data as consistent with an evolved boldness response, leading to greater shyness and lower vulnerability to fishing in highly exploited streams.

Fig. 4. Relationships between specific growth rates and fork length during predator display and angling tests in tanks on age-0 year amago salmon originating from a (*a*) high and (*b*) low fishing pressure stream.



Recreational fishing mortality can be very high in some localities and strongly affect fish populations demographically (Post et al. 2002; Lewin et al. 2006). In particular, heavy catch-and-kill type angling is known to substantially alter age and size distributions within salmonid and other fish populations (e.g., Goedde and Coble 1981; Braña et al. 1992). Size and age truncation was also present in our work where we observed differences in fork length and age among HP and LP streams. In fact, although the population in the exploited HP stream was not numerically less abundant (similar to the coastal fisheries case reported by Alós et al. 2015), the HP population hosted overall smaller and younger fishes compared with the population in the LP stream. Amago salmon in HP streams are traditionally removed after capture, and hence the stock composition in terms of a truncated size and age distribution was not unexpected. The lower vulnerability of large, fecund individuals expressed in HP environments may also safeguard against population collapses. To conclude, fishing-induced adaptive changes, be it evolution or plasticity or both, towards lower vulnerability are likely to carry costs for fishing quality and the index quality of fishery-dependent data while safeguarding population viability in the face of exploitation. However, the presence of more shy individuals in heavily exploited system may have undesired food web effects and could alter ecosystem function (Laundré et al. 2014), which should be studied in the future.

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References

Alós, J., Palmer, M., and Arlinghaus, R. 2012. Consistent selection towards low activity phenotypes when catchability depends on encounters among human predators and fish. PLoS ONE, **7**(10): e48030. doi:10.1371/journal.pone.0048030. PMID:23110164.

Alós, J., Palmer, M., Catalan, I.A., Alonso-Fernández, A., Basterretxea, G., Jordi, A., Buttay, L., Morales-Nin, B., and Arlinghaus, R. 2014. Selective exploitation of spatially structured coastal fish populations by recreational anglers may lead to evolutionary downsizing of adults. Mar. Ecol. Prog. Ser. **503**: 219–233. doi:10.3354/meps10745.

Alós, J., Palmer, M., Trías, P., Díaz-Gil, C., and Arlinghaus, R. 2015. Recreational angling intensity correlates with alteration of vulnerability to fishing in a carnivorous coastal fish species. Can. J. Fish. Aquat. Sci. **72**(2): 217–225. doi:10.1139/cjfas-2014-0183.

Ariyomo, T.O., Carter, M., and Watt, P.J. 2013. Heritability of boldness and aggressiveness in the zebrafish. Behav. Genet. **43**(2): 161–167. doi:10.1007/s10519-013-9585-y. PMID:23354973.

Arlinghaus, R. 2006. On the apparently striking disconnect between motivation and satisfaction in recreational fishing: the case of catch orientation of German anglers. N. Am. J. Fish. Manage. **26**(3): 592–605. doi:10.1577/M04-220.1.

Arlinghaus, R., Bork, M., and Fladung, E. 2008*a*. Understanding the heterogeneity of recreational anglers across an urban–rural gradient in a metropolitan area (Berlin, Germany), with implications for fisheries management. Fish. Res. **92**(1): 53–62. doi:10.1016/j.fishres.2007.12.012.

Arlinghaus, R., Klefoth, T., Kobler, A., and Cooke, S.J. 2008*b*. Size selectivity, injury, handling time, and determinants of initial hooking mortality in recreational angling for northern pike: the influence of type and size of bait. N. Am. J. Fish. Manage. **28**(1): 123–134. doi:10.1577/M06-263.1.

Arlinghaus, R., Matsumura, S., and Dieckmann, U. 2009. Quantifying selection differentials caused by recreational fishing: development of modeling framework and application to reproductive investment in pike (*Esox lucius*). Evol. Appl. **2**: 335–355. doi:10.1111/j.1752-4571.2009.00081.x. PMID:25567885.

Askey, P.J., Richards, S.A., Post, J.R., and Parkinson, E.A. 2006. Linking angling catch rates and fish learning under catch-and-release regulations. N. Am. J. Fish. Manage. **26**(4): 1020–1029. doi:10.1577/M06-035.1.

Biro, P.A., and Post, J.R. 2008. Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. Proc. Natl. Acad. Sci. U.S.A. **105**(8): 2919–2922. doi:10.1073/pnas.0708159105. PMID:18299567.

Braña, F., Nicieza, A.G., and Toledo, M.M. 1992. Effects of angling on population structure of brown trout, *Salmo trutta* L., in mountain streams of northern Spain. Hydrobiologia, **237**(1): 61–66. doi:10.1007/BF00008428.

Brauhn, J.L., and Kincaid, H. 1982. Survival, growth, and catchability of rainbow trout of four strains. N. Am. J. Fish. Manage. **2**(1): 1–10. doi:10.1577/1548-8659(1982)2<1:SGACOR>2.0.CO;2.

Diaz Pauli, B., Wiech, M., Heino, M., and Utne-Palm, A.C. 2015. Opposite selection on behavioural types by active and passive fishing gears in a simulated guppy *Poecilia reticulata* fishery. J. Fish Biol. **86**(3): 1030–1045. doi:10.1111/jfb.12620. PMID:25619538.

Dochtermann, N.A., Schwab, T., and Sih, A. 2015. The contribution of additive genetic variation to personality variation: heritability of personality. Proc. R. Soc. B Biol. Sci. **282**(1798). [Online ahead of print.] doi:10.1098/rspb.2014.2201. PMID:25392476.

Endou, S., Tsuboi, J., and Iwata, T. 2006. Effects of damming on the persistence of white-spotted charr and red-spotted masu salmon populations. Jpn. J. Conserv. Ecol. **11**(1): 4–12. [In Japanese with English summary.]

Evangelista, C., Britton, R.J., and Cucherousset, J. 2015. Impacts of invasive fish removal through angling on population characteristics and juvenile growth rate. Ecol. Evol. **5**(11): 2193–2202. doi:10.1002/ece3.1471. PMID:26078856.

Goedde, L.E., and Coble, D.W. 1981. Effects of angling on a previously fished and an unfished warmwater fish community in two Wisconsin lakes. Trans. Am. Fish. Soc. **110**(5): 594–603. doi:10.1577/1548-8659(1981)110<594:EOAOAP>2.0.CO;2.

Härkönen, L., Hyvärinen, P., Paappanen, J., and Vainikka, A. 2014. Explorative behavior increases vulnerability to angling in hatchery-reared brown trout (*Salmo trutta*). Can. J. Fish. Aquat. Sci. **71**(12): 1900–1909. doi:10.1139/cjfas-2014-0221.

Härkönen, L., Hyvärinen, P., Paappanen, J., and Vainikka, A. 2015. Behavioural variation in Eurasian perch populations with respect to relative catchability. Acta Ethol. [Online ahead of print.] doi:10.1007/s10211-015-0219-7.

Heino, M., and Godø, O.R. 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. Bull. Mar. Sci. **70**(2): 639–656.

Hutchings, J.A. 2009. Avoidance of fisheries-induced evolution: management implications for catch selectivity and limit reference points. Evol. Appl. **2**(3): 324–334. doi:10.1111/j.1752-4571.2009.00085.x. PMID:25567884.

Iguchi, K., Matsubara, N., and Hakoyama, H. 2001. Behavioural individuality assessed from two strains of cloned fish. Anim. Behav. **61**(2): 351–356. doi:10.1006/anbe.2000.1612.

Januchowski-Hartley, F.A., Graham, N.A.J., Cinner, J.E., and Russ, G.R. 2015. Local fishing influences coral reef fish behavior inside protected areas of the Indo-Pacific. Biol. Conserv. **182**(1): 8–12. doi:10.1016/j.biocon.2014.11.024.

Jørgensen, C., Enberg, K., Dunlop, E.S., Arlinghaus, R., Boukal, D.S., Brander, K., Ernande, B., Gårdmark, A., Johnston, F., Matsumura, S., Pardoe, H., Raab, K., Silva, A., Vainikka, A., Dieckmann, U., Heino, M., and Rijnsdorp, A.D. 2007. Managing evolving fish stocks. Science, **318**(5854): 1247–1248. doi:10.1126/science.1148089. PMID:18033868.

Klefoth, T., Skov, C., Krause, J., and Arlinghaus, R. 2012. The role of ecological context and predation risk-stimuli in revealing the true picture about the genetic basis of boldness evolution in fish. Behav. Ecol. Sociobiol. **66**(4): 547–559. doi:10.1007/s00265-011-1303-2.

Klefoth, T., Pieterek, T., and Arlinghaus, R. 2013. Impacts of domestication on angling vulnerability of common carp, *Cyprinus carpio*: the role of learning, foraging behaviour and food preferences. Fish. Manage. Ecol. **20**(2–3): 174–186. doi:10.1111/j.1365-2400.2012.00865.x.

Laundré, J.W., Hernández, L., Medina, P.L., Campanella, A., López-Portillo, J., González-Romero, A., Grajales-Tam, K.M., Burke, A.M., Gronemeyer, P., and Browning, D.M. 2014. The landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance? Ecology, **95**(5): 1141–1152. doi:10.1890/13-1083.1. PMID:25000746.

Lewin, W.C., Arlinghaus, R., and Mehner, T. 2006. Documented and potential biological impacts of recreational fishing: insights for management and conservation. Rev. Fish. Sci. **14**: 305–367. doi:10.1080/10641260600886455.

Matthias, B.G., Allen, M.S., Ahrens, R.N.M., Beard, T.D., Jr., and Kerns, J.A. 2014. Hide and seek: interplay of fish and anglers influences spatial fisheries management. Fisheries, **39**(6): 261–269. doi:10.1080/03632415.2014.903836.

Nakano, S. 1995. Individual differences in resource use, growth and emigration under the influence of a dominance hierarchy in fluvial red-spotted masu salmon in a natural habitat. J. Anim. Ecol. **64**(1): 75–84. doi:10.2307/5828.

Näslund, J., Bererhi, B., and Johnsson, J.I. 2015. Design of emergence test arenas can affect the results of boldness assays. Ethology, **121**(6): 556–565. doi:10.1111/eth.12368.

Niemelä, P.T., and Dingemanse, N.J. 2014. Artificial environments and the study of 'adaptive' personalities. Trends Ecol. Evol. **29**(5): 245–247. doi:10.1016/j.tree.2014.02.007. PMID:24629720.

O'Farrell, M.R., and Botsford, L.W. 2006. The fisheries management implications of maternal-age-dependent larval survival. Can. J. Fish. Aquat. Sci. **63**(10): 2249–2258. doi:10.1139/f06-130.

Olsen, E.M., Heupel, M.R., Simpfendorfer, C.A., and Moland, E. 2012. Harvest selection on Atlantic cod behavioral traits: implications for spatial management. Ecol. Evol. **2**(7): 1549–1562. doi:10.1002/ece3.244. PMID:22957161.

Post, J.R., Sullivan, M., Cox, S., Lester, N.P., Walters, C.J., Parkinson, E.A., Paul, A.J., Jackson, L., and Shuter, B.J. 2002. Canada's recreational fisheries: the invisible collapse? Fisheries, **27**(1): 6–17. doi:10.1577/1548-8446(2002)027<0006:CRF>2.0.CO;2.

Raat, A.J.P. 1985. Analysis of angling vulnerability of common carp, *Cyprinus carpio* L., in catch-and-release angling in ponds. Aquacult. Fish. Manage. **16**(2): 171–187. doi:10.1111/j.1365-2109.1985.tb00305.x.

Réale, D., Reader, S.M., Sol, D., McDougall, P.T., and Dingemanse, N.J. 2007. Integrating animal temperament within ecology and evolution. Biol. Rev. **82**(2): 291–318. doi:10.1111/j.1469-185X.2007.00010.x. PMID:17437562.

Saura, M., Morán, P., Brotherstone, S., Caballero, A., Álvarez, J., and Villanueva, B. 2010. Predictions of response to selection caused by angling in a wild population of Atlantic salmon (*Salmo salar*). Freshw. Biol. **55**(4): 923–930. doi:10.1111/j.1365-2427.2009.02346.x.

Sutter, D.A.H., Suski, C.D., Philipp, D.P., Klefoth, T., Wahl, D.H., Kersten, P., Cooke, S.J., and Arlinghaus, R. 2012. Recreational fishing selectively captures individuals with the highest fitness potential. Proc. Natl. Acad. Sci. U.S.A. **109**(51): 20960–20965. doi:10.1073/pnas.1212536109. PMID:23213220.

Tsuboi, J., and Endou, S. 2008. Relationships between catch per unit effort, catchability, and abundance based on actual measurements of salmonids in a mountain stream. Trans. Am. Fish. Soc. **137**(2): 496–502. doi:10.1577/T06-259.1.

Tsuboi, J., Iwata, T., Morita, K., Endou, S., Oohama, H., and Kaji, K. 2013. Strategies for the conservation and management of isolated salmonid populations: lessons from Japanese streams. Freshw. Biol. **58**(5): 908–917. doi:10.1111/fwb.12096.

Uusi-Heikkilä, S., Wolter, C., Klefoth, T., and Arlinghaus, R. 2008. A behavioral perspective on fishing-induced evolution. Trends Ecol. Evol. **23**(8): 419–421. doi:10.1016/j.tree.2008.04.006. PMID:18582988.

Uusi-Heikkilä, S., Whiteley, A.R., Kuparinen, A., Matsumura, S., Venturelli, P.A., Wolter, C., Slate, J., Primmer, C.R., Meinelt, T., Killen, S.S., Bierbach, D., Polverino, G., Ludwig, A., and Arlinghaus, R. 2015. The evolutionary legacy of size-selective harvesting extends from genes to populations. Evol. Appl. **8**(6): 597–620. doi:10.1111/eva.12268. PMID:26136825.

van Poorten, B.T., and Post, J.R. 2005. Seasonal fishery dynamics of a previously unexploited rainbow trout population with contrasts to established fisheries. N. Am. J. Fish. Manage. **25**(1): 329–345. doi:10.1577/M03-225.1.

White, G.C., Burnham, K.P., Otis, D.L., and Anderson, D.R. 1978. User's manual for program CAPTURE. Utah State University Press, Logan, Utah.

Wilson, A.D.M., Binder, T.R., McGrath, K.P., Cooke, S.J., and Godin, J.-G.J. 2011. Capture technique and fish personality: angling targets timid bluegill sunfish, *Lepomis macrochirus*. Can. J. Fish. Aquat. Sci. **68**(5): 749–757. doi:10.1139/f2011-019.

Wilson, A.D.M., Brownscombe, J.W., Sullivan, B., Jain-Schlaepfer, S., and Cooke, S.J. 2015. Does angling technique selectively target fishes based on their behavioural type? PLoS ONE, **10**(8): e0135848. doi:10.1371/journal.pone.0135848. PMID:26284779.

Wootton, R.J. 1992. The environment, organisms and relationships. *In* Fish ecology. Chapman & Hall, New York. pp. 1–24.

Yamamoto, T., Ueda, H., and Higashi, S. 1998. Correlation among dominance status, metabolic rate and otolith size in masu salmon. J Fish Biol. **52**(2): 281–290. doi:10.1111/j.1095-8649.1998.tb00799.x.

Zuur, A.F., Leno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M. 2009. Mixed effects models and extensions in ecology with R. Springer-Verlag, New York.