Age is not just a number – senescence affects how fish populations respond to different fishing regimes

Pauliina Anna Ahti (✉ pauliina.a.s.ahti@jyu.fi)  
University of Jyväskylä  https://orcid.org/0000-0002-6216-9616

Silva Uusi-Heikkilä  
University of Jyväskylä: Jyvaskylan Yliopisto

Timo J Marjomäki  
University of Jyväskylä: Jyvaskylan Yliopisto

Anna Kuparinen  
University of Jyväskylä: Jyvaskylan Yliopisto

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Age is not just a number – senescence affects how fish populations respond to different fishing regimes

Pauliina A. Ahti¹,²*, Silva Uusi-Heikkilä¹, Timo J. Marjomäki¹, Anna Kuparinen¹

¹ Department of Biological and Environmental Sciences, P.O. Box 35, 40014 University of Jyväskylä, Finland
² Institute of Biodiversity, Animal Health, and Comparative Medicine, College of Medical, Veterinary, and Life Sciences, University of Glasgow, Glasgow, G12 8QQ UK

* Corresponding author: Pauliina A. Ahti, Department of Biological and Environmental Sciences, P.O. Box 35, 40014 University of Jyväskylä, Finland, telephone: +358-41-492-4459, e-mail: pauliina.a.s.ahti@jyu.fi

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Abstract

The presence of senescence in natural populations remains an unsolved problem in biology. Described as an age-dependent increase in natural mortality (known as actuarial senescence) and an age-dependent decrease in fecundity (known as reproductive senescence), the role of senescence in nature is still poorly understood. Based on empirical estimates of reproductive and actuarial senescence, we explored how senescence affects the population dynamics of *Coregonus albula*, a small, schooling salmonid fish. Using an empirically-based eco-evolutionary model, we investigated how the presence or absence of senescence affects how the fish population responds to pristine, intensive harvest, and recovery phases. Our results showed that at an individual level, the presence of senescence was accompanied by life-history trade-offs, i.e. lower asymptotic length and smaller size and younger age at maturity, both in the presence and absence of fishing. At the population level, the response to different fisheries selection patterns depended on the presence or absence of senescence. Importantly, the results indicate that through the life-history trade-offs between early reproduction and late life survival, the young and small individuals can have an important role in population recovery, especially when senescence is present. Since most life-history and fisheries models ignore senescence, they may be over-estimating reproductive capacity and under-estimating natural mortality. Our results highlight the need for increasing biological realism in these models to ensure the successful management of our natural resources.
Introduction

Senescence is considered a fundamentally fitness decreasing trait, and its presence and role in natural populations remains an unsolved problem in biology (Monaghan et al. 2008; Selman et al. 2012; Nussey et al. 2013). Senescence is described as age-dependent increase in natural mortality (known as actuarial senescence), and age-dependent decrease in fecundity (known as reproductive senescence). For much of the 20th century it was thought that very few animals in the wild experience senescence because external factors such as predators, diseases or environmental stressors would kill them before the consequences of aging would commence (Medawar 1952). Today, it is well known that this is not the case and evidence for senescence across taxa is accumulating (Nussey et al. 2013). Several studies of wild populations have shown that trade-offs exist between early and late life performance (Jensen 1996; Bonsall and Mangel 2004; Lemaître et al. 2014; Maklakov and Chapman 2019), likely contributing to the onset or development of senescence in an individual. The early vs. late life performance has been tested in many vertebrates and has gained a lot of support, but tests in fishes are scarce, mainly owing to the difficulty of testing for senescence in species with indeterminate growth (Heino and Kaitala 1999; Reznick et al. 2002; Lemaître et al. 2015).

Life-history trade-offs may take place between functions as well as within the same function. For instance, increased growth rate and increased reproductive effort early in life and higher natural mortality rate later in life are known to be linked (Kirkwood and Rose 1991; Lester et al. 2004). Similarly, investment in future reproductive effort is thought to be of lesser value in terms of fitness benefits than current reproductive effort,
mainly due to the uncertainty of future reproduction (Zhang and Hood 2016). Following the close link between life history characters and senescence, it is therefore likely, as hypothesised by Benoît et al. (2018), that assuming that increased allocation to reproduction in early life leads to an increased rate of ageing later, fishing-induced changes in maturation age and senescence could actually be linked. Indeed, the natural mortality rate of many fish populations is thought to have increased in the recent decades (Gislason et al. 2010).

While most fishes express indeterminate growth and high longevity (Carey and Judge, 2000), it has been suggested that fish experience delayed senescence relative to birds and mammals, facilitated in part by the capacity for increasing fecundity with age (Reznick et al. 2002). Indeed, female body size and reproductive output in fish are known to be positively correlated, indicating that the older and larger the fish, the higher its reproductive output. Most fisheries and fish population models (Beverton-Holt, 1957; Enberg et al., 2010; Andersen and Beyer, 2015; Zimmermann and Jørgensen, 2015) and life-history models (Roff, 1983; Brunel et al., 2013; Charnov et al., 2013) assume that body size (weight) scales isometrically with reproductive output. Recent meta-analysis has provided cues that the scaling might even be hyper-allometric in some cases (Barneche et al. 2018), further stressing the role of large and old individuals for population growth or, in case of over-exploitation, for recovery. Additionally, in fisheries and life-history models, the natural mortality of fish is often assumed to be independent of the age or size of the fish (Gislason et al. 2010). Models with increasing fecundity with age and size, and age- and size-independent natural mortality essentially describe fish as having no reproductive or actuarial senescence at all.
While rarely included in fisheries and life-history models, senescence in fish was first documented over 60 years ago (Gerking 1957; Comfort 1960, 1963; Woodhead and Ellett 1966, 1967, 1969a, b). Over the past few decades, evidence for both reproductive (Reznick et al. 2006; Benoît et al. 2018) and actuarial (Beverton et al. 2004; Uriarte et al. 2016) senescence as well as general deterioration with age (Patnaik et al. 1994; Hendry et al. 2004; Morbey et al. 2005; Carlson et al. 2007) in fish has started to accumulate. While the importance of old and large individuals for the reproductive pool is evident, the common conservation measure of relying on the reproductive effort of large individuals could have detrimental effects on the recovery and resilience of fish populations if actuarial or reproductive senescence is indeed wide-spread in fishes (Le Bris et al. 2015). Given that senescence influences the reproductive outcome and natural mortality rate, it would also have major consequences to our understanding of fish population dynamics and would thereby affect our management efforts of fish populations.

Sustainable fish populations are vital not only for food security around the world (Merino et al. 2012), but also for healthy biodiversity and climate regulation (Jackson 2008). Several fish populations that have collapsed as a result of fishing, have not recovered or are recovering slower than expected even after significant declines in fishing effort (Hutchings and Reynolds 2004). The reasons behind the lack of recovery are complex and likely include factors such as habitat destruction, climatic conditions, trends in prey-predator relationships, and changes in life-history traits (Dulvy et al. 2003a; Hutchings and Reynolds 2004; Olsen et al. 2009). While much research effort has been put into understanding the links between life-history traits such as body size, growth rate, size
and age at maturity, and population dynamics (Ahti et al. 2020), the role of reproductive and actuarial senescence in population dynamics and population recovery remains poorly understood.

Monitoring and measuring reproductive or actuarial senescence in nature is notoriously difficult, particularly for fish, and the fishes with the most data tend to be the fishes that are the most heavily fished, therefore likely caught before senescence commences. Here, we used empirical data to parameterise an existing eco-evolutionary model (Kuparinen et al. 2011) to overcome these obstacles and to illuminate the role of senescence in fish population dynamics and population recovery under two different fishery selection schemes. As opposed to experimental or empirical studies, the simulation model allows us to control the presence and absence of senescence and explore how, all else being equal, it influences fish population dynamics in the presence and absence of fishing. We used vendace (Coregonus albula, Linnaeus), an economically and culturally important freshwater salmonid, as a model species. Specifically, we address the following questions: 1) How does the presence or absence of senescence influence the population dynamics of fish, in terms of biomass and number of fish prior to fishing? And 2) how does the response to different fishery selection schemes differ depending on the presence or absence of senescence? Our results provide insights into the effects of senescence on population dynamics before, during, and after harvest, and how including it in fisheries and life-history models may improve our understanding of population dynamics and facilitate management efforts.

Materials and methods
To explore the role of senescence in *Coregonus Albula* (Linnaeus) life-histories and populations, we used an individual-based model that incorporates empirical growth, fecundity, and survival data with the principles of quantitative genetics and demographic processes. The core of this mechanistic model lies in the strong negative correlations among the von Bertalanffy (vB) growth model parameters $L_\infty$ (asymptotic length), and $k$ (intrinsic growth coefficient, i.e. how fast the fish length is approaching $L_\infty$) and the size at maturity (von Bertalanffy 1938, 1949; Quince et al. 2008). Since the simulation model has been described in detail elsewhere (Kuparinen et al. 2011), we will here limit the model description to a general description of the modelling approach and the main features and additions specific to our study design. While the empirical data are from Lake Puulavesi in Central Finland, the results can be generalised to any fish with similar life-history properties.

**General description of the modelling approach**

The eco-evolutionary model includes five main components (Fig 1a - e). These are four dependent sets of variables: growth, fecundity, survival, population demographics, and an independent variable: senescence.

Life history traits such as size and age at maturity are thought to be controlled by many loci (Roff 2002). In fishes, the correlation of size at maturity and $L_\infty$ is a well-known life-history invariant (Charnov 1993). Thus, in the growth component (Fig. 1a), we utilised empirical length-at-age data back-calculated from fish scales to model the $L_\infty$. The $L_\infty$ was set to be an evolving trait so that the genotype coding $L_\infty$ of each individual was described by 10 diploid loci with two alleles in each. The alleles were inherited in the classic Mendelian way, so that each offspring received one randomly drawn allele from...
the mother, and one from the father. Each allele was coded as 0 or 1 and the sum of alleles across the ten loci was coupled with a normally distributed random number (mean zero) to describe phenotypic variability, and then the sum was linearly translated to values of $L_\infty$. The standard deviation of the normally distributed random number was adjusted to yield a realistic heritability of 0.2-0.3 (Mousseau and Roff 1987). The $v_B$ growth parameter $k$ and the size at maturity were then determined based on $L_\infty$. (For more on $k$ see below “Model parametrisation”). We used the empirical data to determine that the maturation size threshold was at 67% of their $L_\infty$ (mean size at 2 years of age) and no earlier than on their second autumn, which is in line with literature (Jensen 1998; Karjalainen et al. 2016). This way, we ensured that the fish in the model will mature once they reach 67% of their $L_\infty$, but never before they reach their second autumn. Thus, fish younger than two years old, or two-year-olds smaller than 67% of their $L_\infty$ could not yet reproduce.

The fecundity component (Fig. 1b) is based on a length-weight relationship, which was specifically calculated for *C. albula* from Lake Puulavesi. Using this length-weight relationship and published empirical data on egg numbers and female weights (Karjalainen et al. 2016), we fitted a linear model for the fecundity-weight relationship. The survival component (Fig. 1c) includes an empirically based (Marjomäki et al. 2014; Karjalainen et al. 2016) probability ($P = 0.002$) for a fertilized egg to hatch and the juvenile to survive until 2 years of age. The sex of the juveniles was drawn from a Bernoulli trial with a probability of 0.5. Mating occurred randomly, so that for each mature female a random mate was drawn from a group of mature males. The maximum
lifetime for each individual was limited to 6 years, according to local estimations in Lake Puulavesi (Marjomäki and Huolila 1994).

The population component (Fig. 1d) describes density dependency so that at 75% of the population carrying capacity, the individual growth is reduced to 50% of that predicted by the individual’s vB growth curve (its $L_\infty$ and k parameters). Additionally, egg production was set to be density dependent so that the closer the population was to its carrying capacity, the fewer eggs were produced.

The fifth component of the eco-evolutionary model describes senescence in its two forms: reproductive senescence and actuarial senescence (Fig. 1e). The reproductive senescence was modelled by multiplying the linear model for fecundity by the gonadosomatic index (GSI) for the year class in question. When no reproductive senescence was modelled, only the linear model for fecundity was used. Actuarial senescence was modelled by increasing the rate of natural mortality each year, as opposed to keeping natural mortality rate constant throughout lifetime as in the scenario with no actuarial senescence. All the other components were kept identical in the simulations (Fig. 1f), but the presence and absence of reproductive and actuarial senescence was altered.

Each population in each scenario was then allowed to "live" for 500 years, and the individuals and populations were traced at annual time steps. At each annual step, the growth, reproduction, and mortality of each individual fish was simulated to get the population data for the next year. During those 500 years, the populations experienced three consecutive phases: 200 years of pristine phase, 100 years of intense fishing, and 200 years of recovery (Fig. 1f). The output data of particular interest, i.e. asymptotic
length ($L_\infty$), biomass (BM), and number of fish (N) was collected annually. Each simulation was replicated 100 times.

*Parametrisation of the model*

The empirical data were collected from Lake Puulavesi, an oligotrophic lake located in Central Finland. Its areal coverage is approximately 330 km$^2$, with an average depth of 9.2 m and the deepest part reaching 62 m. The samples for vendace age and growth determination were collected from different basins of Lake Puulavesi between 1977 and 2017. The model is based on empirically observed growth trajectories (total N = 93, female N = 62, male N = 31). The age was determined from the annuli of vendace scales located below pelvic fins. The radius of the entire scale (S) and the radius from scale focus to the annulus i ($S_i$) were measured from the anterior part of the scale that was magnified (20–40 x) using a microfiche reader. The ages were as follows: 3-year-olds N = 34; 4-year-olds N = 20; 5-year-olds N = 37; and 6-year-olds N = 2. Because the length at age was back-calculated, the older the fish, the more information it provided from the previous years. Vendace is known to reach maturity usually on their second autumn, so it was here assumed that all the specimens were mature. The back-calculation of length at age ($L_t$) of each individual was done using the Monastyrky’s equation $L_t = L \times \left(\frac{S_t}{S}\right)^b$ (Monastyrsky 1930), where $L$ = the measured total length when the fish was caught, $S_t$ = the width of annulus at age t, $S$ = radius of the entire scale, and $b = 0.641$. The value of 0.641 for the exponent $b$ is an estimate from several Finnish vendace stocks (Marjomäki and Huolila 2001).
The empirically collected weight data (N = 27) and the growth trajectories calculated above were used to calculate the length–weight relationship \( W = a \times L^b \) (Ricker 1975). In this equation \( W \) = fresh weight in grams (precision 0.1 g) and \( L \) = length in cm (precision 1 mm). The parameter \( a \) (scaling coefficient for the weight at length of the fish) the parameter \( b \) (shape parameter for the body form of the species) were calculated to be \( a = 0.007 \), and \( b = 0.003 \). The lengths varied between 120 and 170 mm (mean 146 mm, s.d. = 8.63), and the weights varied between 12 and 27 g, (mean 18.7 g, s.d. = 3.7). The length – weight relationship is important because weight scales with fecundity, and therefore plays a crucial role in population dynamics. In this particular study, it also forms the basis that reproductive senescence is modelled on.

Back-calculated individual growth trajectories from Lake Puulavesi were summarised using a non-linear least-squares fit of the vB growth equation which was fit for our data:

\[
L_t = L_\infty - (L_\infty - L_0)e^{-kt},
\]

where \( L_t \) = length at age t, \( L_\infty \) = asymptotic length, \( L_0 \) = length at t = 0, and \( k \) = the intrinsic individual growth rate. The association between the vB parameters \( L_\infty \) and \( k \) was estimated using an empirically based linear regression model which yielded the following fit:

\[
\ln(k) = 1.27 - 0.13 \times L_\infty \text{ with residual s.d. = 0.30.}
\]

In the scenarios with no reproductive senescence (i.e. how most life-history and fisheries models describe reproduction), fecundity was based purely on the linear function for individual fecundity per gram body weight: 39.06 + 118.47 x wet mass in grams (Table 1) derived from empirical data (Karjalainen et al. 2016). For ease of comparison against the reproductive senescent scenario, we assigned a “fecundity factor” of 1 for each age group, meaning no change in fecundity with age (Table 1).
Karjalainen et al. (2016) showed an age-dependent decrease in gonadosomatic index (GSI), a pattern that could be indicative of reproductive senescence. We used this GSI as a proxy for reproductive senescence (Table 1). As we only had GSI data for fish up to four years old, the GSI for 5- and 6-year-old fish was linearly extrapolated from the existing data. We used linear extrapolation, because we are interested in the mechanistic changes in population, and not specifically only in vendace. Instead of using the absolute GSI values to describe reproductive senescence in the model, we standardised the effect of reproductive senescence so that the GSI for age group 1 was set to be the baseline and have a fecundity factor of 1 (i.e. no change, same as the non-senescent population), and the following age groups from 2 to 6 were assigned a fecundity factor proportional to that of age group 1. The fecundity factor was calculated by dividing the GSI of age group 1 by the GSI of the age group in question, so for instance to get the fecundity factor for age group 4 would be as follows: GSI for age group 1/ GSI for age group 4. The linear function for fecundity (described above) was then multiplied by the appropriate fecundity factor for each age group (Table 1) to model reproductive senescence. This way, as the fish ages, its reproductive output declines with age.

When actuarial senescence was not modelled, the natural mortality rate was coded to be an age-independent constant of \( M = 0.257 \) in all adult age groups (Table 1).

To model actuarial senescence, we coded a natural mortality rate \( (M) \) that increases with age. The senescence scenario was modelled so that a baseline natural mortality of \( M = 0.2 \) was set for 2 year olds, and the added mortality rate per each age group was adjusted to proportion from Marjomäki (2005) and is shown in Table 1. The difference
between natural mortality imposed by actuarial senescence and fishing mortality is that natural mortality as a result of actuarial senescence increases with age, while the fishing mortality is size-dependent.

To allow for a careful investigation of the resulting demographic structures, the actual resulting natural mortality at the population level was scaled to be identical in all scenarios. This means that the total natural mortality over time in all scenarios is the same, but for populations with no actuarial senescence the mortality rate was unchanged over age classes, and for the populations with actuarial senescence present, the mortality increased with age. So, whether the natural mortality remained unchanged over age classes or increased with age, the total natural mortality for a population over time was equal, only the distribution among age classes differed.

An increase in natural mortality following sexual maturity and reproduction is an important trade-off in life-history evolution (Kuparinen et al. 2011). To take this into account, and to add biological realism in the model, a survival cost of reproduction i.e. increased mortality rate after having become sexually mature was added to the natural mortality rate in every scenario, for every maturing fish. The survival cost of reproduction was estimated to be the increase in mortality rate from age group 1 to age group 2 as per Marjomäki (2005), and this was applied once in every scenario, whether actuarial or reproductive senescence was modelled or not.

Simulation design

The initial starting population was 2000 individuals. The population size was selected due to model optimisation and plays no role in the results of the study. Each scenario
was then simulated for 1000 years. All populations reached a state of ecological stability in approximately 600 years. One hundred ecologically and evolutionarily stable populations were saved for all scenarios, and these populations were then randomly sampled to be used as the starting population in further simulations.

Simulations were run for 500 years. The population was kept in a pristine equilibrium state for 200 years before fishing was simulated for a period of 100 years. Fishing started in year 200 and ceased in year 300, and populations were then allowed to recover for 200 years. Vendace is traditionally fished by seining and trawling, which means that the retention probability increases with the size of the fish to a certain size and is constant after that. To mimic seining or trawling selection and to describe length-dependent gear selectivity in the population, we used a logistic curve $r(l) = \frac{\exp(a+bl)}{1+\exp(a+bl)}$, where $r(l)$ is the retention probability of a fish of length $l$, and $a = -9$ and $b = 0.85$ are shape parameters, so that 50% retention probability is reached at length $-a/b$ (Kuparinen et al. 2009). We also ran separate simulations for gill net fishing by describing a dome-shaped selectivity curve $r(l) \sim \exp \left( -\frac{(l-\mu)^2}{2\sigma} \right)$, where $r(l)$ is the retention probability of a fish of length $l$, $\mu = 12$ (fish length in cm at which the selection curve peaks), and $\sigma = 0.5$ (standard deviation describing the width of the curve around its peak). For simplicity hereafter, when we discuss trawling, a logistic selection curve is assumed, and when we discuss gillnetting, a dome-shaped selection curve is assumed. Regardless of the fishing method, the fishing mortality ($F$) of the fully selected size class was set to 0.7, which is considered a realistic level of magnitude for intensively fished populations (Viljanen 1986). The fishing mortality in terms of biomass was kept identical.
for the senescent and non-senescent scenarios. All scenarios were explored across pristine, harvest and recovery periods over 500 years. We created 100 independent replicates for each scenario.

All simulations and analyses were conducted using R version 1.1.456 (R Core Team, 2018).

Results

Populations in all scenarios had reached an equilibrium and therefore showed only minor temporal fluctuations in any of the population parameters before fishing commenced in year 200. However, scenarios including actuarial senescence consistently differed from those that did not include actuarial senescence. These differences were seen before, during and after fishing in all parameters investigated. Given that actuarial senescence appeared to be the major cause of the differences (Fig. 2), likely due to the relatively low reduction in reproductive output with age (Fig. S1, S2), we focus most of the present work on two instead of four scenarios: a scenario with both reproductive and actuarial senescence and a scenario with no senescence. Additionally, reproductive and actuarial senescence are known to be linked (Kirkwood and Shanley 2010), so exploring either both types of senescence together or none at all is biologically more relevant than separating the senescence types.

Asymptotic length

The populations with senescence had a consistently lower $L_\infty$ than those with no senescence. For both the senescent and non-senescent scenarios, fishing caused a decline in $L_\infty$ (Fig. 3a, b), and the decline caused by trawling was larger than the decline
caused by gillnetting, regardless of the presence of senescence. However, the type of fishing played a role in the relative change within a scenario. The senescent scenario had a smaller decline in $L_\infty$ than the non-senescent scenario when trawled (Fig. 4a). The opposite occurred when gillnetting was applied: the senescent scenario had a larger drop in $L_\infty$ as a result of dome-shaped fishing compared to the non-senescent scenario (Fig. 4b). When fishing was ceased after 100 years, $L_\infty$ started to increase slowly in all scenarios, but in none of the scenarios did the $L_\infty$ recover back to the level prior to fishing. Associated changes in the vB growth parameter $k$, and average size and age at maturation are shown in supplementary material (Fig S3 a, b, c, d, respectively).

**Biomass**

In the absence of fishing, whether pristine or recovery phase, the scenario with senescence produced a lower biomass than the scenario without senescence (Fig. 3c, d). When fishing pressure was applied the biomass of both populations declined. Trawling (Fig. 3c) caused a larger drop than gillnetting (Fig. 3d). However, when trawled, the population with senescence maintained a higher biomass than the one without senescence (Fig. 3c). In the gillnetting scenario, the senescent population had a slightly lower biomass during fishing compared to the non-senescent population (Fig. 3d).

Regardless of the type of fishing, the relative drop in biomass for populations with senescence was smaller than for those with no senescence (Fig. 4 c, d). When trawling was applied, the level of biomass stayed relatively constant for both senescent and non-senescent scenarios (Fig. 4c). However, gillnetting caused a sharp decline in biomass then a sharp increase and then a slow, continuous decline for both scenarios (Fig. 4d).
The decline did not level off at any point during hundred years of fishing. When fishing was ceased, all scenarios experienced a rapid increase in biomass with an initial peak (that exceeded the level prior to fishing in gillnetting scenario), and then a sharp drop. These peaks and drops were larger in the gillnetting scenario compared to the trawling scenario. While all scenarios eventually settled to little variation and a slow, increasing trend, in two hundred years of recovery, no population had recovered to the pre-fishing levels.

**Number of fish**

The number of individuals ($N$) was consistently higher for populations with senescence, than for those without, regardless of fishing type or the presence or absence of fishing (Fig. 3e, f). The start of trawling caused a rapid initial decline in the number of fish, but as trawling continued, the $N$ increased in both senescent and non-senescent scenarios, however it never reached the pre-fishing level (Fig. 3e). This was different from gillnetting, which caused a steady increase in the $N$ during fishing, above the pre-fishing levels (Fig. 3f). As fishing was ceased, the populations that were trawled experienced a rapid initial increase in $N$, and then a declining trend. When gillnetting was ceased, it caused a slow decline in the number of fish. No scenario reached the pre-fishing level in two hundred years of recovery.

In both trawling and gillnetting scenarios, the relative change in the number of fish was smaller for the senescent scenario, compared to the non-senescent scenario (Fig. 4e, f). However, as the fishing continued, the difference between the senescent and non-senescent scenarios declined.
Discussion

Many collapsed fish populations have not recovered even after significant reductions in fishing pressure, or are recovering slower than expected (Hutchings and Reynolds 2004). Our individual-based eco-evolutionary simulations shed light on how reproductive and actuarial senescence affect fish population dynamics under different fishing selection regimes. Populations with senescence evolved to have a lower $L_\infty$, and during fishing the $L_\infty$ declined further. However, the senescent and non-senescent populations responded differently to different fishing selection regimes: when fishing by trawling (described by a logistic selection curve), the relative decline in $L_\infty$ in the senescent population was less than in the non-senescent population. When fishing by gillnet (described by a dome-shaped selection regime), the opposite occurred, and the senescent population experienced a proportionately larger decline in $L_\infty$. The effect of senescence on population dynamics in terms of biomass and number of fish appeared to be density dependent. When the population was relaxed from strong density dependency during trawling, populations with senescence maintained a higher biomass and had a higher $N$ than populations with no senescence present. When gillnetting was applied, the senescent population maintained higher numbers, but the total biomass was lower than the non-senescent population’s biomass. Given the sensitivity of fisheries models to the mass-fecundity relationship and total mortality rates, and the common practice of relying on the reproductive effort of old, large individuals, these results draw attention to the importance of considering senescence as a life-history trait affecting population dynamics and recovery.

Asymptotic length
Populations experiencing senescence evolved to have smaller asymptotic length and coupled with this was a higher intrinsic growth rate, and smaller size and younger age at maturation. These trends were present both when there was no fishing and therefore density-dependent processes regulated the population size, and when fishing had relaxed the population from strong density-dependent competition. Both extrinsic mortality (fishing) and intrinsic mortality (actuarial senescence) led to a declining asymptotic length. This may indicate the presence of a trade-off between increased investment in growth and/ or reproduction early in life (as asymptotic length was associated with earlier reproduction and higher growth rate) and decreased survival later in life. The well-known effects of fishing-induced evolution i.e. selection toward smaller size, smaller size at maturation, and higher growth rate (Heino et al. 2015; Hunter et al. 2015; Uusi-Heikkilä et al. 2015) may therefore enhance the trade-offs associated with senescence and the evolution of life-history traits. Additionally, if increased allocation of resources to reproduction early in life is associated with decreased survival later in life (Kirkwood and Rose 1991), fishing-induced evolution may be indirectly promoting the evolution of senescence through selecting for smaller size and age at maturity.

An interesting effect was seen in the response of senescent and non-senescent fish to different fishing methods when comparing the pristine, fishing, and recovery phases within scenarios. Trawling caused a larger absolute decline in asymptotic length (Fig. 3a) than did gillnetting (Fig. 3b) for both senescent and non-senescent populations. However, in the trawling scenario the asymptotic length of the senescent population declined proportionately less than that of the non-senescent population (Fig. 4a). The
opposite occurred in the gillnetting scenario (Fig. 4b), where the asymptotic length of
the senescent population declined proportionately more from the pristine phase to the
fishing phase compared to the non-senescent population. In the 200 years of recovery,
the recovery rates of asymptotic length in senescent and non-senescent populations
also varied. The different response of senescent and non-senescent fish to different
fishing methods is an important notion, as the presence or absence of senescence can
affect the magnitude of the change in lifehistory traits in response to fishing. Further, the
change in lifehistory characters directly and indirectly affects the population level
response.

Population level consequences of senescence

The changes in asymptotic length, and associated changes in growth rate, and size and
age at maturity translated to changes in population level variables. As the carrying
capacity of both senescent and non-senescent populations were the same, and the
asymptotic length of the fish decreased as a result of senescence and/ or fishing, the
senescent population could contain a higher number of fish through pristine, fishing and
recovery phases. However, the response of the senescent and non-senescent
populations in terms of biomass differed during fishing, and the type of fishing affected
the response.

In absolute terms, the senescent population maintained a higher biomass during
trawling than the non-senescent population (Fig. 3c). Our simulation allowed for control
over the fishing mortality, and the catch in terms of biomass was set identical for the
senescent and non-senescent populations. Before the fishing started, the population
with senescence had a lower biomass than that of the non-senescent population. Since
the absolute biomass of the catch is the same in both populations, this means that the proportional catch from the senescent population (with initially lower biomass) is higher than the catch from the non-senescent population (which had a higher biomass initially). Therefore, the lower asymptotic length of the senescent population (Fig. 3a) did not lead to them being less likely to get caught, but indeed the opposite. Regardless of being more likely to get caught, the senescent population maintained a higher number and higher biomass than the non-senescent population. The explanation for the higher biomass and the higher number of senescent population compared to the non-senescent population is likely in the lifehistory trade-offs. The population with senescence has evolved to have a lower asymptotic length and therefore they mature and start reproducing younger and at a smaller size. Fishing as a source of external mortality pushes the age and size at maturity even younger and smaller, so the higher biomass and number of fish is likely maintained by this earlier reproduction and not lesser fishing mortality. This is an important notion, as management practices tend to focus on saving the big fish (Birkeland and Dayton 2005; Barneche et al. 2018). While we do not deny the importance of big fish, we wish to draw attention to the important contribution that smaller fish can have in population recovery, especially in extensively exploited populations.

Gillnetting presents a different kind of selection curve than trawling. While the logistic selection curve of trawling allows virtually no escapement of the larger fishes, the dome-shaped selection curve of gillnetting selects the mid-sized and allows the escapement of small and large fish. This kind of selection curve leads to a less skewed population in terms of size, and consequently age. As a result, the responses of senescent population
and the non-senescent population to gillnetting in terms of biomass did not differ as much as they did to trawling. However, the drop in biomass from pristine phase to fishing phase was relatively smaller for the senescent population (Fig. 4d), despite the larger relative drop in asymptotic length (Fig. 4b). Like the situation in trawling scenario, the enhanced reproduction of younger and smaller fish is likely to drive the relatively higher biomass of the senescent population.

The present study showed a decline in the age and size at maturity for senescent populations, and fishing enhanced this trend further. However, the changes (or the direction of the change) in life-history traits as a result of fishing depend on many factors including species, fishing effort, and environmental conditions. In their meta-analysis, Rochet (1998) controlled for the effect of phylogeny and showed on 77 stocks that fishing induced a decline in age at maturity but an increase in size at maturity. If this were to occur in addition to senescence, it could be speculated that this would likely lead to similar results than in the present study: younger age but larger size at reproduction would probably mean that the reproductive output is even higher if fecundity is assumed to scale isometrically with body size, as most lifehistory and fisheries models do, thereby highlighting the role of young individuals in population recovery even more. However, the increased density of young fish may eventually lead to higher density dependent mortality at younger age classes, or decline in food availability, which could indirectly affect recruitment (Abrams and Rowe 1996). More studies are needed to understand the recruitment dynamics under different density scenarios.
While the asymptotic length of senescent and non-senescent fish responds to different fishing selection regimes differently, the population level consequences of senescence might be partially density dependent (Graves and Mueller 1993). During high external mortality it might be better to invest in reproduction rather than grow large. In other words, given that senescent fish are smaller to start with, senescence may buffer the population against high external mortality by pushing for earlier reproduction. Indeed, looking at the other side of the coin, high rate of external mortality is expected to accelerate the rate of senescence (Williams 1957) and as a trade-off potentially select for earlier reproduction.

The density-dependent consequences of senescence can be seen when the effects of reproductive and actuarial senescence are teased apart (Fig. 2). While the populations with actuarial and reproductive senescence have lower asymptotic length before fishing pressure is applied, under fishing pressure this population maintains higher asymptotic length than a population with actuarial senescence only. This suggests that during high external mortality, if the population experiences both types of senescence (actuarial and reproductive), then maintaining a larger body size becomes beneficial in order to maximise fitness in terms of producing as many offspring as possible. On the other hand, for a population with only actuarial senescence, their reproduction does not suffer in terms of declining GSI with age, so therefore smaller body size carries smaller fitness penalty compared to populations that experience both types of senescence.

Implications to fisheries science

Exploitation and over-exploitation are major causes for the decline of fisheries (Perissi et al. 2017) and even extinction of fish populations (Dulvy et al. 2003b). The traditional
density-dependent population growth theory suggests that at low abundance populations should grow at a fast rate. Following this, fish stocks should recover quickly after fishing has been ceased. Yet, despite large-scale fishing moratoriums, many fish stocks have not fully recovered from intense fishing and remain low (Myers and Barrowman 1997; Bailey 2011; Rougier et al. 2012; Pedersen et al. 2017), or are recovering at a lower rate than expected (Hutchings and Reynolds 2004). While the reasons behind the lack of recovery are complex, the failure of fishing moratoriums to result in stock recovery warrants a closer investigation at the life-history evolution and trade-off in fish, and the potential demographic consequences thereof.

Based on the evidence for the presence of senescence in fish (Gerking 1957; Comfort 1960, 1963; Woodhead and Ellett 1966, 1967, 1969a, b; Patnaik et al. 1994; Woodhead 1998; Beverton et al. 2004; Reznick et al. 2006; Hendry et al. 2004; Reznick et al. 2004; Morbey et al. 2005; Carlson et al. 2007; Terzibasi Tozzini et al. 2013; Uriarte et al. 2016; Benoît et al. 2018), taking senescence into consideration in fisheries stock assessments could improve the accuracy of stock assessment and success in management. As described by Le Bris et al. (2015), fisheries models that predict population dynamics often assume that individual fecundity increases with the increasing size of fish. These models are particularly sensitive to variations in the fecundity–mass relationship (Le Bris et al. 2015). Therefore, for species that undergo senescence, estimates of fecundity that ignore senescence may prove to be incorrect. As discussed above, the smaller and younger fish may have an important role in population recovery.
Similarly, due to lack of age-specific natural mortality data, typical fisheries models assume a constant rate of natural mortality regardless of the age and size of the fish, or a rate of natural mortality that scales with body size raised to a negative power (summarised in Gislason et al., 2010), thereby assuming a decreased rate of natural mortality as the individual grows and ages. For species experiencing senescence, ignoring changes in natural mortality with age could lead to unrealistically low mortality estimates. Additionally, it could mask the importance of young individuals in population recovery, hindering our management efforts further. Recruitment and natural mortality are the basic building blocks of stock assessment, and therefore ignoring the ways that senescence can change them could lead to biased estimates of fish population sizes. Inaccuracies in stock assessment models, whether related to reproductive capacity or mortality rates, may risk the sustainability of fishing.

Importantly, the practice of conserving old and large individuals (Birkeland and Dayton 2005), may not be sufficient, and could even be harmful if senescence is indeed widely present in fishes. While old and large individuals have important functions in the wider ecosystem as predators (Petchey et al. 2008), trainers of young ones in migration and feeding (Petitgas et al. 2010), and in contributing to the gene pool (Uusi-Heikkilä et al. 2015), their role in maintaining population resiliency through recruitment may not be as pivotal as is thought. On the one hand, this may be because if senescence is widely present in fishes, then relying on large individuals could be misleading if their natural mortality is higher than estimated, and their reproductive output is lower than estimated. On the other hand, it may be because we are under-estimating the role of smaller and younger individuals and their reproductive capacity. Early life reproduction may be an
important contributor to population resiliency and recovery, perhaps more so than late
life reproduction.

Senescence can mask changes in life-history responses to fishing. As demonstrated in
the present study, the presence or absence of senescence affects how the population
responds to different fishing selections regimes: while trawling reduced the asymptotic
length of non-senescent population more, gillnetting reduced the asymptotic length of
the senescent population more. Depending on the fishing method in question, the
magnitude of change in life-history characters may be higher or lower than anticipated if
senescence is present. As a result, the population level response will change too.

Failure to consider senescence as a fish life-history trait with trade-offs and population
level consequences will hinder our progress in understanding fish population resiliency.
Declarations

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**Figure legends**

**Fig 1.** A schematic diagram of the modelling approach. (A) The fish length-at-age was back-calculated from fish scales. These data were then used to fit the von Bertalanffy growth equation to model the $L_\infty$. The $L_\infty$ was set to be an evolving trait so that the genotype coding the $L_\infty$ of each individual was described by 10 diploid loci with two alleles in each, one from the mother, one from the father. (B) The length-weight relationship was specifically calculated for *C. albula* from Lake Puulavesi. Using this length-weight relationship and published empirical data on egg numbers and female weights (Karjalainen et al. 2016), we fitted a linear model for the fecundity-weight relationship, so that as the fish body size increases, so does the egg production. (C) The probability of a fertilised egg to hatch and the juvenile to survive until 2 years of age was set to ($P = 0.002$) and the sex of the juveniles was drawn from a Bernoulli trial with a probability of 0.5. (D) The population component describes density dependency so that at 75% of the population carrying capacity, the individual growth is reduced to 50% of that predicted by the individual’s vB growth curve. Additionally, egg production was set to be density dependent so that the closer the population was to its carrying capacity, the fewer eggs were produced. (F) Reproductive senescence and actuarial senescence are the independent variables in the model. The reproductive senescence was modelled by multiplying the linear model for fecundity by the fecundity factor based on the gonadosomatic index (GSI) for the year class in question. When no reproductive senescence was modelled, only the linear model for fecundity was used. Actuarial senescence was modelled by increasing the rate of natural mortality each year, as opposed to keeping natural mortality rate constant throughout lifetime as in the scenario.
with no actuarial senescence. (F) Equipped with the above characters, the populations were then allowed to live for 500 years and traced at annual time steps. The first 200 years the populations lived in pristine conditions, then the populations were fished either by trawling or gillnetting for 100 years, and finally the populations were allowed to recover for 200 years.

**Fig 2.** The mean of the asymptotic length (cm) of fish over 500 years (first hundred years not shown). The dashed lines denote the start (year 200) and end (year 300) of fishing. The solid lines denote the asymptotic length mean in hundred replicated scenarios. The black line describes a scenario with reproductive and actuarial senescence, red line a scenario with actuarial senescence only, blue line a scenario with no senescence, and green line a scenario with reproductive senescence only.

**Fig. 3.** Results for the (a, b) asymptotic length (cm), (c, d) biomass (units), and (e, f) the number (N) of fish. In a, c, and d the fishing simulated trawling (logistic selection) and in b, d and f the fishing simulated gillnetting (dome-shaped selection). The solid black lines represent hundred independent replicates of the scenario with senescence, the red lines represent hundred independent replicates of the scenario with no senescence present. The dashed lines denote the start (year 200) and end (year 300) of fishing.

**Fig. 4.** The relative percentage change (a, b) asymptotic length (cm), (c, d) biomass (units), and (e, f) the number (N) of fish. In a, c, and d the fishing simulated trawling (logistic selection) and in b, d and f the fishing simulated gillnetting (dome-shaped
selection). The change has been scaled so that years 1 – 100 were considered as the starting point and given a value of 0. Changes in all of the parameters (asymptotic length, BM, N) after that are relative changes compared to years 1 – 100. The black lines denote a scenario with senescence, the red lines denote a scenario without senescence. The dashed lines denote the start (year 200) and end (year 300) of fishing. Given the scale of the Y axis, the 95% confidence intervals are virtually invisible.

Appendix S1. The lifetime cumulative number of offspring in each age group during the last ten years before fishing commences and the population is in equilibrium, and during the last ten years of intensive fishing (after 90 years of constant fishing). The red boxplots denote scenarios without senescence and black and white boxplots denote scenarios with both actuarial and reproductive senescence present.

Appendix S2. The lifetime cumulative number of offspring in each age group during the last ten years before fishing commences and the population is in equilibrium, and during the last ten years of intensive fishing (after 90 years of constant fishing). The green boxplots denote scenarios with reproductive senescence and blue boxplots denote scenarios with actuarial senescence present.

Appendix S3. Results for the (a) asymptotic length (cm), (b) intrinsic growth rate $k$, (c) average size (cm) at maturation, and (d) average age (years) at maturation over hundred years (first hundred years not shown). The black lines represent hundred
independent replicates of the scenario with senescence, the red lines represent hundred independent replicates of the scenario with no senescence present. The dashed lines denote the start (year 200) and end (year 300) of fishing.
A schematic diagram of the modelling approach. (A) The fish length-at-age was back-calculated from fish scales. These data were then used to fit the von Bertalanffy growth equation to model the $L_\infty$. The $L_\infty$ was set to be an evolving trait so that the genotype coding the $L_\infty$ of each individual was described by 10 diploid loci with two alleles in each, one from the mother, one from the father. (B) The length-weight relationship was specifically calculated for C. albula from Lake Puulavesi. Using this length-weight relationship and published empirical data on egg numbers and female weights (Karjalainen et al. 2016), we fitted a linear model for the fecundity-weight relationship, so that as the fish body size increases, so does the egg production. (C) The probability of a fertilised egg to hatch and the juvenile to survive until 2 years of age was set to $(P = 0.002)$ and the sex of the juveniles was drawn from a Bernoulli trial with a probability of 0.5. (D) The population component describes density dependency so that at 75% of the population carrying capacity, the individual growth is reduced to 50% of that predicted by the individual’s vB growth curve. Additionally, egg production was set to be density dependent so that the closer the population was to its carrying capacity, the fewer eggs were produced. (F) Reproductive senescence and actuarial senescence are the independent variables in the model. The reproductive senescence was modelled by multiplying the linear model for fecundity by the fecundity factor based on the gonadosomatic index (GSI) for the year class in question. When no reproductive senescence was modelled, only the linear model for fecundity was used. Actuarial senescence was modelled by increasing the rate of natural mortality each year, as opposed to keeping natural mortality rate constant throughout
lifetime as in the scenario with no actuarial senescence. (F) Equipped with the above characters, the populations were then allowed to live for 500 years and traced at annual time steps. The first 200 years the populations lived in pristine conditions, then the populations were fished either by trawling or gillnetting for 100 years, and finally the populations were allowed to recover for 200 years.

**Figure 2**

The mean of the asymptotic length (cm) of fish over 500 years (first hundred years not shown). The dashed lines denote the start (year 200) and end (year 300) of fishing. The solid lines denote the asymptotic length mean in hundred replicated scenarios. The black line describes a scenario with reproductive and actuarial senescence, red line a scenario with actuarial senescence only, blue line a scenario with no senescence, and green line a scenario with reproductive senescence only.
Results for the (a, b) asymptotic length (cm), (c, d) biomass (units), and (e, f) the number (N) of fish. In a, c, and d the fishing simulated trawling (logistic selection) and in b, d and f the fishing simulated gillnetting (dome-shaped selection). The solid black lines represent hundred independent replicates of the scenario with senescence, the red lines represent hundred independent replicates of the scenario with no senescence present. The dashed lines denote the start (year 200) and end (year 300) of fishing.
Figure 4

The relative percentage change (a, b) asymptotic length (cm), (c, d) biomass (units), and (e, f) the number (N) of fish. In a, c, and d the fishing simulated trawling (logistic selection) and in b, d and f the fishing simulated gillnetting (dome-shaped selection). The change has been scaled so that years 1 – 100 were considered as the starting point and given a value of 0. Changes in all of the parameters (asymptotic length, BM, N) after that are relative changes compared to years 1 – 100. The black lines denote a
scenario with senescence, the red lines denote a scenario without senescence. The dashed lines denote the start (year 200) and end (year 300) of fishing. Given the scale of the Y axis, the 95% confidence intervals are virtually invisible.

**Supplementary Files**

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- S1.png
- S2.png
- S3.png