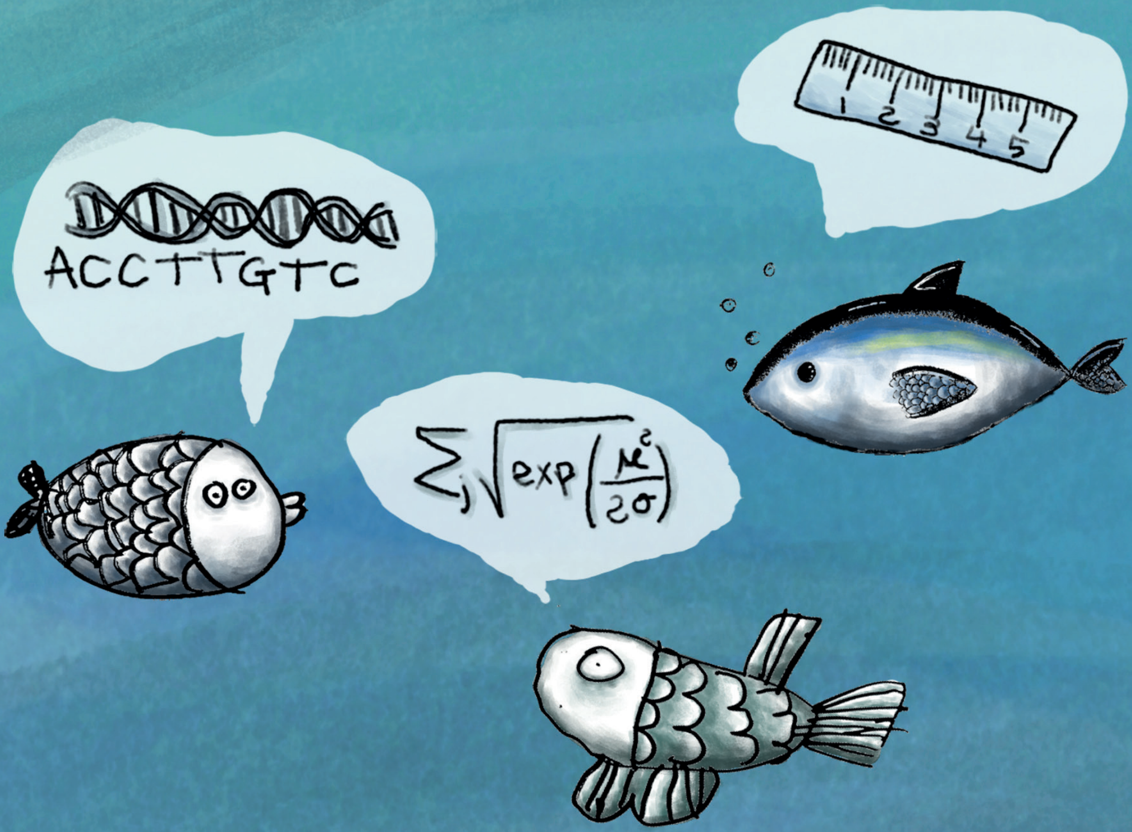
JYU DISSERTATIONS 464

The interplay between fish life-history traits, population dynamics, and ecosystems



Pauliina A. Ahti

2021

UNIVERSITY OF JYVÄSKYLÄ
FACULTY OF MATHEMATICS
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JYU DISSERTATIONS 464

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The Interplay between Fish Life-History Traits, Population Dynamics, and Ecosystems

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ABSTRACT

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Diss.

Aquatic ecosystems are going through an unprecedented decline in biodiversity. This is clearly reflected in the phenomenal declines in fisheries catches and collapses of many fish populations. Different levels of biological organisation interact in complex ways, and changes in fish life-history traits are reflected at population and ecosystem levels. However, the mechanisms behind those interactions are not well understood, and some interactions are completely unknown. This work uses mathematical modelling to explore how senescence, an often-ignored life-history trait affects fish population dynamics and response to fishing. Simulations demonstrate that senescence leads to evolutionary trajectory towards declining asymptotic length and population response to different fishing selection regimes depends on the presence of senescence. The link from population dynamics to life-history evolution is explored through population oscillations. Mathematical simulations show that oscillation wavelength shorter than the maximum lifespan of the fish produce marked differences in the evolution of asymptotic length. Wavelengths longer than the maximum lifespan in turn manifest in ecological effects seen as biomass fluctuations. The combination of the length and amplitude of the oscillation wave determine the direction of the change. Finally, the link between a single species and ecosystem is explored by introducing an invasive species in a food web model. The invasive species sets off a bottom-up effect seen in the decline of biomass. This effect propagates through all trophic levels in the model, including top predator fishes. These findings illuminate some previously unknown or poorly understood links between different levels of biological organisation that will help us better manage and conserve the aquatic nature.

Keywords: Eco-evolutionary dynamics; food web; invasive species; life-history; population fluctuations; senescence; trade-offs.

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TIIVISTELMÄ

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Akvaattisten ekosysteemien biologinen monimuotoisuus on viime vuosikymmeninä heikentynyt ennennäkemättömällä tavalla. Tämä heijastuu selvästi kalasaaliiden vähenemisenä ja monien kalakantojen romahtamisena. Eri tasot biologisessa organisaatiossa ovat monimutkaisessa vuorovaikutuksessa keskenään, ja kalojen elinkierto-ominaisuuksien muutokset heijastuvat myös populaatio- ja ekosysteemitasoilla. Näiden vuorovaikutusten takana olevia mekanismeja ei kuitenkaan ymmärretä hyvin, ja jotkut yhteydet ovat täysin tuntemattomia. Vanheneminen on usein huomiotta jätetty elinkierto-ominaisuus. Tässä työssä tutkitaan matemaattisten mallien avulla, kuinka vanheneminen ja kalastus vaikuttavat kalojen populaatiodynamiikkaan. Simulaatiot osoittavat, että vanheneminen on yhteydessä evoluutioon kohti lyhyempää asymptoottista pituutta ja vaikuttaa siihen, kuinka populaatio vastaa kalastukseen. Populaatiodynamiikan yhteyttä elinkierto-ominaisuuksiin tutkitaan simuloimalla populaation biomassan vaihtelua. Matemaattiset simulaatiot osoittavat, että jos vaihtelun aallonpituus on lyhyempi kuin kalojen maksimielinikä, aiheuttaa se merkittäviä eroja asymptoottisen pituuden evoluutiossa. Kun populaation vaihtelun aallonpituus on pidempi kuin kalan maksimielinikä, se näkyy lähinnä ekologisina vaikutuksina biomassan muutoksessa. Vaihtelun aallonpituuden ja amplitudin yhdistelmä määrää muutoksen suunnan. Lopuksi tutkitaan yhden lajin ja ekosysteemin välistä yhteyttä lisäämällä vieraslaji ravintoverkkomalliin. Vieraslaji aiheuttaa alhaalta ylöspäin menevän vaikutuksen, joka näkyy biomassan vähenemisenä. Tämä vaikutus näkyy mallin kaikilla trofiatasoilla, myös ravintoverkon huipulla olevissa kaloissa. Tämä tutkimus paljastaa aiemmin tuntemattomia tai huonosti ymmärrettyjä yhteyksiä biologisten organisaatioiden eri tasojen välillä. Nämä tulokset auttavat meitä suojelemaan vesiluontoamme paremmin.

Avainsanat: Eko-evolutiivinen dynamiikka; elinkierto-ominaisuus; kalastus; populaation vaihtelut; ravintoverkko; seneskenssi; vieraslaji.

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LIST OF ORIGINAL PUBLICATIONS

The dissertation is based on the following original papers, which will be referred to in the text by their Roman numerals I–IV.

I Pauliina A. Ahti, Anna Kuparinen & Silva Uusi-Heikkilä 2020. Size does matter – the eco-evolutionary effects of changing body size in fish. *Environmental Reviews* 28: 311–324.

II Pauliina A. Ahti, Silva Uusi-Heikkilä, Timo J. Marjomäki & Anna Kuparinen 2021. Age is not just a number–Mathematical model suggests senescence affects how fish populations respond to different fishing regimes. *Ecology and Evolution* 11: 13363–13378.

III Pauliina A. Ahti, Silva Uusi-Heikkilä & Anna Kuparinen 2021. Plenty of fish in the sea? The eco-evolutionary consequences of population fluctuations. Submitted manuscript.

IV Pauliina A. Ahti, Tommi Perälä, Linda Haltiner, Piet Spaak, Hui Zhang & Anna Kuparinen 2021. Invasion of the ecosystem snatchers: The non-native quagga mussel causes a bottom-up effect in an aquatic food web model**.** Manuscript.

Author contributions:

I PAA wrote the article and did the literature research, AK provided comments, SUH contributed to writing the article.
II PAA wrote article, did the analyses, AK provided the initial model and PAA and AK further developed it, SUH provided comments, TJM provided empirical data and comments on the manuscript.
III PAA wrote article, did the analyses, and developed the model. AK provided the initial model, contributed to its development, and commented the manuscript. SUH commented the manuscript.
IV PAA conceived the idea, wrote article, and did the analyses, TP developed the model and contributed to writing, LH, PS, and HZ provided empirical data and commented the manuscript, AK provided the initial model and commented the manuscript.

ABBREVIATIONS

ATN	allometric trophic network
GSI	gonadosomatic index
L_∞	asymptotic length
LRO	lifetime reproductive output
ODE	ordinary differential equation
r	intrinsic rate of per capita population growth
M	instantaneous natural mortality
F	instantaneous fishing mortality

The future is in the hands of those who explore... and from all the beauty they discover while crossing perpetually receding frontiers, they develop for nature and for humankind an infinite love.

The sea, once it casts its spell, holds one in its net of wonder forever.

Jacques Yves Cousteau

1 INTRODUCTION

1.1 Background

The planet Earth is accurately known as the water-world. Over 71 % of the earth's surface is covered by water. It has been estimated, that approximately 25 % of the world's species live in marine ecosystems (Mora *et al.* 2011), and that some 55 % of all fish species are found in freshwater ecosystems (Anon. 2021a). However, of the oceans alone, more than 80 % remain unknown to science (Anon. 2021b). Despite being poorly understood, these aquatic ecosystems play a vital role for life on earth. Oceans and lakes are important carbon sinks (Sabine *et al.* 2004; Anderson *et al.* 2020), produce at least half of the oxygen on earth (Anon. 2021c), and provide important ecosystem services in the form of recreational activities, climate regulation, and shoreline protection as well as food.

The biodiversity in the oceans (Payne *et al.* 2016) and lakes (Harper *et al.* 2021) is going through an unprecedented decline. For humans, this is perhaps most clearly seen in the phenomenal declines in fisheries catches (Pauly and Zeller 2016), and the catastrophic collapse of entire fish populations (Neuenhoff *et al.* 2019). The traditional theory of density dependence predicts that at low abundance, the recovery of fish populations should be fast (Hilborn and Walters 1992). However, after decades of overexploitation, many fish populations are failing to recover despite large reductions in fishing pressure (Worm *et al.* 2009, Hutchings 2015).

The reasons for the lack of recovery are complex, and probably species or at least trophic level specific. Factors such as changing water temperature, predation, continued fishing, harvest induced evolution, and life-history changes have been documented to contribute to poor population recovery (Swain *et al.* 2011). Over the past decades, research has focused on life-history changes, particularly those related to body size, and shown that life-history changes may play a major role in the recovery ability of a fish population (Kuparinen and Hutchings 2012, Audzijonyte *et al.* 2013). Importantly, through alterations in the reproductive output and survival, life-history changes extend their influence to the entire population, and through predator–prey dynamics, to the surrounding ecosystem (Kuparinen *et al.* 2014, Brose *et al.* 2016). This may form a feed-back loop so that changes in the ecosystem and populations feed back to life-histories.

It is obvious, given the number of collapsed fish populations (Jackson *et al.* 2001, Hunter *et al.* 2015, Neuenhoff *et al.* 2019), that not only could fisheries management be improved, but also our fundamental understanding of the eco-evolutionary dynamics of fish populations has several gaps. Traditional fisheries management is heavily focussed on harvest rates and stock biomass (Skern-Mauritzen *et al.* 2016). However, biological systems are far more complex than that, and cannot be reduced to a simple figure of stock biomass. Life-histories affect populations and vice versa, and species interact with each other so that a change in one species reflects to another species and the surrounding ecosystem (Frank *et al.* 2007, Bundy *et al.* 2009).

Senescence is a life-history trait that, to my knowledge, has received no attention in terms of its role in fish population dynamics. Senescence, by its very definition, means age-dependent changes in natural mortality and reproductive output. Natural mortality and reproductive output are the basic building blocks of fisheries models, yet most models completely ignore the possibility of senescence (Gislason *et al.* 2010), despite strong evidence that senescence is indeed present in fishes (Gerking 1957, Comfort 1963, Woodhead and Ellett 1969, Patnaik *et al.* 1994, Woodhead 1998, Beverton *et al.* 2004, Hendry *et al.* 2004, Reznick *et al.* 2004, 2006, Morbey *et al.* 2005, Carlson *et al.* 2007, Terzibasi Tozzini *et al.* 2013, Uriarte *et al.* 2016, Benoît *et al.* 2018, Žák and Reichard 2020). Another knowledge gap is the feedback loop from natural population oscillations to life-history evolution. While the connection between changes in population density due to fishing and life-history traits has been well studied (Kuparinen and Hutchings 2012, Kuparinen *et al.* 2014, Heino *et al.* 2015), the understanding of how natural fluctuations, which are commonplace in nature across taxa (MacArthur 1955), affect the life-history evolution of fish is scarce. In essence, the selection due to natural population oscillations forms the baseline from which evolution due to harvest can be understood. Importantly, none of these feedback interactions between life-histories and population dynamics exist in a vacuum. Rather, they exist as part of a complex ecosystem with different trophic levels, predator–prey dynamics, and various stressors ranging from fishing to invasive species.

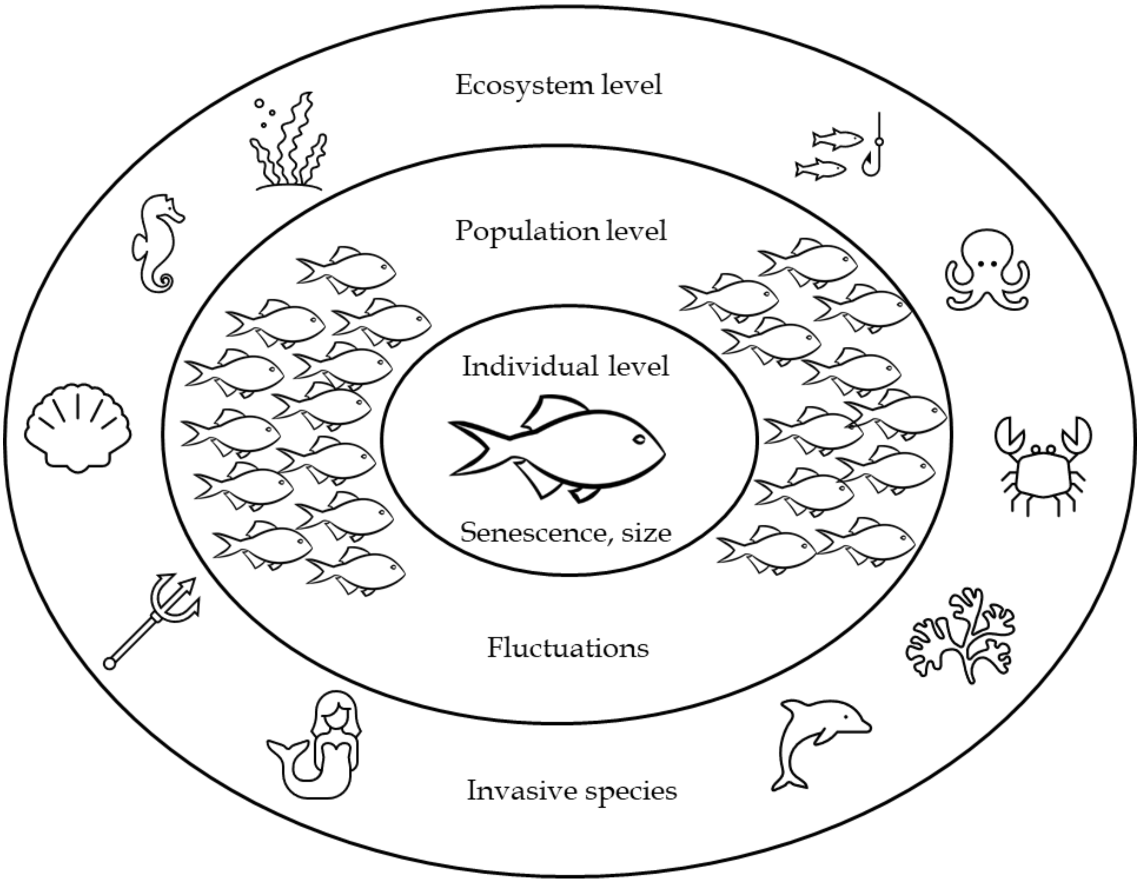

FIGURE 1 Schematic illustration of the research approach.

To address these issues and knowledge gaps, this dissertation explores the links and feedback loops between life-histories, population dynamics, and ecosystems (Fig. 1). First, I review the causes and consequences of changes in a key ecological trait linked to many life-history traits: the body size (I). Next, using an individual-based mechanistic simulation model, I explore the role of an important and often-ignored life-history trait, senescence, in the eco-evolutionary dynamics of a fish population (II). Third, instead of searching for the causes of fish population fluctuations like most research to date, using the same mechanistic model as in (II), I choose a novel approach and investigate the evolutionary and ecological consequences of population fluctuations (III). Finally, using the Allometric Trophic Network (ATN) model, I investigate the impact of an aggressive invasive species on a lake ecosystem (IV). These objectives are further detailed in section 1.6.

1.2 The eco-evolutionary effects of changing body size

Body size holds a key role in ecology and is used as a proxy for many life-history traits such as reproductive output (Barneche *et al.* 2018), size and age at maturity (Jensen 1996), and survival (White *et al.* 2013). While changes in body size and associated traits have been recorded in commercially exploited fish populations, it is notoriously difficult to disentangle the exact factors behind such changes. Populations in the wild are under several simultaneous selection agents and stressors. Apart from size selective fishing, also agents such as temperature (Cheung *et al.* 2012), dissolved oxygen (Pauly and Cheung 2018), and predation (Reznick and Endler 1982) are thought to select for different life-history traits. The mechanisms behind such changes are still poorly understood, however, as is well illustrated by the debate around the gill–oxygen limitation theory. It has been suggested that the reduced dissolved oxygen that comes coupled with increasing water temperature leads to the inability of the gill surface area to support large bodies and as a consequence, small bodies become selected for (Pauly and Cheung 2018). The opposing view suggests that it is not the oxygen content that determines the size of the gills, but the lifestyle and the habitat determine the need for oxygen, and consequently the size of an individual (Lefevre *et al.* 2018, Audzijonyte *et al.* 2019).

While our understanding of the exact mechanisms behind the changes in life-history traits is incomplete, there is a large theoretical framework consisting of ecological literature and theories explaining body size. For temperature, the main theories are Bergmann’s rule (Bergmann 1874), James’ rule (James 1970), Temperature–Size rule (Atkinson 1994), and the Metabolic Theory of Ecology (West *et al.* 1997). The contested effects of dissolved oxygen are explained by the gill-oxygen limitation theory (Pauly 1981) and opposing views (Lefevre *et al.* 2018, Audzijonyte *et al.* 2019). The framework for size selective fisheries is set by the breeder’s equation (Lush 1937). Finally, the theories behind the effects of predation on body size are, for instance, the “Bigger is better” hypothesis (Miller *et al.* 1988) and the Optimal Foraging Theory (MacArthur and Pianka 1966).

Anthropogenic and natural selection agents may select toward opposing directions. While fishing and increasing water temperature are commonly associated with decreasing body size (Cheung *et al.* 2012, Hunter *et al.* 2015), natural selection in the form of predation may select towards fast growing, large individuals as larger individuals might be better protected from predators (Allain *et al.* 2003, Meekan *et al.* 2006). However, predation by invasive species has been documented to cause an opposite effect toward declining size and age at maturity (Heins *et al.* 2016). The different selective forces by native and invasive predators hint how the ecosystem level processes intertwine with individual processes.

Body size is also linked with many behavioural traits which can directly or indirectly enhance or reduce individual fitness, tying life-history traits with the population dynamics and wider ecosystem even tighter. Many size-related behavioural traits are linked with boldness and may affect the willingness to forage (Walsh *et al.* 2006). Foraging behaviour in turn may affect fitness, vulnerability to predators, as well as energy flow through the entire ecosystem (Johansen *et al.* 2015). Large body size can also carry a fitness benefit in terms of reproductive success, as mate and territory selection may favour larger individuals (Fleming and Gross 1994).

Body size correlates with lifetime reproductive output (LRO) (Barneche *et al.* 2018), which translates to intrinsic rate of per capita population growth (*r*), a measure that can be thought of as a population level analogue to LRO (Denney *et al.* 2002). The population level consequences of body size changes bring about the much-debated question of whether these changes are genetic adaptations or plastic responses. There is no indisputable scientific consensus about this, and importantly, it likely depends on the selective agent. Further, changes in the body size can affect predator–prey relations through gape-limited predation, as changing body size affects when the prey reaches size refuge (Persson *et al.* 1996, Palkovacs and Post 2009). As the infamous case of Atlantic cod (*Gadus morhua*) illustrates, changes in fish life-history traits can then propagate to population collapse (Olsen *et al.* 2004) and send waves through the entire ecosystem (Frank *et al.* 2005).

1.3 The interplay between life-history traits and population dynamics

The core of fish stock assessment is based on recruitment and natural mortality (Hilborn and Walters 1992), and stock assessment models are particularly sensitive to variations in fecundity-mass relationship (Le Bris *et al.* 2015). Senescence is a life-history trait that is described as declining reproductive output with age, (reproductive senescence), and increasing natural mortality with age (actuarial senescence). As such, senescence directly affects the core of stock assessment. Senescence was long thought absent in nature, as animals were thought to be eaten by predators or die of other causes before senescence would commence. However, today evidence for senescence across taxa is accumulating (Nussey *et al.* 2013).

Most fisheries (Beverton and Holt 1957, Zimmermann and Jørgensen 2015) and life-history (Roff 1983, Charnov *et al.* 2013) models assume that reproductive output scales isometrically with body size (weight). Additionally, due to the difficulty of achieving accurate, species specific natural mortality rates, natural mortality is often considered an age independent constant or scaled with body size raised to a negative power (Gislason *et al.* 2010). Such models describe fish as not experiencing senescence at all, despite the fact that the first reports of senescence in fish are from the 1950s (Gerking 1957) and evidence for both reproductive and actuarial senescence in fish is fast accumulating (Beverton *et al.* 2004, Uriarte *et al.* 2016, Benoît *et al.* 2018, Žák and Reichard 2020).

While the importance of large and old individuals in population recovery is evident (Barneche *et al.* 2018), if senescence is indeed present in fishes, we may be overestimating reproductive capacity and underestimating natural mortality rate, thereby skewing the very building blocks of stock assessment. A careful consideration of different life-history traits that are linked to the sensitive parameters of fecundity and natural mortality and incorporating them in fisheries projections could improve the management strategies of our natural resources.

1.4 Population dynamics feed back to life-history evolution

Oscillating fish populations have interested scientists for decades, not least because of the financial instability and economic catastrophes they may cause (Sette 1961). A large body of literature aims to explain the causes behind strong oscillation patterns. These causes are divided into intrinsic factors such as predator—prey dynamics, critical period during early life stages, and density dependence (Houde 1987, Bakun and Cury 1999, Minto *et al.* 2008), and extrinsic factors such as oceanographic and other environmental drivers (Cury and Roy 1989, Lehodey *et al.* 2006).

Fisheries-induced evolution, which is based on size-selective harvest on the one hand, and density-mediated selection on the other, has received a lot of research attention over the past decades as scientists are trying to understand what kind of evolutionary and ecological impacts fishing may have (Heino *et al.* 2015). However, the consequences of natural variations in population density have received a lot less research attention. Population fluctuations, by definition, induce variation in population density. Density in turn is an important factor regulating fish growth (Lorenzen and Enberg 2002), reproduction (Schwartzlose *et al.* 1999, Leips *et al.* 2009), and survival (Minto *et al.* 2008).

The effects of density can be complex, as on the one hand low population density is often associated with larger body size due to more energy being available per individual (Cyr *et al.* 1997, Lorenzen and Enberg 2002, Hazlerigg *et al.* 2012). On the other hand, increased competition during high population density is thought to select for larger body size (Calsbeek and Cox 2010, Bouffet-Halle *et al.* 2021). While the direction and strength of the selection may depend on the species and the context, it is clear that changes in population density can drive life-history evolution (Kuparinen *et al.* 2014), and as explored in II, life-histories can drive population dynamics. Natural ecosystems are in a state of constant change from natural and anthropogenic agents. These agents have the capacity to leave an evolutionary signature in the population, and therefore form a feedback loop between population dynamics and life-histories.

1.5 The big picture: how one species affects the entire ecosystem

The eco-evolutionary feedback loops extend far beyond individuals and populations. Species do not exist in a vacuum, but in a complex ecosystem where predator—prey dynamics, competition, parasitism, mutualism, and other biotic and abiotic processes constantly interact.

Invasive, non-native species are affecting ecosystems in various ways by causing losses of native biodiversity (Mcneely 2001) and diminishing biodiversity (Doherty *et al.* 2016). Lake ecosystems are known to be particularly vulnerable to invasive species (Havel *et al.* 2015) due to the relatively closed nature of them and the substantial stress they already face from climate change, land use, and other anthropogenic stressors (Sala *et al.* 2000). The effects of invasive species can be seen at all levels of biological organisation (Simon and Townsend 2003), and they can profoundly alter the entire food web (David *et al.* 2017).

Theoretical ecological network research has shown that occupying a lower trophic level can predict a successful ecosystem invasion (Romanuk *et al.* 2009). Indeed, the quagga mussel (*Dreissena rostriformis bugensis*), a filter feeding herbivore often found at the second trophic level in a food web, is known to be one of the most successful and aggressive freshwater invaders in the world (Karatayev *et al.* 2015a, b). Studies in the Great Lakes have shown changes in water clarity (Yousef *et al.* 2017), near complete disappearance of the key food item *Diporeia* amphipod (Nalepa *et al.* 2009), significant diet shifts at higher trophic levels (Madenjian *et al.* 2015), and changes in fisheries catches (Ebener *et al.* 2008, Fera *et al.* 2017), all of which have been attributed, at least partially, to the arrival of *Dreissena* mussels in the Great Lakes.

The quagga mussel is spreading in North America and in Europe, and even replacing the notorious zebra mussel (*Dreissena polymorpha*) in many freshwater bodies (Wilson *et al.* 2006, Matthews *et al.* 2014, Karatayev *et al.* 2015b). The quagga mussel was first found in Lake Constance in 2016, and anecdotal notes suggest its average population density now exceeds 5 000 individuals m^{-2}. Lake Constance is an important drinking water reservoir for over 5 million people and provides a large number of ecosystem services from fishing and recreation to nature conservation (Hammerl and Gattenhoehner 2003, Petri 2006). How the invasion of the lake by the quagga mussel affects the entire lake ecosystem, is currently not understood.

While a lot of research exists on the impacts of invasive species on lake ecosystems, these studies often focus on only a single phenomenon in the ecosystem. Capturing an ecosystem-wide image of how an invasive, non-native species may affect its new habitat is challenging due to the complex nature of ecosystems. However, food web modelling is a powerful tool that can help us understand the role of a single species in the wider ecosystem context (David *et al.* 2017). Food web modelling explores how different trophic levels interact with each other. Therefore, by incorporating an invasive species into a food web model, we can study how a single species, or even variations in its life-history traits, may affect the structure of the food web.

1.6 Objectives

Given the unprecedented decline in aquatic biodiversity (Harper *et al.* 2021), and the phenomenal collapses in fisheries catches (Pauly and Zeller 2016), it is vital that we improve our fundamental understanding of basic ecology and evolution, and then take this knowledge to make evidence-based decisions. This Ph.D. dissertation is set to explore the fundamental links between life-histories, populations, and ecosystems.

The aim is approached firstly, by investigating how fish life-history traits reflect to population dynamics (I, II), and, secondly, how population dynamics feed back to life-history evolution (III). Then the role of an individual species in an ecosystem is explored by investigating how an aggressive invasive species with varying rates of mortality affects a lake ecosystem (IV).

To address these issues, the following questions will be asked:

A) Body size is a key ecological trait under various selection pressures. What is the current understanding of the role of body size in population dynamics and ecosystem function? (I)
B) Does senescence, an often-ignored life-history trait in fish, affect the population dynamics, and if so, how does it interact with different fishing selection regimes? (II)
C) What are the ecological and evolutionary effects of fish population fluctuations? (III)
D) Can a single species, with variations in its life-history traits, affect the entire ecosystem? What are the ecosystem-wide effects of an invasive species in a lake ecosystem? (IV)

2 METHODS

2.1 Study systems

Given that the focus of this dissertation was on the ecological and evolutionary mechanisms, rather than in a specific species or a specific ecosystem, the study systems were selected based on the data available for each question. To explore the role of senescence (II) and population oscillations (III) in the eco-evolutionary dynamics of a fish population, empirical data for a commercially and culturally important, small, schooling salmonid fish *Coregonus albula* (vendace) from Lake Puulavesi was used. Previous research has indicated that *C. albula* may undergo reproductive (Karjalainen *et al.* 2016b) and actuarial (Marjomäki 2005) senescence, and it is known to exhibit strong population oscillations (Marjomäki and Huolila 2001). Lake Puulavesi in Central Finland has an aerial coverage of approximately 330 km^2, a maximum depth of 62 m, and an average depth of 9.2 m. The collected data cover the period between 1977 and 2017.

For the ecosystem interactions and effects of an invasive species (IV), a network model of Lake Constance (German: Bodensee) was used. Lake Constance is situated on the border of Switzerland, Austria, and Germany, and supplied by the River Rhine. Lake Constance is divided into three main parts: Upper Lake Constance, Lower Lake Constance, and Lake Rhine. As one of the largest freshwater bodies in Europe, its total area is approximately 476 km^2, maximum depth 252 m, and mean depth 101 m. The invasive species of interest here was *Dreissena rostriformis bugensis* (quagga mussel), one of the most aggressive freshwater invaders in the world, and first found in Lake Constance in 2016.

2.2 Individual-based model

To explore the role of senescence in fish population dynamics, and the eco-evolutionary consequences of population fluctuations, an existing individual-based model (Kuparinen *et al.* 2012) was parametrised for *C. albula.* Here, a general description of the modelling approach is provided, and further details can be found in II and III. The model consists of five main components: growth, fecundity, population demographics, survival, and senescence (Fig. 2).

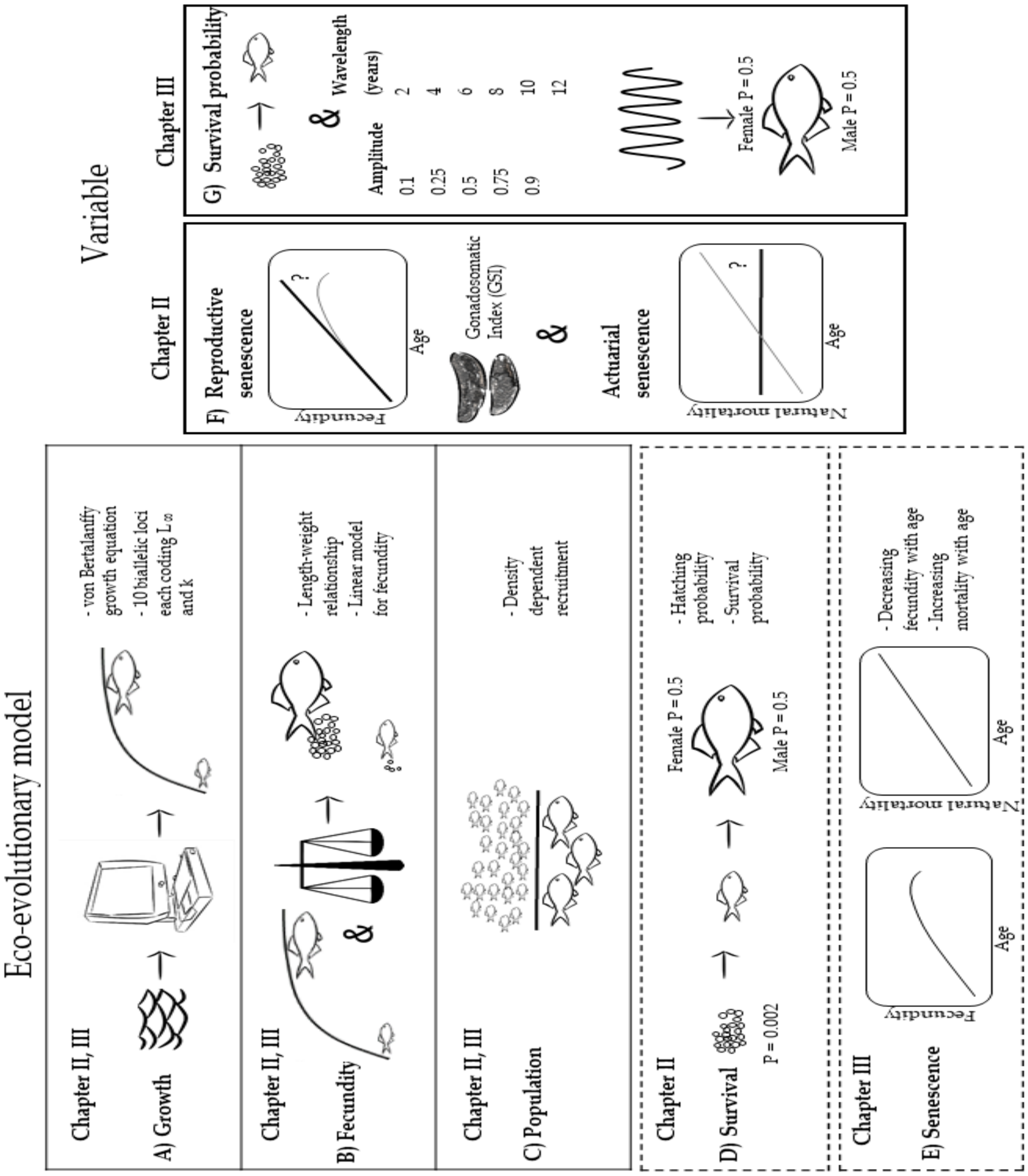

FIGURE 2 Schematic summary of the Individual-Based Modelling approach. “Chapter” refers to the corresponding publication or manuscript (cont. next page).

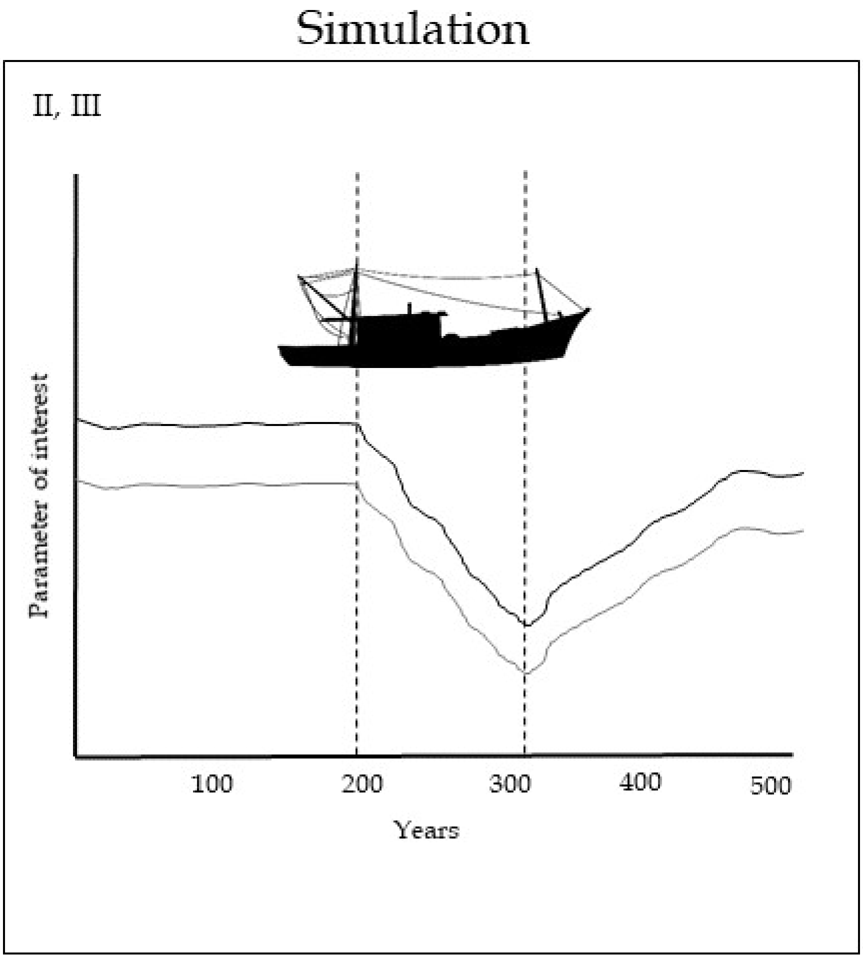

FIGURE 2 Schematic summary of the Individual-Based Modelling approach (continued from previous page).

Fig. 2 illustrates the main components of the model, and the model development done for II and III (labelled accordingly in Fig. 2 boxes). Both II and III included identical growth, fecundity, and population demographic components, and the differences between II and III are shown in the boxes with dashed lines. For II, the survival probability of fish from hatching to their second autumn was set to 0.002, and the main question was the effect of presence vs. absence of senescence on the population dynamics (Fig. 2f). For III, the senescence developed in II was incorporated as always present, and the attention was in the survival component (Fig. 2g). Instead of the constant survival probability (Fig. 2d) as in II, the III focused on oscillating survival probability (Fig. 2g).

The growth trajectories (Fig. 2a, II, III) are based on back-calculated length-at-age data for *C. albula* from Lake Puulavesi. For the back-calculation, the Monastyrsky's equation (Monastyrsky 1930) was used:

$$L_t = L \times \left(\frac{S_t}{S}\right)^b,$$

where L_t = the total length measured when the fish was caught, L= the back-calculated length, S_t = the distance of the annulus from the scale focus at age t,, S = the radius of the scale, and b = 0.641, which is an estimate from several vendace stocks across Finland (Marjomäki and Huolila 2001). The growth trajectories from these back-calculations were then summarised using the von Bertalanffy (vB) growth curve (von Bertalanffy 1938, 1949) as follows:

$$L(t) = L_\infty - (L_\infty - L_0)e^{-kt},$$

where $L(t)$ = fish length at age t, L_∞= asymptotic length, L_0= length at age $t = 0$, and k = the intrinsic individual growth rate, i.e. how fast an individual approaches L_∞. Given that life-history traits such as age and length at maturity are known to be inherited (Roff 2002) and linked to L_∞, the genotype coding L_∞ for each individual was described by two diploid loci with two alleles each, one from the mother, one from the father. The alleles were coded as 0 or 1. To add phenotypic plasticity, a normally distributed number with a mean of 0 and s.d. of 4 was then added to the sum of alleles, and linearly translated to L_∞. The standard deviation of this normally distributed number was adjusted so that the heritability of the L_∞ stayed at the realistic range of 0.2–0.3 (Mousseau and Roff 1987). The vB parameters k and L_∞ are known to have a strong negative correlation, which was estimated by fitting a linear regression model

$$\ln(k) = 1.27 - 0.13 \text{ x } L_\infty$$

with a residual s.d. = 0.30. *C. albula* is known to mature on their second year, so based on the empirical data and previous research (Jensen 1998, Karjalainen *et al.* 2016a) the maturation threshold was set to 67 % of their L_∞ (the mean size of two-year-olds) and no earlier than on their second autumn.

To estimate fecundity (Fig. 2b, II, III), the growth trajectories above and empirical weight data were used to calculate the length–weight relationship. This was done following the method of Ricker (1975):

$$W = a \times L^b,$$

where W = fresh weight in grams, L = length in cm (precision 1 mm), and the parameters a = 7e-06, and b = 2.943. The a and b were calculated from empirical data, and a is a scaling coefficient for the weight at length of the fish, and b is the shape parameter for the body form of the species. Using this length–weight relationship and published data on egg numbers (Karjalainen *et al.* 2016b), a linear model for the weight–fecundity relationship

$$39.06 + 118.47 \text{ x wet mass in grams}$$

was fitted so that as the weight of the fish increases, so does the egg production.

The population component (Fig. 2c, II, III) describes density dependence in the growth of an individual (Marjomäki and Kirjasniemi 1995) along its vB growth trajectory, and in the egg production of each female. The density dependence was continuous, so that as the population density increases, the growth rate and egg production of an individual continuously decrease. As an example, at 85 % of population carrying capacity, the individual's growth rate was reduced to 50 % of that predicted by the vB curve. Both the individual growth rate and the egg production were described through the following equation: growth time available for the individual or the egg production is

$$\frac{e^{\left(a+b*\frac{BM}{CC}\right)}}{\left(1+e^{\left(a+b*\frac{BM}{CC}\right)}\right)},$$

where BM = biomass in units, CC = carrying capacity in units, and a and b parameters describe the slope. These values are arbitrary and chosen to stabilise the population size and to keep it from growing indefinitely.

In II, the survival (Fig. 2d) of an individual from hatching to its second year was set to $P = 0.002$, following empirical estimates from previous works (Marjomäki *et al.* 2014, Karjalainen *et al.* 2016b), and in both II and III the sex of the individual was drawn from a Bernoulli trial with a $P = 0.5$ and the maximum lifetime was set to 7 years following local estimates (Marjomäki and Huolila 2001). In III, survival (Fig. 2g) was used to create oscillation in the population, as oscillating population was the topic of interest. The oscillation was produced by creating a cosine wave with five different amplitudes (0.1, 0.25, 0.5, 0.75, 0.9) and six different wavelengths (2, 4, 6, 8, 10, 12 years) as follows:

$$Oscillation = 1 + a * \cos(t * 2 * \pi / WL),$$

Where t described time, a = the amplitude of the wave, and WL = the wavelength of the wave in years. The cosine function was then multiplied by the baseline survival probability of $P = 0.002$. In total, 30 different oscillation scenarios were produced.

Senescence component (Fig. 2f) was the focus of research in II. For a scenario with no reproductive senescence, the reproductive output was described through the linear function for individual fecundity per gram body weight, as described above. For scenarios with reproductive fecundity, a gonadosomatic index

$$\text{GSI} = (\text{gonad weight} / \text{total tissue weight}) \times 100$$

was calculated based on data from Karjalainen *et al.* (2016b) and extrapolated for age groups 5–7 and used as a proxy for reproductive senescence. The effect of reproductive senescence was standardised so that the GSI for age group 1 was set to be the baseline and was given a fecundity factor of 1. For all the other age groups, the fecundity factor was proportional to that of age group 1, so that for instance, the fecundity factor for age group 4 was calculated as follows:

$$\text{GSI for vendace age group 1} / \text{GSI for age group 4}$$

The linear function for fecundity was then multiplied by the fecundity factor of the age group in question. When no actuarial senescence was modelled, the instantaneous mortality rate was set to $M = 0.257$ for all age groups. When actuarial senescence was modelled, the instantaneous natural mortality rate was set to $M = 0.2$ for two-year-olds, and the added mortality rate for each age group was adjusted to proportion from Marjomäki (2005). The exact values are shown in II (Table 1). The baseline natural mortality was chosen so that at the population level, the natural mortality rate over time was identical in both the scenario with and without actuarial senescence, only the distribution of it across different age groups differed. This allowed for a careful investigation of actuarial senescence while everything else was kept constant. In III, the actuarial and reproductive senescence were incorporated into all the scenarios as described, and no scenario without senescence was run (Fig. 2e).

2.2.1 Simulation design

In both II and III, the initial population size was 2000 individuals, and the initial body size was 4 cm. Neither of these metrics affected the results and were chosen purely based on model optimisation. A burn-in simulation was then ran until the population reached an ecological and evolutionary stability. Then 50–100 stable populations were saved to be used as random starting populations in further simulations. The simulations were then run for 500–600 years during which fishing took place for 100 years. To mimic seining or trawling (II and III), a logistic curve was used as follows

$$r(l) = \left(\frac{\exp(a+bl)}{1+\exp(a+bl)}\right),$$

where $r(l)$ = 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). To mimic gill net fishing (II) a dome-shaped selectivity curve was described as follows:

$$r(l) \sim exp\left(-\frac{(l-\mu)^2}{2\sigma}\right),$$

where $r(l)$ = 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). In all cases, the fishing mortality (F) was set to 0.7 for the fully selected size class (Viljanen 1986). All scenarios were explored through pristine, harvest and recovery phases and were replicated 50–100 times. Data of interest were saved at annual time steps.

2.3 Allometric Trophic Network (ATN)

The ATN model developed by Brose *et al.* (2006), parametrised for Lake Constance by Boit *et al.* (2012), and further expanded to include fish life-history structure by Kuparinen *et al.* (2016) was used to study how the invasive quagga mussel *Dreissena rostriformis bugensis* affects the food web in a lake ecosystem (IV).

The modelled food web includes 33 functional guilds, which are summarised in Table 1 in IV. The functional guilds include particulate and dissolved organic carbon, six functional groups, i.e. guilds of phytoplankton, heterotrophic bacteria, nanoflagellates, five functional groups of ciliates, four functional groups of rotifers, cladocerans, copepods, and perch and whitefish for which five different life stages were modelled. Additionally, to explore how the arrival of quagga mussel affects the food web, a filter feeding quagga mussel was added in the food web. The quagga mussel affects the food web primarily through forming a new feeding link as it feeds on phytoplankton. Given the success of quagga mussel as an invader, it is usually present in high numbers. As a result, its feeding volume is high and therefore the presence of quagga mussel may affect the entire food web through reducing the biomass of primary producers.

The ATN model is based on ordinary differential equations that describe the change in biomass density based on the flow of carbon (µgC m^{-3}) in an ecosystem (Fig. 3).

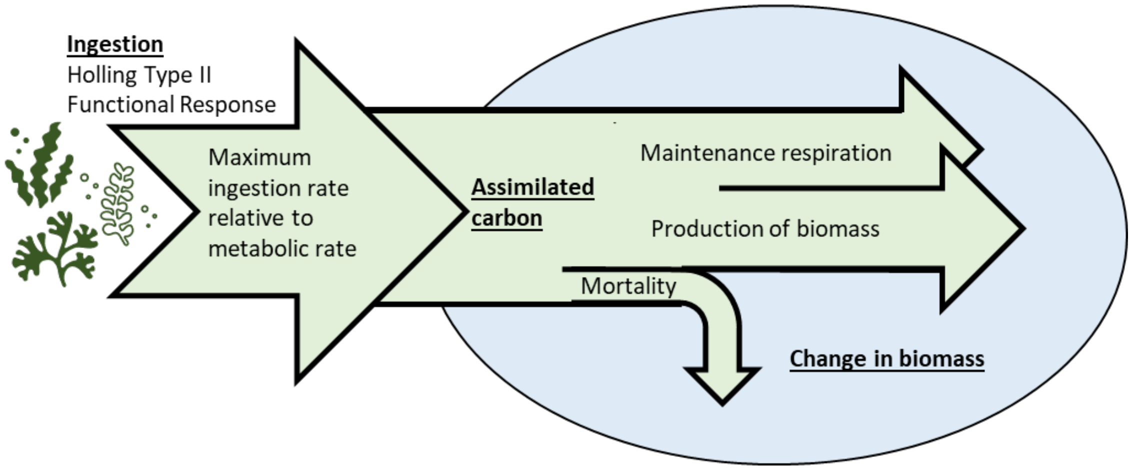

FIGURE 3 Schematic illustration of the carbon flow in the Allometric Trophic Network modelling approach.

The previously developed (Brose *et al.* 2006, Boit *et al.* 2012, Kuparinen *et al.* 2016) model describes the rate of change in the biomass density for producers, consumers other than fishes, and fishes as follows:

The rate of change in the biomass density of producers is described through increase in biomass density due to intrinsic growth and loss in biomass density due to predation by herbivores, as follows

$$\dot{B}_i = r_i B_i G_i(\boldsymbol{B})(1 - s_i) - \sum_j \frac{x_j y_{ji} B_j F_{ji}(\boldsymbol{B})}{e_{ji}},$$

where r_i is the mass-specific intrinsic growth rate of producer i, B_i is the biomass density of producer i in μg of carbon per m^3 of water, $G_i(\boldsymbol{B}) = 1 - (\sum_{j=producers} c_{ij} B_j)/K$ is the limiting factor in the logistic growth of the producers that includes the producer competition coefficients c_{ij} and carrying capacity K. The producer competition coefficient and carrying capacity are shared by all the autotrophs in the model. Further, s_i is the fraction of exudation, x_i is the mass-specific metabolic rate of consumer i based on allometric scaling, y_{ij} is the maximum consumption rate of guild i feeding on guild j, e_{ij} is the assimilation efficiency that describes the loss of biomass through excretion, $F_{ij}(\boldsymbol{B})$ is the is the Holling Type II (Holling 1959a, b) functional response:

$$F_{ij}(\boldsymbol{B}) = \frac{\omega_{ij} B_j{}^q}{B0_{ij}{}^q + d_{ij} B_i B0_{ij}{}^q + \sum_{l=\mathrm{Resources}} \omega_{il} B_l{}^q},$$

where $\boldsymbol{B}$ is the vector of the biomass densities of all herbivore guilds, ω_{ij} is the resource preference parameter for the feeding interaction between consumer i

and its resource guild j, B_j is the biomass density of the resource guild j, $B0_{ij}$ is the "half saturation density" of resource j at which consumer i achieves half of its maximum feeding rate on resource j, when feeding only on resource j in the absence of intraspecific feeding interference, d_{ij} is the coefficient of intraspecific feeding interference of species i feeding on species j, and $q = 1.2$ is the Hill's exponent. The half saturation densities $B0_{ij}$ and intraspecific feeding interference were d_{ij} are determined as in Bland *et al.* (2019).

The rate of change in the biomass density of consumers other than fish is described through gains from feeding, and losses due to the maintenance of bodily functions and getting eaten by predators, as follows:

$$\dot{B}_i = -f_m x_i B_i + f_a x_i B_i \sum_j F_{ij}(\boldsymbol{B}) - \sum_j \frac{x_i y_{ji} F_{ji}(\boldsymbol{B})}{e_{ji}},$$

where f_m is the bodily maintenance through respiration, and f_a is the fraction of assimilated carbon used for the production of biomass.

The rate of change in the biomass density of immature fishes (i.e. larvae and juveniles) is the same as for other consumers:

$$\dot{B}_i = -f_m x_i B_i + f_a x_i B_i \sum_j F_{ij}(\boldsymbol{B}) - \sum_j \frac{x_i y_{ji} F_{ji}(\boldsymbol{B})}{e_{ji}}.$$

The fish reproduction is dependent on the resources available so that the rate of biomass allocated to reproduction ($\dot{B}_i^+$) is determined by the consumption gains and maintenance losses so that when maintenance losses are greater than the consumption gains, reproduction is impaired (Perälä and Kuparinen 2020), as follows:

$$\dot{B}_i^+ = \begin{cases} P_i I_i \cdot \dfrac{\mathcal{G}_i^{\,2}}{2\mathcal{L}_i}, & \mathcal{G}_i < \mathcal{L}_i \\ P_i I_i \cdot \left(\mathcal{G}_i - \frac{1}{2}\mathcal{L}_i\right), & \mathcal{G}_i \geq \mathcal{L}_i \end{cases}$$

Here, P_i is the proportion of mature biomass of adult fish guild i, I_i is a fraction of the mature fish biomass invested in reproduction, $\mathcal{G}_i$ is the consumption gain $f_a x_i B_i \sum_j y_{ij} F_{ij}(\boldsymbol{B})$, and $\mathcal{L}_i$ is the maintenance loss $-f_m x_i B_i$. Because the biomass used for reproduction is no longer available for growth, the rate of change in the biomass density of mature fishes (i.e. all other age groups but larvae and juveniles) is described as follows:

$$\dot{B}_i = -f_m x_i B_i + f_a x_i B_i \sum_j y_{ij} F_{ij}(\boldsymbol{B}) - \dot{B}_i^+ - ES_i B_i,$$

where E is an instantaneous rate of fishing which is detailed below.

In the beginning of the simulation, during growth season $Y = 1$, the biomass vector $\boldsymbol{B}_1(0)$ describes the biomass of all the guilds in equilibrium so that the starting value for $\dot{B}_{Y,i}^+ = 0, \forall i \in \{mature\ fish\ guilds\}, \forall$Y. Each year after the growth season *Y* the fraction of mature fish biomass allocated to reproduction $\dot{B}^{+}_{Y,i}(t^{end})$ makes up the larvae biomass of the next year *Y*+1 for that species so that

$$B_{Y+1,i}(0) = \sum_{a=2}^{4} B^{+}_{Y,i+2a}(t^{end}), \qquad i \in \text{larvae}$$

The initial juvenile, two- and three-year-old (y.o.) fish biomass in year *Y*+1 consist of the biomasses of their previous age classes (i.e. larvae, juvenile, and two-year old) at the end of the growth season in year Y as follows:

$$B_{Y+1,i}(0) = B_{Y,i-2}(t^{end}), \qquad i \in \text{juvenile}, 2, 3\ \text{y.o.}$$

And finally, the oldest age group of 4+ year old fish is made up of the three- and four-year-old fish of the previous year's growth season:

$$B_{Y+1,i}(t^{end}) = B_{Y,i}(t^{end}) + B_{Y,i-2}(t^{end}), \qquad i \in 4\ \text{y.o. and older}$$

The two, three and four + year-old fish in the model were then subjected to size-selective fishing so that the larger fish were targeted with an instantaneous fishing effort *E* = 0.75/90 d (as the growth season is 90 days) and selectivity of 1 for 20 cm long fish, and nominal selectivity for fish smaller than 15 cm or larger than 45 cm.

The quagga mussel was first reported in Lake Constance in 2016, and currently very little data are available on its effects on the lake. This is the first time it has been incorporated into a food web model. Anecdotal notes suggest the quagga mussel is fed on by some species of fish, and in the shallows some birds. However, no reliable data on this exist. Due to the lack of mortality data for quagga mussel, it was modelled with four different instantaneous mortality rates: 0.0, 0.1, 0.2, and 0.3. The scenarios were then compared to a simulated scenario with no quagga mussel present, i.e. the situation before the invasion.

The rate of change in the biomass density ($\dot{B}_i$) of the quagga mussel (denoted as guild *i*) is modelled by considering gains from feeding governed by the Holling Type II Functional Response (Holling 1959a, b) and maximum ingestion rate relative to metabolic rate, and losses due to the maintenance of bodily functions through respiration, production of biomass, and the four different background mortality scenarios, as follows:

$$\dot{B}_i = -f_m x_i B_i + \sum_{j \in \text{Resources}_i} f_a x_i y_{ij} F_{ij}(\boldsymbol{B}) - M_i B_i.$$

Here, Resources_i is the set of indices of the functional groups that quagga mussel feeds upon, and M_i is the added quagga mussel instantaneous mortality rate.

The mass specific metabolic rate x_i of all functional groups is calculated from the carbon body mass m (µg of carbon per individual) using allometric scaling laws

$$x_i = a\left(\frac{m_R}{m}\right)^A,$$

where the allometric scaling constant $a = 0.314$ (Brose *et al.* 2006), the allometric scaling exponent $A = 0.15$ (Killen *et al.* 2007, 2010), and m_R is the carbon body mass of the reference producer guild (Alg1).

The simulation was ran for 300 years, of which the first 100 years were considered as the burn-in period and discarded. The following 100 years the simulated food web was kept in pristine state and the last 100 years fishing took place.

3 RESULTS AND DISCUSSION

3.1 Overview

Using senescence and population oscillations as examples, this dissertation demonstrates a clear feedback loop from life-history traits to population dynamics (II), and vice versa from population dynamics to the evolution of life-history traits (III). The effects were seen both at ecological and evolutionary levels. Individual life-histories are critical in determining population level demographic processes, whether the population is under disturbance or not (II, III). These results can scale up to the ecosystem level, as the presence or absence of a single species can affect the entire ecosystem, and variations in its life-history traits can affect the magnitude of the observed effect (IV).

3.2 The effect of life-history traits on population dynamics (II)

Senescence is an often-ignored life-history trait for populations in the wild, particularly so for fishes, given their tendency for indeterminate growth and therefore the capacity for increasing fecundity with age (Carey and Judge 2000, Reznick *et al.* 2002). However, whether a simulated population experiences senescence or not, affects how they respond to different fishing regimes.

In the initial simulations, the effects of reproductive and actuarial senescence were tested in combination and individually against a scenario with no senescence at all. Likely due to the relatively low reduction in reproductive output with age, the reproductive senescence alone appeared to have only minor effects on any life-history parameters investigated. Consequently, for all the remaining analyses, only two scenarios were used: one with both reproductive and actuarial senescence, and one with no senescence at all. This decision was supported by empirical data as well as literature that suggests that reproductive and actuarial senescence are known to be linked and often occur simultaneously (Kirkwood and Shanley 2010). Additionally, this provided a useful way to explore how the traditional view used in fisheries models, i.e. fish are described as not experiencing senescence at all, compares to biologically more realistic scenario where fish do undergo senescence, as suggested by various studies (Gerking 1957, Comfort 1963, Woodhead and Ellett 1969, Patnaik *et al.* 1994, Woodhead 1998, Beverton *et al.* 2004, Hendry *et al.* 2004, Reznick *et al.* 2004, 2006, Morbey *et al.* 2005, Carlson *et al.* 2007, Terzibasi Tozzini *et al.* 2013, Uriarte *et al.* 2016, Benoît *et al.* 2018, Žák and Reichard 2020), many of which focus on commercially harvested species such as salmon, mackerel, herring, and anchovy.

Generally, senescence resulted in a lower asymptotic length, coupled with higher intrinsic growth rate and evolution towards younger age at maturation (Fig. 4 and 5 in II). These results are similar to those often reported for FIE (Heino *et al.* 2015), suggesting both extrinsic (fishing) and intrinsic (actuarial senescence) mortality have similar consequences in terms of life-history trade-offs between increased investment in growth and/or reproduction early in life and decreased survival later in life. As such, it could be speculated that FIE indirectly promotes the evolution of senescence through evolution towards smaller size and age at maturity and consequently decreased survival later in life. Indeed, the natural mortality rates of fish are thought to have increased over the past decades, particularly in fished populations (Jørgensen and Holt 2013).

3.2.1 The evolutionary effect of senescence in response to fishing

Importantly, the presence or absence of senescence affects how the population responds to different fishing regimes. For trawling, described here by a logistic selection curve, the evolutionary response by the senescent scenario was smaller than that of the non-senescent scenario, that is, the decline in asymptotic length in response to trawling was less for the senescent than the non-senescent scenario (Fig. 4a in II). It could be that senescence (intrinsic mortality) “pre-adapts” the population to the consequences of trawling (extrinsic mortality). The evolutionary pressure for change for these already smaller individuals that mature at a younger age and smaller size, may not be as high as for the non-senescent populations.

In contrast, gillnetting, which has a dome-shaped retention curve, brought about an opposing response, and the senescent scenario now had a stronger evolutionary response to fishing than the non-senescent scenario (Fig. 4b in II). The non-senescent scenario has a higher number of older and larger individuals to start with. Gillnetting allows for the escape of some of the larger individuals which the non-senescent population has more of, so as a result a higher asymptotic length could be maintained. Vice versa, the higher number of smaller individuals in the senescent scenario, and the lower retention of smaller individuals promotes selection towards smaller size. These contrasting evolutionary responses of senescent and non-senescent scenarios to different types of fishing highlight the importance of carefully considering the life-history traits of the species under management.

3.2.2 The ecological effects of senescence in response to fishing

Apart from the evolutionary response to fishing, the scenarios with and without senescence differed in their ecological response. This is expected, as evolutionary and ecological process are not separate. The carrying capacity was the same in both scenarios, so therefore the senescent scenario where the fish size on average was smaller, could maintain a higher number of fish throughout pristine, harvest and recovery phases in both trawling and gillnetting scenarios (Fig. 3e, f in II). In the trawling scenario, the same applied for biomass (Fig. 3c, 4c in II). It is likely, that the life-history trade-offs between lower survival later in life (actuarial senescence) and higher reproductive effort earlier in life explain the higher biomass for the senescent scenario in the trawling scenario. This reflects the "pre-adaptation" seen in the asymptotic length of the senescent population in the trawling scenario. The biomass trend was similar but not as strong in the gillnetting scenario (Fig. 4d in II), likely facilitated by the dome-shaped retention curve of gillnetting which allows for the escape of the larger fish, and the increased reproduction of younger and smaller fish.

3.3 Population dynamics feed back to life-history evolution (III)

Population oscillations present, by their very definition, cyclical changes in the population density over time. While the effects of population density on fish body size, for instance, have been studied (Bouffet-Halle *et al.* 2021), the effects of fluctuating population, a common occurrence in nature, are poorly understood. This chapter demonstrates how different wavelengths and amplitudes yield different ecological and evolutionary results, and that these results are intimately connected to an important life-history character: the maximum lifespan of an individual (in this case, seven years).

3.3.1 The evolutionary signature of population dynamics

Fluctuations with a wavelength shorter than the maximum lifespan of the fish yielded clear evolutionary differences in the asymptotic length of the fish. The wavelengths of 4 and 6 years revealed an evolution toward higher asymptotic length with increasing amplitude (Fig. 2 in III), while a two-year oscillation caused a reverse trajectory: evolution toward lower asymptotic length with increasing amplitude. These results are likely explained by the number of juveniles (< 1-year-olds) and recruits (1–2-year-olds) that largely control the population density. When the oscillation was 4 or 6 years, sparser years occurred in between, allowing the fish to grow large in the absence of density dependent competition (Cyr *et al.* 1997, Lorenzen and Enberg 2002, Hazlerigg *et al.* 2012). The two-year oscillation, however, maintained a relatively constant density as a year with few juveniles was compensated by the previous year with many (Fig. 7 in III) juveniles. As a result, the increasing amplitude meant that the density and density dependent competition for energy increased too, and therefore the asymptotic length evolved shorter with increasing amplitude.

3.3.2 The ecological consequences of population dynamics

Once the wavelength exceeded the maximum lifespan of the individual, the evolutionary differences largely diminished. Instead, the effects were ecological, in the form of biomass oscillation (fig. 5 in III). Increasing wavelength and amplitude resulted in increasing oscillation during pristine, harvest and recovery phases. However, the two-year cyclicity stood out with the contrasting evolutionary direction. While during harvest in all other scenarios there was an inverse relationship between amplitude and biomass, reflecting the changes in asymptotic length, the two-year cyclicity yielded a positive correlation between amplitude and biomass. This is explained by the same phenomenon as was seen in II, where the smallest fish were strong at maintaining a high biomass due to the associated early reproduction. This was further supported by the fish with the mean size asymptotic length showing the highest fitness in terms of LRO (van Daalen and Caswell 2017), suggesting that indeed life-history traits are optimised rather than maximised (Enberg *et al.* 2012).

3.4 The interaction between an individual and the ecosystem (IV)

The quagga mussel (*Dreissena rostriformis bugensis*) is one of the most impactful and notorious aquatic invaders in the world (Higgins and Vander Zanden 2010). Predicting its impacts on aquatic ecosystems could help us mitigate the negative effects it may cause, or at least help us understand how to best live with it. The ATN model proved successful in exploring the mechanistic effects an invading species may cause in the structure and dynamics of a food web.

The addition of quagga mussel in the food web parametrised for Lake Constance revealed a bottom-up effect that propagated through all the trophic levels investigated (Fig. 1 in IV). To understand the dynamics within the food web, the changes were investigated as relative changes in the proportion of the total food web biomass, in other words, how much did the proportion of each investigated guild change in the total food web as a result of the addition of the invader.

The lower the quagga mussel mortality rate, the higher its biomass was in the food web. Consequently, the magnitude of all further results inversely correlated with the mortality rate of the quagga mussel, demonstrating how a single life-history trait of a species can influence the entire ecosystem. As quagga mussel feeds on phytoplankton, a decline in the phytoplankton biomass proportional to the total food web biomass was both expected and observed. While the consumer biomass increased, the increase was caused by the quagga mussel alone. If the quagga mussel was excluded from the consumers, the consumer biomass declined too. Importantly, the effect of quagga mussel was also reflected at the highest trophic levels with declines in the proportion of whitefish and perch biomasses, even when they were not fished. Whitefish and perch are commercially important species in Lake Constance (Baer *et al.* 2016) (as well as in many other lakes). In the food web model, whitefish and perch were subjected to fishing, and fishing appeared to amplify the effects of the quagga mussel invasion in the food web, so that the decline in producer biomass was larger when the system was fished. Additionally, the biomass of quagga mussel increased when the food web was fished. The change in consumer, whitefish and perch biomass was also amplified, but this was due to the removal of fish.

The changes in the biomasses were also accompanied with a slight decline in the food web connectance. Connectance is a food web property that describes the fraction of all the possible links between guilds that are realised, and it shifted from 0.148 (before invasion) to 0.145 (after invasion). While the change is small, it is an important reminder of the structural changes that one species can cause in a food web. Generally, lower connectance is associated with higher vulnerability to future invasions (Romanuk *et al.* 2009). However, food webs with low connectance tend to lose fewer species to extinction as a result of invasions, while food webs with higher connectance, although theoretically harder to invade, suffer more in terms of biodiversity loss as a result of non-native invasions (Romanuk *et al.* 2017). The connectance in the modelled food web remains relatively high. Therefore, once an invader has managed to settle in, it is likely that its impact on the food web structure is high. These results, together with the known high number of invasive species in Lake Constance (Gergs and Rothhaupt 2015, Clusa *et al.* 2021) alert to the possibility of an invasional meltdown. Lake Constance may currently be undergoing or be on the brink of an invasional meltdown.

Food web modelling is a promising tool to study the ecosystem-wide impacts of invasive species. However, making predictions about the ecosystem-wide impacts of invasive species based on food web models currently requires further advances in methodologies. Such advances include the addition of more biotic and abiotic factors in the model, and ways to analyse the resulting complex data. Currently, no predictions should be made solely based on the food web results, given the simplicity of the model. However, the food web models provide a way to illuminate the mechanisms of how the invader can affect the ecosystem, as well as pinpoint areas that more data are needed for. Combined with high-resolution empirical data, ecological networks can help us gain a full picture of how different levels of biological organisation interact.

3.5 Conclusion

This dissertation aimed to explore the fundamental links between life-history traits, population dynamics, and ecosystems. Using body size, senescence, population oscillations, and invasive species as examples, I demonstrate that while life-history traits can significantly influence population dynamics (I, II), population dynamics feed back to life-histories and are capable of leaving a strong evolutionary signature in the population (III), and a single species with a varying life-history trait can affect the ecology of the entire ecosystem (IV). Improving our understanding of this interplay between life-histories, population dynamics and ecosystems equips us to better manage our shared natural resources.

While it is well known that different levels of biological organisation interact in complex ways (Elser *et al.* 2000, Brown *et al.* 2004, Woodward *et al.* 2010), this dissertation draws attention to often-ignored natural phenomena within those links. Senescence is a wide-spread trait across taxa (Nussey *et al.* 2013) and was first documented in fishes in the 1950's (Gerking 1957), yet fisheries science literature as well as population biological literature almost entirely ignore the presence of senescence in fishes, and the idea that it could reflect to population dynamics. Article II demonstrates that senescence does indeed reflect to the evolutionary trajectory of the asymptotic length in the population, as well as how the population responds to different fishing gear.

While senescence was associated with declining asymptotic length, article I describes how fish body size can affect populations and ecosystems, and article III shows a clear feedback loop from population oscillations to the evolution of asymptotic length. These results describe life-histories and populations as sensitive entities that are intimately linked. Even a small change at one level (II) can reflect to another level of biological organisation and back (III). The understanding that natural population oscillations can feed back to the evolutionary trajectories within a population has important implications for fisheries science, as fishing has been demonstrated to amplify population fluctuations (Anderson *et al.* 2008). Whether the feedback loop between natural or fishing induced oscillations and body size is stabilised by some other factor, or whether it is a snowball effect that pushes evolutionary trajectory in one direction is a question for future research.

While these mechanistic models allow for a theoretical investigation of the interplay between life-histories and population dynamics and are vital in advancing the fundamental eco-evolutionary theory, it is important to note when thinking about applications that species do not exist alone, but rather, in a complex ecosystem. For instance, in II and III, fish with medium and small body size gained a fitness advantage in the form of earlier reproduction. However, in an ecosystem context, smaller individuals would likely be more vulnerable to predators and therefore natural selection could operate in an opposite direction, as discussed in I. This is particularly true in aquatic ecosystems where many predators are gape-limited, and it is therefore beneficial to grow big and grow fast to reach size refuge (Urban 2007).

Further, the effects of senescence and population fluctuations were investigated in a single species model. Given the wide-spread existence of both senescence (Nussey *et al.* 2013) and population fluctuations (MacArthur 1955, Shelton and Mangel 2011) in nature, exploring their links to the wider ecosystem could give us a better understanding of their role in nature and illuminate any potential feedback links. Both anecdotal conversations with fisheries scientists and literature often suggest that senescence is irrelevant for fish populations, as fishes are caught before senescence commences. However, this view ignores the very core of this dissertation, which is describing the links between different levels of biological organisation, ecosystem included. Not all fish species are heavily fished (Melnychuk *et al.* 2021), some are not at all as they are not considered suitable food, but they still play an important role in the entire ecosystem function, and may well undergo senescence. As such, they may indirectly affect other species too, including those fished, making senescence relevant for every species. In a similar manner, fluctuations in populations are wide-spread in nature, and predator–prey fluctuations, whether in or out of synchrony are well studied (Small *et al.* 1993, Bjørnstad *et al.* 1999). However, the role of population fluctuations in the wider ecosystem context is poorly understood and require further studies. Importantly, the ecosystem-wide outlook highlights an important message that whether a species is an important species for fisheries, should not determine whether its biology and ecology are important to study. Species important to fisheries do not exist alone but rely on a healthy ecosystem.

Taking the ecosystem context into account, IV investigated the role that a single, non-native, invading species can play in an ecosystem food web. The theoretical exploration of an invasive species in a food web model demonstrated a bottom-up effect of declining biomass that extended all the way from primary producers to the highest trophic level. In the model, the invading species had one life-history trait, natural mortality rate, that varied, and the variation in the mortality rate extended its effects to all other trophic levels investigated. While food web models are useful for illuminating the ecosystem-wide mechanisms an invader, or any other change in the ecosystem, can cause, they too, have limitations. Like the mechanistic model used for studying life-history evolution and population dynamics, the ATN-model used to study food web dynamics is a simplistic presentation of the reality, and the ATN-model, for instance, currently lacks abiotic drivers. Also, the model uses functional groups which necessarily leaves out many species and their complex interactions ranging from predator–prey dynamics to parasitism, mutualism, competition, territorialism, sexual selection, as well as evolution. However, to capture an ecosystem-wide image of how one species or trait can affect communities, populations and ecosystems, food web modelling is one of the only methods available at the moment.

In biological research each method has shortcomings. While modelling may give an overly simplistic image, the challenge with laboratory work is how to generalise it to the "real world", and empirical work on the other hand often focuses on one question only, missing the forest from the trees. Instead of focusing on the shortcomings, it is important to understand and acknowledge the shortcomings, so that we can then use complementary methods to produce biologically relevant high-quality data at high and low resolutions to gain a holistic understanding of the nature around us.

The sincere hope is that by gaining a deeper understanding of how life at different levels of biological organisation is tied together, we will be in a better position to manage and protect our environment. Only by understanding, may we successfully conserve our common nature, and thus leave it in a better condition for those who come after us.

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YHTEENVETO (RÉSUMÉ IN FINNISH)

Kalojen elinkierto-ominaisuuksien, populaatiodynamiikan ja ekosysteemin vuorovaikutus

Maapallon pinta-alasta yli 70 % on veden peitossa. Akvaattiset ekosysteemit eli meret, järvet ja joet ovat elintärkeitä maapallon ilmaston säätelyssä. Ne tarjoavat monenlaisia ekosysteemipalveluita, kalastusta, ruoan tuotantoa, rantaviivojen suojelua sekä monenlaisia virkistymismahdollisuuksia uimareille, veneilijöille, sukeltajille ja muille luonnosta nauttijoille. Akvaattisten ekosysteemien biologinen monimuotoisuus on kuitenkin viime vuosikymmeninä heikentynyt ennennäkemättömällä tavalla. Tämä on ehkä selkeimmin nähtävissä monien kalakantojen katastrofaalisena romahtamisena sekä kalasaaliiden heikkenemisenä.

Perinteinen kalastuksentutkimus nojautuu kompensoivan tiheysriippuvuuden periaatteeseen, jonka mukaan harvaksi kalastetut kalapopulaatiot kasvavat nopeasti, kun kalastus lopetetaan. Kalapopulaatiot ympäri maailmaa kuitenkin osoittavat, että näin ei ole käynyt. Atlantin turska on tästä kuuluisa esimerkki. Turskakannat Kanadan itäisellä rannikolla romahtivat 1990-luvulla, eivätkä ole vuosikymmenien kalastuskiellosta huolimatta palautuneet ennalleen. Syyt tälle ovat moninaisia. Tekijät, kuten veden lämpötilan muutos, turskan saalistus hylkeiden taholta, kalastuksen aiheuttamat elinkierto-ominaisuuksien muutokset sekä paikoittain jatkunut kalastus selittänevät osaltaan, miksi populaatio ei ole palautunut ennalleen.

Moninaisten syiden kirjo myös osoittaa aukkoja biologisessa ymmärryksessämme, joihin tämä väitöskirja pyrkii tuomaan lisää tietoa. Kuinka elinkierto-ominaisuudet, kuten sukukypsyysikä, elinikä, lisääntymiskyky ja luonnollinen kuolevuus vaikuttavat populaatiotason ilmiöihin, kuten kalapopulaation biomassaan? Entä kuinka populaatiotason ilmiöt, kuten vaihtelut biomassassa, vaikuttavat elinkierto-ominaisuuksien evoluutioon? Ja kuinka nämä yksilö- ja populaatiotason muutokset ilmenevät ekosysteemin tasolla?

Vanheneminen (seneskenssi) on ilmiö, jota biologiassa kuvataan lisääntymiskyvyn laskulla ja luonnollisen kuolevuuden nousulla. Kalastusta ja sitä, kuinka paljon voimme kalastaa kestävästi, tutkitaan matemaattisilla malleilla, jotka kuvaavat kalapopulaation vaihtelua. Tällä hetkellä nuo mallit eivät ota huomioon kalojen vanhenemista. Tämä tarkoittaa sitä, että mallissa oletetaan, että kalan todennäköisyys kuolla luonnollisista syistä pysyy koko ajan samana tai pienenee iän (eli koon) myötä, ja kalan lisääntymiskyky kasvaa kalan koon (eli iän) mukana, eikä missään vaiheessa laske vanhenemisen vuoksi. Kalojen seneskenssille on kuitenkin empiiristä tutkimusnäyttöä jo 1950-luvulta saakka. Tässä väitöskirjassa tutkittiin yksilöpohjaisella eko-evolutiivisella mekanistisella mallilla sitä, miten kalan vanheneminen näkyy paitsi populaatiotasolla myös kalan evoluution kannalta. Mallissa käytettiin esimerkkilajina muikkua.

Mallissa kaloille, joiden elinkierto-ominaisuuksiin kuului vanheneminen, kehittyi evoluution seurauksena pienempi teoreettinen maksimikoko kuin niille, joille vanhenemista ei mallinnettu. Eliön koko on keskeinen tekijä ekologisissa ja evolutiivisissa prosesseissa, sillä se vaikuttaa mm. lisääntymiskykyyn, seksuaalivalintaan, kilpailukykyyn reviireistä ja ruoasta sekä alttiuteen jäädä saaliiksi. Kalastuksen kannalta vanheneminen vaikutti siihen, kuinka kalapopulaatio vastaa kalastuksen kokovalikoivuuteen. Kun mallinnettu vanheneva kalapopulaatio altistettiin troolaukselle, populaation evolutiivinen ja ekologinen vaste koon ja biomassan suhteen oli pienempi kuin ei-vanhenevan. Kun taas kalastus tapahtui verkoilla, oli vanhenevan populaation evolutiivinen vaste suurempi. Nämä tulokset osoittavat, että se, oletammeko kalan vanhenevan biologisessa mielessä, vaikuttaa siihen, kuinka se reagoi kalastukseen.

Siinä missä elinkierto-ominaisuus, kuten vanheneminen, voi vaikuttaa kaloihin populaatiotasolla, myös populaatiotason tapahtumat voivat vaikuttaa yksilöiden elinkierto-ominaisuuksiin ja evoluutioon. Yksilöiden kasvun ja lisääntymiskyvyn tiheysriippuvuusteoria on tästä hyvä esimerkki. Syyt kalapopulaatioiden tiheyden vaihtelun taustalla ovat kiinnostaneet kalastajia ja tutkijoita vuosisadan verran. Populaatioiden tiheyden vaihtelun syitä on tutkittu paljon, mutta ymmärrys siitä, mitä tiheyden vaihtelu aiheuttaa itse kalapopulaatiolle, on vähäinen. Tässä väitöskirjassa asiaa tutkittiin matemaattisen mallinnuksen avulla.

Käyttäen edelleen muikkua esimerkkilajina kalapopulaatioiden tiheyden vaihtelulle mallinnettiin 30 eri skenaariota, niin että vaihtelun aallonpituus oli pienimmillään 2 ja suurimmillaan 12 vuotta ja amplitudi vaihteli 10–90 % biomassan keskiarvon ylä- ja alapuolella. Tärkeäksi tekijäksi osoittautui kalan maksimielinikä. Kun aallonpituus oli lyhyempi kuin kalan eliniän pituus, aiheutti se merkittäviä muutoksia kalan maksimikoon evolutiiviseen kehitykseen. Kehityksen suunta riippui aallonkorkeuden ja -pituuden yhdistelmästä. Kun aallonpituus puolestaan oli pidempi kuin kalan eliniän pituus, seuraukset näkyivät lähinnä ekologisena vaihteluna kalojen biomassassa. Nämä tulokset osoittavat tärkeän, ennen tuntemattoman linkin kalan elinkierto-ominaisuuden (maksimielinikä) ja populaatiodynamiikan välillä. Ottaen huomioon, että kalastuksen tiedetään vahvistavan kalojen tiheyden vaihtelua, on tämän linkin tunteminen erityisen tärkeää, jotta voimme arvioida, kuinka muutokset populaation tiheydessä vaikuttavat elinkierto-ominaisuuksiin ja kuinka elinkierto-ominaisuuden puolestaan heijastavat takaisin populaatiotason ilmiöihin.

Koska luonnossa lajit ovat vuorovaikutuksessa keskenään saalistuksen, kilpailun, parasitismin, mutualismin ja muiden biologisten ilmiöiden kautta, on tärkeää tarkastella eliöiden asemaa kokonaisessa ekosysteemissä. Ravintoverkon mallinnus tarjoaa tähän nykyisellään yhden harvoista tavoista, joilla voidaan tutkia eri lajien välisiä yhteyksiä yhdessä ekosysteemissä. Tässä väitöskirjassa yksittäisen lajin ja sen elinkierto-ominaisuuksien vaihtelun merkitystä ekosysteemissä tutkittiin vieraslajin avulla. Quagga-simpukka on yksi maailman tehokkaimmin leviävistä makean veden vieraslajeista. Se on peräisin Ponto-Kaspian alueelta ja on levinnyt ihmistoiminnan seurauksena Pohjois-Amerikassa ja Euroopassa moniin järviin ja aiheuttanut merkittäviä muutoksia järvien ekosysteemeissä. Bodenjärvi sijaitsee Saksan, Itävallan, ja Sveitsin rajalla, ja quagga-simpukka havaittiin siellä ensimmäisen kerran vuonna 2016. Vuonna 2021 sen tiheys on arviolta 5 000 yksilöä m^{-2}.

Simpukan vaikutusta järviekosysteemiin tutkittiin Bodenjärven ravintoverkkomallin avulla. Koska simpukan luonnollisesta kuolevuudesta Bodenjärvessä ei ole vielä tutkimustietoa, kuolevuudelle annettiin mallissa eri vaihtoehtoja niin, että todellinen kuolevuus todennäköisesti osuu mallinnettujen kuolevuuksien suuruusluokkaan. Quagga-simpukka syö perustuottajia eli leväplanktonia erittäin tehokkaasti, joten oletuksena oli, että simpukan vaikutus ekosysteemiin olisi laaja. Malli paljasti alhaalta ylös kulkevan vaikutuksen kaikkien ekosysteemin trofiatasojen läpi niin, että simpukkamäärän kasvaessa biomassa väheni kaikilla tasoilla, mukaan lukien mallin huippusaalistajat eli kalat. Ahven ja siika ovat kalastukselle tärkeitä lajeja Bodenjärvessä, ja niiden kalastus vahvensi simpukan vaikutusta entisestään. Malli demonstroi, kuinka yksi laji ja vaihtelut sen elinkierto-ominaisuudessa (kuolleisuudessa) voivat ulottaa vaikutuksensa koko ekosysteemiin.

Vaikka mallit ovat aina yksinkertaistuksia monimutkaisesta biologisesta todellisuudesta, ne antavat mahdollisuuden tutkia ekologisia ja evolutiivisia mekanismeja sekä kysymyksiä, joiden tutkiminen ei muutoin olisi mahdollista. Tuloksia on aina tulkittava muun tutkimustiedon valossa, mikä korostaakin erilaisten tutkimusmetodien tärkeyttä. Erilaiset metodit kuvaavat biologisia ilmiöitä aina hieman eri näkökulmasta ja eri resoluutiolla. Kun niistä saadut tulokset yhdistetään, pystytään muodostamaan paras mahdollinen yleiskuva tutkitusta ilmiöstä.

Tämän väitöskirjan tutkimustulokset syventävät nykyistä ymmärrystämme siitä, miten yksilöiden elinkierto-ominaisuudet, populaatiot ja ekosysteemit kietoutuvat yhteen. Oli kyse sitten kalastuksesta tai vesiluonnon suojelusta, on tärkeää, että perustamme päätöksemme ja toimintamme tutkittuun tietoon ja parhaaseen mahdolliseen ymmärrykseen ekosysteemien toiminnasta. Vain ymmärtämällä ekosysteemien toimintaa voimme suojella niitä ja jättää ne aina vain parempaan kuntoon seuraavia sukupolvia varten.

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ORIGINAL PAPERS

I

SIZE DOES MATTER — THE ECO-EVOLUTIONARY EFFECTS OF CHANGING BODY SIZE IN FISH

by

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REVIEW

Size does matter — the eco-evolutionary effects of changing body size in fish

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Abstract: Body size acts as a proxy for many fitness-related traits. Body size is also subject to directional selection from various anthropogenic stressors such as increasing water temperature, decreasing dissolved oxygen, fisheries, as well as natural predators. Changes in individual body size correlate with changes in fecundity, behaviour, and survival and can propagate through populations and ecosystems by truncating age and size structures and changing predator–prey dynamics. In this review, we will explore the causes and consequences of changing body size in fish in the light of recent literature and relevant theories. We will investigate the central role of body size in ecology by first discussing the main selective agents that influence body size: fishing, increasing water temperature, decreasing dissolved oxygen, and predation. We will then explore the impacts of these changes at the individual, population, and ecosystem levels. Considering the relatively high heritability of body size, we will discuss how a change in body size can leave a genetic signature in the population and translate to a change in the evolutionary potential of the species.

Key words: body size, fisheries, environmental change, evolution, life-history trait, plasticity.

Résumé : La taille corporelle agit comme un indicateur de nombreux traits reliés à la capacité d'adaptation. La taille corporelle est aussi sujette à une sélection directionnelle émanant de différents facteurs de stress anthropiques tels que l'augmentation de la température de l'eau, la diminution de l'oxygène dissous, les pêcheries, ainsi que les prédateurs naturels. Les changements de la taille corporelle individuelle sont corrélés avec des changements de fécondité, de comportement et de survie, et ils peuvent se propager à travers les populations et les écosystèmes en tronquant des structures d'âge et de taille et en modifiant la dynamique prédateur–proie. Dans cet article de synthèse, les auteurs exploreront les causes et les conséquences des changements de la taille corporelle chez le poisson à la lumière de la littérature récente et des théories pertinentes. Ils examineront le rôle central joué par la taille corporelle en écologie en discutant d'abord des principaux agents de sélection qui influencent la taille corporelle : la pêche, l'augmentation de la température de l'eau, la diminution de l'oxygène dissous et la prédation. Ils exploreront ensuite les impacts de ces changements au niveau de l'individu, de la population et de l'écosystème. Considérant l'héritabilité relativement élevée de la taille corporelle, les auteurs discuteront comment un changement de taille corporelle peut laisser une signature génétique dans la population et se traduire par une modification du potentiel d'évolution de l'espèce. [Traduit par la Rédaction]

Mots-clés : taille corporelle, pêcheries, changement environnemental, évolution, trait du cycle biologique, plasticité.

Introduction

Historically, before the influence of modern humans and industrialization, most species responded to the changing climate by shifting ranges (Cabanne et al. 2016). In the present day, as anthropogenically driven, rapidly changing climate is accompanied by a range of other selective agents, biological responses are likely to be more complex (Parmesan et al. 2000). Threats such as increasing temperature (Barnett et al. 2005), acidification (Orr et al. 2005), reduced dissolved oxygen (Garcia et al. 2005), pollution (Moore 2008), overfishing (Jackson et al. 2001), and habitat destruction (Nordhaus et al. 2018) are posing serious challenges to our oceans, often acting in concert. To survive the change, species have three options: disperse to a more suitable habitat, adjust through phenotypic plasticity, or adapt through evolutionary change. How well an organism can respond to a change depends largely on its plasticity and evolutionary potential (Hoffmann and Willi 2008).

Conventionally, research has focused on either ecological responses such dispersal or phenotypic plasticity or evolutionary responses such as genetic adaptation, and this distinction was based on the assumption that ecological and evolutionary responses occur at vastly different time scales. However, it is now widely documented that evolutionary change can occur over ecologically relevant time scales (Stockwell et al. 2003; Carroll et al. 2007) and that these processes are not independent of each other (Hanski 2012). Consequently, to fully understand the ecological and evolutionary processes in nature, we need to move beyond just documenting the ecological or evolutionary change towards exploring the impact of the change in a wider concept.

Many natural and anthropogenic stressors are inducing selection pressure on a key ecological trait: the body size of an organism. Body size, like many other traits, has both plastic (Crozier and Hutchings 2014) and genetic (Mousseau and Roff 1987; Garcia De Leaniz et al. 2007) components. It acts as an easy-to-measure proxy for many life-history characters such as lifetime reproductive success (Barneche et al. 2018), size and age at maturity (Jensen 1996), and survival (White et al. 2013). Many functions in an organism's life, including energetics, resource use, susceptibility to

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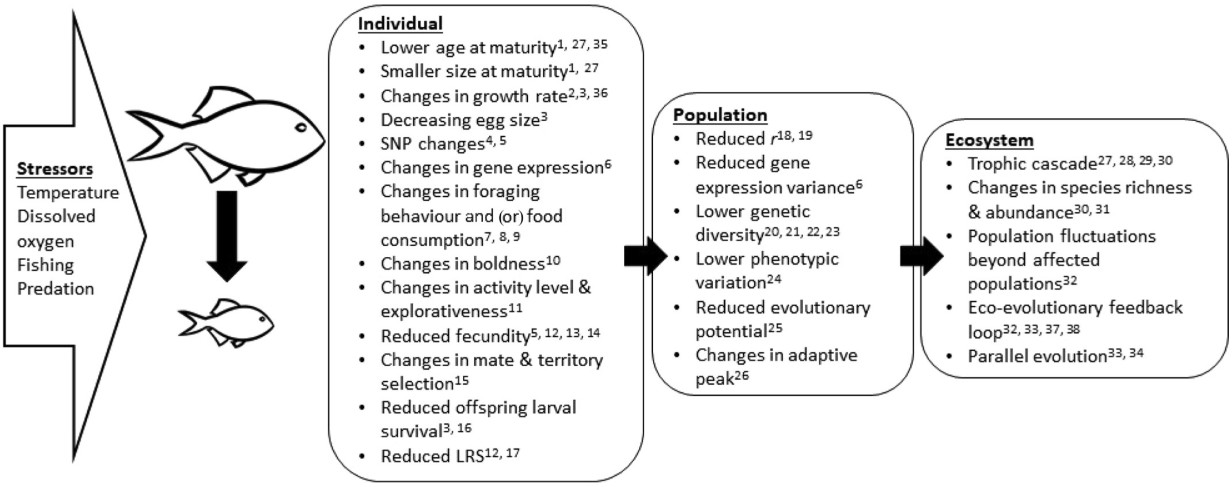
Fig. 1. A summary of how different external stressors may affect fish body size and how the change in body size or associated life-history traits may propagate through different levels of biological organization. The superscript denotes an example study on the topic: (1) Hunter et al. 2015; (2) Nusslé et al. 2009, 2011; (3) Conover and Munch 2002; (4) van Wijk et al. 2013; (5) Uusi-Heikkilä et al. 2015; (6) Uusi-Heikkilä et al. 2017; (7) Walsh et al. 2006; (8) Salinas et al. 2012; (9) Biro et al. 2004, Biro and Post 2008; (10) Uusi-Heikkilä et al. 2008; (11) Uusi-Heikkilä et al. 2015; (12) Barneche et al. 2018; (13) Dick et al. 2017; (14) Savage et al. 2004; (15) Fleming and Gross 1994; (16) Berkeley et al. 2004; (17) Hixon et al. 2014; (18) Audzijonyte and Kuparinen 2016; (19) Dunlop et al. 2015; (20) Hauser et al. 2002; (21) Pinsky and Palumbi 2014; (22) Hutchinson et al. 2003; (23) Jakobsdóttir et al. 2011; (24) Olsen et al. 2009; (25) Reznick et al. 1997; (26) Edeline et al. 2007; (27) Olsen et al. 2004; (28) Frank et al. 2005; (29) Ohlberger et al. 2017; (30) Shackell et al. 2009; (31) Daufresne et al. 2009; (32) Kuparinen et al. 2016; (33) Becks et al. 2012; (34) Elmer and Meyer 2011; (35) Heins et al. 2016; (36) Reznick et al. 2001; (37) Persson et al 1996; and (38) Nilsson et al. 2019. Abbreviations: SNP, single nucleotide polymorphism; LRS, lifetime reproductive success; r, intrinsic rate of per capita population growth rate.



predators, species interactions, and several population parameters, are functions of its body size (Werner and Gilliam 1984).

The question of whether organisms have the evolutionary potential to respond to anthropogenic stressors fast enough is becoming increasingly more important. Unlike terrestrial organisms, fishes, being immersed in water, are in intimate contact with their physical and chemical environments, making them particularly sensitive to any changes in their environment (Cossins and Crawford 2005). Compared with air, oxygen availability in the water is much lower, and due to the higher viscosity of water, more effort is needed to utilize it (Verberk et al. 2011). Increasing water temperature and decreasing oxygen content, even without the pressure from fisheries, have been predicted to lead to sharp declines in fish body sizes (van Rijn et al. 2017). Regardless of the cause, changes in body size occur at the level of an individual and scale up to population, community, and ecosystem levels (Pörtner 2002; Pörtner and Peck 2010). The nature of the change, whether it is plastic or genetic, determines whether the change is likely to be reversible or lead to adaptation. The more the trait under selection changes and the more links there are between the trait variation and ecological interactions, the more important the role of contemporary evolution to ecological processes becomes (Hairston et al. 2005).

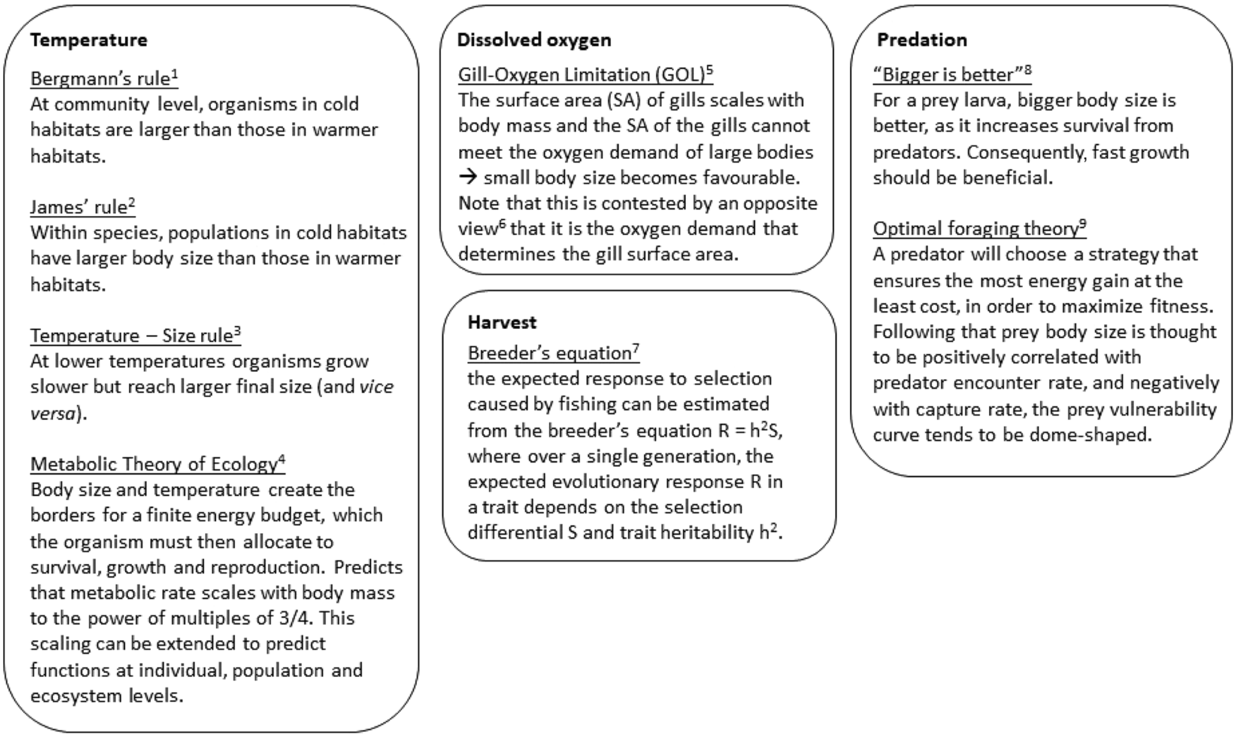
Here, we review the recent literature on the causes and consequences of changing body size in fish and its links to ecological and evolutionary processes. While there is a large selection of important and relevant literature focusing on body size in fish (Uusi-Heikkilä et al. 2008; Devine et al. 2012; Enberg et al. 2012; Audzijonyte et al. 2013; Heino et al. 2013, 2015; Diaz Pauli and Heino 2014; Diaz Pauli and Sih 2017; Hollins et al. 2018), much of it tends to focus on fishing as a selective agent. We believe that it is necessary to expand our investigations into how different selective agents (i.e., not only fishing) affect body size, a key measure in ecology and a central theme in several ecological theories. To achieve this, we draw attention not only to fishing, but also to what we consider to be the main (or at least relatively well-studied) abiotic factors, i.e., increasing temperature and dissolved oxygen, as well as a major biotic factor, i.e., predation, in driving selection on body size. Other agents exist as well, e.g., pH, water chemistry, primary production, light, and mate choice, and more studies are needed to understand their roles in selection. Additionally, there is currently a knowledge gap on how different selection agents or stressors interact, and we call for more research effort on the synergistic effects of multiple stressors. It should also be noted that a single selective agent may select for various traits such as body size, growth rate, and natural mortality schedules. Most of the current literature is descriptive and fails to consider the far-reaching effects of changing body size. Given the rapidly changing environment and the various selection pressures imposed by it, it is crucial to investigate the role of changing body size in a wider perspective beyond fisheries science to understand how those changes may affect the entire ecosystem over ecological and evolutionary time.

With body size, we refer to metrics such as asymptotic length, size-at-age, body mass, and growth rate. Although size-at-age is a state, and growth is a process, these metrics are closely linked, as growth is necessary to reach a certain size (Enberg et al. 2012). Also, size-at-age can be considered a proxy for growth (Heino et al. 2015). We will first provide an overview of the main ecological theories behind the mechanistic functioning of different selective agents, namely, increasing temperature coupled with decreasing dissolved oxygen, fishing, and predation. We will then use examples from relevant literature to discuss how changes in body size can influence other life-history traits of an individual fish and propagate through different levels of biological organization through to population and ecosystem levels at ecologically and evolutionarily relevant time scales (Fig. 1).

The ecological theories behind different stressors as selection agents

In this section, we summarize the selection agents we focus on, namely, temperature, dissolved oxygen, harvesting, and natural

Fig. 2. A summary of the main ecological theories behind the discussed stressors as selection agents. The superscript denotes the reference: (1) Bergmann 1847; (2) James 1970; (3) Atkinson 1994; (4) West et al. 1997; (5) Pauly 1981; (6) Lefevre et al. 2017; Audzijonyte et al 2019; (7) Lush 1937; (8) Miller et al. 1988; and (9) MacArthur and Pianka 1966.



Temperature

Bergmann's rule[1]
At community level, organisms in cold habitats are larger than those in warmer habitats.

James' rule[2]
Within species, populations in cold habitats have larger body size than those in warmer habitats.

Temperature – Size rule[3]
At lower temperatures organisms grow slower but reach larger final size (and *vice versa*).

Metabolic Theory of Ecology[4]
Body size and temperature create the borders for a finite energy budget, which the organism must then allocate to survival, growth and reproduction. Predicts that metabolic rate scales with body mass to the power of multiples of 3/4. This scaling can be extended to predict functions at individual, population and ecosystem levels.

Dissolved oxygen

Gill-Oxygen Limitation (GOL)[5]
The surface area (SA) of gills scales with body mass and the SA of the gills cannot meet the oxygen demand of large bodies → small body size becomes favourable. Note that this is contested by an opposite view[6] that it is the oxygen demand that determines the gill surface area.

Harvest

Breeder's equation[7]
the expected response to selection caused by fishing can be estimated from the breeder's equation $R = h^2S$, where over a single generation, the expected evolutionary response R in a trait depends on the selection differential S and trait heritability h^2.

Predation

"Bigger is better"[8]
For a prey larva, bigger body size is better, as it increases survival from predators. Consequently, fast growth should be beneficial.

Optimal foraging theory[9]
A predator will choose a strategy that ensures the most energy gain at the least cost, in order to maximize fitness. Following that prey body size is thought to be positively correlated with predator encounter rate, and negatively with capture rate, the prey vulnerability curve tends to be dome-shaped.

predators, and provide an overview of the main ecological theories behind the selective mechanisms (Fig. 2).

Temperature and dissolved oxygen

Temperature is known to affect organisms at community, population, and individual levels. This effect is embodied by three rules: Bergmann's rule (Bergmann 1847), James' rule (James 1970), and the temperature–size rule (Atkinson 1994). Bergmann's rule predicts that at the community level, organisms in cold habitats are larger than those in warmer habitats. While not universal (Belk and Houston 2002; Ashton and Feldman 2003; Fisher et al. 2010), many taxa, including birds and mammals (Meiri et al. 2003), as well as marine (Fernández-Torres et al. 2018; Saunders and Tarling 2018) and freshwater (Knouft 2004; Daufresne et al. 2009; Rypel 2014) fishes, are known to conform to Bergmann's rule. This rule is known to apply particularly to freshwater species in cold waters (Rypel 2014). However, at least for freshwater fish, this pattern may be disrupted by non-native species (Blanchet et al. 2010). At the population level, James' rule (James 1970) predicts that within species, populations with smaller body size tend to be found in warmer habitats. As with Bergmann's rule, James' rule is not universal but does hold for some fishes in the marine (Pörtner et al. 2008; Cappo et al. 2013) and freshwater (Daufresne et al. 2009) environments. Temperature is a particularly important aspect in the life of ectothermic organisms such as most fishes, as they rely on an external source for body heat. The well-established temperature–size rule (Atkinson 1994) predicts that at lower temperatures, organisms grow slower but reach larger size at maturity (or inversely at higher temperatures organisms have higher growth rate but lower final size). Indeed, it has been proposed that shrinking body size is one of the universal responses to global warming, alongside range shifts and life cycle mismatches (Daufresne et al. 2009; Sheridan and Bickford 2011). Declines in body size has been observed in marine (Daufresne et al. 2009; Cheung et al. 2012; Baudron et al. 2014) and freshwater (Baudron et al. 2011; Forster et al. 2012) fishes, ranging from warm water to cold water species in every ocean basin and in freshwater environments (Daufresne et al. 2009; Cheung et al. 2012).

Coupled with increasing water temperature is a decreased level of dissolved oxygen. Warm water, whether marine or fresh, holds less oxygen than cold water, and water mass can become undersaturated with oxygen due to excess organic carbon and other anthropogenic processes (Rabalais et al. 2010). Oxygen limitation together with increasing temperature may have synergistic effects on aquatic life, as limited oxygen can further impair the tolerance for warmer temperatures (Pörtner and Knust 2007; Verberk et al. 2016). Warm water causes two opposing effects: on the one hand, warmer water holds less oxygen; on the other hand, warmer temperature increases the anabolic oxygen demand of fish, complicating the oxygen need vs. oxygen supply equation. Following this imbalance, it has been suggested that the surface area of the gills cannot meet the oxygen demand of large bodies, a phenomenon explained by the gill – oxygen limitation (GOL) theory (Pauly 1981; Pauly and Cheung 2018). Consequently, small body size may become favourable. However, while the trend of decreasing body size with increasing temperature and decreasing oxygen is evident in both marine (Pörtner and Knust 2007) and freshwater (Andrews et al. 1973; Pedersen 1987; Pauli et al. 2017) environments, the underlying mechanisms of the GOL theory are currently being debated. It has been suggested that the scaling of gills with body mass, the basis for the GOL theory, is erroneous, and because gills are a folded surface, they can indeed scale proportionally with body mass (Lefevre et al. 2017). Lefevre et al. (2017)

suggest that it is the oxygen demand that determines the gill surface area, and not vice versa. Instead of gill size determining the body size of an individual, lifestyle and habitat determine the demand for oxygen, which, in turn, determines the size of an individual (Lefevre et al. 2017). Audzijonyte et al. (2019) further discuss this approach and point out that gills are dynamic and some fish are capable of increasing or decreasing their mass-specific oxygen consumption within days. Increasing the gill size comes with costs, however, as dynamic modification of gills is likely to incur energetic costs and fish may be more susceptible to parasites, diseases, and toxins in the water (Audzijonyte et al. 2019). Indeed, as with many things in nature, fish growth and size are optimized rather than maximized (Enberg et al. 2012). Audzijonyte et al. (2019) also discuss the potential role of acclimation as well as epigenetic and evolutionary responses to temperature changes. They suggest that while acclimation is unlikely to fully compensate for the increased metabolic rate as temperature increases, adaptation is undoubtedly occurring through epigenetic and evolutionary responses (Audzijonyte et al. 2019). However, Audzijonyte et al. (2019) limit their epigenetic and evolutionary discussion mainly to temperature and not changing oxygen levels. Additionally, they highlight alternative intrinsic and extrinsic explanations for the decrease in body size to encourage further research into the mechanisms behind decreasing body size with temperature in aquatic ectotherms.

The metabolic theory of ecology (MTE) provides a link between the different levels of biological organization. Metabolism, the process by which the body converts food to energy to maintain life, sets the pace for all biological activities (West et al. 1997; Brown et al. 2004; Savage et al. 2004*b*, 2004*a*; West and Brown 2005). Allometric scaling laws demonstrate how body size and temperature create the borders for a finite energy budget, which the organism must then allocate to survival, growth, and reproduction (West et al. 1997; Brown et al. 2004; Savage et al. 2004*b*, 2004*a*; West and Brown 2005). Kleiber's law predicts that the respiratory metabolic rate (R) scales with body mass (M) to the power of ¾ ($R \propto M^{3/4}$) (Kleiber 1932). Using the fundamental laws of biology, chemistry, and physics, this theory was further expanded by West et al. (1997) to use multiples of ¾ to scale up and predict essentially any biological process from genomes to ecosystems (Brown et al. 2004; Savage et al. 2004*a*; West and Brown 2005). This framework became known as the "quarter power law", or metabolic theory of ecology, and it demonstrates how body size and metabolism can be powerful in predicting not only biological traits in the individual, but also functions at the population and ecosystem levels. Indeed, MTE has been successful in predicting the latitudinal diversity gradient (Bailly et al. 2014), population density (Barneche et al. 2016), species distribution and abundance (White et al. 2017), and life-span variation (Scarnecchia et al. 2015) in fish, as well as estimating the flux and storage of carbon in marine, freshwater, and terrestrial ecosystems (Schramski et al. 2015). However, there are several studies not supporting MTE in the aquatic realm (Terribile and Diniz-Filho 2009; Arandia-Gorostidi et al. 2017), and a scientific debate over the validity of MTE remains (Kozlowski and Konarzewski 1998, 2005; Brown et al. 2004, 2005; Savage et al. 2004*b*; Etienne et al. 2006).

Harvesting and natural predators

Given that most fisheries are highly size-selective and target large individuals and that body size is known to have a relatively high heritability (Mousseau and Roff 1987; Garcia De Leaniz et al. 2007), fisheries have the potential to induce evolutionary changes in fished populations when the strength of selection is adequately high (Allendorf and Hard 2009; Heino et al. 2015). Using basic quantitative genetics, the expected response to selection caused by fishing can be estimated from the breeder's equation $R = h^2S$, where over a single generation, the expected evolutionary response (R) in a trait depends on the selection differential (S) and trait heritability (h^2) (Lush 1937). Following this equation, the selection on body size, regardless of the cause, can leave a genetic signature in the population. Indeed, experimental (Uusi-Heikkilä et al. 2015), empirical (Hunter et al. 2015), and mathematical modelling (Ratner and Lande 2001) work is suggesting that harvest-induced evolution is occurring.

Natural selection often drives selection on body size towards a different direction than anthropogenic selective agents. While fisheries often target large body size, natural mortality tends to favour large body size (Edeline et al. 2007; Olsen and Moland 2011). Juvenile fish experience very high rates of mortality during their early life-history stages, and this mortality is often nonrandom with respect to size (Sogard 1997). From the prey's point of view, the "bigger is better" hypothesis (Miller et al. 1988) suggests that for a prey larva, bigger body size is better, as it increases survival from predators. Consequently, it should be beneficial to grow fast and large to avoid predators. Organisms rarely grow to their full potential, however, as the presence of compensatory growth (Metcalfe and Monaghan 2001) in nature illuminates, and growth is optimized rather than maximized (Enberg et al. 2012).

From the predator's point of view, the optimal foraging theory (MacArthur and Pianka 1966) suggests that a predator will choose a strategy that ensures the most energy gain at the least cost to maximize fitness. Following that prey body size is thought to be positively correlated with predator encounter rate and negatively correlated with capture rate, the prey vulnerability curve tends to be dome-shaped (Fuiman and Magurran 1994). A dome-shaped curve would suggest that both smaller and larger individuals are at less risk from predators, and the middle-sized individuals are at the highest risk.

We have here focussed on what we consider to be the main selection agents on body size. While increasing temperature, decreasing dissolved oxygen, and harvesting tend to select towards smaller body size, natural selection in the form of predator avoidance may select for either small or large body size.

Individual-level consequences of selection

Changing body size

Temperature was found to be the main cause of declining body size in an empirically based study in the North Sea (Baudron et al. 2014). The study used over 40 years of data from several databases and found reductions in the body size of six out of eight commercially important species (Baudron et al. 2014). In the northern North Sea, haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*), herring (*Clupea harengus*), and Norwegian pout (*Trisopterus esmarkii*), and in the southern North Sea, whiting, sole (*Solea solea*), and female plaice (*Pleuronectes platessa*) all expressed an average decrease of 16% in asymptotic length (L_∞), coinciding with an increase of <2% in the seawater temperatures (Baudron et al. 2014). Similarly, a comprehensive study by Daufresne et al. (2009) used long-term analyses of fishes (brown trout, herring, sprat) in the Baltic Sea and French rivers, experimental plankton data, and a review of other published work to show a decrease in size-at-age and mean body sizes at individual, population, and community levels. These changes applied in both freshwater and marine environments.

In addition to temperature, fishing alone is thought to exert selection pressure on body size. On the west coast of Scotland, the Firth of Clyde was once a productive estuary supporting commercially important demersal fisheries, mainly targeting cod (*Gadus morhua*), haddock (*M. aeglefinus*), and whiting (*M. merlangus*) (Bailey et al. 2011). After decades of intense harvest and the collapse of many fisheries, a decrease in age and size at maturation was demonstrated in all three species using probabilistic maturation reaction norms (PMRNs) (Hunter et al. 2015). The significant decline in the abundance of large fish in the Clyde may be partially explained by these changes in age and size at maturation (Hunter et al. 2015). Temperature and abundance were shown to have only marginal effects on this, and the shift towards earlier age and smaller size at maturation was attributed, at least in part, to fishing (Hunter et al. 2015).

Disentangling the effects of changing temperature and fishing can be notoriously difficult, and more research effort is needed to understand the potential synergistic effects of multiple stressors. In an attempt to differentiate between the effects of fishing and temperature, Genner et al. (2010) investigated the variability of demersal fish assemblages in the English Channel. They documented size-dependent responses to changing climate and fishing and showed that the temporal trends in the abundance of smaller-bodied fish followed thermal trends, while the abundance of large-bodied fish declined steadily and independently of the thermal regime. Large-bodied fish also showed the greatest declines in body size. Regardless of the root cause of changing body size, the combination of climate change and fisheries may act in concert. Daufresne et al. (2009) noticed that reduction in body size was larger in marine species subjected to heavy fishing than in species not subjected to such heavy fishing, suggesting the potential presence of additive effects. In turn, Clark et al. (2012) showed that in coho salmon (*Oncorhyncus kisutch*), smaller individuals showed a clear advantage in recovery following exhaustive exercise mimicking catch-and-release fishing, suggesting that fishing-induced selection against large individuals may be enhanced by the better stress-related survival of smaller individuals. Importantly, different stressors may affect fish at different stages of their life, and the effects of the stressor may carry over to different life stages (Cline et al. 2019). Although not directly measuring size per se, Cline et al. (2019) studied sockeye salmon (*Oncorhynchus nerka*) and showed that increased temperature during the freshwater phase increased the prevalence of salmon spending only one year in freshwater. This carried over to the ocean life history by increasing the sockeye maturation age and hence the time of return to the natal river (Cline et al. 2019). At the same time, hatchery-augmented pink and chum salmon compete with the sockeye salmon in the ocean, and the size of returning sockeye negatively correlates with the biomass of hatchery-produced salmon. Cline et al. (2019) suggest that competition reduces the size of sockeye salmon, which then drives delayed maturation, highlighting the complexity of several selection agents acting on life-history traits. The different responses of different size-class fishes stress the importance of considering the life histories of individual species when predicting responses to any natural or anthropogenic stressors.

Predation is one of the most important selective forces driving the evolution of life histories (Day et al. 2002). Depending on the context, predation can drive evolution towards smaller (Heins et al. 2016) or larger (Reznick et al. 2001) body size, as would be the prediction of the dome-shaped curve of prey vulnerability as a result of optimal foraging. Understanding the selection caused by predation is particularly timely, as the potential increase in invasive species is thought to be among the consequences of climate change (Dukes and Mooney 1999; Rahel and Olden 2008; Mainka and Howard 2010). Invasive species can markedly alter local ecosystem function and drive changes in the life-history evolution of native species. For instance, an illegally introduced invasive pike in the Alaskan Scout Lake preys on the native threespine stickleback (*Gasterosteus aculaeatus*) (Heins et al. 2016). It has caused significant, directional changes in the life-history traits of the stickleback towards declining size and age at maturity. The sticklebacks shifted from maturing at the age of 2 years to reaching maturity already at the age of 1 year, at a significantly smaller size (Heins et al. 2016). An opposite effect was seen in the well-known guppy (*Poecilia reticulata*) experiments. Reznick et al. (2001) showed that guppies in the high-predation environment grew faster but also reached higher asymptotic lengths than those inhabiting low-predation sites. Reznick et al. (2001) suggested that the higher growth rate and higher asymptotic length were in part due to high-predation areas also having higher resource availability. This could be caused by abiotic factors such as the higher light level in the area resulting in higher primary productivity, or it could be a consequence of predators lowering prey biomass, thus freeing more nutrients per capita (Reznick et al. 2001). Compared with selection induced by fisheries, natural selection often operates in the opposite direction, favouring larger size (Olsen and Moland 2011). The fitness landscape then becomes dynamic, moving in the direction of the stronger selection force (Edeline et al. 2007).

Over the last two decades, experimental studies have started to reveal the genetic basis of changing body size. However, while experimental studies allow for the control of confounding factors, they lack the density dependence present in nature and thus alone cannot be directly translated to describe processes taking place in the nature. Most of this experimental evidence comes from harvesting studies on freshwater, marine, and brackish species, and the results have indicated no differences in the mechanistic changes as a result of harvest depending on the salinity of the water. Following positively size-selected harvest (i.e., large individuals removed from the population, selection similar to most fisheries) of the Atlantic silverside (*Menidia menidia*) over four generations, Conover and Munch (2002) reported significantly lower body weight and slower growth rate of the positively size-selected line. Later, using the same selection lines, Salinas et al. (2012) showed that some of these changes were reversible, some partially reversible, and some did not show any signs of reversibility after five generations of the cessation of fishing. While this common garden approach suggested that some of the changes were likely to be genetic, the direct evidence for genetic changes caused by size-selective harvesting was provided over a decade later. Van Wijk et al. (2013) subjected guppies to three generations of positively and negatively size-selective harvest and quantified the phenotypic and genetic responses to selection. The phenotypic responses to directional selection were similar to those observed by Conover and Munch (2002): positively size-selected harvest led to a reduction in adult body size. Van Wijk et al. (2013) used 17 candidate loci to study genetic changes in response to size-selective harvesting and demonstrated changes in seven of them. At least three of their candidate loci were associated with body size. Following a similar harvest design over five generations, an experimental study on zebrafish (*Danio rerio*) provided further evidence on declining body size and changes in associated life-history characters after intensive directional selection (Uusi-Heikkilä et al. 2015). Uusi-Heikkilä et al. (2015) utilized 384 single nucleotide polymorphisms (SNPs) and identified 21 outlier SNPs responding to directional selection, thus demonstrating contemporary evolutionary changes in the experimentally exploited populations. With the same experimental selection lines, Uusi-Heikkilä et al. (2017) studied harvest-induced changes in gene expression by sequencing the transcriptomes of individual fishes. They demonstrated that size-selective harvesting had changed the expression of over 4000 genes, and some of these changes were associated with changes at the sequence level. Importantly, they showed that the changes in gene expression were slow to reverse. Further, in 2019, Therkildsen and colleagues showed that the phenotypic responses to harvest selection may in fact be underlain by divergent genomic shifts, meaning fishing may potentially cause genomic changes comparable with distinct populations in nature (Therkildsen et al. 2019). Experimental studies such as these can further our understanding of the nature of the changes and help us monitor and manage fish populations in an efficient way.

Changes in growth rate

The fight for survival begins at the egg phase and continues through the larval stage into adulthood and eventual mortality. This survival is often nonrandom with respect to size. The “bigger is better” hypothesis suggests that fast- and large-growing larvae may better avoid predators. The size-selective mortality of the sprat *Spratelloides gracilis* provided evidence for this hypothesis, as selection was operating against small- and slow-growing individuals (Meekan et al. 2006). Allain et al. (2003) reported similar trends in anchovies (*Engraulis encrasicolus*) and attributed survival to faster larval growth rate. While the juvenile stage is of crucial importance as it determines the future cohort sizes, juvenile growth rates can be altered by size-selective harvest (Conover and Munch 2002; Walsh et al. 2006), changing temperatures (Meekan et al. 2003; Baudron et al. 2011, 2014; Rogers et al. 2011), and predation (Reznick et al. 2001; Heins et al. 2016).

Body size and growth rate are closely associated, and for animals with indeterminate growth, this close association is often described by the von Bertalanffy equation. There is a strong negative correlation between the von Bertalanffy growth parameters L_∞ (asymptotic length) and k (the intrinsic individual growth rate), suggesting the presence of a trade-off. Following this, if asymptotic length decreases, the growth rate would be expected to increase (and vice versa); however, depending on the selective agent, selection on body size may influence growth rate differently.

Baudron et al. (2011) used over three decades of length and age data to fit the von Bertalanffy growth model and investigated the growth response of North Sea haddock (*Melanogrammus aeglefinus*) to different temperature scenarios. They showed that increasing temperature was linked to a decrease in L_∞. This finding was coupled with an increase in the growth rate during early life stages (Baudron et al. 2011), in line with the von Bertalanffy growth model (where L_∞ and k correlate negatively) and as predicted by the temperature–size rule. A similar increase in juvenile growth rate with an increasing temperature appears to be relatively common, as it has also been detected in the North Sea cod (Rindorf et al. 2008), Northeast Arctic cod (Michalsen et al. 1998), and Norwegian coastal cod (Otterlei et al. 1999), and holds true across spatial scales (Brander 1995). In some cases, temperature may select directly for increased juvenile growth rate. Thresher et al. (2007) examined otolith data dating back to 1861 and reported a significant change in the growth rate of six out of eight studied species. Three of these species were shallow-water fishes (<250 m) and thus had been subjected to increasing water temperatures over the past century and showed increasing juvenile growth rates. The remaining three species were deep-water species, and temperature reconstructions inferred from deep-water corals fitted the growth curves of the older, deep-water species, which showed no increase in juvenile growth rates (Thresher et al. 2007). More recently, Morrongiello et al. (2019) were the first to report fishing-induced shifts in thermal reaction norms in marine fish, highlighting the potential synergistic effects of harvest and changing temperature. By fishing out the largest individuals that have a high thermal capacity, we might be weakening the species' adaptive potential to respond to climate change (Morrongiello et al. 2019).

While the fish in the study by Morrongiello et al. (2019) attained faster adult growth rates (partially due to release from density dependence as a result of fishing), a typical selection pressure from fisheries tends to select towards lower growth rate (Enberg et al. 2012). Empirical studies of the alpine freshwater whitefish *Coregonus palaea* (Nusslé et al. 2009), *Coregonus albellus*, and *Coregonus fatioi* (Nusslé et al. 2011), all subject to steady and heavy fishing pressure, have shown declines in the average adult (but not juvenile) growth rate, as well as significant selection differentials over several generations. Studies in the laboratory have provided further evidence for changes in growth rate. Experimental harvesting studies have revealed declines in juvenile growth rate following positively size-selective harvest over four generations (Conover and Munch 2002). The parental harvest extended its influence into the next generation, causing changes also in the larval growth rates. The larvae of positively size-selected parents evolved to grow slower than the larvae of negatively size-selected parents, potentially subjecting slow-growing larvae to higher predation pressure in nature (Conover and Munch 2002).

It is thought that the natural mortality of many fish populations has been increasing in the recent decades (Gislason et al. 2010). Following the presence of life-history trade-offs in nature (Jensen 1996; Lemaitre et al. 2015), it could be that increased growth rate early in life is associated with increased mortality late in life. Indeed, accelerated growth rate is known to be linked to shorter life-span in many species (Metcalfe and Monaghan 2003), and a recent meta-analysis suggested a link between growth rate and natural mortality in fish (Gislason et al. 2010). The link between faster growth rate and higher natural mortality (or shorter life-span, which in a controlled laboratory environment, corresponds to higher natural mortality) has also been shown experimentally in three-spined sticklebacks (Lee et al. 2013). By inducing changes in fish growth rate, we may also be indirectly altering fish natural mortality rates.

Big and bold? Linking body size and behaviour

Body size is known to correlate with many behavioural traits, which can enhance or reduce individual fitness. For example, after five generations of harvesting, small Atlantic silverside (*Menidia menidia*) showed reduced willingness to forage under a threat of predation compared with the large ones, potentially reducing individual energy flow and thereby reducing fitness (Walsh et al. 2006). Later, using the same experimental populations, Salinas et al. (2012) showed that the changes in food consumption did not recover after the cessation of fishing. This kind of change in food consumption is likely to influence the population growth rate and productivity (Conover and Munch 2002). Uusi-Heikkilä et al. (2015) investigated behavioural changes in juvenile zebrafish and showed that negatively size-selected fish (i.e., small individuals removed) were more active, explorative, and bolder than positively size-selected fish (i.e., large individuals removed) and that this shift in behaviour was accompanied by genetic changes (but see Sbragaglia et al. 2019). Although not demonstrated by the zebrafish study, it can be speculated that larger fish have higher energy demand, and therefore, they are more active and bolder in searching of food (Réale et al. 2010). In turn, this could make them more vulnerable not only to natural predators, but also to fishing gear.

Fishing gear selection is a two-way street. While behaviour can influence the vulnerability to fishing, selective fishing can cause behavioural changes. As an example, Sutter et al. (2012) focused on behaviour instead of size and showed that aggression, intensity of parental care, and reproductive fitness positively correlated with vulnerability to angling. Similarly, physiological traits such as anaerobic swimming performance and metabolic demand are known to be linked to vulnerability to fishing (Killen et al. 2015). Fishing can also be the cause of behavioural changes, as the gear retention probability depends on the fishing gear in question, and the selection curves are often nonlinear with respect to size (Kuparinen et al. 2009). Because size and behavioural traits are linked and fishing often selects a certain size regime, the selection likely also affects behavioural traits. Obviously, vulnerability also depends on the fishing gear at hand. Behavioural changes associated with body size have also been studied in the context of fish farming, as it provides a semi-natural laboratory in which to study contemporary evolution. Farmed fish that have been selected for higher growth rates are expressing changes in boldness (Biro et al. 2004). The fish under selection tend to take more risks while foraging, grow faster, and survive at a lower rate than their wild conspecifics (Biro et al. 2004; Biro and Post 2008).

In addition to fishing and fish farming, behavioural characters may be indirectly impacted by temperature. Given that fishes are mainly ectothermic, increasing water temperature will likely affect metabolic rates, which, in turn, may alter feeding behaviour and activity. Scott et al. (2017) showed that this kind of response is size-dependant. On the Great Barrier Reef in Australia, the common coral trout (*Plectropomus leopardus*) shows more active foraging behaviour during hotter months than colder months, but when the water temperature exceeds 30 °C, foraging frequency declines. This may suggest the presence of a temperature threshold beyond which *P. leopardus* cannot compensate for the increased basal metabolic rate with increased foraging activity (Scott et al. 2017). They also showed that larger individuals spent more time completely inactive in increasing temperatures compared with their smaller conspecifics (Scott et al. 2017). This kind of behavioural change may have far-reaching effects, from insufficient foraging and abnormal spawning-related movements to predator–prey relationships (Scott et al. 2017). Studying the same species, Johansen et al. (2015) demonstrated that while *P. leopardus*, a predatory species, may be able to increase food intake in response to increased metabolic demand due to increased water temperature, the lower trophic levels may not be able to provide this energy. This highlights the importance of considering the wider ecosystem, not just one species, when predicting the influence of natural or anthropogenic stressors.

An interesting link between changing sea temperature, body size, and activity level was also discovered by van Rijn et al. (2017). They studied 74 fish species across space in the Mediterranean Sea, ranging from small bottom-associated gobies to large pelagic tunas, and demonstrated that body size decreased with increasing temperature, as predicted by the temperature–size rule. Additionally, they found that the activity level of the species was strongly correlated with the decrease in body size, so that large, active species showed the strongest decline in size in response to increasing temperature (van Rijn et al. 2017). This highlights the complexity of several selective agents acting simultaneously. As discussed earlier, fisheries selection may select for a certain type of behaviour or activity level, and as shown here, activity level is linked to body size response to warming. This provides an interesting connection between fishing, changing temperature, activity level, and body size and warrants further research into the potential synergistic effects of multiple stressors.

Changes in reproduction

A commonly used proxy for individual fitness is the lifetime reproductive success (LRS), which can simply be described as the total number of offspring an individual produces during its lifetime (Mousseau and Roff 1987). The reproductive output of an individual tends to increase with body size (Hixon et al. 2014), thus contributing to the individual's fitness. In a meta-analysis of 342 species of marine fishes from 15 different orders, Barneche et al. (2018) quantified this increase and estimated how selection towards smaller body size may reduce fecundity. They controlled for phylogenetic non-independence and scaled female mass and reproductive energy output, including fecundity, egg volume, and egg energy, to show that large females reproduce disproportionally more than small females. A similar trend has been seen in experimental studies, where positively size-selected harvest has led to reduction in fecundity (lower spawning probability, fewer eggs both absolutely and relatively) in zebrafish (Uusi-Heikkilä et al. 2015). Similarly, a study on the Atlantic silverside subjected to five generations of size-selective harvest showed marked reductions in egg volume, larval size at hatching, larval growth rate, and larval survival probability (Walsh et al. 2006). The correlation of body size and fecundity has been documented in various fish species both intraspecifically (Dick et al. 2017) and interspecifically (Savage et al. 2004*b*; Hayward and Gillooly 2011). It is important to note, however, that the strength of the correlation depends on the species in question (Barneche et al. 2018), and that like other animals in the wild (Nussey et al. 2013), at least some fish experience actuarial (Beverton et al. 2004; Uriarte et al. 2016) and reproductive (Reznick et al. 2006; Benoît et al. 2018) senescence, meaning that the reproductive capacity of fish may not increase indefinitely with size. Therefore, predictions about reproductive capacity based on body size alone should be made with caution.

The mechanisms of how larger body size benefits the reproductive output vary, however, and some are related to behaviour. In coho salmon (*O. kisutch*), larger female body size has been associated with an advantage in mate and territory selection (Fleming and Gross 1994). Bigger size appears to be beneficial, as it allows for increased egg production, better access to nesting territories, and improved nest digging (Fleming and Gross 1994). Further, the changes in body size are often accompanied by associated changes in population age structure. The truncation of age structure can potentially enhance the effects of declining body size at individual and population levels. As an example, longevity may be advantageous as it can increase population recruitment variability (in timing), particularly in long-lived fish species, thereby making the population less vulnerable in unstable environments (Longhurst 2002). Maternal age can also contribute to the fitness of offspring. The larvae of older black rockfish (*Sebastes melanops*) showed over three times faster growth rate than the larvae of younger rockfish, and they survived starvation better (Berkeley et al. 2004). Because body size and reproductive output are often positively correlated (Barneche et al. 2018), changes in individual body size can have multigenerational impacts, truncate the population age and size structure, and potentially lower the population growth rate.

How do changes in body size translate to population dynamics?

The intrinsic rate of per-capita population growth rate (r) can be thought of as a population-level analogue to LRS. Although r cannot be directly translated from LRS, body size is a strong correlate for both (Denney et al. 2002; Anderson et al. 2008). Indeed, Uusi-Heikkilä et al. (2015) modelled their results from the zebrafish studies and found that in the absence of fishing, a positively size-selected (large individuals removed) population had slower population growth rate than negatively and randomly size-selected populations. In their modelling study, Audzijonyte and Kuparinen (2016) showed that earlier maturation that evolved during fishing, reduced r after fishing had been halted. They also showed that decreased adult body size reduced the reproductive output and increased adult natural mortality. However, species' age-specific survival and trophic position were also important in determining r: a species inhabiting the offshore environment and exposed to few predators did not suffer, in terms of population growth rate, as much from reduced body size as a species living nearshore and being intensively predated by other fish. A density-dependent population response to fishing was predicted by the model of Dunlop et al. (2015), who observed that as fishing began, r first declined as the largest individuals were removed from the reproductive pool, but once density-dependent processes started regulating the population, r and reproductive output increased. After a moratorium, the opposite occurred: at first r increased temporarily but was eventually counteracted by density-dependent processes, leading to a reduction in r (Dunlop et al. 2015). This kind of delayed response can explain how evolution may impede stock recovery after harvest (Dunlop et al. 2015).

The form of selection will affect the outcome of the selection: stabilizing selection favours the intermediate phenotype, and disruptive selection favours the extreme phenotypes. Directional selection occurs when selection favours one phenotype over another so that the frequency of this phenotype in a population becomes higher than before selection. On the one hand, studies have shown that stabilizing selection can lead to decreasing phenotypic and genetic variation (Olsen et al. 2009), which is known to reduce population fitness (Reed and Frankham 2003). On the other hand, if the selection is disruptive, it may increase the genetic variance in a population (Edeline et al. 2009), potentially increasing population fitness. Thus, by understanding the selection mode of different fishing methods and the genetic outcome they may produce, we could minimize the damage that harvesting can cause.

While human-induced trait selection may drive selection in one direction, natural selection may favour another direction. This trend was quantified by Carlson et al. (2007) as they studied the effect of natural selection and harvest-induced selection on Windermere pike (*Esox lucius*). They showed that while fishery selection favoured small pike, natural selection acted against small pike. Further, natural selection was stabilizing, suggesting that bigger body size is not always beneficial, while harvest-induced selection was disruptive, likely a sign that the smallest and the largest individuals were not caught by the fishery (Carlson et al. 2007). Thus, harvest-induced selection may modify the natural adaptive landscape of populations. Changes in the adaptive peak were further explored by Edeline et al. (2007), as they showed that the adaptive peak moves in the direction imposed by the stronger selective force and that trait changes follow the movement of the peak. The modification of the adaptive peak is dynamic, so that during fishing, harvest selection was the dominating force, and when fishing was relaxed, natural selection became the dominating force. After the fishing pressure ceased, a shift toward faster growth was accompanied by a decrease in reproductive investment, suggesting a trade-off between growth and reproductive investment (Edeline et al. 2007). These movements of the adaptive peak were seen under a relatively low fishing pressure (1.1%–7.3%), while commercial fishing pressure is typically in the order of 45%–99% (Edeline et al. 2007).

Genetic and phenotypic variation

While selective harvesting is known to affect several traits in harvested populations (Walsh et al. 2006), the nature of selection can affect the outcome. Some fish populations have not managed to recover following depletion, but others show signs of reversal after intense harvest (Murawski 2010; Costello et al. 2016). While the recovery of a population likely depends on several factors, extrinsic and intrinsic, the effect of fishing depends on the form of selection it causes. Edeline et al. (2009) demonstrated empirically that harvest-induced selection in pike could actually increase variance in fitness-related traits such as body size when the harvest is disruptive. Disruptive selection leads to a higher fitness for the phenotypic extremes, which gives rise to increased trait variability (Edeline et al. 2009). An opposing effect of fishing has been seen in the brown trout (*Salmo trutta*) (Haugen et al. 2008) and Atlantic cod (Olsen et al. 2009) in which stabilizing selection led to a decrease in phenotypic variance with respect to body size. Furthermore, the nature of genetic architecture of the trait under selection may influence the outcome of the harvest-induced selection (Kuparinen and Hutchings 2016). A striking example of the importance of the genetic patterns behind inherited traits comes from the Atlantic salmon (*S. salar*) in which the genetic architecture behind age at maturity was recently identified to be controlled by a large effect locus explaining nearly 40% of phenotypic variation in age at maturity (Barson et al. 2015). Simulations indicate that if the trait (here age at maturity) is under the control of a single sexually dimorphic locus, the selection response is likely divergent or disruptive, and if the trait is controlled by multiple loci, the response is unidirectional (Kuparinen and Hutchings 2016).

According to classic evolutionary theory, for populations with small effective population size (N_e) and little genetic variation, the evolutionary potential to respond to future challenges may be limited and the consequences of genetic drift and stochastic events may be serious. Selection and declining population size may cause erosion in the genetic variation of a population, potentially leading to the accumulation of deleterious alleles and therefore decreasing the population fitness (Marty et al. 2015). A genetic bottleneck has the potential to cause inbreeding depression in populations with small effective population size (Palstra and Ruzzante 2008), and in the worst case, this could send the population into an extinction vortex.

The empirical evidence for reduced genetic variation as a result of harvest or in small populations is, however, contradictory. While heavy harvesting has been associated with lower genetic diversity in some populations (Hauser et al. 2002; Pinsky and Palumbi 2014), others show no signs of this (Ruzzante et al. 2001; Therkildsen et al. 2010). This maintenance of genetic diversity may be due to large effective population size despite harvesting (Therkildsen et al. 2010) or the mixing of populations (Ruzzante et al. 2001). Additionally, a recent meta-analysis (Wood et al. 2016) found no correlation between declining population size and genetic variation. Similarly, the consequences of reduced genetic diversity in nature can be variable. An experimental relocation study found no correlation between reduced genetic variability and fitness (survival and growth) (Yates et al. 2019). Instead, the habitat quality had a significant effect on the fitness of individuals and species extinction (Yates et al. 2019). While this study highlights the importance of habitat conservation, it does not inform on the importance of genetic variation on an evolutionary time scale. It has been suggested that factors such as epigenetic variation, in addition to genetic variation, soft sweeps from standing genetic variation, polygenic and balancing selection, and repeated adaptation may help maintain the evolutionary potential of species (Bernatchez 2016).

In some cases, fishing can result both in strong directional selection and in declining population size, thereby being a candidate for the cause of potentially irreversible changes in genetic and phenotypic variation. Empirical (Hauser et al. 2002) and experimental (Uusi-Heikkilä et al. 2015) studies, as well as a meta-analysis of 140 fish species (Pinsky and Palumbi 2014), have shown that harvest can lead to declines in genetic variation (both sequence and gene expression levels). Genetic diversity has been shown to correlate with population fitness and to explain almost 20% of the variation in it (Reed and Frankham 2003). Additionally, high genetic diversity (Reusch et al. 2005), as well as phenotypic diversity (Morrongiello et al. 2019), can buffer ecosystems from extreme climatic events by ensuring complimentary genotypes and improving recovery after perturbations. Apart from avoiding genetic bottlenecks and maintaining evolutionary potential, another reason for the importance of preserving genetic variation is that it may be linked to the rate of evolution. In the Trinidadian guppies, for instance, male guppies showed a higher rate of evolution than female guppies, apparently due to higher genetic variation in males (Reznick et al. 1997). The lower genetic variation in females likely slowed down the evolutionary change in age and size at maturity (Reznick et al. 1997). Now, with a rapidly changing environment, fast adaptation may be needed, highlighting the role of genetic variation as it holds the evolutionary key for the swift adaptation of species to their environment.

In recent years, studies have found declines in genetic and phenotypic variations, but the root cause of these is somewhat unclear. Olsen et al. (2009) used nine decades of commercially and recreationally harvested cod length data from the Norwegian Skagerrak coast and showed that while the mean length of juvenile Atlantic cod had not changed, the variation had decreased. They found evidence for selection against both large- and fast-growing and small- and slow-growing juveniles, likely a sign of stabilizing selection. The reasons behind this were speculated to be various and non-exclusive, e.g., climatic conditions, trends in biotic factors (abundance of conspecifics, predator–prey relationships), changes in breeding phenology, natural selection, or harvest (Olsen et al. 2009). In the same location, Rogers et al. (2011) showed that temperature and population density had a pronounced effect on the variation in the growth rates of juvenile Atlantic cod. While warm spring temperatures resulted in larger juvenile cod, they also reduced length variation within a cohort (Rogers et al. 2011). While the cod on the Norwegian coast showed declines in phenotypic variation, the North Sea cod off the coast of Flamborough Head, U.K., showed declines in genetic variation (Hutchinson et al. 2003). This decline coincided with the time of high population exploitation rates, shifts towards younger age and smaller size at maturity, and demographic changes on a population level (Hutchinson et al. 2003).

Intraspecific variation in life-history traits such as age or size at maturation can affect ecological dynamics on the population level, irrespective of whether the trait variation is genetically based or not (Bolnick et al. 2011). Life-history variation within species can stabilize ecosystems and dampen temporal variability, a phenomenon known as the portfolio effect. The heavily exploited sockeye salmon in Bristol Bay, Alaska, shows a high degree of population and life-history diversity (Schindler et al. 2010). Schindler et al. (2010) quantified this variability by modelling empirical data and showed that because of the life-history variation, the temporal variability in annual salmon returns is 2.2 times lower than what it would be if the population were homogenous with respect to life histories. This is important because the salmon fishery is a major source of income to the local communities, and therefore, low variation in income is desirable (Schindler et al. 2010). This study highlights the importance of preserving within-species variation from both ecological and economic perspectives (Schindler et al. 2010).

A study on Atlantic cod in Iceland has provided clues to the link between life-history variation and genetic changes. Jakobsdóttir et al. (2011) used a historical data set spanning nearly six decades to study the genotypic frequencies in Atlantic cod. They showed that the frequency of the *Pan* I^{BB} genotype decreased over the course of 60 years and that this decrease coincided with the increases in fishing effort and intensity, as well as with the collapse of the numbers of older individuals in the population (Jakobsdóttir et al. 2011). Their results strongly suggest that the different *Pan* I genotypes correspond to different life-history strategies, so that different *Pan* I genotypes mature at different ages (Jakobsdóttir et al. 2011). As suggested by the portfolio effect, the decrease in intraspecific life-history variation may make the population more vulnerable to stochastic events or adverse conditions (Bolnick et al. 2011). Ignoring the genetic and phenotypic variations and evolutionary potential of species can reduce the efficiency of conservation efforts or even make some actions harmful.

Ecosystem-level effects of the changing body size

Predator–prey relationship

An ecosystem consists of the abiotic environment and the species and their functional characters that live in it (Hooper et al. 2005). Predator–prey relationships are the cornerstone of ecosystem dynamics (Bailey et al. 2010), and a phenotypic change in one species can induce ecological and evolutionary changes in other species interacting with it (Agrawal 2001). The predator–prey relationship is characterized by prey survival on the one hand and predator foraging strategy on the other hand. As a result, a change in the body size of one species can affect the other species in the food web. Most predatory fish tend to be gape-limited, and thus both prey and predator body size are likely to influence the outcome of predator–prey encounters. The predator gape limitation determines when prey will reach a size refuge from the predator, which, in turn, can have community-wide effects. Persson et al. (1996) studied size-structured perch (*Perca fluviatilis*) populations in four lakes in Sweden. Two of these lakes had perch, and two had perch and pike (*Esox lucius*). All lakes had predators, because perch are known to be cannibalistic. Given that predatory perch is smaller than predatory pike, in lakes with perch only, perch reached size refuge earlier than in lakes in which pike were also present. Persson et al. (1996) found that the lakes differed in size-dependent mortality and growth rates, as well as perch habitat use, so that the presence of pike increased the size at which perch reached size refuge, increased the growth rate, and limited their resource use. In the lakes with no pike present, perch utilized both the hypolimnion and epilimnion habitats and thus were also found below the thermocline. The authors attributed these differences to the differences in the size at which perch reached size refuge, illustrating how size-dependent predation can feed back to the ecosystem function by altering the habitat use of the species (Persson et al. 1996). Growth rate and body size may even determine who becomes a prey and who is a predator. A study by Nilsson et al. (2019) documented a predator–prey role reversal for pike and stickleback. While pike is usually a predator and stickleback a prey, they provided evidence that juvenile pike mortality is size-dependant and corresponds to stickleback gape limitation (Nilsson et al. 2019). In the presence of increasing water temperature or human-induced changes in body size and growth rate, this kind of predator–prey role reversals may add to the hindrance of population recovery.

While size-dependent predation can have ecological effects on the environment, as described in the study by Persson et al. (1996) mentioned in the previous paragraph, the cause and effect are likely more complex. Size-related evolutionary and ecological changes can also drive changes in the ecosystem, and these may further feed back into the ecosystem. In their experimental study, Palkovacs et al. (2009) compared the effects of ecological (invasive guppies, *P. reticulata*), evolutionary (different guppy life histories as a result of different predation pressure), and coevolutionary (coevolution of guppies and the small fish *Rivulus*) agents driving ecosystem change in Trinidadian river ecosystems. They concluded that guppy evolution and guppy–*Rivulus* coevolution caused significant changes in the surrounding ecosystem, while guppy invasion did not. Another example of evolutionary change affecting the ecosystem comes from the gape-limited predatory alewife (*Alosa pseudoharengus*), which has diverged in its foraging traits (Palkovacs and Post 2009). Anadromous alewives are capable of preying on larger prey than their landlocked counterparts, and this, in turn, has significantly affected the size structure of its prey, crustacean zooplankton (Palkovacs and Post 2009). These studies provide evidence that evolutionary changes in one species can have an impact on the entire ecosystem. Human-induced evolutionary changes on various species and their effects on ecosystems have further been reviewed by Palkovacs et al. (2012) and Fraser (2013).

Trophic cascade

The tale of Atlantic cod is an iconic example of how changes have propagated through different levels of biological organization in nature. The intensely fished northern cod population in southern Labrador and eastern Newfoundland collapsed in the early 1990s, and despite a decades-long moratorium, the stocks have not fully recovered (Neuenhoff et al. 2019; Sguotti et al. 2019). The reasons for the lack of recovery are complex and include several hypotheses such as changing sea water temperatures, predation by seals, continued fishing, and life-history changes due to fishing (Swain et al. 2011). Olsen et al. (2004) showed that the fishery collapse was preceded by a rapid phenotypic change toward younger age and smaller size at maturity, and the study strongly suggested that there was an evolutionary component behind this change. It is likely that this has contributed to the slow recovery of the stocks (Olsen et al. 2004), and similar trends have been recorded in many other top predators (Hutchings and Baum 2005). The collapse of cod and other large predator populations in the Northwest Atlantic marine ecosystem led to a cascade involving four trophic levels (Frank et al. 2005). Following the collapse of large predators, the abundance of smaller fish and benthic macroinvertebrates increased markedly. The increase in smaller fish, in turn, influenced the abundance of zooplankton and phytoplankton, followed by a response in nitrate concentrations. This top-down trophic cascade has likely further impeded the recovery of the cod population by altering food webs (Frank et al. 2005).

Similarly, in the Northeast Pacific, marked declines in the abundance of the oldest and largest individuals of Chinook salmon (*O. tshawytscha*) and changes in the age and size structure of the population coincide with a decline in the length-at-age of the fish (Ohlberger et al. 2017). Intriguingly, while the decrease in the length-at-age was clear, the cause of it was not. Ohlberger et al. (2017) hypothesized that the changes could be a result of size-selective harvesting, changing temperatures, interspecific competition, or, more likely, predation by large apex predators such as the resident killer whale, the numbers of which have increased following a harvest ban in the 1970s. The loss of the oldest and largest individuals of the Chinook salmon population is of concern because it can have a negative impact on the long-term viability of the population (Ohlberger et al. 2017). Another ecosystem-level example comes from the Northwest Atlantic, where the combination of size-selective harvest and changing climate caused reductions in the body sizes of functional top predators, which, in turn, contributed to the increase in prey biomass (Shackell et al. 2009). This demographic change was also weakly associated with a decline in zooplankton and an increase in phytoplankton abundance, indicating a cascading effect through the food web involving three trophic levels (Shackell et al. 2009).

As discussed, not only fishing, but also changing water temperature, has been associated with shifts towards smaller body size in fish, affecting populations and communities. A comprehensive meta-analysis by Daufresne et al. (2009) demonstrated an increase in the proportion of small-sized species with increasing temperature, in terms of both species richness and abundance (Daufresne et al. 2009). The latter result includes a latitude-related component and is in line with not only the temperature–size rule, but also ecogeographical rules such as Bergmann's rule or James' rule (Daufresne et al. 2009). Warming-induced changes in body size and resulting consequences at the population and community levels have also been reviewed by Ohlberger (2013). These are important studies showing how the changing climate can have an impact at individual, population, and community levels and even change the species composition of an ecosystem.

The explicit demonstration of changes propagating through different levels of biological organization is challenging, but in addition to empirical examples discussed earlier, modelling and microcosm studies are showing similar trends. In a modelling study, Kuparinen et al. (2016) used a network model to demonstrate how declining body size together with advanced maturation may magnify fluctuations in fished populations. They showed that this fluctuation can extend to other species in the ecosystem and may continue long after fishing has ceased (Kuparinen et al. 2016). A microcosm study on predator–prey (rotifer–algae) interactions showed that the prey evolution affected the growth of the predator population more than the actual abundance of prey and that the changes in predator abundance, in turn, affected the prey evolution, suggesting an eco-evolutionary feedback loop (Becks et al. 2012). While these particular results cannot be directly extrapolated to fish communities, changes in fish body size are also likely to influence other species, especially when predation is gape-limited. Indeed, examples of parallel evolution in fishes such as the cichlids, threespine sticklebacks, and guppies are illuminating the tight linkage that exists between the genetics of an individual and the ecological environment surrounding it (Elmer and Meyer 2011).

Conclusion

Changes in body size at an individual level can propagate through different levels of the biological organization. Given the current rapid environmental change, organisms will have to adjust, adapt, or move, probably more quickly than ever before. Adaptation requires evolutionary change, and evolutionary change requires building material: genetic variability. Evolutionary change can occur at ecologically relevant time scales, and therefore it is vital for conservation biologists and decision makers to understand both the ecology of an organism and the genetic architecture that enables evolution. Changes in body size and correlated life-history characters following harvest, changing temperature and dissolved oxygen, and predation have been demonstrated empirically (Nusslé et al. 2009, 2011; Baudron et al. 2014; Hunter et al. 2015; Ohlberger et al. 2017), experimentally (Reznick et al. 1990; Conover and Munch 2002; van Wijk et al. 2013; Uusi-Heikkilä et al. 2015), and through mathematical modelling (Kuparinen et al. 2016). Consequently, the outcomes of these changes can vary from behavioural changes (McCormick 2009; Sutter et al. 2012) to changes in reproductive output (Hixon et al. 2014) and can extend their influence to the next generation (van Wijk et al. 2013) and the entire ecosystem (Frank et al. 2005) regardless of whether the change is genetic or not (Bolnick et al. 2011). The genetic basis of the change matters, however, because first, genetic change allows for the evolutionary adaptation to the changing environment, and second, evolutionary change may be hard, if not impossible, to reverse (Salinas et al. 2012; Uusi-Heikkilä et al. 2017). Should the changes be indeed genetic and, therefore, likely hard to reverse, the consequences that extend from declining body size through to population size and stability (Audzijonyte and Kuparinen 2016) to ecosystem functions (Frank et al. 2005; Ohlberger et al. 2017) may also be hard to reverse.

In addition to reversibility, understanding the genetic basis of the changes occurring in nature is vital from the biodiversity management perspective. From the multiple stressors affecting our oceans today, some are easier controlled than others. Managing fisheries selection regimes, for instance, is easier and quicker to control than changing climate. If we utilize the genetic knowledge and fishing methods that conserve variation, we may be maintaining a higher genetic variability (Edeline et al. 2009), as well as population stability (Bolnick et al. 2011). Higher genetic variability, in turn, is what forms the basis for evolutionary potential. In this way, we may better conserve the biodiversity not only now, but also in the future.

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II

AGE IS NOT JUST A NUMBER—MATHEMATICAL MODEL SUGGESTS SENESCENCE AFFECTS HOW FISH POPULATIONS RESPOND TO DIFFERENT FISHING REGIMES

by

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ORIGINAL RESEARCH

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Age is not just a number—Mathematical model suggests senescence affects how fish populations respond to different fishing regimes

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Abstract

Senescence is often described as an age-dependent increase in natural mortality (known as actuarial senescence) and an age-dependent decrease in fecundity (known as reproductive senescence), and its role in nature is still poorly understood. Based on empirical estimates of reproductive and actuarial senescence, we used mathematical simulations to explore 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 the eco-evolutionary dynamics of a fish population during pristine, intensive harvest, and recovery phases. Our simulation results showed that the presence or absence of senescence affected how the population responded to the selection regime. At an individual level, gillnetting caused a larger decline in asymptotic length when senescence was present, compared to the nonsenescent population, and the opposite occurred when fishing was done by trawling. This change was accompanied by evolution toward younger age at maturity. At the population level, the change in biomass and number of fish in response to different fishery size-selection patterns depended on the presence or absence of senescence. 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 to understand the combined effects of life-history characters such as senescence and fisheries selection regime to ensure the successful management of our natural resources.

KEYWORDS
eco-evolutionary dynamics, fisheries, life-history, senescence, trade-offs

1 | 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; Nussey et al., 2013; Selman et al., 2012). Senescence is often described as age-dependent increase in natural mortality (known as actuarial senescence) and age-dependent decrease in reproductive function (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, 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 (Bonsall & Mangel, 2004; Jensen, 1996; Lemaitre et al., 2014; Maklakov & Chapman, 2019), likely contributing to the onset or development of senescence in an individual. The early- versus 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 & Kaitala, 1999; Lemaître et al., 2015; Reznick et al., 2002).

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 & 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 & Hood, 2016). Following the close link between life-history characters and senescence, it is therefore likely, that increased allocation to reproduction in early life leads to an increased rate of aging later as hypothesized by the antagonistic pleiotropy (Williams, 1957) and disposable soma theories (Kirkwood, 1977). As a consequence, fishing-induced changes in maturation age and senescence could actually be linked (Benoît et al., 2018). Indeed, the natural mortality rate of many fish populations is thought to have increased in the recent decades (Gislason et al., 2010).

Given that most fishes express indeterminate growth and high longevity (Carey & 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). Other works suggest they may completely lack senescent deterioration (Sauer et al., 2021; Vaupel et al., 2004). Indeed, female body size and reproductive output in fish are known to be positively correlated in many species, indicating that the older and larger the fish, the higher its reproductive output. Most fisheries and fish population models (Andersen & Beyer, 2015; Beverton & Holt, 1957; Enberg et al., 2010; Zimmermann & Jørgensen, 2015) and life-history models (Brunel et al., 2013; Charnov et al., 2013; Roff, 1983) assume that body size (weight) scales isometrically with reproductive output. Recent meta-analysis has provided cues that the scaling might even be hyperallometric (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 (Comfort, 1960, 1963; Gerking, 1957; Woodhead & Ellett, 1966, 1967, 1969a, 1969b). Over the past few decades, evidence for both reproductive (Benoît et al., 2018; Reznick et al., 2006; Žák & Reichard, 2020) and actuarial (Beverton et al., 2004; Uriarte et al., 2016) senescence as well as general deterioration with age (Carlson et al., 2007; Hendry et al., 2004; Morbey et al., 2005; Patnaik et al., 1994) 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 life-histories and population dynamics.

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). 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 (Bailey, 2011; Myers & Barrowman, 1997; Pedersen et al., 2017; Rougier et al., 2012), or are recovering at a lower rate than expected (Hutchings & 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., 2003; Hutchings & 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 parameterize an existing eco-evolutionary model (Kuparinen et al., 2011) to overcome these obstacles (i.e., measuring senescence from a fish that has been caught and is therefore no longer in the nature contributing to the population dynamics) 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: (a) How does the presence or absence of senescence influence the population dynamics of fish, in terms of asymptotic length, biomass, and number of fish in a pristine environment? And (b) 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 in pristine and harvested populations.

2 | 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 correlation of the von Bertalanffy (vB) growth model parameters L_∞ (asymptotic length), and k (intrinsic growth coefficient, i.e., how fast the fish length is approaching L_∞) (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 modeling 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 generalized to any fish with similar life-history properties.

2.1 | General description of the modeling approach

The eco-evolutionary model includes five main components (Figure 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_∞ is a well-known life-history invariant (Charnov, 1993). Thus, in the growth component (Figure 1a), we utilized empirical length-at-age data back-calculated from fish scales to model the L_∞. The L_∞ was set to be an evolving trait so that the genotype coding L_∞ of each individual was described by 10 diploid loci with two alleles in each. The alleles were inherited in the

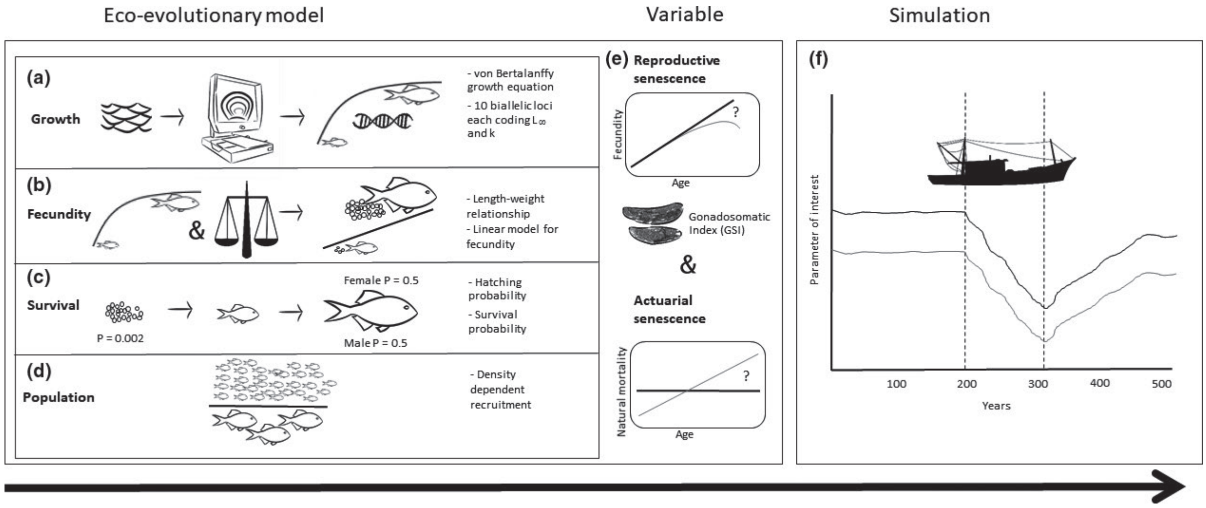

FIGURE 1 A schematic diagram of the modeling approach. (a) The fish length-at-age was back-calculated from fish scales. These data were then used to fit the von Bertalanffy growth equation to model the L_∞. The L_∞ was set to be an evolving trait so that the genotype coding the L_∞ of each individual 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 fertilized egg to hatch and the juvenile to survive until 2 years of age was set to $p = .002$ 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, for instance, at 85% 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. (e) Reproductive senescence and actuarial senescence are the independent variables in the model. The reproductive senescence was modeled 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 modeled, only the linear model for fecundity was used. Actuarial senescence was modeled 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

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_∞. The standard deviation of the normally distributed random number was adjusted to yield a realistic heritability of 0.2–0.3 (Mousseau & Roff, 1987). The vB growth parameter *k* and the size at maturity were then determined based on L_∞ (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_∞ (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_∞, but never before they reach their second autumn. Thus, fish younger than two years old, or fish smaller than 67% of their L_∞ could not yet reproduce. The age at maturation was allowed to evolve, but had a restriction so that it could not go below 2 years.

The fecundity component (Figure 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 (Figure 1c) includes an empirically based (Karjalainen et al., 2016; Marjomäki et al., 2014) probability ($p = .002$) 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 7 years, according to local lifespan estimations in Lake Puulavesi (Marjomäki & Huolila, 1994).

The population component (Figure 1d) describes density dependency through an individual's progress along its growth trajectory. Growth continuously slows down as population density increases. For example, at 85% of the population carrying capacity (measured in biomass units, carrying capacity is 75 units), the individual growth is reduced to 50% of that predicted by the individual's vB growth curve (its L_∞ and *k* parameters) (see Kuparinen et al. (2011) Figure 1 for an illustration of how growth continuously slows down). This effect of population density on the individual growth was described as follows: growth time available for the individual $= \frac{e^{\left(a+b*\frac{BM}{CC}\right)}}{\left(1+e^{\left(a+b*\frac{BM}{CC}\right)}\right)}$, where BM = biomass in units, CC = carrying capacity in units, and *a* and *b* parameters describe the slope how the growth slows down. Additionally, using the same function the egg production by individual females (based on their body size) was set to be density-dependent so that the closer the size of the spawning population was to the total population carrying capacity, the fewer eggs were produced. Inversely, the sparser the population, the more eggs were produced. Notably, while the exact numeric choices were somewhat arbitrary, implementation of these two density-dependent mechanisms was necessary for stabilizing the population size and to keep it from exploding. The mechanisms were kept unchanged throughout the simulations and, thus, do not affect the results which are derived from the comparison of alternative simulation scenarios.

The fifth component of the eco-evolutionary model describes senescence in its two forms: reproductive senescence and actuarial senescence (Figure 1e). The reproductive senescence was modeled by multiplying the linear model for fecundity by the gonadosomatic index (GSI, = (gonad weight/total tissue weight) × 100) for the year class in question. When no reproductive senescence was modeled, only the linear model for fecundity was used. Actuarial senescence was modeled 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 (Figure 1f), but the presence and absence of reproductive and actuarial senescence were 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 were 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 (Figure 1f). The output data of particular interest, that is, asymptotic length (L_∞), biomass (*BM*), and number of fish (*N*) were collected annually. Each simulation was replicated 100 times.

2.2 | Parametrization of the model

The empirical data were collected from Lake Puulavesi, an oligotrophic lake located in Central Finland. Its area 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. While ideally the samples would have been collected from a pristine lake, no such lakes exist in Finland, and therefore, the data were collected from a lake with an average amount of fishing taking place (Marjomäki & Huolila, 2001). The model is based on empirically observed growth trajectories of vendace (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×) 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 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 & Huolila, 2001).

The empirical 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 = 7e−06, and $b = 2.943$. The lengths varied between 120 and 170 mm (mean 146 mm, $SD = 8.63$), and the weights varied between 12 and 27 g, (mean 18.7 g, $SD = 3.7$). 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 modeled on.

Back-calculated individual growth trajectories from Lake Puulavesi were summarized using a nonlinear 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_∞ = asymptotic length, L_0 = length at $t = 0$, and k = the intrinsic individual growth rate. The association between the vB parameters L_∞ and k was estimated using an empirically based linear regression model which yielded the following fit: $\ln(k) = 1.27 - 0.13 * L_\infty$ with residual $SD = 0.30$.

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 × 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 the relation of body and gonad weight which we used to calculate gonadosomatic index (GSI), a pattern that could be indicative of reproductive senescence given it has been used as a proxy in other studies (Benoît et al., 2018; Hendry et al., 2003). 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-, 6 and 7-year-old fish was linearly extrapolated from the existing data. We used linear extrapolation, because we are interested in the mechanistic changes in a population, and not specifically only in vendace. Instead of using the absolute GSI values to describe reproductive senescence in the model, we standardized 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 nonsenescent 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.

When actuarial senescence was not modeled, the instantaneous 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 an instantaneous natural mortality rate (M) that increases with age. The senescence scenario was modeled 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

TABLE 1 A summary of the average lengths, median gonadosomatic indices (GSI), actuarial senescence, and reproductive senescence parameters

	Empirical data					
Age [years]	**1**	**2**	**3**	**4**	**5**	**6+**
Average length [mm]	89	114	130	137	146	147
Median GSI	25	24,747	23,184	18,841	NA	NA
	Natural mortality (M) for each year class					
Scenario without actuarial senescence	NA	0.257	0.257	0.257	0.257	0.257
Scenario with actuarial senescence	NA	0.2	0.258	0.314	0.372	0.428
	Fecundity factor					
Scenario without reproductive senescence	x 0	x 1	x 1	x 1	x 1	x 1
Scenario with reproductive senescence	x 0	x 0.990	x 0.927	x 0.754	x 0.612	x 0.498

Note: The natural mortality parameters for actuarial senescence describe how the natural mortality is spread across year classes. Natural mortality is expressed as an instantaneous rate. Fecundity was calculated as 39.060 + 118.470 * wg, where wg = weight in grams at age t. For populations not experiencing senescence, this was multiplied by a fecundity factor of one each year, meaning fecundity did not change with age. For populations experiencing reproductive senescence, this was multiplied by the fecundity factor shown above, simulating declining fecundity with age. For fish under the reproductive age of 2, the fecundity factor was zero, and therefore, no reproduction took place. The fecundity factor describes the relative change in gonadosomatic index (GSI) over age classes.

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 natural mortality at the population level was set 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 rate remained unchanged over age classes or increased with age, the total realized natural mortality for a population over time was equal, only the distribution among age classes differed.

An increase in natural mortality following sexual maturity 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 maturation, that is, 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 maturation 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 modeled or not.

2.3 | Simulation design

The initial starting population was 2,000 individuals and the initial body size was 4 cm. The population size and the initial body size were selected due to model optimization and play no role in the results of the study. A burn-in simulation of 1,000 years was then run for each scenario. All populations reached a state of ecological stability in approximately 600 years. The population carrying capacity is 75 units. The populations leveled off at around 56–61 units. One hundred ecologically and evolutionarily stable populations were saved for all scenarios, and these populations were then 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 (Salmi, 1998), 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 $r(l) = \left(\frac{\exp(a+bl)}{1+\exp(a+bl)}\right)$, where $r(l)$ = 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 (for reasons why we assume gillnetting to have a dome-shaped selectivity curve, see (Kuparinen et al., 2009)) $r(l) \sim \exp\left(-\frac{(l-\mu)^2}{2\sigma}\right)$, where $r(l)$ = 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 seining or 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 nonsenescent scenarios. All scenarios were explored across pristine, harvest and recovery periods over 500 years. We created 100 independent replicates for each scenario.

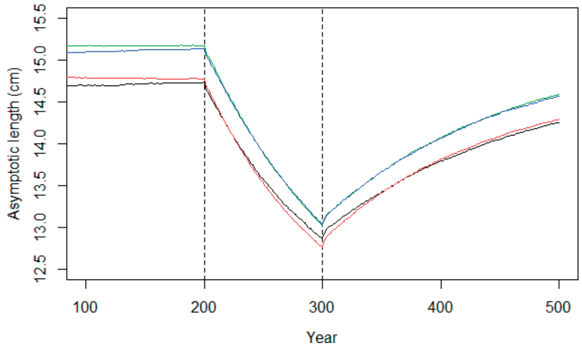

FIGURE 2 The mean of the asymptotic length (cm) of fish over 500 years (first hundred years not shown). The dashed lines denote the start (year 200) and end (year 300) of fishing. The solid lines denote the asymptotic length mean in hundred replicated scenarios. The black line describes a scenario with 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

All simulations and analyses were conducted using R version R-4.0.3 (R Core Team, 2018). The code is available in the Supplementary material.

3 | 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 (Figure 2). 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 output variables investigated. Given that actuarial senescence appeared to be the major cause of the differences (Figure 2), likely due to the relatively low reduction in reproductive output with age (Figures S1 and 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. This is because the GSI is based on empirical data (Karjalainen et al., 2016), so comparing a scenario based on actual empirical data to a scenario where both reproductive and actuarial senescence are assumed completely absent enables us to investigate the potential differences between models that include and do not include empirical life-history characteristics of senescence. Additionally, reproductive and actuarial senescence are known to be linked (Kirkwood & Shanley, 2010), so exploring either both types of senescence together or none at all is biologically more relevant than separating the senescence types.

No trends toward different life-history strategies were seen between the different simulation replicates in either the scenarios with senescence (Figure S3) or without senescence (Figure S4).

3.1 | Asymptotic length, body size, and age

The populations with senescence had a consistently lower L_∞ than those with no senescence. For both the senescent and nonsenescent scenarios, fishing caused a decline in L_∞ (Figure 3a,b), and the decline caused by trawling (Figure 3a) was larger than the decline caused by gillnetting (Figure 3b), 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_∞ than the nonsenescent scenario when trawled (Figure 4a). The opposite occurred when gillnetting was applied: The senescent scenario had a larger drop in L_∞ as a result of dome-shaped fishing compared to the nonsenescent scenario (Figure 4b). When fishing was ceased after 100 years, L_∞ started to increase slowly in all scenarios, but in none of the scenarios did the L_∞ 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 Figure 5a,b,c,d, respectively.

Investigation into the variation among individuals in the evolved asymptotic length showed no alternative life-history strategies at any stage before, during, or after fishing, and in both the senescent and nonsenescent scenarios the asymptotic length distribution was approximately normally distributed (Figure S5). The variation in fish body size (not asymptotic length) (Figure S6) and age structure (Figure S7) revealed a shift toward smaller and younger individuals during fishing, much like seen in Figures 3 and 4 for the average asymptotic length. When looking at the size and age distribution together (Figure 6), it can be seen that in the senescent scenarios both trawling (Figure 6c,d) and gillnetting (Figure 6e,f) led to a slight reduction in the variation of body size in the older age groups, compared to the scenario with no senescence (Figure 6d for trawling, Figure 6f for gillnetting). One hundred years after fishing was ceased, these differences had largely diminished (Figure 6g-j).

3.2 | Biomass

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

Regardless of the type of fishing, the relative drop in biomass for populations with senescence was smaller than for those with no senescence (Figure 4c,d). When trawling was applied, the level of biomass stayed relatively constant for both senescent and nonsenescent scenarios (Figure 4c). However, gillnetting caused a sharp decline in biomass then a sharp increase and then a slow, continuous decline for both scenarios (Figure 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 as large fish were again free from harvest and then a sharp drop as density-dependent processes started controlling the population again. These peaks and drops were larger in the gillnetting scenario than in 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 prefishing levels.

3.3 | 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 (Figure 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 nonsenescent scenarios, and however, it never reached the prefishing level (Figure 3e). This was different from gillnetting, which caused a steady increase in the *N* during fishing, above the prefishing levels (Figure 3f). As fishing was ceased, the populations in trawling scenarios 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 prefishing 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 nonsenescent scenario (Figure 4e,f). However, as the fishing continued, the difference between the senescent and nonsenescent scenarios declined.

4 | DISCUSSION

Changes in fish life-history characters are known to scale up to the ecosystem level (Kuparinen et al., 2016). At the same time, many collapsed fish populations have not recovered even after significant reductions in fishing pressure or are recovering slower than expected (Hutchings & Reynolds, 2004). The causes for the lack of recovery are complex (Swain et al., 2011), but a careful look at the life-history characters of different species may enable us to better predict the response of fish populations to fishing. Our

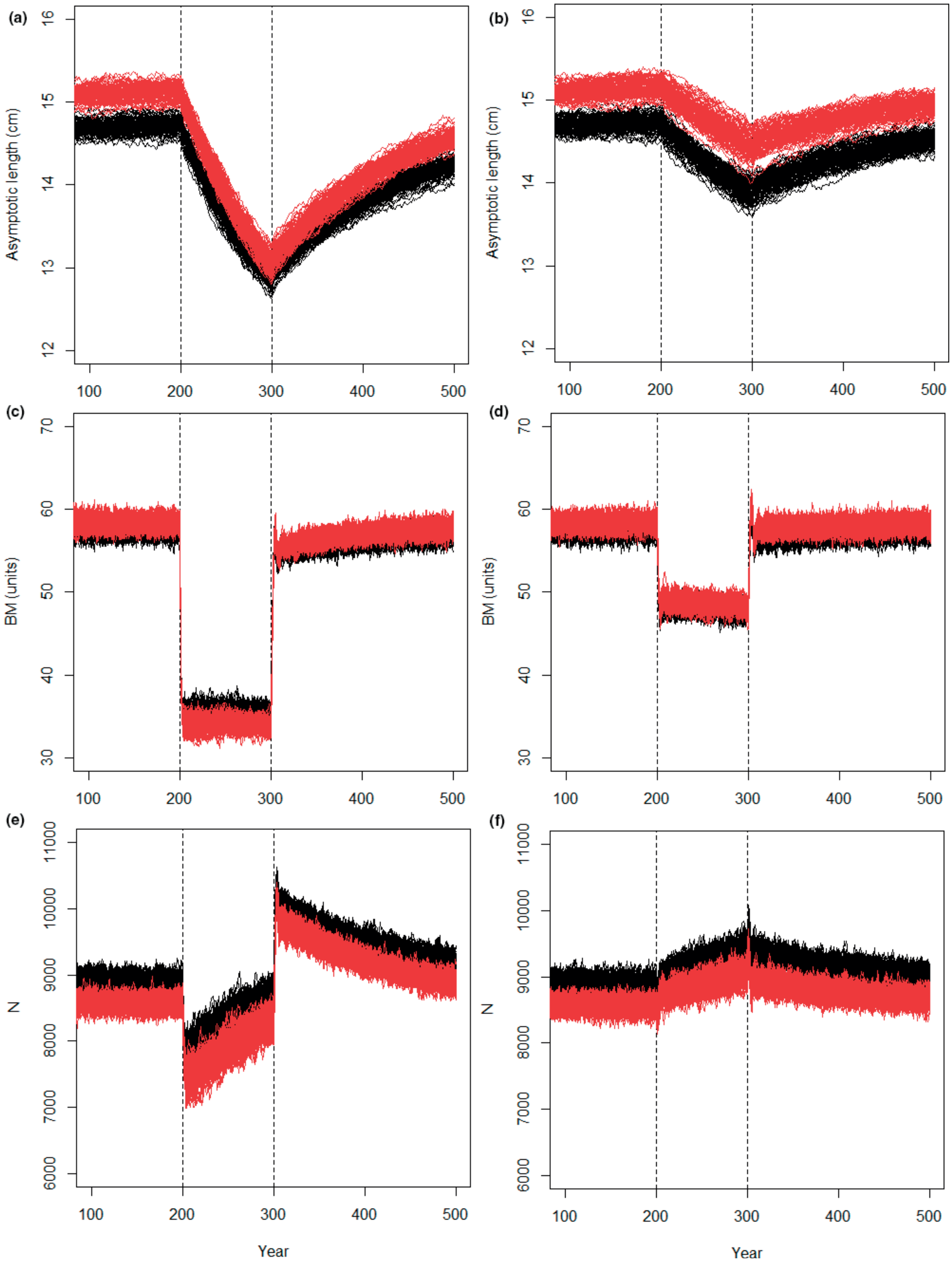
(a)
Asymptotic length (cm)
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FIGURE 3 Results for the (a, b) asymptotic length (cm), (c, d) biomass (units), and (e, f) the number (*N*) of fish. In (a, c, and e), the fishing simulated trawling (logistic selection) and in (b, d, and f) the fishing simulated 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

individual-based eco-evolutionary simulation model sheds light on how often ignored life-history characters, namely, reproductive and actuarial senescence, may affect fish population dynamics under different fishing selection regimes. While the asymptotic length of senescent and nonsenescent fish responds to different fishing selection regimes with a different magnitude, the population level consequences of senescence might be partially density dependent (Graves & Mueller, 1993). During high external mortality, it might be better to invest in reproduction rather than grow large. Indeed, 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.

An interesting connection raises from the potential link between senescence, other life-history traits associated with senescence, and fisheries induced evolution. In scenarios with senescence, populations evolved to have a smaller asymptotic length and coupled with this was a higher intrinsic growth rate, as well as evolution toward 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 lower asymptotic length was associated with higher growth rate and maturation at a younger age) and decreased survival later in life. The well-known effects of fishing-induced evolution, that is, 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 & Rose, 1991), then fishing-induced evolution could be indirectly promoting the evolution of senescence through selecting for smaller size and age at maturity.

The different response of senescent and nonsenescent scenarios to trawling and gillnetting shows that the presence or absence of senescence can affect the magnitude of the change in life-history traits in response to fishing. The evolutionary response to trawling in terms of asymptotic length was smaller in the senescent scenario than in the nonsenescent scenario. It could be speculated that the smaller asymptotic length of the senescent scenarios "pre-adapts" the population to the consequences of fishing by trawling. As the fish have a smaller asymptotic length to start with, and trawling removes specifically the large fish, the relative change in their asymptotic length is therefore not as large as in the scenarios with no senescence where the asymptotic length is higher to start with. Additionally, as the fish in the senescent scenario matured younger and smaller already before any fishing-induced evolution took place, the evolutionary pressure for change is not as high as it would be for the nonsenescent scenario where fish are larger and mature larger and older.

Gillnetting, on the other hand, allows some of the larger individuals to escape, and as a result, the evolutionary response in asymptotic length is smaller than in the trawling scenario. However, the magnitude of the response is the opposite from the trawling scenario: When gillnetting was applied, the senescent population had a stronger response in asymptotic length than did the nonsenescent population. On the one hand, given that the nonsenescent scenario would have more old and large fish alive than the senescent scenario, those old and large individuals could help keep the asymptotic length in the population higher than in the senescent scenario. In the senescent scenario, on the other hand, the proportion of smaller fish was higher to start with, making the asymptotic length decline more in response to fishing as more smaller fish would pass on more genes for lower asymptotic length. These different responses of senescent and nonsenescent scenarios to different fishing regimes highlight the importance of considering life-history traits when managing fish populations that are exposed to different types of fishing selection, especially as these differences are seen even when the variation in age and size structures between scenarios are very small.

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 nonsenescent populations was 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 nonsenescent 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 nonsenescent population. Our simulation allowed for control over the fishing mortality, and the catch in terms of biomass was set identical for the senescent and nonsenescent populations. Before the start of fishing, the population with senescence had a lower biomass than that of the nonsenescent 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 nonsenescent population (which had a higher biomass initially). Therefore, the lower asymptotic length of the senescent population 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 nonsenescent population in trawling.

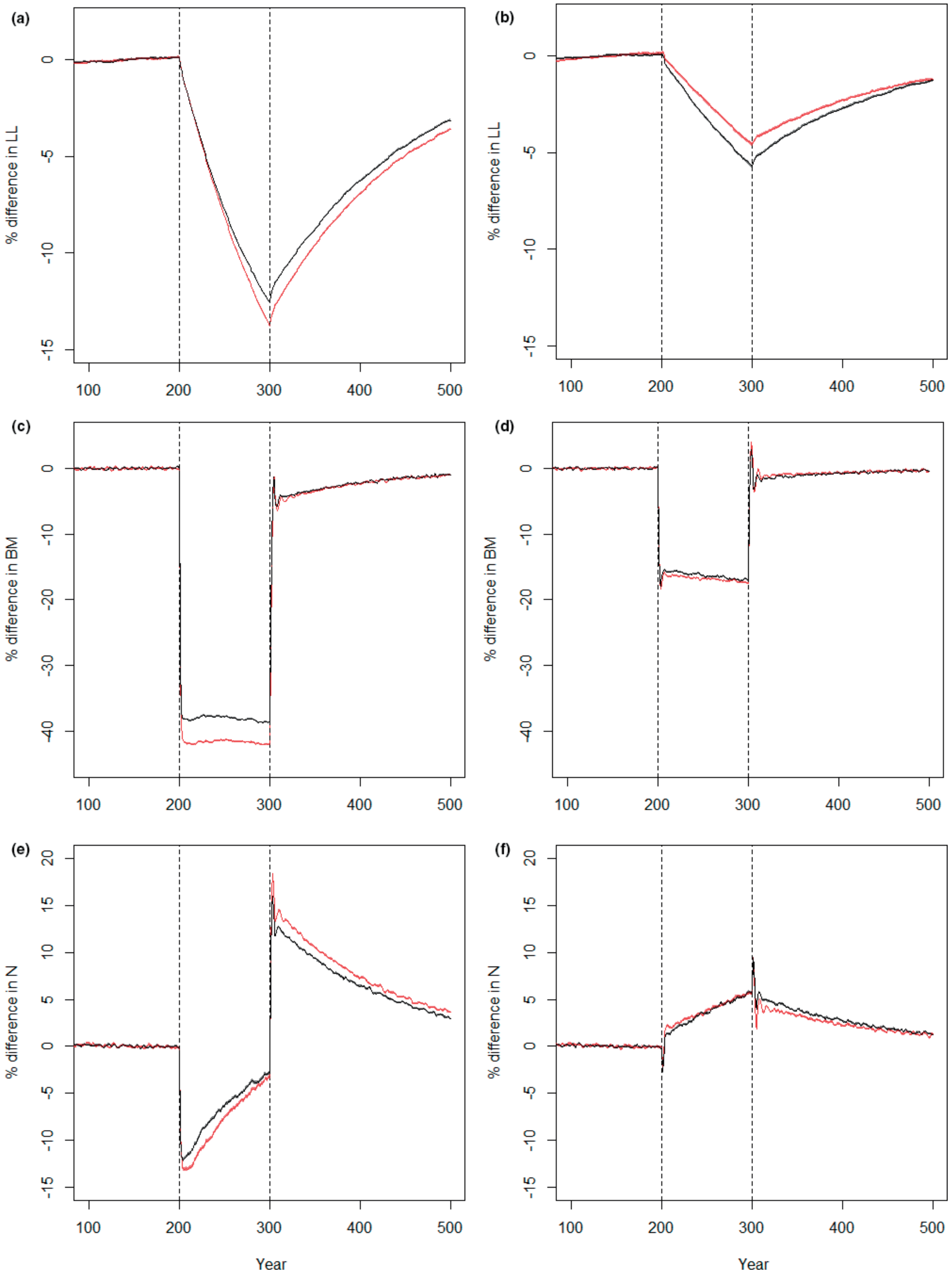
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FIGURE 4 The relative percentage change (a, b) asymptotic length (cm), (c, d) biomass (units), and (e, f) the number (*N*) of fish. In (a, c, and e), the fishing simulated trawling (logistic selection) and in (b, d and f) the fishing simulated gillnetting (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, and 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

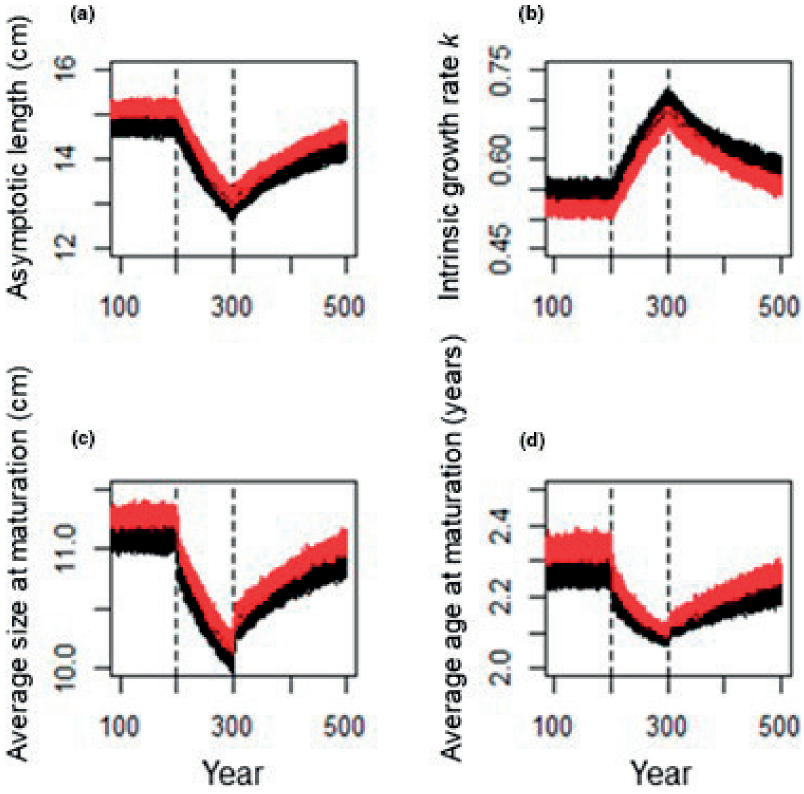

FIGURE 5 Results for the (a) asymptotic length (cm), (b) intrinsic growth rate *k*, (c) average size (cm) at maturation, and (d) average age (years) at maturation over hundred years (first hundred years not shown). The black lines represent hundred independent replicates of the scenario with senescence, and 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

The explanation for the higher biomass and the higher number of fish in the senescent scenario during trawling compared to the nonsenescent scenario is likely in the life-history 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 also reflected in the fact that compared to the nonsenescent scenario, the senescent scenario had a smaller size variation of old individuals, but the size variation of young individuals did not differ from that in the nonsenescent scenario. Consequently, due to the carrying capacity restriction, the truncated size structure in the older age groups for the senescent scenario allowed for more variation in the size structure of the younger age groups, and therefore potentially higher reproductive output, given that body size influences fecundity.

Gillnetting presents a different kind of selection curve than trawling. While the logistic selection curve of trawling allows virtually no escape of the larger fishes, the dome-shaped selection curve of gillnetting selects the mid-sized and allows the escape of small and large fish. This kind of selection curve leads to a less skewed population in terms of size and age (Figure 6). While the fish in the senescent scenario were smaller, there were more of them than in the nonsenescent scenario. As a result, the responses of the senescent and the nonsenescent scenarios to gillnetting in terms of biomass did not differ as much as they did to trawling. Like in the trawling scenario, the increased reproduction of younger and smaller fish is likely to drive the relatively higher biomass of the senescent population.

Based on the evidence for the presence of senescence in fish (Benoît et al., 2018; Beverton et al., 2004; Carlson et al., 2007; Comfort, 1960, 1963; Gerking, 1957; Hendry et al., 2004; Morbey et al., 2005; Patnaik et al., 1994; Reznick et al., 2004, 2006; Terzibasi Tozzini et al., 2013; Uriarte et al., 2016; Woodhead, 1998; Woodhead & Ellett, 1966, 1967, 1969a, 1969b; Žák & Reichard, 2020), 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

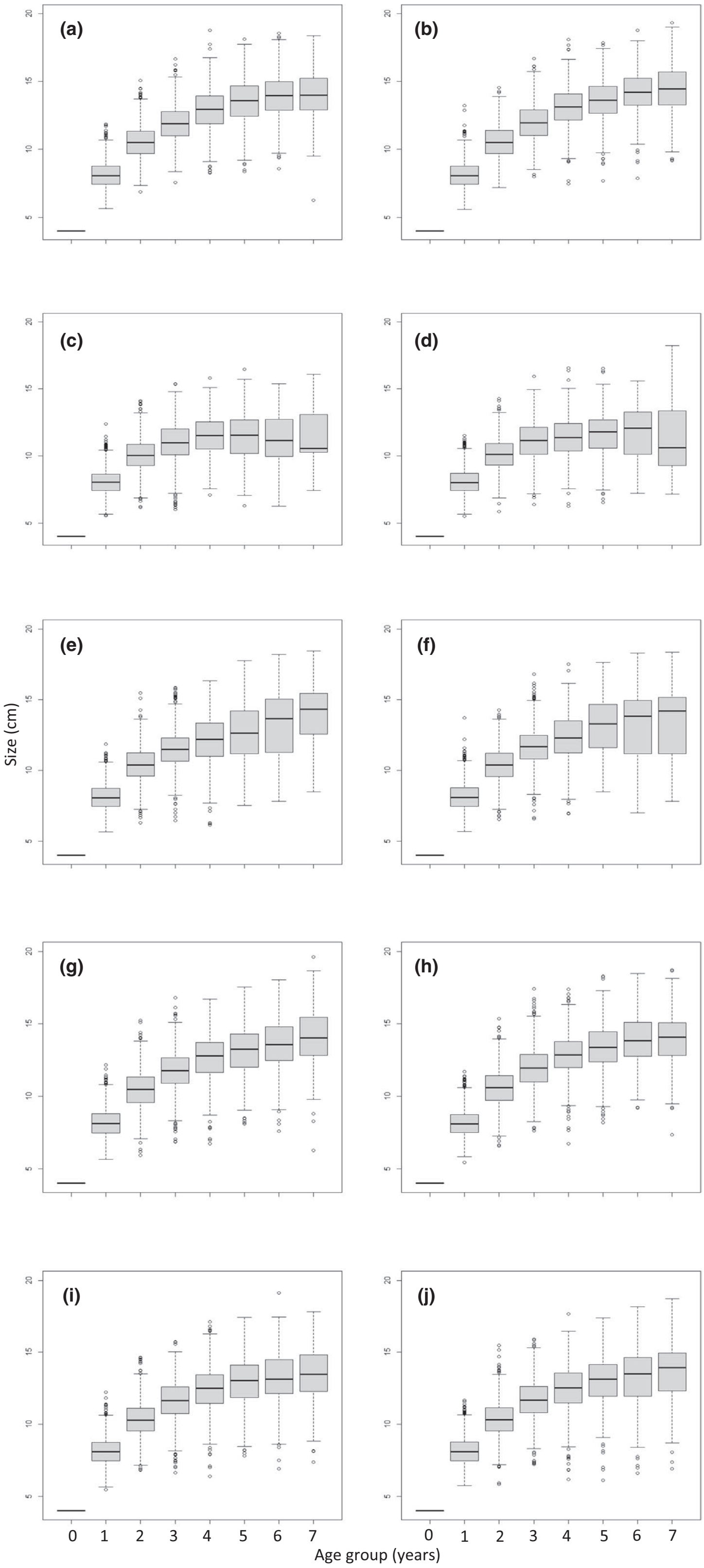

FIGURE 6 The fish size (cm) distribution by age groups. The different panels are as follows: (a) Senescence scenario before fishing, (b) No senescence scenario before fishing, (c) Senescence scenario during fishing (logistic selection), (d) No senescence scenario during fishing (logistic selection), (e) Senescence scenario during fishing (dome-shaped selection), (f) No senescence scenario during fishing (dome-shaped selection), (g) Senescence scenario after fishing (logistic selection), (h) No senescence scenario after fishing (logistic selection), (i) Senescence scenario after fishing (dome-shaped selection), and (j) No senescence scenario after fishing (dome-shaped selection)

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.

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 (summarized in Gislason et al., 2010), thereby assuming a decreased rate of natural mortality as the individual grows and ages. While accurate for many species, for species experiencing senescence, ignoring increasing natural mortality with age could lead to unrealistically low mortality estimates, as well as skewed fecundity estimates given that the old and large individuals may not be there to reproduce. 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.

Senescence can mask changes in life-history responses to fishing. As demonstrated in the present study, the presence or absence of senescence can affect how the population responds to different fishing selections regimes: while trawling reduced the asymptotic length of nonsenescent 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 depending on whether senescence is present or not. 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.

The shortage of pristine environments brings limitations to all ecological studies. This was no different in the current work. Our model was parametrized with data from a fished population because it is impossible to collect data from a pristine population given that as soon as the data are collected the population is no longer pristine. It is likely, however, that this has no effect in the results of the study, as the study focuses on large mechanisms instead of absolute numbers, and most populations of concern for fisheries management are also fished. Similarly, mathematical simulation modeling allows for data generation based on collected empirical data, and the relatively low sample size of 93 individuals was therefore sufficient for the present work. By their very nature models are simplifications of the real world, and before used to predict phenomena in other populations, the life-history characters of such populations should be cautiously considered.

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CONFLICT OF INTEREST

The authors declare no conflict of interests.

AUTHOR CONTRIBUTIONS

Pauliina A. Ahti: Conceptualization (equal); formal analysis (lead); writing-original draft (lead); writing-review & editing (lead). **Silva Uusi-Heikkilä:** Supervision (equal); writing-review & editing (supporting). **Timo J. Marjomäki:** Resources (equal); writing-review & editing (supporting). **Anna Kuparinen:** Conceptualization (equal); funding acquisition (equal); supervision (equal); writing-review & editing (supporting).

DATA AVAILABILITY STATEMENT

The code used for the simulations is accessible in Dryad at https://doi.org/10.5061/dryad.c866t1g7j.

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III

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by

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IV

INVASION OF THE ECOSYSTEM SNATCHERS: THE NON-NATIVE QUAGGA MUSSEL CAUSES A BOTTOM-UP EFFECT IN AN AQUATIC FOOD WEB MODEL

by

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