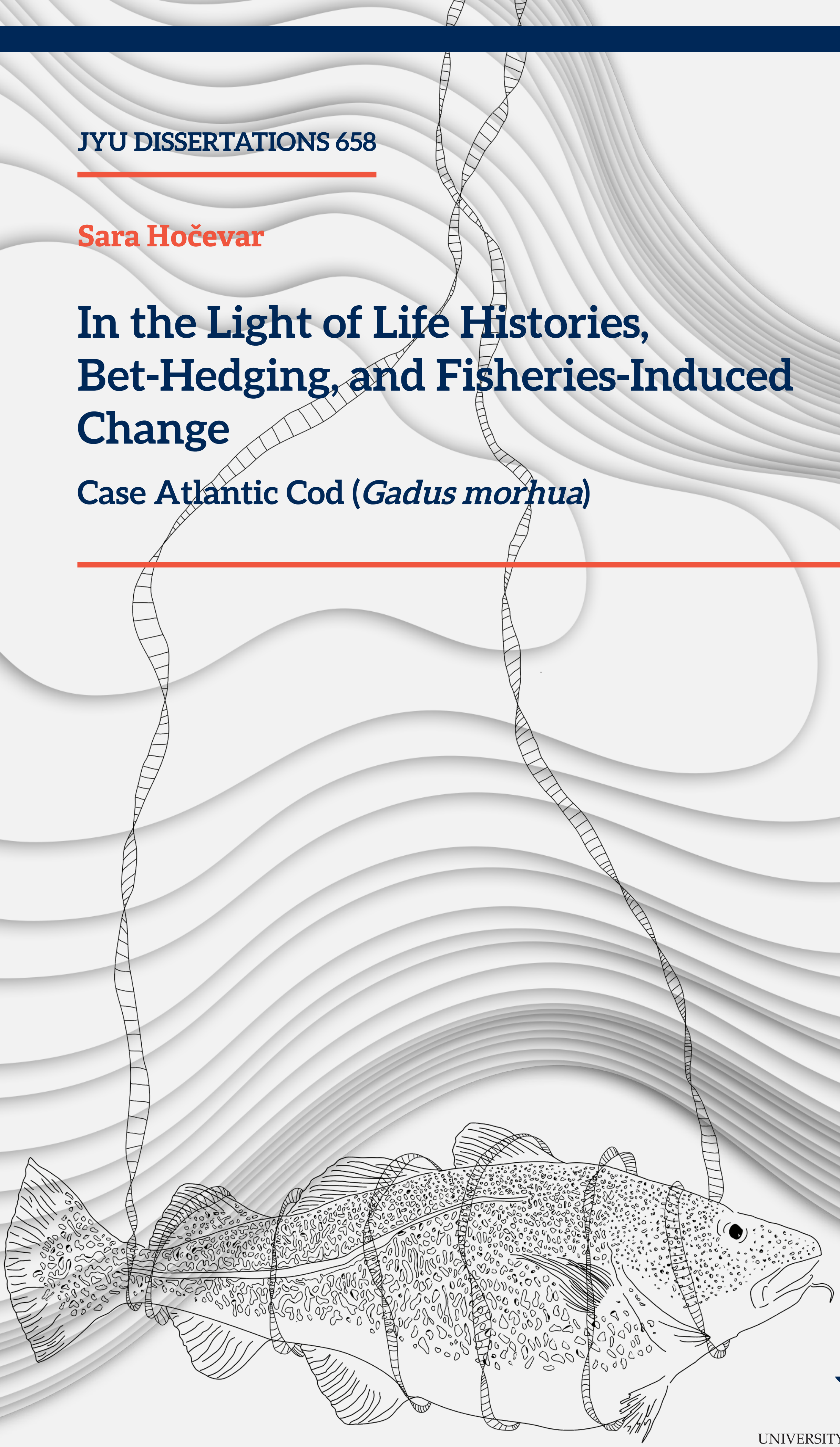
JYU DISSERTATIONS 658

Sara Hočevar

In the Light of Life Histories, Bet-Hedging, and Fisheries-Induced Change

Case Atlantic Cod (*Gadus morhua*)



UNIVERSITY OF JYVÄSKYLÄ
FACULTY OF MATHEMATICS
AND SCIENCE

JYU DISSERTATIONS 658

Sara Hočevar

In the Light of Life Histories, Bet-Hedging, and Fisheries-Induced Change

Case Atlantic Cod (*Gadus morhua*)

Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella
julkisesti tarkastettavaksi Ylistönrinteen auditoriossa YAA303
kesäkuun 2. päivänä 2023 kello 12.

Academic dissertation to be publicly discussed, by permission of
the Faculty of Mathematics and Science of the University of Jyväskylä,
in Ylistönrinne, auditorium YAA303, on June 2, 2023, at 12 o'clock.

JYVÄSKYLÄN YLIOPISTO
UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 2023

Editors
Timo Marjomäki
Department of Biological and Environmental Science, University of Jyväskylä
Päivi Vuorio
Open Science Centre, University of Jyväskylä

Cover art by Sara Hočevar.

ISBN 978-951-39-9640-6 (PDF)
URN:ISBN:978-951-39-9640-6
ISSN 2489-9003

Permanent link to this publication: http://urn.fi/URN:ISBN:978-951-39-9640-6

ABSTRACT

Hočevar, Sara
In the light of life histories, bet-hedging, and fisheries-induced change: case Atlantic cod (*Gadus morhua*)
Jyväskylä: University of Jyväskylä, 2023, 62 p. + original papers
(JYU Dissertations
ISSN 2489-9003; 658)
ISBN 978-952-39-9640-6 (PDF)
Diss.

Nature is full of complex phenomena, non-linearity, random chances, and less random changes. These conditions promote diversity among and within species, in their life histories and ecological roles. In this thesis, I untangled some of the evolutionary and ecological advantages that the life history diversity of the iconic Atlantic cod, *Gadus morhua*, generates and maintains at different levels of biological organisation. I explored the eco-evolutionary dynamics by applying the mechanistic models to empirical systems; one parameterized for Atlantic cod, and another for a newly built Skagerrak food web. Analyses of fitness components revealed that multiple-batch spawning is a risk-spreading strategy of cod, an adaptation to hedge its evolutionary bets when the environmental conditions impacting the survival of egg batches are uncertain and destructive. Because multiple-batch spawning is a size-related trait, the size-selective fishing was found to cause a lingering eco-evolutionary change, not only by selective removal of bigger and older individuals, but also by an unforeseen removal of individuals with the greatest risk-spreading potential. These findings reveal that the risk-spreading benefits multiple-batch spawning provides, are not advantageous under size-selective fishing, considering it does not protect the fitness nor demographic structure of Atlantic cod. I have tackled the role of the co-existing Fjord cod and North Sea cod ecotypes for the food web topology and functioning in a coastal pelagic food web of Skagerrak and found that the intraspecific differences in life-history traits and ontogenetic dietary shifts between the ecotypes led to counterintuitive opposing impact on the fish community. Skagerrak food web proved less robust to the loss of a smaller stationary Fjord cod ecotype, of which absence induced a decline in the biomass of several economically valuable harvested species. Diversity was a silver lining of the four papers, all cautioning about the causes and consequences of fisheries-induced changes that reduce such diversity at any of the three levels: individual, populational, food web.

Keywords: Atlantic cod; bet-hedging; eco-evolutionary dynamics; fisheries-induced evolution; fitness; food web; life histories.

Sara Hočevar, University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FI-40014 University of Jyväskylä, Finland

TIIVISTELMÄ

Hočevar, Sara
Elinkiertonäkökulma riskin hajauttamiseen ja kalastuksen aiheuttamiin muutoksiin: tutkimuslajina Atlantin turska
Jyväskylä: Jyväskylän yliopisto, 2023, 62 s. + alkuperäiset julkaisut
(JYU Dissertations
ISSN 2489-9003; 658)
ISBN 978-952-39-9640-6 (PDF)
Diss.

Luonto on täynnä monimutkaisia ilmiöitä, epälineaarisuutta ja enemmän tai vähemmän satunnaisia muutoksia. Nämä olosuhteet ylläpitävät vaihtelua lajien välillä ja lajien sisällä elinkierto-ominaisuuksissa sekä yksilöiden ekologisissa rooleissa. Tässä väitöskirjassa tutkin biologisen systeemin eri tasoilla evolutiivisia ja ekologisia hyötyjä, jotka liittyvät Atlantin turskalla (*Gadus morhua*) havaittuun vaihteluun elinkierto-ominaisuuksissa. Tutkin eko-evolutiivista dynamiikkaa hyödyntäen empiirisille systeemeille kehitettyjä mekanistisia malleja Atlantin turskalle sekä Skagerrakin ravintoverkolle. Kelpoisuuden analysointi osoitti, että turskan kudun jakaminen useisiin kutukertoihin on riskin hajauttamisstrategia eli adaptaatio, joka tukee munien selviytymistä vaihtelevassa ja epävakaassa ympäristössä. Kyky kutea useassa osassa riippuu kalan ruumiin koosta. Siksi valikoiva kalastus ei ainoastaan vähennä suurien, vanhojen kutukalojen osuutta populaatiossa vaan myös poistaa ne yksilöt, joilla on paras kyky riskin hajauttamiseen. Valikoiva kalastus syö riskin hajauttamisen kelpoisuushyödyt, koska kalastus ei suojele Atlantin turskan evolutiivista kelpoisuutta eikä populaation demografista rakennetta. Tutkin myös kahden turskaekotyypin, rannikko- ja pohjanmerenturskan, rooleja Skagerrakin pelagisen ravintoverkon rakenteessa ja toiminnassa. Turskan ekotyyppien välisillä eroilla elinkierto-ominaisuuksissa ja ravinnon käytössä on yllättäviä vaikutuksia koko kalayhteisöön: Skagerrakin ravintoverkko on herkempi pienemmän rannikkoekotyypin vähenemiselle, ja ekotyypin häviäminen johti monen muun kaupallisesti kalastetun kalalajin biomassojen vähenemiseen. Väitöskirjan neljän tutkimusartikkelin yhteinen nimittäjä on vaihtelu, ja kaikki artikkelit varoittavat seurauksista, joita voi aiheutua, jos kalastus vähentää vaihtelua yksilöiden välillä tai populaatio- ja ekosysteemitasolla.

Avainsanat: Atlantin turska; eko-evolutiivinen dynamiikka; elinkierto-ominaisuudet; kalastuksen aiheuttama evoluutio; kelpoisuus; ravintoverkko; riskin hajauttaminen.

Sara Hočevar, Jyväskylän yliopisto, Bio- ja ympäristötieteiden laitos PL 35, 40014 Jyväskylän yliopisto

Author's address Sara Hočevar
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland
sara.s.hocevar@jyu.fi

Supervisors Professor Anna Kuparinen
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland

Professor Jeffrey A. Hutchings
Department of Biology
Dalhousie University
Canada

Reviewers Professor Andrew Simons
Department of Biology
Carleton University
1125 Colonel By Drive, Ottawa, ON K1S 5B6
Canada

Professor Eric Palkovacs
Department of Ecology and Evolutionary Biology
University of California, Santa Cruz
130 McAllister Way, Santa Cruz, CA 95060
USA

Opponent Professor Per Lundberg
Department of Biology
Lund University
Ekologihuset, Sölvegatan 37, 223 62 Lund
Sweden

To fish, bees, and trees,

and their keepers.

CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This doctoral thesis consists of a summary and four original papers, which are referred to in the text by their Roman numerals (I–IV).

I Hočevar S., Hutchings J.A. & Kuparinen A. 2021. Multiple-batch spawning as a bet-hedging strategy in highly stochastic environments: An exploratory analysis of Atlantic cod. *Evolutionary Applications* 14: 1980–1992. https://doi. org/10.1111/eva.13251

II Hočevar S., Hutchings J.A. & Kuparinen A. 2022. Multiple-batch spawning: a risk-spreading strategy disarmed by highly intensive size-selective fishing rate. *Proceedings of the Royal Society B: Biological Sciences* 289, 20221172. https://doi.org/10.1098/rspb.2022.1172

III Hočevar S., Perälä T., Olsen E., Falkenhaug T. & Kuparinen A. *Contrasting trophic roles of Atlantic cod ecotypes in a coastal pelagic food web*. Manuscript.

IV Hočevar, S. & Kuparinen A. 2021. Marine food web perspective to fisheries-induced evolution. *Evolutionary Applications* 14: 2378–2391. https://doi. org/10.1111/eva.13259

Authors' contribution to the original publications.

Publication	I	II	III	IV
Conceptualization	SH, JH, AK	SH, JH, AK	SH, AK, EO, TF	SH, AK
Data simulations	SH	SH	SH, TP	
Formal analysis	SH	SH	SH	
Drafting the manuscript	SH	SH	SH	SH
Finalizing	SH, JH, AK	SH, JH, AK	SH, TP, EO, TF, AK	SH, AK

SH = Sara Hočevar, JH = Jeffrey A. Hutchings, AK = Anna Kuparinen, EO = Esben Olsen, TF = Tone Falkenhaug, TP = Tommi Perälä

1 INTRODUCTION

1.1 What's in the sea? Today's stocks and major threats

Almost two centuries have passed since Charles Darwin boarded the second voyage of His Majesty's ship Beagle to explore new lands of South America. As he ventured around the world between December 1831 and October 1836, he kept a colourful journal on the variety of species he encountered and the ideas he grasped. From varying amounts of ink released by cuttlefish to a peculiar defence behaviour of a porcupinefish, from various arts of fishing to a breakfast served with fish and coffee one April morning at Campos Novos in Brazil; Darwin described fish to be diverse and plentiful, supporting an astonishing amount of marine and terrestrial life, including birds and near-shore communities (Darwin 1996). It was only five decades later at the International Fisheries Exhibition in London, when fishermen shared their worries on witnessed declining catches with one of Darwin's most vocal advocates, Thomas H. Huxley. At that time Huxley found the multitude of most important sea fisheries to be so abundant and considered fishing mortality so minor compared to natural mortality that he dismissed the fishermen's fears by stating:

"…the cod fishery, the herring fishery, the pilchard fishery, the mackerel fishery, and probably all the great sea fisheries, are inexhaustible: that is to say, that nothing we do seriously affects the number of the fish."(Huxley 1883).

After another century, during which the fisheries underwent a technological and digital revolution, Jeffrey A. Hutchings and his mentor Ransom A. Myers uncovered that one of the commercially most important stocks, the northern cod stock *Gadus morhua* L. of Newfoundland, has been declining in size and reported catches. They demonstrated that the decline was not due to the environmental reasons of colder temperatures, as claimed by Canadian governmental officials, but due to the eco-evolutionary consequences of overfishing (Hutchings and Myers 1994). Since then, a long history of high exploitation rates beyond maximum sustainable yield has been identified among multiple other fish stocks around the globe and has led to the collapse of many (Pinsky *et al.* 2011). Consequentially, a steep increasing trend in global landings or catches of marine fishes, plateaued in the 1990s (Fig. 1a) and the annual return rate turned out to be negative more frequently (Fig. 1b). As the global human population continues to grow (Fig. 1c), the demand for sustainable protein also increases, especially in the United States and the European Union (Pauly 2019). Fisheries provide at least 15 % of the global animal protein consumption and sustain other food sectors, including aquaculture, poultry, and livestock (Béné *et al.* 2015). And yet, despite being a valuable natural resource, the necessity to improve and apply management practices to fish sustainably continues to persist. The latest report of the FAO still shows an increasing trend in the percentage of overfished reported marine stocks, with less than 10 % being considered underfished since 2015 (FAO 2022). Interestingly, it is the Atlantic cod, Atlantic herring (*Clupea harengus*), and European pilchard (*Sardina pilchardus*) fisheries, previously pointed out by Huxley, which today not only still belong to the ten fisheries with the greatest landings, but whose stocks are also overfished beyond the global average. Some sort of absurdity. While in 1968 the cod fisheries reported the highest landings, 3.9 million tons, which accounted for 6.5 % of the total global landings that year, the productivity of the cod stocks and the efficiency of cod fisheries declined tremendously thereafter, accounting for 0.8 % in 2008 (Fig. 1d). As comparison, already the sum of the three countries that have the highest reported average annual cod landings, Russia, Norway, and Iceland, exceeded the cod global catch of 2008 (Fig. 2).

Therefore, while the consequences of climate change such as ocean acidification, rising temperature and increased upper stratification threaten marine ecosystems, it appears that unsustainable fishing itself might be the central threat to the health of the oceans and the fisheries economy (Halpern *et al.* 2007). Whether by harming the habitat with destructive fishing practices such as heavy trawling or by polluting the habitats with microplastic and spreading of a harmful species through ghost fishing. In addition to critically reducing stocks through overfishing, overlooked bycatch, unreported and unregulated illegal fishing, or over-reported catches that disguise the real state of a stock, fishing can lead to irreversible ecological and evolutionary change; also referred to as fisheries-induced evolution (Law 2000).

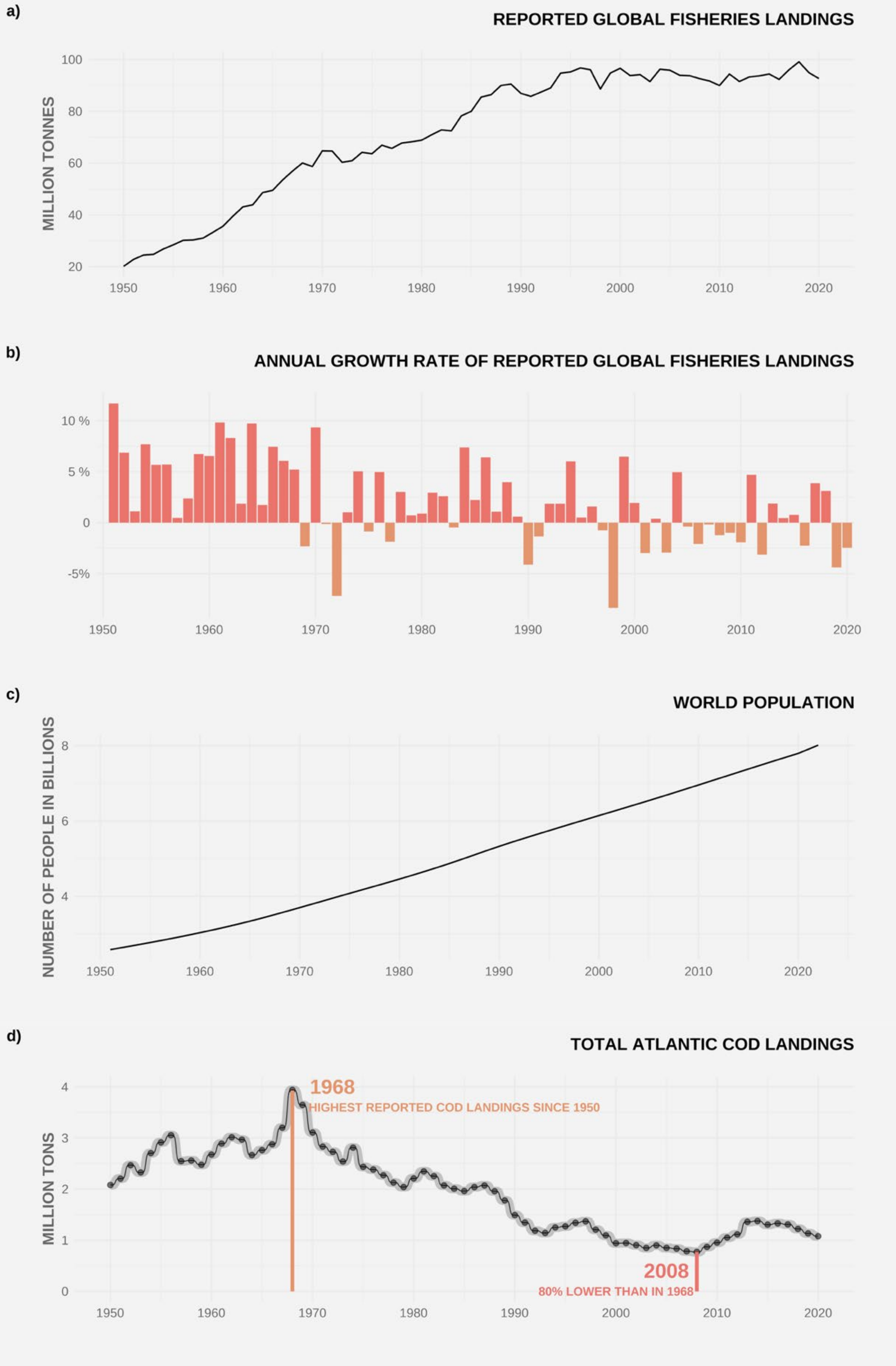


FIGURE 1 Historic time series illustrating the status of global fisheries (a,b), human population (c), and cod fisheries (d). Fisheries datasets have been obtained from the FishStatJ software version v4.02.08 curated by the Food and Agriculture Organization of the United Nations (FAO 2022) and from the world population dataset (Worldometer 2023). Fisheries landings do not include bycatch.

1.2 Fishing, fisheries, and fisheries-induced evolution

Fishing can act as a selective agent by increasing the mortality rate and decreasing the chance for reproduction of a targeted resource. But in particular, it is *fisheries* exploitation that exerts long-term mortality on a wider scale and thus has the potential to alter the phenotypic and genotypic landscape of fished populations. If the fishing strategy favours a certain heritable trait and non-randomly changes the course of natural mortality in a fished stock, the directional selection can cause a change in gene frequencies and genetic variation and thus, lead to evolution by means of fisheries selection (Law and Grey 1989, Law 2000, Kuparinen and Merilä 2007, Law 2007, Hutchings and Fraser 2008). Therefore, the key mechanism of fisheries-induced evolution is the heritability of the selected trait (h^2) and the intensity of a non-random selection (S), for which the outcome is paradoxically often the opposite of what fisheries long for, i.e., large fish.

While unequivocal direct empirical evidence for fisheries-induced evolution in wild populations is arguably still lacking (Pinsky *et al.* 2021), the observations of genotypic frequencies (Jakobsdóttir *et al.* 2011) and phenotypic changes in historic time-series of exploited stocks (Olsen *et al.* 2009) are suggestive of fisheries-induced genetic change. Theoretical and experimental comparative common-garden studies clearly linked fisheries-induced genetic change to phenotypic changes (Conover and Munch 2002, Audzijonyte *et al.* 2013, Uusi-Heikkilä *et al.* 2015). The reason lies in the controlled settings these studies offer for manipulating the rate and direction of selection, creating a less complex environment to tease apart the evolutionary change that is caused by fishing selection *per se* from the changes which are the aftermath of phenotypical plasticity and demographic processes (reviewed in Jørgensen *et al.* 2007, Heino *et al.* 2015). Different fishing strategies have been observed to generate different evolutionary changes. For example, the type of fishing gear has been linked to changes in behavioural traits. While passive fishing methods, such as gill nets, angling or traps, select for bolder individuals, active gear, such as trawling or seine, may select for more shy individuals (Arlinghaus *et al.* 2017, Díaz Pauli and Sih 2017). Mesh size is also an essential character in size-selective fishing and has been linked to changes in maturation schedule (Sharpe and Hendry 2009) and subsequent change in associated traits (Jørgensen *et al.* 2009).

Yet, fisheries do not act in a controlled manner. Along with fisheries-driven selectivity, depleted stocks simultaneously face a full-blown force of reduced population size, altered density-dependent dynamics, and unrelenting natural and sexual selectivity that can all fundamentally affect the life histories of exploited populations (Hutchings and Kuparinen 2021).

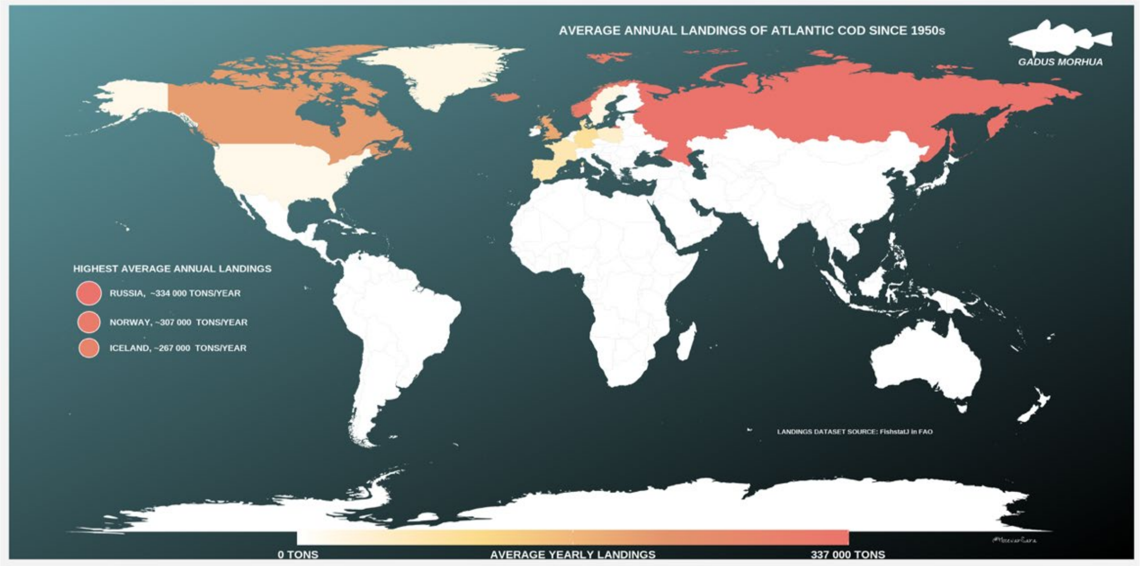


FIGURE 2 World map illustrating average reported annual landings of cod fisheries by country. Average annual landings have been estimated from FishStatJ database (FAO 2022).

1.3 Life histories

Life histories are a unique set of inherited evolutionary constraints and have undergone development within the environment that vary throughout an individual's life. Understanding the vast diversity of life histories is to understand the coadapted evolution and interactions of life-history traits with the surrounding biotic and abiotic environment, which is one of the greatest puzzles in natural science (Fisher 1930, Stearns 1976). Life-history traits are the features of species that can shape their reproductive potential while being shaped by natural selection (Cole 1954, Charnov and Schaffer 1973).

Variations among life history traits pertain to the age and size of maturation, mating frequency, maternal costs, size and the number of offspring, or lifespan and emerge among and within species (Hutchings 2021). While a female humpback whale (*Megaptera novaeangliae*) gives birth to one offspring every 2 to 3 years (Clapham 1996), Atlantic cod can spawn more than 14 million eggs in a single spawning season (Thorsen *et al.* 2010). A range of fecundity potential can also be observed within different stocks of Atlantic cod as they have adapted to their local environmental conditions. Cod in the Irish sea can mature at 1.6 years and 36 cm body length, while cod in the Barents Sea mature much later and at a bigger size, 7.2 years and 78 cm, respectively (Thorsen *et al.* 2010). Earlier maturation can be an adaptation to high mortality in later life, as the probability to be fished increases with fish size and age (Olsen and Moland 2011), or it can be a consequence of a faster growth rate in warmer regions (Nash *et al.* 2010). If other life-history traits like the reproductive lifespan or maternal costs are being ignored, and if potential fecundity is based solely on the stock-specific length–weight relationship and a constant average oocyte diameter, a 90 cm cod from the Irish sea cod could spawn 80 % more eggs than a 90 cm cod from the Barents Sea (Thorsen *et al.* 2010). However, life history traits tend to covary, making the estimates on the actual number of eggs an individual from each stock successfully produces more complex. This complex optimization is the core of life history theory; the allocation of energy reserves among life-history traits that augment the chances to survive and reproduce (Roff 1992). The measure that is being maximized and can encompass the optimality of the life-history trait combination, conditioned by the constraints and trade-offs, is *fitness*.

1.4 Fitness

The origin of the fitness concept dates back to Darwin's term on the *origin of species by means of natural selection or the preservation of favoured races in the struggle for life* (Darwin 1859), which led sociologist Herbert Spencer to conceive the term *survival of the fittest* (Spencer 1864). Darwin later adopted the term on Wallace's suggestion that *Natural Selection* might be a too metaphorical expression, and fitness has been placed into the centre of the evolutionary paradigm. Yet, the concept lacks a universal definition whilst causing plenty of confusion (Dawkins 1982), a perplexity that Stearns depicted by describing fitness as *something everyone understands but no one can define precisely* (Stearns 1976).

Fitness and its measures are context-dependent approximations. From an individual's potential to survive and reproduce, to a genotype's reproductive contribution or frequency relative to another genotype with a different combination of alleles located at the same locus, what defines fitness is a question-specific challenge. While *genotypic fitness* usually follows the fitness of a single locus, fitness in life history studies tends to portray the average contribution of multiple loci, and thus rather follows a *phenotypic fitness* or *fitness of a trait,* that evolution maximises over a longer time span (Fisher 1930). In ecology, fitness is frequently used as the *lifetime reproductive success*, a realized number of immediate offspring an individual produces over its life. Another common theoretical version is *Darwinian fitness,* which accounts for the immediate offspring and genes passed to the next generation, and for their success to produce offspring of their own, which is also describing fitness as the average fitness of all individuals sharing the same genotype. Hamilton went a step further by rising the importance of following the proportional individual's contribution to the reproductive success of its relatives, the indirect fitness, in addition to the individual's own reproductive success, direct fitness (Hamilton 1964). To counter a challenge of traceability in Hamilton's *inclusive fitness* approach, Orlove swapped the perspective into *personal fitness* which instead of following the contribution of an individual to the fitness of its relatives, it follows the contribution of relatives to the fitness of an individual (Orlove 1979).

Along with multiple conceptualizations of fitness, the methods to quantify fitness have developed too. Fisher applied the continuous population growth model (Lotka 1907) to the life-history evolution (Fisher 1930) and derived r which he named the *Malthusian parameter of population increase*. The parameter r, also called the *rate of natural increase per head* (Lotka 1907) or *an intrinsic rate of increase* (Cole 1954) describes the difference between the per capita birth and death rates in a continuous time. It stems from a density-independent population with non-overlapping generations, inhabiting a constant stable environment, where time is discrete, and the life-history evolution is expected to maximize the proportional rate of change in population size from one time step to the next. However, populations in nature generally do not grow indefinitely, are density-dependent, compete for limiting resources, are often exposed to variation in temporal and spatial environmental conditions, and are age-structured, with intrinsic demographic stochasticity, which can, for instance, arise from variation in age-scheduled reproduction. Therefore, the most suited quantitative life-history model to calculate fitness as the product of life-history optimization in life-history research depends upon the question and the set of biological assumptions pertaining to the populational dynamics of the species, phenotype or genotype in its explicit environment (Metz *et al.* 1992, Benton and Grant 2000, Roff 2008), with a typical focus on the observed life-history trait or a strategy (Stearns 2000).

1.5 Bet-hedging

Change is the essence of natural environments. When the magnitude of abrupt changes exceeds the organism's ability to survive and reproduce, changes can lead to a decline in the population or even its extinction (Kaiho 2022). Some species have adjusted to the changing multi-dimensional environmental conditions with the adaptive strategies known as risk-averse and risk-spreading strategies. As their name suggest, these adaptations either increase the chance of survival and reproduction by actively avoiding the risk of low success to increase the average success, or by spreading the risk on the evolutionary time scale by reducing the variance in success (Meyers and Bull 2002).

Bet hedging is a strategy, where genotypes hedge their bets against environmental uncertainty and reduce the reliance of genotypic success on the outcome of a single environmental condition (Slatkin 1974). In a temporally fluctuating environment, a bet-hedging strategy trades the average reproductive success or the *arithmetic mean fitness* for the reduced variance in the reproductive success to maximize the long-run reproductive success or the *geometric-mean fitness* (Gillespie 1974). The geometric-mean principle can signify what evolution maximizes in a temporally variable environment, as it is sensitive to the variance in reproductive success over the generation (Sæther and Engen 2015).

Bet hedging traits and strategies can reduce the variance in the long-term reproductive success of a genotype at the individual or at the population level

(Seger and Brockmann 1987). At the individual level, the strategy maximizes the geometric mean fitness of an individual by reducing the reproductive success following the proverb "bird in the hand is worth two in the bush", where contributing a lower number of offspring at no or lower risk is advantageous over an uncertain chance of producing more with a high risk of producing none. This type of bet-hedging tends to select for an optimal trait value and is typically referred to as conservative bet-hedging (Seger and Philippi 1989) or perhaps a more suitable description, one extreme end on a continuum (Starrfelt and Kokko 2012). On the other end of the continuum is diversified bet-hedging. This strategy involves phenotypic variance among individuals within or among generations. By increasing the variation within a generation, this strategy lowers the arithmetic mean fitness within generations, but reduces the variation in arithmetic mean fitness among-generations, leading to long-term success. Therefore, diversifying bet-hedging optimizes the geometric mean fitness of a genotype following the phrase "don't put all your eggs in one basket"(Frank and Slatkin 1990).

Many species may benefit from bet-hedging. Some of these potentially include spore-producing bacteria (Veening *et al.* 2008), polymorphic insects (Witek *et al.* 2006), or desert plants producing seeds with varying dormancy periods and delayed germination (Evans *et al.* 2007, Philippi 1993) to increase the chance that at least some seeds germinate at favourable conditions, i.e. rainfall. However, only a few empirical examples have been able to provide sufficient quantitative evidence of bet-hedging (Simons 2011).

1.6 Multiple-batch spawning

Reproductive biology encompasses multiple life-history variables, some of which may resemble bet-hedging; potentially a widespread and frequent response to environmental uncertainty (Crean and Marshall 2009). Diversity in the timing of oocyte development, countless maturity schedules, various mating modes, a range of fecundity characteristics including the size, number and buoyancy of eggs, diverse degrees of reproductive effort and paternal care, or the variety in the onset and location of spawning; these are all just some of the variables that reflect the eco-evolutionary adaptations of teleost species to a large variation in the mortality that offspring and adults encounter in the aquatic environment (Rowe and Hutchings 2003, Smith and Wootton 2016). One of the variables is also spawning frequency.

Spawning frequency describes the number of spawning events within a spawning season (Lowerre-Barbieri *et al.* 2011) and different strategies can be divided into two main patterns: semelparity and iteroparity (Young 1981, Roff 1992, Stearns 1992). While semelparous species, such as Pacific salmon (*Oncorhynchus nerka*), spawn only once in their life and subsequently die (Crespi and Teo 2002), iteroparous species, such as Atlantic cod, survive spawning and can repeat it several times during the span of their life (Kjesbu *et al.* 1996).

Spawning success and the rate of adult mortality plays an important role in which of the spawning patterns is more likely to evolve. If the variation in the spawning success of species is high and egg mortality is higher relative to adult mortality, a long reproductive span with multiple reproductive events is advantageous (Murphy 1968). Iteroparous spawning patterns can be further split into total spawning and multiple batch spawning strategies. Total spawners spawn all their eggs in one single event within one spawning season, while multiple-batch spawners spawn several batches within one spawning season. Among multiple-batch spawners, there can be further variation in fecundity, which is determinate or indeterminate. If the fecundity is determinate, a batch-spawning female has all the eggs that will be spawned during the upcoming season already in her ovaries as oocytes before spawning starts. On the other hand, if the fecundity is indeterminate, the batch-spawning female does not necessarily have all the eggs present as oocytes before the onset of spawning and can develop more eggs later during the spawning season (Wootton and Smith 2014). While the latter strategy may be considered as an adaptive phenotypic plasticity, given the female's influence on the number of spawned batches in response to stored energy or favorable environmental conditions, determinate multiple batch spawning can be viewed as non-plastic. A protracted spawning season with a pre-determined number of spawning events is common in several taxonomic groups, especially in fish species occupying the boreal and temperate waters (Ganias *et al.* 2015), including Atlantic cod (Hutchings and Rangeley 2011). Size of body cavity limits the number of eggs fish can spawn per/at a spawning event (Sadovy 1996). Therefore, the prolonged spawning that facilitates higher fecundity may have evolved to overcome the somatic constraints, an adaptation favored in conditions with a high environmental unpredictability newly released eggs experience in the ocean.

But while, in theory, a prolonged spawning period with several batches that each may experience different environmental conditions and thus, different probabilities of surviving seems beneficial, empirical evidence on whether this reproductive strategy is indeed bet-hedging is difficult to obtain (Simons 2011). An example of bet hedging, illustrated in Fig. 3, depicts two Atlantic cod genotypes: one has a multiple-batch spawning strategy and the other (a hypothetical opposite) has a single-batch spawning strategy.

Ceteris paribus, and the distribution of eggs is the only difference between the two genotypes, then in order to explore that multiple-batch spawning is a bet-hedging strategy (Fig. 3), at least three premises should be fulfilled. First, there should be some variability in the environment, creating more and less favourable conditions (blue and red, respectively) for batches to hatch. Second, the multiple batch spawning strategy needs to have associated costs to the arithmetic mean fitness, where the arithmetic mean fitness of a multiple-batch spawner is lower than it is in the absence of this costly strategy, here single-batch spawners. Third, the strategy should minimize the among-generational variance in arithmetic mean fitness, leading to a higher geometric mean fitness of multiple-batch spawners compared to the geometric mean fitness of single-batch spawners. This would allow the multiple-batch spawning genotype to evolutionarily outperform the single-batch spawning genotype. In such conditions, multiple-batch spawning could be a bet-hedging strategy, rendering the genotype more robust to environmental uncertainty.

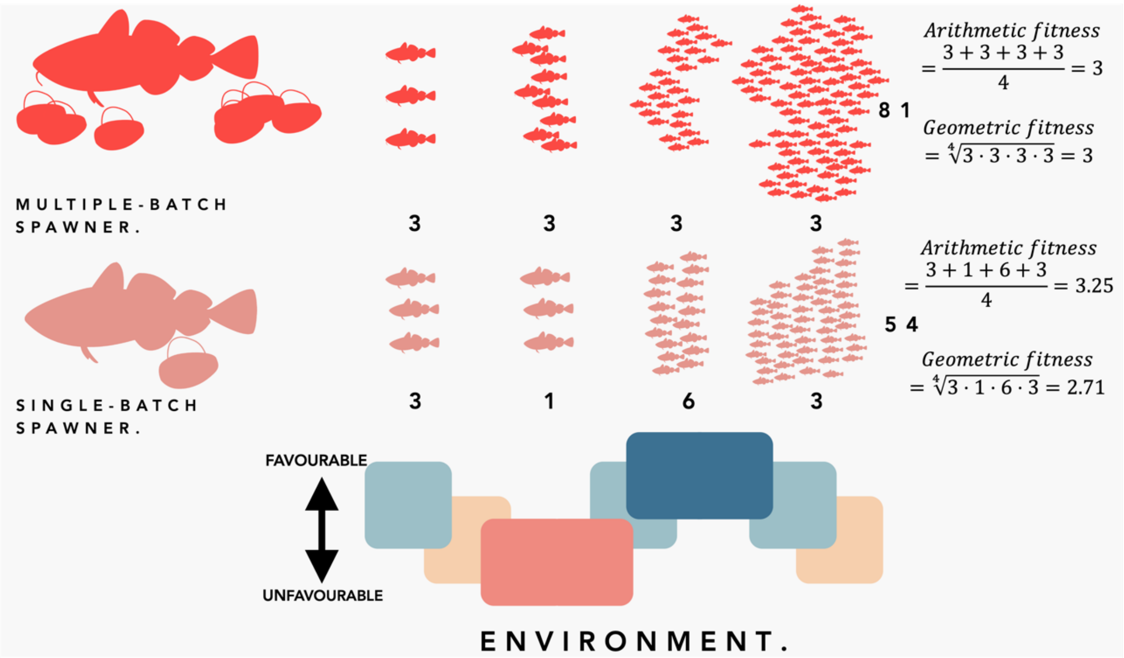


FIGURE 3 Illustration of a snip into geometric-mean fitness advantage of a bet hedging strategy with the example following the multiple-batch spawner (in red) and single-batch spawner (in pink) in a fluctuating environment with more (blue) or less (salmon pink) favourable conditions over four spawning seasons. The visualization is adapted based on Simons (2011).

1.7 From life histories to food webs

Many life-history traits and strategies of fish, including multiple-batch spawning (Kjesbu *et al.* 1996), correlate to the individual body mass and size, which ultimately influence the quantity and quality of the progeny or the reproductive output (Trippel and Neil 2004, Barneche *et al.* 2018). At the populational level, this relation translates to the relationship between the number of spawners and the number of recruits, a link central to fisheries management (Hilborn and Walters 1992). Given the overexploitation of fisheries does not only change the abundance of stocks, but also changes the demographic distribution in age and size, the fisheries-induced ecological and evolutionary changes can substantially alter the productivity potential of the stock. Changes in the demographic distribution of a stock feedback to reproductive and recruitment potential, because the contribution to populational growth depends on the age and size class the individuals belong to (Marshall *et al.* 1998, Morgan and Brattey 2005, Rideout and Morgan 2010, Ohlberger *et al.* 2020). In addition to life history traits, ecological traits such as home range, trophic status, diet niche or secondary production (Woodward and Hildrew 2002) tend to also scale allometrically with the body mass of an individual. Therefore, any profound eco-evolutionary change leading to alteration in the populational dynamics of a single species can instigate further change in the structure of the surrounding community or in the functioning of its ecosystem (Rochet and Benoît 2012, Kuparinen *et al.* 2016a). However, how evident this change might be, depends also on the topology of the food web, and its density of interactions or connectedness (O'Gorman *et al.* 2010).

The functional role of species additionally affects the extent of the impact a species may have on the stability of the ecosystem. Keystone species and ecosystem engineers, forming strong direct interactions or supporting a large number of weak indirect connections, can already at a small populational size induce disproportionally large effects or shifts within an ecosystem (Paine 1966), potentially resulting in trophic cascades (Coleman and Williams 2002). A decline in the biomass of top predators can also induce changes in the mean biomass or the biomass variance at other trophic levels (Uusi-Heikkilä *et al.* 2022) that transcends beyond the direct link to lower trophic species. For example, the overfishing of Atlantic cod, one of the dominant predators in the northwest Atlantic shelf ecosystem of Nova Scotia in the 1980s, resulted in a restructured ecosystem (Frank *et al.* 2005). Once the abundance of Atlantic cod declined, the abundance of small pelagic fishes and benthic macroinvertebrates increased, causing higher predatory pressure on herbivorous zooplankton, which in turn led to an increase in phytoplankton abundance and ultimately, resulted in altered nutrient cycling of the ecosystem. In some cases, top–down control even exceeds climate control when the prey biomass links more closely to the changes in the biomass of their predators than the changing environmental conditions (Worm and Myers 2003). Therefore, besides the functional role a species has in the ecosystem, the magnitude of a top–down control varies also depending on the strength of each direct predator–prey relationship. This has been observed in a biomass time series of Atlantic cod and northern shrimp (*Pandalus borealis*), which showed that geographic differences, local climate or the extent of anthropogenic perturbations uniquely influence the strength of the relationship by reducing or increasing the biomass of predators or their prey (Worm and Myers 2003).

In addition to changes in the population dynamics of a single species, ecosystems can also show sensitivity to changes in the life-history and functional diversity that occur at the intraspecific level (Raffard *et al.* 2021). Mesocosm studies, monitoring different taxonomic groups from plants (Crutsinger *et al.* 2006) to fish (Harmon *et al.* 2009, Palkovacs and Post 2009), revealed that unique ecological effects can emerge from distinctive genotypical and phenotypical trait variation among individuals within a population. Another example are the ecotypes of Atlantic cod. Generally, a larger migratory cod ecotype that forages in deep waters and a smaller coastal cod ecotype that forages in shallower waters occur on both sides of the Atlantic (Hemmer-Hansen *et al.* 2013). Ecotypes, described as individuals within a population capable of interbreeding but with distinctive genotypes, are an outcome of intraspecific adaptation to local environmental conditions (Hufford and Mazer 2003) that can coexist on a small geographical scale (Knutsen *et al.* 2018). Therefore, a problem arises, when the nursery, foraging or spawning habitats of these unique ecotypes overlap and are subject to the same conservation actions or exploitation measurements. Overlooking intraspecific differences exposes the ecotypes with different growth rates and maturation schedules (Olsen *et al.* 2004) to the same truncation in the size structure, but different selective pressure on the age classes, which may make one ecotype more sensitive to exploitation than the other and therefore unevenly impair the recovery potential of each (Hutchings 2005). Because ecotypes differ in their life-history traits, foraging traits, and diet niches, disentangling their role in the ecosystem might be as vital to our understanding of ecosystem functioning as is revealing the role of species.

1.8 Thesis aim and objectives

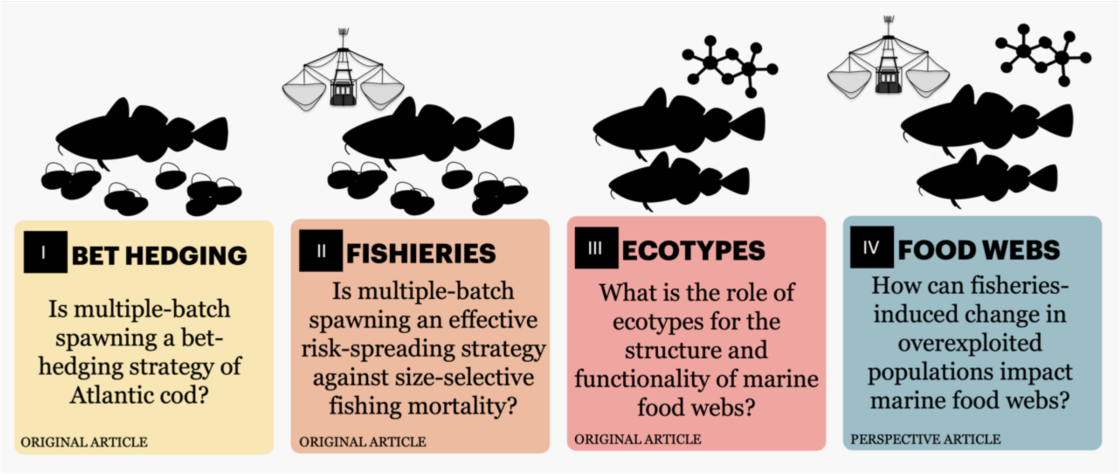
Evolutionary and ecological consequences of life history diversity shape individual survival, growth and reproduction, and can also induce a broader impact within populations or even the surrounding community, the connected food web, or the entire ecosystem. Following the interplay between the evolution and ecology in nature is mesmerising, but disentangling the influence of the multiple selective pressures and trade-offs among the underlying life history traits and strategies can be notoriously challenging. In this thesis, I aim to untangle some of the evolutionary and ecological advantages that the life history diversity of the iconic Atlantic cod, *Gadus morhua*, generates and maintains at different levels of biological organisation. By addressing four specific research objectives (Fig. 4), I explore how body size-related life-history traits and strategies impact the reproductive potential of an individual, the across-generational fitness of a population, and the functioning of a marine food web. I apply two mechanistically motivated modelling approaches to reason the complex interactions that arise in varying environmental settings.

In paper I, I study whether the reproductive strategy of multiple-batch spawning in Atlantic cod constitutes a bet-hedging. To do so, I use an eco-evolutionary individual-based model and simulate two distinct populations of Atlantic cod in stochastically fluctuating environmental scenarios. One population includes a genotype with a multiple-batch spawning strategy, that is typical for cod, and labels the individuals as multiple-batch spawners, whilst the other population presents a hypothetical opposite, and includes a genotype with a single-batch spawning strategy, and individuals labelled as single-batch spawners. While all being equal apart from the costly diversification of eggs among multiple spawned batches or uncostly diversification of eggs into one single spawned batch, I delineate the fitness consequences of the multiple-batch spawning strategy under different levels of environmental stochasticity. By following the fitness components of arithmetic mean fitness, variance in arithmetic mean fitness and geometric mean fitness, I determine whether the strategy is a bet-hedging.

In II, I explore the sensitivity of multiple-batch spawning to size-selective fishing. Because the number of batches that can be spawned per spawning season increases with maternal body size in cod, I investigate how a fisheries-induced change in the population size structure affects the geometric mean fitness. By adding fishing mortality into the eco-evolutionary individual-based model (I), and by exposing multiple-batch spawning and single-batch spawning cod populations to different intensities of size-selective fishing mortality, I illuminate the eco-evolutionary advantages and disadvantages that the multiple-batch spawning strategy contributes to the populational dynamics of Atlantic cod.

In III, I intertwine evolution and ecology into intraspecific diversity and explore the consequences of their interplay within the food web. I use an Allometric Trophic Network (ATN) model to incorporate the two Atlantic cod ecotypes: the North Sea cod ecotype and the Fjord cod ecotype, that grow at different rates and follow different trajectories in asymptotic size. I link the two cod ecotypes to semi-overlapping ontogenetic dietary niches within the ATN model, which I parameterised for the coastal pelagic food web in Skagerrak. By systematically observing changes in food web functioning that reflect changed food web topology, I illuminate the scale and direction of change that is sustained by intraspecific diversity of the two co-existing ecotypes at different trophic levels of the food web, and which can be compromised when any or both ecotypes are lost from the ecosystem.

In IV, I review and interlink studies exploring ecological and evolutionary consequences of altered genotypic or phenotypic variance of teleost species in marine ecosystems. The objective was to investigate potential pathways through which a fisheries-induced change in evolutionary or ecological dynamics and diversity of overfished fish stocks can lead to wide-ranging food web consequences. This allowed me to grasp the magnitude and multitude of potential direct and indirect mechanisms through which an eco-evolutionary change can resonate and to reason why such changes may be hard to distinguish, detect or may remain obscure.


I **BET HEDGING**

Is multiple-batch spawning a bet-hedging strategy of Atlantic cod?

ORIGINAL ARTICLE

II **FISHIERIES**

Is multiple-batch spawning an effective risk-spreading strategy against size-selective fishing mortality?

ORIGINAL ARTICLE

III **ECOTYPES**

What is the role of ecotypes for the structure and functionality of marine food webs?

ORIGINAL ARTICLE

IV **FOOD WEBS**

How can fisheries-induced change in overexploited populations impact marine food webs?

PERSPECTIVE ARTICLE

FIGURE 4 Graphical representation of the four main research objectives explored in this doctoral thesis.

2 METHODS

2.1 Atlantic cod

Atlantic cod is used as the study species in I, II, and III. There are two main reasons for this choice: the historic exploitation of Atlantic cod stocks, and the intriguing, yet fairly well researched, life history diversity of Atlantic cod. This species is a native fish to the continental shelves of the North Atlantic. High fecundity, adaptability, and a wide dietary niche equipped Atlantic cod to become a widespread and abundant species, dominating continental shelves from Greenland and the Barents Sea in the north, to Cape cod and the Celtic Sea in the south (Rose 2019). The latitudinal distribution range of some stocks in the southernmost regions has shifted towards the north in the last decades, a consequence of the warming average annual temperature in the ocean (Drinkwater 2005), pushing the species towards new territories with a recent northernmost location of Atlantic cod being observed in the Svalbard fjords (Spotowitz *et al.* 2022). To account for the diversity in life histories among Atlantic cod populations inhabiting different habitats, the fisheries manage cod through 26 main stocks or management units (Rose 2019) and collect information on stock size, biological characteristics, and populational structure. Most of these management units are further divided into divisions and subdivisions (Fig. 5).

Atlantic cod displays a distinctive spawning behaviour. At the onset of the spawning season, cod aggregates to cold spawning grounds, where spawning males establish a hierarchy with dominance behaviour, often linked to body size and expressed through a temporal occupation of small territories, forming a spawning lek (Windle and Rose 2007). Spawning males then court a spawning female, by drumming, which communicates their readiness to spawn, and by circling her (Rowe and Hutchings 2004). Such mating behaviour allows the female to assess the physical characteristics of a spawning male and choose the one that may secure the highest fertilization rate for her eggs (Hutchings *et al.* 1999). Once the female is ready to spawn a batch of eggs, she swims with the male of her choice beneath her, grasped into a 'ventral mount'. Vicinity of the urogenital openings and close release of eggs and sperm increases the fertilization success of the selected male and limits the opportunity of satellite males to fertilize more eggs and thus enhance the genetic variation of the recently spawned eggs (Rowe and Hutchings 2003). Spawning occurs early in the year, between February and April, near the first spring phytoplankton bloom. During this time a female can spawn hundreds of thousands or several millions of up to 3 mm sized eggs protracted over 20 batches (Kjesbu *et al.* 1996). The eggs are surrounded by extracellular reproductive ovarian fluid, which may prolong their viability, increase the fertilization window, and thereby influence postmating sexual selection (recent evidence from zebrafish by Pinzoni *et al.* 2023). The timing of the spawning season provides a suitable opportunity window for the pelagic fertilised eggs, which hatch within three weeks into drifting yolk-sac larva and undergo ontogenetic development in the absence of parental care. They metamorphose into feeding larvae and free-swimming juveniles at the peak time of secondary production, heterotrophic biomass or zooplankton prey (Cushing 1990).

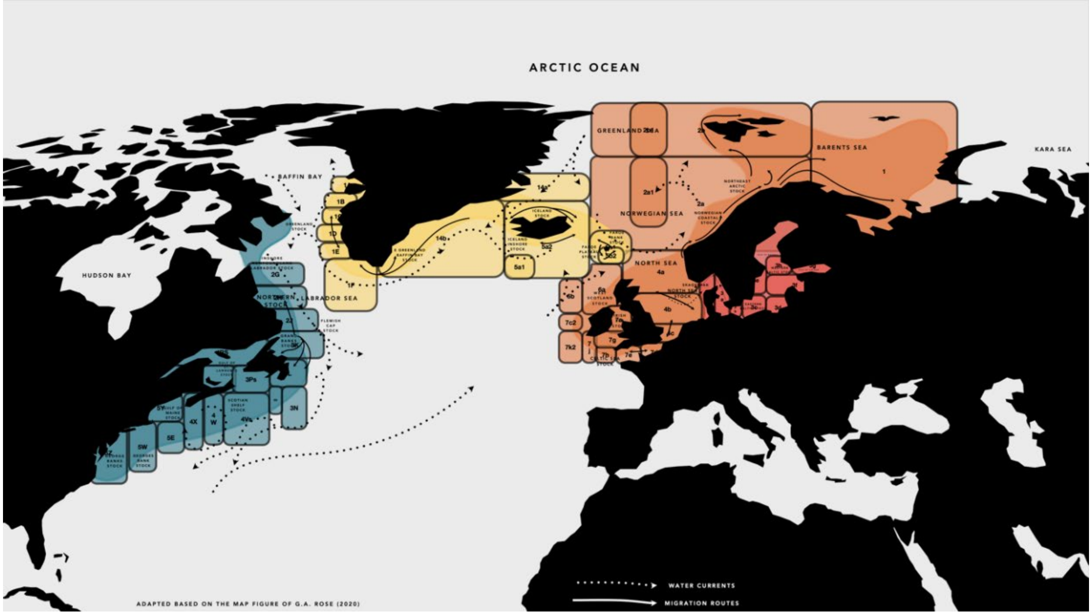


FIGURE 5 Graphical representation of the geographical distribution, migratory routes, management units and subdivisions of Atlantic cod.

2.2 Skagerrak

Skagerrak, a strait connecting the North Sea and the Kattegat (Fig. 6), is used as the study site in III. Skagerrak food web was parameterized for the ATN model for the first time, using information on the composition and biological characteristics of marine species observed in this strait. The moderately productive mesotrophic shelf ecosystem of Skagerrak (Karageorgis *et al.* 2003) is characterized by an inflow of water masses from the North Sea through the warmer Atlantic Current and the colder Jutland Coastal Current, and the outflow of less saline water from the Baltic Sea and local freshwater river discharge (Kristiansen and Aas 2015). This counterclockwise gyre of water currents influences the seasonal dynamics in plankton communities (Gran-Stadniczeñko *et al.* 2019) and the transport of pelagic eggs and larval drift from the North Sea to Skagerrak (André *et al.* 2016). As a result, the oceanographic processes can influence the connectivity of populations and potentially contribute to their differentiations. Such example is the population structure of Atlantic cod that resides in the coastal Norwegian Skagerrak.

The population structure consists of the coastal Fjord cod ecotype and offshore North Sea cod ecotype (Knutsen *et al.* 2018). The Fjord cod ecotype shows spawning-site fidelity by spawning in sheltered coastal fjords (e.g. Risør fjord in Fig. 6), while the North Sea cod ecotype may migrate to spawn in the North Sea, indicating a natal homing behavior, and have the eggs and larvae carried with ocean currents back to Skagerrak (Stenseth *et al.* 2006). Differences in spawning dynamics may contribute to reproductive isolation and lead to differentiations between the North Sea and Fjord cod ecotypes, which has been observed in genetic (Barth *et al.* 2017), phenotypic (Olsen *et al.* 2004, Kuparinen *et al.* 2016b, Knutsen *et al.* 2018) and ecological (Kristensen *et al.* 2021) traits, and which is maintained despite the spatial and temporal overlaps. The life-history (Kuparinen *et al.* 2016b) and dietary differences (Hop *et al.* 1992, Floeter & Temming 2003, Kristensen *et al.* 2021) between the ecotypes were accounted for in the ATN to observe the influence of their phenotypic and ecological divergence on the coastal pelagic food web in Skagerrak.

The information on the remaining species of the fish community in Skagerrak was obtained for parameterization of the ATN from one of the longest ongoing monitoring programs, the beach seine survey led by the Institute of Marine Research at Flødevigen research station in Norway. Alf Dannevig, whose father founded the marine research station in Flødevigen, started the sampling in 1919 and since then fine-meshed seine hauls have been deployed every September along the Norwegian Skagerrak coast (Dannevig 1949, Olsen *et al.* 2009, Barceló *et al.* 2016). Each of the 21 fish species that has been consistently occurring in the beach seine survey data or in stomach content analyses of harbor seals from Norwegian Skagerrak, was divided into 5 age classes and linked to its prey and predators based on the literature.

The species composition of zooplankton and phytoplankton community in the Skagerrak ATN was estimated from a 3-year data series also collected and systematically curated by the Institute of Marine Research at Flødevigen research station. Samples were taken twice a month between August and November at Arendal Station 2 (58° 23′ N 08° 49′ E), positioned 1 nautical mile off the Norwegian Skagerrak coast at 75 m depth (Falkenhaug *et al.* 2022).

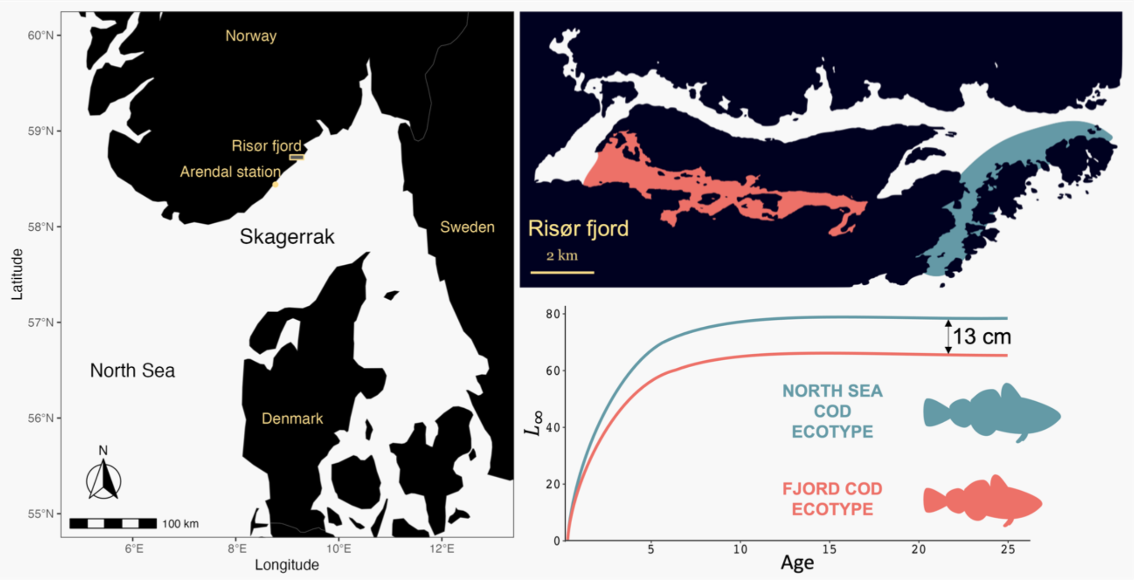


FIGURE 6 Study area of paper III, demonstrating the location of the research station Arendal and the habitat location of the North Sea cod ecotype (in blue) and the Fjord cod ecotype (in red) as observed in Risør fjord. The locations and asymptotic length (L_∞) trajectories of both ecotypes are adapted based on Kuparinen *et al.* 2016b.

2.3 Individual-based model

The individual-based mechanistic cod model was initially developed in 2012 (Kuparinen *et al.* 2012) to explore how the survival costs related to reproductive investment and behavior influence stock productivity through other life-history traits. Since then, the model has been applied to a variety of questions to find answers and learn about problems that may be difficult to uncover otherwise, e.g., *in situ*. These include questions pertaining to the ecological and evolutionary dynamics of cod: to illuminate the consequences of fisheries-induced evolution in life histories for population growth rate (Kuparinen and Hutchings 2012), net reproductive rate (Kuparinen *et al.* 2014a), effective population size (Kuparinen *et al.* 2016c), and eco-evolutionary rescue (Kuparinen and Uusi-Heikkilä 2020), to explore how the Allee effect impedes populational recovery (Kuparinen and Hutchings 2014, Kuparinen *et al.* 2014b), and to investigate the impact of environmental recruitment variability on stock productivity and recovery (Kuparinen *et al.* 2014c). The model has been also applied to other fish species, e.g. Atlantic salmon, to disentangle the role of single-locus vs. multi-loci genetic architecture of life history traits that are under fisheries selection (Kuparinen and Hutchings 2017, 2019, Oomen *et al.* 2020), or in European hake to compare the eco-evolutionary consequences of different fishing practices (Jusufovski and Kuparinen 2014) and combined size-selective fishing and predation mortality (Jusufovski and Kuparinen 2020).

The model used in I and II, is parameterized for Atlantic cod and describes the annual demographic processes of somatic growth, reproduction and mortality of each individual female and male in a density-dependent population. The fundamental evolving traits are the asymptotic length L_∞ and the intrinsic growth rate k, which are uniquely inherited from the individual's parents via the classical Mendelian principle. L_∞ and k are the von Bertalanffy parameters (von Bertalanffy 1938) that relate to other life history and fitness traits, such as maturation age, maturation size, and the number of spawned eggs.

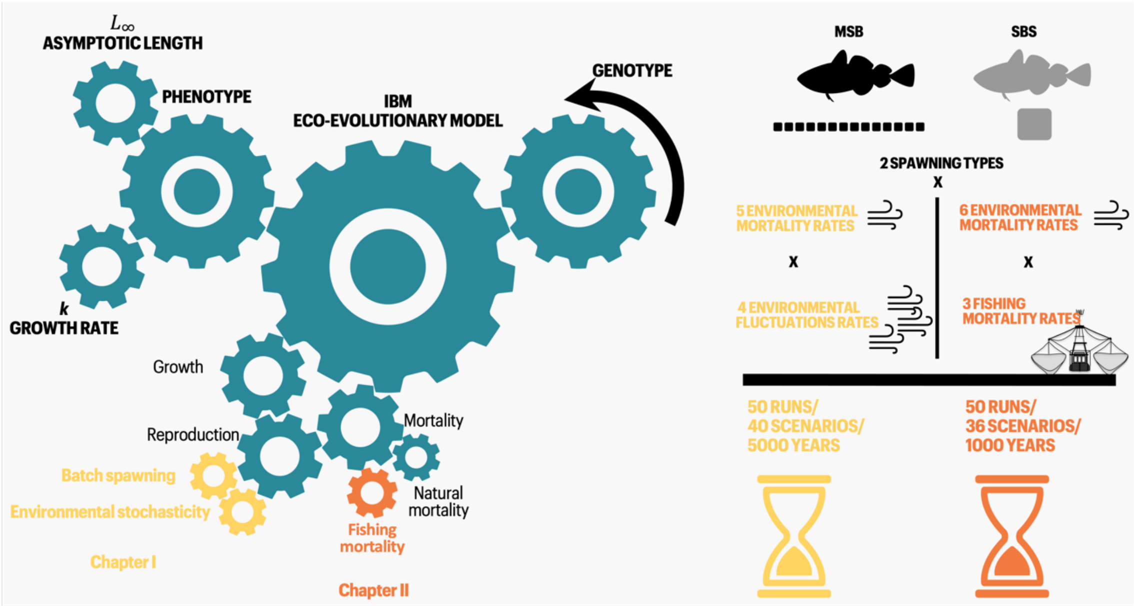


FIGURE 7 Schematic illustration of the core mechanisms considered in the individual-based model developed by Kuparinen et al. (2012) in blue with the added extensions that were developed for the purpose of paper I (in yellow) and II (in orange). The right-hand side illustrates the multifactorial approach of paper I (in yellow) and II (in orange) that was applied to the multiple-batch spawning (MBS) cod population (in black) and single-batch spawning (SBS) population (in gray).

In paper I, the original individual-based model (Kuparinen *et al.* 2012) was expanded by adding a batch spawning strategy and environmental stochasticity, which defines whether a spawned batch survives or is destroyed (Fig. 7). The batch spawning strategy of multiple and single-batch spawning individuals were portrayed, as both scenarios were needed to delineate the benefits of multiple-batch spawning in cod. While in both strategists the total potential number of spawned eggs depended on the female's body mass at the beginning of the spawning season, the difference between the two was in egg distribution and batch-spawning costs. Single-batch spawning females spawned all the eggs at once, which led to all eggs experiencing the same environmental stochasticity that determined whether the batch survived or was completely destroyed. On the other hand, multiple-batch spawning females spawned eggs in several batches, the number of which depended on body mass. This caused each spawned batch to experience different environmental stochasticity and each subsequent batch a decrease in survival probability due to spawning costs. Cod populations with and without the multiple-batch spawning strategy were simulated separately and exposed to 20 different scenarios with varying environmental stochasticity. Environmental stochasticity was portrayed through a combination of environmental pressure and environmental fluctuations in batch mortality rate.

In II, multiple and single-batch spawning populations were exposed to size-selective fishing. Fishing selection reflected the common S-shaped selectivity curve of bottom trawling cod fisheries and the applied instantaneous fishing mortality rates of 0.1, 0.2, and 0.3, described low, intermediate, and high fishing exploitation of cod. The simulation design included 50 replicas of 36 scenarios, testing multiple and single-batch spawning cod in a multi-factorial approach under six different conditions of environmental pressure that reflect external factors, which drive mortality change in batch survival (in II referred to as the environmental forcing) and 3 different fishing mortality rates acting on individuals with a size of at least 45 cm.

Further details of the simulation design, that was performed in R (R Core Team 2021), and the empirically based mechanisms of the eco-evolutionary model, including newly added extensions, are specified in paper I and II.

2.4 Allometric trophic network

The allometric trophic network (ATN) model is a mathematical model that links allometrically scaled bioenergetic models describing the dynamics of populations (Yodzis and Innes 1992) with structural models describing the complexity of food webs (Williams and Martinez 2004). Synthesized for the first time in 2006 (Brose *et al.* 2006), the ATN addressed one of the classic challenges in ecology, i.e. the complex-stability theory (May 1974), and highlighted the body mass ratio in predator–prey interactions as one of the essential properties of empirical food webs that may stabilize natural ecosystems. The ATN has been actively developed to embrace and integrate mechanistic observations from different research areas at different biological organizations, e.g. the metabolic theory (Brown *et al.* 2004), modified functional response (Williams and Martinez 2004), nutrient cycling (Boit *et al.* 2012), life-histories (Kuparinen *et al.* 2016a), evolution (Perälä and Kuparinen 2020) and was parameterized for an alpine lake food web in Lake Constance (Boit *et al.* 2012).

The core of the ATN is the collection of ordinary differential equations that describe biomass dynamics between each pair of trophic species or a node that interacts within the food web (Fig. 8). Biomass changes in each node depend on its estimated carbon concentrations, and mass or size-scaled processes. In phytoplankton nodes, these involve the intrinsic growth rates of producers that are limited by the carrying capacity of the environment and the deduction of biomass lost to consumers. In consumer nodes, the metabolic rate scales with the body mass and influences the gain from each resource or prey and the biomass losses that arise from the maintenance of basic physiological functions and from consumer or predation pressure. The extent of the gained and lost biomass due to species interactions is also influenced by the consumer's preference for its prey and resources, and by the consumer's susceptibility to predation or consumption. This relationship is described by the intermediate Holling type II–III functional response (Williams and Martinez 2004).

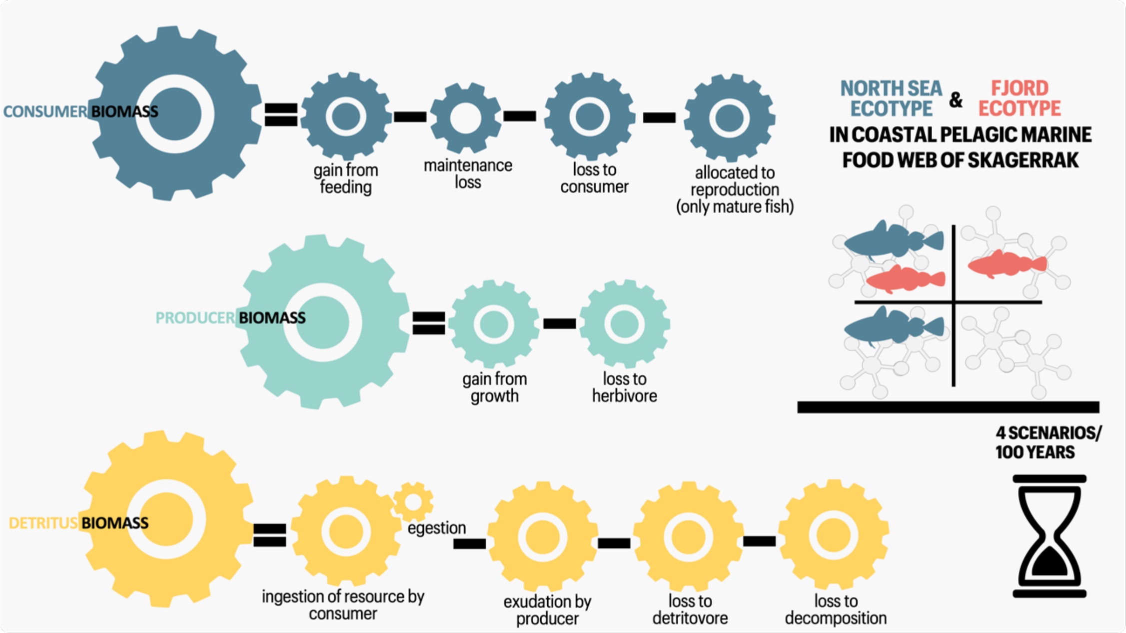


FIGURE 8 Schematic illustration of the core mechanisms considered in the allometric trophic network (ATN) model version developed in Kuparinen *et al.* (2016). The ATN describes the rate of change in the biomass of detritus (yellow), producers (teal), and consumers (blue). The right-hand side illustrates the four simulated food web scenarios of paper III, that explored the impact of the North Sea cod ecotype (blue) and the Fjord cod ecotype (red) on the food web topology and functioning in Skagerrak.

In III, Skagerrak food web structure was applied to the ATN framework (version from Kuparinen *et al.* 2016a) to simulate the annual dynamics of phytoplankton production and consumer consumption. Four food web scenarios were tested to observe the impact of Atlantic cod ecotypes on the food web topology and functioning: 1) with both cod ecotypes present, 2) with the North Sea ecotype missing, 3) with the Fjord cod ecotype missing, and 4) with both cod ecotypes missing. The food web outputs were compared by evaluating 18 food web metrics. The food web metrics included non-weighted metrics of connectance, generality, vulnerability, trophic level, omnivory, modularity, assortativity and robustness. The biomass-weighted metrics of connectance, generality, vulnerability, and trophic position were also estimated to account for the biomass changes within the food web. Simulations were run in MATLAB (MATLAB 2018) for 100 simulated years that each consisted of a 90-days growth season.

A full description of the model parameterization including the applied ordinary differential equations, simulation design and analyzed food web properties are provided in III.

3 RESULTS AND DISCUSSION

3.1 Role of a diversifying strategy under a varying environment (I)

Determinate multiple-batch spawning has been referred to as a bet-hedging strategy of Atlantic cod (e.g. Rowe *et al.* 2008), but evidence in support of this speculation has been missing. By integrating theoretical and empirical aspects of the multiple-batch spawning reproductive strategy (I) in an eco-evolutionary cod model (Kuparinen *et al.* 2012), fitness dynamics under different environmentally stochastic scenarios directly affecting the batch survival could be explored. Analyses of simulation results provided support for the previous hypothesis, offered novel insights into the fitness consequences of a costly multiple-batch spawning strategy and demonstrated the environmental conditions under which multiple-batch spawning constitutes a bet-hedging (I).

Spawning several batches proved to be an advantageous spawning strategy under spatially and temporally fluctuating environmental conditions. It increased batch survival by providing a number of reproductive opportunities, which boosted the chances that at least some batches encounter favorable environmental conditions and endure the early threats impacting survival (I). The higher survival rates at the early egg stage led to higher hatching success and greater chances of producing at least one successfully surviving offspring that reached the age of maturity. The lower chance of complete spawning failure at the individual level was reflected in more even reproductive outputs among multiple-batch spawning females at the populational level, and in a reduced within-generation variance in reproductive output (I). This led to a reduced variance in the average reproductive output among generations at the genotypic level, also referred to as the across-generational variance in arithmetic mean fitness (Fig. 3 in I). Because the geometric mean is sensitive to variance in the arithmetic mean (Gillespie 1974, Slatkin 1974, Seger and Brockmann 1987, Seger and Philippi 1989), the across-generational geometric mean in fitness increased with environmental fluctuations (I).

A life-history mechanism that has supported the spawning tactics and also led to the lower variance in reproductive output at the individual level was the increased evolutionary pressure for a bigger average asymptotic length, maturation at a bigger size, and a lower variance in asymptotic length under fluctuating environmental conditions (I). The observation is consistent with the life-history theory that predicts the evolutionary advantage of delayed maturation and more reproductive events if mortality in earlier life stages is high or variable (Murphy 1968). Since multiple-batch spawning is a size-related trait (Fig. 2 in I), the number of shed batches per spawning season increased with female body size, providing greater distribution of eggs in a variable environment that mitigated batch mortality rate (I). Investment into somatic growth became thus advantageous with higher environmental stochasticity, especially under high environmental pressure and environmental fluctuations.

A particularly interesting finding was that, under the least stochastic environmental scenario, where no unpredictable environmental fluctuations were applied to environmental pressure, the evolutionary pressure to invest into somatic growth was comparatively lower in the presence of the multiple-batch spawning strategy (I, II). The main reason for this observation seems to be the allocation of costs between somatic growth, the evolving life history trait, and reproduction, the batch spawning strategy. An allocation into bigger size proved to not be as necessary in the absence of environmental fluctuations, suggesting that the multiple-batch spawning strategy offsets for the benefits that bigger body size may provide (II). So, the dilemma of multiple-batch spawners is to what optimal size to grow in order to shed the optimal number of batches and optimally increase the chances of encountering the optimal conditions, while still optimally managing the optimal extent of associated spawning costs, realized in the lower average reproductive output. Unfortunately, the answer is not straightforward; the optimum trade-off between costs and benefits depends on the life history of the multiple-batch spawner in question and on the characteristics of selection pressures driven by the environmental setting, including the anthropogenic effects (II).

The reproductive effort allocated into the spawning of multiple batches traded off the investment into the egg survival potential (see below) and as such made multiple-batch spawning a costly strategy. This led to a decline in average arithmetic mean fitness under unpredictable environmental fluctuations and the highest environmental pressure scenarios (I). A synchronous decrease in variance in the arithmetic mean fitness across generations generated an increase in geometric mean fitness across generations, indicating the environmental conditions when multiple-batch spawning acts as a bet-hedging trait (I). The survival potential of each spawned egg batch in model (I) depended on the egg volume, diameter and dry weight which have been observed to decrease throughout the spawning season in cod (Bleil and Oeberst 1998). But while the egg quality (Roney *et al.* 2018) and quantity of spawned eggs per batch (Kjesbu *et al.* 1996) followed a dome-shaped curve in captivity, the eco-evolutionary cod model considered the spawning costs to increase linearly throughout the spawning period (I). Therefore, although the eggs spawned in the first batches tend to be smaller compared to the eggs spawned in the middle of the spawning season (Kjesbu *et al.* 1996, Roney *et al.* 2018), plausibly reflecting yet another risk-spreading or even a bet-hedging trait, a diversifying bet-hedging through the variable offspring size (Marshall *et al.* 2008), the larvae hatched from the first batches may experience a lower density-dependent intraspecific competition for zooplankton prey and thus have higher chances to feed and prevent or shorten starvation periods. On the other hand, the eggs spawned at the end of the spawning season, have a smaller egg volume, therefore lower chances to survive during longer starvation periods. Moreover, a later onset of ontogenetic development likely makes later spawned eggs weaker rivals in intraspecific interactions, as well as more susceptible to cannibalism (Puvanendran *et al.* 2008). To depict these multifold intraspecific interacting possibilities, the model used a linear decrease in batch survival probability (I) as opposed to the empirically observed dome-shaped.

Besides the size-related batch spawning strategy, the model purposefully did not account for any other size or age-dependent maternal traits that may increase the survival chances of eggs and the newly hatched larvae. For example, larvae of older females have been observed to grow faster and survive longer starvation periods (Berkeley *et al.* 2004). Therefore, while the results of the model indicated selection towards females of larger size that spawn more batches and altogether more eggs as the environmental fluctuations in batch mortality increase (I), the selection may be even stronger and occur at lower environmental stochasticity if additional empirically observed size and age-related benefits related to larval survival would be included to the model. Hence, after the exploration of fitness benefits that arise exclusively from the distribution of egg batches (I), the influence of selective fishing could be perused only by focusing on the environmental scenarios with different environmentally induced increase in batch mortality rate, referred to as environmental pressure rates in paper I or environmental forcing in II.

3.2 Role of a diversifying strategy under size-selective fishing (II)

Fishing tends to be non-random. The fisheries target, intensity, method, location and time can be highly selective and eventually lead to a phenotypic change in life-history traits of harvested stocks (Hutchings and Baum 2005, Sharpe and Hendry 2009). These changes can reflect a plastic response to altered density-dependent growth (Eikeset *et al.* 2016) as well as signal a rapid or a contemporary evolution in life-history traits that occurs only over few generations (Jakobsdóttir *et al.* 2011). Given that the rate of anthropogenically-induced change can be more than twice stronger (Darimont *et al.* 2015), faster (Jørgensen *et al.* 2007, Devine *et al.* 2012) and act in the opposite direction of natural selection (Monk *et al.* 2021), strategies adapted to cope with high natural mortalities may turn out suboptimal under fishing mortality.

It seems likely that multiple-batch spawning is one of such strategies. During the simulated period of size-selective fishing, the fitness of cod populations dropped when the adults suffered fishing mortality (Fig. 3 in II). The removal of larger and older cod with greater reproductive potential (Barneche *et al.* 2018) reduced the spawners' contribution to recruitment. Consequently, this resulted in up to 75 % fitness losses (II). Decline in fitness of multiple-batch spawners under lowest environmental forcing was comparable to a population consisting of individuals without the risk-spreading strategy, the single-batch spawners. Still, the distribution of eggs across several batches provided some gains in fitness. Fitness value, calculated as a geometric mean in realized reproductive output across generations, remained unaffected by increasing environmental forcing in egg batch mortality rate or the early life stage of cod (II). However, the nature of fitness gains provided by risk-spreading under increasing environmental forcing depended on the intensity of fishing. When the fishing intensity was low (F = 0.1) multiple-batch spawners had a higher fitness than single-batch spawners. But interestingly, the advantage of multiple-batch spawning disappeared during the moderate fishing intensity (F = 0.2) and became a disadvantage under the highest fishing intensity (F = 0.3). The same trend in fitness dynamics persisted even after a more than 300 years long moratorium, when fishing completely ceased. These findings imply that multiple-batch spawning can quickly turn into a maladaptive strategy (relative to single-batch spawning) under size-selective fishing.

Fisheries-induced life history changes were visible in the average asymptotic length of fished populations (Fig. 2 in II). Fishing led to a smaller asymptotic length, favouring individuals that grow faster and mature at an earlier age. The trend replicates the observations from wild overharvested populations, where the proportion of older and larger individuals declines (Olsen and Moland 2011). Although fishing in the model ceased as soon as the population dropped to 15 % of its pre-fishing biomass, and the populational biomass had bounced with some lag to the carrying capacity of the environment, the asymptotic length did not fully recover. Slow recovery, despite a moratorium of several centuries, signifies that the decline in average body size was not only a plastic response to low populational density, but an evolutionary downsizing of genetic variation.

The spawning strategy additionally influenced the extent of the decline in size and speed of recovery. Despite that multiple-batch spawning populations sustained the fishing longer under low fishing intensity (F = 0.1), the advantage diminished with higher fishing rates. Thus, while the evolution of asymptotic length in multiple-batch spawning populations was not sensitive to changing environmental forcing rates, not during and not after fishing, single-batch spawning populations were. In the absence of multiple-batch spawning, the evolution toward bigger size in order to spawn more eggs became more advantageous as environmental mortality was higher. The aftermath of this were smaller dips in body size during fishing, and quicker recovery, assisted by natural selection.

Identifying the shifts in fitness-related traits and strategies that are a consequence of harvest selection can offer some explanation or pinpoint on the reasons for slow recovery of overexploited stocks (Hutchings 2005). The findings of II show that fish with a multiple-batch spawning strategy are more sensitive to large-size-selective fishing and that the strategy can additionally impede recovery. A decline in asymptotic length under different environmental scenarios likely generates stronger lingering fitness consequences in multiple-batch spawning cod-like species, because the strategy is adapted to uncertain mortality at an earlier age, but not to selective mortality in later adult life.

3.3 Role of a diverse demographic structure for stock productivity (I, II)

Low survival of the earliest life stages influences recruitment and can be a source of variability in population dynamics. Cod undergoes a high egg mortality with strong interannual variation. For example, the instantaneous egg mortality rate of cod can be twice higher and three times more variable between years, compared to the mortality of haddock (*Melanogrammus aeglefinus*) eggs, another batch-spawner (Langangen *et al.* 2014). But the life-history differences between these two gadoids, including the longer spawning period of cod, may dampen the variability in early egg mortality and contribute to the lower recruitment variability that is usually observed in cod stocks (Fogarty *et al.* 2001, Johannesen *et al.* 2022). A diverse demographic structure can better balance interannual variations in mortality rate at earlier life stages through compensatory density-dependent mortality. Lower mortality of larvae at lower population density may prevent variation at the recruitment level or sustain them less pronounced in the population dynamics (Ohlberger and Langangen 2015). Given the spawning stock biomass does not plainly reflect changes in the distribution of year classes, preserving a diverse size and age structure is of the critical importance as are more accurate measurements of reproductive potential (Fitzhugh *et al.* 2012).

Differences in the potential of various reproductive traits are size and age-specific, generally positively related to both (Wright and Trippel 2009, Lowerre-Barbieri *et al.* 2011). This makes especially late-maturing species sensitive to high age-truncation, which can generate faster growth rates and lead to population instability (Anderson *et al.* 2008). Fisheries truncation in demographic structure may also reduce the benefit of risk spreading strategies. The observed cushioning effect of the multiple-batch spawning strategy does not seem to shield the demographic age and size structures from fisheries downsizing (Fig. 4 in II). While the distribution of eggs mitigated the environmental forcing rates and preserved the shape of demographic structure in multiple-batch spawning population, the diversity in demographic structure declined with increased fishing intensity. Truncated populations were younger under fishing exploitation, had a smaller average size and a decreased influx of recruits. Consequently, lower reproductive output of overfished stocks as well as higher interannual variance generated a lower across-generational fitness in truncated demographic structure.

The role of a prolonged spawning strategy for the stock productivity may differ among different cod stocks. These differences may not be only due to life-history variations among stocks adapted to different geographic areas, but also due to differences of surrounding intraspecific and interspecific interactions, given these rapidly change in time. This can cause the benefit of risk-spreading traits and strategies, such as multiple-batch spawning, to be less detectible in certain populations. For instance, although the age and size structure of the Barents Sea cod stock influenced the abundance and distribution of eggs, the spatial egg distribution itself was not observed to be a strong link to recruitment (Stige *et al.* 2017). Likewise, the findings of the eco-evolutionary cod model show that the impact of multiple-batch spawning and thus, a temporally prolonged spawning period, does not generate a notable impact on the populational dynamics when the environmental conditions are rather stable or only slightly variable (II). However, when looking across different rates of environmental conditions, the results of the model indeed resonate the buffering power of the multiple-batch spawning strategy against higher environmental fluctuations (I), and the strategy's influence on the individual reproductive output and stock's productivity (II).

3.4 Role of intraspecific diversity for food web functioning (III)

Besides reproductive strategies (I), numerous other traits and physiological processes relate closely to body size of an individual, in particular among species in aquatic ecosystems. Individual size is one of the key life-history characteristics, that confines the individual's ecological possibilities, such as resource acquisition (Andersen *et al.* 2016). From food web perspective, individuals shape the structure and functioning of marine food webs through predator–prey interactions and these generally depend on the body size (Brose *et al.* 2006, Trebilco *et al.* 2013). So, if the differences in life histories among species have the potential to scale up and impact the food web dynamics through foraging characteristics and occupied niches (Raffard *et al.* 2021), so can the differences in life histories that occur within species (Palkovacs and Post 2009, Des Roches *et al.* 2013). The ATN model can capture the complex interactions among and within species and offers possibility to explore what impact size-related life-history differences have for the biomass flow in a food web (Boit *et al.* 2012, Bland *et al.* 2019, Vesterinen *et al.* 2021).

Newly build Skagerrak ATN portrayed the coastal pelagic food web in Skagerrak through five North Sea cod ecotype guilds, five Fjord cod ecotype guilds, 109 fish guilds, and 13 phytoplankton, 12 flagellate and 14 zooplankton aggregated functional guilds (III). The food web consisted of 8.5 % realized feeding links, which is half lower compared to the food webs from nearby regions, constructed for the benthic community in German Bright in the North Sea (Olivier *et al.* 2019) and the pelagic Gulf of Riga in the Baltic Sea (Kortsch *et al.* 2021). A greater number of nodes partitioned into life-histories to account for ontogenetic dietary shifts was one of the main reasons for this low food web parameter in Skagerrak.

Removal of one or both cod ecotypes from the food web led to a reduced food web generality with a lower average number of prey per consumer and to an increased vulnerability with a higher average number of predators per prey. Simultaneously, the robustness of the food web to a random removal of guilds decreased too and led to earlier occurrence of secondary extinctions (III). Contribution to food web generality indicates that the ecotypes are well connected and thus, the number of their ecological interactions reduce the competition and pressure on a specific prey, which may otherwise become rare or get extinct. This means that the ecotypes could contribute to food web diversity and its stability by supporting prey coexistence. The contribution could also depend on the eco-evolutionary characteristics of the ecotype, since the Skagerrak food web became less robust and had a lower generality and higher vulnerability in the absence of the smaller Fjord cod ecotype (III). Likewise, 16 other food web metrics showed different sensitivity to ecotype-specific removal, supporting the observations from other systems that the re-wiring of food web topology is sensitive to intraspecific diversity (Palkovacs and Post 2009, Raffard *et al.* 2019, Mougi 2020, Raffard *et al.* 2021).

Further, the findings provide evidence that intraspecific variability can give rise to a unique functioning of the food web and impact its biomass flow (III). Differences in life histories and ontogenetic dietary shifts between the co-existing cod ecotypes had a distinctive regulatory influence on the food web functioning that could be observed at upper trophic levels but dampened towards lower trophic levels (Fig. 2 in III). A removal of the Fjord cod ecotype had a negative impact on the entire fish community in Skagerrak, leading to a more than 2 % decline in their biomass, relative to a food web with both ecotypes. Contrary, the removal of the North Sea ecotype generated a more than a 3 % increase in the biomass of the fish community. These results suggest that the Fjord ecotype controls the intensity of the predatory pressure of North Sea cod on the fish community in Skagerrak via an allometrically coupled effect of size-related traits and dietary niche. The biomass changes were particularly evident in the older age classes of whiting (*Merlangius merlangus*), pollock (*Pollachius pollachius*), herring, mackerel (*Scomber scombrus*) and group of flatfish, all being valuable economically harvested species. The fish community showed the strongest sensitivity in relative biomass change probably because these were the directly or closest linked prey and predators of the older cod ecotypes. On the other end, the density-dependent regulation, predator diversity and life-history omnivory may have contributed to dampening of the biomass change among zooplankton and phytoplankton guilds (Kratina *et al.* 2012, Heath *et al.* 2014).

The intraspecific overlap in dietary niche at the earliest life-stages resulted in a high competition between the ecotypes as cod larvae exploited the same zooplankton prey, copepods (III). As the ecotypes age, differences in size become greater (Kuparinen *et al.* 2016b) and the ontogenetic dietary shifts tend to diverge due to different dietary preferences (Knutsen *et al.* 2018). Consequently, the faster and bigger growing North Sea cod ecotype overtook the Fjord ecotype at age 2, which led to a reduced overlap in life-stage-depended dietary niche. This lowered direct competition between the same age classes and contributed to a different overall ecological impact of the ecotypes. Concurrently, while at smaller sizes the interspecific predatory pressure from whiting, herring, mackerel, pollock, haddock and saithe (*Pollachius virens*) was allocated rather evenly between the larvae of the two ecotypes, the differences in growth trajectories eventually led to different vulnerabilities to predation. For example, owing to a faster growth, the North Sea larvae escaped the predation from older age classes of haddock and mackerel, while the 3-year-olds escaped the predation from the oldest saithe age class (III). Differences in ecological role among or within species are one of the mechanisms that prevents conflict, permits coexistence, and maintains diversity (Bolnick *et al.* 2011).

That being said, the ATN version used to explore Skagerrak does not integrate the food web within its abiotic environment. Biomass of producers in the ATN is not controlled by abiotic conditions, such as light or temperature, that would link the food web structure within the ecosystem. Although producers cannot grow indefinite, as all phytoplankton guilds share the same carrying capacity and compete for limited resources, the model considers carrying capacity to be fixed throughout the growth season. A recent integration of seasonality to the ATN showed that seasonal changes in abiotic factors, influencing the amount of available resources in the system, impact primary producers and lower trophic levels (Eloranta *et al.* 2023). While the seasonality version of the ATN was not necessary in the quest of the research question in III, it would be a reasonable enhancement of the biological realism in the model. Nevertheless, although the ATN has its own inherent limitations, it has several strengths. In particular, the inclusion of life-history stages that account for empirical growth relationships and developmental differences in energy allocations between growth and reproduction in fish is one of them. This makes the linking to ontogenetic dietary shifts and predator switching in the food web more realistic (Bland *et al.* 2019). Different modelling approaches have been developed to explore how size scaling from individuals' characteristics reflects at higher levels of biological organizations (Blanchard *et al.* 2017). Then again, exploring the role of intraspecific diversity at a finer eco-evolutionary scale, where smaller differences in size-based feeding, growth and reproduction differ across life-history stages, may be challenging with modelling approaches that do not integrate this structural realism.

3.5 Diversity and fisheries-induced eco-evolutionary change (I, II, III, IV)

Genome-wide data analysis in the northern cod from Newfoundland and the northeast Arctic cod from the Lofoten archipelago did not detect any strong change in allele frequency in otolith and scale samples collected before and after a decades long period of intense fishing (Pinsky *et al.* 2021). Yet, experimental studies on guppies (van Wijk *et al.* 2013) and zebrafish (Uusi-Heikkilä *et al.* 2015, Uusi-Heikkilä *et al.* 2017) have detected genetic change after only few generations of size-selective fishing. While the possibility of a delicate undetectable smaller genetic change occurring across multiple loci could explain why genetic signals of selection remained hidden (Yeaman 2015), genetic change may as well not be that significant in the wild. Lack of evidence for fisheries-induced evolution from genome-wide data (Pinsky *et al.* 2021) suggests it is the ecological change induced by fisheries which is steering the course of wild populations beyond the evolutionary (Hutchings and Kuparinen 2021).

Disparity between wild and laboratory observations is likely due to complex interactions that resolve in nature. These include but are not limited to gene flow between stocks (Breistein *et al.* 2022), population size, a diffused fishing selectivity, and the phenotypic plastic response to lightened density-dependent mechanisms (Conover & Baumann 2009). Whether with genetic basis or through persistent ecological drivers, fisheries alter the expression of life history traits in overharvested populations by disrupting their demography. The density-dependent response of faster growth rate and consequential earlier maturation coupled with phenotypic change in size have not been only observed in a wide range of stocks (e.g. Hunter *et al.* 2015, reviewed in IV) but their rate of change has shown to be corelated to fishing intensity (Sharpe and Hendry 2009). This can prove especially damaging when population size becomes too small and falls under the Allee effect, zone of impaired recovery (Perälä *et al.* 2022), where even in the absence of fishing the natural mortality can be enough to cause a depensatory density-dependent dynamics (Kuparinen and Hutchings 2014). In that sense truncation of phenotypic diversity can be as dangerous as genetic, with one positive detail: the loss of big old fat fecund fish (Hixon *et al.* 2014) is not necessary irreversible on a contemporary scale. Therefore, rebuilding depleted abundances and restoring a diversity in populational age and size structure is essential in sustaining the potential of the iconic Atlantic cod.

Individuals, populations, and food webs are connected in the oceans through direct and indirect interactions (III, IV). Any adequate change that occurs at the individual level and has a potential to scale to population fitness (I) and size structure (II) can potentially resonate through the food web (III). In the same sense, the impact of fishing removal of individuals sharing precise set of features can transcend beyond the target of fishing (IV). The intensity and selectivity of fisheries, leading to changes in population size and in life history traits has been observed to disturb the ecological interactions within the food web by altering the overall behavior of populations, their competition for resources and vulnerability to predators (Rochet and Benoît 2012, Audzijonyte *et al.* 2014, Uusi-Heikkilä *et al.* 2015, Kuparinen *et al.* 2016a, Díaz Pauli and Sih 2017).

In addition to fisheries-induced ecological change, other modelling approaches looked closer into the role of adaptive trait change along with a demographic effect: the fisheries-induced eco-evolutionary change within food webs. For example, a model following the evolution of a competition-defense tradeoff within a food web consisting of four discrete trophic levels showed that fisheries-induced eco-evolutionary change in top-predators has the potential to induce harvest-mediated evolution at lower trophic levels and that the eco-evolutionary change can feedback to harvested species (Wood *et al.* 2018). Similar effects have been observed in a case study in Lake Constance. The implementation of an evolutionary component into the ATN model, the evolution of asymptotic length and reproductive investment, displayed a distinctive eco-evolutionary life-history effect cascading from large and small-harvested fishes downwards to primary producers (Perälä and Kuparinen 2020).

Loss of intraspecific diversity can also reflect in food web dynamics (III). However, III has not involved any fishing selectivity nor implemented evolutionary change and has only studied food web sensitivity to an absolute loss of genotypic and functional richness in both or only one of the cod ecotypes. Average trophic position of size-selectively harvested Atlantic cod has been observed to decline considerably more when maturation age and size are treated as adaptive traits, which additionally affects the demographic structure (Kindsvater and Palkovacs 2017). Integrating the Skagerrak food web into the ATNE (Perälä and Kuparinen 2020) and imposing size-selective fishing selection on cod ecotypes may be an instructive follow up to thesis (I, II, III, IV). Simulating size-selective fishing in North Sea and Fjord cod ecotypes may then elucidate the relevance of considering the intraspecific diversity in life histories for food web functioning when managing evolving stocks. Differences in the instantaneous fishing mortality, disproportional selective pressure on demographic structure, lessened bet-hedging strategy (I), timing of when a trait becomes maladaptive (II) and the impact scale on the food web (III, IV) could prove counterintuitive.

4 CONCLUDING REMARKS

I write my thesis in a city where one of the greatest architects took his first drawing lessons. Once he stated:

"Nothing is as dangerous in architecture as dealing with separated problems. If we split life into separated problems, we split the possibilities to make good building art. "
Alvar Aalto

In the thesis, I come to a similar conclusion. Nature is full of complex phenomena, chaos, non-linearity, and random chances, which make predictions uncertain and conclusions relative. Studies embracing this complexity and piercing through multiple levels of biological organisation are intimidating as well as insightful and can offer a comprehensive perspective. If the reader permits a slightly over-reaching claim: by applying mechanistic modelling tools to empirical systems, I fulfilled the initial aim of the thesis, the pursuit of eco-evolutionary benefits arising from diversity in Atlantic cod.

Diversity was the silver lining of the 4 papers; benefits of diversifying the chances of offspring survival, the value of a diverse size structure in a population, the influence of the eco-evolutionary diversity within species on the food web, and the consequence of fisheries selection that reduce such diversity at any of the three levels: individual, populational, food web. I have learned that multiple-batch spawning is a risk-spreading strategy of cod, an adaptation to overcome the somatic constraints and hedge its evolutionary bets when the environmental conditions impacting the survival of egg batches are uncertain and destructive. I discovered that size-selective fishing causes lingering eco-evolutionary change, not only by selective removal of bigger and older individuals, but also by an unforeseen removal of individuals with the greatest risk-spreading potential, resulting in a lower across-generational fitness, truncated demographic structure, while the high intensity of size-selective fishing shifted the multiple-batch spawning into a maladaptive strategy. I disclosed that the risk-spreading benefits multiple-batch spawning provides, are not advantageous under size-selective fishing, considering it does not protect the fitness nor demographic structure of Atlantic cod. I have tackled the role of cod ecotypes for the food web topology and functioning and found that while the effect of the different ecotypes on the food web was somewhat anticipated, owing to the intraspecific differences in life-history traits and ontogenetic dietary shifts, their opposing impact on the fish community was counterintuitive. This raises a rather applicative question, on whether scientific advice and fisheries managing units should account for distinct eco-evolutionary features of North Sea cod and Fjord cod ecotypes. The latest scientific advice from the International Council for the Exploration of the Sea for Atlantic cod in the North Sea, eastern English Channel and Skagerrak warned about the existence of reproductively isolated populations within stocks, however, it is not clear how or if these were implemented into the advice (ICES 2022). European Union Delegation and Norwegian Delegation followed the advice for total available catches for Atlantic cod and set provisional catches in Skagerrak to 3095 tonnes with 2995 tonnes allocated to all European Union members, and 100 tonnes to Norwegian vessels (Anon. 2023). Besides Skagerrak, overlapping offshore and inshore cod have been identified in several stocks along the coast of both sides of the Atlantic. Therefore, if feasible, this intraspecific diversity should be managed cautiously.

As in nature, the human social system is coupled with trade-offs. Trade-offs balance the system, but the point of balance is subject to adjustment, depending on unfolding changes in what is invested and what is gained. Along with a profuse number of trade-offs with trade-offs within trade-offs, governing seems a daunting task. Especially as human systems can be more chaotic and random than nature itself. Still, yet another recent report (IPCC 2023) is warning us how staggering our role can be. So, we need to find optimal socio-ecological trade-offs. One of these is being more involved in adjusting our exploitation rates and targets in order to limit the human-induced pressure on mechanisms that maintain the high diversity and productivity of the oceans. So that in exchange we can harvest healthier fish and secure fish protein for those who rely on it the most. Sharing science-based evidence in a sincere and understandable manner to decision-makers is a scientist's reward to the public in return for the taxpayers investment in science (Hutchings 2022). The scientist's part in a trade-off for a blue future.

I am grateful for so many moments and memories that have been created throughout this five-year-long journey, which has turned the acknowledgement section into one of the hardest parts to write, purely out of fear to fail in finding the right words. Overall, it was never about the goal but about the journey. A genuine cliché. It was so worthwhile and enjoyable because of everyone I had the pleasure to meet, whether for a split moment in time, or was lucky to travel along with for a little while, or even luckier if I still can. I am grateful for all.

The first time I took a train to Jyväskylä, it was all out of plain curiosity to learn more about how R software can be used for ecological research. Little have I known this green city by Lake Päijänne, would become yet another place to call home. Anna, I would have never guessed that only a few hours later after sharing some hot tea while playing with the probabilities in the Bernoulli trial that winter afternoon, you would offer me a PhD in the most casual Finnish way and pull me into eco-evolutionary research. Since that day on you have been a wonderful mentor to me. I admire your sometimes almost magical way of elucidating the most complex problems through the most simple and coherent wording. This often made me wonder whether to start voice recording our meetings and save the transcripts for future discussions. Thank you for teaching me how to pursue answers, while letting me have the freedom to ask the questions. Thank you for believing in me, for always fully supporting me in every choice, in whatever I wanted to do or wherever I wanted to go. Thank you for being my dive buddy in my first actual dive into the shallow but murky freshwaters of Finland (although I don’t think it was the wisest choice, as I felt too much of a responsibility to keep an eye on our PI). I absolutely adored our trip to the Swiss Alps (including the most delicious Brezel mit Butter!), and it holds a special place in my heart. You are one of the strongest and most brilliant scientists I know, and I have been always so proud to have you be my mentor.

I have been incredibly lucky in having two excellent mentors providing me with guidance that went beyond research. My deepest gratitude goes to Jeff, for being an impeccable role model in what a genuine meaning of a scientist is. With youthful curiosity, delightful intellect, transparency and honesty about the knowns and the unknowns, meaningful exchange of ideas, enthusiastic explanations of life history theory, and a great zeal for saving Atlantic cod and improving the fisheries. I dearly cherish his warm-hearted lessons. Some of these are advice on how to better understand reviewer 2, advice in Göteborg on what to focus on while giving a presentation, and advice on art paintings to see in Delft when I visit the Netherlands. I am thankful that despite being a prolific writer and active academic, Jeff would know how to elegantly comment on my first drafts with the most encouraging praise of their excellence while butchering them with edits, comments, and *kind suggestions,* turning the text into bleeding red, which managed to shape my chaotic rambling into an effective communication. I loved that. I will be better at whatever I do in the future, because of the superb entanglement of qualities I had a chance to witness in Jeff.

I owe my greatest thanks to Professor Per Lundberg, for accepting to be my honourable opponent, making the closure to my doctoral journey particularly special. Sometimes unknowingly scientists can be superstars to disoriented students. Some of mine were Professor Andrew Simons and Professor Eric Palkovacs. I am thankful to both for taking the time to pre-examine my thesis, for the kind reviews, and constructive feedback, and especially for publishing thought-provoking and absorbing work. I wish to thank my follow-up group, Leena and Outi, for encouraging me and for gently offering support in the toughest time. I am grateful to Timo, for his uplifting words, diligent and patient editing of my thesis, and for being one of the best lecturers I have ever had; his enthusiasm in explaining Baranov's catch equation will remain imprinted in my mind. Thank you to Nina Pekkala and Päivi Vuorio, for making the submitting and publishing stages run smoothly.

All this research would not be possible without our kind collaborators from Flødevigen, including Esben Olsen, Tone Falkenhaug and Lars-Johan Naustvoll, who have been diligently collecting data through years of biodiversity monitoring in Skagerrak and have generously shared their knowledge to empower the ATN model. I am thankful to everyone who I had a chance to meet during my visit at the IMR station in Flødevigen, but especially to Esben, for the opportunity to join him and the technical group for a few days on board for the famous Dannevig's beach seine survey and catch age-0 cod juveniles for the first time. Thank you, Rebekah and Susanne, for making the visit to Oslo and Arendal, especially welcoming.

These five years would not be the same without the *EcoEvoAqua* research group filled with beautiful and curious minds of the past and present group members, including Tommi, Milko, Ines, Tiina, Sami, Eevi, Silva, Antti, Etsuko, Jaakko, Mikksu, Sabrina, Maria, Pauliina and Jouni. Tommi, you have a quick-witted mind with startling programming skills that can solve the most challenging problem, while all along keeping your coolness with a touch of humour. Thank you for always helping me out whenever I would get stuck with code, try to reason a crazy equation, need another pair of eyes to check a manuscript, even answering my SMS (so not 90s), but especially for being like a big brother who is there through good and bad, while it rambles about his garden, perch fishing, and in between shares some wisdom on life. Ines and Milko, sharing the office with you was an absolute pleasure. All our frequency-dependent conversations about code, science, and life that would run into deepness for hours (although we would still always end up with so much to say before Milko placed his next coffee cup on top of his victorious collection), have brightened my days and fuelled to keep going on. I am so grateful to both for truly caring, making me laugh, and for being always there, my wonderful friends. Sami, Eevi, Tiina, Sabrina, Tommi and Ines thank you for the so much-needed online coffee breaks and our synergetic pursuit in Gloomhaven Jaws of the Lion (there are still dark chambers waiting to be conquered). Silva and Antti, your enthusiasm is contagious and a comforting contrast to the respectfully-undramatic-stilled-down swag of the Aquatic section.

Somewhere along the way, almost by sheer fluke, I got to meet one of the most passionate, creative, and hearty young scientists, who understood that boxplots could communicate information more efficiently and pleasantly. Chloe, thank you for sharing a pure joy for data visualization. Data is beautiful. It was such a pleasure running a workshop at Oikos Finland with you, and creating a course on data processing and visualization. This quest became even more fun because after we befriended Eric at Hiisi, you reminded me there is a whole bunch of people just one floor above. Thank you to the very first boardgame friends Andrii, Danny, Ilmur, Justine, Noora, Santtu, Stephan, and the whole freshly expanded family. *Winter is coming* sounds a bit less frightening when there is a boardgame to be played with you. I am thankful to Annis, Cecilie, and Lara, for our online Writing boot camp where we could cheer for each other and share daily writing plans and other truly short-term goals. Annis, thank you for being such an enjoyable friend, for always finding time to go for a walk around the block and for casual chilling. I am grateful to all the bright and kind scientists I had a chance to interact with along the way however briefly, whether at the department, sauna, on the tennis court or in Pori, among others, Lucy, Mateo, Ilze, Chiara, Mariana, Skylar, Sara C., Lutz, Emily, Yagmur, Paulina, Cindy, Marco, Tjaša, Irma, Mikko, Daniel, Ari and Ville. Time is relative and not necessarily only measured in quantity. I am thankful to good professors for the great lectures, for valuable correspondence, and for shared suggestions which have inspired my research. I also wish to acknowledge stock overflow, R community, and FishBase, for being an open source, allowing for an uninterrupted knowledge flow that lessens differences in education. Years of research abroad have jeopardized my mother tongue. I am grateful to my Bachelor's and Master's mentors Alenka Malej and Barbara Boldin, and to Professor Lovrenc Lipej, for their instantaneous intervention in improving my summary in Slovene.

Along with moving to Jyväskylä came a geographical distance from friends and family. You have always had my back, made me laugh from thousands of kilometers away and have never made me feel that anything would have changed between us when our lives have. Ana B., Ana K., Ana P., Ema, Consuelo, Ines, Katja, Mateja, Peter, thank you dearly for that.

I am greatly thankful to my whole loving family who has been always rooting for me in whatever I did. To my mum and dad, for taking me and my little brothers to the seaside every summer, letting us run wild around the forest, and rising us with a love for nature. *Mami in oči, hvala iz srca.* To my darling brothers, Žan and Urh, of whom I am so proud, for letting me be their geeky sister. To my grandmas for hearty dishes and warm hugs. To my dear grandpa for the opportunity and all the stories. To Anica and Arnold, for my first English dictionary and a subscription to National Geographic magazine, both opened a whole new world for me. To my beloved, Ruben, for everything that is and is yet to come.

POVZETEK (RÉSUMÉ IN SLOVENE)

O življenjskem krogu, strategijah zavarovanja pred tveganjem, ter o ribiško-povzročenih spremembah: primer atlantske trske (*Gadus morhua*)

Narava je polna kompleksnih pojavov, nepredvidljivosti, naključnjih dejanj in manj naključnjih sprememb. Ti pogoji poganjajo in vzdržujejo evolucijske in ekološke procese, ki vodijo v biotsko raznolikost med vrstami in znotraj njih. Do sedaj je bilo opisanih več kot 35 000 vrst rib, katerih znotrajvrstna raznolikost presega samo število vrst. Vsaka populacija se naravnim okoljskim razmeram prilagaja prek evolucije z edinstvenimi življenjskimi strategijami, ki jim zagotavljajo najboljšo možno razporeditev energije med preživetjem in razmnoževanjem. Končni cilj teh prilagoditev je zagotoviti potomce za naslednjo generacijo, z dednimi lastnostmi, ki nudijo najboljšo predispozicijo za njihovo preživetje do spolne zrelosti in uspešno razmnoževanje v danem okolju. Na ta način ugodne prilagoditve zagotovijo ne samo visok razmnoževalni doprinos posameznika, ampak predvsem visok razmnoževalni uspeh osebkov specifičnega genotipa v populaciji ali dolgoročni fitnes. Življenjski krog in strategije tako odražajo odvijajoče se dolgotrajno izoblikovanje genetske raznolikosti populacije, njenih genotipskih prilagoditev in plastičnih fenotipskih odrazov na okolje, ki se je izoblikovalo prek večgeneracijske izpostavljenosti neusmerjenim mehanizmom evolucije kot so naključne mutacije, genetski zdrs in pretok genov, ter prek večgeneracijske izpostavljenosti usmerjenim mehanizmom evolucije, kot je naravna selekcija. S tem se poraja pomembno vprašanje današnjega časa, in sicer, kako te evolucijsko najuspešnejše strategije naravnih populacij delujejo pod usmerjeno nenaravno smrtnostjo, umetno selekcijio moderne dobe, ki jo usmerja človek?

Ribištvo je prešlo tehnološko in digitalno revolucijo in spremenilo plovila v tovarniške ladje, ki lahko natančno izsledijo lokacijo visoke gostote rib, povečajo ulov ter ga procesirajo in zamrznejo nemudoma na krovu. S tem se podaljša razpoložljiv čas zadrževanja plovil na morju in čas namenjen ribolovu, kar posledično vodi v večji izlov. Ker ribolov ni naključen, ampak poveča verjetnost smrtnosti pri osebkih s specifičnimi lastnostmi bolj kot pri tistih, ki le-teh nimajo, prekomeren ribolov pozroča usmerjeno selekcijo in s tem vpliva na evolucijske in ekološke spremembe v populaciji, ki se lahko posledično opazijo tudi širše v samem ekosistemu. Najpogostejše odbirno merilo ribolova je telesna velikost ribe. S tem, ko izlovijo osebke večje rasti iz populacije, se poveča pogostost osebkov z genotipom manjše rasti, ki imajo običajno počasnejšo telesno rast, postanejo zreli pri zgodnejši starosti in manjši telestni velikosti, ter izležejo manjše število iker v svoji razmnoževalni življenjski dobi. V primeru, da fenotipska velikost odraža genetsko zasnovo, lahko le-ta vodi v nepovraten evolucijski odklon povprečne telesne velikosti v populaciji. V nasprotnem primeru, torej če genetska podlaga ostane nespremenjena in fenotipska sprememba v povprečni velikosti rib odraža plastičen odziv na ekološke spremembe, ki so povezane z manjšo številčnostjo populacije in manjšo populacijsko gostoto, je sprememba v odklonu telesne velikosti lahko obnovljiva.

V doktorskem delu sem obelodanila nekatere evolucijske in ekološke prednosti, ki jih raznolikost v življenjskem krogu ikonične ribje vrste, atlantske trske (*Gadus morhua L.*), ustvarja in ohranja na več ravneh biološke organizacije. V okviru štirih raziskovalnih ciljev sem odkrivala kako prilagojene življenjske lastnosti in strategije, tesno povezane z velikostjo telesa ribe, vplivajo na razmnoževalni potencial posamezne ribje samice ali ikrnice, na uspešnost populacije in na delovanje prehranjevalnega spleta. Odgovore na raziskovalna vprašanja sem iskala z dvema mehanicistično motiviranima modeloma, ki sta zaobjela kompleksnost biotskih in abiotskih interakcij ter s primerjavo različnih okoljskih scenarijev privedla do novih spoznanj.

V prvem objavljenem delu ugotavljam ali je razmnoževanje z večkratnim drstenjem znotraj ene sezone prilagoditvena strategija atlantske trske, katere namen je zavarovanje pred tveganjem izgube potomstva. Z eko-evolucijskim modelom, ki sledi celotnemu življenju vsake posamezne ribe v populaciji in združuje teoretične in empirične izsledke večjega števila študij o dedovanju, razvoju, rasti, razmnoževanju in smrtnosti posameznega osebka, sem primerjala evolucijski uspeh ribje populacije, ki vključuje strategijo večkratnega drstenja znotraj vsake sezone, z evolucijskim uspehom ribje populacije, ki te strategije nima in odlaga vse ikre enkrat znotraj vsake sezone. Torej, zakaj in pod kakšnimi pogoji je večkratno drstenje zmagovalna strategija, ki zagotavlja boljši dolgoročni uspeh populacije ali njen fitnes? Analize fitnesa so pokazale, da je večkratno drstenje evolucijsko prilagojena strategija, ki zmanjša visoko zgodnjo smrtnost iker. Z drstenjem v več intervalih znotraj sezone trska poveča verjetnost, da se vsaj nekatere ikre izležejo v ugodnih okoljskih pogojih. Večja kot je ikrnica, več iker lahko drsti, prek več intervalov jih razporedi in tudi zagotovi boljši razmnoževalni uspeh. Ta strategija je prednostna pod naravno selekcijo na dolgi rok, saj zmanjša varianco v razmnoževalnem uspehu med posamezniki znotraj generacije kot tudi med generacijami in s tem zagotavlja višji dolgoročni uspeh ali fitness genotipa. Ta strategija se izplača predvsem, ko je okolje, ki vpliva na preživetje ikrnic, nepredvidljivo, spremenljivo in nevarno.

V drugem objavljenem delu preučujem ali je strategija razpršitve tveganja, večkratno drstenje atlantske trske, učinkovita tudi proti umetni selekciji v obliki velikostno-selektivnega ribolova. Ker je število drstitev v drstitveni sezoni povezano z velikostjo telesa trske, me je zanimalo kako sprememba v velikostni strukturi populacije, ki jo povzroča prekomeren selektivni ribolov, vpliva na fitnes genotipa. Razširitev eko-evolucijskega modela z dodano ribiško smrtnostjo je pokazala ekološke in evolucijske prednosti ter slabosti drstitvene strategije pod različnimi intenzitetami ribolova. Natančneje, velikostno-selektivni ribolov je povzročil dolgotrajne spremembe v populacijski strukturi ne samo zaradi selektivnega odstranjevanja večjih in starejših osebkov, temveč tudi zaradi nepričakovanega odstranjevanja posameznikov z največjim potencialom obvladovanja tveganja reprodukcijskega neuspeha. S tem sem razkrila, da so prednosti razpršitve tveganja, ki ga večkratno drstenje zagotavlja, neučinkovite pri velikostno-selektivnemu ribolovu, saj ne ščiti fitnesa in demografske strukture atlantske trske. Intenziven ribolov je vodil v manjšo povprečno telesno velikost populacije in v njeno počasnejše okrevanje. Kljub popolni prepovedi ribolova, populacija ni zmogla obnoviti velikostne demografske strukture, kar kaže da odklon v povprečni velikosti ni zgolj plastičen odziv na zmanjšano populacijsko gostoto, temveč tudi posledica evolucijskega zmanjševanja genetske raznolikosti. To dokazuje, da lahko prekomerni ribolov že v roku nekaj let spremeni nekatere prvotno uspešne življenjske strategije v neugodne, in s tem zmanjša produktivnost ribjih zalog.

V tretjem delu sem analizirala doprinos medvrstne raznolikosti k strukturi in delovanju morskega prehranjevalnega spleta. S pomočjo dolgoročnih študij, ki že več desetletij spremljajo sestavo in delovanje fitoplanktona, zooplanktona in ribjih združb v norveškem delu morja Skagerrak, sem pripravila alometrični trofični model za prehranjevalni splet Skagerraka. Model tako sestavlja 148 trofičnih skupin, ki se povezujejo z 1864 prehranjevalnimi vezmi. V splet sta ključena tudi dva ekotipa atlantske trske in sicer ekotip Severnega morja in ekotip fjorda. Ekotipa se kljub temu, da sobivata, razlikujeta v genetskih, fenotipskih in ekoloških značilnostih. Medtem, ko ekotip Severnega morja doseže večjo telesno velikost in ima hitrejšo rast, je hkrati tudi bolj mobilen in načeloma migrira v drstitvenem času v Severno morje ter se kasneje vrača v obalne pelagične vode Skagerraka za hranjenje. Za razliko od severnega ekotipa, fjordski ekotip doseže manjšo telesno velikost in ima počasnejšo rast, je manj mobilen ter se tako drsti kot tudi prehranjuje v Skagerraku. Fjordski ekotip se v fjordih Skagerraka običajno prehranjuje v večjih globinah kot ekotip Severnega morja, kar se odraža tudi na izotopski sestavi, ki nakazujejo, da ekotip Severnega morja pleni več pelagičnega plena, fjordski ekotip pa več bentoškega plena. Vključitev ekotipov v prehranjevalni splet in sistematsko opazovanje njunih tako posameznih kot skupnih vplivov na strukturo in delovanje prehrambenega spleta, je pokazalo, da ima medvrstno razlikovanje med ekotipoma v ontogenetskih spremembah prehranjevanja nasproten vpliv na produktivnost ribje združbe. Poleg tega se je prehranjevalni splet Skagerraka izkazal kot bolj občutljiv na izgubo fjordskega ekotipa atlantske trske, saj se je robustnost prehranjevalnega spleta na napredvidljive ekološke katastrofe, ki bi privedle do izgube posamičnih vrst, močneje zmanjšala pri odstranistvi fjordskega ekotipa kot pa pri odstranitvi ekotipa Svernega morja. Te ugotovitve opozarjajo na kritično potrebo po upoštevanju in vključevanju medvrstne raznolikosti v programe, ki se zavzemajo za ohranjanje narave, in katerih cilj je zagotovitev trajnostnega ribištva.

V četrtem objavljenem delu sem pregledala študije, ki raziskujejo ekološke in evolucijske posledice spremenjene genotipske in fenotipske variance med populacijami morskih rib kostnic. Cilj prispevka je bil predstaviti vidik možnih mehanizmov, prek katerih lahko ribiško-povzročene spremembe v evolucijski ali ekološki dinamiki prelovljenih ribjih zalog vodijo do obsežnih posledic v ekosistemu. V tem doktorskem delku je bila rdeča nit raznolikost. Izsledki vseh štirih del opozarjajo na mehanizme in potencialne posledice do katerih lahko privede prekomeren ribolov z visoko nenaravno smrtnostjo in selektivnimi metodami ter vpliva na raznolikost na kateri koli od treh ravni biološke organizacije: individualni, populacijski in ekosistemski.

REFERENCES

Andersen K.H., Berge T., Gonçalves R.J., Hartvig M., Heuschele J., Hylander S., Jacobsen N.S., Lindemann C., Martens E.A., Neuheimer A.B., Olsson K., Palacz A., Prowe A.E.F., Sainmont J., Traving S.J., Visser A.W., Wadhwa N. & Kiørboe T. 2016. Characteristic sizes of life in the oceans, from bacteria to whales. *Ann. Rev. Mar. Sci.* 8: 217–241. https://doi.org/10.1146/annurev-marine-122414-034144

Anderson C.N.K., Hsieh C., Sandin S.A., Hewitt R., Hollowed A., Beddington J., May R.M. & Sugihara G. 2008. Why fishing magnifies fluctuations in fish abundance. *Nature* 452: 835–839. https://doi.org/10.1038/nature06851

André C., Svedäng H., Knutsen H., Dahle G., Jonsson P., Ring A., Sköld M. & Jorde P.E. 2016. Population structure in Atlantic cod in the eastern North Sea-Skagerrak-Kattegat: early life stage dispersal and adult migration. *BMC Res. Notes* 9, 63. https://doi.org/10.1186/s13104-016-1878-9

Anon. 2023. Agreed record of conclusions of fisheries consultations between Norway and the European Union on the regulation of fisheries in Skagerrak and Kattegat for 2023. https://www.regjeringen.no/contentassets/db5400fed30b48f1be1f9f072c042803/noway-eu-skagerrak-agreement.pdf. Accessed 1.5.2023.

Arlinghaus R., Laskowski K.L., Alós J., Klefoth T., Monk C.T., Nakayama S. & Schröder A. 2017. Passive gear-induced timidity syndrome in wild fish populations and its potential ecological and managerial implications. *Fish Fish.* 18: 360–373. https://doi.org/10.1111/faf.12176

Audzijonyte A., Kuparinen A. & Fulton E.A. 2013. How fast is fisheries-induced evolution? Quantitative analysis of modelling and empirical studies. *Evol. Appl.* 6: 585–595. https://doi.org/10.1111/eva.12044

Audzijonyte A., Kuparinen A. & Fulton E.A. 2014. Ecosystem effects of contemporary life-history changes are comparable to those of fishing. *Mar. Ecol. Prog. Ser.* 495: 219–231. https://doi.org/10.3354/meps10579

Barceló C., Ciannelli L., Olsen E.M., Johannessen T. & Knutsen H. 2016. Eight decades of sampling reveal a contemporary novel fish assemblage in coastal nursery habitats. *Glob. Change Biol.* 22: 1155–1167. https://doi.org/10.1111/gcb.13047

Barneche D.R., Robertson D.R., White C.R. & Marshall D.J. 2018. Fish reproductive-energy output increases disproportionately with body size. *Science* 360: 642–645. https://doi.org/10.1126/science.aao6868

Barth J.M.I., Berg P.R., Jonsson P.R., Bonanomi S., Corell H., Hemmer-Hansen J., Jakobsen K.S., Johannesson K., Jorde P.E., Knutsen H., Moksnes P., Star B., Stenseth N.C., Svedäng H., Jentoft S. & André C. 2017. Genome architecture enables local adaptation of Atlantic cod despite high connectivity. *Mol. Ecol.* 26: 4452–4466. https://doi.org/10.1111/mec.14207

Béné C., Barange M., Subasinghe R., Pinstrup-Andersen P., Merino G., Hemre G. & Williams M. 2015. Feeding 9 billion by 2050 – Putting fish back on the menu. *Food Secur.* 7: 261–274. https://doi.org/10.1007/s12571-015-0427-z

Benton T.G. & Grant A. 2000. Evolutionary fitness in ecology: Comparing measures of fitness in stochastic, density-dependent environments. *Evol. Ecol. Res.* 2: 769–789.

Berkeley S.A., Chapman C. & Sogard S.M. 2004. Maternal age as a determinant of larval growth and survival in a marine fish, Sebastes melanops. *Ecology* 85: 1258–1264. https://doi.org/10.1890/03-0706

Blanchard J.L., Heneghan R.F., Everett J.D., Trebilco R. & Richardson A. J. 2017. From bacteria to whales: using functional size spectra to model marine ecosystems. *Trends Ecol. Evol.* 32: 174–186. https://doi.org/10.1016/j.tree.2016.12.003

Bland S., Valdovinos F.S., Hutchings J.A. & Kuparinen A. 2019. The role of fish life histories in allometrically scaled food-web dynamics. *Ecol. Evol.* 9: 3651–3660. https://doi.org/10.1002/ece3.4996

Bleil M. & Oeberst R. 1998. The spawning of cod (Gadus morhua morhua) under controlled conditions of captivity, quantity and quality of spawned eggs. *ICES J. Mar. Sci.* C. M. 1998/DD:3: 1–27.

Boit A., Martinez N.D., Williams R.J. & Gaedke U. 2012. Mechanistic theory and modelling of complex food-web dynamics in Lake Constance. *Ecol. Lett.* 15: 594–602. https://doi.org/10.1111/j.1461-0248.2012.01777.x

Bolnick D.I., Amarasekare P., Araújo M.S., Bürger R., Levine J.M., Novak M., Rudolf V.H.W., Schreiber S.J., Urban M.C. & Vasseur D.A. 2011. Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.* 26: 183–192. https://doi.org/10.1016/j.tree.2011.01.009

Breistein B., Dahle G., Johansen T., Besnier F., Quintela M., Jorde P.E., Knutsen H., Westgaard J., Nedreaas K., Farestveit E. & Glover K.A. 2022. Geographic variation in gene flow from a genetically distinct migratory ecotype drives population genetic structure of coastal Atlantic cod (Gadus morhua L.). *Evol. Appl.* 15: 1162–1176. https://doi.org/10.1111/eva.13422

Brose U., Williams R.J. & Martinez N.D. 2006. Allometric scaling enhances stability in complex food webs. *Ecol. Lett.* 9: 1228–1236. https://doi.org/10.1111/j.1461-0248.2006.00978.x

Brown J.H., Gillooly J.F., Allen A.P., Savage V.M. & West G.B. 2004. Toward a metabolic theory of ecology. *Ecology* 85: 1771–1789. https://doi.org/10.1890/03-9000

Charnov E.L. & Schaffer W.M. 1973. Life-history consequences of natural selection: Cole's result revisited. *Am. Nat.* 107: 791–793. https://doi.org/10.1086/282877

Clapham P.J. 1996. The social and reproductive biology of Humpback Whales: an ecological perspective. *Mamm. Rev.* 26: 27–49. https://doi.org/10.1111/j.1365-2907.1996.tb00145.x

Cole L.C. 1954. The population consequences of life history phenomena. *Q. Rev. Biol.* 29: 103–137. https://doi.org/10.1086/400074

Coleman F.C. & Williams S.L. 2002. Overexploiting marine ecosystem engineers: potential consequences for biodiversity. *Trends Ecol. Evol.* 17: 40–44. https://doi.org/10.1016/s0169-5347(01)02330-8

Conover D.O. & Baumann H. 2009. The role of experiments in understanding fishery-induced evolution. *Evol. Appl.* 2: 276–290. https://doi.org/10.1111/j.1752-4571.2009.00079.x

Conover D.O. & Munch S.B. 2002. Sustaining fisheries yields over evolutionary time scales. *Science* 297: 94–96. https://doi.org/10.1126/science.1074085

Crean A.J. & Marshall D.J. 2009. Coping with environmental uncertainty: dynamic bet hedging as a maternal effect. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* 364: 1087–1096. https://doi.org/10.1098/rstb.2008.0237

Crespi B.J. & Teo R. 2002. Comparative phylogenetic analysis of the evolution of semelparity and life history in salmonid fishes. *Evolution* 56: 1008–1020. https://doi.org/10.1111/j.0014-3820.2002.tb01412.x

Crutsinger G.M., Collins M.D., Fordyce J.A., Gompert Z., Nice C.C. & Sanders N.J. 2006. Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science* 313: 966–968. https://doi.org/10.1126/science.1128326

Cushing D.H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Adv. Mar. Biol.* 26: 249–293. https://doi.org/10.1016/s0065-2881(08)60202-3

Dannevig A. 1949. The variation in growth of young codfish from the Norwegian Skagerrak coast. *Fisk.dir. Skr., Havundersøkelser* 9: 1–22.

Darimont C.T., Fox C.H., Bryan H.M. & Reimchen T.E. 2015. The unique ecology of human predators. *Science* 349: 858–860. https://doi.org/10.1126/science.aac4249

Darwin C. 1859. *On the origin of species by means of natural selection, or, the preservation of favoured races in the struggle for life*. John Murray, London.

Darwin C. 1996. *The voyage of the Beagle*. Wordsworth Editions, Herts.

Dawkins R. 1982. *The extended phenotype: the long reach of the gene*. Oxford University Press, Oxford.

Des Roches S., Shurin J.B., Schluter D. & Harmon L.J. 2013. Ecological and evolutionary effects of stickleback on community structure. *PLoS ONE* 8, e59644. https://doi.org/10.1371/journal.pone.0059644

Devine J.A., Wright P.J., Pardoe H.E. & Heino M. 2012. Comparing rates of contemporary evolution in life-history traits for exploited fish stocks. *Can. J. Fish. Aquat. Sci.* 69: 1105–1120. https://doi.org/10.1139/f2012-047

Díaz Pauli B. & Sih A. 2017. Behavioural responses to human-induced change: why fishing should not be ignored. *Evol. Appl.* 10: 231–240. https://doi.org/10.1111/eva.12456

Drinkwater K.F. 2005. The response of Atlantic cod (Gadus morhua) to future climate change. *ICES J. Mar. Sci.* 62: 1327–1337. https://doi.org/10.1016/j.icesjms.2005.05.015

Eikeset A.M., Dunlop E.S., Heino M., Storvik G., Stenseth N.C. & Dieckmann U. 2016. Roles of density-dependent growth and life history evolution in accounting for fisheries-induced trait changes. *Proc. Natl. Acad. Sci. U.S.A* 113: 15030–15035. https://doi.org/10.1073/pnas.1525749113

Eloranta A.P., Perälä T. & Kuparinen A. 2023. Effects of temporal abiotic drivers on the dynamics of an allometric trophic network model. *Ecol. Evol.* 13, e9928. https://doi.org/10.1002/ece3.9928

Evans M.E.K., Ferrière R., Kane M.J. & Venable D.L. 2007. Bet hedging via seed banking in desert evening primroses (Oenothera, Onagraceae): demographic evidence from natural populations. *Am. Nat.* 169: 184–194. https://doi.org/10.2307/4125316

Falkenhaug T., Broms C., Bagøien E. & Nikolioudakis N. 2022. Temporal variability of co-occurring Calanus finmarchicus and C. helgolandicus in Skagerrak. *Front. Mar. Sci.* 9, 779335. https://doi.org/10.3389/fmars.2022.779335

FAO Fisheries and Aquaculture Department, Statistics and Information Service. 2022. FishStatJ: Universal software for fishery statistical time series. Version v4.02.08. https://www.fao.org/fishery/en/statistics/software/fishstatj Accessed 31.1.2023

Fisher R.A. 1930. *The genetical theory of natural selection*. Clarendon Press, Oxford.

Fitzhugh G.R., Shertzer K.W., Kellison T.G. & Wyanski D. M. 2012. Review of size- and age-dependence in batch spawning: implications for stock assessment of fish species exhibiting indeterminate fecundity. *Fish. Bull.* 110: 413–425.

Floeter J. & Temming A. 2003. Explaining diet composition of North Sea cod (Gadus morhua): prey size preference vs. prey availability. *Can. J. Fish. Aquat. Sci.* 60: 140–150. https://doi.org/10.1139/f03-007

Fogarty M.J., Myers R.A. & Bowen K.G. 2001. Recruitment of cod and haddock in the North Atlantic: a comparative analysis. *ICES J. Mar. Sci.* 58: 952–961. https://doi.org/10.1006/jmsc.2001.1108

Frank K.T., Petrie B., Choi J.S. & Leggett W.C. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308: 1621–1623. https://doi.org/10.1126/science.1113075

Frank S.A. & Slatkin M. 1990. Evolution in a variable environment. *Am. Nat.* 136: 244–260. https://doi.org/10.1086/285094

Ganias K., Lowerre-Barbieri S.K. & Cooper W. 2015. Understanding the determinate–indeterminate fecundity dichotomy in fish populations using a temperature dependent oocyte growth model. *J. Sea Res.* 96: 1–10. https://doi.org/10.1016/j.seares.2014.10.018

Gillespie J.H. 1974. Natural selection for within generation variance in offspring number. *Genetics* 76: 601–606. https://doi.org/10.1093/genetics/76.3.601

Gran-Stadniczeñko S., Egge E., Hostyeva V., Logares R., Eikrem W. & Edvardsen B. 2019. Protist diversity and seasonal dynamics in Skagerrak plankton communities as revealed by metabarcoding and microscopy. *J. Eukaryot. Microbiol.* 66: 494–513. https://doi.org/10.1111/jeu.12700

Halpern B.S., Selkoe K.A., Micheli F. & Kappel C.V. 2007. Evaluating and ranking the vulnerability of global marine ecosystems to anthropogenic threats. *Conserv. Biol.* 21: 1301–1315. https://doi.org/10.1111/j.1523-1739.2007.00752.x

Hamilton W.D. 1964. The genetical evolution of social behaviour. II. *J. Theor. Biol.* 7: 17–52. https://doi.org/10.1016/0022-5193(64)90039-6

Harmon L.J., Matthews B., Des Roches S., Chase J.M., Shurin J.B. & Schluter D. 2009. Evolutionary diversification in stickleback affects ecosystem functioning. *Nature* 458: 1167–1170. https://doi.org/10.1038/nature07974

Heath M.R., Speirs D.C. & Steele J.H. 2014. Understanding patterns and processes in models of trophic cascades. *Ecol. Lett.* 17: 101–114. https://doi.org/10.1111/ele.12200

Heino M., Díaz Pauli B. & Dieckmann U. 2015. Fisheries-induced evolution. *Annu. Rev. Ecol. Evol. Syst.* 46: 461–480. https://doi.org/10.1146/annurev-ecolsys-112414-054339

Hemmer-Hansen J., Nielsen E.E., Therkildsen N.O., Taylor M.I., Ogden R., Geffen A.J., Bekkevold D., Helyar S., Pampoulie C., Johansen T. & Carvalho G.R. 2013. A genomic island linked to ecotype divergence in Atlantic cod. *Mol. Ecol.* 22: 2653–2667. https://doi.org/10.1111/mec.12284

Hilborn R. & Walters C.J. 1992. *Quantitative fisheries stock assessment: choice, dynamics and uncertainty*. Chapman and Hall, London.

Hixon M.A., Johnson D.W. & Sogard S.M. 2014. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES J. Mar. Sci.* 71: 2171–2185. https://doi.org/10.1093/icesjms/fst200

Hop H., Gjøsæter J. & Danielssen D.S. 1992. Seasonal feeding ecology of cod (Gadus morhua L.) on the Norwegian Skagerrak coast. *ICES J. Mar. Sci.* 49: 453–461. https://doi.org/10.1093/icesjms/49.4.453

Hufford K.M. & Mazer S.J. 2003. Plant ecotypes: genetic differentiation in the age of ecological restoration. *Trends Ecol. Evol.* 18: 147–155. https://doi.org/10.1016/s0169-5347(03)00002-8

Hunter A., Speirs D.C. & Heath M.R. 2015. Fishery-induced changes to age and length dependent maturation schedules of three demersal fish species in the Firth of Clyde. *Fish. Res.* 170: 14–23. https://doi.org/10.1016/j.fishres.2015.05.004

Hutchings J.A. 2005. Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (Gadus morhua). *Can. J. Fish. Aquat. Sci.* 62: 824–832. https://doi.org/10.1139/f05-081

Hutchings J.A. 2021. *A primer of life histories: ecology, evolution, and application*. Oxford University Press, Oxford.

Hutchings J.A. 2022. Tensions in the communication of science advice on fish and fisheries: northern cod, species at risk, sustainable seafood. *ICES J. Mar. Sci.* 79: 308–318. https://doi.org/10.1093/icesjms/fsab271

Hutchings J.A. & Baum J.K. 2005. Measuring marine fish biodiversity: temporal changes in abundance, life history and demography. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* 360: 315–338. https://doi.org/10.1098/rstb.2004.1586

Hutchings J.A. & Fraser D.J. 2008. The nature of fisheries- and farming-induced evolution. *Mol. Ecol.* 17: 294–313. https://doi.org/10.1111/j.1365-294x.2007.03485.x

Hutchings J.A. & Kuparinen A. 2021. Throwing down a genomic gauntlet on fisheries-induced evolution. *Proc. Natl. Acad. Sci. U.S.A* 118, e2105319118. https://doi.org/10.1073/pnas.2105319118

Hutchings J.A. & Myers R.A. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, Gadus morhua, of Newfoundland and Labrador. *Can. J. Fish. Aquat. Sci.* 51: 2126–2146. https://doi.org/10.1139/f94-214

Hutchings J.A. & Rangeley R.W. 2011. Correlates of recovery for Canadian Atlantic cod (Gadus morhua). *Can. J. Zool.* 89: 386–400. https://doi.org/10.1139/Z11-022

Hutchings J.A., Bishop T.D. & McGregor-Shaw C.R. 1999. Spawning behaviour of Atlantic cod, Gadus morhua: evidence of mate competition and mate choice in a broadcast spawner. *Can. J. Fish. Aquat. Sci.* 56: 97–104. https://doi.org/10.1139/cjfas-56-1-97

Huxley T.H. 1883. *Inaugural meeting of the fishery congress, papers of the conferences held in connection with the Great International Fisheries Exhibition*. William Clowes and Sons Ltd, London.

ICES 2022. Cod (Gadus morhua) in subarea 4, division 7.d, and subdivision 20 (North Sea, eastern English Channel, Skagerrak). Report of the ICES Advisory Committee, ICES Advice 2022, cod.27.47d20. https://doi.org/10.17895/ices.advice.21406881

IPCC 2023. *Climate change 2023: mitigation of climate change. Working group III contribution to the IPCC sixth assessment report of the Intergovernmental Panel on Climate*. Cambridge University Press, Cambridge.

Jakobsdóttir K.B., Pardoe H., Magnússon Á., Björnsson H., Pampoulie C., Ruzzante D.E. & Marteinsdóttir G. 2011. Historical changes in genotypic frequencies at the Pantophysin locus in Atlantic cod (Gadus morhua) in Icelandic waters: evidence of fisheries-induced selection? *Evol. Appl.* 4: 562–573. https://doi.org/10.1111/j.1752-4571.2010.00176.x

Johannesen E., Keith D., Fogarty M.J., Shackell N. & Frank K.T. 2022. Persistent differences in recruitment variability among co-occurring North Atlantic groundfish species. *ICES J. Mar. Sci.* 79: 2430–2441. https://doi.org/10.1093/icesjms/fsac181

Jørgensen C., Ernande B. & Fiksen Ø. 2009. Size-selective fishing gear and life history evolution in the Northeast Arctic cod. *Evol. Appl.* 2: 356–370. https://doi.org/10.1111/j.1752-4571.2009.00075.x

Jørgensen C., Enberg K., Dunlop E.S., Arlinghaus R., Boukal D.S., Brander K., Ernande B., Gårdmark A.G., Johnston F., Matsumura S., Pardoe H., Raab K., Silva A., Vainikka A., Dieckmann U., Heino M. & Rijnsdorp A.D. 2007. Ecology: Managing Evolving Fish Stocks. *Science* 318: 1247–1248. https://doi.org/10.1126/science.1148089

Jusufovski D. & Kuparinen A. 2014. Contrasting evolutionary and ecological management objectives in the context of sustainable harvesting. *Evol. Ecol. Res.* 16: 133–142.

Jusufovski D. & Kuparinen A. 2020. Exploring individual and population eco-evolutionary feedbacks under the coupled effects of fishing and predation. *Fish. Res.* 231, 105713. https://doi.org/10.1016/j.fishres.2020.105713

Kaiho K. 2022. Relationship between extinction magnitude and climate change during major marine and terrestrial animal crises. *Biogeosciences* 19: 3369–3380. https://doi.org/10.5194/bg-19-3369-2022

Karageorgis A.P., Kaberi H.G., Tengberg A., Zervakis V., Hall P.O.J. & Anagnostou C.L. 2003. Comparison of particulate matter distribution, in relation to hydrography, in the mesotrophic Skagerrak and the oligotrophic northeastern Aegean Sea. *Cont. Shelf Res.* 23: 1787–1809. https://doi.org/10.1016/j.csr.2003.06.004

Kindsvater H.K. & Palkovacs E.P. 2017. Predicting eco-evolutionary impacts of fishing on body size and trophic role of Atlantic cod. *Copeia* 105: 475–482. https://doi.org/10.1643/ot-16-533

Kjesbu O.S., Solemdal P., Bratland P. & Fonn M. 1996. Variation in annual egg production in individual captive Atlantic cod (Gadus morhua). *Can. J. Fish. Aquat. Sci.* 53: 610–620. https://doi.org/10.1139/f95-215

Knutsen H., Jorde P.E., Hutchings J.A., Hemmer-Hansen J., Grønkjær P., Jørgensen K.M., André C., Sodeland M., Albretsen J. & Olsen E.M. 2018. Stable coexistence of genetically divergent Atlantic cod ecotypes at multiple spatial scales. *Evol. Appl.* 11: 1527–1539. https://doi.org/10.1111/eva.12640

Kortsch S., Frelat R., Pecuchet L., Olivier P., Putnis I., Bonsdorff E., Ojaveer H., Jurgensone I., Strāķe S., Rubene G., Krūze Ē. & Nordström M.C. 2021. Disentangling temporal food web dynamics facilitates understanding of ecosystem functioning. *J. Anim. Ecol.* 90: 1205–1216. https://doi.org/10.1111/1365-2656.13447

Kratina P., LeCraw R.M., Ingram T. & Anholt B.R. 2012. Stability and persistence of food webs with omnivory: Is there a general pattern? *Ecosphere* 3, 50. https://doi.org/10.1890/es12-00121.1

Kristensen M.L., Olsen E.M., Moland E., Knutsen H., Grønkjær P., Koed A., Källo K. & Aarestrup K. 2021. Disparate movement behavior and feeding ecology in sympatric ecotypes of Atlantic cod. *Ecol. Evol.* 11: 11477–11490. https://doi.org/10.1002/ece3.7939

Kristiansen T. & Aas E. 2015. Water type quantification in the Skagerrak, the Kattegat and off the Jutland west coast. *Oceanologia* 57: 177–195. https://doi.org/10.1016/j.oceano.2014.11.002

Kuparinen A. & Hutchings J.A. 2012. Consequences of fisheries-induced evolution for population productivity and recovery potential. *Proc. R. Soc. B: Biol. Sci.* 279: 2571–2579. https://doi.org/10.1098/rspb.2012.0120

Kuparinen A. & Hutchings J.A. 2014. Increased natural mortality at low abundance can generate an Allee effect in a marine fish. *R. Soc. Open Sci.* 1, 140075. https://doi.org/10.1098/rsos.140075

Kuparinen A. & Hutchings J.A. 2017. Genetic architecture of age at maturity can generate divergent and disruptive harvest-induced evolution. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* 372, 20160035. https://doi.org/10.1098/rstb.2016.0035

Kuparinen A. & Hutchings J.A. 2019. When phenotypes fail to illuminate underlying genetic processes in fish and fisheries science. *ICES J. Mar. Sci.* 76: 999–1006. https://doi.org/10.1093/icesjms/fsz002

Kuparinen A. & Merilä J. 2007. Detecting and managing fisheries-induced evolution. *Trends Ecol. Evol.* 22: 652–659. https://doi.org/10.1016/j.tree.2007.08.011

Kuparinen A. & Uusi-Heikkilä S. 2020. Atlantic cod recovery from the Allee effect zone: contrasting ecological and evolutionary rescue. *Fish Fish.* 21: 916–926. https://doi.org/10.1111/faf.12470

Kuparinen A., Hardie D.C. & Hutchings J.A. 2012. Evolutionary and ecological feedbacks of the survival cost of reproduction. *Evol. Appl.* 5: 245–255. https://doi.org/10.1111/j.1752-4571.2011.00215.x

Kuparinen A., Hutchings J.A. & Waples R.S. 2016c. Harvest-induced evolution and effective population size. *Evol. Appl.* 9: 658–672. https://doi.org/10.1111/eva.12373

Kuparinen A., Keith D.M. & Hutchings J.A. 2014b. Allee effect and the uncertainty of population recovery. *Conserv. Biol.* 28: 790–798. https://doi.org/10.1111/cobi.12216

Kuparinen A., Keith D.M. & Hutchings J.A. 2014c. Increased environmentally driven recruitment variability decreases resilience to fishing and increases uncertainty of recovery. *ICES J. Mar. Sci.* 71: 1507–1514. https://doi.org/10.1093/icesjms/fsu021

Kuparinen A., Stenseth N.C. & Hutchings J.A. 2014a. Fundamental population-productivity relationships can be modified through density-dependent feedbacks of life-history evolution. *Evol. Appl.* 7: 1218–1225. https://doi.org/10.1111/eva.12217

Kuparinen A., Boit A., Valdovinos F.S., Lassaux H. & Martinez N.D. 2016a. Fishing-induced life-history changes degrade and destabilize harvested ecosystems. *Sci. Rep.* 6, 22245. https://doi.org/10.1038/srep22245

Kuparinen A., Roney N.E., Oomen R.A., Hutchings J.A. & Olsen E.M. 2016b. Small-scale life history variability suggests potential for spatial mismatches in Atlantic cod management units. *ICES J. Mar. Sci.* 73: 286–292. https://doi.org/10.1093/icesjms/fsv181

Langangen Ø., Stige L.C., Yaragina N.A., Vikebø F.B., Bogstad B. & Gusdal Y. 2014. Egg mortality of northeast Arctic cod (Gadus morhua) and haddock (Melanogrammus aeglefinus). *ICES J. Mar. Sci.* 71: 1129–1136. https://doi.org/10.1093/icesjms/fst007

Law R. 2000. Fishing, selection, and phenotypic evolution. *ICES J. Mar. Sci.* 57: 659–668. https://doi.org/10.1006/jmsc.2000.0731

Law R. 2007. Fisheries-induced evolution: present status and future directions. *Mar. Ecol. Prog. Ser.* 335: 271–277. https://doi.org/10.3354/meps335271

Law R. & Grey D.R. 1989. Evolution of yields from populations with age-specific cropping. *Evol. Ecol.* 3: 343–359. https://doi.org/10.1007/bf02285264

Lotka A.J. 1907. Relation between birth rates and death rates. *Science* 26: 21–22. https://doi.org/10.1126/science.26.653.21.b

Lowerre-Barbieri S.K., Ganias K., Saborido-Rey F., Murua H. & Hunter J.R. 2011. Reproductive timing in marine fishes: variability, temporal scales, and methods. *Mar. Coast. Fish.* 3: 71–91. https://doi.org/10.1080/19425120.2011.556932

Marshall C.T., Kjesbu O.S., Yaragina N.A., Solemdal P. & Ulltang Ø. 1998. Is spawner biomass a sensitive measure of the reproductive and recruitment potential of Northeast Arctic cod? *Can. J. Fish. Aquat. Sci.* 55: 1766–1783. https://doi.org/10.1139/f98-062

Marshall D.J., Bonduriansky R. & Bussière L.F. 2008. Offspring size variation within broods as a bet-hedging strategy in unpredictable environments. *Ecology* 89: 2506–2517. https://doi.org/10.1890/07-0267.1

MATLAB 2018. Version 9.4 (R2019b). The MathWorks Inc. , Natick, Massachusetts.

May R.M. 1974. *Stability and complexity in model ecosystems*. Princeton University Press, Princeton.

Metz J.A.J., Nisbet R. M. & Geritz S.A.H. 1992. How should we define 'fitness' for general ecological scenarios? *Trends Ecol. Evol.* 7: 198–202. https://doi.org/10.1016/0169-5347(92)90073-k

Meyers L.A. & Bull J.J. 2002. Fighting change with change: adaptive variation in an uncertain world. *Trends Ecol. Evol.* 17: 551–557. https://doi.org/10.1016/s0169-5347(02)02633-2

Monk C.T, Bekkevold D., Klefoth T., Pagel T., Palmer M. & Arlinghaus R. 2021. The battle between harvest and natural selection creates small and shy fish. *Proc. Natl. Acad. Sci. U.S.A* 118, e2009451118. https://doi.org/10.1073/pnas.2009451118

Morgan M.J. & Brattey J. 2005. Effect of changes in reproductive potential on perceived productivity of three Northwest Atlantic cod (Gadus morhua) stocks. *ICES J. Mar. Sci.* 62: 65–74. https://doi.org/10.1016/j.icesjms.2004.10.003

Mougi A. 2020. Natural selection contributes to food web stability. *PLoS ONE* 15, e0227420. https://doi.org/10.1371/journal.pone.0227420

Murphy G.I. 1968. Pattern in life history and the environment. *Am. Nat.* 102: 391–403. https://doi.org/10.1086/282553

Nash R.D.M., Pilling G.M., Kell L.T., Schön P. & Kjesbu O.S. 2010. Investment in maturity-at-age and -length in northeast Atlantic cod stocks. *Fish. Res.* 104: 89–99. https://doi.org/10.1016/j.fishres.2010.03.001

O'Gorman E.J., Jacob U., Jonsson T. & Emmerson M.C. 2010. Interaction strength, food web topology and the relative importance of species in food webs. *J. Anim. Ecol.* 79: 682–692. https://doi.org/10.1111/j.1365-2656.2009.01658.x

Ohlberger J. & Langangen Ø. 2015. Population resilience to catastrophic mortality events during early life stages. *Ecol. Appl.* 25: 1348–1356. https://doi.org/10.1890/14-1534.1

Ohlberger J., Schindler D.E., Brown R.J., Harding J.M.S., Adkison M.D., Munro A.R., Horstmann L. & Spaeder J. 2020. The reproductive value of large females: consequences of shifts in demographic structure for population reproductive potential in Chinook salmon. *Can. J. Fish. Aquat. Sci.* 77: 1292–1301. https://doi.org/10.1139/cjfas-2020-0012

Olivier P., Frelat R., Bonsdorff E., Kortsch S., Kröncke I., Möllmann C., Neumann H., Sell A.F. & Nordström M.C. 2019. Exploring the temporal variability of a food web using long-term biomonitoring data. *Ecography* 42: 2107–2121. https://doi.org/10.1111/ecog.04461

Olsen E.M. & Moland E. 2011. Fitness landscape of Atlantic cod shaped by harvest selection and natural selection. *Evol. Ecol.* 25: 695–710. https://doi.org/10.1007/s10682-010-9427-9

Olsen E.M., Carlson S.M., Gjøsæter J. & Stenseth N.C. 2009. Nine decades of decreasing phenotypic variability in Atlantic cod. *Ecol. Lett.* 12: 622–631. https://doi.org/10.1111/j.1461-0248.2009.01311.x

Olsen E.M., Knutsen H., Gjøsæter J., Jorde P.E., Knutsen J.A. & Stenseth N.C. 2004. Life-history variation among local populations of Atlantic cod from the Norwegian Skagerrak coast. *J. Fish Biol.* 64: 1725–1730. https://doi.org/10.1111/j.0022-1112.2004.00402.x

Oomen R.A., Kuparinen A. & Hutchings J.A. 2020. Consequences of single-locus and tightly linked genomic architectures for evolutionary responses to environmental change. *J. Hered.* 111: 319–332. https://doi.org/10.1093/jhered/esaa020

Orlove M.J. 1979. A reconciliation of inclusive fitness and personal fitness approaches: A proposed correcting term for the inclusive fitness formula. *J. Theor. Biol.* 8: 577–586. https://doi.org/10.1016/0022-5193(79)90055-9

Paine R.T. 1966. Food web complexity and species diversity. *Am. Nat.* 100: 65–75. https://doi.org/10.1086/282400

Palkovacs E.P. & Post D.M. 2009. Experimental evidence that phenotypic divergence in predators drives community divergence in prey. *Ecology* 90: 300–305. https://doi.org/10.1890/08-1673.1

Pauly D. 2019. *Vanishing fish: shifting baselines and the future of global fisheries*. Greystone Books, Vancouver.

Perälä T. & Kuparinen A. 2020. Eco-evolutionary dynamics driven by fishing: From single species models to dynamic evolution within complex food webs. *Evol. Appl.* 13: 2507–2520. https://doi.org/10.1111/eva.13058

Perälä T., Hutchings J.A. & Kuparinen A. 2022. Allee effects and the Allee-effect zone in northwest Atlantic cod. *Biol. Lett.* 18: 3–8. https://doi.org/10.1098/rsbl.2021.0439

Philippi T. 1993. Bet-hedging germination of desert annuals: beyond the first year. *Am. Nat.* 142: 474–487. https://doi.org/10.1086/285550

Pinsky M.L., Jensen O.P., Ricard D. & Palumbi S.R. 2011. Unexpected patterns of fisheries collapse in the world's oceans. *Proc. Natl. Acad. Sci. U.S.A* 108: 8317–8322. https://doi.org/10.1073/pnas.1015313108

Pinsky M.L., Eikeset A.M., Helmerson C., Bradbury I.R., Bentzen P., Morris C., Gondek-Wyrozemska A.T., Baalsrud H.T., Brieuc M.S.O., Kjesbu O.S., Godiksen J.A., Barth J.M.I., Matschiner M., Stenseth N.C., Jakobsen K.S., Jentoft S. & Star B. 2021. Genomic stability through time despite decades of exploitation in cod on both sides of the Atlantic. *Proc. Natl. Acad. Sci. U.S.A.* 118, e2025453118. https://doi.org/10.1073/pnas.2025453118

Pinzoni L., Poli F., Grapputo A., Rasotto M.B. & Gasparini C. 2023. Female Reproductive Fluid Increases the Opportunities for postmating sexual selection by prolonging the egg fertilization window. *Am. Nat.* 201: 491–499. https://doi.org/10.1086/722798

Puvanendran V., Laurel B.J. & Brown J.A. 2008. Cannibalism of Atlantic cod Gadus morhua larvae and juveniles on first-week larvae. *Aquat. Biol.* 2: 113–118. https://doi.org/10.3354/ab00044

R Core Team. 2021. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.

Raffard A., Santoul F., Cucherousset J. & Blanchet S. 2019. The community and ecosystem consequences of intraspecific diversity: a meta-analysis. *Biol. Rev.* 94: 648–661. https://doi.org/10.1111/brv.12472

Raffard A., Cucherousset J., Montoya J.M., Richard M., Acoca-Pidolle S., Poésy C., Garreau A., Santoul F. & Blanchet S. 2021. Intraspecific diversity loss in a predator species alters prey community structure and ecosystem functions. *PLoS Biol.* 19, e3001145. https://doi.org/10.1371/journal.pbio.3001145

Rideout R.M. & Morgan M.J. 2010. Relationships between maternal body size, condition and potential fecundity of four north-west Atlantic demersal fishes. *J. Fish Biol.* 76: 1379–1395. https://doi.org/10.1111/j.1095-8649.2010.02570.x

Rochet M. & Benoît E. 2012. Fishing destabilizes the biomass flow in the marine size spectrum. *Proc. R. Soc. B: Biol. Sci.* 279: 284–292. https://doi.org/10.1098/rspb.2011.0893

Roff D.A. 1992. *The evolution of life histories: theory and analysis*. Chapman and Hall, New York.

Roff D.A. 2008. Defining fitness in evolutionary models. *J. Genet* 87: 339–348. https://doi.org/10.1007/s12041-008-0056-9

Roney N.E., Oomen R.A., Knutsen H., Olsen E.M. & Hutchings J.A. 2018. Temporal variability in offspring quality and individual reproductive output in a broadcast-spawning marine fish. *ICES J. Mar. Sci.* 75: 1353–1361. https://doi.org/10.1093/icesjms/fsx232

Rose G.A. 2019. *Atlantic cod: a bio-ecology*. John Wiley & Sons Ltd, Chichester.

Rowe S. & Hutchings J.A. 2003. Mating systems and the conservation of commercially exploited marine fish. *Trends Ecol. Evol.* 18: 567–572. https://doi.org/10.1016/j.tree.2003.09.004

Rowe S. & Hutchings J.A. 2004. The function of sound production by Atlantic cod as inferred from patterns of variation in drumming muscle mass. *Can. J. Zool.* 82: 1391–1398. https://doi.org/10.1139/z04-119

Rowe S., Hutchings J.A., Skjæraasen J.E. & Bezanson L. 2008. Morphological and behavioural correlates of reproductive success in Atlantic cod Gadus morhua. *Mar. Ecol. Prog. Ser.* 354: 257–265. https://doi.org/10.3354/meps07175

Sadovy Y.J. 1996. Reproduction of reef fishery species. In: Polunin N. V. C. & Roberts C. M. (eds.), *Reef fisheries*, Chapman and Hall, London, pp. 15–59.

Sæther B. & Engen S. 2015. The concept of fitness in fluctuating environments. *Trends Ecol. Evol.* 30: 273–281. https://doi.org/10.1016/j.tree.2015.03.007

Seger J. & Brockmann H.J. 1987. What is bet-hedging? In: Harvey P. H. & Partridge L. (eds.), *Oxford surveys in evolutionary biology*, Oxford University Press, Oxford, pp. 182–211.

Seger J. & Philippi T. 1989. Hedging one's evolutionary bets, revisited. *Trends Ecol. Evol.* 4: 41–44.

Sharpe D.M.T. & Hendry A.P. 2009. Life history change in commercially exploited fish stocks: an analysis of trends across studies. *Evol. Appl.* 2: 260–275. https://doi.org/10.1111/j.1752-4571.2009.00080.x

Simons A.M. 2011. Modes of response to environmental change and the elusive empirical evidence for bet hedging. *Proc. R. Soc. B: Biol. Sci.* 278: 1601–1609. https://doi.org/10.1098/rspb.2011.0176

Slatkin M. 1974. Hedging one's evolutionary bets. *Nature* 250: 704–705. https://doi.org/10.1038/250704b0

Smith C. & Wootton R.J. 2016. The remarkable reproductive diversity of teleost fishes. *Fish Fish.* 17: 1208–1215. https://doi.org/10.1111/faf.12116

Spencer H. 1864. *The principles of biology*. Williams and Norgate, London.

Spotowitz L., Johansen T., Hansen A., Berg E., Stransky C. & Fischer P. 2022. New evidence for the establishment of coastal cod Gadus morhua in Svalbard fjords. *Mar. Ecol. Prog. Ser.* 696: 119–133. https://doi.org/10.3354/meps14126

Starrfelt J. & Kokko H. 2012. Bet-hedging-a triple trade-off between means, variances and correlations. *Biol. Rev.* 87: 742–755. https://doi.org/10.1111/j.1469-185x.2012.00225.x

Stearns S.C. 1976. Life-history tactics: a review of the ideas. *Q. Rev. Biol.* 51: 3–47. https://doi.org/10.1086/409052

Stearns S.C. 1992. *The evolution of life histories*. Oxford University Press, New York.

Stearns S.C. 2000. Life history evolution: successes, limitations, and prospects. *Sci. Nat.* 87: 476–486. https://doi.org/10.1007/s001140050763

Stenseth N.C., Jorde P.E., Chan K., Hansen E., Knutsen H., André C., Skogen M.D. & Lekve K. 2006. Ecological and genetic impact of Atlantic cod larval drift in the Skagerrak. *Proc. R. Soc. B: Biol. Sci.* 273: 1085–1092. https://doi.org/10.1098/rspb.2005.3290

Stige L.C., Yaragina N.A., Langangen Ø., Bogstad B., Stenseth N.C. & Ottersen G. 2017. Effect of a fish stock's demographic structure on offspring survival and sensitivity to climate. *Proc. Natl. Acad. Sci. U.S.A* 114: 1347–1352. https://doi.org/10.1073/pnas.1621040114

Thorsen A., Witthames P.R., Marteinsdóttir G., Nash R.D.M. & Kjesbu O.S. 2010. Fecundity and growth of Atlantic cod (Gadus morhua L.) along a latitudinal gradient. *Fish. Res.* 104: 45–55. https://doi.org/10.1016/j.fishres.2010.03.020

Trebilco R., Baum J.K., Salomon A.K. & Dulvy N.K. 2013. Ecosystem ecology: size-based constraints on the pyramids of life. *Trends Ecol. Evol.* 28: 423–431. https://doi.org/10.1016/j.tree.2013.03.008

Trippel E.A. & Neil S.R. 2004. Maternal and seasonal differences in egg sizes and spawning activity of northwest Atlantic haddock (Melanogrammus aeglefinus) in relation to body size and condition. *Can. J. Fish. Aquat. Sci.* 61: 2097–2110. https://doi.org/10.1139/f04-125

Uusi-Heikkilä S., Perälä T. & Kuparinen A. 2022. Fishing triggers trophic cascade in terms of variation, not abundance, in an allometric trophic network model. *Can. J. Fish. Aquat. Sci.* 79: 947–957. https://doi.org/10.1139/cjfas-2021-0146

Uusi-Heikkilä S., Sävilammi T., Leder E., Arlinghaus R. & Primmer C.R. 2017. Rapid, broad-scale gene expression evolution in experimentally harvested fish populations. *Mol. Ecol.* 26: 3954–3967. https://doi.org/10.1111/mec.14179

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

van Wijk S.J., Taylor M.I., Creer S., Dreyer C., Rodrigues F.M., Ramnarine I.W., van Oosterhout C. & Carvalho G.R. 2013. Experimental harvesting of fish populations drives genetically based shifts in body size and maturation. *Front. in Ecol. Environ.* 11: 181–187. https://doi.org/10.1890/120229

Veening J.W., Stewart E.J., Berngruber T.W., Taddei F., Kuipers O.P. & Hamoen L.W. 2008. Bet-hedging and epigenetic inheritance in bacterial cell development. *Proc. Natl. Acad. Sci. U.S.A* 105: 4393–4398. https://doi.org/10.1073/pnas.0700463105

Vesterinen M., Perälä T. & Kuparinen A. 2021. The effect of fish life-history structures on the topologies of aquatic food webs. *Food Webs* 29, e00213. https://doi.org/10.1016/j.fooweb.2021.e00213

von Bertalanffy L. 1938. A quantitative theory of organic growth. *Hum. Biol.* 10: 181–213.

Williams R.J. & Martinez N.D. 2004. Stabilization of chaotic and non-permanent food-web dynamics. *Eur. Phys. J. B* 38: 297–303. https://doi.org/10.1140/epjb/e2004-00122-1

Windle M.J.S. & Rose G.A. 2007. Do cod form spawning leks? Evidence from a Newfoundland spawning ground. *Mar. Biol.* 150: 671–680. https://doi.org/10.1007/s00227-006-0385-2

Witek M., Sliwinska E.B., Skórka P., Nowicki P., Settele J. & Woyciechowski M. 2006. Polymorphic growth in larvae of Maculinea butterflies, as an example of biennialism in myrmecophilous insects. *Oecologia* 148: 729–733. https://doi.org/10.1007/s00442-006-0404-5

Wood Z.T., Palkovacs E.P. & Kinnison M.T. 2018. Eco-evolutionary feedbacks from non-target species influence harvest yield and sustainability. *Sci. Rep.* 8, 6389. https://doi.org/10.1038/s41598-018-24555-0

Woodward G. & Hildrew A.G. 2002. Body-size determinants of niche overlap and intraguild predation within a complex food web. *J. Anim. Ecol.* 71: 1063–1074. https://doi.org/10.1046/j.1365-2656.2002.00669.x

Wootton R.J. & Smith C. 2014. *Reproductive biology of teleost fishes*. John Wiley & Sons Ltd, Chichester.

Worldometer 2023. *Current world population*. https://www.worldometers.info/world-population/#table-historical. Accessed 31.1.2023.

Worm B. & Myers R.A. 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. *Ecology* 84: 162–173. https://doi.org/10.1890/0012-9658(2003)084[0162:MAOCSI]2.0.CO;2

Wright P.J. & Trippel E.A. 2009. Fishery-induced demographic changes in the timing of spawning: consequences for reproductive success. *Fish Fish.* 10: 283–304. https://doi.org/10.1111/j.1467-2979.2008.00322.x

Yeaman S. 2015. Local adaptation by alleles of small effect. *Am. Nat.* 186: 74–89. https://doi.org/10.1086/682405

Yodzis P. & Innes S. 1992. Body size and consumer-resource dynamics. *Am. Nat.* 139: 1151–1175. https://doi.org/10.1086/285380

Young T.P. 1981. A general model of comparative fecundity for semelparous and iteroparous life histories. *Am. Nat.* 118: 27–36. https://doi.org/10.1086/283798

ORIGINAL PAPERS

I

MULTIPLE-BATCH SPAWNING AS A BET-HEDGING STRATEGY IN HIGHLY STOCHASTIC ENVIRONMENTS: AN EXPLORATORY ANALYSIS OF ATLANTIC COD

by

Sara Hočevar, Jeffrey A. Hutchings & Anna Kuparinen 2021

Evolutionary applications 14: 1980–1992.

DOI: 10.1111/eva.13251

Received: 18 October 2020 | Revised: 30 April 2021 | Accepted: 3 May 2021
DOI: 10.1111/eva.13251

ORIGINAL ARTICLE

Evolutionary Applications Open Access WILEY

Multiple-batch spawning as a bet-hedging strategy in highly stochastic environments: An exploratory analysis of Atlantic cod

Sara Hočevar[1] | **Jeffrey A. Hutchings**[1,2,3,4] | **Anna Kuparinen**[1]

[1]Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland
[2]Department of Biology, Dalhousie University, Halifax, NS, Canada
[3]Institute of Marine Research, Flødevigen Marine Research Station, His, Norway
[4]Department of Natural Sciences, University of Agder, Kristiansand, Norway

Correspondence
Sara Hočevar, Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland.
Email: sara.s.hocevar@jyu.fi

Funding information
Academy of Finland, Grant/Award Number: 317495; Natural Sciences and Engineering Research Council of Canada; European Research Council, Grant/Award Number: COMPLEX-FISH 770884

Abstract

Stochastic environments shape life-history traits and can promote selection for risk-spreading strategies, such as bet-hedging. Although the strategy has often been hypothesized to exist for various species, empirical tests providing firm evidence have been rare, mainly due to the challenge in tracking fitness across generations. Here, we take a 'proof of principle' approach to explore whether the reproductive strategy of multiple-batch spawning constitutes a bet-hedging. We used Atlantic cod (*Gadus morhua*) as the study species and parameterized an eco-evolutionary model, using empirical data on size-related reproductive and survival traits. To evaluate the fitness benefits of multiple-batch spawning (within a single breeding period), the mechanistic model separately simulated multiple-batch and single-batch spawning populations under temporally varying environments. We followed the arithmetic and geometric mean fitness associated with both strategies and quantified the mean changes in fitness under several environmental stochasticity levels. We found that, by spreading the environmental risk among batches, multiple-batch spawning increases fitness under fluctuating environmental conditions. The multiple-batch spawning trait is, thus, advantageous and acts as a bet-hedging strategy when the environment is exceptionally unpredictable. Our research identifies an analytically flexible, stochastic, life-history modelling approach to explore the fitness consequences of a risk-spreading strategy and elucidates the importance of evolutionary applications to life-history diversity.

KEYWORDS
Atlantic cod, bet-hedging, environmental stochasticity, fitness, multiple-batch spawning, risk-spreading

1 | INTRODUCTION

Natural environmental conditions change continuously across multiple spatial and temporal scales. While some of the fluctuations can be predictable and of low magnitude, others are uncertain, occurring with varying degrees of intensity, periodicity and stochasticity. Stochasticity can be integral to the shaping of genotypes, phenotypes and populations, either concomitantly or not (for a detailed review, see Lenormand et al., 2009). Environmental stochasticity influences the ecological processes of a population, determines the rate and direction of its evolutionary change (Frank & Slatkin, 1990; May, 1973) and can even lead to its extinction (Lande, 1993). Hence, to mitigate challenges arising from prevailing environmental uncertainty, organisms have evolved a diversity of life-history strategies (Kussell & Leibler, 2005; Maynard Smith, 2010; Meyers & Bull, 2002; Moran, 1992; Stearns, 1976; Tufto, 2015). One of these is bet-hedging (Gillespie, 1973, 1974, 1975; Slatkin, 1974).

Bet-hedging is a costly genotypic strategy that maximizes long-run or geometric mean fitness across generations by trading off the arithmetic mean in reproductive output and its variance (Cohen, 1966; Gillespie, 1974; Lewontin & Cohen, 1969; Seger & Brockmann, 1987; Simons, 2002; Yoshimura & Clark, 1991). In other words, bet-hedging can act as a 'portfolio effect' (Markowitz, 1952) through which the diversification of assets, here partitioning of offspring among batches, reduces the risk and stabilizes the returns, that is geometric mean fitness of a genotype.

Organisms can spread risk among their offspring on a temporal or spatial scale, in a conservative or diversified way, or even as a complex combination of all the above (Haaland et al., 2019; Scheiner, 2014). While conservative bet-hedging maximizes fitness by reducing the variance in fitness at the individual level, diversifying bet-hedging does so by reducing the correlation in expected fitness among individuals in the same population (Starrfelt & Kokko, 2012). Examples of bet-hedging strategies appear in a wide range of systems and forms (Childs et al., 2010; Philippi & Seger, 1989) such as iteroparity (Cole, 1954; Ranta et al., 2002), seed dormancy (Cohen, 1966; Simons, 2009), seed dispersal (Beckman et al., 2018; Snyder, 2011), flowering schedule (Simons & Johnston, 2003), timing of sexual reproduction (Tarazona et al., 2017), embryonic diapause (Furness et al., 2015) and hatching asynchrony (Laaksonen, 2004).

Simons (2011) extensively reviewed over 100 studies on bet-hedging, categorizing them based on the strength of the empirical evidence. Although bet-hedging life histories have been reported for a variety of species and hypothesized for even more, from bacteria (Beaumont et al., 2009) to vertebrates (Lips, 2001; Mahony & Thumm, 2002), the strength of the evidence for most has been limited or, as Simons (2011) put it, the evidence has been elusive. He proposed six, ranked evidence conditions that need to be met: (I) recognize a bet-hedging trait; (II) monitor the unpredictable environment; (III) observe differences in the trait among populations; (IV) demonstrate differences in fitness dynamics; (V) validate whether the trait is favoured under relevant varying environments; and (VI) test the optimality of the trait under a range of conditions of fluctuating selection (Simons, 2011).

Few studies possess sufficient empirical support to fulfil the highest three and most data-demanding categories of evidence for bet-hedging (i.e. categories IV–VI; Simons, 2011). The majority of those that do fulfil these conditions are on plants (Childs et al., 2010; Simons & Johnston, 2003). This general lack of evidence can be attributed to the very considerable challenges of recognizing the adaptive significance of a trait that is bet-hedged and the difficulty of tracking across-generational fitness in a stochastically fluctuating environment. In our study, we attempt to overcome these challenges and aspire to provide support for or against the fifth evidence category on bet-hedging significance of multiple-batch spawning strategy.

Multiple-batch spawning is a reproductive strategy common among marine fishes, such as gadoids and flounders, for example haddock (*Melanogrammus aeglefinus*), pollock (*Pollachius virens*), whiting (*Merlangus merlangus*), halibut (*Hippoglossus hippoglossus*) and dab (*Limanda limanda*) (Murua & Sabrido-Rey, 2003). Yet, the fitness benefits of the multiple-batch strategy have not been comprehensively explored. To sustain population resilience in a stochastic environment, bet-hedging could be crucial for multiple-batch spawning fish populations. A strategy of broadcast spawning on multiple spawning grounds, multiple times (Kjesbu, 1989) and over prolonged periods (Hutchings & Myers, 1994; Kjesbu et al., 1996) might act as a portfolio effect by reducing the risk of complete reproductive failure. The production of multiple egg batches within a spawning season, the number of which increases with female weight and body size (Kjesbu et al., 1996; Roney et al., 2018), could enable a batch spawner to spread the environmental risk among its offspring and mitigate the fitness consequences of environmental fluctuations. As a trade-off in diversification, the variance in reproductive output of a multiple-batch spawner could be lower, boosting the across-generational geometric mean fitness, at the expense of producing a lower average number of offspring.

To tackle the question of whether multiple-batch spawning yields the predicted fitness benefits of a bet-hedging strategy, we used Atlantic cod, *G. morhua* (Linnaeus, 1758), as a focal species in this study. Atlantic cod, one of the most studied batch spawning fish species, has been speculated to be a conservative bet-hedger (e.g. Hutchings & Rangeley, 2011), but never in fact tested for it. Here, we test this hypothesis by expanding an eco-evolutionary model parameterized for cod (Kuparinen et al., 2012). Our primary objectives are to (i) observe how multiple-batch spawning affects populational dynamics; (ii) evaluate the fitness consequences of multiple-batch spawning within a spawning season, under different levels of environmental stochasticity; (iii) inspect the variance in reproductive output within generations; and (iv) analyse the proportion of successful spawning seasons.

2 | MATERIALS AND METHODS

There can be several risk distribution strategies acting on different stages or processes in a species at any given time. This complication has potential to obscure the fitness consequences of any one component of the bet-hedging strategy (Simons, 2011). Thus, we focused solely on the component of multiple-batch spawning.

TABLE 1 Summarizing the main underlying empirically derived variables of the eco-evolutionary model

Variable	Description	Equation	Value	Unit	Source
L	Length calculated each year for every individual following the Von Bertalanffy growth curve	$L_{(t)} = L_\infty - \left(L_\infty - L_0\right) \cdot e^{-kt}$ $\log(k) = -0.609 - 0.013 \cdot L_\infty$	$L_{(t)}$	cm	von Bertalanffy (1938) Kuparinen et al. (2012)
W	Weight calculated each year for every individual from the length-weight relationship	$W_t = 3.52 \cdot 10^{-6} \cdot L_t^{3.19}$	$W_{(t)}$	kg	Kuparinen et al. (2012)
L_{mat}	Length at maturity	$L_{\mathrm{mat}} = 0.66 \cdot L_\infty$	L_{mat}	cm	Jensen (1997)
N_{batches}	Number of spawned batches calculated each year for every mature female	$N_{\mathrm{batches}} = \frac{21.156}{1+\exp\left(\frac{55.014 - L_{\mathrm{fork}(t)}}{10.141}\right)}$	$N_{\mathrm{batches}(t)}$		Roney et al. (2018)
N_{eggs}	Number of spawned eggs, calculated each year for every mature female	$N_{eggs} = \left(\frac{0.48 \cdot (W_t + 0.37)}{1.45} + 0.12\right) \cdot 10^{-6}$	$N_{\mathrm{eggs}(t)}$		Hutchings (2005)
$\mathrm{Costs}_{\mathrm{MBS}}$	Costs of multiple-batch spawning strategy, calculated each year for every mature female spawning more than one batch	$\mathrm{Costs}_{\mathrm{MBS}} = \sum_{\mathrm{batch}=1}^{N_{\mathrm{batches}}} 1 - 0.00523 \cdot (\mathrm{batch} - 1)$	$\mathrm{Costs}_{\mathrm{MBS}(t)}$		Roney et al. (2018)

2.1 | Multiple-batch spawning and environmental stochasticity

We examined whether multiple-batch spawning constitutes a bet-hedging strategy by exploring its eco-evolutionary impacts on fitness dynamics under varying levels of environmental stochasticity affecting batch survival. We did so by implementing an individual-based mechanistic model developed by Kuparinen et al. (2012) which characterizes the eco-evolutionary dynamics and demographic processes of Atlantic cod. The main evolving trait of the model is body size, which fits our research design since batch production, fecundity and spawning duration are size-related traits. Given that the model's configuration and parameterization have been thoroughly described elsewhere (Kuparinen et al., 2012, 2014), we outline below only the main features (Table 1). Here, we focus on a detailed description of newly implemented batch spawning strategies and components of generated environmental stochasticity in batch survival.

We simulated the fecundity of every mature female at the start of each spawning season through juvenile production and survival. The production of eggs was a positively dependent function of the female's weight derived from the empirically based length (L)–weight (W) relationship $W_t = 3.52 \cdot 10^{-6} \cdot L_t^{3.19}$. The egg number was calculated based on the empirical relationship as $\mathrm{eggs} = \left(\frac{0.48 \cdot (W_t + 0.37)}{1.45} + 0.12\right) \cdot 10^{-6}$ (Hutchings, 2005; Kuparinen et al., 2012). We portrayed the life-history strategy of multiple-batch spawning cod in the model as the occurrence of multiple reproductive events within a single spawning season. To highlight how the strategy feeds back on the population dynamics of cod, we compared it to a separately simulated hypothetical population with no such risk-spreading strategy, that is single-batch spawners. While individuals in a multiple-batch spawning population distribute their eggs among several batches, individuals in a single-batch spawning population only have one reproductive event within each spawning season and, thus, practise the tactic of 'placing all your eggs in one basket' (Figure 1). The number of eggs that a multiple-batch spawning female produced in one spawning season was distributed evenly among batches.

The number of batches depended on body size. At each annual step, the number of batches for each mature female was derived from an empirically based nonlinear regression fit between the fork length $L_{\mathrm{fork}(t)}$ and batch number N_{batches}, where $N_{\mathrm{batches}} = \frac{21.156}{1+\exp\left(\frac{55.014 - L_{\mathrm{fork}(t)}}{10.141}\right)}$ (parameterized based on an empirical data set collected from Risør fjord in coastal Skagerrak by Roney et al., 2018; Figure 2). Before the nonlinear regression was fitted, the lower value of 0 batches at size 25 cm and higher value of 21 batches at 100 cm were added to the experimentally gathered data to account for somatic constraints. We based these constraints on data of maximum observed batch number in captive Norwegian coastal cod (Kjesbu et al., 1996) and limited the function by setting the maximum available number of batches to 21 to prevent the continuous increase of produced batches with a female's size.

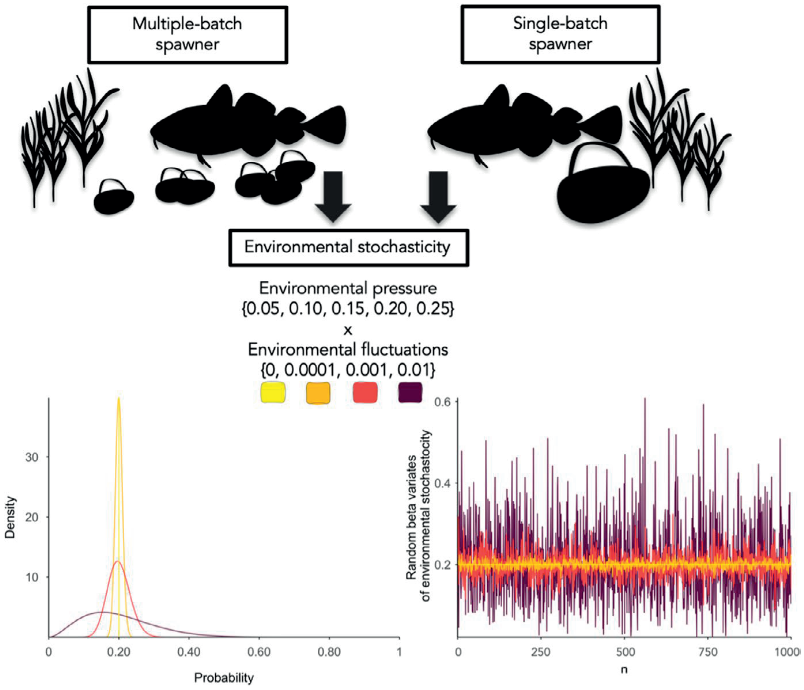


FIGURE 1 The schematic diagram demonstrates the multiple-batch and single-batch spawning cod populations simulated under a stochastic environment with varying rate of environmental pressure (0.05–0.25) and environmental fluctuations (0–0.01). The first graph is illustrating the probability density function for the beta distribution where mean environmental pressure applied to batch survival equals 0.20 and fluctuates depending on the environmental fluctuation rate (0, 0.0001, 0.001, 0.01). Correspondingly, the second graph is demonstrating the random, beta-generated batch mortality rates, drawn from each probability density function

To make multiple-batch spawning a costly trait, we introduced costs to batch survival (right-sided bar plot on Figure 2). We set these costs based on empirical findings, following the spawning dynamics of 73 wild-caught Norwegian coastal cod in Skagerrak and their offspring quality (Roney et al., 2018). Larval length and yolk-sac volume of offspring spawned in an experimental spawning basin at the Institute of Marine Research Flødevigen exhibited declining trends during the spawning period. Given that later spawned batches produced smaller larvae at hatch, we added an assumption that shedding of the first or single batch had no associated costs, while for every consecutive batch, shed within the same season, the batch spawning costs increased. Because larvae length tends to correlate with survival probability, we applied the trade-off in costs of batch production and risk-spreading potential in a gradually decreasing survival probability of each batch from 1.00 to 0.89 for the first to 21st produced batch, respectively (Roney et al., 2018; following the mortality function described by Pepin, 1991). Therefore, while single-batch spawners experienced no such batch spawning costs, as they could shed only one batch per spawning season, the average costs of multiple-batch spawners varied depending on how many batches an individual has shed in a spawning season.

We introduced environmental stochasticity to batch survival as the environmental pressure (0.05, 0.10, 0.15, 0.20, 0.25) and environmental fluctuations (0, 0.0001, 0.001, 0.01) and varied them in a full factorial manner (Figure 1). We define environmental pressure as a change in the mean batch mortality rate that could be driven, for example by any combination of ecological, environmental or anthropogenic factors. On the other hand, environmental fluctuations are defined as a change in the variance of batch mortality rate and can be generated by the stochasticity about the ecological, environmental or anthropogenic factors. Hence, we separately exposed multiple-batch and single-batch spawning populations to each of 20 simulated environmental scenarios and compared their fitness performances. Higher rates of environmental pressure and fluctuations were dismissed upon trial testing, since the stochasticity became overwhelming and drove the populations simulated in our study towards extinction. When the added environmental fluctuations were preset to zero, the scenario was considered nonstochastic. Under these circumstances, we applied a constant environmental pressure to a batch or batches as a success probability in a Bernoulli trial to determine the survival of an entire batch or group of batches. While the environmental pressure under such nonstochastic scenarios remained constant, the outcome of successful survival of a batch or batches could still vary among seasons and individuals as it was newly drawn in every spawning season for every mature female.

By contrast, the stochastic scenario was characterized by the presence of a variance in the form of continuous environmental fluctuations around mean rates of environmental pressure (Figure 1). The final environmental stochastic rate applied to batches was preadjusted, based on the rate of environmental pressure and environmental fluctuation, using a beta distribution parameterized by the α and β shape parameters (see Tables S1 and S2), and was drawn for every batch in every spawning season. To derive the final survival outcome of each batch, we applied the final environmental stochastic rate as a success probability in a Bernoulli trial to each batch separately, meaning that, for each batch, we drew a random number (0 or 1) as to whether the batch either dies or survives (i.e. a predator or environmental disaster destroyed a whole batch). Subsequently, to determine the final number

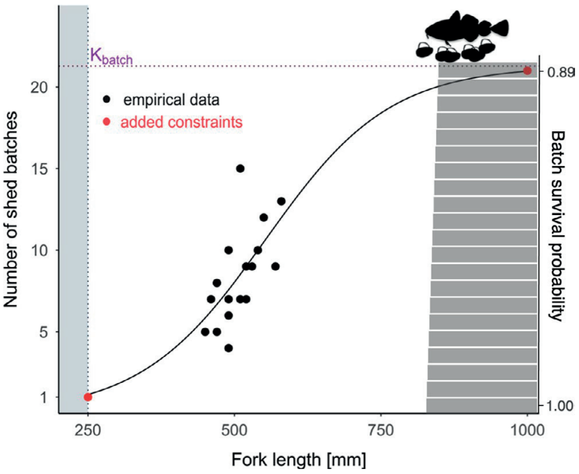


FIGURE 2 Relationship between mature female size, batch number and batch survival probability. The empirically gathered data (black) on the abundance of batches were plotted against the fork length of mature female cod and added constraints (red). A sigmoid curve given by a solid line was fitted to the data set and used in the simulation process. Vertical blue-shaded area indicates the female size smaller than 250 mm, which were not considered mature in our model. Grey-shaded bar chart on the right side of the figure illustrates the batch survival probability assigned to every batch according to the order at which female has shed it in the spawning period (values based on Roney et al., 2018). As a result, the batch survival probability is decreasing with increasing order number at which batch is shed (*y*-axis)

of offspring, we summed the number of eggs from survived batches for every multiple-batch spawning female and multiplied the sum with a natural survival rate from the egg stage to 3-year-old recruit estimated to be $1.13 \cdot 10^{-6}$ for northern cod (Hutchings, 2005). The same process was adopted for the single-batch spawning population.

Thus, we created a combination of 40 different scenarios, comprising multiple-batch spawning populations under 20 distinct conditions of environmental stochasticity and single-batch spawning populations under 20 distinct conditions of environmental stochasticity (Figure 1).

2.2 | Mechanistic model of Atlantic cod

The mechanistic model (Kuparinen et al., 2012) follows the life stages of each individual fish in a population at annual time steps and combines genetic and optimization approaches through the use of heritable growth trajectories. The trajectories were derived from least square fits of empirically gathered 258 cod growth trajectories (Kuparinen et al., 2012), using the von Bertalanffy growth model $L_{(t)} = L_\infty - \left(L_\infty - L_0\right) \cdot e^{-kt}$, where $L_{(t)}$ is the length of a fish at age t, L_∞ is the asymptotic body length, L_0 is the length at $t = 0$ and k (year − 1) is the growth coefficient which describes the rate at which L_∞ is reached (von Bertalanffy, 1938). Two observed associations underpin the model: (i) the observed negative correlation between L_∞ and k, where $\log(k) = -0.609 - 0.013 \cdot L_\infty$, and (ii) the ratio of the length at maturity L_{mat} and L_∞, where $L_{\mathrm{mat}} = 0.66 \cdot L_\infty$ (Jensen, 1997) when $30\ \mathrm{cm} \le L_\infty \le 120\ \mathrm{cm}$ (Kuparinen et al., 2012).

Each individual carried a genotype of 10 unlinked, diploid loci with 2 alleles (0 and 1) that followed classical Mendelian inheritance. The sum of these 10 loci, that could range from 0 to 20, coded for the genotypic value of L_∞ and, thus, allowed for evolution of growth to occur. Ten loci were sufficient in describing the trait distribution smoothly; adding additional loci did not affect the simulations. Final phenotypic value, generated as an environmental variation (s.d. = 3.5) around the genotypic trait value, coded for the phenotypic L_∞ value that provided a basis for the estimation of other relevant size-based traits. To initiate the external fertilization process, a mature male was randomly assigned to a mature female, and the sex of offspring was determined by a 50/50 Bernoulli trial (Kuparinen et al., 2012).

In addition to the demographic processes of reproduction and survival described in the batch spawning component of the model, density-dependent growth and natural mortality were also simulated at each annual time step on the individual level, and the state of the population was tracked accordingly. Growth of each individual was defined by its von Bertalanffy parameters (L_∞ and k) and additionally altered by density-dependent population dynamics. Time available for growth at each annual step was bounded between 0 and 1. If the population reached or exceeded the carrying capacity, the individual's growth time and progress along its growth trajectory was reduced in accordance with a logistic equation $e^{15-17.6\cdot c}\left(1 + e^{15-17.6\cdot c}\right)^{-1}$, where c is the ratio between the biomass of the population and its carrying capacity. Populations of multiple-batch and single-batch spawners had the same preset carrying capacity in all scenarios. At low population density, the individual's time spent on growth within one year was close to 1, allowing an individual almost a full annual growth increment along its von Bertalanffy curve (see Figure S1). Therefore, the population density affected fecundity by regulating the individual's growth, which impacts (i) the time the individual needs to reach 66% of its asymptotic length and mature and (ii) the age when reproduction starts.

An instantaneous rate of natural mortality rate of 0.15, which was not applied until individuals had reached 3 years of age (see above), was assumed to be equal for all individuals of age 3 years or older (Kuparinen et al., 2012). If the individual was mature, the mortality rate was additionally increased by 0.10 to account for the survival cost of reproduction (following Kuparinen et al., 2012), resulting in an instantaneous rate of 0.25, which corresponds with the estimated natural mortality of many cod populations (Beverton et al., 1994). Using the binomial distribution, the model simulated the survival of every individual at each annual step with the maximum lifespan set to 25 years.

2.3 | Simulation design

To achieve reproducibility of the code and results, we initialized a pseudorandom number generating sequence in a repeatable manner before each scenario run in R software (R Core Team, 2019) and allowed the loop to iterate and produce 50 replica simulations. As bet-hedging is predicted to have the greatest benefits in stochastic environments (Simons, 2011), we produced several combinations of runs to generate quantitative data (Figure 1). In the run of each scenario, we initialized the simulations with a preadapted cod population to separately simulate a population consisting of only multiple-batch spawners and a population consisting of only single-batch spawners under each of the environmentally stochastic scenarios for 5000 years. This time interval was sufficient as it was beyond the time needed for the populations to reach their dynamic eco-evolutionary equilibriums (Figure S2).

To investigate the potential underlying feedbacks of the bet-hedging strategy on life histories, we looked into the dynamics of the last 2500 years of the population in each run by recording the population variables and life-history traits at each annual step. The primary recorded output data were total number of recruits produced in one year, and annual population averages of L_∞ and *k*, abundance, biomass and mortality rate. These outputs of 50 replica simulations per run were then summarized across replicates by recording the mean, coefficient of variance and standard deviation of each variable in every year.

For the last 300 years of each simulation process, we tracked the individual fitness of every mature fish and recorded its total number of successfully shed batches, batch size and realized reproductive output over the individual's lifespan. The total reproductive output of every mature individual was recorded as the sum of the realized number of 3-year-old recruits produced in the lifetime of the original individual. To explore whether multiple-batch spawning is a bet-hedging strategy of Atlantic cod, we looked into across-generational fitness elements of multiple-batch spawning populations under simulated environmentally stochastic scenarios and compared them to a single-batch spawning population. Across-generational fitness elements included the arithmetic mean fitness $\overline{W}_{\mathrm{AM}}$, variance in arithmetic mean fitness among generations or cohorts, and geometric mean fitness $\overline{W}_{\mathrm{GM}}$. We measured the arithmetic mean fitness $\overline{W}_{\mathrm{AM}}$ and its variance across generations for each scenario as an average realized lifetime reproductive output of a generation and the across-generational geometric mean in fitness $\overline{W}_{\mathrm{GM}}$ as the nth root of the product of average realized lifetime reproductive output of every generation following $\overline{W}_{\mathrm{GM}} = \left(\overline{W}_{\mathrm{AM1}} \cdot \overline{W}_{\mathrm{AM2}} \cdot \ldots \cdot \overline{W}_{\mathrm{AM}n}\right)^{1/n}$ (Seger & Brockmann, 1987), where *n* is a number of generations or cohorts.

Fitness outputs were pooled together per run, and the mean, variance and coefficient of variation of each variable were recorded. Statistical analyses of relationships and trends were done using Welch's two-sample *t* test (Welch, 1947), nonparametric Kruskal–Wallis test (Kruskal & Wallis, 1952) and simple linear regression (Kenney & Keeping, 1962). All simulations and analyses were performed in the open-source software R (R Core Team, 2019), and figures were produced using the package tidyverse (Wickham et al., 2019).

3 | RESULTS

3.1 | Population dynamics of each of the spawning strategists

Separately simulated multiple-batch and single-batch spawning cod populations exposed to 20 variations of environmentally stochastic scenarios (Figure 1) were analysed to investigate whether the costly spawning of multiple batches might be considered a bet-hedging strategy in Atlantic cod. In all 2000 simulations (2 spawning strategies * 20 different environmental scenarios * 50 replica simulations of each spawning population), the populations adapted from initial conditions to the new specific environments in fewer than 2500 years, maintaining a stable dynamic thereafter (Figure S2).

Mean population size for all scenarios was 5311 individuals (s.d. 623 individuals across scenarios) and exhibited a declining trend (up to a 33.10% decrease) as the environmental fluctuations and pressure on batch survival or batch mortality rate increased. Coefficient of variation in population size was greater overall for single-batch spawning populations (Table S3) and significantly increased with increasing environmental pressure on batch survival: from 2.28 (CV) under the least pressured environmental scenarios to 3.20 (CV) under the most pressured environmental scenarios in multiple-batch spawning populations, and from 2.37 (CV) under the least pressured environmental scenarios to 3.52 (CV) under the most pressured environmental scenarios in single-batch spawning populations.

Environmental fluctuations had no significant effect on either population size or CV in population size of single-batch spawners but did affect multiple-batch spawners (Table S4), causing a significant difference between scenarios with and without any applied environmental fluctuations. In particular, population size was more variable under scenarios with no environmental fluctuations as it varied from s.d. 165 individuals to s.d. 134 individuals under scenarios with environmental fluctuations. However, there was no significant variation among scenarios with different environmental fluctuation rates. The same dynamics were observed for population biomass and its CV (Tables S3 and S4).

Multiple-batch spawning cod populations had significantly lower realized average mortality rate compared to single-batch spawning populations (Figure S3a). While the realized mortality rate did not differ among different environmental fluctuating rates in single-batch spawning populations, it increased significantly in multiple-batch spawning populations when environmental fluctuations were applied to each batch separately (Table S4).

3.2 | Fitness components

Under increasing environmental fluctuations, multiple-batch spawners experienced a significant increasing trend in long-run geometric mean fitness $\overline{W}_{\mathrm{GM}}$, resulting in a higher long-run $\overline{W}_{\mathrm{GM}}$ under most unpredictable and uncertain environmental conditions (Figure 3a). Both strategies had an increasing trend in $\overline{W}_{GM}$ with increasing environmental pressure (Figure 4a), but the relationship was significant, albeit weak, only in multiple-batch spawning populations (Table S6). The difference in $\overline{W}_{GM}$ across all environmentally stochastic scenarios differed significantly between multiple-batch and single-batch spawning populations by being lower in the multiple-batch spawning population (Table S5) as their $\overline{W}_{GM}$ values were lower under conditions when the environmental fluctuations were absent or low, and/or the environmental pressure was weak.

The variance in $\overline{W}_{AM}$ across-generations was higher overall in multiple-batch spawning populations (Table S5) and had a significant decreasing trend with increasing environmental fluctuations (Figure 3c; Table S6). This significance and decreasing trend were due to higher variance in $\overline{W}_{AM}$ among generations under nonstochastic conditions, while the variance among single-batch spawning cod generations increased in the presence of environmental fluctuations. In contrast, environmental pressure had no significant effect on the variance in $\overline{W}_{AM}$ among generations of either multiple- or single-batch spawners.

Multiple-batch spawners had overall significantly higher arithmetic mean in fitness $\overline{W}_{AM}$ compared to single-batch spawners (Table S5) due to greater realized reproductive output in the absence of environmental fluctuations (Figure 3b). While the environmental pressure had no significant effect on $\overline{W}_{AM}$ for either strategy, the presence of environmental fluctuations significantly decreased the $\overline{W}_{AM}$ of multiple-batch spawners (Table S6). This effect resulted in a lower $\overline{W}_{AM}$ for multiple-batch spawners when exposed to the highest environmental pressure and environmental fluctuations, hence, experiencing elevated environmental uncertainty and mortality (Figure 3b and Figure 4b).

The environmental scenarios where the three fitness components: (i) high long-run geometric mean fitness $\overline{W}_{GM}$, (ii) low arithmetic mean in fitness $\overline{W}_{AM}$ and (iii) low across-generational variance in $\overline{W}_{AM}$ overlap illustrate that multiple-batch spawning is a bet-hedging strategy (Figure 4 grey-shaded area).

3.3 | Variance in reproductive output within generations

Multiple-batch spawning populations had a lower variance in within-generational reproductive output than single-batch spawning populations (Figure S3 and Table S3). The two components of environmental stochasticity—the environmental fluctuations and environmental pressure applied to batch mortality—had a significant effect on the variance in within-generational reproductive output of multiple-batch spawning populations (Table S4).

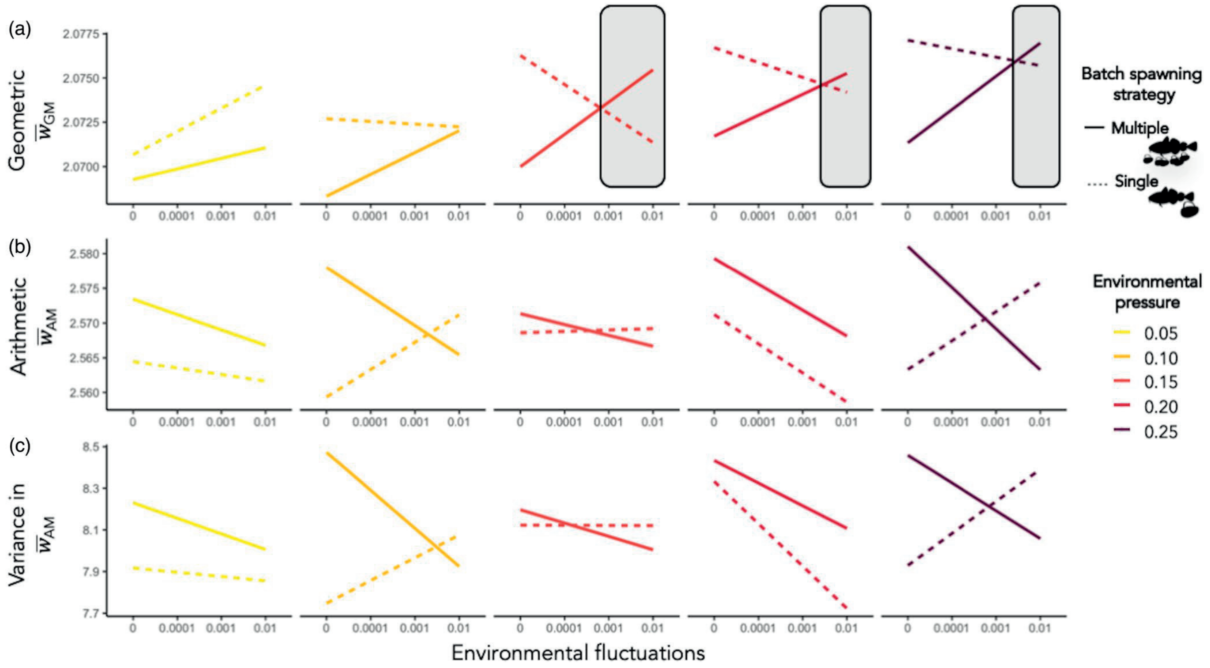


FIGURE 3 Trends of three fitness components: across-generational geometric mean in fitness ($\overline{W}_{GM}$), across-generational average reproductive output or arithmetic mean in fitness ($\overline{W}_{AM}$) and across-generational variance in arithmetic mean fitness (variance in $\overline{W}_{AM}$) plotted against increasing rate of environmental fluctuations (*x*-axis), and grouped by increasing environmental pressure applied to batch survival (colours). Linear regression trends, that were based on the average value of each observed variable across all generations per every run of each spawning type, are illustrated by a solid line for multiple-batch spawners and by a dashed line for single-batch spawners. Grey-shaded area indicates the environmental conditions under which a costly multiple-batch spawning evolutionary outperforms the single-batch spawning strategy

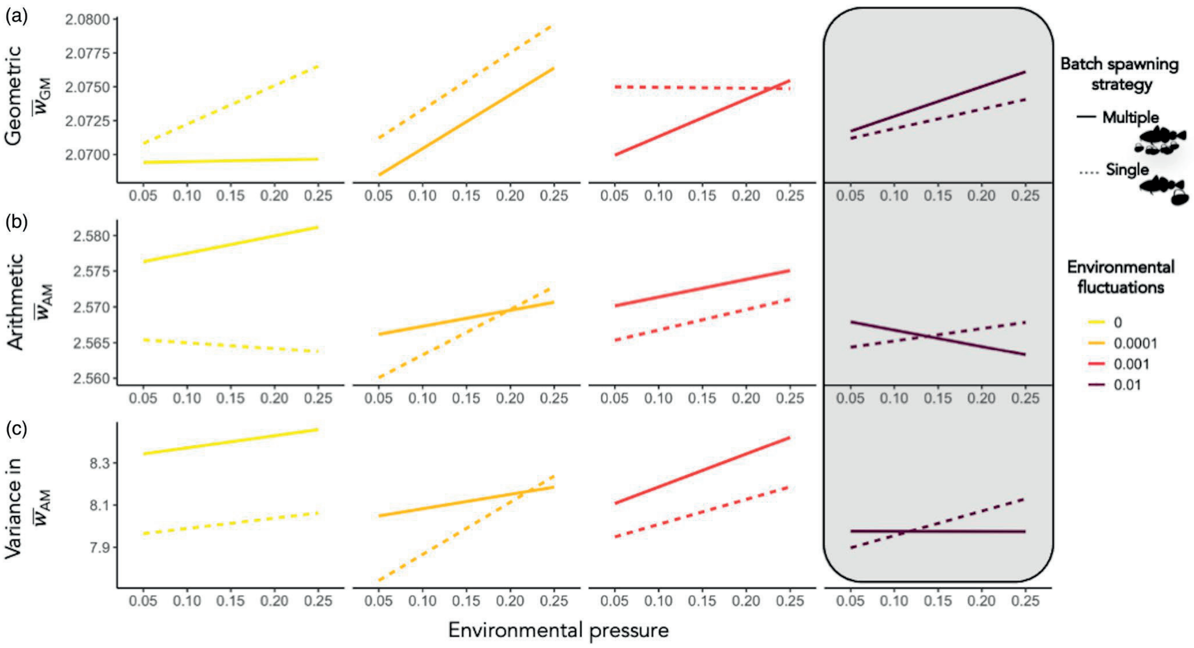


FIGURE 4 Trends of three fitness components: across-generational geometric mean in fitness ($\overline{W}_{GM}$), across-generational average reproductive output or arithmetic mean in fitness ($\overline{W}_{AM}$) and across-generational variance in arithmetic mean fitness (variance in $\overline{W}_{AM}$) plotted against increasing rate of environmental pressure (*x*-axis), and grouped by increasing environmental fluctuations applied to batch survival (colours). Linear regression trends, that were based on the average value of each observed variable across all generations per every run of each spawning type, are illustrated by a solid line for multiple-batch spawners and by a dashed line for single-batch spawners. Grey-shaded area indicates the environmental conditions under which multiple-batch spawning strategy constitutes a bet-hedging, as the $\overline{W}_{GM}$ increases at the cost of reduced $\overline{W}_{AM}$

However, post hoc Dunn's test revealed that the effects were significant only due to the increased variance under the most pressured environments (0.25) and predictable environmental conditions (0). The scenarios with environmental fluctuations (0.0001, 0.001, 0.01) did not differ significantly in the within-generational variance of reproductive output.

3.4 | Spawning success

The proportion of successful spawning seasons in a population, when an individual produced at least one successfully surviving offspring, reaching age 3 (recruitment age when juveniles become catchable by fishing), per season, differed between populations of multiple-batch and single-batch spawners (Table S5). The average frequency of such occasions was significantly higher and more consistent in multiple-batch spawning populations when environmental conditions were less predictable and more stressful (Figure 5a,b). In contrast, the scenarios with no environmental fluctuations (0) and low pressure applied to batch survival (0.05) were more favourable to single-batch spawning populations which exhibited higher spawning success under such conditions (Figure 5a,b). The success probability of mature fish was on average higher and more predictable in the presence of the multiple-batch spawning strategy (Figure 5c).

4 | DISCUSSION

It has been hypothesized that multiple-batch spawning in fishes might comprise a bet-hedging strategy and yield high fitness returns (e.g. Hutchings & Rangeley, 2011). In the present study, we used Atlantic cod as a model species and extended the eco-evolutionary mechanistic model of Kuparinen et al. (2012) to theoretically and empirically explore the hypothesis by evaluating the fitness consequences of such a risk-spreading trait.

The most interesting finding to emerge from the simulations of our empirically parameterized eco-evolutionary model is that the costly multiple-batch spawning strategy can constitute a bet-hedging trait under sufficiently uncertain natural environments. The multiple-batch spawning strategy of individuals exposed to fluctuating environmental conditions served to reduce the variance in arithmetic mean fitness across generations, reflecting the decreasing variance in offspring output within generations.

The fitness of spawners under stochastic environments is governed by the geometric mean in their reproductive success (Gillespie, 1974) rather than the average mean, which fails to account for environmental variability (Lewontin & Cohen, 1969). We followed the across-generational fitness and found that the multiple-batch spawning strategy maximizes geometric mean fitness by lowering the across-generational variance in arithmetic

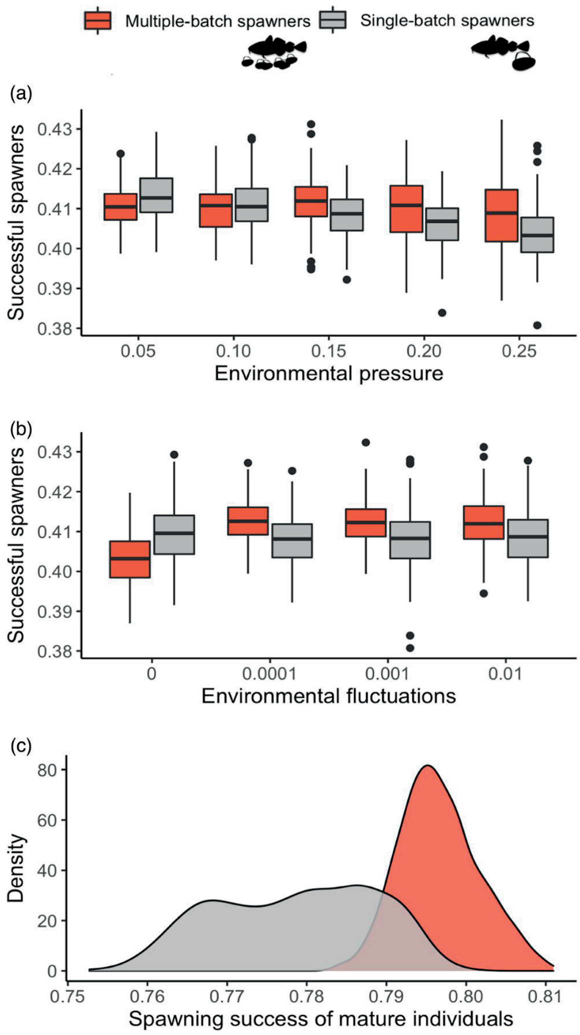


FIGURE 5 The effect of multiple-batch spawning strategy on spawning success under the components of increasing environmental stochasticity. The two boxplots show the difference in the proportion of successful spawners in a population of multiple-batch (red) and single-batch spawners (grey) against increasing environmental pressure (a) and fluctuations (b) applied to batch survival. The proportions were calculated as the total number of all successful events of all mature individuals in the last 300 years and divided by the total sum of succeeded and failed spawning events of all mature individuals in the last 300 years. The density plot (c) illustrates concentrated values over the interval of successful spawning seasons of mature individuals, being right-skewed and more concentrated in the presence of a multiple-batch spawning strategy

mean fitness (Figure 3). These fitness dynamics are indicative of a bet-hedging strategy. Once the arithmetic mean fitness decreases due to the appended costs of the strategy, and when the decrease in arithmetic mean is synchronous with the increase in across-generational geometric mean fitness, multiple-batch spawning performs as a bet-hedging (Figure 4) and evolutionarily outperforms the costless single-batch spawning strategists (Figure 3 grey-shaded area).

A fundamental component of our results lies in the qualitative, rather than quantitative, output. Firstly, we are primarily interested in the directions in which multiple-batch spawning confers advantages, such as reduced long-term variance in fitness or increased probability of non-zero reproductive spawning years, rather than numerical differences between multiple-batch spawners and single-batch spawners. Secondly, although one might be tempted to conclude that our statistically significant quantitative differences are of little biological consequence, we would caution against such a conclusion. Seemingly small phenotypic differences at the species or population level can have considerably greater consequences within a multi-species or ecosystem context (Bassar et al., 2010; El-Sabaawi et al., 2015).

By producing several batches per spawning season (Kjesbu et al., 1996; Roney et al., 2018), batch spawners distribute eggs among multiple batches, thereby spreading the risk on both spatial and temporal scales. This results, on average, in increased survival probabilities for each egg and, as identified in the present study, a decreased realized populational mortality rate, highlighting how early life stages shape the vital rates of adults (Hjort, 1914). Concomitantly, the high spawning success and lower reproductive variance associated with multiple-batch strategy under highly unpredictable and intense environmental perturbations presented the underlying reason for the increased fitness that was maximized across generations.

On the other hand, under scenarios in which temporal and spatial fluctuations were absent and all batches endured equal environmental pressure, each time that a fish spawned, the average output of successfully surviving offspring varied considerably within and across generations, resulting in a higher arithmetic and lower geometric mean fitness compared to the single-batch spawning strategy. This suggests that, apart from bypassing the physiological constraints imposed by egg shedding, solely from the isolated perspective of egg batch effects on fitness dynamics, the costs of the multiple-batch spawning strategy are too high and fitness benefits too low to pay off under fairly stable environmental circumstances in the long run. Therefore, multiple-batch spawning of Atlantic cod is plausibly selected for to endure greater natural stochasticity. The outcome could be common among batch spawning fish species that are exposed to similar selective pressures and that share similar trade-off in life-history traits and costs of reproduction (Longhurst, 2002).

Several studies have demonstrated why, in a purely spatially varying or a fine-grained environment (Levins, 1968), a bet-hedging response would not evolve or be favoured (Haaland et al., 2020; Moran, 1992). A costly strategy requires a certain ratio of spatial-temporal variation and a trade-off in fitness to be advantageous and adaptive. Environmental settings where individuals face different environmental variability only on a spatial scale within generations gain fitness additively as reflected by the arithmetic mean fitness, whereas environmental variability on an exclusively temporal scale across generations gain fitness multiplicatively as reflected by the geometric mean fitness (Haaland et al., 2020).

The externally applied environmental stochasticity in our model might have, to some degree, generated such a fine-grained environmental setting as it was newly drawn for each batch of every female within each generation. However, there are at least three reasons why our simulations also accounted for temporal fluctuations, thus steering the environments towards coarser graininess. Firstly, the environmental setting of fluctuating scenarios (Figure 1) was newly drawn for every spawning season, adding the temporal aspect of changes from one year to the next and, as such, generated conditions where a bet-hedging strategy could unfold. Secondly, the presence of temporal variability was additionally endorsed by our calculations of arithmetic and geometric fitness, for which the values were never equal, indicating that the environments were not constant but rather fluctuating through time because of external stochasticity simulating the biotic and abiotic change (Orr, 2009). And lastly, the 20 diverse but discrete environmental scenarios enabled us to obtain a broad glimpse into a coarse-grained setting. Notwithstanding these points, the modelling of a more detailed year-to-year interchangeable environmental pressure on spawning dynamics might reveal further effects of the multiple-batch spawning strategy on fitness components of cod populations.

The mechanistic model that we used is, as any other model, a simplification of a natural system, one that includes simplifying assumptions; these need to be considered for model interpretation. For instance, one of the assumptions was a uniform distribution of egg sizes and abundance within and among egg batches. This simplification could reduce the effect of the selective pressure on larger phenotypes. Kjesbu (1989), Kjesbu et al. (1996), for example, found that abundance and mean weight of eggs of Norwegian coastal cod varied among batches and spawning seasons. While the egg abundance follows a dome-shaped curve, which can be right or left-skewed, the mean size of offspring decreases towards the end of the spawning period (Kjesbu et al., 1996; Roney et al., 2018). In addition, it is known that natural selection can favour variability in egg size within batches (Koops et al., 2003; Olofsson et al., 2009). Our primary reason for omitting these relationships was to isolate the multiple-batch production trait and to focus solely on its unique diversifying influence on fitness.

Taking into account the model's assumptions, we can conclude that multiple-batch spawning contributes to the long-term persistence of cod genotypes under stochastic environmental conditions, where the cost–benefit ratio is low, and reduces the probability of reproductive failure (Figure 5). In contrast, the strategy of laying all eggs at once in every spawning season would increase the survival uncertainty of the batches, resulting in a game with two outcomes: success or complete reproductive failure. Here, we found that the within- and across-generational reproductive variance associated with such a single-batch spawning strategy would be higher and result in lower fitness when faced with strong environmental stochasticity, as it is more sensitive to the number of complete reproductive failures.

The novelty of our work lies in the direct comparison of across-generational geometric mean fitness between risk-spreading and nonrisk-spreading cod populations. Our modelling approach provided empirically anchored support for the hypothesis that multiple-batch spawning is advantageous and adaptive in stochastically variable environments. Following Simons (2011), such a direct test falls at least into the second highest strength of evidence category (V), which involves the bet-hedging trait to be validated whether it is favoured under relevant varying environments. We manipulated the magnitude of selection through the degree of environmental stochasticity and found that the presence of the trait significantly stabilized fitness of cod under most fluctuating environmental settings.

Extensive theoretical work has been developed on the maximization of geometric fitness under stochastic conditions (Cohen, 1966; Lewontin & Cohen, 1969; Simons, 2002; Starrfelt & Kokko, 2012; Yoshimura & Clark, 1991), but some ambiguities persist (Metz et al., 1992; Sæther & Engen, 2015). For example, Tal and Tran (2020) have stressed the need to re-consider or upgrade the approach of the maximized geometric mean fitness in the search of a bet-hedging trait. In the present study, we derived the mean geometric fitness using standard nth roots of the multiplicative approach (Seger & Brockmann, 1987). We observed the cod population in our model to be flexible; whenever the rate of egg batch mortality equalled or exceeded 0.30, the population collapsed within the first 100 years and became extinct. This makes ecological sense, given that several mortality rates were combined in our model during the lifespan of an individual to simulate natural environmental conditions, including increased juvenile mortalities (Anderson & Gregory, 2000), and survival and reproduction costs (Lambert & Dutil, 2000). That said, a more detailed exploration of extinction probabilities was beyond the scope of our study, and we did not pursue the differences between the two genotype populations in their resilience to extinction.

Another ambiguity involves false dichotomy. Starrfelt and Kokko (2012) concluded that the usual partitioning of conservative and diversification bet-hedging should not be treated only as two discretely separate categories. Their point was that the benefit of bet-hedging can also derive from their combination; reduced variance on the individual fitness level can represent a conservative part of the trait, and reduced fitness correlations among individuals can present a diversifying part of the trait. As a result, they proposed that the two strategies be considered as endpoints along a continuous scale. Recent theoretical research illustrated how they might coexist (Haaland et al., 2019). Similarly, the trait examined in the present study seems to encompass elements of both conservative and diversification bet-hedging. Multiple-batch spawning is a positive size-based trait that reduces individual-level variance in fitness and, thus, resembles a conservative type of bet-hedging (Haaland et al., 2020; Starrfelt & Kokko, 2012), while at least two rationales could reflect the diversifying characteristics of bet-hedging: the stock demographic structure and subpopulation connectivity (e.g. *stock complex*).

The benefits of a multiple-batch spawning might be integrated across multiple levels of biological organization. For instance, Shelton et al. (2015) showed that spawning stock age structure has a significant effect on the recruitment dynamics of Atlantic cod. Therefore, the eradication of one cohort due to a natural catastrophe or anthropogenic impact such as overfishing (Hutchings, 2005) could reduce the diversity in size-structure of a population and consequently increase the fitness correlation among individuals or, in another words, repress the diversifying bet-hedging fitness benefits that the multiple-batch spawning of unfished populations might offer.

A spatial distribution in metapopulation structure could also be detrimental through larval dispersal or even adult migration (Hu & Wroblewski, 2009). Genetic analyses of North Sea and coastal inshore and offshore cod populations in the Norwegian Skagerrak have revealed an alternating connectivity among coexisting subpopulations (Knutsen et al., 2004), which display a fine-scaled differentiation in life-history characteristics (Kuparinen et al., 2016). Although the subpopulations appear to be more linked in some years than others (Knutsen et al., 2004), the connectivity ensures higher diversity of life histories in a subpopulation and minimizes the correlation in spawning potential of stock. In contrast, populational fragmentation via local extinctions (Hutchings & Myers, 1994) could disrupt the connectivity with neighbouring areas through perished adult links or decreased recruit inflow, which can have a far-reaching effect in maintaining gene flow to locally depleted stocks or in mitigating poor spawning seasons (Stenseth et al., 2006). Thus, the benefits of dividing eggs into several batches could, hypothetically, arise from both individual- and population-level considerations. However, to test our speculations, we would need to further explore the fitness correlations among individuals of each strategists.

Our results highlight that producing several egg batches per spawning period increases spawning success of batch spawners. This might be related to prolonged spawning seasons expanding the time window for optimal abiotic conditions to occur and influence the variation in survival probability within an egg batch. Early-stage survival of fish is known to be a highly stochastic process (Ohlberger et al., 2014), and multiple factors contribute to successful recruitment and fitness, from favourable abiotic conditions driven by currents (Hjort, 1914) to biotic processes of bottom-up control (Cushing, 1990), habitat complexity (Theodorou et al., 2013), and density-dependent regulation (Fromentin et al., 2001; Kuparinen et al., 2014). For example, given that the probability of egg and larval transport to suitable habitats can be strongly influenced by the timing of release coinciding with the favourable environmental conditions (e.g. Huserbråten et al., 2018), it is conceivable that the multiple-batch spawning strategy would increase the probability of these coincidentally occurring events. Multiple-batch spawning is also likely to affect the dynamics of a temporal 'match'/'mismatch' between the peak abundance of larvae and their prey, such that variability in offspring production is inversely related to the length of spawning season (Mertz & Myers, 1994). The empirical modelling study of cod by Kristiansen et al. (2011) supports our findings; offspring survival increased as the spatial and temporal overlap between fish larvae and their prey increased. The duration of overlap during the spawning period was more beneficial to recruitment than the co-occurrence of peak prey and larvae abundance, which further underscores the risk-spreading benefits of prolonged spawning among batch spawners.

In summary, we show that the risk-spreading mechanism of producing multiple batches facilitates cod to endure greater environmental stochasticity. The number of batches, which increases with maternal body size, contributes significantly to across-generational fitness of populations experiencing highly unpredictable environmental perturbation. This relation invokes new rather applicative questions such as could a size-selective fishing pressure have a magnified impact on the effective size-structure of a cod population and cod-like species because of a size-related spawning trait? Could the fishing of larger individuals abduct the population of the security mechanism that the bet-hedging ensure and consequently diminish its portfolio effect? Since several stocks of batch spawning fish species have been subjected to overfishing and are still in a rebuilding phase (e.g. Hutchings & Kuparinen, 2020), the role of traits that enable populations to reduce susceptibility to environmental variation may be vital to species recovery and success. Bet-hedging strategies such as batch spawning can yield high fitness returns and should therefore be integrated in proactive stock management, including the setting of reference points. Spawning type influences the reproductive dynamics of stocks, which is the underlying reference for management implications. We suggest that recognizing stress-coping mechanisms of species and understanding their dynamics under naturally and anthropogenically induced stressful conditions is a critical issue that needs to be tackled to fill the knowledge gaps on fitness dynamics of harvested stocks and to achieve sustainable use of natural resources.

ACKNOWLEDGEMENTS

This study was funded by the Academy of Finland (project grant 317495 to A.K.), Natural Sciences and Engineering Research Council of Canada (NSERC; Discovery Grants to J.A.H. and A.K.) and the European Research Council (COMPLEX-FISH 770884 to A.K.). The present study reflects only the authors' view; the European Research Council is not responsible for any use that may be made of the information it contains. We would like to thank the anonymous reviewers who provided many helpful suggestions, which significantly improved the final version of the manuscript.

CONFLICT OF INTEREST

We have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

Data for this study are available at the Dryad Digital Repository: https://doi.org/10.5061/dryad.g1jwstqn0.

ORCID

Sara Hočevar https://orcid.org/0000-0002-1294-0927

REFERENCES

Anderson, J. T., & Gregory, R. S. (2000). Factors regulating survival of northern cod (NAFO 2J3KL) during their first 3 years of life. *ICES Journal of Marine Science*, *57*(2), 349–359.

Bassar, R. D., Marshall, M. C., López-Sepulcre, A., Zandonà, E., Auer, S. K., Travis, J., Pringle, C. M., Flecker, A. S., Thomas, S. A., Fraser, D. F., & Reznick, D. N. (2010). Local adaptation in Trinidadian guppies alters ecosystem processes. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(8), 3616–3621.

Beaumont, H. J. E., Gallie, J., Kost, C., Ferguson, G. C., & Rainey, P. B. (2009). Experimental evolution of bet hedging. *Nature*, *462*(7269), 90–93.

Beckman, N. G., Bullock, J. M., & Salguero-Gómez, R. (2018). High dispersal ability is related to fast life-history strategies. *Journal of Ecology*, *106*(4), 1349–1362.

Beverton, R. J. H., Hylen, A., & Oestvedt, O. J. (1994). Growth, maturation, and longevity of maturation cohorts of Northeast Arctic cod. *ICES Marine Science Symposia*, *198*, 482–501.

Childs, D. Z., Metcalf, C. J. E., & Rees, M. (2010). Evolutionary bet-hedging in the real world: Empirical evidence and challenges revealed by plants. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1697), 3055–3064.

Cohen, D. (1966). Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology*, *12*(1), 119–129.

Cole, L. C. (1954). The population consequences of life history phenomena. *The Quarterly Review of Biology*, *29*(2), 103–137.

Cushing, D. H. (1990). Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. *Advances in Marine Biology*, *26*, 249–293.

El-Sabaawi, R. W., Bassar, R. D., Rakowski, C., Marshall, M. C., Bryan, B. L., Thomas, S. N., Pringle, C. M., Reznick, D. N., & Flecker, A. S. (2015). Intraspecific phenotypic differences in fish affect ecosystem processes as much as bottom–up factors. *Oikos*, *124*(9), 1181–1191.

Frank, S. A., & Slatkin, M. (1990). Evolution in a variable environment. *The American Naturalist*, *136*(2), 244–260.

Fromentin, J. M., Myers, R. A., Bjørnstad, O. N., Stenseth, N. C., Gjøsæter, J., & Christie, H. (2001). Effects of density-dependent and stochastic processes on the regulation of cod populations. *Ecology*, *82*(2), 567–579.

Furness, A. I., Lee, K., & Reznick, D. N. (2015). Adaptation in a variable environment: Phenotypic plasticity and bet-hedging during egg diapause and hatching in an annual killifish. *Evolution*, *69*(6), 1461–1475.

Gillespie, J. H. (1973). Natural selection with varying selection coefficients: A haploid model. *Genetical Research*, *21*, 115–120.

Gillespie, J. H. (1974). Natural selection for within-generation variance in offspring number. *Genetics*, *76*(3), 601–606.

Gillespie, J. H. (1975). Natural selection for within-generation variance in offspring number. 2. Discrete haploid models. *Genetics*, *81*, 403–413.

Haaland, T. R., Wright, J., & Ratikainen, I. I. (2020). Generalists versus specialists in fluctuating environments: A bet-hedging perspective. *Oikos*, *129*(6), 879–890. https://doi.org/10.1111/oik.07109

Haaland, T. R., Wright, J., Tufto, J., & Ratikainen, I. I. (2019). Short-term insurance versus long-term bet-hedging strategies as adaptations to variable environments. *Evolution*, *73*(2), 145–157.

Hjort, J. (1914). Fluctuations in the great fisheries of Northern Europe, viewed in the light of biological research. *Rapports Et Procès-Verbaux Des Réunions Du Conseil Permanent International Pour L'exploration De La Mer*, *20*, 1–228.

Hu, L., & Wroblewski, J. S. (2009). Conserving a subpopulation of the northern Atlantic cod metapopulation with a marine protected area. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *19*(2), 178–193.

Huserbråten, M. B. O., Moland, E., & Albretsen, J. (2018). Cod at drift in the North Sea. *Progress in Oceanography*, *167*, 116–124.

Hutchings, J. A. (2005). Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, *62*(4), 824–832.

Hutchings, J. A., & Kuparinen, A. (2020). Implications of fisheries-induced evolution for population recovery: Refocusing the science and refining its communication. *Fish and Fisheries*, *21*(2), 453–464.

Hutchings, J. A., & Myers, R. A. (1994). What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Canadian Journal of Fisheries and Aquatic Sciences*, *51*(9), 2126–2146.

Hutchings, J. A., & Rangeley, R. W. (2011). Correlates of recovery for Canadian Atlantic cod (*Gadus morhua*). *Canadian Journal of Zoology*, *89*(5), 386.

Jensen, A. L. (1997). Origin of relation between K and Linf and synthesis of relations among life history parameters. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*(5), 987–989.

Kenney, J., & Keeping, E. (1962). *Mathematics of statistics*. Van Nostrand.

Kjesbu, O. S. (1989). The spawning activity of cod, *Gadus morhua* L. *Journal of Fish Biology*, *34*(2), 195–206.

Kjesbu, O. S., Solemdal, P., Bratland, P., & Fonn, M. (1996). Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, *53*(3), 610–620.

Knutsen, H., André, C., Jorde, P. E., Skogen, M. D., Thuróczy, E., & Stenseth, N. C. (2004). Transport of North Sea cod larvae into the Skagerrak coastal populations. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(1546), 1337–1344.

Koops, M. A., Hutchings, J. A., & Adams, B. K. (2003). Environmental predictability and the cost of imperfect information: Influences on offspring size variability. *Evolutionary Ecology Research*, *5*, 29–42.

Kristiansen, T., Drinkwater, K. F., Lough, R. G., & Sundby, S. (2011). Recruitment variability in North Atlantic cod and match-mismatch dynamics. *PLoS One*, *6*(3), e17456.

Kruskal, W. H., & Wallis, W. A. (1952). Use of ranks in one-criterion variance analysis. *Journal of the American Statistical Association*, *47*(260), 583–621.

Kuparinen, A., Hardie, D. C., & Hutchings, J. A. (2012). Evolutionary and ecological feedbacks of the survival cost of reproduction. *Evolutionary Applications*, *5*(3), 245–255.

Kuparinen, A., Keith, D. M., & Hutchings, J. A. (2014). Increased environmentally driven recruitment variability decreases resilience to fishing and increases uncertainty of recovery. *ICES Journal of Marine Science*, *71*(6), 1507–1514.

Kuparinen, A., Roney, N. E., Oomen, R. A., Hutchings, J. A., & Olsen, E. M. (2016). Small-scale life history variability suggests potential for spatial mismatches in Atlantic cod management units. *ICES Journal of Marine Science: Journal Du Conseil*, *73*(2), 286–292.

Kuparinen, A., Stenseth, N. C., & Hutchings, J. A. (2014). Fundamental population–productivity relationships can be modified through density-dependent feedbacks of life-history evolution. *Evolutionary Applications*, *7*(10), 1218–1225.

Kussell, E., & Leibler, S. (2005). Phenotypic diversity, population growth, and information in fluctuating environments. *Science*, *309*(5743), 2075–2078.

Laaksonen, T. (2004). Hatching asynchrony as a bet-hedging strategy – An offspring diversity hypothesis. *Oikos*, *104*(3), 616–620.

Lambert, Y., & Dutil, J. (2000). Energetic consequences of reproduction in Atlantic cod (*Gadus morhua*) in relation to spawning level of somatic energy reserves. *Canadian Journal of Fisheries and Aquatic Sciences*, *57*(4), 815–825.

Lande, R. (1993). Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist*, *142*(6), 911–927.

Lenormand, T., Roze, D., & Rousset, F. (2009). Stochasticity in evolution. *Trends in Ecology and Evolution*, *24*(3), 157–165.

Levins, R. (1968). *Evolution in changing environments*. Princeton University Press.

Lewontin, R. C., & Cohen, D. (1969). On population growth in a randomly varying environment. *Proceedings of the National Academy of Sciences of the United States of America*, *62*(4), 1056–1060.

Lips, K. R. (2001). Reproductive trade-offs and bet-hedging in Hyla calypsa, a Neotropical treefrog. *Oecologia*, *128*(4), 509–518.

Longhurst, A. (2002). Murphy's law revisited: Longevity as a factor in recruitment to fish populations. *Fisheries Research*, *56*(2), 125–131.

Mahony, M., & Thumm, K. (2002). Hatching dynamics and bet-hedging in a temperate frog, *Pseudophryne australis* (Anura: Myobatrachidae). *Amphibia-Reptilia*, *23*(4), 433–444.

Markowitz, H. (1952). Portfolio selection. *The Journal of Finance*, *7*(1), 77–91.

May, R. M. (1973). Stability in randomly fluctuating versus deterministic environments. *The American Naturalist*, *107*(957), 621–650.

Maynard Smith, J. (2010). *Evolution and the theory of games*. Cambridge Univ. Press.

Mertz, G., & Myers, R. A. (1994). Match/mismatch predictions of spawning duration versus recruitment variability. *Fisheries Oceanography*, *3*(4), 236–245.

Metz, J. A. J., Nisbet, R. M., & Geritz, S. A. H. (1992). How should we define 'fitness' for general ecological scenarios? *Trends in Ecology and Evolution*, *7*(6), 198–202.

Meyers, L. A., & Bull, J. J. (2002). Fighting change with change: Adaptive variation in an uncertain world. *Trends in Ecology and Evolution*, *17*(12), 551–557.

Moran, N. A. (1992). The evolutionary maintenance of alternative phenotypes. *The American Naturalist*, *139*(5), 971–989.

Murua, H., & Sabrido-Rey, F. (2003). Safety assessment for geological disposal of radioactive wastes set 4–6 heat transfer in the engineered barriers. *Journal of Northwest Atlantic Fishery Science*, *33*, 23–31.

Ohlberger, J., Rogers, L. A., & Stenseth, N. C. (2014). Stochasticity and determinism: How density-independent and density-dependent processes affect population variability. *PLoS One*, *9*(6), e98940.

Olofsson, H., Ripa, J., & Jonzén, N. (2009). Bet-hedging as an evolutionary game: The trade-off between egg size and number. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1669), 2963–2969.

Orr, H. A. (2009). Fitness and its role in evolutionary genetics. *Nature Reviews Genetics*, *10*(8), 531–539.

Pepin, P. (1991). Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. *Canadian Journal of Fisheries and Aquatic Sciences*, *48*, 503–518.

Philippi, T., & Seger, J. (1989). Hedging one's evolutionary bets, revisited. *Trends in Ecology and Evolution*, *2*, 41–44.

R Core Team (2019). *A language and environment for statistical computing*. R foundation for Statistical Computing.

Ranta, E., Tesar, D., & Kaitala, V. (2002). Environmental variability and semelparity vs. iteroparity as life histories. *Journal of Theoretical Biology*, *217*(3), 391–396.

Roney, N. E., Oomen, R. A., Knutsen, H., Olsen, E. M., & Hutchings, J. A. (2018). Temporal variability in offspring quality and individual reproductive output in a broadcast-spawning marine fish. *ICES Journal of Marine Science*, *75*(4), 1353–1361.

Sæther, B., & Engen, S. (2015). The concept of fitness in fluctuating environments. *Trends in Ecology and Evolution*, *30*(5), 273–281.

Scheiner, S. M. (2014). Bet-hedging as a complex interaction among developmental instability, environmental heterogeneity, dispersal, and life-history strategy. *Ecology and Evolution*, *4*(4), 505–515.

Seger, J., & Brockmann, H. J. (1987). *What is bet-hedging?* Oxford University Press.

Shelton, A. O., Hutchings, J. A., Waples, R. S., Keith, D. M., Akçakaya, H. R., & Dulvy, N. K. (2015). Maternal age effects on Atlantic cod recruitment and implications for future population trajectories. *ICES Journal of Marine Science*, *72*(6), 1769–1778.

Simons, A. M. (2002). The continuity of microevolution and macroevolution. *Journal of Evolutionary Biology*, *15*(5), 688–701.

Simons, A. M. (2009). Fluctuating natural selection accounts for the evolution of diversification bet hedging. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1664), 1987–1992.

Simons, A. M. (2011). Modes of response to environmental change and the elusive empirical evidence for bet hedging. *Proceedings: Biological Sciences*, *278*(1712), 1601–1609.

Simons, A. M., & Johnston, M. O. (2003). Suboptimal timing of reproduction in *Lobelia inflata* may be a conservative bet-hedging strategy. *Journal of Evolutionary Biology*, *16*(2), 233–243.

Slatkin, M. (1974). Hedging one's evolutionary bets. *Nature*, *250*(5469), 704–705.

Snyder, R. E. (2011). Leaving home ain't easy: Non-local seed dispersal is only evolutionarily stable in highly unpredictable environments. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1706), 739–744.

Starrfelt, J., & Kokko, H. (2012). Bet-hedging—A triple trade-off between means, variances and correlations. *Biological Reviews*, *87*(3), 742–755.

Stearns, S. C. (1976). Life-history tactics: A review of the ideas. *The Quarterly Review of Biology*, *51*(1), 3–47.

Stenseth, N. C., Jorde, P. E., Chan, K. S., Hansen, E., Knutsen, H., André, C., Skogen, M. D., & Lekve, K. (2006). Ecological and genetic impact of Atlantic cod larval drift in the Skagerrak. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1590), 1085–1092.

Tal, O., & Tran, T. D. (2020). Adaptive bet-hedging revisited: Considerations of risk and time horizon. *Bulletin of Mathematical Biology*, *82*(4), 50.

Tarazona, E., García-Roger, E. M., & Carmona, M. J. (2017). Experimental evolution of bet hedging in rotifer diapause traits as a response to environmental unpredictability. *Oikos*, *126*(8), 1162–1172.

Theodorou, P., Snorrason, S. S., & Ólafsdóttir, G. Á. (2013). Habitat complexity affects how young of the year Atlantic cod *Gadus morhua* perceive predation threat from older conspecifics. *Journal of Fish Biology*, *82*(6), 2141–2146.

Tufto, J. (2015). Genetic evolution, plasticity, and bet-hedging as adaptive responses to temporally autocorrelated fluctuating selection: A quantitative genetic model. *Evolution*, *69*(8), 2034–2049.

Von Bertalanffy, L. (1938). A quantitative theory of organic growth (inquiries on growth laws ii). *Human Biology*, *10*(2), 181–213.

Welch, B. L. (1947). The generalization of 'Student's' problem when several different population variances are involved. *Biometrika*, *34*(1/2), 28–35.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms, J., Robinson, D., Seidel, D., Spinu, V., … Yutani, H. (2019). Welcome to the tidyverse. *Journal of Open Source Software*, *4*(43), 1686.

Yoshimura, J., & Clark, C. W. (1991). Individual adaptations in stochastic environments. *Evolutionary Ecology*, *5*(4), 173–192.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Hočevar S, Hutchings JA, Kuparinen A. Multiple-batch spawning as a bet-hedging strategy in highly stochastic environments: An exploratory analysis of Atlantic cod. *Evolutionary Applications*. 2021;14:1980–1992. https://doi.org/10.1111/eva.13251

II

MULTIPLE-BATCH SPAWNING: A RISK-SPREADING STRATEGY DISARMED BY HIGHLY INTENSIVE SIZE-SELECTIVE FISHING RATE

by

Sara Hočevar, Jeffrey A. Hutchings & Anna Kuparinen 2022

Proceedings of the Royal Society B: Biological Sciences 289, 20221172.

DOI: 10.1098/rspb.2022.1172

PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Research

Cite this article: Hočevar S, Hutchings JA, Kuparinen A. 2022 Multiple-batch spawning: a risk-spreading strategy disarmed by highly intensive size-selective fishing rate. *Proc. R. Soc. B* **289**: 20221172.
https://doi.org/10.1098/rspb.2022.1172

Received: 16 June 2022
Accepted: 8 August 2022

Subject Category:
Evolution

Subject Areas:
biological applications, evolution, ecology

Keywords:
Atlantic cod, bet-hedging, fitness, fisheries-induced evolution, multiple-batch spawning, size-selective fishing

Author for correspondence:
Sara Hočevar
e-mail: sara.hocevar@icloud.com

Multiple-batch spawning: a risk-spreading strategy disarmed by highly intensive size-selective fishing rate

Sara Hočevar[1], Jeffrey A. Hutchings[1,2,3,4] and Anna Kuparinen[1]

[1]Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä 40014, Finland
[2]Department of Biology, Dalhousie University, Halifax NS B3H 4R2, Canada
[3]Institute of Marine Research, Flødevigen Marine Research Station, N-4817 His, Norway
[4]Department of Natural Sciences, University of Agder, N-4604 Kristiansand, Norway

SH, 0000-0002-1294-0927; JAH, 0000-0003-1572-5429; AK, 0000-0002-7807-8946

Can the advantage of risk-managing life-history strategies become a disadvantage under human-induced evolution? Organisms have adapted to the variability and uncertainty of environmental conditions with a vast diversity of life-history strategies. One such evolved strategy is multiple-batch spawning, a spawning strategy common to long-lived fishes that 'hedge their bets' by distributing the risk to their offspring on a temporal and spatial scale. The fitness benefits of this spawning strategy increase with female body size, the very trait that size-selective fishing targets. By applying an empirically and theoretically motivated eco-evolutionary mechanistic model that was parameterized for Atlantic cod (*Gadus morhua*), we explored how fishing intensity may alter the life-history traits and fitness of fishes that are multiple-batch spawners. Our main findings are twofold; first, the risk-spreading strategy of multiple-batch spawning is not effective against fisheries selection, because the fisheries selection favours smaller fish with a lower risk-spreading effect; and second, the ecological recovery in population size does not secure evolutionary recovery in the population size structure. The beneficial risk-spreading mechanism of the batch spawning strategy highlights the importance of recovery in the size structure of overfished stocks, from which a full recovery in the population size can follow.

1. Introduction

More than 34 000 species of fish have been described so far [1]. The diversity of life histories among them is vast and even exceeds the number of species [2]. Each species developed a unique strategy to allocate its energy budget among the selected life-history traits, each one with the ultimate goal: to maximize the number of next-generation spawners, fitness, before being vanquished by natural mortality [3,4].

Some species have adapted to minimize the high natural mortality rates and increase the survival of the earliest life stages with reproductive strategies in spawning patterns [5]. Some teleosts optimize their reproductive success and reduce the risk of offspring mortality with spawning location and are demersal spawners—spawning their eggs on different kinds of a substrate (e.g. capelin *Mallotus villosus* [6]), while some are pelagic spawners—spawning their eggs into a water column (e.g. European pilchard *Sardina pilchardus* [7]). Extensive variability also exists in spawning regularity and the number of spawning episodes. Species may be semelparous spawners, spawning all the eggs only once in their life (e.g. Chinook salmon *Oncorhynchus tshawytscha* [8]), or iteroparous spawners, spawning eggs for multiple years. The former can be parted into total spawners, which spawn a batch of eggs once within a season (e.g. Atlantic herring *Clupea harengus*) or multiple-batch spawners (MBS), which spawn

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.6158611.

THE ROYAL SOCIETY
PUBLISHING

several batches of eggs within a season (e.g. haddock *Melanogrammus aeglefinus*). Some batch spawning fish may even skip spawning in years when environmental cues favour investment into somatic growth instead of reproduction [9]. Batch spawners can be further classified as determinant batch spawners (e.g. European sea bass *Dicentrarchus labrax* and plaice *Pleuronectes platessa*) or indeterminate batch spawners (e.g. European anchovy *Engraulis encrasicolus* and sole *Solea solea*), depending on whether the number of vitellogenic oocytes is determined before the start of the spawning season or whether it is formed continuously throughout the spawning season [10,11].

Spawning strategies of teleosts, characterized by the spawning frequency and fecundity have been fine-tuned over hundreds of millions of years of evolution to the optimal trade-off among survival, growth and reproductive traits to challenge natural mortality. But how do these evolutionary winning strategies perform when exposed to the *non-natural mortality* of the modern epoch? Could the advantage of risk-mitigating spawning strategies become a disadvantage under human-induced mortality?

Reconstructions from historical records have demonstrated that some of today's commercially fished stocks represent merely a remnant of once highly abundant populations [12,13]. For example, cod fisheries date back to the pre-Mesolithic Stone Age [14], but intense fishing practices have depleted most stocks only in recent decades, with some stocks collapsing to less than 5% of their pre-industrial fishing values [13]. As a consequence, some stocks may have passed their tipping point of recovery as reflected by the Allee effects [15,16]. Regardless of stricter fisheries regulations, moratoriums and the decades passed, stocks such as Canadian stocks, have yet to recover their biomasses from their critical zones [13].

In the present study, we explore the extent of the impact that size-selective fishing has on the risk-spreading strategy of MBS. Our focal species is the iconic Atlantic cod (*Gadus morhua*), a determinant demersal spawner with a wide geographic range and a long history of fishing exploitation [17]. Life-history characteristics set cod among the most fecund species with a long reproductive lifespan, late maturation, increasing maternal investment with age and repetitive broadcast spawning. Some of these reproductive traits, including the duration of the spawning period and the frequency of spawning events, tend to correlate positively with body size in cod [18,19]. The spawning dynamics of cod, in which fish shed eggs in multiple batches within every spawning season [18], grant a spatial and temporal risk-spreading effect [20]. This diverse distribution of egg batches contributes to higher across-generational fitness and can act as a bet-hedging strategy under environmental conditions when odds of survival are low and hard to predict [21].

We apply an individual-based eco-evolutionary model [22] to investigate the performance of batch spawning strategy under human-induced mortality, in form of size-selective fishing. To encompass the wide spectrum of risk that this risk-spreading strategy provides, from risk-averse, where eggs are shed across as many batches as the female's body size can support, to risk-prone, where all the eggs are shed at once, we compare multiple-batch spawning cod to its hypothetical opposite: a single-batch spawning cod. With this approach, we disentangle the far-reaching effects that the batch spawning strategy as such promotes. In particular, we look into the influence of spawning strategy on (i) fisheries-induced evolution of fish body size, (ii) changes in fitness dynamics and survival of recruits that join the adult population, and (iii) alteration of population age structure. Overall, we highlight the eco-evolutionary role of a multiple-batch spawning strategy under size-selective fishing and show that this risk-spreading strategy is not resilient to fishing selection.

2. Methods

(a) Extended mechanistic cod model

The individual-based mechanistic model, developed and thoroughly described by Kuparinen *et al.* [22], follows each individual cod within a population at each annual time step from the start to the end of its simulated life. In the years between, the individuals undergo the processes of natural and fishing mortality, growth, and, if mature, reproduction. The fish lengths (L) follow their von Bertalanffy growth trajectories [23], and the integral evolving trait of the model is the asymptotic maximum length L_∞. This model parameter represents the basis for other size-related life-history [24] and fitness traits [18,19]. To create an initial genetic pool of L_∞ values, the model integrates the negative correlation between the growth rate k and L_∞ estimated from 258 growth trajectories of an unexploited cod population from a lake in the Canadian Arctic [25].

At the time of birth, each recruit inherits a unique genetic value of L_∞ from its parents via classical Mendelian principles. After accounting for normally distributed environmental noise (s.d. = 3.5) around the genotypic value (ranging between 0 and 20), the phenotypic value of L_∞ is set, resulting in a naturally observed heritability of 0.2–0.3 [26]. The ratio between the population's biomass and carrying capacity in the corresponding year was used as a measure of density dependence, and it negatively affected the somatic growth of individuals along their von Bertalanffy growth curves [22].

(b) Spawning strategy

The spawning season occurs once a year for every individual that reaches the maturation threshold set to 66% of its individual asymptotic maximum length L_∞ [27]. The number of eggs a mature female produces is positively correlated to its body weight (table 1), following empirically based age-specific fecundity [28], while the weight is derived from the empirically based length–weight relationship [22,28].

To identify the impact of size-selective fishing on spawning dynamics, we simulated populations in the presence and absence of a multiple-batch spawning strategy. This allowed us to separately generate and track the populational dynamics of multiple-batch and single-batch spawning individuals. Each batch spawning female (i.e. a *MBS*) imitates the risk-spreading strategy of Atlantic cod. Such a female spawns its eggs in multiple batches in several pulses during an extended spawning season. The number of spawned batches is positively correlated to female body size [19] and the relation is derived from the fitted data on the number of batches and female fork length $L_{\mathrm{fork}(t)}$ (table 1) gathered on cod from coastal Skagerrak (fig. 2 in [21]). We implemented batch spawning costs to the model because we consider multiple-batch spawning a bet-hedging trait [21] which acts with associated costs to mean arithmetic fitness [31–33]. Spawning mortality costs gradually increase from 0 to 0.11 for every subsequently shed egg batch, to reflect the empirical observation of Norwegian coastal cod [19] (fig. 2 in [21]), where larval length and yolk-sac volume declined in the latest batches. We applied the spawning costs separately as a decreased

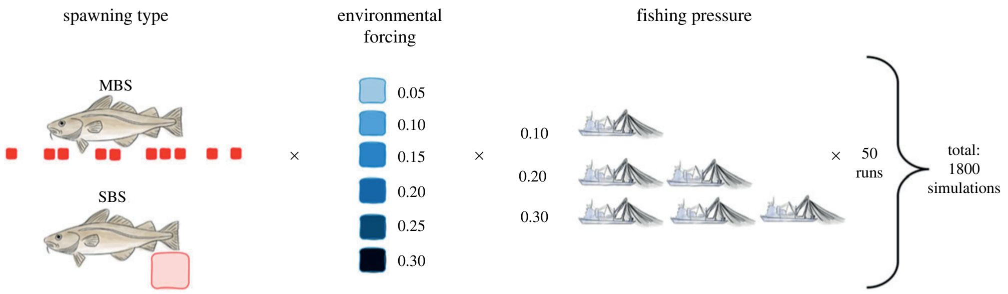


Figure 1. Schematic demonstration of the study's simulation design. Fish populations consisted of individuals with one spawning type: MBS or SBS. While fish with the former strategy shed their eggs among multiple batches within each spawning season, the fish of the later strategy deployed the same number of eggs in one spawning event. We performed 50 replica simulations of every population exposed to one of six environmental forcing rates and one of three fishing pressure rates, linked in a multi-factorial manner.

Table 1. Descriptions of equations and sources underpinning the empirically derived variables of the individual-based mechanistic model.

description	equation	source
length (L)–weight (W) relationship	$W_t = 3.52 \cdot 10^{-6} \cdot L_t^{3.19}$	Kuparinen *et al.* [22]
age-specific fecundity (N_{eggs})	$N_{\text{eggs}} = \left(\frac{0.48 \cdot (W_t + 0.37)}{1.45} + 0.12\right) \cdot 10^{-6}$	Hutchings [28]
batch number (N_{batches})	$N_{\text{batches}} = \frac{21.156}{1 + \exp((55.014 - L_{\text{fork}(t)})/10.141)}$	derived in Hočevar *et al.* [21] based on empirical data from Roney *et al.* [29]
multiple-batch spawning costs ($Costs_{MBS}$)	$Costs_{MBS} = \sum_{\text{batch}=1}^{N_{\text{batches}}} 1 - 0.00523 \cdot (\text{batch} - 1)$	derived in Hočevar *et al.* [21] based on empirical data from Roney *et al.* [29]
size-based fishing *selectivity* (*L(t)* is the length of an individual at the time of fishing)	$selectivity = \frac{\exp(-12.5 + 0.25 \cdot L(t))}{1 + \exp(-12.5 + 0.25 \cdot L(t))}$	Kuparinen & Hutchings [30]

survival probability to each shed egg batch. On the other hand, the model assumes that every female that is not a MBS, but a *total* or *single-batch spawner* (SBS), releases all eggs annually in a single spawning event and suffers no associated spawning costs.

(c) Environmental forcing

We introduced the environmentally induced increase in mortality rate, hereafter environmental forcing, into the model through a batch mortality rate. We tested six rates of environmental forcing (0.05, 0.10, 0.15, 0.20, 0.25 and 0.30). The interval captured the most sustainably endurable environmental mortality (higher tested rates resulted in frequent collapses among populations). To simplify the study design, we considered two contrasting scenarios where an entire egg batch dies or survives. The outcome is uniquely drawn randomly each time for each shed batch, imitating the risk-spreading effect of shedding multiple batches. The environmental forcing rates are applied to each batch individually along with the related spawning costs as a success probability in a Bernoulli trial every time a MBS produces an egg batch. Similarly, the environmental forcing is introduced to SBS in such a way that the survival of a single produced batch is drawn randomly based on a Bernoulli trial and determines whether the batch survives or dies.

(d) Recruitment

The final number of individuals that a MBS or a SBS recruits to the population is determined by applying the juvenile survival probability, as the probability of survival from egg to recruit, 1.13×10^{-6} [28] in a Bernoulli trial to the sum of all eggs of every batch for the first 3 years of individual's life. Once the offspring reaches 3 years of age, they experience an annual instantaneous rate of natural mortality (M) of 0.15, which at maturity increases by 0.1 due to reproductive costs. The lifespan maximum of every individual cannot exceed 25 years [22].

(e) Size-selective fishing

During the fishing season, every individual that is longer than the minimum size threshold of 45 cm can be fished, following the empirically parameterized sigmoid size-selective model (table 1). The model imitates the most used fishing gear in cod fisheries—the bottom trawls—which tend to exert stronger selection on larger sized individuals (electronic supplementary material, figure S1). We applied the product of a pre-determined instantaneous fishing mortality rate, F (year^{-1}), ($F = 0.1$, 0.2 and 0.3) and an individual-based selectivity as the survival probability in a Bernoulli trial [30] to determine whether the individual is captured by the trawl or not. We discontinued trawling as soon as the population biomass dropped to 15% of its initial pre-fishing capacity.

(f) Simulation design and analyses

We investigated the response of spawning dynamics to fishing pressure by running the model under separate scenarios and analysing their outputs. As a result, 50 replicates for each of the 36 scenarios were simulated (figure 1). Each population, representing one of the two spawning strategies, was exposed to six environmental forcing rates (0.05, 0.10, 0.15, 0.20, 0.25 and 0.30) and three fishing mortality rates (0.1, 0.2 and 0.3) in

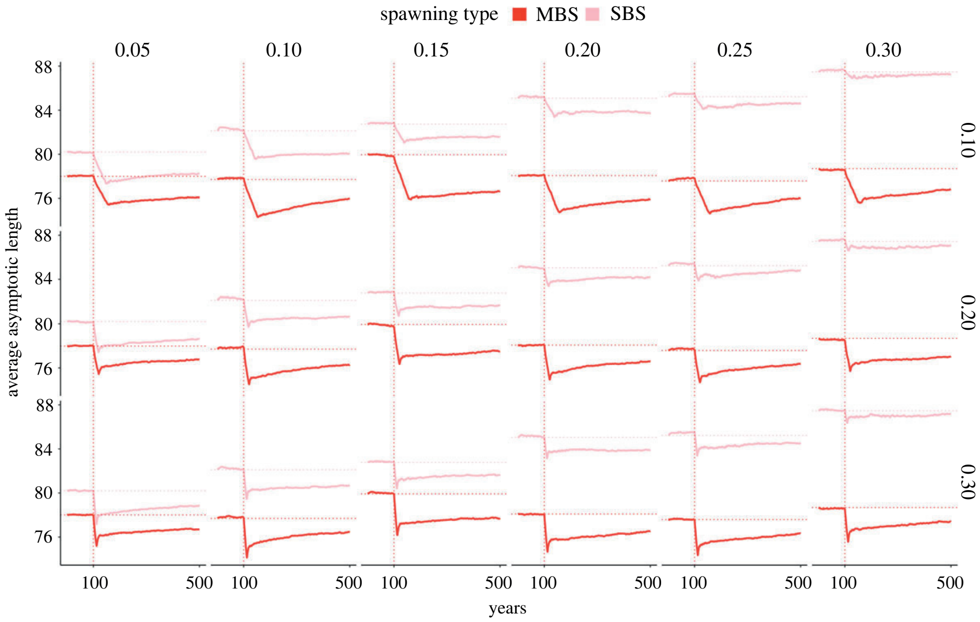


Figure 2. Selection in asymptotic length (L_∞) of Atlantic cod under environmental forcing rates and fisheries-induced pressure. The average asymptotic lengths of the populations with MBS (red coloured line) and SBS (light pink coloured line) strategy are plotted against time. The panels indicate row-wise the fishing effort and column-wise the environmental forcing, applied to the populations throughout the entire simulation. The vertical dashed line illustrates the onset of fishing that was ceased as soon as the population dropped to 15% of its initial biomass and horizontal dashed lines depict the value of L_∞ before the fishing started.

a full factorial manner. Instantaneous fishing mortalities greater than 0.30 resulted in increasingly rapid population depletions, limiting our resolution of the ongoing populational dynamics during fishing, and were thus not investigated.

We allowed the populations, of which the initial size was 2000 individuals, to adapt to the simulated environmental forcing scenarios for 5000 years before starting the *in silico* experiment. Then, each of the pre-adapted 36 scenarios was simulated for 500 years, wherein the first 100 years, the populations lived under the corresponding environmental forcing, in the following 300 years (or until the biomass dropped to 15% of its initial condition) under environmental forcing and added fishing pressure, and in the last 100 years (or the remaining years until year 500) again solely under environmental forcing. During each simulated time step, we recorded population biomass and abundance, catch biomass and individuals' asymptotic maximum length L_∞, maturation age and size. We also followed the across-generational fitness, derived as the geometric mean or the *n*th root of the product of average realized lifetime reproductive generational output [33].

Simulations and data analyses were conducted in the open-source statistical programming language R [34]. We used a collection of R packages 'tidyverse' for data visualization [35].

3. Results

(a) Evolution of life-history traits under natural and fishing selection

The evolution of L_∞ distinctively differed between the two spawning strategies (figure 2). In both cases, L_∞ began declining immediately after the start of size-selective fishing, illustrating the selective direction of fishing pressure towards smaller body sizes. The proportional reduction in L_∞ differed between the multiple-batch and single-batch spawning strategists. A population comprised MBS exhibited more substantial fisheries-induced selection towards smaller body sizes, which dropped in general by approximately 3% and had a steeper negative slope with increasing realized fishing mortality rate, compared to a population comprised SBS. This led to MBS being on average 1.36 cm smaller than SBS under the same fishing mortality rates.

Single-batch spawning populations showed a tendency in selection for bigger body size as the environmental perturbations increased while L_∞ of MBS showed no such trend and remained within a narrow range despite changes in environmental forcing. Fishing ceased under all simulated scenarios when populations declined to 15% of the initial biomass. Shortly after the cessation of fishing, the declining trend in L_∞ of both spawning strategies ceased and thereafter began a slow recovery process, which was not fully reached even after more than 300 years long moratorium or no-fishing period. Although SBS exhibited stronger recovery potential in L_∞ than MBS (figure 2), they also exhibited higher sensitivity to environmentally induced perturbations, evidenced by a prolonged lag in its post-fishing recovery in biomass to carrying capacity (electronic supplementary material, figure S2). The greater the environmental perturbations, the longer the lag time to rebuild the pre-fishing biomass. The multiple-batch spawning population showed no such sensitivity to environmental perturbations.

(b) Fitness shaped by fishing

The type of spawning strategy and exposure to environmental forcing and fishing pressure influenced the across-generational fitness (figure 3). The fitness of both strategists declined by up to 75% during intense harvest and recovered

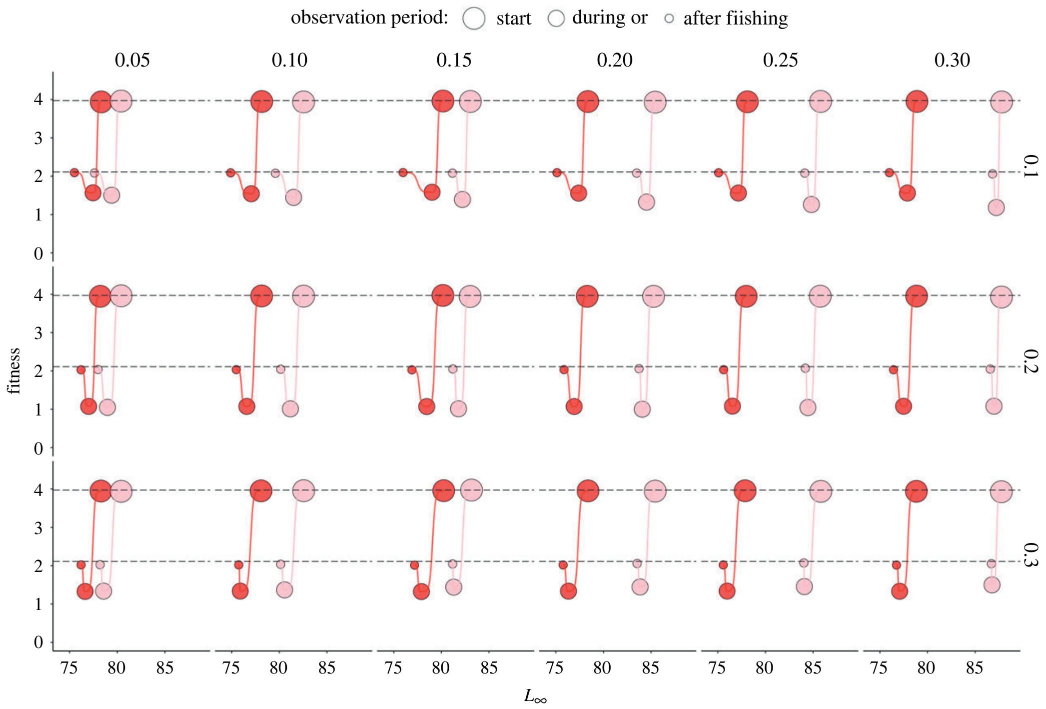


Figure 3. Fitness before, during and after fishing period calculated as a geometric mean of realized reproductive output across cohorts living in that period. Fitness is plotted against average asymptotic length (L_∞) and faceted according to fishing pressure (row-wise) and environmental forcing (column-wise). The red and pink points represent the mean values of 50 replica simulations for each scenario combination of multiple (MBS) and single (SBS) batch spawning strategists, respectively. The black dashed lines indicate the highest fitness value before (3.97) and after (2.10) fishing period.

after fishing was ceased to 53% of the pre-fishing value (for a closer view of initial fitness: electronic supplementary material, figure S3A). The recovery rate was the lowest under the strongest fishing pressure (recovered to 51% of pre-fishing value).

Multiple-batch spawning populations had higher fitness than single-batch spawning populations during fishing when fishing intensity was 0.10 and 0.20, and lower fitness when fishing intensity was 0.30 (for a closer view: electronic supplementary material, figure S3B). Differences in fitness between the two strategies increased with increasing environmental forcing, as multiple-batch spawning populations were not sensitive to environmental change, while single-batch spawning populations were. Post-fishing fitness of multiple-batch spawning populations was higher than that of the single-batch spawning populations only after recovering from the least intensive fishing period (0.10), while single-batch spawning population showed better recovery in fitness after more intensive fishing periods (0.20, 0.30) (for a closer view: electronic supplementary material, figure S3C). Overall, compared to populations comprised SBS, multiple-batch spawning populations experienced a lower proportion of failed spawning seasons before, during and after fishing. The proportion of failed events among MBS increased from approximately 0.4 before fishing to approximately 0.6 during fishing and did not change with increasing environmental mortality, while fishing mortality had an effect (electronic supplementary material, figure S4).

We did not observe any consistent trend in the average realized individual fitness, calculated as the abundance of recruits divided by the abundance of mature adults, except that the post-fishing realized individual fitness of MBS was always lower than before and during fishing (maximum difference for MBS: 0.026 and for SBS: 0.015) (electronic supplementary material, figure S5). We also found that the interannual variance in individual fitness increased with fishing intensity during fishing and was lower among MBS (electronic supplementary material, figure S6).

(c) Length of fishing period and catch biomass

Recovery in recruitment abundance began once population biomass dropped below 15% of initial biomass and fishing activities ceased. Under the lowest fishing pressure, the multiple-batch spawning strategy enabled the population to endure size-selective fishing for 9 to 46 years longer than SBS (median length of the fishing period at 0.10 for MBS 51 years and for SBS 35 years). However, under fishing pressure of 0.20 and 0.30, the resilience of the multiple-batch strategy to fishing mortality decreased or even vanished, reducing the difference between MBS and SBS to 2–8 years and 0–4 years, respectively (percentage comparison in the electronic supplementary material, figure S7).

Multiple-batch spawning strategy kept the biomass of recruits consistently higher compared to SBS, and the difference between the two strategies in their recruitment abundance increased with increased environmental forcing, from the lowest difference of 8% under the least fatal environment to the biggest difference of 36% under most fatal environment (electronic supplementary material, figure S7). The advantage under most fatal environmental conditions

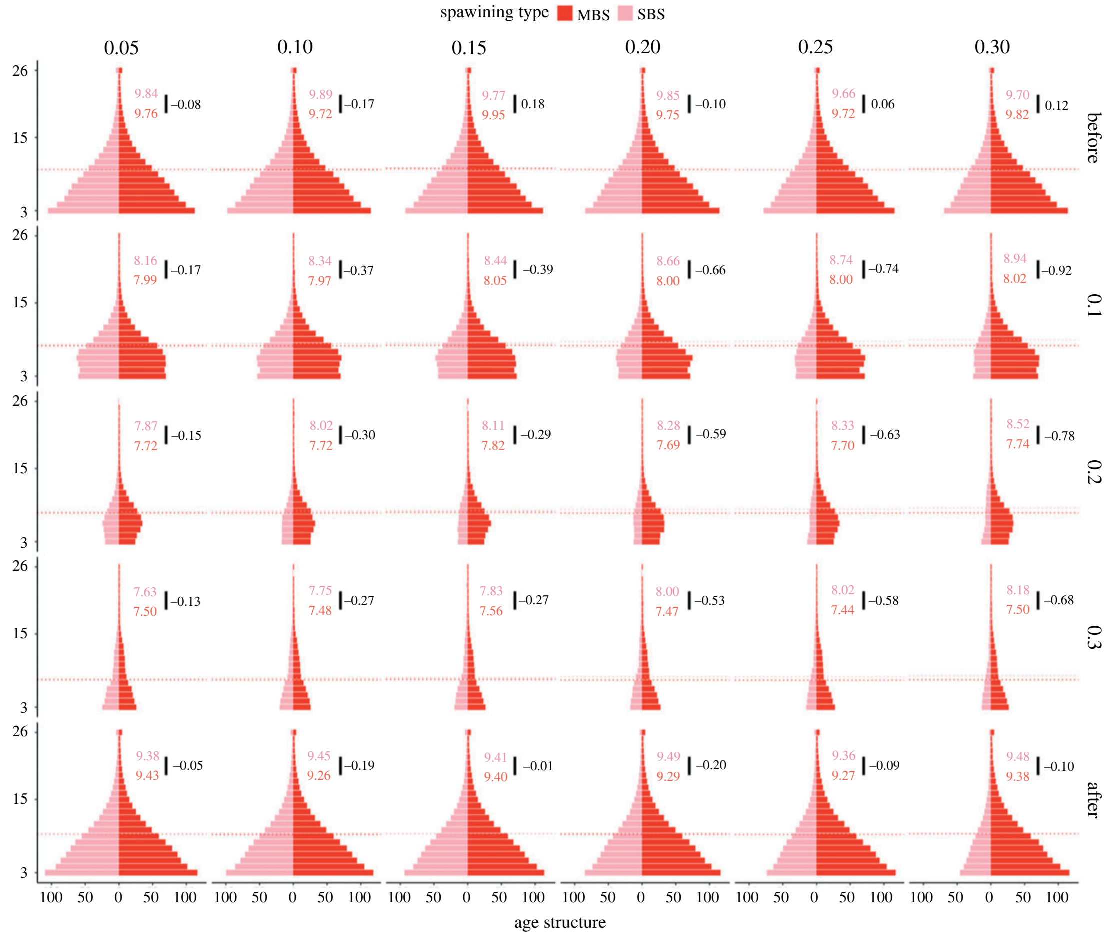


Figure 4. The age structure of a multiple (MBS; red coloured) and single (SBS; pink coloured) batch spawning cod population. Row-wise the panels depict the demographical structure of cod stock before fishing, during increasing fishing pressure and after fishing. The changes in the populational age structure can be observed also among environmental forcing rates (column-wise). The horizontal dashed lines indicate the average age of each population pyramid and numbers show the difference in the average age at maturation between the strategies.

decreased with greater fishing pressure, to 35% and 32% under 0.20 and 0.30 of fishing pressure, respectively, and consequently, fishing had to be terminated sooner.

Catch biomass decreased with increasing environmental mortality rates, and the decrease was steeper among SBS compared to MBS. By contrast, increasing fishing pressure resulted in higher annual catch biomass, with its trend steeper and higher among multiple-batch than single-batch spawning cod. The total catch biomass of both strategists decreased with higher fishing intensity (electronic supplementary material, figure S8).

(d) Age structure

To determine whether spawning strategy affects the overall age distribution of cod stocks, we portrayed the pre-fishing, during-fishing and post-fishing cohort abundance in populational pyramids of corresponding years (figure 4). In the pre-fishing period, younger classes dominated both strategies, reflecting a fast-growing pace of populations. Introduced fishing changed the distribution of age classes of cod populations considerably by shifting the shape of the population pyramid from expansive towards constrictive. In particular, under the fishing mortalities of 0.1 and 0.2, the populational pyramid narrowed at the bottom, illustrating a decreasing influx of recruits. Younger classes reclaimed the dominance under the highest fishing intensity 0.3, but the shape was not as triangular as in the pre-fishing time. In terms of abundance, the differences between the two strategies became more pronounced with increased environmental forcing, as the multiple-batch spawning strategy showed higher reproductive potential.

During the rebuilding phase, both strategies recovered their shape of populational age structure to that of the pre-fishing status, but SBS did not manage to recover to the pre-fishing abundance. The post-fishing populational pyramids remained slimmer under scenarios of greater environmental forcing. MBS had an overall higher mean age compared to SBS (13.44 years and 13.25 years, respectively), but as the fishing intensity increased, the difference between the two strategies decreased with an advantage accruing to SBS, who had higher mean age under the greatest fishing pressure (0.3), showing lower sensitivity to fishing than MBS as their average age decreased more rapidly and intensively (MBS: 26% or 14.22–10.66 and SBS 20% or 14.03–11.23). On the other hand, the mean populational age of MBS remained unaffected with increasing environmental forcing (decrease in the mean age of 0.08%), while SBS showed higher sensitivity and decreased the mean age with increasing environmental forcing by 3.25%.

Age at maturity decreased with the intensity of size-selective fishing in both strategies and was not able to fully recover under the moratorium. The tendency towards later maturation increased with the environmental mortality rate only in single-batch spawning populations (figure 4).

4. Discussion

This empirically and theoretically motivated study provides a compelling perspective on how under a strong fisheries-induced selection the fitness advantage of a risk-spreading strategy can counterintuitively turn into a disadvantage. We find that reproductive strategy, in light of interactions between environmental variability and fishing mortality, can influence selection on life-history (figure 2) and fitness dynamics (figure 3). Our key finding is that while the multiple-batch spawning strategy increases the across-generational fitness under the natural selection by reducing the variance in fitness, the size-selective fisheries diminish the risk-spreading benefits of the strategy by selecting against larger sized females, that is, the phenotype that can shed the highest number of batches and thus provides the greatest risk-spreading effect. We applied several rates of natural and fishing-induced selection on simulated Atlantic cod populations with and without a multiple-batch spawning strategy. The discrete full factorial approach allowed us to distinguish the eco-evolutionary benefits of batch spawning from other life-history traits and to evaluate the extent to which this risk-spreading strategy contributes to the fitness of fished populations. Our findings support research highlighting the value that life-history diversity provides for stock productivity [36,37] (reviewed in [38]), while the individual-based modelling approach offers a novel perspective on the consequences of alternative fishing mortalities for individual fitness and population viability.

The asymptotic maximum body length during fishing rapidly decreased in our study, as we selectively started removing cod longer than 45 cm (figure 2). Given that the asymptotic length correlates with the size of maturation in our model, the fishing-induced change selected for earlier- and smaller-maturing individuals whether in the presence or absence of a multiple-batch spawning strategy. These findings are consistent with the life-history theory which predicts that size-selective fishing of larger individuals favours reduced age and size at maturation [39,40]. Life-history change in response to fishing was evident during and after fishing, having the effect of slowing subsequent population growth towards full recovery, which was never fully attained (additional tests showed no full recovery in the asymptotic length even after more than 4800 years of moratorium). The magnitude of the size difference between multiple- and single-batch spawning populations differed by 2 to 11 cm (figure 2). Given that weight (and thus fecundity) can be approximated as L^3 [41], these size differences can have a substantial influence on reproductive output [29]. For example, based on weight-specific fecundity [28], a cod of 78 cm (average size of MBS before fishing) lays about 100 000 eggs fewer than a cod of 80 cm (average size of SBS before fishing). Yet, our results suggest that because of the risk-spreading effect and the distribution of eggs across a different spatial and temporal scale, ensured by the multiple-batch spawning strategy, cod do not need to grow in size as they would in the absence of the multiple-batch strategy to gain the same long-term fitness as an individual adopting the single-batch strategy. This suggests that the risk-spreading strategy could offset a smaller body size.

Our results suggest that maximizing the number of batches over the batch size is a winning reproductive tactic for cod in a highly variable environment when there is no size-selective fishing, which is similar to the benefits of maximizing the number of eggs over the egg size to ensure higher reproductive output among some fish spawners [42]. We observed that the benefit of shedding multiple batches lies in the allocation of survival probability across the environmental spectrum, which provides stability and allows the population to persist despite natural environmental perturbations. The strategy can even act as a risk-spreading strategy that safeguards fitness against environmental fluctuations [43] or a bet-hedging strategy when the uncertainty and mortality driven by the environment are high and the across-generational fitness profits from low variation in reproductive success despite the associated costs of the strategy [21,33]. Diversification of eggs reduces variance in offspring survival probability [44] and increases survival of early life stages, by increasing the probability that some offspring will experience optimal feeding conditions and experience larval development in a favourable environmental setting (e.g. hydrological and climatic).

Yet, we observed that despite the risk-spreading benefits that batch spawning provides for cod, truncation in the size structure of harvested batch spawning stocks leads to stronger losses in fitness when fishing mortality is high. These findings are consistent with studies that find the selective forces of fisheries to be very different if not the opposite of natural and have the potential to surpass natural selection in some harvested populations [45,46]. We found that the more intense the size-selective fishing, the sooner the fish matured and the lower their populational fitness was after fishing (figure 2). This outcome could be due to the evolutionary downsizing of body size. Fishing tends to truncate the size structure in harvested population, resulting in a higher proportion of adults of smaller size, producing a lower number of batches with a lower number of eggs [38,47–50].

Nonetheless, it is important to stress that our model includes several assumptions. Irrefutably these pre-set assumptions provoke a question on the possibility of variation in the model outcomes if we modify their premise. For example, some of such assumptions are the size and age at maturity, which were not under a direct fishing selection. Size at maturity was derived from its correlation to the asymptotic length while age at maturity was additionally a subject to density-dependent processes. Therefore, the possibility of a change in the direction of the evolutionary regime shift within the two traits could be challenged. Age-at-length can be a plastic trait in some fish species [51,52]. A neural network analysis of a long-term dataset showed that changes in maturation trends in stocks such as Norwegian spring-spawning herring have varied before, during and after the stock collapse period, and the reason could have been in the ecological drivers related to changing stock abundance [51]. Nevertheless, the life history of a species can affect the populational response to fishing selection. As opposed to herring, which is a pelagic SBS, demersal stocks such as cod and cod-like species, sharing a similar spawning strategy, tend to display a stronger decline in age and size at maturity [49].

The outcome of our study is consistent with empirical observations of overfished cod stocks, cautioning that fishing can be a strong selective agent, especially in populations that undergo uninterrupted heavy exploitation for several decades and can lead to a fitness deficit of heavily overfished stocks [28,46,53]. While some commercially overexploited stocks such as North Sea cod stock are showing signs of recovery [54], stocks such are Northern cod stocks struggle to recover their biomasses [13]. The results presented here warn that the abundance recovery to pre-fishing condition does not necessarily mean that the across-generational fitness has recovered as well. In other words, ecological recovery does not guarantee evolutionary recovery. For example, we found that neither multiple-batch nor their hypothetic opposite, the single-batch spawning populations, were able to recover their long-term fitness to the pre-fishing value that they had as pristine or unfished populations (figure 3). Unlike Le Bris *et al.* [55], who did not observe that batch spawning would considerably impact the population resilience of cod, our results suggest that a multiple-batch spawning strategy could additionally slow the recovery, especially after highly intense fishing (electronic supplementary material, figure S3C). The contrasting conclusion between these two modelling studies may be due to the absence of an evolutionary component in the age- and size-structured population model [55]. While the size and time needed to rebuild the biomasses are comparable, our results underscore the value of incorporating an evolving trait within mechanistic models that follow the post-fishing recovery potential. This can prove especially critical if selective fishing changes the frequency of a heritable trait (asymptotic length) that is so closely related to populational reproductive success [56].

Implications of batch spawning strategy for the management of cod stocks could be in the reduced variance of fitness. The batch spawning strategy reduces the variance in across-generational fitness, rending cod genotypes less susceptible and more resilient to environmental change, which could benefit stock predictions and return more stable catches. Our results show that if fishing mortality is low the biomass of the multiple-batch spawning population is greater, enabling fishing to last longer and consequently, return higher and more stable total catch biomass, regardless of the environmental conditions (electronic supplementary material, figures S7 and S8). The relationship between the stock spawning biomass and the recruitment is considered the beacon of fisheries science, but the metric of stock reproductive potential needs a more objective measure that embraces the nonlinearity and asymmetry of this relationship [57–59].

The diversity of reproductive strategies is indeed high [2,10,11], which makes a partition of components that define the reproductive potential highly complex, species-specific and unfeasible to generalize. We mechanistically estimated the eco-evolutionary performance of a batch spawning strategy in light of fisheries-induced evolution and found it to be yet another mechanism sensitive to highly selective human-induced mortality. Risk-spreading benefits of batch spawning strategy underpin that truncating the age and size structure of stocks such as cod truncates their ability to reduce the variance in fitness and resist natural environmental change, resulting in impaired capacity to recover.

Data accessibility. Simulation code and input files for the eco-evolutionary model used in this manuscript are available on the Dryad Digital Repository [60].

Electronic supplementary material is available online [61].

Authors' contributions. S.H.: conceptualization, formal analysis, methodology, visualization, writing—original draft and writing—review and editing; J.A.H.: conceptualization, funding acquisition, methodology, supervision and writing—review and editing; A.K.: conceptualization, funding acquisition, methodology, supervision and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This study was funded by the Academy of Finland (project grant 317495 to A.K.), Natural Sciences and Engineering Research Council of Canada (NSERC; Discovery Grants to J.A.H. and A.K.) and the European Research Council (COMPLEX-FISH 770884 to A.K.).

Acknowledgements. This paper is dedicated to the memory of Jeffrey A. Hutchings, for his limitless pursuit of unveiling the enigmas of life histories. We are thankful to Tommi Perälä for helpful comments and discussion on this work. We thank two anonymous reviewers for their insightful remarks and efforts towards improving our manuscript. The present study reflects only the authors' view; the European Research Council is not responsible for any use that may be made of the information it contains.

References

1. Froese R, Pauly D. 2022 FishBase. See www.fishbase.org.
2. Hutchings JA. 2021 *A primer of life histories: ecology, evolution, and application*. New York, NY: Oxford University Press.
3. Roff D. 1992 *The evolution of life histories: theory and analysis*. New York, NY: Chapman and Hall.
4. Stearns SC. 1992 *The evolution of life histories*. New York, NY: Oxford University Press.
5. Wootton RJ, Smith C. 1984 *Reproductive biology of teleost fishes*. New York, NY: John Wiley & Sons.
6. Penton PM, Davoren GK, Montevecchi WA, Andrews DW. 2012 Beach and demersal spawning in capelin (*Mallotus villosus*) on the northeast Newfoundland coast: egg developmental rates and mortality. *Can. J. Zool.* **90**, 248–256. (doi:10.1139/Z11-132)
7. Olivar MP, Salat J, Palomera I. 2001 Comparative study of spatial distribution patterns of the early stages of anchovy and pilchard in the NW Mediterranean Sea. *Mar. Ecol. Prog. Ser.* **217**, 111–120. (doi:10.3354/meps217111)
8. Bourret SL, Caudill CC, Keefer ML. 2016 Diversity of juvenile Chinook salmon life history pathways. *Rev. Fish Biol. Fish.* **26**, 375–403. (doi:10.1007/s11160-016-9432-3)
9. Jørgensen C, Ernande B, Fiksen Ø, Dieckmann U. 2006 The logic of skipped spawning in fish. *Can. J. Fish. Aquat. Sci.* **63**, 200–211. (doi:10.1139/f05-210)
10. Mcbride RS, Somarakis S, Fitzhugh GR, Albert A, Yaragina NA, Wuenschel MJ, Alonso-Fernández A, Basilone G. 2015 Energy acquisition and allocation to egg production in relation to fish reproductive strategies. *Fish Fish.* **16**, 23–57. (doi:10.1111/faf.12043)
11. McEvoy LA, McEvoy J. 1992 Multiple spawning in several commercial fish species and its consequences for fisheries managment.pdf. *J. Fish Biol.* **41**, 125–136. (doi:10.1111/j.1095-8649.1992.tb03874.x)
12. Thurstan RH, Roberts CM. 2010 Ecological meltdown in the Firth of Clyde, Scotland: two centuries of change in a coastal marine ecosystem. *PLoS ONE* **5**, 7. (doi:10.1371/journal.pone.0011767)
13. Schijns R, Froese R, Hutchings JA, Pauly D. 2021 Five centuries of cod catches in Eastern Canada.

ICES J. Mar. Sci. **78**, 2675–2683. (doi:10.1093/icesjms/fsab153)

14. Enghoff IB, MacKenzie BR, Nielsen EE. 2007 The Danish fish fauna during the warm Atlantic period (ca. 7000–3900 BC): forerunner of future changes? *Fish. Res.* **87**, 167–180. (doi:10.1016/j.fishres.2007.03.004)
15. Hutchings JA. 2015 Thresholds for impaired species recovery. *Proc. R. Soc. B* **282**, 1809. (doi:10.1098/rspb.2015.0654)
16. Perälä T, Kuparinen A. 2017 Detection of Allee effects in marine fishes: analytical biases generated by data availability and model selection. *Proc. R. Soc. B* **284**, 20171284. (doi:10.1098/rspb.2017.1284)
17. Rose GA. 2007 *Cod: the ecological history of the North Atlantic fisheries*. St. John's, Canada: Breakwater Books.
18. Kjesbu OS, Solemdal P, Bratland P, Fonn M. 1996 Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **53**, 610–620. (doi:10.2493/jjspe.59.1683)
19. Roney NE, Oomen RA, Knutsen H, Olsen EM, Hutchings JA. 2018 Temporal variability in offspring quality and individual reproductive output in a broadcast-spawning marine fish. *ICES J. Mar. Sci.* **75**, 1353–1361. (doi:10.1093/icesjms/fsx232)
20. Hutchings JA, Rangeley RW. 2011 Correlates of recovery for Canadian Atlantic cod (*Gadus morhua*) 1. *Can. J. Zool.* **89**, 386–400. (doi:10.1139/Z11-022)
21. Hočevar S, Hutchings JA, Kuparinen A. 2021 Multiple-batch spawning as a bet-hedging strategy in highly stochastic environments: an exploratory analysis of Atlantic cod. *Evol. Appl.* **14**, 1980–1992. (doi:10.1111/eva.13251)
22. Kuparinen A, Hardie DC, Hutchings JA. 2012 Evolutionary and ecological feedbacks of the survival cost of reproduction. *Evol. Appl.* **5**, 245–255. (doi:10.1111/j.1752-4571.2011.00215.x)
23. Von Bertalanffy L. 1938 A quantitative theory of organic growth (inquiries on growth laws II). *Hum. Biol.* **10**, 181–213.
24. Charnov EL. 1993 *Life history invariants*. Oxford, UK: Oxford University Press.
25. Hardie DC, Hutchings JA. 2011 The ecology of Atlantic cod (*Gadus morhua*) in Canadian arctic lakes. *Arctic* **64**, 137–150. (doi:10.14430/arctic4095)
26. Mousseau TA, Roff DA. 1987 Natural selection and the heritability of fitness components. *Heredity* **59**, 181–197. (doi:10.1038/hdy.1987.113)
27. Jensen AL. 1997 Origin of relation between K and Linf and synthesis of relations among life history parameters. *Can. J. Fish. Aquat. Sci.* **54**, 987–989. (doi:10.1139/f97-007)
28. Hutchings JA. 2005 Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **62**, 824–832. (doi:10.1139/f05-081)
29. Roney NE, Oomen RA, Knutsen H, Olsen EM, Hutchings JA. 2018 Fine-scale population differences in Atlantic cod reproductive success. *Ecol. Evol.* **8**, 11 634–11 644. (doi:10.1002/ece3.4615)
30. Kuparinen A, Hutchings JA. 2012 Consequences of fisheries-induced evolution for population productivity and recovery potential. *Proc. R. Soc. B* **279**, 2571–2579. (doi:10.1098/rspb.2012.0120)
31. Gillespie JH. 1974 Natural selection for within-generation variance in offspring number. *Genetics* **76**, 601–606. (doi:10.1093/genetics/76.3.601)
32. Slatkin M. 1974 Hedging one's evolutionary bets. *Nature* **250**, 704–705. (doi:10.1038/250704b0)
33. Seger J, Brockmann H. 1987 What is bet-hedging? *Oxford Surveys Evol. Biol.* **4**, 182–211.
34. R Core Team. 2020 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See Https://www.R-project.org/.
35. Wickham H *et al.* 2019 Welcome to the tidyverse. *J. Open Source Softw.* **4**, 1686. (doi:10.21105/joss.01686)
36. Hixon MA, Johnson DW, Sogard SM. 2014 Structure in fishery populations. *ICES J. Mar. Sci.* **71**, 2171–2185. (doi:10.1093/icesjms/fst200)
37. Ohlberger J, Thackeray SJ, Winfield IJ, Maberly SC, Vøllestad LA. 2014 When phenology matters: age–size truncation alters population response to trophic mismatch. *Proc. R. Soc. B* **281**, 20140938. (doi:10.1098/rspb.2014.0938)
38. Secor DH. 2007 The year-class phenomenon and the storage effect in marine fishes. *J. Sea Res.* **57**, 91–103. (doi:10.1016/j.seares.2006.09.004)
39. Kuparinen A, Merilä J. 2007 Detecting and managing fisheries-induced evolution. *Trends Ecol. Evol.* **22**, 652–659. (doi:10.1016/j.tree.2007.08.011)
40. Law R, Grey DR. 1989 Evolution of yields from populations with age-specific cropping. *Evol. Ecol.* **3**, 343–359. (doi:10.1007/BF02285264)
41. Froese R. 2006 Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. *J. Appl. Ichthyol.* **22**, 241–253. (doi:10.1111/j.1439-0426.2006.00805.x)
42. Duarte CM, Alcaraz M. 1989 To produce many small or few large eggs: a size-independent reproductive tactic of fish. *Oecologia* **80**, 401–404. (doi:10.1007/BF00379043)
43. Simons AM. 2011 Modes of response to environmental change and the elusive empirical evidence for bet hedging. *Proc. R. Soc. B* **278**, 1601–1609. (doi:10.1098/rspb.2011.0176)
44. Childs DZ, Metcalf CJE, Rees M. 2010 Evolutionary bet-hedging in the real world: empirical evidence and challenges revealed by plants. *Proc. R. Soc. B* **277**, 3055–3064. (doi:10.1098/rspb.2010.0707)
45. Olsen EM, Moland E. 2011 Fitness landscape of Atlantic cod shaped by harvest selection and natural selection. *Evol. Ecol.* **25**, 695–710. (doi:10.1007/s10682-010-9427-9)
46. Swain DP, Sinclair AF, Hanson JM. 2007 Evolutionary response to size-selective mortality in an exploited fish population. *Proc. R. Soc. B* **274**, 1015–1022. (doi:10.1098/rspb.2006.0275)
47. Charbonneau JA, Keith DM, Hutchings JA. 2019 Trends in the size and age structure of marine fishes. *ICES J. Mar. Sci.* **76**, 938–945. (doi:10.1093/icesjms/fsy180)
48. Fitzhugh GR, Shertzer KW, Todd Kellison G, Wyanski DM. 2012 Review of size- and age-dependence in batch spawning: implications for stock assessment of fish species exhibiting indeterminate fecundity. *Fish. Bullet.* **110**, 413–425.
49. Hutchings JA, Baum JK. 2005 Measuring marine fish biodiversity: temporal changes in abundance, life history and demography. *Phil. Trans. R. Soc. B* **360**, 315–338. (doi:10.1098/rstb.2004.1586)
50. Stige LC, Yaragina NA, Langangen Ø, Bogstad B, Chr Stenseth N, Ottersen G. 2017 Effect of a fish stock's demographic structure on offspring survival and sensitivity to climate. *Proc. Natl Acad. Sci. USA* **114**, 1347–1352. (doi:10.1073/pnas.1621040114)
51. Engelhard GH, Heino M. 2004 Maturity changes in Norwegian spring-spawning herring Clupea harengus: compensatory or evolutionary responses? *Mar. Ecol. Prog. Ser.* **272**, 245–256. (doi:10.3354/meps272245)
52. De Roos AM, Boukal DS, Persson L. 2006 Evolutionary regime shifts in age and size at maturation of exploited fish stocks. *Proc. R. Soc. B* **273**, 1873–1880. (doi:10.1098/rspb.2006.3518)
53. Sguotti C, Otto SA, Frelat R, Langbehn TJ, Ryberg MP, Lindegren M, Durant JM, Chr. Stenseth N, Möllmann C. 2018 Catastrophic dynamics limit Atlantic cod recovery. *Proc. R. Soc. B* **286**, 20182877. (doi:10.1098/rspb.2018.2877)
54. Van Gemert R, Andersen KH. 2018 Challenges to fisheries advice and management due to stock recovery. *ICES J. Mar. Sci.* **75**, 1864–1870. (doi:10.1093/icesjms/fsy084)
55. Le Bris A, Pershing AJ, Hernandez CM, Mills KE, Sherwood GD. 2015 Modelling the effects of variation in reproductive traits on fish population resilience. *Mar. Sci.* **72**, 2590–2599. (doi:10.1093/icesjms/fsv154)
56. Lowerre-Barbieri S *et al.* 2017 Reproductive resilience: a paradigm shift in understanding spawner-recruit systems in exploited marine fish. *Fish Fish.* **18**, 285–312. (doi:10.1111/faf.12180)
57. Cooper WT, Barbieri LR, Murphy MD, Lowerre-Barbieri SK. 2013 Assessing stock reproductive potential in species with indeterminate fecundity: effects of age truncation and size-dependent reproductive timing. *Fish. Res.* **138**, 31–41. (doi:10.1016/j.fishres.2012.05.016)
58. Lowerre-Barbieri SK, Lowerre JM, Barbieri LR. 1998 Multiple spawning and the dynamics of fish populations: inferences from an individual-based simulation model. *Can. J. Fish. Aquat. Sci.* **55**, 2244–2254. (doi:10.1139/f98-105)
59. Marshall CT, Kjesbu OS, Yaragina NA, Solemdal P, Ulltang Ø. 1998 Is spawner biomass a sensitive measure of the reproductive and recruitment potential of Northeast Arctic cod? *Can. J. Fish. Aquat. Sci.* **55**, 1766–1783. (doi:10.1139/f98-062)
60. Hočevar S. 2022 Data from: Multiple-batch spawning: a risk spreading strategy disarmed by highly intensive size-selective fishing. Dryad DIgital Repository. (doi:10.5061/dryad.3j9kd51m2)
61. Hočevar S, Hutchings JA, Kuparinen A. 2022 Multiple-batch spawning: a risk-spreading strategy disarmed by highly intensive size-selective fishing rate. Figshare. (doi:10.6084/m9.figshare.c.6158611)

III

CONTRASTING TROPHIC ROLES OF ATLANTIC COD ECOTYPES IN A COASTAL PELAGIC FOOD WEB

by

Sara Hočevar, Tommi Perälä, Esben Olsen, Tone Falkenhaug
& Anna Kuparinen 2023

Manuscript.

Request a copy from the author.

IV

MARINE FOOD WEB PERSPECTIVE RO FISHERIES-INDUCED EVOLUTION

by

Sara Hočevar & Anna Kuparinen 2021

Evolutionary applications 14: 2378–2391.

DOI: 10.1111/eva.13259

Received: 9 November 2020 | Revised: 28 May 2021 | Accepted: 31 May 2021
DOI: 10.1111/eva.13259

SPECIAL ISSUE ARTICLE

Evolutionary Applications Open Access WILEY

Marine food web perspective to fisheries-induced evolution

Sara Hočevar | **Anna Kuparinen**

Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland

Correspondence
Sara Hočevar, Department of Biological and Environmental Science, University of Jyvskylä, Jyväskylä, Finland.
Email: sara.s.hocevar@jyu.fi

Funding information
Academy of Finland, Grant/Award Number: 317495; H2020 European Research Council, Grant/Award Number: 770884

Abstract

Fisheries exploitation can cause genetic changes in heritable traits of targeted stocks. The direction of selective pressure forced by harvest acts typically in reverse to natural selection and selects for explicit life histories, usually for younger and smaller spawners with deprived spawning potential. While the consequences that such selection might have on the population dynamics of a single species are well emphasized, we are just beginning to perceive the variety and severity of its propagating effects within the entire marine food webs and ecosystems. Here, we highlight the potential pathways in which fisheries-induced evolution, driven by size-selective fishing, might resonate through globally connected systems. We look at: (i) how a size truncation may induce shifts in ecological niches of harvested species, (ii) how a changed maturation schedule might affect the spawning potential and biomass flow, (iii) how changes in life histories can initiate trophic cascades, (iv) how the role of apex predators may be shifting and (v) whether fisheries-induced evolution could codrive species to depletion and biodiversity loss. Globally increasing effective fishing effort and the uncertain reversibility of eco-evolutionary change induced by fisheries necessitate further research, discussion and precautionary action considering the impacts of fisheries-induced evolution within marine food webs.

KEYWORDS
eco-evolutionary change, fisheries-induced evolution, life history, marine food webs, recovery potential, size-selective fishing, trophic cascades

1 | INTRODUCTION

Human exploitation of marine resources dates back to a prehistoric era. Excavations from Vanguard and Gorham's coastal caves by Gibraltar convey the appetite of our closest relatives, Neanderthals, whose diet included marine mammals, seafood and fish (Stringer et al., 2008). The exploitation intensity has extensively amplified since, and the human population became much reliant on environmental, economic and social benefits sustained by marine ecosystems (Konar et al., 2019). Increased fishing pressure has been ensuring livelihood to a quarter of a billion people and has contributed substantially to the global economy (Teh & Sumaila, 2013). Yet, applied fishing methods have not been sustainable. A majority of commercially fished stocks are considered overfished (FAO, 2020), and effective catch per unit of effort is decreasing despite that the size of the fishing fleet has doubled since the 1950s (Rousseau et al., 2019). The future could still be optimistic as the status of global fish stocks is not homogenous but rather considerably varying among fisheries and locations, demonstrating the influence of successful management strategies (Hilborn et al., 2021). The general trend implies that while poorly managed stocks continue to decline, the biomass of well-managed stocks is in stabilising or rebuilding state (Worm & Branch, 2012). Nevertheless, notwithstanding the intensity of management implementations, some restrictions have still proved insufficient by not accounting for the interlinking effects of biotic and abiotic environmental conditions, nor for the possibility of regime shits (Perälä et al., 2020; Shelton et al., 2006).

Long-term exposure to intense and selective fishing does not only alter the species composition and deplete their biomasses but can also incite a genetic change in heritable traits (Law, 2007). The selective evolution can be attributed to fisheries when heritable trait shifts of exploited fish stocks are a consequence of underlying genetic changes induced directly by fishing activity and thus not driven by the environmental nor trophic drivers (Kuparinen & Merilä, 2007). Although heavily harvested stocks often show trajectories towards 'live fast, die young', fishing can induce selection on different traits, depending on fishing strategy and gear. Phenotypic plasticity (Kuparinen & Merilä, 2007), genetic swamping (Pukk et al., 2013) and demographic effects, such as genetic drift (Kuparinen & Hutchings, 2017), can also trigger similar trajectories as fisheries-induced evolution (FIE), making FIE difficult to recognize (Heino & Dieckmann, 2009; Laugen et al., 2014). Moreover, the genetic architecture of a trait exposed to fishing mortality can also affect the extent of eco-evolutionary changes in harvested species (Kuparinen & Hutchings, 2017).

In the last decades, the evidence on FIE has been presented and challenged several times (Andersen & Brander, 2009; Browman et al., 2008; Jørgensen et al., 2007; Kuparinen & Merilä, 2007; Pinsky et al., 2021), ever since the seminal study on Arcto-Norwegian cod, demonstrating the selective force of age-specific harvest (Law & Grey, 1989). Notwithstanding remaining debates and challenges, to this day, a mounting body of literature indicates that FIE is supported not only theoretically but also empirically (Alós et al., 2014; Jakobsdóttir et al., 2011; Uusi-Heikkilä et al., 2015; Young et al., 2020). However, while we are becoming more familiar with the consequences that FIE can have on population dynamics of a single species (Dunlop et al., 2015; Enberg et al., 2010; Hollins et al., 2018; Hutchings & Fraser, 2008; Kuparinen & Merilä, 2007), we are just beginning to grasp the array and intensity of its far-reaching effects on the dynamics of the entire marine food webs.

Human-mediated removal of selected individuals within a population can change the structure of a food web (e.g. Daskalov et al., 2007). The consequence of fishing can be seen as altered predation regimes which can cascade down the food web and result in eco-evolutionary changes at lower, nontargeted species (Perälä & Kuparinen, 2020; Wood et al., 2018). Given the FIE has the potential to alter biological traits of species or their life-history stages significantly, the induced changes could manifest in a modified ecological role of species under harvest, their trophic position and interactions (Audzijonyte et al., 2013). Moreover, since marine food webs are globally connected (Albouy et al., 2019), the generated eco-evolutionary changes in species traits within the food web may have the potential to widely propagate across the ecosystems and modify their functioning and, ultimately, services and nature's contribution to people (Díaz et al., 2018).

In this perspective, we look at the current status of scientific knowledge on the influence of FIE within marine food webs (Figure 1). Although only a minority of the findings that follow stems explicitly from studies that have succeeded to detect FIE, the perceived mechanisms are alike and, therefore, instructive to each other (Hutchings & Kuparinen, 2021). Fishing impacts that deprive population genetic diversity or induce a direct demographic truncation (Kuparinen et al., 2016) by size-selective biomass removal can be ecologically analogous to evolutionary shifts towards smaller body size. Bearing that in mind, we briefly explore five pathways through which FIE, driven by size-selective fishing, might influence the intrinsic structure and functioning of marine food webs. We highlight (i) how FIE in physiological, behavioural and life-history traits might shift the ecological niche of harvested species, (ii) whether altered maturation schedule and stock productivity could impact biomass flow, (ii) how modified life histories can trigger trophic cascades and (iv) how the declining body size of apex predators may modify their functional role. Finally, we look at (v) the weakened recovery potential of depleted stocks and how it may accelerate biodiversity loss.

2 | BODY SIZE AND SHIFTING ECOLOGICAL NICHE

Nonrandom fishing exploitation can exert a selective pressure and induce evolutionary changes in physiological, behavioural and life-history traits of fished stocks (Diaz Pauli & Sih, 2017; Jørgensen et al., 2007; Kuparinen & Festa-Bianchet, 2017; Olsen et al., 2004; Uusi-Heikkilä et al., 2015). The most common driver of FIE is a long-term size-selective harvest under which the population endures altered rate, probability and timing of fishing mortality. Although this fishing type has been predominantly studied, FIE does not require fishing to be necessary size selective (Biro & Post, 2008). Size-regulated management applications in commercially harvested stocks and observed life-history changes that are measurable make size-selective driver of FIE simpler to explore. For example, the costs of size-selecting harvest are maximized short-term benefits, which can be seen in selection for slower or faster growth rates, or truncated age and size distribution (Hsieh et al., 2006; Jørgensen et al., 2009; Kindsvater & Palkovacs, 2017). Fishing season, location, gear limits or minimum landing sizes expose individuals that fall under these fishing bounds to fishing mortality, which generally exceeds natural mortality and has the opposite trend; the vulnerability to fishing increases with the body size of an individual (Hansen et al., 2011).

Body size is a central biological trait that correlates strongly to several life-history and behavioural traits (e.g. Walsh et al., 2006) and portrays the underlying characteristics of food webs (Brose et al., 2006; Trebilco et al., 2013; Woodward et al., 2005). The size continuum, where larger individuals eat smaller ones, is typical of marine food webs. The diet portfolio (i.e. number of available prey

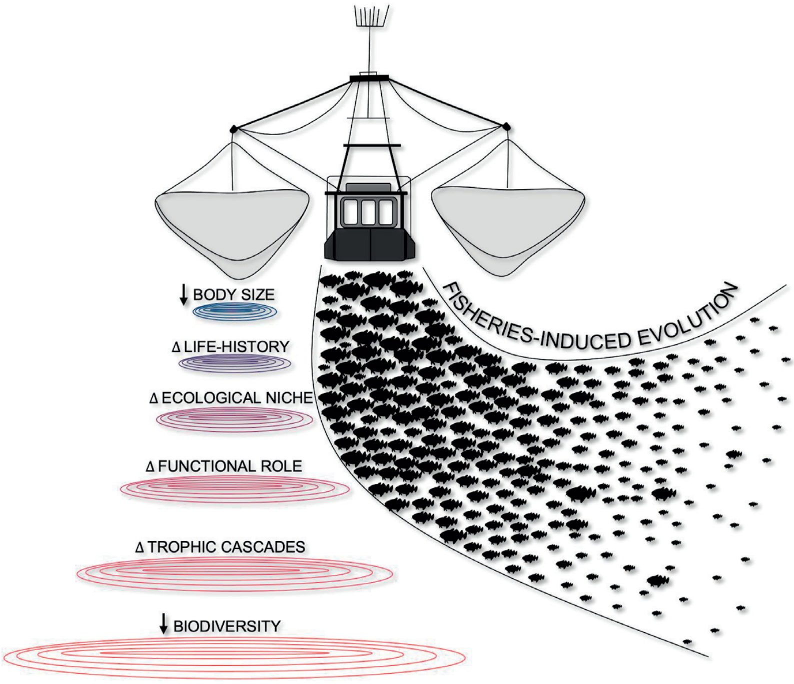


FIGURE 1 Fisheries-induced evolution resonating through different levels of biological organization within the marine food web. Starting with changes in body size and life-history traits at the individual level, moving to altered ecological and functional role at species level, to trophic cascades and biodiversity loss at the community level. The illustration is a simplified summary of the main mechanisms discussed in this perspective.

taxa) of marine species is closely size-related and can become more diverse with increasing body size of consumers (Nordström et al., 2015). As the diet expands, the species becomes more generalist by preying upon a broader range of prey species, allowing it to be disproportionally less dependent on a single prey species. While the extent of the influence that size has on the diet composition differs among fishes (Barbini et al., 2018; Schafer et al., 2002), the general trends show a positive correlation between body size and trophic niche width. Thus, as the fisheries select against large adult body size, the dietary range of harvested species may become narrower and its risk-spreading effect less significant. This could reduce the resilience of harvested species to prey fluctuations or to increased intraspecific competition for resources (Jacobson et al., 2018). Simultaneously, fisheries-induced changes in the size distribution could reshuffle predator–prey interactions or decrease the number of feeding links, and thus narrow the available range for diet switching among alternative prey species. Loss of feeding links could result in an impoverished trophic diversity (measured as the number of species or life-history stages at different trophic levels) and ecosystem productivity (Poisot et al., 2013).

A small size truncation can significantly expose harvested species to a greater number of potential predators and considerably increase its natural mortality rate up to 50 per cent, while in other instances, predation rate can decline (Audzijonyte et al., 2013a). The decline may be due to smaller individuals being predated upon less or due to a behavioural shift in predator avoidance, where in order to escape predator pressure, harvested populations with a reduced size structure relocate to a safer areas or refugia (Audzijonyte, Kuparinen, & Fulton, 2013). The process could be reversely compared with ontogenetic shifts in movements and habitat use (Reis-Filho et al., 2019) where younger and smaller individuals tend to cluster in less exposed areas with milder competition for space and resources, resulting in a lower success rate of predator attacks (Van De Wolfshaar et al., 2006).

Shifts in spatial distribution may also occur due to plastic or evolutionary changes in behavioural traits of harvested stocks (Diaz Pauli & Sih, 2017). Depending on the type of fisheries and fishing gear (i.e. passive such as longlines or active such as trawling), fisheries can promote a certain type of behaviour (i.e. shy or bold) (Arlinghaus et al., 2017; Diaz Pauli & Heino, 2014; Diaz Pauli & Sih, 2017; Kuparinen et al., 2009; Uusi-Heikkilä et al., 2008). Because these behavioural traits tend to be at least phenotypically correlated with body size, bolder individuals could be inevitably selected against more frequently, irrespective of fishing gear (Biro & Post, 2008). Fast-growing fish that tend to be more active or bolder have higher metabolic demands and need to spend more time on foraging, which increases their vulnerability to fishing. Some harvested stocks with plausible fisheries-induced changes in behavioural patterns can be seen to dive deeper (Handegard et al., 2003), to relocate their spawning grounds to habitats that are less accessible to fishing gears (Opdal & Jørgensen, 2015) or, as fishing gear selectivity experiment has shown (Özbilgin & Glass, 2004), to learn how to escape from fishing meshes (i.e. developmental plasticity).

Altered behavioural patterns and truncated size structure can influence interspecies interactions through which energy and resources are transferred between trophic levels (Trebilco et al., 2013). Body size tends to correlate with higher trophic position positively and with the abundance negatively, directing the energy flow from abundant, smaller body sized nodes (i.e. species or life-history stages of species) to less abundant, larger body sized nodes (Jacob et al., 2011; Nordström et al., 2015). These properties form the basis of the size spectrum models recently applied to analyse, for example, fisheries-induced changes in the ecosystems (Jennings & Blanchard, 2004). Size hierarchy in predator–prey interactions constitutes the food-web topology and improves its stability (Blanchard et al., 2011; Riede et al., 2011). Moreover, because body size correlates with life history, the predator–prey size ratio could be affected by fisheries-induced changes in growth rate, determining the time an individual spends in each size class.

3 | MATURATION SCHEDULE AND BIOMASS FLOW

The most typically observed aftermath of overexploiting harvesting practices is the tendency to select for earlier maturation age in fish (Hutchings, 2005; Olsen et al., 2004; Swain, 2011). Traits related to maturation timing can change faster than other life-history traits, which may contribute to their susceptibility to FIE (Audzijonyte et al., 2013b). Although the trend of maturing at earlier age tends to be associated with a decrease in stock abundance and a release of density-dependent processes that allow for a faster somatic growth rate (Roff, 2002), selection experiments have shown that fishing can also be a driving force of phenotypic and genotypic change in heavily exploited stocks (reviewed by Diaz Pauli & Heino, 2014). Intensive fishing mortality and selective removal of larger and often late-maturing individuals can change the allelic frequency of the inherited trait in a population. This can consequently increase the probability that genetic encoding, favoured by fishing, will be passed to the next generation. For example, 37 commercially harvested fish stocks mainly inhabiting marine food webs of temperate regions showed evolutionary changes in maturation schedule and probabilistic maturation reaction norms, both highly correlated with fishing intensity (Sharpe & Hendry, 2009).

The maturation schedule is often a proximate determinant of individual fitness, including age-related survival probability and reproductive output (Hutchings, 2005). Individual fitness can translate to a stock reproductive potential based on the combined effects of population abundance, sex ratio, age and size structure (Morgan & Brattey, 2005). Therefore, by selecting for earlier-maturing life histories, size-selective harvest can exert a directional pressure on an individual's energy allocation invested into reproductive and somatic growth and can, thereby, affect the stock productivity (Ohlberger et al., 2020). Paradoxically, a selection for life histories adapted to fishing exploitation can lead to depleted reproductive potential. Smaller female spawners tend to produce fewer and less viable eggs, which decreases an individual's lifetime fecundity, population's total egg production and stock's productivity (Birkeland & Dayton, 2005; Ohlberger et al., 2020; Walsh et al., 2006), resulting in a reduced yield and economic losses (Laugen et al., 2014). We might be underestimating the possible aftereffects of FIE on the biomass increase and variation within trophic networks (Jennings & Blanchard, 2004), given the influx of recruits is often disproportionately larger among bigger and older females compared with smaller and younger ones (Barneche et al., 2018).

Size diversity of fish life-history stages can notably influence the biomass flow and increase food-web stability (Bland et al., 2019). Indeterminate somatic growth is typical among fish, meaning that age and body size correlate closely (von Bertalanffy, 1938). Therefore, the consequences of fisheries-induced changes that select for earlier maturation at smaller body size have the potential to destabilize the food-web functioning by truncating the age or size structure of the harvested population (Table 1). Such food webs can endure higher vulnerability to environmental changes and intensify fishing mortality unless the fishing effort is relaxed (Brose et al., 2006; Kuparinen et al., 2016). A simulation study of a food-web model empirically parameterized for the Lake Constance ecosystem showed that by decreasing the body size ratio between the feeding links, fishing increases the biomass fluctuation of harvested species and co-existing species in the food web (Kuparinen et al., 2016). The magnitude of fluctuations became especially severe and displayed a longer-lasting effect when evolutionary changes due to selective removal of old and large individuals were heritable and considered within the food-web architecture. Although the harvested fish species have recovered substantially once the simulated fishing was ceased, the population's recovery had not reached its prefishing values when traits were heritable. These model predictions illustrate the indispensable impact of a selective harvest, inflicted directly on the population dynamics of harvested species (Anderson et al., 2008; Hsieh et al., 2006) and implicitly on the dynamics of the ecosystem (Kuparinen et al., 2016; Perälä & Kuparinen, 2020).

4 | ALTERED LIFE HISTORIES AND TROPHIC CASCADES

Stocks can be regulated by the availability of resources and the consumers' presence. Both restrains intertie the role of the stock within the food web, which makes it susceptible to trophic cascades. Intense harvest has a potential to change the strength of the trophic cascades on a short scale due to ecologically induced changes arising from the removal of fish biomass (Altieri et al., 2012; Mumby et al., 2006) or on a long scale due to evolutionary-induced life-history changes (Audzijonyte, Kuparinen, & Fulton, 2013; De Roos et al., 2006; Kuparinen et al., 2016; Perälä & Kuparinen, 2020; Start, 2018; Wood et al., 2018). By definition, trophic cascades entail the changes in abundance or biomass density of a functional group or population to propagate beyond one trophic link (Pace et al., 1999; Paine, 1966). An example can be the top-down cascades in the food web of Scotian Shelf that were induced by overfishing of Atlantic cod and other large predators (Scheffer et al., 2005). The absence of the top predators influenced the community structure and competitive interactions. Predation and competition release increased the abundance of small pelagic fishes and benthic invertebrates, which reduced the abundance of larger zooplankton species and reduced grazing pressure on phytoplankton, leading to lower levels

TABLE 1 Fisheries-induced evolution in marine food webs. Potential pathways through which fisheries-induced evolution may alter the structure and functioning of marine food webs

Potential driver of FIE	Individual consequence	Population consequences	Food-web consequence	Challenges
Higher mortality of a particular genotype	Compromised genetic diversity	Population may become less resilient or adaptable to environmental changes and regime shifts	The probability of missing links increases, and the food web may pass the tipping point of trophic cascades	What is the tipping point at which the fisheries-induced changes in intraspecies interactions translate to interspecies interactions? How can this tipping point be identified or predicted?
Higher fishing mortality of larger individuals	Changes in somatic growth rate, smaller body size, smaller differences in body size among life-history stages	Truncated size structure and size diversity of life histories can magnify the fluctuations in abundance of the fished population due to higher intraspecific competition for resources and more potential predators	The reduced body size ratio among existing feeding links can further decrease the food-web stability by increasing the biomass fluctuations among links	Can fisheries-induced changes in growth rate shape the growth rates of their feeding links and thus alter the functionality of marine food webs?
Higher fishing mortality of older individuals	Earlier maturation at smaller body size, higher maternal costs, reduced reproductive output and risk-spreading effect	Low recruitment biomass that is released during a shorter spawning window may result in more frequent mismatch occasions, and a weaker, longer and more uncertain population recovery potential	Strong fluctuations in the biomass of recruits could destabilize the trophic flow in the food web and reduce its buffering capacity to environmental variability	Could fisheries-induced changes in altered maturation schedule reduce the temporal and spatial synchrony in ecological efficiency of feeding links? To what extend could mismatch events affect the stability of marine food webs?
Higher fishing mortality of bolder individuals	Gear avoidance, timid individuals, decreased foraging efficiency, shorter spawning migrations, reduced parental care	Population with a prevalent proportion of timid behavioural type may have compromised metabolic rate and reproductive success	Timid individuals might connect to a lower number of trophic links and thus reduce food-web connectivity and robustness	How can FIE in traits that influence the metabolic rate impact the trophic efficiency of marine food webs?
Higher fishing mortality in the oldest life-history stages of apex predators	Vulnerability to predation, ontogenetic changes in diet and narrower diet portfolio	Increased natural mortality rate and altered functional role	With downsized life histories, the number of feeding links may decline along with prey switching and predator control and shift the control to species at lower trophic levels	Could marine food webs become more prone to extinction if the diet niche of apex predators narrows with downsized life-history stages?

of nutrients. Similar ecological cascading mechanisms, triggered by harvesting, have been reported worldwide, from simpler food webs in reef communities (Mumby et al., 2006), kelp forest (Tegner & Dayton, 2000) and saltmarsh ecosystems (Altieri et al., 2012), to complex ecosystems in the open ocean (Frank et al., 2005).

Ecological changes that cascade through the food webs can also generate an adaptive response in species that are not directly targeted by fishing. Re-balanced abundance and biomass open pathway for evolutionary changes arising in traits that are influenced by density-dependent processes. For instance, a modelling study tracking the evolution of a genotypic-based competition–defence trade-off showed that the eco-evolutionary response to fishing could cascade downward to nontargeted species (Wood et al., 2018). The two underlying mechanisms driving the cascades were feeding availability and predator vulnerability. The food web constituted of four trophic levels. As the harvest of top predators started, the food web showed typical top-down cascade: the abundance of top predators declined, leading to increase in secondary consumers, decrease in primary consumers and increase in producers. Simultaneously, the tracking of the competition–defence trade-off showed that the impact of FIE and its direction alternated among trophic levels in a corresponding manner alike to the ecological top-down cascade. This pattern highlights that fishing can generate ecological and evolutionary cascades just through the biomass removal due to changes in prey density and predation regime.

FIE in life-history traits of fished species may lead to trophic cascades as well. The maturation schedule is a strong contingent of reproductive success and population dynamics. This connection essentially provokes the assumption that depleted stocks with altered spawning potential and higher recruitment variability may make the food web more sensitive to top-down or bottom-up cascades. For example, the reduced disparity between the life-history stages of harvested species undergoing ontogenetic shifts could increase the potential for mismatch events (Cushing, 1990). Maturation at bigger body size in broadcast spawners is often positively related to the duration of spawning season and the number of spawning events (Kjesbu et al., 1996), which leads to greater chances of finding favourable conditions for larval survival (James et al., 2003). Therefore, a truncated size diversity of life-history stages may lower the likelihood of newly hatched larvae overlapping in time and space with the peak of its prey availability or quality. The consequences could be reduced recruitment success and increased temporal fluctuations in the abundance of harvested stocks (Hsieh et al., 2006; Siddon et al., 2013), which could feedback ecological cascades.

To quantify the impact that fisheries-induced changes in life-history evolution may have on the aquatic food webs, Perälä and Kuparinen (2020) extended the allometric trophic network and allowed two life-history traits of adult fished stocks to evolve with time. They simulated small and large size-selective fishing of perch in Lake Constance and tracked how the evolutionary changes in the asymptotic body size and reproductive costs develop within each of the five life-history stages (larvae, juveniles, and 2-year, 3-year and 4+ year adults). Findings showed that fishing type can influence the direction and the extent of evolutionary change in body size. Ecological and evolutionary changes driven by the large size-selective fishing generated stronger biomass changes within the perch life stages and within the food web compared with small size-selective fishing. Key mechanisms behind this were changes in metabolic rates and maintenance costs of harvested individuals along with their body size changes, as well as changes in the maintenance costs due to changes in the timing of maturity, that is the survival costs of reproduction (Bell, 1980). Therefore, populations exposed to large size-selective fishing had more truncated body size, which has contributed to the increased feeding rate of younger life stages and predatory pressure of their prey (including fish larvae).

Interestingly, the presence of evolution seems to have played an especially strong role for the ecological cascades in the food web under small size-selective fishing, where the ecological changes in biomasses of some functional groups would be hardly observable otherwise (Perälä & Kuparinen, 2020). This counterintuitive outcome could be an artefact of the model's assumptions and limitations. For example, the modelling approach has not fully emulated the mechanisms of a food web as perch was the only species susceptible to evolutionary changes, and the diet was not evolving along with body size, meaning that food-web feedbacks may be quite conservative. Findings emphasize that recognising the origin and predicting the outcomes of coupled eco-evolutionary cascades can be challenging.

Trophic cascades can emerge from a complex interaction of biological mechanisms and human-mediated drivers that can have amplifying or buffering effects. Multiple anthropogenic drivers can synergistically destabilize the system not just by the removal of feeding links but also by the introduction of new ones. For instance, the trophic cascades in the food web of the Black sea show ecological changes triggered by overfishing, eutrophication and the introduction of invasive species (Daskalov et al., 2007). The cascades generated by the overfishing of top predators propagated downwards by altering the predator–prey interactions, while the introduction of invasive ctenophore induced an upward cascade due to high predatory pressure on eggs and larvae of commercial stocks. Despite that trophic cascade can occur within the food webs independently of fishing exploitation, modelling and empirical evidence suggest that fishing at one or multiple levels can provoke or neutralize the motion of trophic cascades. The intensity of cascades can be highly context-dependent and can vary on a regional or local scale with environmental conditions and community structure (Pinkerton & Bradford-Grieve, 2014; Shears et al., 2008). While in some systems, fishing can be a limiting factor that triggers cascading effects in biomass or abundance directly through the community structure and functioning, in other instances, the induced fluctuations can be buffered through the fishing activity itself (Andersen & Pedersen, 2010).

5 | FADING APEX PREDATORS

Apex predators are species at the highest trophic level of their ecosystem. Due to their large body size, the adults do not tend to have natural predators, and thus are not regulated by top-down control but rather by prey-availability (i.e. bottom-up control) and self-regulating processes (Wallach et al., 2015). Populations of apex predators across ecosystems have been under substantial declines, pushing several to the verge of functional extinction or pass it (Pauly et al., 1998; Ripple et al., 2014). Despite their low densities, apex predators are essential in maintaining the ecosystem in a balanced structure and healthy state through predation (Estes et al., 2011). Given this control, the overfishing of their populations can quickly cascade down the food web and increase the biomass of their prey species, usually mesopredators, which often tend to be species of fisheries interest. For instance, overexploitation of large sharks along the northwest Atlantic coast has severely depleted shark populations and truncated their size structure with up to 17–47% decline in body lengths (Myers et al., 2007). This eased control over their mesopredatory elasmobranch prey, including cownose ray (*Rhinoptera bonasus*), which became exceptionally abundant (Figure 2). With increased ray population, the pressure for its prey, commercially harvested bay scallop (*Argopecten irradians*), increased, which has resulted in a collapse of scallop fishery (Myers et al., 2007).

While the diet of most fish species is gape-limited, as they tend to swallow a whole prey at once, apex predators can also prey upon bigger species (e.g. Lucifora et al., 2009). During their ontogenetic dietary shifts, apex predators can predate on all trophic levels (Navia et al., 2016). Size-related traits such as life histories, metabolic rate, diet, feeding and haunting behaviour, and habitat preferences constitute the functional role of apex predators that shape marine communities (Heithaus et al., 2008). Given their functional role within the food web, apex predators tend to exhibit high topological uniqueness (Navia et al., 2016), meaning that there are not many species of similar network position. Therefore, replacing their function effectively would be difficult (Prugh et al., 2009).

Losing apex predators from the food web is not a solitary risk. Their unique life histories also constitute trophic diversity. Although life histories might not always be directly interlinked to the trophic level, their loss can affect the energy and biomass flow from one trophic level to another (Bland et al., 2019). Shifting life histories could reduce not just phenotypic diversity but also functional diversity, and thus through altered food-web structure impact the productivity of the system (Poisot et al., 2013). Downsized size structure of apex predators may increase predation risk to their earlier life stages, as the probability of being predated by more species would increase if the time spent at the earlier life stage is longer. Buffering capacity of a food web can decline if the trophic diversity is reduced and may amplify the sensitivity of a food web to environmental variability (Kuparinen et al., 2019). Trophic levels provide a buffering effect that dampens biomass variations with progressing levels. Therefore, if size-selective fishing truncates life histories of apex predators, we might lose some of this protecting support that trophic and functional diversity ensure.

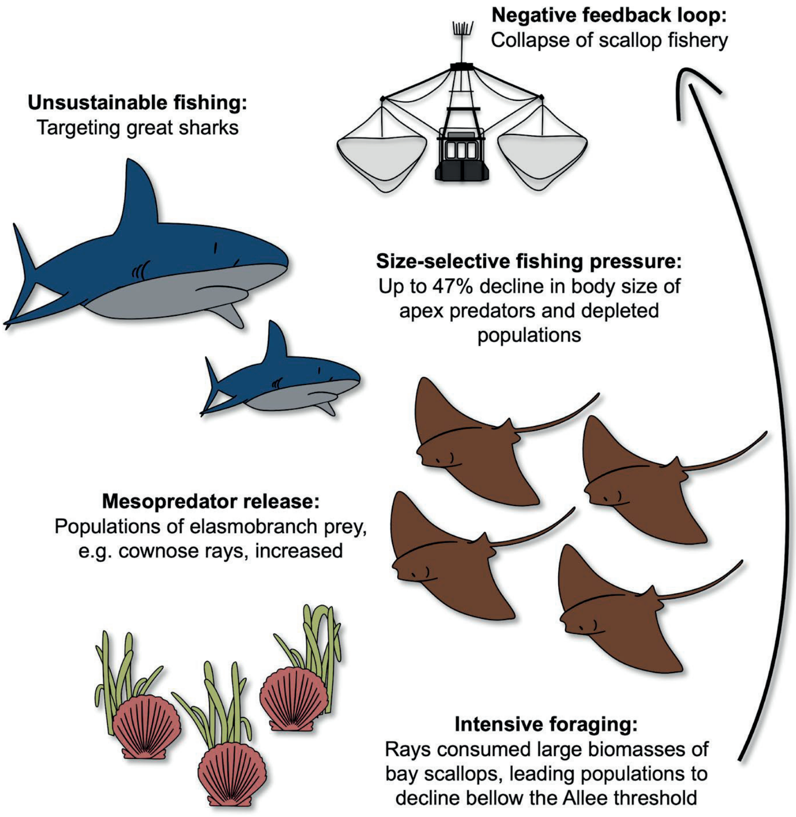


FIGURE 2 Example of cascading effects with a feedback loop generated by selective fishing of apex predators. Adopted based on Myers et al. (2007)

6 | RECOVERY POTENTIAL AND BIODIVERSITY DECLINES

Species life history underlines its population dynamics and influences its response to exploitation rates and extinction risk (Jennings et al., 1999; Jusufovski & Kuparinen, 2020; Rowe & Hutchings, 2003). Depending on the type of fishing selectivity, modelling studies point that the rate and time of recovery in an evolutionary change in a selected trait are slow and not necessarily certain (De Roos et al., 2006; Perälä & Kuparinen, 2020). FIE may contribute to a delayed population recovery, lead to a weaker recovery or prevent full recovery of the heavily harvested stock by driving it beyond its stabilization threshold (Hutchings, 2015). The iconic case is the Northwest Atlantic cod fishery, where the spawning biomass had been depleted beyond 94%, resulting in ecological collapse (Hutchings & Myers, 1994). The stock has yet not reached its prefishing size structure nor abundance despite reinforced moratorium and management mitigations (Brander, 2007; Hutchings & Kuparinen, 2020).

This case is critical as it points at the complexity of recognising the extent to which the FIE *per se* may have delayed the recovery (Figure 3) (Hutchings & Kuparinen, 2021; Pinsky et al., 2021). For instance, the increased natural mortality rates, environmental conditions, ongoing fishing activities and depensation effects have all influenced the lack of rebuilding (Shelton et al., 2006). Allee effect seems to have also been a significant contributor that has not just delayed or impaired the recovery period but has also greatly increased the uncertainty of recovery, as the population growth rate becomes lower and more variable at low abundance (Kuparinen et al., 2014). A meta-analysis of 153 depleted marine stocks also elucidates how unpredictable can the recovery be (Neubauer et al., 2013). When analysed as separate effects, the historic intensity and duration of exploitation can shorten the recovery period (Neubauer et al., 2013). This outcome was suggested to be the aftermath of plastic and evolutionary changes in maturation schedule that may have increased the population growth rate when a population is exposed to long-moderate or short-intensive fishing. When the historic intensity and duration of exploitation were analysed as the interaction, the impact on the rebuilding of population biomass was negative and had prolonged the recovery time. The findings of this meta-analysis are consistent with the modelling study from Lake Constance (Kuparinen et al., 2016), which showed that the rate or extent of recovery from eco-evolutionary changes induced by FIE is not as fast nor as efficient as it is the recovery from ecological changes. Signs of severe depletion and collapsed fisheries can be seen from different parts of the globe (Myers & Worm, 2005; Neubauer et al., 2013; Sadovy de Mitcheson et al., 2013), and so are the consequences of overexploitation that have reduced species abundance and diversity in these depleted systems (Byrnes et al., 2007; Daskalov et al., 2007; Poisot et al., 2013; Rochet & Benoît, 2012; Thurstan & Roberts, 2010).

The diversity of species is declining, and fish species of larger body sizes are at high risk of extinction (FAO, 2020; Olden et al., 2007). Fishing activity can be deemed one of the main external drivers for extinctions within marine ecosystems, whether owing to direct overfishing or indirect habitat loss and fragmentation. Harvesting predatory species at higher trophic levels can destabilize trophic diversity and biomass flow within the food webs (Essington et al., 2006; Rochet & Benoît, 2012) and thus accelerate biodiversity loss. Predators promote the diversity of their prey in multiple ways, including through the active selection of the most abundant prey or dominant competitor, through the territorial distribution, consumer density and feeding rate (Koen-Alonso & Yodzis, 2005; Ryabov et al., 2015). Selective fishing against larger body size can shift the trophic position of a predator, the size range of its prey, trophic efficiency, predation rate and density. Trophic generality (i.e. number of prey taxa in the diet) tends to positively correlate with body size, meaning that the number of species preyed upon by a predator can become lower if the predator's body size declines (Nordström et al., 2015). Moreover, reduced size diversity of life-history stages can also compromise the robustness of predator's diet due to narrower ontogenetic diet shifts, which may otherwise secure a buffering impact for predator–prey dynamics and food-web stability (Bland et al., 2019).

Beside trophic generality, trophic vulnerability (i.e. number of predator taxa) also tends to correlate with body size (Nordström et al., 2015). This correlation is negative and becomes especially relevant when the harvested species is a forage fish at the lower trophic level. Forage fish species tend to be well connected within the food web, and thus supporting the energy transfer from their resources to their predators. Therefore, fisheries-induced evolutionary and ecological changes in the distribution of their size or life-history stages can potentially impact the structure of a food web in two linear directions: through the altered upward or downward biomass flow. The robustness of a food web can also depend on the extent of trophic vulnerability of missing species. Some studies suggest that the extinction of the most vulnerable species that support many predator species tends to lead to the fastest collapse of the food web while the role of generality triggers less secondary extinctions (e.g. Jacob et al., 2011). Therefore, species (or life histories) that can decrease food-web stability by going missing are not necessary only large species at the highest trophic levels but also small, highly linked species at lower trophic levels (Jacob et al., 2011; Navia et al., 2016).

Intertwined changes in declining body size, shifting diet, survival probability, spatial distribution and behavioural changes induced by overfishing can considerably modify the ecological role of species, alter the trophic structure of communities and reduce the value of fisheries catches (Essington et al., 2006). Although theoretical and empirical studies show that the recovery ability of a stock experiencing eco-evolutionary changes due to overexploiting fishing practices can be substantially impaired and delayed (Eikeset et al., 2016; Hutchings & Kuparinen, 2020; Kuparinen et al., 2016; Kuparinen & Hutchings, 2012), these findings also indirectly suggest that a release of high fishing pressure holds the potential to rebuild the abundance of depleted species and to modify the food-web structure yet again (Bieg & McCann, 2020; Ellingsen et al., 2020; Fung et al., 2013).

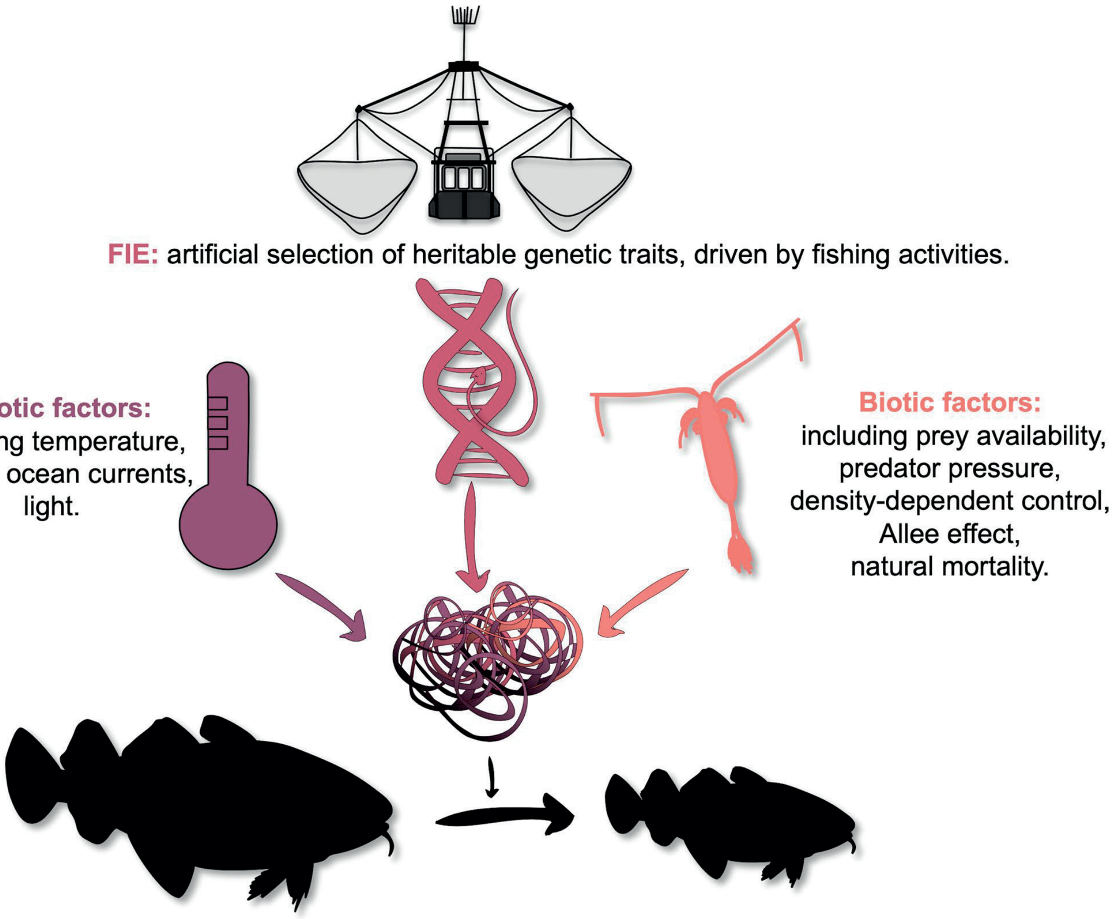


FIGURE 3 Schematic illustration depicting the complexity of identifying the extent of fisheries-induced evolution apart from biotic and abiotic drivers

7 | ANTHROPO-PREDATOR WITH CONCLUDING REMARKS

Fisheries have become an integral part of marine food webs and have, along with climate-induced changes, showed a considerable potential to modify the structure and function of ecosystems by gradually altering eco-evolutionary processes (Audzijonyte, Kuparinen, & Fulton, 2013; Kuparinen et al., 2016; Pauly et al., 1998; Perälä & Kuparinen, 2020; Wood et al., 2018). Emerging evidence from diverse marine systems attests how through fishing ventures, the role of humans in ecosystem structure and functioning has intensified beyond, and unlike, one of the apex predators. We selectively strip the food webs of the individuals in a fully grown, reproductively most successful life stages at three times higher rate than the most voracious predators (Darimont et al., 2015). Doing so, we provoke faster phenotypic changes that are at least somewhat induced by size-selective fishing (Audzijonyte, Kuparinen, Gorton, et al., 2013; Sharpe & Hendry, 2009).

Interestingly, although our trophic level within marine food webs is high, it does not exceed that of natural apex predators (Roopnarine, 2014). The reason could partially lie in the fishing-down-the-food-web strategy since due to depleted stocks at high trophic levels, fisheries shifts to stocks at lower trophic levels (Pauly et al., 1998). As we overfish authorized stocks, we extend our diet portfolio and move farther offshore, searching for new, yet unfished taxa (Pauly, 2020). The increased technological development has facilitated us to easily shift our ecological niche, quickly find prey, effectively avoid predators and, arguably, obviate top-down, bottom-up and density-dependent control (Darimont et al., 2015; Wallach et al., 2015). These features distinguish us from apex predators and revolve us into sort of an»Anthropo-predator«, as our impact on the ecosystems has notably amplified during Anthropocene, the epoch of human-induced changes (Moll et al., 2021; Waters et al., 2016).

The time calls for embracing the responsibility in our functional role. Evolutionary changes in the life history of harvested populations and direct fishing impacts increase the probability of regime shifts within the ecosystems, and these might be hard to reverse (Conversi et al., 2015). It is, therefore, crucial to act sooner than later. Action and research are not mutually exclusive; thus, we encourage applicative studies on the impacts that FIE can trigger within marine food webs. In the meantime, we need to speculate based on incomplete knowledge and mitigate the contemporary consequences to prevent borrowing fish from future generations.

ACKNOWLEDGMENTS

We are grateful to anonymous reviewers for valuable comments on the manuscript. This work was supported by the Academy of Finland (project grant 317495 to A.K.) and the European Research Council (COMPLEX-FISH 770884 to A.K.). The present study reflects only the authors' view; the European Research Council is not responsible for any use that may be made of the information it contains.

CONFLICT OF INTEREST

We have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no data sets were generated or analysed during the current study.

ORCID

Sara Hočevar https://orcid.org/0000-0002-1294-0927
Anna Kuparinen https://orcid.org/0000-0002-7807-8946

REFERENCES

Albouy, C., Archambault, P., Appeltans, W., Araújo, M. B., Beauchesne, D., Cazelles, K., Cirtwill, A. R., Fortin, M. J., Galiana, N., Leroux, S. J., Pellissier, L., Poisot, T., Stouffer, D. B., Wood, S. A., & Gravel, D. (2019). The marine fish food web is globally connected. *Nature Ecology and Evolution*, *3*(8), 1153–1161. https://doi.org/10.1038/s41559-019-0950-y

Alós, J., Palmer, M., Linde-Medina, M., & Arlinghaus, R. (2014). Consistent size-independent harvest selection on fish body shape in two recreationally exploited marine species. *Ecology and Evolution*, *4*(11), 2154–2164. https://doi.org/10.1002/ece3.1075

Altieri, A. H., Bertness, M. D., Coverdale, T. C., Herrmann, N. C., & Angelini, C. (2012). A trophic cascade triggers collapse of a salt-marsh ecosystem with intensive recreational fishing. *Ecology*, *93*(6), 1402–1410. https://doi.org/10.1890/11-1314.1

Andersen, K. H., & Brander, K. (2009). Expected rate of fisheries-induced evolution is slow. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(28), 11657–11660. https://doi.org/10.1073/pnas.0901690106

Andersen, K. H., & Pedersen, M. (2010). Damped trophic cascades driven by fishing in model marine ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1682), 795–802. https://doi.org/10.1098/rspb.2009.1512

Anderson, C. N. K., Hsieh, C., Sandin, S. A., Hewitt, R., Hollowed, A., Beddington, J., May, R. M., & Sugihara, G. (2008). Why fishing magnifies fluctuations in fish abundance. *Nature*, *452*(1), 835–839. https://doi.org/10.1038/nature06851

Arlinghaus, R., Laskowski, K. L., Alós, J., Klefoth, T., Monk, C. T., Nakayama, S., & Schröder, A. (2017). Passive gear-induced timidity syndrome in wild fish populations and its potential ecological and managerial implications. *Fish and Fisheries*, *18*(2), 360–373. https://doi.org/10.1111/faf.12176

Audzijonyte, A., Kuparinen, A., & Fulton, E. A. (2013). How fast is fisheries-induced evolution? Quantitative analysis of modelling and empirical studies. *Evolutionary Applications*, *6*(4), 585–595. https://doi.org/10.1111/eva.12044

Audzijonyte, A., Kuparinen, A., Gorton, R., & Fulton, E. A. (2013). Ecological consequences of body size decline in harvested fish species: Positive feedback loops in trophic interactions amplify human impact. *Biology Letters*, *9*(2), https://doi.org/10.1098/rsbl.2012.1103

Barbini, S. A., Sabadin, D. E., & Lucifora, L. O. (2018). Comparative analysis of feeding habits and dietary niche breadth in skates: the importance of body size, snout length, and depth. *Reviews in Fish Biology and Fisheries*, *28*(3), 625–636. https://doi.org/10.1007/s11160-018-9522-5

Barneche, D. R., Robertson, D. R., White, C. R., & Marshall, D. J. (2018). Fish reproductive-energy output increases disproportionately with body size. *Science*, *360*(May), 642–645. https://doi.org/10.1126/science.aao6868

Bell, G. (1980). The Costs of Reproduction and Their Consequences. *The American Naturalist*, *116*(1), 45–76. https://doi.org/10.1086/283611

Bieg, C., & McCann, K. S. (2020). Fisheries restoration potential: Optimizing fisheries profits while maintaining food web structure. *Food Webs*, *25*, e00168. https://doi.org/10.1016/j.fooweb.2020.e00168

Birkeland, C., & Dayton, P. K. (2005). The importance in fishery management of leaving the big ones. *Trends in Ecology and Evolution*, *20*(7), 356–358. https://doi.org/10.1016/j.tree.2005.03.015

Biro, P. A., & Post, J. R. (2008). Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(8), 2919–2922. https://doi.org/10.1073/pnas.0708159105

Blanchard, J. L., Law, R., Castle, M. D., & Jennings, S. (2011). Coupled energy pathways and the resilience of size-structured food webs. *Theoretical Ecology*, *4*(3), 289–300. https://doi.org/10.1007/s12080-010-0078-9

Bland, S., Valdovinos, F. S., Hutchings, J. A., & Kuparinen, A. (2019). The role of fish life histories in allometrically scaled food-web dynamics. *Ecology and Evolution*, *9*(6), 3651–3660. https://doi.org/10.1002/ece3.4996

Brander, K. M. (2007). The role of growth changes in the decline and recovery of North Atlantic cod stocks since 1970. *ICES Journal of Marine Science*, *64*(2), 211–217. https://doi.org/10.1093/icesjms/fsl021

Brose, U., Williams, R. J., & Martinez, N. D. (2006). Allometric scaling enhances stability in complex food webs. *Ecology Letters*, *9*(11), 1228–1236. https://doi.org/10.1111/j.1461-0248.2006.00978.x

Browman, H. I., Law, R., Marshall;, C. T., Kuparinen, A., Merila;, J., Jorgensen, C., Enberg, K., Dunlop, E. S., Arlinghaus, R., Boukal, D. S., Brander, K., Ernande, B., Gardmark, A., Johnston, F., Matsumura, S., Pardoe, H., Raab, K., Silva, A., Vainikka, A., … Rijnsdorp, A. D. (2008). The role of fisheries-induced evolution. *Science*, *320*(5872), 47b–50b. https://doi.org/10.1126/science.320.5872.47b

Byrnes, J. E., Reynolds, P. L., & Stachowicz, J. J. (2007). Invasions and extinctions reshape coastal marine food webs. *PLoS One*, *2*(3), 1–7. https://doi.org/10.1371/journal.pone.0000295

Conversi, A., Dakos, V., Gårdmark, A., Ling, S., Folke, C., Mumby, P. J., Greene, C., Edwards, M., Blenckner, T., Casini, M., Pershing, A., & Möllmann, C. (2015). A holistic view of marine regime shifts. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1659), 1–8. https://doi.org/10.1098/rstb.2013.0279

Cushing, D. H. (1990). Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology*, *26*, 249–293. https://doi.org/10.1016/S0065-2881(08)60202-3

Darimont, C. T., Fox, C. H., Bryan, H. M., & Reimchen, T. E. (2015). The unique ecology of human predators. *Science*, *349*(6250), 858–860. https://doi.org/10.1126/science.aac4249

Daskalov, G. M., Grishin, A. N., Rodionov, S., & Mihneva, V. (2007). Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proceedings of the National*

Academy of Sciences of the United States of America, *104*(25), 10518–10523. https://doi.org/10.1073/pnas.0701100104

De Roos, A. M., Boukal, D. S., & Persson, L. (2006). Evolutionary regime shifts in age and size at maturation of exploited fish stocks. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1596), 1873–1880. https://doi.org/10.1098/rspb.2006.3518

Diaz Pauli, B., & Heino, M. (2014). What can selection experiments teach us about fisheries-induced evolution? *Biological Journal of the Linnean Society*, *111*(3), 485–503. https://doi.org/10.1111/bij.12241

Diaz Pauli, B., & Sih, A. (2017). Behavioural responses to human-induced change: Why fishing should not be ignored. *Evolutionary Applications*, *10*(3), 231–240. https://doi.org/10.1111/eva.12456

Díaz, S., Pascual, U., Stenseke, M., Martín-López, B., Watson, R. T., Molnár, Z., Hill, R., Chan, K. M. A., Baste, I. A., Brauman, K. A., Polasky, S., Church, A., Lonsdale, M., Larigauderie, A., Leadley, P. W., van Oudenhoven, A. P. E., van der Plaat, F., Schröter, M., Lavorel, S., … Shirayama, Y. (2018). Assessing nature's contributions to people. *Science*, *359*(6373), 270–272. https://doi.org/10.1126/science.aap8826

Dunlop, E. S., Eikeset, A. M., & Stenseth, N. C. (2015). From genes to populations: How fisheries-induced evolution alters stock productivity. *Ecological Applications*, *25*(7), 1860–1868. https://doi.org/10.1890/14-1862.1

Eikeset, A. M., Dunlop, E. S., Heino, M., Storvik, G., Stenseth, N. C., & Dieckmann, U. (2016). Roles of density-dependent growth and life history evolution in accounting for fisheries-induced trait changes. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(52), 15030–15035. https://doi.org/10.1073/pnas.1525749113

Ellingsen, K. E., Yoccoz, N. G., Tveraa, T., Frank, K. T., Johannesen, E., Anderson, M. J., Dolgov, A. V., & Shackell, N. L. (2020). The rise of a marine generalist predator and the fall of beta diversity. *Global Change Biology*, *26*(5), 2897–2907. https://doi.org/10.1111/gcb.15027

Enberg, K., Jørgensen, C., & Mangel, M. (2010). Fishing-induced evolution and changing reproductive ecology of fish: The evolution of steepness. *Canadian Journal of Fisheries and Aquatic Sciences*, *67*(10), 1708–1719. https://doi.org/10.1139/F10-090

Essington, T. E., Beaudreau, A. H., & Wiedenmann, J. (2006). Fishing through marine food webs. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(9), 3171–3175. https://doi.org/10.1073/pnas.0510964103

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., … Wardle, D. A. (2011). Trophic downgrading of planet earth. *Science*, *333*(6040), 301–306. https://doi.org/10.1126/science.1205106

FAO (2020). *The State of World Fisheries and Aquaculture 2020*. Sustainability in action.

Frank, K. T., Petrie, B., Choi, J. S., & Leggett, W. C. (2005). Ecology: Trophic cascades in a formerly cod-dominated ecosystem. *Science*, *308*(5728), 1621–1623. https://doi.org/10.1126/science.1113075

Fung, T., Farnsworth, K. D., Shephard, S., Reid, D. G., & Rossberg, A. G. (2013). Why the size structure of marine communities can require decades to recover from fishing. *Marine Ecology Progress Series*, *484*, 155–171. https://doi.org/10.3354/meps10305

Handegard, N. O., Michalsen, K., & Tjøstheim, D. (2003). Avoidance behaviour in cod (Gadus morhua) to a bottom-trawling vessel. *Aquatic Living Resources*, *16*(3), 265–270. https://doi.org/10.1016/S0990-7440(03)00020-2

Hansen, M. J., Fayram, A. H., & Newman, S. P. (2011). Natural mortality in relation to age and fishing mortality on walleyes in escanaba lake, wisconsin, during 1956–2009. *North American Journal of Fisheries Management*, *31*(3), 506–514. https://doi.org/10.1080/02755947.2011.593929

Heino and Dieckmann, 2009Heino, M., & Dieckmann, U. (2009). Fisheries-induced Evolution. Encyclopedia of Life Sciences, September. https://doi.org/10.1002/9780470015902.a0021213

Heithaus, M. R., Frid, A., Wirsing, A. J., & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends in Ecology and Evolution*, *23*(4), 202–210. https://doi.org/10.1016/j.tree.2008.01.003

Hilborn, R., Hively, D. J., Loke, N. B., de Moor, C. L., Kurota, H., Kathena, J. N., Mace, P. M., Minto, C., Parma, A. M., Quiroz, J. C., & Melnychuk, M. C. (2021). Global status of groundfish stocks. *Fish and Fisheries*, 1–18. https://doi.org/10.1111/faf.12560

Hollins, J., Thambithurai, D., Koeck, B., Crespel, A., Bailey, D. M., Cooke, S. J., Lindström, J., Parsons, K. J., & Killen, S. S. (2018). A physiological perspective on fisheries-induced evolution. *Evolutionary Applications*, *11*(5), 561–576. https://doi.org/10.1111/eva.12597

Hsieh, C., Reiss, C. S., Hunter, J. R., Beddington, J. R., May, R. M., & Sugihara, G. (2006). Fishing elevates variability in the abundance of exploited species. *Nature*, *443*(October), 859–862. https://doi.org/10.1038/nature05232

Hutchings, J. A. (2005). Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (Gadus morhua). *Canadian Journal of Fisheries and Aquatic Sciences*, *62*(4), 824–832. https://doi.org/10.1139/f05-081

Hutchings, J. A. (2015). Thresholds for impaired species recovery. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1809), https://doi.org/10.1098/rspb.2015.0654

Hutchings, J. A., & Fraser, D. J. (2008). The nature of fisheries- and farming-induced evolution. *Molecular Ecology*, *17*(1), 294–313. https://doi.org/10.1111/j.1365-294X.2007.03485.x

Hutchings, J. A., & Kuparinen, A. (2020). Implications of fisheries-induced evolution for population recovery: Refocusing the science and refining its communication. *Fish and Fisheries*, *21*(2), 453–464. https://doi.org/10.1111/faf.12424

Hutchings, J. A., & Kuparinen, A. (2021). Throwing down a genomic gauntlet on fisheries-induced evolution. *Proceedings of the National Academy of Sciences*, *118*(20), e2105319118. https://doi.org/10.1073/pnas.2105319118

Hutchings, J. A., & Myers, R. A. (1994). What can be learned from the collapse of a renewable resource? Atlantic cod, Gadus morhua, of Newfoundland and Labrador. *Canadian Journal of Fisheries and Aquatic Sciences*, *51*(9), 2126–2146. https://doi.org/10.1139/f94-214

Jacob, U., Thierry, A., Brose, U., Arntz, W. E., Berg, S., Brey, T., Fetzer, I., Jonsson, T., Mintenbeck, K., Möllmann, C., Petchey, O. L., Riede, J. O., & Dunne, J. A. (2011). The role of body size in complex food webs: A cold case. *Advances in Ecological Research*, *45*, 181–223. https://doi.org/10.1016/B978-0-12-386475-8.00005-8

Jacobson, P., Gardmark, A., Ostergren, J., Casini, M., & Huss, M. (2018). Size-dependent prey availability affects diet and performance of predatory fish at sea: A case study of Atlantic salmon. *Ecosphere*, *9*(1), https://doi.org/10.1002/ecs2.2081

Jakobsdóttir, K. B., Pardoe, H., Magnússon, Á., Björnsson, H., Pampoulie, C., Ruzzante, D. E., & Marteinsdóttir, G. (2011). Historical changes in genotypic frequencies at the Pantophysin locus in Atlantic cod (Gadus morhua) in Icelandic waters: Evidence of fisheries-induced selection? *Evolutionary Applications*, *4*(4), 562–573. https://doi.org/10.1111/j.1752-4571.2010.00176.x

James, A., Pitchford, J. W., & Brindley, J. (2003). The relationship between plankton blooms, the hatching of fish larvae, and recruitment. *Ecological Modelling*, *160*(1–2), 77–90. https://doi.org/10.1016/S0304-3800(02)00311-3

Jennings, S., & Blanchard, J. L. (2004). Fish abundance with no fishing: Predictions based on macroecological theory. *Journal of Animal Ecology*, *73*(4), 632–642. https://doi.org/10.1111/j.0021-8790.2004.00839.x

Jennings, S., Greenstreet, S. P. R., & Reynolds, J. D. (1999). Structural change in an exploited fish community: A consequence of differential fishing effects on species with contrasting life histories. *Journal of Animal Ecology*, *68*(3), 617–627. https://doi.org/10.1046/j.1365-2656.1999.00312.x

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

Jørgensen, C., Ernande, B., & Fiksen, Ø. (2009). Size-selective fishing gear and life history evolution in the Northeast Arctic cod. *Evolutionary Applications*, *2*(3), 356–370. https://doi.org/10.1111/j.1752-4571.2009.00075.x

Jusufovski, D., & Kuparinen, A. (2020). Exploring individual and population eco-evolutionary feedbacks under the coupled effects of fishing and predation. *Fisheries Research*, *231*, 105713. https://doi.org/10.1016/j.fishres.2020.105713

Kindsvater, H. K., & Palkovacs, E. P. (2017). Predicting eco-evolutionary impacts of fishing on body size and trophic role of atlantic cod. *Copeia*, *105*(3), 475–482. https://doi.org/10.1643/ot-16-533

Kjesbu, O. S., Solemdal, P., Bratland, P., & Fonn, M. (1996). Variation in annual egg production in individual captive Atlantic cod (Gadus morhua). *Canadian Journal of Fisheries and Aquatic Sciences*, *53*, 610–620. https://doi.org/10.2493/jjspe.59.1683

Koen-Alonso, M., & Yodzis, P. (2005). Multispecies modelling of some components of the marine community of northern and central Patagonia, Argentina. *Canadian Journal of Fisheries and Aquatic Sciences*, *62*(7), 1490–1512. https://doi.org/10.1139/f05-087

Konar, M., Qiu, S., Tougher, B., Vause, J., Tlusty, M., Fitzsimmons, K., Barrows, R., & Cao, L. (2019). Illustrating the hidden economic, social and ecological values of global forage fish resources. *Resources, Conservation and Recycling*, *151*(February), 104456. https://doi.org/10.1016/j.resconrec.2019.104456

Kuparinen, A., Boit, A., Valdovinos, F. S., Lassaux, H., & Martinez, N. D. (2016). Fishing-induced life-history changes degrade and destabilize harvested ecosystems. *Scientific Reports*, *6*, 1–9. https://doi.org/10.1038/srep22245

Kuparinen, A., & Festa-Bianchet, M. (2017). Harvest-induced evolution: Insights from aquatic and terrestrial systems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1712), 20160036. https://doi.org/10.1098/rstb.2016.0036

Kuparinen, A., & Hutchings, J. A. (2012). Consequences of fisheries-induced evolution for population productivity and recovery potential. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1738), 2571–2579. https://doi.org/10.1098/rspb.2012.0120

Kuparinen, A., & Hutchings, J. A. (2017). Genetic architecture of age at maturity can generate divergent and disruptive harvest-induced evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1712), 20160035. https://doi.org/10.1098/rstb.2016.0035

Kuparinen, A., Keith, D. M., & Hutchings, J. A. (2014). Allee effect and the uncertainty of population recovery. *Conservation Biology*, *28*(3), 790–798. https://doi.org/10.1111/cobi.12216

Kuparinen, A., Kuikka, S., & Merilä, J. (2009). Estimating fisheries-induced selection: Traditional gear selectivity research meets fisheries-induced evolution. *Evolutionary Applications*, *2*(2), 234–243. https://doi.org/10.1111/j.1752-4571.2009.00070.x

Kuparinen, A., & Merilä, J. (2007). Detecting and managing fisheries-induced evolution. *Trends in Ecology and Evolution*, *22*(12), 652–659. https://doi.org/10.1016/j.tree.2007.08.011

Kuparinen, A., Perälä, T., Martinez, N. D., & Valdovinos, F. S. (2019). Environmentally-induced noise dampens and reddens with increasing trophic level in a complex food web. *Oikos*, *128*(4), 608–620. https://doi.org/10.1111/oik.05575

Laugen, A. T., Engelhard, G. H., Whitlock, R., Arlinghaus, R., Dankel, D. J., Dunlop, E. S., Eikeset, A. M., Enberg, K., Jørgensen, C., Matsumura, S., Nusslé, S., Urbach, D., Baulier, L., Boukal, D. S., Ernande, B., Johnston, F. D., Mollet, F., Pardoe, H., Therkildsen, N. O., … Dieckmann, U. (2014). Evolutionary impact assessment: Accounting for evolutionary consequences of fishing in an ecosystem approach to fisheries management. *Fish and Fisheries*, *15*(1), 65–96. https://doi.org/10.1111/faf.12007

Law, R. (2007). Fisheries-induced Evolution : Present Status and Future Directions, *Marine Ecology Progress Series*, *335*, 271–278.

Law, R., & Grey, D. R. (1989). Evolution of yields from populations with age-specific cropping. *Evolutionary Ecology*, *3*(4), 343–359. https://doi.org/10.1007/BF02285264

Lucifora, L. O., García, V. B., Menni, R. C., Escalante, A. H., & Hozbor, N. M. (2009). Effects of body size, age and maturity stage on diet in a large shark: Ecological and applied implications. *Ecological Research*, *24*(1), 109–118. https://doi.org/10.1007/s11284-008-0487-z

Moll, R. J., Killion, A. K., Hayward, M. W., & Montgomery, R. A. (2021). A Framework for the Eltonian Niche of humans. *BioScience*, 1–14, biab055. https://doi.org/10.1093/biosci/biab055

Morgan, M. J., & Brattey, J. (2005). Effect of changes in reproductive potential on perceived productivity of three Northwest Atlantic cod (Gadus morhua) stocks. *ICES Journal of Marine Science*, *62*(1), 65–74. https://doi.org/10.1016/j.icesjms.2004.10.003

Mumby, P. J., Dahlgren, C. P., Harborne, A. R., Kappel, C. V., Micheli, F., Brumbaugh, D. R., Holmes, K. E., Mendes, J. M., Broad, K., Sanchirico, J. N., Buch, K., Box, S., Stoffle, R. W., & Gill, A. B. (2006). Fishing, trophic cascades, and the process of grazing on coral reefs. *Science*, *311*(5757), 98–101. https://doi.org/10.1126/science.1121129

Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P., & Peterson, C. H. (2007). Cascading effects of the loss of apex predatory sharks. *Science*, *315*, 1846–1850.

Myers, R. A., & Worm, B. (2005). Extinction, survival or recovery of large predatory fishes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *360*(1453), 13–20. https://doi.org/10.1098/rstb.2004.1573

Navia, A. F., Cruz-Escalona, V. H., Giraldo, A., & Barausse, A. (2016). The structure of a marine tropical food web, and its implications for ecosystem-based fisheries management. *Ecological Modelling*, *328*, 23–33. https://doi.org/10.1016/j.ecolmodel.2016.02.009

Neubauer, P., Jensen, O. P., Hutchings, J. A., & Baum, J. K. (2013). Resilience and recovery of overexploited marine populations. *Science*, *340*(6130), 347–349. https://doi.org/10.1126/science.1230441

Nordström, M. C., Aarnio, K., Törnroos, A., & Bonsdorff, E. (2015). Nestedness of trophic links and biological traits in a marine food web. *Ecosphere*, *6*(9), 1–14. https://doi.org/10.1890/ES14-00515.1

Ohlberger, J., Schindler, D. E., Brown, R. J., Harding, J. M. S., Adkison, M. D., Munro, A. R., Horstmann, L., & Spaeder, J. (2020). The reproductive value of large females: Consequences of shifts in demographic structure for population reproductive potential in Chinook Salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, *77*(8), 1292–1301. https://doi.org/10.1139/cjfas-2020-0012

Olden, J. D., Hogan, Z. S., & Zanden, M. J. V. (2007). Small fish, big fish, red fish, blue fish: Size-biased extinction risk of the world's freshwater and marine fishes. *Global Ecology and Biogeography*, *16*(6), 694–701. https://doi.org/10.1111/j.1466-8238.2007.00337.x

Olsen, E. M., Heino, M., Lilly, G. R., Morgan, M. J., Brattey, J., Ernande, B., & Dieckmann, U. (2004). Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature*, *428*(6986), 932–935. https://doi.org/10.1038/nature02430

Opdal, A. F., & Jørgensen, C. (2015). Long-term change in a behavioural trait: truncated spawning distribution and demography in Northeast

Arctic cod. *Global Change Biology*, *21*(4), 1521–1530. https://doi.org/10.1111/gcb.12773

Özbilgin, H., & Glass, C. W. (2004). Role of learning in mesh penetration behaviour of haddock (Melanogrammus aeglefinus). *ICES Journal of Marine Science*, *61*(7), 1190–1194. https://doi.org/10.1016/j.icesjms.2004.07.001

Pace, M. L., Cole, J. J., Carpenter, S. R., & Kitchell, J. F. (1999). Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution*, *14*(12), 483–488. https://doi.org/10.1016/S0169-5347(99)01723-1

Paine, R. T. (1966). Food web complexity and species diversity. *The American Naturalist*, *100*(910), 65–75. https://doi.org/10.1086/282400

Pauly, D. (2020). *Vanishing Fish: Shifting baseline and the Future of Global fisheries*. Greystone books.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., & Torres, F. (1998). Fishing down marine food webs. *Science*, *279*(5352), 860–863. https://doi.org/10.1126/science.279.5352.860

Perälä, T., Hutchings, J. A., & Olsen, E. M. (2020). *Disentangling Conditional Effects of Multiple Regime Shifts on Atlantic Cod Productivity.*

Perälä, T., & Kuparinen, A. (2020). Eco-evolutionary dynamics driven by fishing: From single species models to dynamic evolution within complex food webs. *Evolutionary Applications*, *13*(10), 2507–2520. https://doi.org/10.1111/eva.13058

Pinkerton, M. H., & Bradford-Grieve, J. M. (2014). Marine science. *ICES Journal of Marine Science*, *71*(7), 1542–1553. https://doi.org/10.1093/icesjms/fst230

Pinsky, M. L., Eikeset, A. M., Helmerson, C., Bradbury, I. R., Bentzen, P., Morris, C., Gondek-Wyrozemska, A. T., Baalsrud, H. T., Brieuc, M. S. O., Kjesbu, O. S., Godiksen, J. A., Barth, J. M. I., Matschiner, M., Stenseth, N. C., Jakobsen, K. S., Jentoft, S., & Star, B. (2021). Genomic stability through time despite decades of exploitation in cod on both sides of the Atlantic. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(15), 1–6. https://doi.org/10.1073/pnas.2025453118

Poisot, T., Mouquet, N., & Gravel, D. (2013). Trophic complementarity drives the biodiversity-ecosystem functioning relationship in food webs. *Ecology Letters*, *16*(7), 853–861. https://doi.org/10.1111/ele.12118

Prugh, L. R., Stoner, C. J., Epps, C. W., Bean, W. T., Ripple, W. J., Laliberte, A. S., & Brashares, J. S. (2009). The rise of the mesopredator. *BioScience*, *59*(9), 779–791. https://doi.org/10.1525/bio.2009.59.9.9

Pukk, L., Kuparinen, A., Järv, L., Gross, R., & Vasemägi, A. (2013). Genetic and life-history changes associated with fisheries-induced population collapse. *Evolutionary Applications*, *6*(5), 749–760. https://doi.org/10.1111/eva.12060

Reis-Filho, J. A., Schmid, K., Harvey, E. S., & Giarrizzo, T. (2019). Coastal fish assemblages reflect marine habitat connectivity and ontogenetic shifts in an estuary-bay-continental shelf gradient. *Marine Environmental Research*, *148*, 57–66

Riede, J. O., Brose, U., Ebenman, B., Jacob, U., Thompson, R., Townsend, C. R., & Jonsson, T. (2011). Stepping in Elton's footprints: A general scaling model for body masses and trophic levels across ecosystems. *Ecology Letters*, *14*(2), 169–178. https://doi.org/10.1111/j.1461-0248.2010.01568.x

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*(6167), 1241484. https://doi.org/10.1126/science.1241484

Rochet, M. J., & Benoît, E. (2012). Fishing destabilizes the biomass flow in the marine size spectrum. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1727), 284–292. https://doi.org/10.1098/rspb.2011.0893

Roff, D. (2002). *Life History Evolution*. Sinauer.

Roopnarine, P. D. (2014). Humans are apex predators. *Proceedings of the National Academy of Sciences*, *111*(9), E796. https://doi.org/10.1073/pnas.1323645111

Rousseau, Y., Watson, R. A., Blanchard, J. L., & Fulton, E. A. (2019). Evolution of global marine fishing fleets and the response of fished resources. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(25), 12238–12243. https://doi.org/10.1073/pnas.1820344116

Rowe, S., & Hutchings, J. A. (2003). Mating systems and the conservation of commercially exploited marine fish. *Trends in Ecology and Evolution*, *18*(11), 567–572. https://doi.org/10.1016/j.tree.2003.09.004

Ryabov, A. B., Morozov, A., & Blasius, B. (2015). Imperfect prey selectivity of predators promotes biodiversity and irregularity in food webs. *Ecology Letters*, *18*(11), 1262–1269. https://doi.org/10.1111/ele.12521

Sadovy de Mitcheson, Y., Craig, M. T., Bertoncini, A. A., Carpenter, K. E., Cheung, W. W. L., Choat, J. H., Cornish, A. S., Fennessy, S. T., Ferreira, B. P., Heemstra, P. C., Liu, M., Myers, R. F., Pollard, D. A., Rhodes, K. L., Rocha, L. A., Russell, B. C., Samoilys, M. A., & Sanciangco, J. (2013). Fishing groupers towards extinction: A global assessment of threats and extinction risks in a billion dollar fishery. *Fish and Fisheries*, *14*(2), 119–136. https://doi.org/10.1111/j.1467-2979.2011.00455.x

Schafer, L. N., Platell, M. E., Valesini, F. J., & Potter, I. C. (2002). Comparisons between the influence of habitat type, season and body size on the dietary compositions of fish species in nearshore marine waters. *Journal of Experimental Marine Biology and Ecology*, *278*(1), 67–92. https://doi.org/10.1016/S0022-0981(02)00337-4

Scheffer, M., Carpenter, S., & de Young, B. (2005). Cascading effects of overfishing marine systems. *Trends in Ecology and Evolution*, *20*(11), 579–581. https://doi.org/10.1016/j.tree.2005.08.007

Sharpe, D. M. T., & Hendry, A. P. (2009). Life history change in commercially exploited fish stocks: An analysis of trends across studies. *Evolutionary Applications*, *2*(3), 260–275. https://doi.org/10.1111/j.1752-4571.2009.00080.x

Shears, N. T., Babcock, R. C., & Salomon, A. K. (2008). Context-dependent effects of fishing: Variation in trophic cascades across environmental gradients. *Ecological Applications*, *18*(8), 1860–1873. https://doi.org/10.1890/07-1776.1

Shelton, P. A., Sinclair, A. F., Chouinard, G. A., Mohn, R., & Duplisea, D. E. (2006). Fishing under low productivity conditions is further delaying recovery of Northwest Atlantic cod (Gadus morhua). *Canadian Journal of Fisheries and Aquatic Sciences*, *63*(2), 235–238. https://doi.org/10.1139/f05-253

Siddon, E. C., Kristiansen, T., Mueter, F. J., Holsman, K. K., Heintz, R. A., & Farley, E. V. (2013). Spatial match-mismatch between juvenile fish and prey provides a mechanism for recruitment variability across contrasting climate conditions in the eastern Bering Sea. *PLoS One*, *8*(12), e84526. https://doi.org/10.1371/journal.pone.0084526

Start, D. (2018). Predator macroevolution drives trophic cascades and ecosystem functioning. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1883), https://doi.org/10.1098/rspb.2018.0384

Stringer, C. B., Finlayson, J. C., Barton, R. N. E., Fernández-Jalvo, Y., Cáceres, I., Sabin, R. C., Rhodes, E. J., Currant, A. P., Rodríguez-Vidal, J., Giles-Pacheco, F., & Riquelme-Cantal, J. A. (2008). Neanderthal exploitation of marine mammals in Gibraltar. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(38), 14319–14324. https://doi.org/10.1073/pnas.0805474105

Swain, D. P. (2011). Life-history evolution and elevated natural mortality in a population of Atlantic cod (Gadus morhua). *Evolutionary Applications*, *4*(1), 18–29. https://doi.org/10.1111/j.1752-4571.2010.00128.x

Tegner, M. J., & Dayton, P. K. (2000). Ecosystem effects of fishing in kelp forest communities. *ICES Journal of Marine Science*, *57*(3), 579–589. https://doi.org/10.1006/jmsc.2000.0715

Teh, L. C. L., & Sumaila, U. R. (2013). Contribution of marine fisheries to worldwide employment. *Fish and Fisheries*, *14*(1), 77–88. https://doi.org/10.1111/j.1467-2979.2011.00450.x

Thurstan, R. H., & Roberts, C. M. (2010). Ecological meltdown in the firth of clyde, Scotland: Two centuries of change in a coastal marine ecosystem. *PLoS One*, *5*(7), e11767. https://doi.org/10.1371/journal.pone.0011767

Trebilco, R., Baum, J. K., Salomon, A. K., & Dulvy, N. K. (2013). Ecosystem ecology: Size-based constraints on the pyramids of life. *Trends in Ecology and Evolution*, *28*(7), 423–431. https://doi.org/10.1016/j.tree.2013.03.008

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

Uusi-Heikkilä, S., Wolter, C., Klefoth, T., & Arlinghaus, R. (2008). A behavioral perspective on fishing-induced evolution. *Trends in Ecology and Evolution*, *23*(8), 419–421. https://doi.org/10.1016/j.tree.2008.04.006

Van De Wolfshaar, K. E., De Roos, A. M., & Persson, L. (2006). Size-dependent interactions inhibit coexistence in intraguild predation systems with life-history omnivory. *American Naturalist*, *168*(1), 62–75. https://doi.org/10.1086/505156

von Bertalanffy, L. (1938). A quantitative theory of organic growth (inquiries on growth laws II). *Human Biology*, *10*, 181–213.

Wallach, A. D., Izhaki, I., Toms, J. D., Ripple, W. J., & Shanas, U. (2015). What is an apex predator? *Oikos*, *124*(11), 1453–1461. https://doi.org/10.1111/oik.01977

Walsh, M. R., Munch, S. B., Chiba, S., & Conover, D. O. (2006). Maladaptive changes in multiple traits caused by fishing: Impediments to population recovery. *Ecology Letters*, *9*(2), 142–148. https://doi.org/10.1111/j.1461-0248.2005.00858.x

Waters, C. N., Zalasiewicz, J., Summerhayes, C., Barnosky, A. D., Poirier, C., Ga uszka, A., Cearreta, A., Edgeworth, M., Ellis, E. C., Ellis, M., Jeandel, C., Leinfelder, R., McNeill, J. R., Richter, D. D., Steffen, W., Syvitski, J., Vidas, D., Wagreich, M., Williams, M., … Wolfe, A. P. (2016). The Anthropocene is functionally and stratigraphically distinct from the Holocene. *Science*, *351*(6269), aad2622. https://doi.org/10.1126/science.aad2622

Wood, Z. T., Palkovacs, E. P., & Kinnison, M. T. (2018). Eco-evolutionary feedbacks from non-target species influence harvest yield and sustainability. *Scientific Reports*, *8*(1), 1–11. https://doi.org/10.1038/s41598-018-24555-0

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J. M., Olesen, J. M., Valido, A., & Warren, P. H. (2005). Body size in ecological networks. *Trends in Ecology and Evolution*, *20*(7), 402–409. https://doi.org/10.1016/j.tree.2005.04.005

Worm, B., & Branch, T. A. (2012). The future of fish. *Trends in Ecology and Evolution*, *27*(11), 594–599. https://doi.org/10.1016/j.tree.2012.07.005

Young, K. A., Cluney, V. A., & Weir, L. K. (2020). Fisheries-induced evolution of alternative male life history tactics in Coho salmon. *Evolutionary Applications*, *13*(6), 1501–1512. https://doi.org/10.1111/eva.12970

How to cite this article: Hočevar, S., & Kuparinen, A. (2021). Marine food web perspective to fisheries-induced evolution. *Evolutionary Applications*, 14, 2378–2391. https://doi.org/10.1111/eva.13259