Long-term changes in life-history traits of Norwegian spring-spawning herring

Marion Claireaux

Thesis for the Degree of Philosophiae Doctor (PhD)
University of Bergen, Norway
2019

UNIVERSITY OF BERGEN

Long-term changes in life-history traits of Norwegian spring-spawning herring

Marion Claireaux

Thesis for the Degree of Philosophiae Doctor (PhD)
at the University of Bergen

Date of defence: 11.01 2019

Year: 2019

Title: Long-term changes in life-history traits of Norwegian spring-spawning herring

Name: Marion Claireaux

Print: Skipnes Kommunikasjon / University of Bergen

Scientific environment

The work presented in this thesis was carried out at the Department of Biology, University of Bergen and the Institute of Marine Research, from August 2015 to October 2018. The candidate Marion Claireaux was affiliated with the research group Pelagic fish (IMR). This work was financially supported by the Research Council of Norway (grant number 243735) through the project ConEvolHer.

Acknowledgements

First and foremost, I want to warmly and sincerely thank my supervisors Katja Enberg and Mikko Heino for giving me the opportunity to study in Bergen, and for guiding and supporting me through this "terra incognita" that the PhD studies represent.

Katja, thank you for making yourself as available as you could when I needed. I realise now I was not prepared for this when I started. Under your supervision, I was able to improve my strengths and identify my weaknesses, so I could start progressing as a scientist and not as a student. Working with you, who manages to combine family and work life in such a successful way, was very inspiring and gave me an optimistic picture of my potential future in science. I also really appreciated that you taught me the importance of rest for work productivity and it helped relieve the load of anxiety, especially during the last few months.

Mikko, thank you for the always pertinent comments about statistical details. You made me discover the subtilities of statistics and I have never been as aware that one must give careful inspection of his/her work before being confident in the results. Even though it is still not perfect, this cautiousness can only serve me well in the future. Thank you also, for your valuable comments on my writing, and for making yourself available even while traveling abroad. Finally, I deeply apologize for my constantly poor colour choices when making graphs and promise to improve on this point in the future.

I want to particularly thank Christian Jørgensen, Bruno Ernande and Marc Mangel for their invaluable comments on my theoretical and statistical work, as well as for helping me get more familiar with the life-history theory and the mixed effect modelling framework. Thank you also to Aril Folkvord for his precious feedbacks on my manuscripts and his support during the last few months. Finally, thank you Fabian Zimmermann for your invaluable help with the writing and the stress management. I do not know how I would have made it without it.

More largely, I want to acknowledge all my colleagues at both BIO and IMR for the pleasant atmosphere and enthusiastic lunch/coffee break discussions. A special mention goes to Nikos Nikolioudakis and Fabian Zimmermann. My hopes to bring you to dance sometimes still did not fade.

I want to also warmly thank Guy Claireaux and Bruno Ernande, who directed my first steps in network creation and without whom I would probably not have had the opportunity to come to Bergen in the first place.

To all my friends in Bergen, you made the last three years here unforgettable. I am now considering this city as my home. Special thank you to all the members of BSI Dans, new or old, that I now consider as my second family.

Ivan, I will never be able to express how grateful I am for the unconditional love and emotional support you showed me, during both the good and bad times. I am not sure I would have been able to hold until the end of my PhD without you. Thank you for helping me organise my ideas, prevent me from panicking, cooking for me in the evening while I was working and saving the apartment from becoming a complete mess during the last month. I hope to be able to give you as much as I received from you during these last two and a half years.

My most sincere apologies to my family for not giving them as many news as I should have. Even though I do not say it as often as I should, your encouragements mean everything to me and I made everything I could to make you proud. I will never be able to express how overjoyed I am that you can be present to my defence, despite the 6000 kilometres trip it represents. Thank you, Elise, for taking the initiative to come and visit me whenever you could. Even though months separated those visits, it always felt as it was only a couple of days since I last saw you.

Abstract

Life-history traits are key determinants of populations' dynamics. Those traits are susceptible to natural selection and are therefore sensitive to the mortality regime and the selection pattern a population experience. Nowadays, almost all natural populations are affected by anthropogenic activities (e.g. urbanisation, loss or segmentation of habitats). More specifically, fish stocks, reproducing in the wild and coping with environmental fluctuations, have been exploited with industrialized efficiency for decades. The effects of fisheries on exploited stocks life-history traits have been widely studied and there is currently no doubt that fisheries-induced evolution is taking place in many of them. Fisheries-induced evolution of life-history traits constitutes a challenge for management, since genetic changes are difficult to reverse, and can lead to a loss of productivity and resilience of the exploited stock. Considering the amount of evidence supporting fisheries-induced evolution, it is therefore surprising that little of it is found in an intensively exploited pelagic fish, the Norwegian spring-spawning herring. Exploited for centuries, the stock collapsed in the late 1960's because of overfishing and took more than 15 years to recover. The fishery went from an open-access fishery to a TAC regulated fishery combined with management regulations such as a minimum landing size of 25 cm. A weak decrease in age at maturation, maybe attributable to fisheries-induced evolution, has been detected, while other traits haven't been studied yet.

The goal of this thesis is to investigate how traits other than age and length at maturation have been affected by the fishing pressure in Norwegian spring-spawning herring. In addition, it gives an overview of how the selection pressures Norwegian Spring-spawning herring is subjected to may have changed during the last century and explain the weakness of the trends observed.

Using multivariate linear (mixed effect) models together with data spanning 80 years, significant residual trends, potentially attributable to genetic changes, were found for the reproductive investment (increase, **Paper II**) and adult growth (decrease, **Paper**

IV). No significant trend could be found in juvenile growth (**Paper IV**). However, the trends observed are weak and year to year variation is still mainly driven by environmental factors. In the case they stem from genetic changes, three possibilities could explain their weakness: (1) They are partly masked by phenotypic plasticity. (2) Changes in the selectivity experienced (**Paper III**) could slow down evolution rates. (3) The current selection pattern (**Paper III**) is driving the long-term trend. In addition, we showed that fishing can induce changes in natural mortality by selecting specific behaviours (**Paper I**), potentially leading to biased estimates for stock size assessment. However, it is not known how much of this pertains to Norwegian spring-spawning herring and warrants more research.

The consequences of the observed trends in Norwegian spring-spawning herring life-history traits for the stock's dynamics are not very clear yet. Even though slower growth could lead to a loss of productivity, consequences would not be as drastic as in stocks were age and size at maturation are largely reduced. Considering the current knowledge about fisheries-induced evolution, it seems that the modern management measures for the Norwegian spring-spawning herring stock are the most desirable and that the potential evolution shown in this thesis is of little consequence for the stock's management compared to environmental variability. Close monitoring of the stock is however necessary to avoid or mitigate any detrimental effect fisheries-induced evolution could have in the future on the stock's productivity and, most importantly, recovery potential.

List of Publications

Claireaux, M., Jørgensen, C. & Enberg, K. (*In press*). Evolutionary effects of fishing gear on foraging behaviour and life-history, Ecology and Evolution.

Claireaux, M., dos Santos Schmidt, T.C., Olsen, E.M., Varpe, Ø., Slotte, A., Heino, M., Enberg, K. (*In prep*). Eight decades of changes in herring reproductive investment: effects of fishing, environment and conspecific density. (*submitted to Ecological Applications*)

Claireaux, M., Folkvord, A., Heino, M., Enberg, K. (*In prep*). The Rosa Lee Phenomenon revisited: Population dynamics, sampling and selectivity affect the apparent changes in growth rate (*manuscript*).

Claireaux, M., Zimmermann, F., Ernande, B., Heino, M., Enberg, K. (*In prep*) Reconstructing growth in Norwegian spring-spawning herring from scale increments: exploring historic population dynamics and their drivers (*manuscript*).

Reprints were made with permission from Ecology and Evolution

Contents

Scientific environment **1**

Acknowledgements **2**

Abstract **4**

List of Publications **6**

Contents **7**

Introduction **9**

1. Evolution *9*

1.1. Survival of the fittest 9

1.2. Life-history theory 10

2. Fisheries-induced evolution *12*

2.1. Global state of fisheries 12

2.2. Fisheries-induced evolution 13

2.3. Fisheries-induced selection 14

3. Methods to detect fisheries-induced evolution *19*

3.1. Statistics/Data 19

3.2. Experiments 20

3.3. Models 20

4. The Norwegian Spring-spawning herring *22*

4.1. Life-history 22

4.2. Short history of the fishery 24

5. The Norwegian Sea-Barents Sea ecosystem *25*

Aim of the thesis **28**

Summary of papers **30**

Discussion 34

1. Detecting evolution 34

  1.1. Data limitation 34

  1.2. Plastic versus genetic changes 36

  1.3. Patterns of selection 37

2. Consequences for fisheries management 39

3. Fishing and natural selectivity 41

Concluding remarks and future perspectives 45

References 48

Introduction

1. Evolution

1.1. Survival of the fittest

The theory of evolution by natural selection (Darwin, 1859; Fisher, 1930), also known as “survival of the fittest”, is probably one of the most famous scientific theories, supported by a wide range of evidence coming from different fields such as geology, ecology and genetics (Dawkins, 2009; Fabian and Flatt, 2012). Evolution occurs at the genotypic level and can be defined as a change in a genotype or allele frequency within a population. In contrast, natural selection happens at the phenotypic level and several conditions are needed for it to lead to evolution (Endler, 1986). As natural selection is the selective removal of individuals from a population based on a trait or set of traits, it can only occur if there is individual variation in the traits considered (i.e. different colours, sizes, growth rates…). The variation in these traits must also be associated to variation in fitness, with the fittest individuals the ones best able to survive and reproduce. This way, natural selection favours individuals with a phenotype best suited to their environment. Finally, for evolution to happen, the variation in the trait considered must be, at least partly, due to variation in the genotype (Endler, 1986).

Inter-individual variations in life-history traits can be the result of different genotypes, but also different environments (Schmalhausen, 1949). The phenotype, on which selection occurs, is the result of the interaction between environment and genotype (Figure 1). The extent of this interaction is called phenotypic plasticity (Gause, 1947; Bradshaw, 1965) and explains why different environments can lead to different phenotypes, even if individuals are genetically close or identical. For example, growth can be influenced by both biotic (i.e. food) and abiotic (i.e. temperature) factors and individuals will not grow the same way depending on the quantity of food or the temperature they experience. In theory, selection on a trait varying only due to environmental factors does not lead to evolution, even though recent studies suggest that this picture is more complicated than previously thought (e.g. Wang et al., 2016).

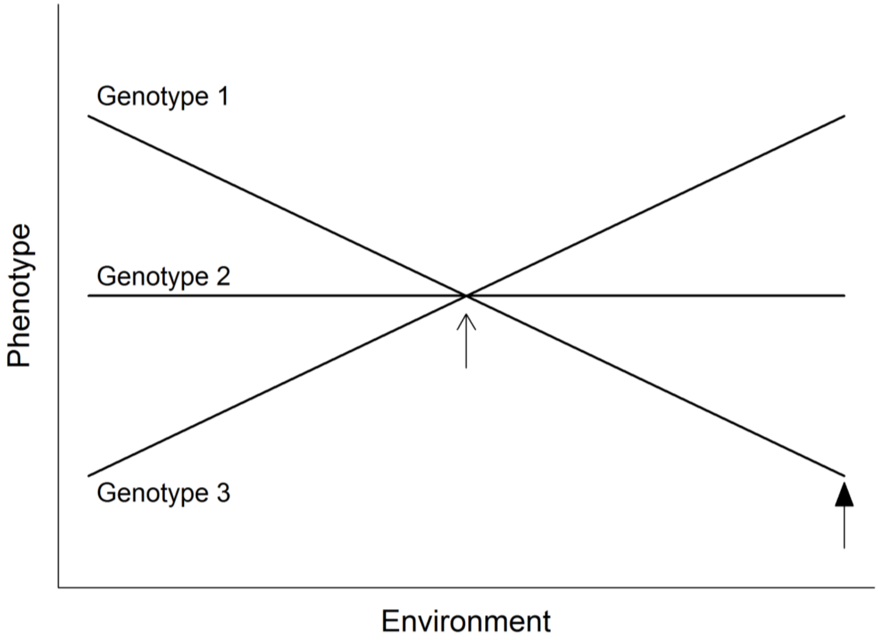


Figure 1: Illustration of the genotype-environment interaction. A given genotype can result in a different phenotype in different environments. The closed and open arrows respectively indicate environments where phenotype variation is and is not associated to genotype variation (Figure adapted from Fabian and Flatt (2012)).

1.2. Life-history theory

The life-history theory aims at answering “Why all the variation?” and gives a framework to predict which traits will be favoured in different environments (Stearns, 1992; Fabian and Flatt, 2012). This theory treats life-history evolution as an optimization problem (Houston and McNamara, 1999; Clark and Mangel, 2000). Its aim is to find the optimal values of life-history traits considering both extrinsic (e.g. predators, food availability, temperature…) and intrinsic factors (i.e. intrinsic trade-offs specific to the organism) that affect an organism's capacity to survive and reproduce (Stearns, 1992; Fabian and Flatt, 2012). Therefore, life-history theory addresses one of the most fundamental issues in evolutionary biology: understanding how species respond and adapt to changes in selective pressures. By observing changes in the environment, we can infer how a population or species might evolve (Reznick et al., 1990b). In contrast, changes in species traits can give us information about how the selective landscape was modified (Mangel, 2017), helping us to understand better our impact on wild populations and ultimately constituting a tool to design adapted management measures (e.g. Heppell, 1998).

1.2.1. Trade-offs shape life-history traits

Life-history traits are the traits determining schedules of mortality and reproduction in populations (i.e. age and size at maturity, reproductive effort, number of offsprings…; Stearns, 1992). The covariation of life-history traits is a central element of the life-history theory. Negative covariation between traits is called a trade-off and occurs when the fitness benefit of increasing one trait is balanced with the fitness cost of decreasing another (Svardson, 1949; Stearns, 1977; Stearns, 1989; Roff, 1992; Stearns, 1992). Trade-offs mark the boundaries of life-histories evolution (Stearns, 1992; Houle, 2001). Particularly, two of them are keys to shape life-history traits: the trade-off between growth and reproduction, and between current reproduction and survival (i.e., future reproduction).

The trade-off between growth and reproduction is caused by competitive allocation of limited resources to one trait versus the other (Stearns, 1989; Stearns, 1992; Roff, 2000). Individuals investing more in growth during a certain period will have fewer resources to put in reproduction and vice-versa. The optimal amount of energy to invest in each trait for an organism heavily depends on the natural conditions it experiences, such as predation pressure (Reznick, 1983). The question of how much to invest into reproduction in one reproductive event, considering the probability of surviving until the next one also needs to be considered (trade-off between current reproduction and survival). Investment in reproduction can be very costly and investing too much can considerably decrease an organism's survival, especially for the first reproductive events (Williams, 1966). If mortality is at low to medium levels, theory predicts that an organism should not compromise its survival by investing all its energy into current reproduction. Because size can influence the natural mortality experienced by an individual (e.g. smaller fish have more chance to be predated on than bigger counterparts; Peterson and Wroblewski, 1984; Tian et al., 2007), it can therefore be advantageous early in life to invest more in growth. In general, bigger organisms have a higher net reproductive effort and can therefore compensate later for the energy they did not put in reproduction earlier (Heino and Kaitala, 1999; Hixon et al., 2013; Barneche et al., 2018). On the other hand, theory predicts that current reproductive investment should increase at the expense of growth and future reproduction when the prospect of survival is bleak, in a last attempt to maximize fitness (Stearns, 1992). Those two trade-offs, among others, therefore constitute essential mechanisms to understand life-histories.

2. Fisheries-induced evolution

2.1. Global state of fisheries

Fisheries constitute an important anthropogenic activity, supporting many countries' economy (Global total capture fisheries production valued at USD 130 billion in 2016; FAO, 2017). It is also a crucial factor of food security, especially in developing countries (e.g. 47 % of the fish produced for food came from fisheries in 2016, with fish demand reaching 20.2 kg per capita in 2015; FAO, 2017). Therefore, it is not surprising that fishing constitutes an important if not the main source of mortality in the exploited stocks across the world (Mertz and Myers, 1998; Stokes and Law, 2000).

For a long time, fisheries have been considered harmless for the resources they exploited, and this might have been true, owing to equipment or vessel limitation (Pauly et al., 2005). The debate on whether marine fishery resources were inexhaustible or not started in the late 1800’s (Smith, 1994), and was settled when the accelerated depletion of coastal systems (Jackson et al., 2001) due to the development of vessels with increased fishing power, among others, showed that fishing could reduce stocks to dangerously low levels. During the post-World War II era, scientific effort was directed toward improving fisheries management by assessing maximum sustainable yield and stock-recruitment relationships (Conover, 2000). However, as the fisheries became more efficient by using newly developed technologies, collapse of some heavily fished stocks (e.g. Peruvian anchovy, Norwegian Spring-spawning herring) demonstrated that the current tools were not sufficient to capture the complex dynamics of marine stocks and that responses of populations to fishing were still very uncertain. Even though fisheries scientists worked on improving recruitment predictions and developed new analytical and computational tools to assess stock dynamics, the considerable increase in the harvesting capacity of fisheries, combined with over-optimistic yield estimates (Pauly, 1996), led to numerous collapses, the most famous being the one of Atlantic cod (Myers et al., 1997).

Despite the achieved progress, it is nowadays impossible to doubt that the current fishing practices still pose a potential threat to stock sustainability: the fraction of marine fish stocks fished within biologically sustainable levels went down to 67 percent in 2015, of which 60 percent were fully fished (i.e. fishing pressure is at the maximum limit of what can be sustained before overfishing occurs). The 33 percent left were fished at biologically unsustainable levels (FAO, 2017).

2.2. Fisheries-induced evolution

In parallel to problems that intense exploitation brings for stock sustainability, fishing-induced genetic changes of life-history traits in exploited stocks are an important source of concerns (Hutchings, 2000; Stokes and Law, 2000; Heino and Godø, 2002; Jørgensen et al., 2007; Kuparinen and Merilä, 2007; Enberg et al., 2009; Enberg et al., 2010; Enberg et al., 2012; Heino et al., 2015a). However, this issue is often wrongly seen as less problematic than other detrimental effects of fishing such as stock depletion. Life-history traits are determinants of populations dynamics, and their evolution can have drastic consequences for stock biomass, stock demographics, economic yield and recovery rates of exploited populations (Walsh et al., 2006; Enberg et al., 2009; Zimmermann and Jørgensen, 2015). Consequences of life-history traits evolution can further extend to the whole ecosystem, affecting predator-prey dynamics, competitive interactions, production of offspring, and other ecological relationships (Jennings and Kaiser, 1998; Hall, 1999; Kaiser and De Groot, 2000; Heino and Godø, 2002).

2.3. Fisheries-induced selection

Fisheries-induced selection works in the same fashion as natural selection. Virtually all forms of fishing are selective, either because of management regulations (e.g. minimum landing size, protected areas, fishing season) protecting certain age/size-classes and maturity stages or because fishermen will preferentially catch the most profitable individuals (Holland and Sutinen, 1999; Salas et al., 2004; Andersen et al., 2012). Fisheries selection can therefore alter the distribution of relevant phenotypic traits within a population. As for natural selection, if fishing is selective for traits showing genetic variability among individuals, it has the potential to induce evolutionary change (Gjedrem, 1983; Carlson and Seamons, 2008).

2.3.1. By reducing the lifespan and removing individuals

Fisheries-induced selection can first arise without fishing targeting specific traits. For example, a uniform rise in fishing mortality across all body sizes can cause selection pressure on many traits such as length and age at maturation, as well as growth rates and reproductive investment (Roff, 1992; Heino and Kaitala, 1999; Conover, 2000; Jørgensen and Fiksen, 2010; **Paper I**), especially for late maturing species. Under normal conditions, because fecundity is correlated with size (Hixon et al., 2013; Barneche et al., 2018; Vignieri, 2018), delaying maturation to spawn at a larger size can present a considerable fitness benefit. However, this works only if mortality is low enough so that individuals can reach the ideal size before dying. The potential gains of enhanced growth, survival and future reproduction are cancelled when a fish gets caught before reproducing, and fishing pressure at moderate to high levels is expected to favour earlier reproduction at smaller sizes (Heino and Godø, 2002; Jørgensen and Fiksen, 2010; Heino et al., 2015b).

With high adult mortality induced by fishing, investment in future reproduction may not pay off. In addition to early reproduction, fishing will therefore favour higher reproductive effort at age at the expense of body growth (Heino and Kaitala, 1999; Rijnsdorp et al., 2005; Enberg et al., 2010; van Walraven et al., 2010; Enberg et al., 2012). However, Heino et al. (2015b) point out that this theory is not widely observed in fish stocks, probably because of (1) no suitable data on gonad weight, (2) measurement difficulties necessitating the use of proxies or (3) possibly less strong selection on the reproductive investment than on other traits.

The removal of biomass can also lead to changes in life-history traits through compensatory responses, even though those changes are mostly due to plasticity rather than evolution (Reznick and Yang, 1993; Rochet, 1998; Law, 2000). Such responses usually come from a relaxation of the competition for resources and generally lead to faster growth, thus reaching the required body size for maturation earlier in life (Jørgensen, 1990; Trippel, 1995; Law, 2000). Those changes being plastic, they are also faster to reverse than fisheries-induced evolution (Law and Grey, 1989; Hutchings and Fraser, 2008).

2.3.2. By selecting specific traits

2.3.2.1. Life-history traits

Fishing gears are almost always selective for specific traits. Size is the most studied trait in relation to gear selectivity, with fishermen traditionally removing the biggest fish as they usually are the most valuable (Zimmermann and Heino, 2013). Even if a certain gear is not strictly selective for size, management regulations such as minimum landing size can introduce an additional source of selectivity. The direct consequence of a selection against bigger sizes is an elevated mortality for large-sized individuals. It therefore becomes more beneficial for individuals to delay their entrance in the fishery by growing slower (Miller, 1957; Fenberg and Roy, 2008; but see Enberg et al., 2012) and maturating at smaller size (Conover and Munch, 2002; Heino and Godø, 2002), potentially leading to a decreased fecundity (Law, 2000; Jørgensen et al., 2007). Smaller fish experience higher predation rates (Peterson and Wroblewski, 1984; Sogard, 1997) and, combined with poorer recruitment through decreased fecundity, such changes can hinder a stock's productivity and amplify fluctuations in abundance (Hsieh et al., 2006; Ottersen et al., 2006; Britten et al., 2016). This pattern is reversed when the smaller length-classes are targeted (Heino and Godø, 2002; Kuparinen et al., 2009) and predictions become more difficult when disruptive selection occurs (Rueffler et al., 2006; Jørgensen et al., 2009). Several solutions to avoid undesired evolution due to size-selectivity have been proposed, such as targeting a specific size range, for instance around maturation size (Jørgensen et al., 2009; Zimmermann and Jørgensen, 2017; Ayllón et al., 2018).

Fishing selectivity can have more direct effects on age at maturation, by targeting certain maturity stages (e.g. when mature and immature individuals are segregated in time or space). Little evolution of age at maturation is to be expected when only mature individuals are selected (Law and Grey, 1989; Heino, 1998; Ernande et al., 2004). However, reduction of adult survival can lead to increased allocation towards reproduction, at the cost of slower adult growth (Reznick, 1983; Stearns, 1992; Enberg et al., 2012). In contrast, targeting immatures will likely induce evolution towards earlier maturation (Ernande et al., 2004). As growth typically slows after maturation, selection for early maturation can result in smaller size at age later in life, with similar consequences for the stock as a direct selection on size.

Finally, life-history traits are correlated with traits related to bioenergetics that can affect a fish's capacity to escape a fishing gear, such as the resting metabolic rate, aerobic scope and swimming capacity. Even though there is a strong potential for fisheries-induced evolution of those traits, they have received little attention and how their evolution will affect life-history traits (and vice-versa) is still to be explored (Hollins et al., 2018).

2.3.2.2. Behaviour

It is easier to show that fishing gears have the capacity to select for behaviours than finding evolution of behavioural traits in wild populations. Evidence in the wild remains scarce, probably because data is not available as it is a difficult trait to measure (Heino et al., 2015b). However, behavioural traits possess a heritable component, which makes them potentially susceptible to fisheries-induced evolution (Mousseau and Roff, 1987; Merilä and Sheldon, 2000).

It is now commonly accepted that different fishing gears can select for different behaviours, such as foraging activity, exploration, aggressivity and habitat preference (Arlinghaus et al., 2017; Diaz Pauli and Sih, 2017) and numerous evidence is coming from selection experiments in the lab or semi-natural ponds (e.g. Biro and Post, 2008; Diaz Pauli et al., 2015), as well as from theoretical models (Andersen et al., 2018; **Paper I**). Correlations between behavioural, physiological and life-history traits also suggest that behaviour-selective fishing could induce indirect selection in other traits. For example, shyer fish (i.e., less aggressive, less willing to take risk in presence of predators) have been found to have lower metabolic rates (Cooke et al., 2007, largemouth bass (*Micropterus salmoides*)), lower energetic requirements (Cutts et al., 2002, Atlantic salmon (*Salmo salar*); Cooke et al., 2007; Nannini et al., 2011, largemouth bass) and more efficient energy conversion (Nannini et al., 2011, largemouth bass). In addition to direct detrimental effects such as lower catchability or maladaptation of the targeted population, changes in one species behaviour could affect its interaction with other species (e.g. predator-prey interaction) and lead to cascading effects at the ecosystem level (see Scheffer et al., 2005 for an example with Atlantic cod (*Gadus morhua*)).

2.3.2.3. Morphological traits

Few evidence of fishing-induced evolution in morphological traits is available, even though they have a higher heritability than life-history traits (Mousseau and Roff, 1987). Heino and Godø (2002) propose that this lack of evidence is due to either a lack of attention to this issue or because changes in morphology are purely plastic. Selection on morphological traits acts in the same way as for other traits, and shapes more easily retained by the gear are selected against (Hamon et al., 2000; Alós et al., 2014). Note that morphology is not limited to somatic growth and changes in shape can be associated with differences in surplus energy (e.g. liver size) and investment in reproduction (e.g. gonad size; Enberg et al., 2012). Consequences of such selection are not very well explored, but, as body shape can affect swimming performance (Ghalambor et al., 2004), this selection could affect individuals' vulnerability to predation and fishing gears. Additionally, direct selection on morphology could indirectly select on traits associated to energy acquisition and allocation (Álvarez and Nicieza, 2005; Burton et al., 2011) with consequences for stock's resilience and productivity.

2.3.2.4. Phenology

Even though variation in phenology (i.e. timing of breeding) plays a critical role in the productivity of fish populations, it also has received less attention than other life-history traits. Quinn et al. (2006, 2007) have shown changes in spawning migration (i.e. run) timing for Atlantic and sockeye salmon, respectively, that could be partly associated with differences between early and late-running fish vulnerability. Acoustic tagging of Atlantic cod also showed that individuals with certain movement patterns were more likely to be fished than others (Olsen et al., 2012). More generally, management measures can impose a fishing intensity varying over time and potentially induce a selection regarding important traits such as spawning or migration date (Quinn et al., 2007; Loher, 2011; Peer and Miller, 2014).

3. Methods to detect fisheries-induced evolution

“Counting fish is just like counting trees - except that they are invisible and keep moving”

John Sheperd, University of South Hampton, New Hampshire, United States

3.1. Statistics/Data

Statistical methods can be used to detect fisheries-induced evolution by isolating a signal attributable to evolutionary adaptation from variations due to demographic and plastic changes (Heino et al., 2002b; Barot et al., 2004a). The most commonly used statistical method to detect fisheries-induced evolution in age and length at maturation is probably the probabilistic maturation reaction norms (PMRNs, Heino et al., 2002a, b, c; Barot et al., 2004b). Reaction norms give age and size specific probabilities for fish with different growth rates to mature. This method therefore allows to disentangle the effect of growth and mortality on the maturation schedule from other sources of variation. However, those sources might be attributable to other factors than fishing (e.g. temperature). Thus, even though they are a promising tool, they cannot give unequivocal evidence of genetic change (but see Kraak, 2007).

The same principle (isolation of a remaining trend attributable to genetic changes) can be applied with multivariate regressions. However, data of good quality, for both the response and explanatory variables, is necessary and, because evolution can take place at a decadal time scale (Law, 2000), the time series needs to be long enough to cover the trend. Statistical models can also get very complex, and one needs to give close attention to the structure of the model (e.g. auto-correlation, heterogeneity, zero-inflation…) to make sure the detected trends are not due to model misspecifications (e.g. Zuur et al., 2007). Alternatively, fisheries-induced selection can be directly included in the model: with a long enough time series, traits in the parents and offspring can be compared and selection gradients calculated using quantitative genetics (Swain et al., 2007). Parent-offspring differences can then be explained by differences in environment experienced and selection differentials. The main problem of those methods is that data for environment (e.g. natural mortality, local temperature) and for some phenotypic traits (e.g. gonad weight) is often scarce or estimated from models (e.g. spawning stock biomass, fishing mortality...; Brooks and Deroba, 2015) depending on a set of assumptions. They therefore do not allow to attribute any trend observed to genetic changes with certainty, and one needs to be aware of the pitfalls they represent when using them.

3.2. Experiments

Controlled experiments offer an opportunity to test the effect of different selections on one or several traits while maintaining other variables constant. They can be used to determine which phenotypic or genetic changes can be attributed to the experimental pressures and are useful to study the effect of co-evolution and combination of selections on different traits (e.g. Conover and Munch, 2002; Biro and Post, 2008; van Wijk et al., 2013; Diaz Pauli et al., 2015). However, uncertainties arise when scaling-up results from small, controlled environments to large and variable systems. One could question the validity of applying conclusions drawn from reared species to wild populations, as well as the adequacy of the simulated selections (Conover and Baumann, 2009; Diaz Pauli and Heino, 2014). Even though, application of their conclusions to exploited populations is difficult, experiments constitute good tools to produce hypotheses concerning changes observed in the wild.

3.3. Models

Models can be used to combine descriptions of known mechanisms at the individual level, and subject them to simulated environmental changes. Response to these changes can then be translated at the population and ecosystem scale. Compensatory processes such as density-dependence can be easily integrated and therefore give a mechanistic overview of the consequences of fishing selection. Predictions made by mechanistic models can then be compared with experiments results or field data to further refine hypotheses and test them with more adapted models, through an iterative modelling-data-modelling cycle (Grimm et al., 1996; Grimm and Railsback, 2005; Figure 2).

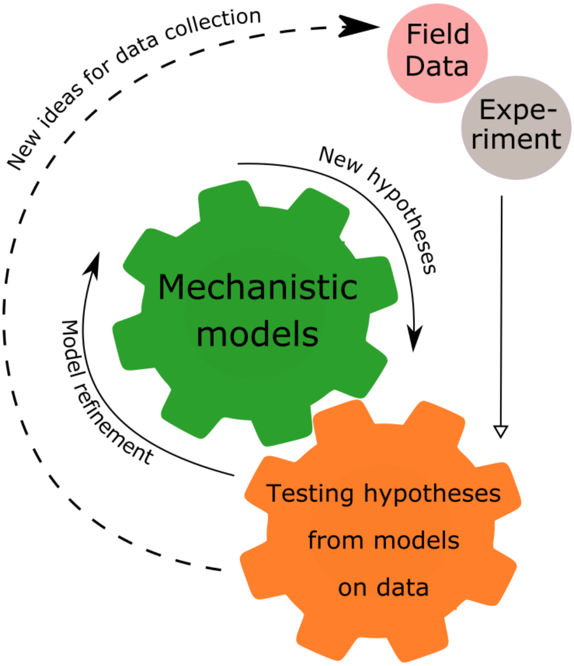


Figure 2: Iterative modelling-data-modelling cycle (reproduced with the authorization of Katja Enberg).

A wide range of models exist, each adapted to answer specific questions. For example, dynamic state-dependent modelling aims at finding optimal life-histories under varying environmental pressures and allows to model rather complex energy acquisition and allocation mechanisms in a relatively simple fashion. (Law and Grey, 1989; Ernande et al., 2004; Jørgensen and Fiksen, 2006; Dunlop et al., 2009; Enberg et al., 2009; Sharpe and Hendry, 2009; Jørgensen and Fiksen, 2010; **Paper I**). Even though this method cannot attribute observed changes to genes or plasticity and produce an estimate of the time scale of the response, it is a very practical tool for hypothesis formulation.

More complex models, such as eco-genetic models, can be required to improve hypotheses formulated by simpler methods. By combining quantitative genetics and adaptive dynamics, they allow to predict the time scale of evolutionary responses to selection pressures while accounting for realistic population structure and life-history detail. However, interpretation and communication of the output can sometimes be challenging (Dunlop et al., 2009; Heino et al., 2015a).

4. Norwegian Spring-spawning herring

4.1. Life-history

The Norwegian spring-spawning herring is a very important species of the Nordic Seas. With a current stock size of 4 million tons (ICES, 2018), it is one of the most important fish stock of the North-East Atlantic. It supports numerous predator populations (e.g. cod, sea birds, whales; Hamre, 1994) and represents an economically valuable resource. Herring is an iteroparous species (i.e. reproduces every year), that can live up to 20-25 years and reach a size of around 40 cm (Beverton et al., 2004). The spawning takes place off the coast of Norway, mainly from January to March (Slotte and Fiksen, 2000). Even though the main spawning grounds are located off Møre (Figure 3), the migration distance depends on size and condition (Slotte, 1999b), and spawning occurs all along the coast. After hatching, the larvae drift northward, with the Norwegian Coastal Current, towards the nursery grounds. While the main nursery grounds are located in the Barents Sea, some individuals may drift towards the fjords (Holst et al., 2004). When year-class strength is low, a higher proportion of the larvae is restricted to the fjords (Toresen, 1990). Experiencing warmer temperatures, those individuals grow faster than their counterparts located in the Barents Sea (Dragesund et al., 1980).

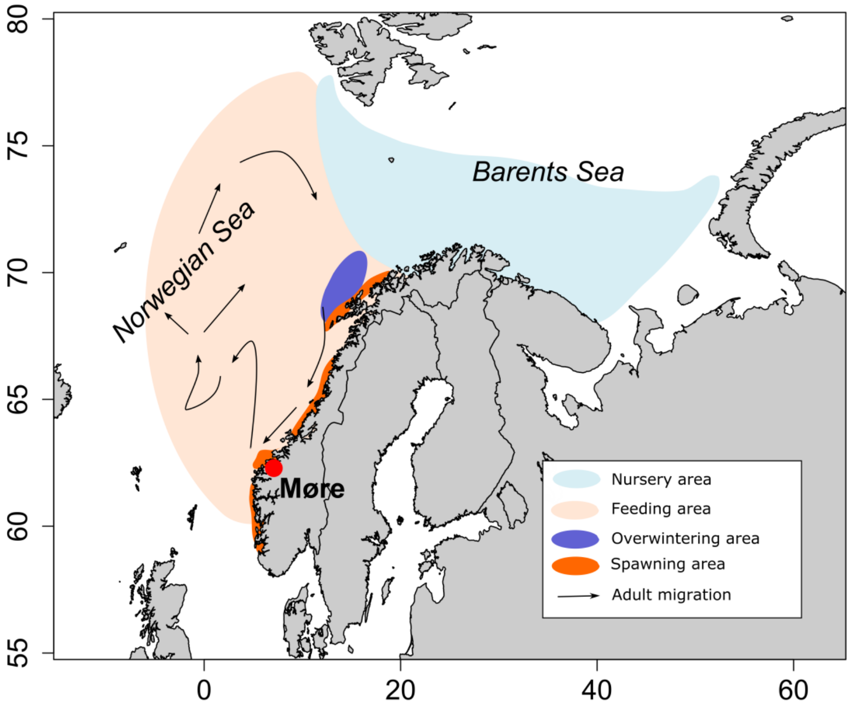


Figure 3: Distribution area and current migration route of Norwegian spring spawning-herring.

Herring starts maturing at an average length of 30 cm, corresponding to an age between 3 and 7 years old (Beverton et al., 2004; Engelhard and Heino, 2004a). It then leaves the nursery grounds to join the adult stock (Dragesund et al., 1980; Huse et al., 2002). After spawning, the adults migrate towards the Norwegian Sea where they feed mainly on copepods (*Calanus finmarchichus* and *C. hyperboreus)*, appendicularians, amphipods and euphausiids (Prokopchuk and Sentyabov, 2006; Bachiller et al., 2016). Around September-October, they migrate back to the overwintering grounds, along the northern part of the Norwegian coast (Figure 3).

Herring is a capital breeder and the amount of energy allocated to growth, reproduction and migration mostly depends on the energy acquired during the relatively short feeding season (Slotte, 1999a; Slotte, 1999b; Stephens et al., 2009; Kennedy et al., 2011).

Environmental factors govern the large-scale variations of the stock. Year-class strength is strongly linked to predation pressures, feeding conditions and temperature, among others, themselves driven by oceanographic processes. In turn, fluctuations in stock size can have a strong impact on the stock's life-history. In the past, migration routes and distances changed with biomass levels (Dragesund et al., 1980; Huse et al., 2010). Growth also depends on year-class strength, among others, and changes in size-at-age can affect a wide range of traits such as migrating potential (Slotte, 1999a; Slotte, 1999b; Slotte et al., 2000), optimal swimming speed (Ware, 1975; Ware, 1978), metabolic rate (Winberg, 1956; Winberg, 1961) and investment in reproduction (Óskarsson et al., 2002; **Paper II**). In addition to driving year-to-year variation, the effects of environmental conditions one year, such as food availability, can also extend over 3 to 4 years (dos Santos Schmidt et al., 2017).

4.2. Short history of the fishery

In a virgin state, the Norwegian Spring-spawning herring stock might have reached 15 to 20 million tons. The fishery is shared between Norway, Russia, the Faroe Islands, Iceland and Europe, and constitutes an important source of employment and economy for all the many countries participating, especially Norway which records the largest annual harvest (Bjørndal et al., 1998; Bjørndal et al., 2004). In the early 1900's, the fishery was an open-access fishery, dominated by small vessels with drift nets, even though the large catches were made with shore seines. In the 30's, an increase in the total catches was registered, due to the apparition of larger vessels operating purse seines (Toresen and Østvedt, 2000; Sandberg, 2010).

New fishing technology got introduced in the early 60's and modernization of the fishery led to an increased efficiency of the fleets (Toresen and Østvedt, 2000).

Together with open-access management regulations for coastal and high sea fisheries, this new equipment allowed for a substantial increase of the catches. The highest annual catch occurred in 1966, with 2 million metric tons fished. From this point, catches drastically decreased, going from 1.5 million to 200 thousand tons. Overfishing caused the stock to collapse (Dragesund et al., 1980; Toresen and Østvedt, 2000) and fishing was banned in the early 1970's. The stock started to recover in 1986, due to the 1983 year-class that showed an exceptionally strong recruitment (Røttingen, 1990; Bjørndal et al., 1998). Together with the strong year-classes of 1991 and 1992 (Sætre et al., 2002), it allowed the stock to fully recover. To avoid a second collapse, new management measures and regulations have been introduced. TACs are currently shared between Iceland, Faroes, Russia, Norway and EU and the fishery targets almost only mature individual, with a minimum landing size of 25 cm (Sandberg, 2010).

5. The Norwegian Sea-Barents Sea ecosystem

The Norwegian Sea-Barents Sea ecosystem is a rich, dynamic system, governed by the influx of Atlantic water through the Faroe-Shetland channel (Hamre, 1994; Saetre and Skjoldal, 2004). When it reaches the Norwegian Coast, a part of the Atlantic waters is directed towards the North Sea, while the rest moves up, along the coast, with the Norwegian Coastal Current. In the Norwegian Sea, this warm inflow meets the cold Arctic waters at the Arctic front (Blindheim et al., 2000; Blindheim and Rey, 2004), forming the physical basis of a very productive area. The warm inflow of Atlantic water together with the Norwegian Coastal waters dominate the southern part of the Barents Sea whereas the northern part is largely composed of cold Arctic waters, mixing at the Polar front (Loeng, 1991). Productivity in this area is driven by the melt of the winter ice edge that stabilizes the upper layers and drives the spring plankton bloom (Sakshaug and Skjoldal, 1989).

The Norwegian Sea-Barents Sea ecosystem variability is driven at a large scale by the North-Atlantic Oscillation (NAO) which influences temperatures and currents in the Norwegian Seas. When the NAO is positive, strong westerly winds blow over Europe, increasing the transport of warm Atlantic water in the Barents Sea and leading to favourable environmental conditions for the recruitment of several main fish populations (Marti and Fedorov, 1963; Sætersdal and Loeng, 1984; Sætersdal and Loeng, 1987; Blindheim et al., 2000; Saetre and Skjoldal, 2004).Those physical processes also affect zooplankton diversity and abundance in the Norwegian Sea (Beaugrand et al., 2002; Loeng and Drinkwater, 2007) determining the feeding conditions for the three main stocks who come to feed in summer: adult Norwegian spring-spawning herring, blue whiting (*Micromesistius poutassou*) and Northeast Atlantic mackerel (*Scomber Scombrus*). Those species mainly feed on *Calanus* sp.p., amphipods, krill, appendicularian and euphausiids (Dalpadado et al., 2000; Prokopchuk and Sentyabov, 2006). Even though the high zooplankton consumption rates and overlapping diet of those three pelagic species might be a source of inter-specific competition (Huse et al., 2012; but see Bachiller et al., 2018), their interactions are somewhat restricted by differences in depth and temperature preferences, (Iversen, 2002; Utne and Huse, 2012; Utne et al., 2012), as well as timing of peak feeding (Hamre, 1980; Dalpadado et al., 2000; Iversen, 2002).

The Northeast Atlantic cod (*Gadus morhua*), polar cod (*boreogadus saida*), capelin (*Mallotus villosus*) and young Norwegian spring-spawning herring are the main fish populations found in the Barents Sea. Those species are mainly supported by the plankton production of the area, even though species interactions are more complex than in the Norwegian Sea (Hamre, 1994; Ushakov and Prozorkevich, 2002). The larval stages of *C. finmarchicus* are the principal food for fish larvae, and an important factor for the recruitment of cod and herring (Dalpadado et al., 2009). Young herring can also feed on capelin larvae, inducing a strong predation pressure on the 0-year group in years of strong year-classes (Gjøsæter, 1998; Hallfredsson and Pedersen, 2009). Capelin abundance in turn affects abundance and condition of cod, its main predator

(Gjøsæter et al., 2009). More generally, herring and capelin constitute the main source of food for a wide range of fish stocks, marine mammals and sea birds. As for the Norwegian Sea, the dynamics of the system and the inter-specific interactions are governed by the inflow of Atlantic water, closely linked to the NAO, which determines distribution, recruitment success and growth of the main species involved (Ottersen et al., 2001; Loeng and Drinkwater, 2007).

Aim of the thesis

Considering the intense exploitation of Norwegian spring-spawning herring, it is surprising that we do not observe changes in length and maturation age similar to the ones occurring in other heavily exploited stocks (Engelhard and Heino, 2004a; Engelhard and Heino, 2004b). However, Norwegian spring-spawning herring constitutes a special case since the fishery mainly targets mature individuals, and this type of selection is known to lead to little changes or even postpone maturation (Law and Grey, 1989; Ernande et al., 2004; Jørgensen et al., 2009). Before this thesis Engelhard and Heino (2004a, b), were the only ones who investigated the potential effect of fishing in Norwegian spring-spawning herring. Working with PRMNs, they suggested that a compensatory response induced by year-class strength is probably the main mechanism behind variations of age and length at maturation and found little evidence for a remaining genetic trend. Even though herring is a very well documented species, no other study on Norwegian spring-spawning herring life-history traits investigated potential fisheries-induced evolution of other traits.

As life-history traits are determinants of a stock's productivity, undetected fisheries-induced evolution can have wide, detrimental effects on a stock's resilience and sustainability. Understanding how fishing, together with environmental factors, drives Norwegian spring-spawning life-history traits and dynamic is therefore important for the proper management of the stock This issue is also highly relevant the management of the entire ecosystem, as herring plays a key role in transferring energy from the lower to the higher levels (Hunt and McKinnell, 2006; Smith et al., 2011). The aims of this thesis are (1) investigating fisheries-induced evolution in other traits than length and age at maturation of Norwegian spring-spawning herring and (2) clarify hypotheses regarding the absence/presence of long-term trends, potentially induced by genetic changes.

Research questions:

- What is the long-term effect of fishing and environment to changes in other traits than age and length-at-maturation? **(Papers II and IV)**
- Can the fishing-induced selection experienced by the stock explain the presence/lack of fisheries-induced evolution of the traits previously studied? **(Paper III)**
- Could the presence/lack of fisheries-induced evolution be explained by other forms of selection than length-selectivity? **(Paper I)**

Summary of papers

Paper I: Evolutionary effects of fishing gear on foraging behaviour and life-history traits

Fishing gears are designed to exploit the natural behaviours of fish, and the concern that fishing may cause evolution of behavioural traits has been receiving increasing attention. The first intuitive expectation is that fishing causes evolution towards reduced boldness because it selectively removes actively foraging individuals due to their higher encounter rate and vulnerability to typical gear. However, life-history theory predicts that fishing, through shortened lifespan, favours accelerated life histories, potentially leading to increased foraging and its frequent correlate, boldness. Additionally, individuals with accelerated life-histories mature younger and at a smaller size, and therefore spend more of their life at a smaller size where mortality is higher. This life history evolution may prohibit increases in risk-taking behaviour and boldness, thus selecting for reduced risk-taking and boldness. Here we aim to clarify which of these three selective patterns ends up being dominant. We study how behaviour-selective fishing affects the optimal behavioural and life-history traits using a state-dependent dynamic programming model. Different gear types were modelled as being selective for foraging or hiding/resting individuals along a continuous axis, including unselective fishing. Compared with unselective harvesting, gears targeting hiding/resting individuals leads towards evolution of increased foraging rates and elevated natural mortality rate, while targeting foraging individuals leads to evolution of decreased foraging rates and lower natural mortality rate. Interestingly, were predicted for traits difficult to observe in the wild (natural mortality and behaviour) whereas the more regularly observed traits (length-at-age, age at maturity, and reproductive investment) showed only little sensitivity to the behavioural selectivity.

Paper II: Eight decades of changes in herring reproductive investment: effects of fishing, environment and conspecific density

Reproductive investment is a central trait for population dynamics and productivity. Fishing is a major driver affecting population structure, dynamics, and adaptation of life-history and behavioural traits. Theory predicts an increase in reproductive investment in response to an elevated mortality and fishing has the capacity to induce evolutionary changes in this trait. In this study, we investigate the contribution of environment, fishing pressure, and intra-specific competition to variation in the reproductive investment of the Norwegian spring-spawning herring (*Clupea harengus*), a stock that has been fished for centuries, and monitored for decades. Growth rate (measured as mean age-at-length), sea surface temperature and fishing pressure were positively correlated with reproductive investment. Fish with a higher post-spawning weight had a lower reproductive investment in the largest length-class. This non-intuitive result reflects the trade-off between growth and reproduction, as, among the large fish, the fast-growing individuals invested less in reproduction and were in better condition after spawning than slow-growers. After accounting for the main environmental variables and fishing pressure, we discovered a weak, but significant positive temporal trend in the reproductive investment, suggesting fisheries-induced evolutionary adaptation in the Norwegian spring-spawning herring.

Paper III: The Rosa Lee Phenomenon revisited: Population dynamics, sampling and selectivity affect the apparent changes in growth rates

Natural and anthropogenic pressures shape the selection landscape populations are subjected to. In turn, this landscape determines optimal combinations of life-history traits and its modification can lead to evolution of wild populations. The Rosa Lee phenomenon can be defined as the difference in growth rates obtained from comparing lengths-at-age back-calculated from scales of older vs younger fish.

Assuming the back-calculation method is adapted, and the sampling of individuals is unbiased, it constitutes an interesting tool to investigate the selection landscape a population experiences. The Rosa Lee phenomenon was detected more than a century ago in Norwegian spring-spawning herring, a fish stock exploited for centuries and monitored for decades. However, what causes this phenomenon in this species is not known. In this paper, we study the Rosa Lee phenomenon in Norwegian spring-spawning herring over the last century and offer possible causes for this phenomenon. We found that the Rosa Lee phenomenon has greatly varied over time and shows that fast-growing fish were favoured when fishing pressure was low but selected against in periods of exploitation. Natural and fishing pressures therefore seem to act in opposite ways, which might present an issue for the stock's sustainability. We could not explain the current selection pattern with natural mortality and size-selective fishing only, suggesting that other selection pressures might be at play (e.g. behavioural selection). Our study demonstrates that the Rosa Lee phenomenon in herring is shaped by multiple factors, and their strength has varied over time. It therefore constitutes a first step to understand the selective forces Norwegian spring-spawning herring is subjected to. A natural continuation of this work is to quantify the relative contribution of environmental and anthropogenic drivers to the Rosa Lee phenomenon.

Paper IV: Reconstructing growth in Norwegian spring-spawning herring from scale increments: exploring historic population dynamics and their drivers

The Norwegian spring-spawning (NSS) stock of Atlantic herring (*Clupea harengus*) is one of the largest fish stocks in the Atlantic Ocean and has an extraordinary long history of commercial fishing and scientific data collection, dating back more than 100 years. In the late 1960's overfishing caused the stock to collapse, and it took around 15 years for it to recover. Despite the intense exploitation, only mixed evidence of fisheries-induced evolution of age and size at maturation as well as investment in reproduction has been observed. Study of the growth patterns over the last 80 years might provide more insights on the presence or absence of fisheries-induced evolution. In the present study we analysed a time series of scale measurements, directly linked to body growth, that spans from 1935 to 2014 and covers all cohorts during this period. We tested a range of mixed-effect models describing potential intrinsic and extrinsic sources of variation in growth, and selected the best fitting model based on AIC weights. Age and cohort were used to represent internal variables, while, stock and cohort biomass, sea surface temperature, the North Atlantic Oscillation, fishing pressure and year were tested as external ones. Age at capture was used as a control for selective apparent mortality. This allowed us to explore the growth dynamic throughout lifetime and throughout the time series of cohorts, as well as possible extrinsic drivers of growth. Age was found to be a key determinant in explaining growth, but our models also revealed density-dependent growth as well as an effect of temperature. The latter was much more pronounced for juveniles, indicating that extrinsic effects play a larger role for growth dynamics at early life stages. A weak positive relationship between fishing and growth was also detected but should be interpreted with care. Furthermore, the random effects revealed a clear temporal pattern toward slower adult growth, but no significant trend was found for juveniles. This suggests that important drivers of change in growth have not been explicitly included, and one of these drivers may be evolution

Discussion

Norwegian spring-spawning herring has been exploited for centuries and the effects of intense fisheries activity have been observed, notably on the demographics, when the stock collapsed in the late 1960’s. Despite its history of intense exploitation, only two studies investigated potential presence of fisheries-induced evolution in Norwegian spring-spawning herring life-history traits (Engelhard and Heino, 2004a; Engelhard and Heino, 2004b), revealing mixed evidence for evolution of age and length at first maturity. This doctoral thesis investigates the effects of fishing pressure on other traits such as behaviour (**Paper I**), reproductive effort (**Paper II**) and growth (**Paper IV**) and draws a picture of the selection pressure experienced by Norwegian spring-spawning herring over the 80 years of data available (**Paper III**). A weak but significant residual trend, possibly attributable to evolution, was found in the reproductive effort (increase, **Paper II**) and adult growth (decrease, **Paper IV**) of Norwegian Spring-spawning herring. The weakness of those trends might be partly explained by the changes in the selection experienced by the stock before, during and after the collapse period (**Paper III**). This thesis also highlighted the capacity of fishing to affect life-history traits as well as behaviour and natural mortality via direct selection on the behaviour (**Paper I**). However, how much this type of selection applies to Norwegian spring-spawning herring is still not certain.

1. Detecting evolution

1.1. Data limitation

The main challenge when studying fisheries-induced evolution is disentangling genetic changes from all other sources of variation in life-history traits. With statistical models, in the ideal case where we can account for all external variables, theory states that a trend in the residuals can be attributed to genetic change (Heino et al., 2015b). However, this ideal case is far from reality and such methods are often limited by data availability. As Heino et al. (2015b) put it, it is not possible to gather all the local temperatures and feeding conditions a fish experienced at each moment of its life. Similarly, time series are sometimes incomplete or too short to be used. For example, we could not include important variables such as zooplankton and volume transport since data are available only from 1994. Even though proxies (e.g. NAO index) can be used in an attempt to capture the share of the variation they explain, it also makes the interpretation more difficult. Finally, some environmental indices cannot be measured accurately, need to be aggregated and/or are estimated from models, with the result depending on the model's assumptions (e.g. Spawning Stock Biomass, fishing mortaliy…; Brooks and Deroba, 2015). Even though this method is often the only way to quantify some variables, one still needs to be cautious when interpreting results from this type of data and be aware of the pitfalls.

As a consequence, other mechanisms not considered in this thesis might account for the trends we detected. For example, migration patterns changed regularly during the last century (Dragesund et al., 1980). However, is not likely that modifications of the migration patterns lead to such gradual trends as those observed. A more likely factor could be changes in oxygen concentrations as reduced oxygen availability can lead to similar effect as fisheries-induced evolution, i.e. decrease in age at maturation and increase in reproductive investment (Diaz Pauli et al., 2017). In the current context of global warming, lower oxygen concentrations could be expected as the waters get warmer, especially towards the Arctic, where the impact is the most important (Hoegh-Guldberg and Bruno, 2010; Lind et al., 2018). Noticeable changes in the temperatures are however reported only from the 2000's and oxygen concentrations are therefore not likely to drive the long-term trends over the last century. Even though the interaction of climate change and fishing selectivity is outside the scope of this thesis, this problematic constitutes an important point for future research, and such environmental considerations will have to be included in future studies on fisheries-induced evolution (Neuheimer and Grønkjær, 2012; Holt and Jørgensen, 2014).

1.2. Plastic versus genetic changes

Phenotypic plasticity has the potential to reduce the effects of selection or to hide genetic changes (Schlichting, 2004; Lande, 2009; but see Pfennig et al., 2010). In theory, as genotypes can produce several phenotypes in response to different environmental conditions (Figure 1), plasticity can be enough to optimise fitness without requiring genetic changes (even though recent studies showed that plastic changes could be heritable to some degree; e.g. Wang et al., 2016). As Pfennig et al. (2010) present it, it does not matter to natural selection how optimal phenotypes arise, and both genetic and plastic responses can be favoured to produce them. Therefore, high levels of plasticity can strongly reduce the effect of selection on the genotypes by placing the population mean close to the optimal value, without genetic changes taking place (Price et al., 2003; but see Wang et al., 2016). Alternatively, different genotypes can also produce the same phenotype (Figure 1) and therefore become undistinguishable without genetic analyses.

Norwegian spring-spawning herring is a very plastic species (Geffen, 2009) and its extreme adaptability to current and past environmental conditions (dos Santos Schmidt et al., 2017) constitutes a challenge in detecting evolutionary changes. Important traits for Norwegian spring-spawning herring life-history such as metabolic rate (Winberg, 1956; Winberg, 1961), optimal swimming speed (Ware, 1975; Ware, 1978), migration efficiency (Slotte, 1999a; Slotte, 1999b; Slotte and Fiksen, 2000; Slotte et al., 2000), age at maturation (Engelhard and Heino, 2004a; Engelhard and Heino, 2004b) and reproductive effort (Óskarsson et al., 2002; **Paper II)**, largely depend on size and growth, even though they can also be directly affected by temperature and feeding conditions. Fluctuations in growth are in turn mainly driven by temperature (Holst, 1996; Ottersen and Loeng, 2000) and year-class strength (Toresen, 1990; Ottersen and Loeng, 2000), and environmental conditions experienced early in life can have repercussions on size at later stages (Brophy and Danilowicz, 2003; Husebø et al., 2007). In addition to these numerous sources of variation, the Norwegian spring-spawning herring stock is composed of two components originating from different nurseries (Northern in the Barents Sea and Southern in the Norwegian fjords) and following distinctive growth patterns (Dragesund et al., 1980; Holst and Slotte, 1998). During the last century, the Southern component dominated in periods of low biomass, while the Northern component constituted the biggest part of the stock otherwise (Holst and Slotte, 1998).

Together, those processes induce important inter-individual and year-to-year variations in Norwegian spring-spawning herring traits, potentially masking eventual changes at the genotype level (Hendry et al., 2008). However, the relative contribution of genotype and environment to Norwegian spring-spawning herring life-history traits has not been quantified yet and warrants more research.

1.3. Patterns of selection

Evolutionary changes can occur at a decadal time scale, much faster than previously thought (Hendry and Kinnison, 1999; Kinnison and Hendry, 2001). In contrast, we studied traits over a period of almost a century, only to find weak trends in the traits considered (**Paper II**, **Paper IV**). Engelhard and Heino (2004b) already formulated several hypotheses, related to the biological properties of the stock, to explain such mixed evidence. Assuming the trends have a genetic basis, additional inferences can be made based on the selection patterns and the fishery history.

The Norwegian spring-spawning herring fishery is relatively unselective compared to demersal stocks where a rapid evolution was found (e.g. Heino et al., 2002c; Law, 2007; Hard et al., 2008). As both harvest rates and intensity of the selection play a role in the evolutionary rates of wild populations (Hendry et al., 2008; Kuparinen et al., 2009), absence of strong selection might have induced relatively slower evolution than in other stocks. Before and after the collapse, mostly mature individuals were targeted, even though small juveniles of age and size not yet relevant for maturation were also caught before the collapse (Toresen and Østvedt, 2000; Toresen and

Jakobsson, 2002; Engelhard and Heino, 2004b). This type of harvesting is known to induce weak selection on maturations schedules (Law and Grey, 1989; Ernande et al., 2004). However, even fisheries that are not very selective are expected to produce evolutionary change when fishing mortality is high enough (Policansky, 1993; Allendorf and Hard, 2009). Strong adult mortality is expected to lead to increased reproductive investment at the detriment of growth (Stearns, 1992). Even though our results go in this direction, we cannot show strong evolutionary change in those two traits and other processes might explain the weakness of the trends.

During the last century, exploitation rates experienced by the Norwegian spring-spawning herring changed, with, most notably, the interruption of the fishery during the collapse. In addition to the relaxed fishing pressure, selective forces were also modified: fast-growers were advantaged over slow-growers while the opposite was true during periods of exploitation (**Paper III**). Such changes in selective pressures have the capacity to slow evolution of populations (Palumbi, 2001). Additionally, in their review and meta-analysis, Hendry and Kinnison (1999) and Kinnison and Hendry (2001) show that, over a long period of time, wild populations alternatively experience periods of fast short-term directional evolution and periods of apparent quasi-stasis. The alternance of these periods can thus make evolution rates appear as slow when taken together. Changes in exploitation rates and selectivity over the last century might therefore play a role in the weakness of the trends detected in Norwegian spring-spawning herring life-history traits.

> "[…] The periods, during which species have undergone modifications, though long as measured by years, have probably been short in comparison with the periods during which they retain the same form"
>
> (Darwin, 1872)

Finally, the trends observed in Norwegian spring-spawning herring traits might be driven by the current selection pattern, thus explaining their lack of strength over 80 years. As this stock has been fished for centuries, the data gathered before the collapse may provide a picture of a stock already adapted to a relatively non-selective fishing pressure. When the fishery re-opened, new management measures were put in place, introducing a new selection pattern (Sandberg, 2010; **Paper III**). It is not yet clear how this new pattern has arisen, and several hypotheses are still to be explored in detail: (1) the fishery could select on other traits, in addition to size, leading to changes more difficult to measure using traditional data (e.g. behaviour, **Paper I**); (2) In addition to fisheries-selection, natural selection pressures have changed, shaping the overall selection landscape in a different way (Carlson et al., 2007; Edeline et al., 2007).

2. Consequences for fisheries management

Fisheries-induced evolution of life-history traits has the capacity to alter population dynamics and can be detrimental to stock biomass, demography and economic yield (Law and Grey, 1989; Conover and Munch, 2002; Jørgensen et al., 2007; Zimmermann and Jørgensen, 2017). Rates of reversibility in evolutionary changes due to fisheries-induced evolution are extremely low (Law and Grey, 1989; Dieckmann and Heino, 2007; Kuparinen and Merilä, 2007; Swain et al., 2007), especially if combined to a major depletion of fish stocks due to over-exploitation (Pandolfi, 2009). Those processes may constitute an obstacle for the stock's recovery and hinder recruitment (Walsh et al., 2006). If fisheries-induced evolution goes undetected, stocks may be wrongly assessed as being within safe biological limits and long-term yield under optimal fishing may be overestimated (Jørgensen et al., 2007; Enberg et al., 2010; Zimmermann and Jørgensen, 2015). In contrast to this alarming picture, other studies showed that fisheries-induced evolution can be of little consequence for recruitment estimations and thus sustainable management (Enberg et al., 2010). Its impact on references points such as MSY (i.e. Maximum Sustainable Yield) and MEY (i.e.

Maximum Economic Yield) is also minor, considering other management challenges such as natural fluctuations and climate change (Zimmermann and Jørgensen, 2015). Even though it decreases the ability of the stock to recover on the long-term, it does not necessarily hinder the initial recovery potential of depleted stocks (Enberg et al., 2009) and the resilience to high fishing pressures (Enberg et al., 2009; Heino et al., 2013). Finally, some types of fisheries-induced selection can result in increased sustainable yields and stock's productivity (Heino, 1998; Zimmermann and Jørgensen, 2017), and can therefore constitute a tool for stock management.

It is still difficult to predict how much of this applies to Norwegian spring-spawning herring. Even though the loss of the bigger individuals and the evolution towards slower growth may impact the stock's productivity, the consequences for the fishery might be less important than in other stocks were age and size at maturation decreased. In addition, mostly mature individuals are targeted, which, in theory, can lead to higher biomass and yield (Heino et al., 2013; Zimmermann and Jørgensen, 2017). However, the current trends in Norwegian spring-spawning herring life-history trait might still lead to undesirable effects on the stock's dynamic. First, bigger females tend to produce more eggs of higher quality (Trippel, 1995; Kjesbu et al., 1996; Óskarsson et al., 2002) and evolution towards slower growth and smaller adult sizes could directly lead to a decline in larval survival and thus stock productivity. Additionally, smaller fish have a higher metabolic rate (Winberg, 1956; Winberg, 1961) and a lower optimal swimming speed (Ware, 1975; Ware, 1978), making it more costly for them to reach optimal spawning grounds, off Møre (Slotte, 1999a; Figure 2; Slotte, 1999b; Slotte and Fiksen, 2000; Slotte et al., 2000). Larvae spawned at this location experience warmer waters during their drift towards the Barents Sea and therefore benefit from an increased in growth and survival probability (Krysov and Ergakova, 1990; Slotte and Fiksen, 2000). Less individuals reaching those spawning grounds in good condition might therefore hinder larval survival and the recruitment of the stock. Alternatively, new migration routes towards new optimal grounds might appear in response to changes in growth (Jørgensen et al., 2008). As recruitment partly depends on environmental conditions (Fiksen and Slotte, 2002), changes in eggs and larvae quality may just strengthen this dependence, leading to more variability and lowering the stock's resilience. Even though the slower growth is compensated by an increase in the reproductive effort (**Paper II**), the consequences in terms of stock's productivity and total egg production are difficult to predict, especially without knowledge about the total mortality experienced by the population.

Considering the actual knowledge about fisheries-induced evolution, the current management of the Norwegian spring-spawning herring stock is probably among the most desirable for a sustainable fishery (Jørgensen et al., 2009; Zimmermann and Jørgensen, 2017; Ayllón et al., 2018). As consequences of the trends we detected in the life-history traits are not certain yet, close monitoring of the stock's life-history traits and cautious management are still necessary to ensure the exploitation of the stock stays sustainable (Biro et al., 2008; Uusi-Heikkilä et al., 2008; Enberg et al., 2010; Heino et al. 2013; Laugen et al. 2014) and does not impact ecosystem dynamics, as herring plays a key role within its ecosystem by transferring energy from the lower to the higher levels (Hunt and McKinnell, 2006; Smith et al., 2011). Precautionary measures could also temper the effects of selection on other traits than size, such as behaviour, that could be occurring without being noticed (**Paper I**). Such selection modifies the level of natural mortality a population experiences and could lead to biased estimations of stock size (discussed further in 3. Fishing and natural selectivity). However, how much this case applies to Norwegian spring-spawning herring is not known and calls for further consideration.

3. Fishing and natural selectivity

In addition to fisheries selectivity, wild populations continually experience natural selection. Fishing and natural mortality can therefore act in the same or in opposite directions (Edeline et al., 2007) and the sum of both forces will shape the adaptive landscape (Hendry et al., 2006; Carlson et al., 2007; Edeline et al., 2007). In rare cases, fishing and natural selection act in similar directions (Edeline et al., 2007), but those two forces oppose each other most of the time. Such opposition may give rise to naturally maladapted phenotypes, which could pose problems for a stock's sustainability (Walsh et al., 2006; Carlson et al., 2007). This last situation seems to apply to Norwegian spring-spawning-herring: in periods of low fishing, where natural selection likely was the dominant factor, fast-growers were favoured, whereas they were selected against when fishing occurred (**Paper III**). However, it would be a mistake to assume that the strength and direction of natural selection in the wild is uniform (Grant & Grant 2002; McAdam & Boutin 2003; Carlson & Quinn 2007). For example, other factors such as biomass levels changed between periods of high and low fishing pressure. Such variations may be a cause or consequence of changes in natural mortality in addition to fishing pressure (Jacobsen and Essington, 2018).

In addition, fishing itself can cause changes in natural mortality, by leading to smaller individuals in the population but also to changes in their behaviour (**Paper I**). It is now well acknowledged that fishing gears are targeting behavioural traits (Recently reviewed in Arlinghaus et al., 2017; Diaz Pauli and Sih, 2017) and that those traits are heritable, even though quantifying the strength of this selection in wild populations may be complicated. As **Paper I** demonstrates, by changing the behaviour of exploited populations, fishing can increase or temper the compensatory response in natural mortality induced by changes in size. The regulation of this response operates through changes in predator-prey dynamics, among others, that can have cascading effects at the ecosystem level (e.g. Scheffer et al., 2005). For fisheries management, such unaccounted variations in natural mortality may lead to biased stock estimations. However, the extent of this response in wild populations is not known, for two reasons: (1) compensatory changes in natural mortality affected by behaviour may not be reflected in the most monitored traits (i.e. age and size at maturation, reproductive investment…; **Paper I**). (2) Natural mortality is influenced by a large range of factors, and the effect of behaviour-selectivity may not be dominant.

How much this type of selection applies to Norwegian spring-spawning herring is not certain. The current selection landscape (**Paper III**) could not be explained by natural mortality and size-selectivity only, suggesting that other types of selectivity, such as behavioural-selectivity, could take place. However, there is no evidence that purse seines, the main gear used to fish herring, induces strong behavioural-selection (Moav and Wohlfarth, 1970; Wilson et al., 1993; Diaz Pauli and Sih, 2017) and it is therefore not likely that this type of selection dominates. Disentangling the respective contribution of fishing and natural mortality components on the selection landscape of Norwegian spring-spawning herring will be required in the future for a better understanding of the stock's dynamics and the evolutionary pressures it is subjected to (Main processes summarised in Figure 4). Even though this task seems very complex, closer study of the natural component of the selection landscape constitutes the next step for a better understanding of the stock's evolutionary dynamic.

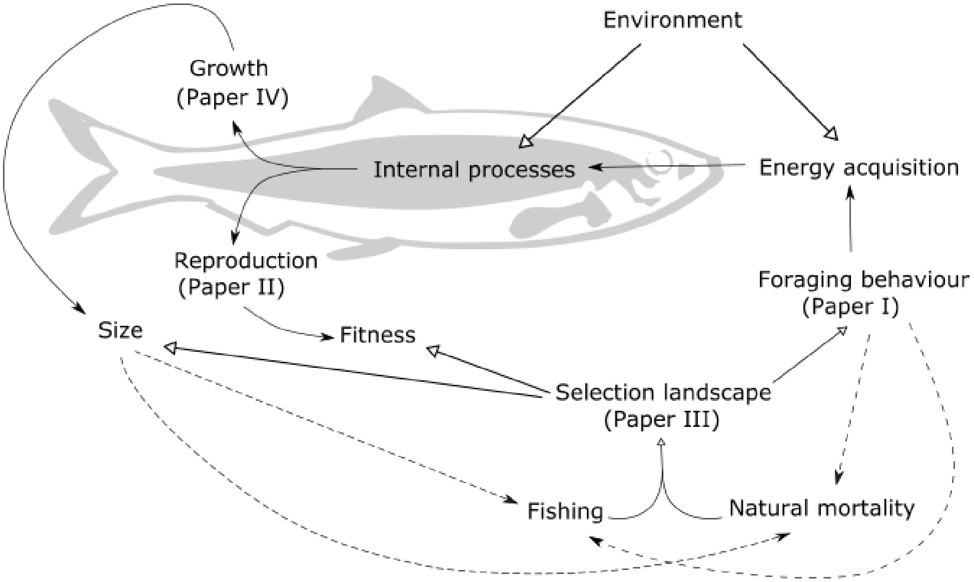


Figure 4: Illustration of the complexity of the processes determining optimal life-history traits. Fishing, natural mortality and environment can directly (i.e. direct selection/effect) and indirectly (i.e. selection/effect on correlated traits) affect life-history traits (white arrow heads). In turn, changes in life-history traits affects the

survival probability of an individual (dashed arrows). Black arrows represent processes inherent to the individual.

Concluding remarks and future perspectives

This thesis provides evidence for weak but significant trends towards increased reproductive effort and decreased adult growth of the Norwegian Spring-spawning herring, potentially attributable to fisheries-induced evolution. The weakness of these trends might come from changes in the selection landscape experienced by the stock during the last century. Other sources of selection than size-selectivity have been explored (e.g. selection on the behaviour), but how much they apply to the case of Norwegian spring-spawning herring is still to be determined.

The results exposed in this thesis complete the picture Engelhard and Heino (2004b) started to paint. Even though more work is still needed to determine if the trends observed have a genetic basis, it constitutes a step towards better knowledge of the stock and could prove useful for future management. An important aspect not included in this thesis is the combined effect of fishing pressure and climate change on Norwegian spring-spawning herring life-history traits, and such consideration should be taken into account in the future.

Now that we have given an overview of the combined effects of fishing and environment on different life-history traits of Norwegian spring-spawning herring, there is a need to go deeper into the mechanisms behind the picture. Norwegian spring-spawning herring being a very plastic species, we could expect to see a very flexible energy allocation or acquisition to compensate for internal or external effects on life-history traits. Energy allocation-based growth models are a category of statistical models that investigate energy allocation and acquisition patterns from individual size-at-age data, easily obtained by back-calculation (Quince et al., 2008a, b; Mollet et al., 2010; Brunel et al., 2013). Those models rely on the fact that somatic growth rate is reduced after maturation, due to the trade-off with reproduction, and allow to estimate important traits such as age at maturation, energy acquisition rates (Figure 5) as well as maintenance and reproductive rates (Quince et al., 2008a; Mollet et al., 2010; Brunel et al., 2013).

The usefulness of those models for Norwegian spring-spawning herring is currently under investigation. Indeed, those models are computationally demanding, require data of good quality and their success depend on the right combination of starting values for the parameters to estimate. In theory, they give us the possibility to obtain a time series for each of the traits related to energy acquisition and allocation previously mentioned. Using generalized linear models or generalized additive models, one could then estimate the variation of those traits explained by environmental or anthropogenic variables and look for residual temporal trends. So far, around 30 cohorts were studied, and some interesting patterns arose: energy acquisition rates covaried with each other but not with age at maturation, suggesting age at maturation may not be the best trait to study the stock's dynamic. Energy acquisition and energy allocation rates to growth and maintenance also seemed higher during the collapse period, while allocation rates to reproduction were lower. Even though those results fit with the findings described in this thesis, the time series is still incomplete and more work in needed to draw a more detailed picture.

Meanwhile, bioenergetics models are being investigated and adapted to herring in particular (Ljungström et al., In prep). Progress in this area will allow for a more mechanistic understanding of the anthropogenic and environmental factors influencing the Norwegian spring-spawning life-history traits.

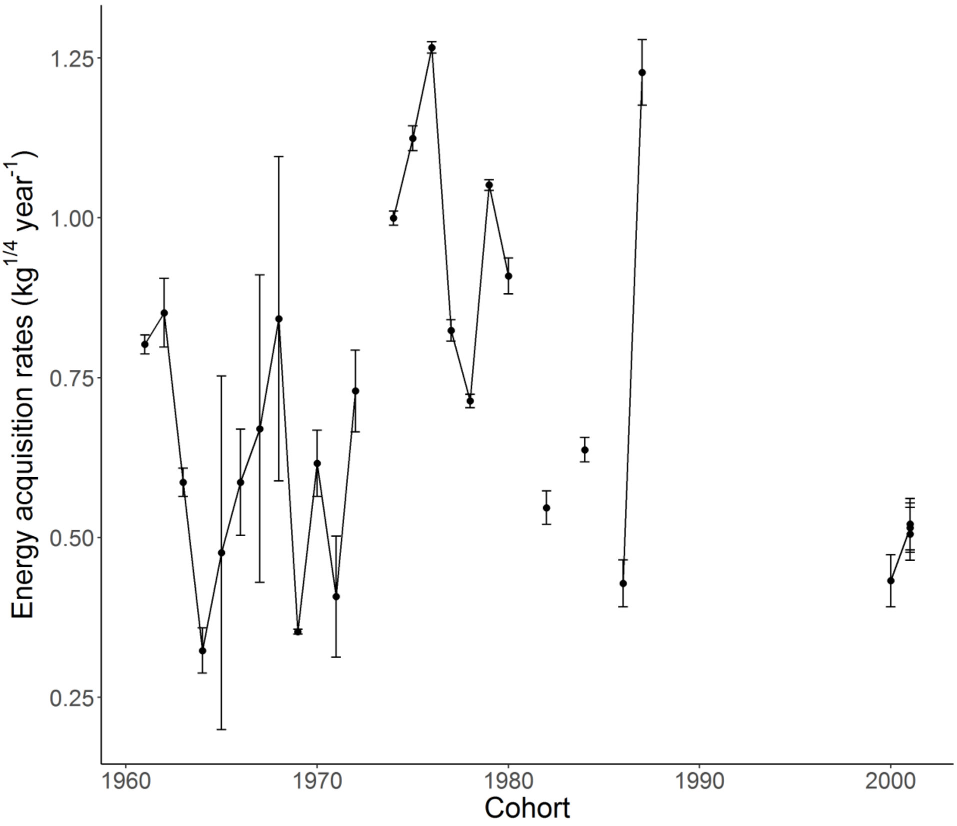


Figure 5: Estimates of energy acquisition rates from an energy allocation growth model for several cohorts of Norwegian spring-spawning herring.

References

Allendorf, F. W., and Hard, J. J. 2009. Human-induced evolution caused by unnatural selection through harvest of wild animals. Proceedings of the National Academy of Sciences, 106: 9987-9994.

Alós, J., Palmer, M., Linde-Medina, M., and Arlinghaus, R. 2014. Consistent size-independent harvest selection on fish body shape in two recreationally exploited marine species. Ecology and Evolution, 4: 2154-2164.

Álvarez, D., and Nicieza, A. 2005. Is metabolic rate a reliable predictor of growth and survival of brown trout (Salmo trutta) in the wild? Canadian Journal of Fisheries and Aquatic Sciences, 62: 643-649.

Andersen, B. S., Ulrich, C., Eigaard, O. R., and Christensen, A.-S. 2012. Short-term choice behaviour in a mixed fishery: investigating métier selection in the Danish gillnet fishery. ICES Journal of Marine Science, 69: 131-143.

Andersen, K. H., Marty, L., and Arlinghaus, R. 2018. Evolution of boldness and life history in response to selective harvesting. Canadian Journal of Fisheries and Aquatic Sciences, 75: 271-281.

Arlinghaus, R., Laskowski, K. L., Alós, J., Klefoth, T., Monk, C. T., Nakayama, S., and Schröder, A. 2017. Passive gear-induced timidity syndrome in wild fish populations and its potential ecological and managerial implications. Fish and Fisheries, 18: 360-373.

Ayllón, D., Railsback, S. F., Almodóvar, A., Nicola, G. G., Vincenzi, S., Elvira, B., and Grimm, V. 2018. Eco-evolutionary responses to recreational fishing under different harvest regulations. Ecology and Evolution. doi: 10.1002/ece3.4270.

Bachiller, E., Skaret, G., Nøttestad, L., and Slotte, A. 2016. Feeding ecology of Northeast Atlantic mackerel, Norwegian spring-spawning herring and blue whiting in the Norwegian Sea. PLOS ONE, 11: e0149238.

Bachiller, E., Utne, K. R., Jansen, T., and Huse, G. 2018. Bioenergetics modeling of the annual consumption of zooplankton by pelagic fish feeding in the Northeast Atlantic. PLOS ONE, 13: e0190345.

Barneche, D. R., Robertson, D. R., White, C. R., and Marshall, D. J. 2018. Fish reproductive-energy output increases disproportionately with body size. Science, 360: 642-645.

Barot, S., Heino, M., O'Brien, L., and Dieckmann, U. 2004a. Estimating reaction norms for age and size at maturation when age at first reproduction is unknown. Evolutionary Ecology Research, 6: 659-678.

Barot, S., Heino, M., O'Brien, L., and Dieckmann, U. 2004b. Long-term trend in the maturation reaction norm of two cod stocks. Ecological Applications, 14: 1257-1271.

Beaugrand, G., Reid, P. C., Ibanez, F., Lindley, J. A., and Edwards, M. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. Science, 296: 1692-1694.

Beverton, R. J., Hylen, A., Østvedt, O.-J., Alvsvaag, J., and Iles, T. C. 2004. Growth, maturation, and longevity of maturation cohorts of Norwegian spring-spawning herring. ICES Journal of Marine Science, 61: 165-175.

Biro, P. A., and 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: 2919-2922.

Bjørndal, T., Gordon, D. V., Kaitala, V., and Lindroos, M. 2004. International management strategies for a straddling fish stock: a bio-economic simulation model of the Norwegian spring-spawning herring fishery. Environmental and Resource Economics, 29: 435-457.

Bjørndal, T., Hole, A. D., Slinde, W. M., Asche, F., and Reithe, S. 1998. Norwegian Spring Spawning Herring-Some Biological and Economic Issues: An Update. Working paper - Foundation for research in economics and business administration.

Blindheim, J., Borovkov, V., Hansen, B., Malmberg, S.-A., Turrell, W., and Østerhus, S. 2000. Upper layer cooling and freshening in the Norwegian Sea in relation to atmospheric forcing. Deep Sea Research Part I: Oceanographic Research Papers, 47: 655-680.

Blindheim, J., and Rey, F. 2004. Water-mass formation and distribution in the Nordic Seas during the 1990s. ICES Journal of Marine Science, 61: 846-863.

Bradshaw, A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. *In* Advances in genetics, pp. 115-155. Elsevier.

Britten, G. L., Dowd, M., and Worm, B. 2016. Changing recruitment capacity in global fish stocks. Proceedings of the National Academy of Sciences, 113: 134-139.

Brooks, E. N., and Deroba, J. J. 2015. When “data” are not data: the pitfalls of post hoc analyses that use stock assessment model output. Canadian Journal of Fisheries and Aquatic Sciences, 72: 634-641.

Brophy, D., and Danilowicz, B. S. 2003. The influence of pre-recruitment growth on subsequent growth and age at first spawning in Atlantic herring (Clupea harengus L.). ICES Journal of Marine Science, 60: 1103-1113.

Brunel, T., Ernande, B., Mollet, F. M., and Rijnsdorp, A. D. 2013. Estimating age at maturation and energy-based life-history traits from individual growth trajectories with nonlinear mixed-effects models. Oecologia, 172: 631-643.

Burton, T., Killen, S., Armstrong, J., and Metcalfe, N. 2011. What causes intraspecific variation in resting metabolic rate and what are its ecological consequences? Proceedings of the Royal Society of London B: Biological Sciences, 278: 3465-3473.

Carlson, S. M., Edeline, E., Asbjorn Vollestad, L., Haugen, T. O., Winfield, I. J., Fletcher, J. M., Ben James, J., et al. 2007. Four decades of opposing natural and human-induced artificial selection acting on Windermere pike (*Esox lucius*). Ecology Letters, 10: 512-521.

Carlson, S. M., and Seamons, T. R. 2008. A review of quantitative genetic components of fitness in salmonids: implications for adaptation to future change. Evolutionary Applications, 1: 222-238.

Clark, C. W., and Mangel, M. 2000. Dynamic state variable models in ecology, Oxford University Press, New York. 289 pp.

Conover, D. O. 2000. Darwinian fishery science. Marine Ecology-Progress Series, 208: 303-307.

Conover, D. O., and Baumann, H. 2009. The role of experiments in understanding fishery-induced evolution. Evolutionary Applications, 2: 276-290.

Conover, D. O., and Munch, S. B. 2002. Sustaining fisheries yields over evolutionary time scales. Science, 297: 94-96.

Cooke, S. J., Suski, C. D., Ostrand, K. G., Wahl, D. H., and Philipp, D. P. 2007. Physiological and behavioral consequences of long-term artificial selection for vulnerability to recreational angling in a teleost fish. Physiological and Biochemical Zoology, 80: 480-490.

Cutts, C. J., Metcalfe, N. B., and Taylor, A. C. 2002. Juvenile Atlantic salmon (*Salmo salar*) with relatively high standard metabolic rates have small metabolic scopes. Functional ecology, 16: 73-78.

Dalpadado, P., Bogstad, B., Eriksen, E., and Rey, L. 2009. Distribution and diet of 0-group cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) in the Barents Sea in relation to food availability and temperature. Polar Biology, 32: 1583.

Dalpadado, P., Ellertsen, B., Melle, W., and Dommasnes, A. 2000. Food and feeding conditions of Norwegian spring-spawning herring (*Clupea harengus*) through its feeding migrations. ICES Journal of Marine Science, 57: 843-857.

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

Darwin, C. R. 1872. The Origin of Species, John Murray, London.

Dawkins, R. 2009. The greatest show on earth: The evidence for evolution, Free Press, Transworld, United Kingdom. 470 pp.

Diaz Pauli, B., and Heino, M. 2014. What can selection experiments teach us about fisheries-induced evolution? Biological journal of the Linnean Society, 111: 485-503.

Diaz Pauli, B., Kolding, J., Jeyakanth, G., and Heino, M. 2017. Effects of ambient oxygen and size-selective mortality on growth and maturation in guppies. Conservation Physiology, 5:cox010.

Diaz Pauli, B., and Sih, A. 2017. Behavioural responses to human-induced change: Why fishing should not be ignored. Evolutionary Applications, 10: 231-240.

Diaz Pauli, B., Wiech, M., Heino, M., and Utne-Palm, A. C. 2015. Opposite selection on behavioural types by active and passive fishing gears in a simulated guppy Poecilia reticulata fishery. Journal of Fish Biology, 86: 1030-1045.

Dieckmann, U., and Heino, M. 2007. Probabilistic maturation reaction norms: their history, strengths, and limitations. Marine Ecology-Progress Series, 335: 253-269.

dos Santos Schmidt, T. C., Slotte, A., Kennedy, J., Sundby, S., Johannessen, A., Oskarsson, G. J., Kurita, Y., et al. 2017. Oogenesis and reproductive investment of Atlantic herring are functions of not only present but long-ago environmental influences as well. Proceedings of the National Academy of Sciences of the United States of America, 114: 2634-2639.

Dragesund, O., Hamre, J., and Ulltang, Ø. 1980. Biology and population dynamics of the Norwegian spring-spawning herring. Rapp p-v réun - Cons int Explor Mer, 177: 43-71.

Dunlop, E. S., Heino, M., and Dieckmann, U. 2009. Eco-genetic modeling of contemporary life-history evolution. Ecological Applications, 19: 1815-1834.

Edeline, E., Carlson, S. M., Stige, L. C., Winfield, I. J., Fletcher, J. M., James, J. B., Haugen, T. O., et al. 2007. Trait changes in a harvested population are driven by a dynamic tug-of-war between natural and harvest selection. Proceedings of the National Academy of Sciences, 104: 15799-15804.

Enberg, K., Jørgensen, C., Dunlop, E. S., Heino, M., and Dieckmann, U. 2009. Implications of fisheries-induced evolution for stock rebuilding and recovery. Evolutionary Applications, 2: 394-414.

Enberg, K., Jørgensen, C., Dunlop, E. S., Varpe, O., Boukal, D. S., Baulier, L., Eliassen, S., et al. 2012. Fishing-induced evolution of growth: concepts, mechanisms and the empirical evidence. Marine Ecology-an Evolutionary Perspective, 33: 1-25.

Enberg, K., Jorgensen, C., and Mangel, M. 2010. Fishing-induced evolution and changing reproductive ecology of fish: the evolution of steepness. Canadian Journal of Fisheries and Aquatic Sciences, 67: 1708-1719.

Endler, J. A. 1986. Natural selection in the wild*,* Princeton University Press, Princetin, New Jersey, USA.

Engelhard, G. H., and Heino, M. 2004a. Maturity changes in Norwegian spring-spawning herring before, during, and after a major population collapse. Fisheries Research, 66: 299-310.

Engelhard, G. H., and Heino, M. 2004b. Maturity changes in Norwegian spring-spawning herring *Clupea harengus*: compensatory or evolutionary responses? Marine Ecology Progress Series, 272: 245-256.

Ernande, B., Dieckmann, U., and Heino, M. 2004. Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. Proceedings of the Royal Society of London Series B-Biological Sciences, 271: 415-423.

Fabian, D., and Flatt, T. 2012. Life History Evolution. Nature Education Knowledge, 3: 24.

FAO 2017. The State of Food Security and Nutrition in the World 2017: Building Resilience for Peace and Food Security*,* FAO.

Fenberg, P. B., and Roy, K. 2008. Ecological and evolutionary consequences of size-selective harvesting: how much do we know? Molecular Ecology, 17: 209-220.

Fiksen, Ø., and Slotte, A. 2002. Stock-environment recruitment models for Norwegian spring spawning herring (*Clupea harengus*). Canadian Journal of Fisheries and Aquatic Sciences, 59: 211-217.

Fisher, R. A. 1930. Genetical theory of natural selection, Oxford University Press, Oxford, UK.

Gause, G. F. 1947. Problems of evolution. Trans. Conn. Acad. Arts Sci.: 17-68.

Geffen, A. J. 2009. Advances in herring biology: from simple to complex, coping with plasticity and adaptability. ICES Journal of Marine Science, 66: 1688-1695.

Ghalambor, C. K., Reznick, D. N., and Walker, J. A. 2004. Constraints on adaptive evolution: The functional trade-off between reproduction and fast-start swimming performance in the Trinidadian guppy (*Poecilia reticulata*). American Naturalist, 164: 38-50.

Gjedrem, T. 1983. Genetic variation in quantitative traits and selective breeding in fish and shellfish. Aquaculture, 33: 51-72.

Gjøsæter, H. 1998. The population biology and exploitation of capelin (*Mallotus villosus*) in the Barents Sea. Sarsia, 83: 453-496.

Gjøsæter, H., Bogstad, B., and Tjelmeland, S. 2009. Ecosystem effects of the three capelin stock collapses in the Barents Sea. Marine Biology Research, 5: 40-53.

Grimm, V., Frank, K., Jeltsch, F., Brandl, R., Uchmanski, J., and Wissel, C. 1996. Pattern-oriented modelling in population ecology. Science of the Total Environment, 183: 151-166.

Grimm, V., and Railsback, S. F. 2005. Individual-based modeling and ecology, Princeton University Press, Princeton, New Jersey, USA.

Hall, S. J. 1999. Effects of fishing on marine ecosystems and communities, Blackwell Science, Oxford, UK.

Hallfredsson, E. H., and Pedersen, T. 2009. Effects of predation from juvenile herring (*Clupea harengus*) on mortality rates of capelin (*Mallotus villosus*) larvae. Canadian Journal of Fisheries and Aquatic Sciences, 66: 1693-1706.

Hamon, T. R., Foote, C. J., Hilborn, R., and Rogers, D. E. 2000. Selection on morphology of spawning wild sockeye salmon by a gill-net fishery. Transactions of the American Fisheries Society, 129: 1300-1315.

Hamre, J. 1980. Biology, exploitation, and management of the northeast atlantic mackrel. Rapp. P.-v. Reun. Cons. into Explor. Mer, 177: 212-242.

Hamre, J. 1994. Biodiversity and exploitation of the main fish stocks in the Norwegian-Barents Sea ecosystem. Biodiversity & Conservation, 3: 473-492.

Hard, J. J., Gross, M. R., Heino, M., Hilborn, R., Kope, R. G., Law, R., and Reynolds, J. D. 2008. Evolutionary consequences of fishing and their implications for salmon. Evolutionary Applications, 1: 388-408.

Heino, J., Melo, A. S., Siqueira, T., Soininen, J., Valanko, S., and Bini, L. M. 2015a. Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. Freshwater Biology, 60: 845-869.

Heino, M. 1998. Management of evolving fish stocks. Canadian Journal of Fisheries and Aquatic Sciences, 55: 1971-1982.

Heino, M., Baulier, L., Boukal, D. S., Ernande, B., Johnston, F. D., Mollet, F. M., Pardoe, H., et al. 2013. Can fisheries-induced evolution shift reference points for fisheries management? ICES Journal of Marine Science, 70: 707-721.

Heino, M., Diaz Pauli, B., and Dieckmann, U. 2015b. Fisheries-Induced Evolution. *In* Annual Review of Ecology, Evolution, and Systematics, pp. 461-480.

Heino, M., Dieckmann, U., and Godø, O. R. 2002a. Estimating reaction norms for age and size at maturation with reconstructed immature size distributions: a new technique illustrated by application to Northeast Arctic cod. ICES Journal of Marine Science, 59: 562-575.

Heino, M., Dieckmann, U., and Godø, O. R. 2002b. Measuring probabilistic reaction norms for age and size at maturation. Evolution, 56: 669-678.

Heino, M., Dieckmann, U., and Godø, O. R. 2002c. Reaction norm analysis of fisheries-induced adaptive change and the case of the Northeast Arctic cod. ICES CM, 2002/Y: 14.

Heino, M., and Godø, O. R. 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. Bulletin of marine science, 70: 639-656.

Heino, M., and Kaitala, V. 1999. Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. Journal of Evolutionary Biology, 12: 423-429.

Hendry, A. P., Farrugia, T. J., and Kinnison, M. T. 2008. Human influences on rates of phenotypic change in wild animal populations. Molecular Ecology, 17: 20-29.

Hendry, A. P., Kelly, M. L., Kinnison, M. T., and Reznick, D. N. 2006. Parallel evolution of the sexes? Effects of predation and habitat features on the size and shape of wild guppies. Journal of Evolutionary Biology, 19: 741-754.

Hendry, A. P., and Kinnison, M. T. 1999. The pace of modern life: Measuring rates of contemporary microevolution. Evolution, 53: 1637-1653.

Heppell, S. S. 1998. Application of life-history theory and population model analysis to turtle conservation. Copeia: 367-375.

Hixon, M. A., Johnson, D. W., and Sogard, S. M. 2013. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. ICES Journal of Marine Science, 71: 2171-2185.

Hoegh-Guldberg, O., and Bruno, J. F. 2010. The impact of climate change on the world’s marine ecosystems. Science, 328: 1523-1528.

Holland, D. S., and Sutinen, J. G. 1999. An empirical model of fleet dynamics in New England trawl fisheries. Canadian Journal of Fisheries and Aquatic Sciences, 56: 253-264.

Hollins, J., Thambithurai, D., Koeck, B., Crespel, A., Bailey, D. M., Cooke, S. J., Lindström, J., et al. 2018. A physiological perspective on fisheries-induced evolution. Evolutionary Applications, 11: 561-576.

Holst, J. 1996. Long term trends in the growth and recruit-ment pattern of the Norwegian spring-spawning herring (*Clupea harengus* Linnaeus 1758). University of Bergen, Norway.

Holst, J., and Slotte, A. 1998. Effects of juvenile nursery on geographic spawning distribution in Norwegian spring-spawning herring (*Clupea harengus* L.). ICES Journal of Marine Science, 55: 987-996.

Holst, J. C., Røttingen, I., and Melle, W. 2004. The herring. The Norwegian Sea Ecosystem: 203-226.

Holt, R. E., and Jørgensen, C. 2014. Climate warming causes life-history evolution in a model for Atlantic cod (*Gadus morhua*). Conservation Physiology, 2.

Houle, D. 2001. Characters as the units of evolutionary change. The character concept in evolutionary biology: 109-140.

Houston, A. I., and McNamara, J. M. 1999. Models of adaptive behaviour: an approach based on state, Cambridge University Press, Cambridge, UK. 378 pp pp.

Hsieh, C.-h., Reiss, C. S., Hunter, J. R., Beddington, J. R., May, R. M., and Sugihara, G. 2006. Fishing elevates variability in the abundance of exploited species. Nature, 443: 859.

Hunt, G. L., and McKinnell, S. 2006. Interplay between top-down, bottom-up, and wasp-waist control in marine ecosystems. Progress in Oceanography, 68: 115-124.

Huse, G., Fernö, A., and Holst, J. C. 2010. Establishment of new wintering areas in herring co-occurs with peaks in the ‘first time/repeat spawner’ratio. Marine Ecology Progress Series, 409: 189-198.

Huse, G., Holst, J. C., Utne, K., Nottestad, L., Melle, W., Slotte, A., Ottersen, G., et al. 2012. Effects of interactions between fish populations on ecosystem dynamics in the Norwegian Sea - results of the INFERNO project Preface. Marine Biology Research, 8: 415-419.

Huse, G., Railsback, S., and Fernø, A. 2002. Modelling changes in migration pattern of herring: collective behaviour and numerical domination. Journal of Fish Biology, 60: 571-582.

Husebø, Å., Slotte, A., and Stenevik, E. K. 2007. Growth of juvenile Norwegian spring-spawning herring in relation to latitudinal and interannual differences in temperature and fish density in their coastal and fjord nursery areas. ICES Journal of Marine Science, 64: 1161-1172.

Hutchings, J. A. 2000. Collapse and recovery of marine fishes. Nature, 406: 882-885.

Hutchings, J. A., and Fraser, D. J. 2008. The nature of fisheries- and farming-induced evolution. Molecular Ecology, 17: 294-313.

ICES. 2018. Report of the Working Group on Widely Distributed Stocks (WGWIDE).

Iversen, S. A. 2002. Changes in the perception of the migration pattern of Northeast Atlantic mackerel during the last 100 years. *In* ICES Marine Science Symposia, pp. 382-390.

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science, 293: 629-637.

Jacobsen, N. S., and Essington, T. E. 2018. Natural mortality augments population fluctuations of forage fish. Fish and Fisheries, 19: 791-797.

Jennings, S., and Kaiser, M. J. 1998. The effects of fishing on marine ecosystems. *In* Advances in marine biology, pp. 201-352. Elsevier.

Jørgensen, C., Dunlop, E. S., Opdal, A. F., and Fiksen, Ø. 2008. The evolution of spawning migrations: state dependence and fishing-induced changes. Ecology, 89: 3436-3448.

Jørgensen, C., Enberg, K., Dunlop, E. S., Arlinghaus, R., Boukal, D. S., Brander, K., Ernande, B., et al. 2007. Managing evolving fish stocks. Science, 318: 1247-1248.

Jørgensen, C., Ernande, B., and Fiksen, Ø. 2009. Size-selective fishing gear and life history evolution in the Northeast Arctic cod. Evolutionary Applications, 2: 356-370.

Jørgensen, C., and Fiksen, Ø. 2006. State-dependent energy allocation in cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 63: 186-199.

Jørgensen, C., and Fiksen, Ø. 2010. Modelling fishing-induced adaptations and consequences for natural mortality. Canadian Journal of Fisheries and Aquatic Sciences, 67: 1086-1097.

Jørgensen, T. 1990. Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus morhua* L.). Journal Du Conseil, 46: 235-248.

Kaiser, M. J., and De Groot, S. J. 2000. The effects of fishing on non-target species and habitats: biological, conservation and socio-economic issues*,* Blackwell Science, Oxford, UK.

Kennedy, J., Skjæraasen, J. E., Nash, R. D. M., Slotte, A., Geffen, A. J., and Kjesbu, O. S. 2011. Evaluation of the frequency of skipped spawning in Norwegian spring-spawning herring. Journal of Sea Research, 65: 327-332.

Kinnison, M. T., and Hendry, A. P. 2001. The pace of modern life II: from rates of contemporary microevolution to pattern and process. Genetica, 112-113: 145-164.

Kjesbu, O. S., Solemdal, P., Bratland, P., and 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.

Kraak, S. B. M. 2007. Does the probabilistic maturation reaction norm approach disentangle phenotypic plasticity from genetic change? Marine Ecology-Progress Series, 335: 295-300.

Krysov, A. I., and Ergakova, L. R. 1990. Distribution and drift of Atlanto-Scandian herring larvae in Norwegian and Lofoten shallows in 1983–1987. *In* Biology and Fishery of the Blue Whiting in the Northeast Atlantic and the Norwegian Spring Spawning Herring, pp. 135-152. Ed. by I. o. M. R. T. Monstad, Bergen. Institute of Marine Research, Bergen.

Kuparinen, A., Kuikka, S., and Merilä, J. 2009. Estimating fisheries-induced selection: traditional gear selectivity research meets fisheries-induced evolution. Evolutionary Applications, 2: 234-243.

Kuparinen, A., and Merilä, J. 2007. Detecting and managing fisheries-induced evolution. Trends in Ecology & Evolution, 22: 652-659.

Lande, R. 2009. Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. Journal of Evolutionary Biology, 22: 1435-1446.

Law, R. 2000. Fishing, selection, and phenotypic evolution. ICES Journal of Marine Science, 57: 659-668.

Law, R. 2007. Fisheries-induced evolution: present status and future directions. Marine Ecology-Progress Series, 335: 271-277.

Law, R., and Grey, D. R. 1989. Evolution of yields from populations with age-specific cropping. Evolutionary Ecology, 3: 343-359.

Lind, S., Ingvaldsen, R. B., and Furevik, T. 2018. Arctic warming hotspot in the northern Barents Sea linked to declining sea-ice import. Nature Climate Change, 8: 634.

Ljungström, G., Claireaux, M., Fiksen, Ø., and Jørgensen, C. In prep. Shifts in fish body size under environmental change: prey characteristics may be a more important driver than temperature.

Loeng, H. 1991. Features of the physical oceanographic conditions of the Barents Sea. Polar research, 10: 5-18.

Loeng, H., and Drinkwater, K. 2007. An overview of the ecosystems of the Barents and Norwegian Seas and their response to climate variability. Deep Sea Research Part II: Topical Studies in Oceanography, 54: 2478-2500.

Loher, T. 2011. Analysis of match–mismatch between commercial fishing periods and spawning ecology of Pacific halibut (Hippoglossus stenolepis), based on winter surveys and behavioural data from electronic archival tags. ICES Journal of Marine Science, 68: 2240-2251.

Mangel, M. 2017. The inverse life-history problem, size-dependent mortality and two extensions of results of Holt and Beverton. Fish and Fisheries, 18: 1192-1200.

Marti, Y., and Fedorov, S. 1963. Features of the population dynamics of marine herring as seen from the Atlanto-Scandian stock. Rapports et Procès-verbaux des Réunions Conseil International pour l'Exploration de la Mer, 154: 91-97.

Merilä, J., and Sheldon, B. 2000. Lifetime reproductive success and heritability in nature. The American Naturalist, 155: 301-310.

Mertz, G., and Myers, R. A. 1998. A simplified formulation for fish production. Canadian Journal of Fisheries and Aquatic Sciences, 55: 478-484.

Miller, R. B. 1957. Have the genetic patterns of fishes been altered by introductions or by selective fishing? Journal of the Fisheries Board of Canada, 14: 797-806.

Moav, R., and Wohlfarth, W. 1970. Genetic correlation between seine escapability and growth capacity in carp. Journal of Heredity, 61: 153-157.

Mollet, F. M., Ernande, B., Brunel, T., and Rijnsdorp, A. D. 2010. Multiple growth-correlated life history traits estimated simultaneously in individuals. Oikos, 119: 10-26.

Mousseau, T. A., and Roff, D. A. 1987. Natural selection and the heritability of fitness components. Heredity, 59: 181-198.

Myers, R. A., Hutchings, J. A., and Barrowman, N. J. 1997. Why do fish stocks collapse? The example of cod in Atlantic Canada. Ecological Applications, 7: 91-106.

Nannini, M., Wahl, D., Philipp, D., and Cooke, S. 2011. The influence of selection for vulnerability to angling on foraging ecology in largemouth bass *Micropterus salmoides*. Journal of Fish Biology, 79: 1017-1028.

Neuheimer, A. B., and Grønkjær, P. 2012. Climate effects on size-at-age: growth in warming waters compensates for earlier maturity in an exploited marine fish. Global Change Biology, 18: 1812-1822.

Olsen, E. M., Heupel, M. R., Simpfendorfer, C. A., and Moland, E. 2012. Harvest selection on Atlantic cod behavioral traits: implications for spatial management. Ecology and Evolution, 2: 1549-1562.

Óskarsson, G. J., Kjesbu, O. S., and Slotte, A. 2002. Predictions of realised fecundity and spawning time in Norwegian spring-spawning herring (*Clupea harengus*). Journal of Sea Research, 48: 59-79.

Ottersen, G., Hjermann, D. Ø., and Stenseth, N. C. 2006. Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. Fisheries Oceanography, 15: 230-243.

Ottersen, G., and Loeng, H. 2000. Covariability in early growth and year-class strength of Barents Sea cod, haddock, and herring: the environmental link. ICES Journal of Marine Science, 57: 339-348.

Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P. C., and Stenseth, N. C. 2001. Ecological effects of the North Atlantic Oscillation. Oecologia, 128: 1-14.

Pandolfi, J. M. 2009. Evolutionary impacts of fishing: overfishing's 'Darwinian debt'. F1000 biology reports, 1.

Pauly, D. 1996. One hundred million tonnes of fish, and fisheries research. Fisheries Research, 25: 25-38.

Pauly, D., Watson, R., and Alder, J. 2005. Global trends in world fisheries: impacts on marine ecosystems and food security. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 360: 5-12.

Peer, A., and Miller, T. 2014. Climate change, migration phenology, and fisheries management interact with unanticipated consequences. North American Journal of Fisheries Management, 34: 94-110.

Peterson, I., and Wroblewski, J. 1984. Mortality rate of fishes in the pelagic ecosystem. Canadian Journal of Fisheries and Aquatic Sciences, 41: 1117-1120.

Pfennig, D. W., Wund, M. A., Snell-Rood, E. C., Cruickshank, T., Schlichting, C. D., and Moczek, A. P. 2010. Phenotypic plasticity's impacts on diversification and speciation. Trends in Ecology & Evolution, 25: 459-467.

Policansky, D. 1993. Fishing as a cause of evolution in fishes. *In* The exploitation of evolving resources, pp. 1-18. Springer.

Price, T. D., Qvarnström, A., and Irwin, D. E. 2003. The role of phenotypic plasticity in driving genetic evolution. Proceedings of the Royal Society of London Series B-Biological Sciences, 270: 1433-1440.

Prokopchuk, I., and Sentyabov, E. 2006. Diets of herring, mackerel, and blue whiting in the Norwegian Sea in relation to *Calanus finmarchicus* distribution and temperature conditions. ICES Journal of Marine Science, 63: 117-127.

Quince, C., Abrams, P. A., Shuter, B. J., and Lester, N. P. 2008a. Biphasic growth in fish I: Theoretical foundations. Journal of Theoretical Biology, 254: 197-206.

Quince, C., Shuter, B. J., Abrams, P. A., and Lester, N. P. 2008b. Biphasic growth in fish II: Empirical assessment. Journal of Theoretical Biology, 254: 207-214.

Quinn, T. P., Hodgson, S., Flynn, L., Hilborn, R., and Rogers, D. E. 2007. Directional selection by fisheries and the timing of sockeye salmon (*Oncorhynchus nerka*) migrations. Ecological Applications, 17: 731-739.

Quinn, T. P., McGinnity, P., and Cross, T. F. 2006. Long-term declines in body size and shifts in run timing of Atlantic salmon in Ireland. Journal of Fish Biology, 68: 1713-1730.

Reznick, D. 1983. The structure of guppy life histories: the tradeoff between growth and reproduction. Ecology, 64: 862-873.

Reznick, D., and Yang, A. P. 1993. The influence of fluctuating resources on life-history - patterns of allocation and plasticity in female guppies. Ecology, 74: 2011-2019.

Reznick, D. A., Bryga, H., and Endler, J. A. 1990. Experimentally induced life-history evolution in a natural population. Nature, 346: 357-359.

Rijnsdorp, A. D., Grift, R. E., and Kraak, S. B. M. 2005. Fisheries-induced adaptive change in reproductive investment in North Sea plaice (*Pleuronectes platessa*)? Canadian Journal of Fisheries and Aquatic Sciences, 62: 833-843.

Rochet, M. J. 1998. Short-term effects of fishing on life history traits of fishes. ICES Journal of Marine Science, 55: 371-391.

Roff, D. 2000. Trade-offs between growth and reproduction: an analysis of the quantitative genetic evidence. Journal of Evolutionary Biology, 13: 434-445.

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

Røttingen, I. 1990. The 1983 year class of Norwegian spring spawning herring as juveniles and recruit spawners.

Rueffler, C., Van Dooren, T. J. M., and Metz, J. A. J. 2006. The evolution of resource specialization through frequency-dependent and frequency-independent mechanisms. American Naturalist, 167: 81-93.

Sætersdal, G., and Loeng, H. 1984. Ecological adaption of reproduction in Arctic Cod.

Sætersdal, G., and Loeng, H. 1987. Ecological adaptation of reproduction in Northeast Arctic cod. Fisheries Research, 5: 253-270.

Saetre, R., and Skjoldal, H. R. 2004. The Norwegian sea ecosystem*,* Tapir Academic Press.

Sætre, R., Toresen, R., and Anker-Nilssen, T. 2002. Factors affecting the recruitment variability of the Norwegian spring-spawning herring (*Clupea harengus* L.). ICES Journal of Marine Science, 59: 725-736.

Sakshaug, E., and Skjoldal, H. R. 1989. Life at the ice edge. Ambio (Sweden).

Salas, S., Sumaila, U. R., and Pitcher, T. 2004. Short-term decisions of small-scale fishers selecting alternative target species: a choice model. Canadian Journal of Fisheries and Aquatic Sciences, 61: 374-383.

Sandberg, P. 2010. Rebuilding the stock of Norwegian spring spawning herring: Lessons learned. In: OECD 2010, Workshop Proceedings on the Economics of Rebuilding Fisheries: Challenges for Sustaining Fisheries. OECD, Paris: 219–234.

Scheffer, M., Carpenter, S., and Young, B. d. 2005. Cascading effects of overfishing marine systems. Trends in Ecology & Evolution, 20: 579-581.

Schlichting, C. 2004. The role of phenotypic plasticity in diversification. Phenotypic plasticity: functional and conceptual approaches: 191-200.

Schmalhausen, I. I. 1949. Factors of evolution: the theory of stabilizing selection.

Sharpe, D. M. T., and Hendry, A. P. 2009. Life history change in commercially exploited fish stocks: an analysis of trends across studies. Evolutionary Applications, 2: 260-275.

Slotte, A. 1999a. Differential utilization of energy during wintering and spawning migration in Norwegian spring-spawning herring. Journal of Fish Biology, 54: 338-355.

Slotte, A. 1999b. Effects of fish length and condition on spawning migration in Norwegian spring spawning herring (*Clupea harengus* L.). Sarsia, 84: 111-127.

Slotte, A., and Fiksen, Ø. 2000. State-dependent spawning migration in Norwegian spring-spawning herring. Journal of Fish Biology, 56: 138-162.

Slotte, A., Johannessen, A., and Kjesbu, O. 2000. Effects of fish size on spawning time in Norwegian spring-spawning herring. Journal of Fish Biology, 56: 295-310.

Smith, A., Brown, C. J., Bulman, C. M., Fulton, E. A., Johnson, P., Kaplan, I. C., Lozano-Montes, H., et al. 2011. Impacts of fishing low-trophic level species on marine ecosystems. Science, 333: 1147-1150.

Smith, T. D. 1994. Scaling fisheries: the science of measuring the effects of fishing, 1855-1955, Cambridge University Press.

Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of marine science, 60: 1129-1157.

Stearns, S. C. 1977. The evolution of life history traits: a critique of the theory and a review of the data. Annual review of ecology and systematics, 8: 145-171.

Stearns, S. C. 1989. Trade-offs in life-history evolution. Functional ecology, 3: 259-268.

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

Stephens, P. A., Boyd, I. L., McNamara, J. M., and Houston, A. I. 2009. Capital breeding and income breeding: their meaning, measurement, and worth. Ecology, 90: 2057-2067.

Stokes, K., and Law, R. 2000. Fishing as an evolutionary force. Marine Ecology-Progress Series, 208: 307-309.

Svardson, G. 1949. Natural selection and egg number in fish. Report of the Institute of Freshwater Research, Drottningholm, 29: 115-122.

Swain, D. P., Sinclair, A. F., and Hanson, J. M. 2007. Evolutionary response to size-selective mortality in an exploited fish population. Proceedings of the Royal Society B: Biological Sciences, 274: 1015-1022.

Tian, T., Fiksen, Ø., and Folkvord, A. 2007. Estimating larval fish growth under size-dependent mortality: a numerical analysis of bias. Canadian Journal of Fisheries and Aquatic Sciences, 64: 554-562.

Toresen, R. 1990. Long-term changes in growth of Norwegian spring-spawning herring. Journal Du Conseil, 47: 48-56.

Toresen, R., and Jakobsson, J. 2002. Exploitation and management of Norwegian spring-spawning herring in the 20th century. *In* ICES Mar. Sci. Symp, pp. 558-571.

Toresen, R., and Østvedt, O. J. 2000. Variation in abundance of Norwegian spring-spawning herring (*Clupea harengus*, Clupeidae) throughout the 20th century and the influence of climatic fluctuations. Fish and Fisheries, 1: 231-256.

Trippel, E. A. 1995. Age at maturity as a stress indicator in fisheries. Bioscience, 45: 759-771.

Ushakov, N. G., and Prozorkevich, D. V. 2002. The Barents Sea capelin–a review of trophic interrelations and fisheries. ICES Journal of Marine Science, 59: 1046-1052.

Utne, K. R., and Huse, G. 2012. Estimating the horizontal and temporal overlap of pelagic fish distribution in the Norwegian Sea using individual-based modelling. Marine Biology Research, 8: 548-567.

Utne, K. R., Huse, G., Ottersen, G., Holst, J. C., Zabavnikov, V., Jacobsen, J. A., Óskarsson, G. J., et al. 2012. Horizontal distribution and overlap of planktivorous fish stocks in the Norwegian Sea during summers 1995–2006. Marine Biology Research, 8: 420-441.

van Walraven, L., Mollet, F. M., van Damme, C. J. G., and Rijnsdorp, A. D. 2010. Fisheries-induced evolution in growth, maturation and reproductive investment of the sexually dimorphic North Sea plaice (*Pleuronectes platessa* L.). Journal of Sea Research, 64: 85-92.

van Wijk, S. J., Taylor, M. I., Creer, S., Dreyer, C., Rodrigues, F. M., Ramnarine, I. W., van Oosterhout, C., et al. 2013. Experimental harvesting of fish populations drives genetically based shifts in body size and maturation. Frontiers in Ecology and the Environment, 11: 181-187.

Vignieri, S. 2018. Big mamas matter for fish. American Association for the Advancement of Science.

Walsh, M. R., Munch, S. B., Chiba, S., and Conover, D. O. 2006. Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. Ecology Letters, 9: 142-148.

Wang, S. Y., Lau, K., Lai, K.-P., Zhang, J.-W., Tse, A. C.-K., Li, J.-W., Tong, Y., et al. 2016. Hypoxia causes transgenerational impairments in reproduction of fish. Nature communications, 7: 12114.

Ware, D. M. 1975. Growth, metabolism, and optimal swimming speed of a pelagic fish. Journal of the Fisheries Research Board of Canada, 32: 33-41.

Ware, D. M. 1978. Bioenergetics of pelagic fish: theoretical change in swimming speed and ration with body size. Journal of the Fisheries Research Board of Canada, 35: 220-228.

Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. The American Naturalist, 100: 687-690.

Wilson, D. S., Coleman, K., Clark, A. B., and Biederman, L. 1993. Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. Journal of Comparative Psychology, 107: 250.

Winberg, G. 1956. Rate of metabolism and food requirements of fish. Fish. Res. Board Can., Transl. Ser., 194: 1-253.

Winberg, G. G. 1961. New information on metabolic rate in fishes. Vopr. Ikhtiol., 1: 157-165.

Zimmermann, F., and Heino, M. 2013. Is size-dependent pricing prevalent in fisheries? The case of Norwegian demersal and pelagic fisheries. ICES Journal of Marine Science, 70: 1389-1395.

Zimmermann, F., and Jørgensen, C. 2015. Bioeconomic consequences of fishing-induced evolution: a model predicts limited impact on net present value. Canadian Journal of Fisheries and Aquatic Sciences, 72: 612-624.

Zimmermann, F., and Jørgensen, C. 2017. Taking animal breeding into the wild: regulation of fishing gear can make fish stocks evolve higher productivity. Marine Ecology Progress Series, 563: 185-195.

Zuur, A., Ieno, E. N., and Smith, G. M. 2007. Analyzing ecological data, Springer Science & Business Media.

Paper I

Received: 9 February 2018 | Revised: 24 July 2018 | Accepted: 3 August 2018
DOI: 10.1002/ece3.4482

ORIGINAL RESEARCH

WILEY Ecology and Evolution Open Access

Evolutionary effects of fishing gear on foraging behavior and life-history traits

Marion Claireaux[1,2] | **Christian Jørgensen**[2] | **Katja Enberg**[1]

[1]Institute of Marine Research, Bergen, Norway
[2]Department of Biological Sciences, University of Bergen, Bergen, Norway

Correspondence
Marion Claireaux, Institute of Marine Research, Bergen, Norway.
Email: marion.claireaux@imr.no

Funding information
Research Council of Norway, Grant/Award Number: 243735; H2020 Marie Skłodowska-Curie Actions, Grant/Award Number: 675997

Abstract

Fishing gears are designed to exploit the natural behaviors of fish, and the concern that fishing may cause evolution of behavioral traits has been receiving increasing attention. The first intuitive expectation is that fishing causes evolution toward reduced boldness because it selectively removes actively foraging individuals due to their higher encounter rate and vulnerability to typical gear. However, life-history theory predicts that fishing, through shortened life span, favors accelerated life histories, potentially leading to increased foraging and its frequent correlate, boldness. Additionally, individuals with accelerated life histories mature younger and at a smaller size and therefore spend more of their life at a smaller size where mortality is higher. This life-history evolution may prohibit increases in risk-taking behavior and boldness, thus selecting for reduced risk-taking and boldness. Here, we aim to clarify which of these three selective patterns ends up being dominant. We study how behavior-selective fishing affects the optimal behavioral and life-history traits using a state-dependent dynamic programming model. Different gear types were modeled as being selective for foraging or hiding/resting individuals along a continuous axis, including unselective fishing. Compared with unselective harvesting, gears targeting hiding/resting individuals led toward evolution of increased foraging rates and elevated natural mortality rate, while targeting foraging individuals led to evolution of decreased foraging rates and lower natural mortality rate. Interestingly, changes were predicted for traits difficult to observe in the wild (natural mortality and behavior) whereas the more regularly observed traits (length-at-age, age at maturity, and reproductive investment) showed only little sensitivity to the behavioral selectivity.

KEYWORDS
behavior, boldness, fishing-induced evolution, foraging rate, life-history traits, mortality, timidity

1 | INTRODUCTION

Even though most food production is now taking place under controlled conditions in farms, fishing is one exception where we rely on wild populations reproducing in their natural habitat, although we exploit them with industrialized technology and efficiency. The traits of wild fish are therefore still subjected to natural selection and may in addition evolve in new directions as they experience selective pressures from fishing and other human activities (Law & Grey, 1989). Identifying these selective drivers and understanding their impact on the evolution of wild populations are necessary for ensuring long-term productivity and sustainability of living resources.

Because fishing gears are designed to exploit the natural behaviors of fish, the concern that fishing may cause evolution of behavioral traits has been receiving increasing attention (Arlinghaus et al., 2017; Biro & Stamps, 2008; Cooke, Suski, Ostrand, Wahl, & Philipp, 2007; Diaz Pauli & Sih, 2017; Leclerc, Zedrosser, & Pelletier, 2017; Uusi-Heikkilä, 2008; Wilson, Clark, Coleman, & Dearstyne, 1994). A key concept in behavioral studies is boldness, defined by placing an individual's level of risk acceptance during behaviors such as foraging, exploration, and defense along a boldness–shyness continuum (Budaev, 1997; Sih, Bell, Johnson, & Ziemba, 2004; Wilson, 1998; Wilson et al., 1994). Risk-taking is often consistent among contexts and situations, and correlated to other traits. For example, individuals more willing to inspect novel objects will also tend to take risks in other settings and move around more. These correlation structures have been termed "animal personalities" or "behavioral syndromes" (Sih et al., 2004; Wilson et al., 1994). Therefore, boldness is not a single trait, but rather a label ascribed by experimenters and modelers to typically co-occurring behavioral traits.

Several studies have found that actively foraging individuals may have higher encounter rates with "passive" fishing gears such as gillnets, traps, and baited hooks and will therefore be selectively removed (Biro & Post, 2008; for trout; Philipp et al., 2009; for largemouth bass *Micropterus salmoides*; Biro & Sampson, 2015; for Australian common yabby, *Cherax destructor*; Diaz Pauli, Wiech, Heino, & Utne-Palm, 2015; for guppies *Poecilia reticulata*). As foraging is a trait typically related to boldness, it is often correlated to other behaviors that are consistent across contexts and situations (Dochtermann, Schwab, & Sih, 2015; Mousseau & Roff, 1987; Sih et al., 2004). The removal of actively foraging individuals, generation after generation, may therefore lead to evolution of multiple traits over time, in what can be summed up as evolution of reduced boldness. This type of selection also takes place when some fish more efficiently escape "active" or moving gears such as trawls (Diaz Pauli et al., 2015).

The expectation, as argued by numerous studies and recently reviewed by Arlinghaus et al. (2017), is that passive gears eliminate bold individuals from the existing trait variation in the population, which causes the evolution of reduced boldness, that is, timidity, over time. Thus, when Arlinghaus et al. (2017) and other studies claim that boldness will decrease due to fishing, the prediction is not that an individual, in the rare case it may encounter a novel object, will approach it more slowly. Instead, the focus is on the behavioral syndrome and that fishing gear, because it exploits certain behaviors related to boldness, may have consequences for correlated traits such as foraging, survival, and in turn population dynamics, trophic interactions, and fisheries yield (Arlinghaus et al., 2017; Biro & Stamps, 2008; Uusi-Heikkilä, 2008). In the remainder of this article, we use the term "boldness" interchangeably with the level of foraging activity, which in our model is the behavior that leads to ingestion of food while at the same time exposing individuals to predation risk. In the model, fish find more food if they are more active, but they also run into predators more frequently, which are common elements of the "bold" behavioral syndrome. Shyer fish have been found to have lower metabolic rates (Cooke et al., 2007; largemouth bass), lower energetic requirements (Cutts, Metcalfe, & Taylor, 2002; Atlantic salmon *Salmo salar*; Cooke et al., 2007; and Nannini, Wahl, Philipp, & Cooke, 2011; largemouth bass), and more efficient energy conversion (Nannini et al., 2011; largemouth bass). Selection on boldness can further have amplified effects on fitness through reproductive behaviors, for example in largemouth bass where Sutter et al. (2012) documented how males that were more vulnerable to angling also were more aggressive and more active in parental care. This body of studies makes compelling arguments that direct selection on foraging behavior will cause evolution toward reduced boldness with potential consequences including reduced growth, reproduction, population resilience, and fisheries productivity.

However, life-history theory predicts that fishing, like other sources of external mortality, mostly selects toward early maturation (Law & Grey, 1989) and accelerated life histories (e.g., faster juvenile growth and smaller length at maturation; see Heino & Godø, 2002 for a detailed discussion). Because life-history traits and behavior are correlated, the general expectation is that accelerated life histories are also associated with a riskier behavior to acquire the resources needed to sustain it (Fraser & Gilliam, 1987; in guppies, *P. reticulata* and Hart's rivulus, *Rivulus hartii*; Biro & Stamps, 2008; Réale et al., 2010). We may therefore expect the elevated mortality from fishing to lead to riskier foraging and bolder individuals over evolutionary time. Even though risky behavior might increase mortality further, it is more beneficial for individuals, under these conditions, to prioritize immediate reproductive gains over long-term survival or future reproduction (Jørgensen & Holt, 2013; Werner & Anholt, 1993). This argument thus reaches the opposite conclusion but, being complex and involving multiple traits, it is not as verbally persuasive.

The story does not stop there, however, because there is even another layer of feedbacks at which life-history traits can have effects. Earlier onset of reproduction is well documented as a main effect that is easily detected in fisheries data (reviewed by Heino, Díaz Pauli, & Dieckmann, 2015), and many exploited fish stocks now have smaller body size than before. Because natural mortality declines with size (Gislason, Daan, Rice, & Pope, 2010), these early-maturing fish spend more of their life at a smaller size where mortality is higher. These fish therefore run into higher risks when foraging, which can prohibit further increases in boldness, simply because the cumulative risk would be too high.

Fishing may thus typically cause three opposing selection patterns for behavioral boldness: direct selection on behavior for reduced boldness; indirect selection through reduced expected life span for increased boldness; and a further route of indirect selection from smaller body size for decreased boldness (Table 1). Which of these three selective forces acting on boldness ends up being numerically dominant likely depends, among other factors, on the type of selectivity of the fishing gear (exactly how accurately does it target behaviors associated with boldness) and the selectivity and level of the other sources of natural and harvesting mortality.

Some evolutionary models have already included effects on both life-history traits and behavior (although rather rudimentarily), and these made the prediction that the risk-taking during foraging,

TABLE 1 Schematic illustration of how fishing gear selectively removing bold individuals may affect evolution of boldness when additional layers of life-history feedback mechanisms are included

Certain types of fishing gear are selectively removing the boldest individuals...		
Expectation ↓: Boldness will evolve to lower values because it is a heritable trait **Applies to:** Verbal arguments in, for example, Biro and Stamps (2008), Arlinghaus et al. (2017). Likely outcome in single-trait experiments **Conclusion:** Boldness cannot be seen in isolation but requires a lifetime integration, and this perspective is therefore likely not applicable to the wild	▼ **...but fishing is also reducing life span...** **Expectation ↑:** Boldness will evolve to higher values because increased mortality favors early reproduction and accelerated life histories **Applies to:** The model by Andersen et al. (2018), which finds selection gradients on lifetime fitness one trait at the time **Conclusion:** Possible transient or short-term effect, because behavior may change or evolve faster than body size	▼ **...and it causes evolution of earlier maturation and smaller size** **Expectation ↓:** Boldness will evolve to lower values because size-dependent predation is higher for smaller-bodied fish, prohibiting increases in risk-taking and boldness **Applies to:** Andersen et al. (2018) (evolutionary transients) and the model and results in this paper (evolutionary endpoints) **Conclusion:** Includes all evolutionary feedbacks, but predictions depend on methodology

a characteristic of boldness, would increase slightly due to fishing (Jørgensen & Fiksen, 2010; Jørgensen & Holt, 2013). This expectation was recently analyzed by Andersen, Marty, and Arlinghaus (2018) in a model where fishing selects on boldness, and fitness is quantified as the expected lifetime reproductive output. The authors interpreted the model as predicting reduced boldness, that is, inducing a timidity syndrome (Arlinghaus et al., 2017). However, while selection toward reduced boldness was true for some parameter combinations, selection toward increased boldness over time took place in most of the parameter space explored (see their figures 4b and 6).

In this study, we present a model that in some respects resembles that of Andersen et al. (2018), although the models and analyses have been developed independently and in parallel. Because the models differ in assumptions and evolutionary methodology, the degree of shared predictions makes a stronger case for how behaviors may evolve due to fishing, while the differences in predictions can be traced back to model-specific assumptions. We aim to clarify theoretical expectations for how fishing activities are selective for behavioral traits, and what consequences are for the evolution of risk-taking behavior, life-history traits, and emergent natural mortality.

2 | MATERIALS AND METHOD

2.1 | Model description

To assess the impacts of behavior-selective fishing on behavioral and life-history traits, we adopted a state-dependent dynamic programming model (based on Jørgensen & Fiksen, 2010; see also Mangel, 1994; Satterthwaite et al., 2009). The model finds optimal lifelong trajectories for foraging, growth, and reproduction. The new element of this version is that we focus on how fishing gears select on behavior along a continuous axis with two different gear types at each end of the spectrum.

In the one end, individuals are vulnerable to fishing gear when actively looking for food or foraging (e.g., gill nets, lures, baited hooks). We will refer to this fishing situation as targeting the "foraging individuals." In the other end of the spectrum, individuals are vulnerable when they are not actively foraging. As an example, purse seines might be selecting individuals that are seeking shelter in the safety of the school (Hamilton, 1971; Krause, Bumann, & Todt, 1992) whereas individuals on the outskirts, where more food is available, might have more chance of escaping the gear. We will call this gear type targeting the "resting/hiding individuals." It is important to note that it is difficult to place precisely the above-mentioned gears on our continuum because it depends on the gear and on the biology of the targeted species. The gears mentioned here are therefore used as an illustration of a concept.

For more clarity, we deliberately avoid the use of "active" and "passive" gear. "Passive" gears are usually defined as catching the fish as a result of the movement of the fish toward the gear and are also considered as stationary (the opposite is true for active gears, Cochrane & Garcia, 2009). However, we see this view as confusing in the context of our study. For example, trawling is considered as an active gear but can target both foraging and resting fish, depending on where and when it is deployed and, therefore, be located at both ends of the continuum we model.

Most gear types select simultaneously for several, both behavioral and morphological, traits. For simplicity and ease of interpretation of results, our model is selecting purely on foraging behavior, and we exclude size selectivity from the current analysis to avoid confusing the effect of behavioral selectivity with the already complex effects of selection on body size (e.g., Jørgensen, Dunlop, Opdal, & Fiksen, 2009; Zimmermann & Jørgensen, 2017). Excluding size selectivity will also allow us to disentangle the effects of fishing mortality and selectivity pattern. Because the model assumes behavioral vulnerability to fishing gear as a continuum, our analysis includes also the case where vulnerability to fishing is not correlated with behavior. Even if this scenario is not likely to occur in reality, it is the assumption used in most previous modeling studies and the one that fisheries management operates with.

The foraging activity affects growth, as well as the individual's exposure to predators and fishing gear. The key trade-offs are as follows: (a) between energy acquisition and survival, as increased foraging leads to increased exposure or vulnerability to predation and (b) allocation of acquired resources between growth and reproduction. We describe the model briefly below. For further details please confer Jørgensen and Fiksen (2010), Jørgensen and Holt (2013) and the Supporting Information Appendix S1. All model variables are summarized in Table 1 and parameters in Table 2.

Net energy intake (R, g year^{-1}) corresponds to the total energy intake subtracted the energetic costs of routine metabolism (e.g., standard respiration, activity):

$$R = h \cdot W^{b} - b_0 \cdot (W+G)^{a}, \tag{1}$$

where W and G, respectively, are the individual's somatic and gonadal weight (in grams), b and a are metabolic exponents, and b_0 is a metabolic constant (see Table 2 for parameter values). Net energy R is allocated between reproduction and growth according to the allocation parameter α, thus determining age and size of sexual maturation and influencing postmature growth rate (Supporting Information Appendix S1, Equations S1 and S2).

Food intake h depends on the individual's foraging strategy ϕ (i.e., more or less active foraging behavior) and food availability E:

$$h = \phi \cdot E. \tag{2}$$

Note that E is a normally distributed random value reflecting autocorrelated stochasticity in food availability, with mean μ_E and standard deviation σ_E (Table 2; see also Holt & Jørgensen, 2014). More intense foraging (higher h) increases growth rate but also leads to higher mortality risk (see below). Energy allocation α and the foraging strategy ϕ are state-dependent; that is, they and are optimized for every combination of the individual states age, length, and current value of food availability.

Total mortality Z (year^{-1}) is split into five components (all in unit year^{-1}) (for more details, see Jørgensen & Fiksen, 2010):

$$Z = M_{\text{fixed}} + M_{\text{size}} + M_{\text{reproduction}} + M_{\text{foraging}} + F, \tag{3}$$

where M_{fixed} is a constant background mortality rate, M_{size} a component due to size-dependent predation irrespective of behavior, $M_{\text{reproduction}}$ a mortality component that increases with more intense reproductive investment, M_{foraging} is the component related to foraging behavior, and F is the fishing mortality (see below). All the parameters used in the model are summarized in Table 3.

Fishing mortality F depends on the foraging strategy ϕ and is otherwise nonselective (i.e., independent of other traits such as size, age, or maturity status). The strength of the association between ϕ and fishing mortality is a continuous variable, which allows us to investigate different gear types and fish ecologies. Fishing mortality F is split into two components: (a) an unavoidable component which the individual will experience regardless of its behavior, and (b) the behavior-dependent mortality component contingent on foraging strategy, where the risk acceptance for the foraging strategy ϕ is scaled with a reference value θ to adjust the sensitivity of the model to γ (described below):

$$F = (1-\gamma) \cdot F_0 + \gamma \cdot \frac{\phi}{\theta} \cdot F_0. \tag{4}$$

The relative importance of these two components can be expected to vary depending on the type of fishery, fishing gear, and species that

TABLE 2 Summary of the variables used in the model. Prefix S denotes equations found in the Supporting Information Appendix S1

Variable	Description	Unit	Equation
α	State-dependent variable: proportion of resources allocated to reproduction	–	S1; S2
ϕ	State-dependent variable: risk acceptance related to foraging	–	2; 4; S6
L	Body length	cm	S3; S5
W	Somatic body mass	g	1; S3; S1; S8
E	Food availability	g$^{1\text{-}b}$·year^{-1}	2
G	Gonad mass	g	1; S1; S8
R	Net intake	g·year^{-1}	1; S1; S2
Q	Gonado-somatic index: weight of the gonads in relation to the total body weight (including gonads)	–	S7; S8
γ	Coefficient for the relation between fishing mortality and foraging strategy	–	4
h	Net available resources	g$^{1\text{-}b}$·year^{-1}	1; 2

TABLE 3 Summary of the parameters used in the model

Parameter	Description	Value	Unit	Equation
a	Metabolic exponent	0.7	–	1
b	Metabolic exponent	0.7	–	1
b_0	Metabolic coefficient	0.3	–	1
q_{ref}	Gonado-somatic index at which $M_{reproduction} = M_{size}$	0.2	–	S7
k	Length–weight relationship coefficient	0.95	$g \cdot cm^{-3}$	S3
c	Size-dependent mortality coefficient	1.2	$year^{-1}$	S5
d	Size-dependent mortality exponent	−0.75	–	S5
p	Cost of carrying gonads exponent	2	–	S7
$\bar{\phi}$	Reference value for the foraging strategy	1.4	–	4
M_{fixed}	Fixed mortality	0.05	$year^{-1}$	S4
μ_E	Mean of the distribution of E	6	–	–
σ_E	Standard deviation of the distribution of E	2.5	–	–

is being harvested. We therefore included the parameter γ ($-1 \le \gamma \le 1$) to describe the effect of foraging on gear exposure. Note that this equation can produce negative values for F depending on the ratio ϕ/θ. This was checked for continuously in our simulations and was not a problem, partly because realistic values for γ lie in the range −0.3 to 0.3, and the majority of our results are reported for this range. The biological interpretation of γ is compounded by effects of the fishing gear and of the harvested species' ecology. Parameter γ describes both the intensity by which the fishing gear selects on certain behaviors, and the magnitude of unavoidable fishing mortality not dependent on behavior.

2.2 | Proportion of mortality attributed to behavior

When $\gamma = 0$, the fishing is completely unselective on behavior, and the probability of being caught is the same for all individuals regardless of their foraging strategy ϕ. For values of γ close to zero, the avoidable part of the fishing mortality is low compared to the unavoidable part, and the overall fishing mortality is only weakly dependent on behavior. When the absolute value of γ is approaching one, the behavior-dependent part becomes the most important component of the fishing mortality and the vulnerability of the fish to fishing is depending almost exclusively on the foraging strategy ϕ adopted.

2.3 | Behavior targeted by fishing

Parameter γ also defines the behavior targeted by the fishery. When γ is positive, the vulnerability to fishing increases with the level of foraging activity, and fishing targets individuals with intense foraging strategy ϕ. When γ is negative, the vulnerability to fishing decreases with the level of foraging activity, and fishing targets individuals with low foraging strategy ϕ (illustrated in the top panel of Figure 1).

Because of the association between foraging behavior and vulnerability to different gear types, the realized fishing mortality F becomes dependent on the value of γ.

2.4 | Optimization method

The continuous equations above are updated in 24 time steps annually, while strategies α and ϕ are optimized with annual resolution.

We used optimization by dynamic programming (Clark & Mangel, 2000; Houston & McNamara, 1999) to find the values for foraging strategy and energy allocation that maximized the expected lifetime gonad production. This method thus finds evolutionary endpoints; that is, the evolutionary adaptations one could expect given sufficient time and supposing constraints remained constant (Clark & Mangel, 2000; Houston & McNamara, 1999; Jørgensen & Fiksen, 2010). Finally, we simulated a population following the optimal strategy in an environment with stochasticity in food availability. We ran 10,000 replicates to obtain mean and standard deviation of each trait.

The model was parameterized so that we obtained coherent life-history traits and trajectories in the absence of fishing, that is, shaped by natural mortality only. Parameter values are summarized in Table 2.

3 | RESULTS

The model predicts that behavior-selective fishing induces changes in the optimal foraging strategy of opposite directions depending on which behavior is targeted. In general, when individuals are targeted while foraging, the optimal strategy is to forage less. On the opposite, when individuals are targeted while hiding/resting, the optimal strategy is to spend more time foraging. The qualitative changes observed in other life-history traits are in line with the general expectations associated with additional mortality: earlier maturation, smaller adult size-at-age, and smaller asymptotic size. However, the intensity of these life-history changes depends on the new optimal foraging strategies induced by behavior-selective fishing (summarized in Figure 1).

3.1 | Vulnerability to fishing gear while foraging (γ)

Varying the vulnerability to fishing gear while foraging (γ) continuously from −0.3 to 0.3 shows clear, directional changes in the optimal life

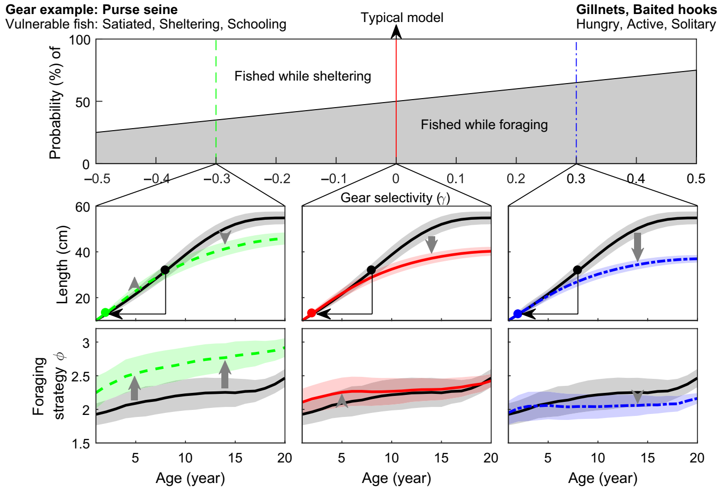


FIGURE 1 Effect of vulnerability to gear γ on optimal life-history and foraging strategies for fishing mortality of 0.1 year^{-1}. In the second row, dots indicate age at first maturation: black ones for populations adapted to natural mortality only, and colored ones after adaptation to fishing mortality (the thin arrow highlights the shift). The solid red line corresponds to the case where fishing is independent of behavior ($\gamma = 0$). The dashed green and dash-dot blue lines correspond to the case where fishing targets passive ($\gamma = -0.3$) and active ($\gamma = 0.3$) individuals, respectively. Shaded areas correspond to the standard deviation of the trait within the population, and grey arrows show the direction of change due to adaptation to fishing

histories, foraging strategy, and emerging natural mortality (Figure 2). Predicted length-at-age for adult fish is generally reduced at $F = 0.1$ year^{-1}, but this reduction is more pronounced when fishing targets foraging individuals (Figure 2a). Length at young ages is largely unaffected by the variation in gear selectivity (Figure 2a). The optimal foraging strategy (ϕ) is unaffected by unselective fishing (Figure 2b). However, behavior-selective fishing influences the optimal foraging strategy, and opposite vulnerability (γ) have opposite effects: targeting hiding/resting individuals ($\gamma < 0$) considerably increases the optimal foraging strategy relatively to nonselective fishing (maximum 20% increase), while targeting foraging individuals ($\gamma > 0$) reduces it (maximum 10% decrease) (Figure 2b). As expected, natural mortality increases, even with unselective fishing (Figure 2c). The model predicts that targeting hiding/resting individuals ($\gamma < 0$) increases consequently the total natural mortality even further, relative to nonselective fishing (maximum 22% increase). This is particularly due to the component of mortality related to foraging. Targeting foraging individuals ($\gamma > 0$) results in somewhat lower total mortality rate than nonselective fishing (maximum 7% decrease) (Figure 2c), but still in an increase compared to no fishing.

3.2 | Interactions between behavioral gear selectivity and the level of fishing mortality

The sensitivity of the various life-history and behavioral traits to intensified fishing mortality depends on the vulnerability to the fishing gear γ (Figure 3). We use three distinct selectivity scenarios to exemplify this: (a) targeting hiding/resting individuals ($\gamma = -0.3$); (b) targeting foraging individuals ($\gamma = 0.3$); and (c) nonselective fishing ($\gamma = 0$). Traits can be grouped into two groups based on how sensitive they are to gear selectivity γ, and interestingly, this correlates with how easily observable the traits are. The first group consists of traits that are difficult to observe or measure, but where the model predicts a considerable impact of behavioral gear selectivity with intensified fishing (Figure 3a,b). The traits in this group the foraging strategy, which may increase or decrease depending on the vulnerability to fishing gear γ, and natural mortality, which increases with intensified fishing for all types of vulnerability γ but more when hiding/resting individuals are targeted ($\gamma = -0.3$; Figure 3b). The second group of traits are more easily observable and measurable, and in many cases already part of standard monitoring of fish stocks and a focus of many models, but are at the same time less sensitive to different gear vulnerability (Figure 3c–e). The traits in this second group are length-at-age (Figure 3c), gonado-somatic index reflecting the reproductive investment (GSI; Figure 3d), and age at maturity (Figure 3e).

Vulnerability to fishing gear while foraging γ also highlights changes in energy allocation. When fishing targets foraging individuals ($\gamma = 0.3$; Figure 3, blue dash-dot lines), the individual fitness is maximized by reduced activity and adoption of safer foraging strategies (i.e., foraging less, Figure 3a, blue dash-dot line). The individual survival thus increases through reduced overall natural mortality (Figure 3b), but at the cost of decreased energy acquisition. This leads to less energy being available for growth and reproduction. On the opposite, when fishing targets hiding/resting individuals ($\gamma = -0.3$; Figure 3 green dotted lines), the survival benefit from safe foraging strategies is reduced. No matter which foraging strategy an individual adopts, it will suffer extra mortality, either from

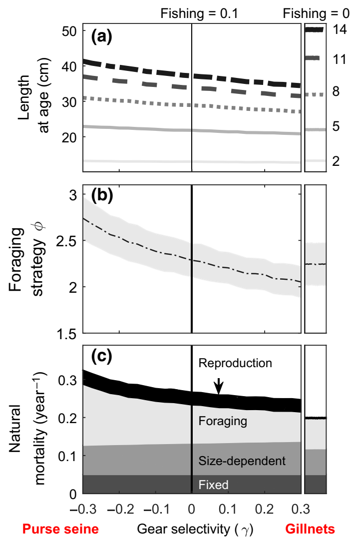


FIGURE 2 Effect of vulnerability to gear γ on predicted optimal values of length-at-age (a), the foraging strategy at age 14 (b), and the emergent natural mortality at age 14 (c). The shaded area for the foraging strategy corresponds to the standard deviation of the trait in the population. We use age 14 as the reference for adult life-history traits because at this age all individuals are mature, even in the absence of fishing. This age is also far enough from the end of the modeled life span to be unaffected by terminal effects when using dynamic programming for optimization (Clark & Mangel, 2000)

fishing or from predation, and adopting a riskier foraging strategy (i.e., increased foraging rate) appears to be the most optimal solution (Figure 3a). Thus, natural mortality increases, but the positive effect of increased energy acquisition compensates for reduced survival probability (Figure 3b). Investment into reproduction is only little affected by vulnerability to the fishing gear (Figure 3d), but appears to have priority over somatic growth because differences in energy acquisition result in differences in adult length, but not in GSI or age at maturation (Figure 3c–e).

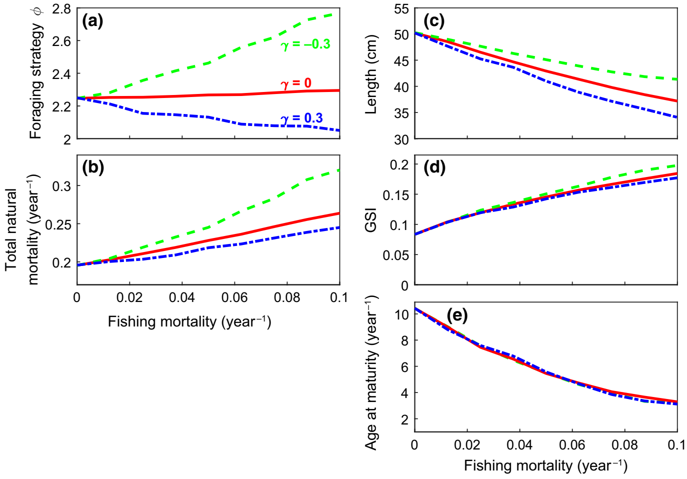
4 | DISCUSSION

In this study, we analyzed a model which predicted that behavior-selective harvesting has the potential to alter life-history traits and emergent natural mortality in addition to the behavioral trait that is directly targeted by the fishing gear. It thus integrates the one direct and two indirect selection routes in Table 1. Our findings support earlier works on evolutionary effects of fishing by predicting earlier age at maturation, increased reproductive investment, smaller asymptotic size, and higher natural mortality (e.g., Dunlop, Enberg, Jørgensen, & Heino, 2009; Enberg, Jørgensen, Dunlop, Heino, & Dieckmann, 2009; Enberg et al., 2012; Jørgensen & Fiksen, 2010; Law & Grey, 1989). Importantly, the model also goes beyond that, in showing that being specific about how gear types interact with a fish species' ecology has implications for the evolution of behavior (see also Andersen et al., 2018), even when indirect selection via life-history traits is included.

4.1 | Fishing can be a driver of reduced boldness

The predictions from our model align with those of Andersen et al. (2018) by showing that behavior may evolve in response to fishing and that different gear types can be selective in different ways. When interpreting these models, it is important to keep in mind that the type of fishing gear and the species' natural behavior together determine the degree of selection on a trait. For example, many fishing techniques use baits or mimic food, which attracts fish while they are foraging. This will selectively harvest fish that more actively search for food or more indiscriminately eat what

FIGURE 3 Effects of fishing mortality on average individual-level traits for different types of vulnerability to gear γ. The traits shown are the mean value of the foraging strategy at age 14 (a), total natural mortality at age 14 (note that total mortality includes also fishing mortality which is not shown here) (b), length-at-age 14 (c), reproductive investment (GSI) at age 14 (d), and mean age at maturity within a population, depending on γ. The red solid lines correspond to the case where fishing is not related to behavior ($\gamma = 0$). The green dashed ($\gamma = -0.3$) and blue dot-dash ($\gamma = 0.3$) lines correspond to the case where fishing targets sheltering (purse seines) and foraging individuals (gill nets), respectively



they find. Baits and lures may thus be effective in capturing active predators and generalists, of which Atlantic cod can serve as an example. It is thus the combination of species biology and gear type that defines an efficient fishery for cod and, in our model, this leads to decreased boldness (Figure 2, positive γ). Andersen et al. (2018) find the same, but only when there is size-selective harvest of big fish only (their figure 6) and when direct selection on behavior is at the high end of their tested range (their figure 4b). It remains to be argued how typical this combination is, but the clearest example may be rod-and-reel angling where lures mimic food and trophy fish are targeted. That our model predicts reduced foraging rates (a characteristic of shyness) for a broader parameter range (as long as fishing gear selectively removes foraging fish) suggests that the phenomenon may occur more widely than suggested by Andersen et al. (2018). The prediction follows from our methodology, where the evolutionary effect of fishing includes reduced body size, at which predation risk is higher to the degree that it prohibits increased foraging rates. The finding is in accordance with the suggestion by Arlinghaus et al. (2017) that passive gears, often selectively removing active individuals, have the potential to induce a "timidity syndrome" in exploited populations.

A further effect that may lead to the evolution of reduced boldness is size-selective fishing, where fish that mature and stop growing before they reach harvestable size may have higher fitness (see examples in Jørgensen et al., 2009). Reduced foraging may therefore evolve if it can contribute to fish staying small. In our model, foraging activity can vary with age and size, so foraging can slow down as fish reach harvestable size, were we to run such a scenario. This is in contrast to Andersen et al. (2018), where boldness is a lifelong trait and where potential benefits at small size and potential costs at large size are weighed together when selection favors either increased or reduced boldness. With harvesting of large fish, the cost of high foraging when large can outweigh its benefits while being small so that boldness would evolve to become lower, as in their figure 6.

Unfortunately, it is difficult to confront our results to observations from wild populations since behaviors such as boldness and mortality are very difficult to observe and estimate, especially in marine fish stocks. Additionally, selection on the behavior usually comes together with selection on size or other traits and disentangling the effects of both selections from population data would be impossible. Also, in large scale fisheries, gears might not discriminate enough between the different behaviors to introduce a significant effect of behavioral selectivity. To answer this question, we would need more knowledge about quantifying the behavioral selectivity of large scale fisheries gears.

4.2 | In pelagic, schooling fish, increased boldness is predicted

Where we draw attention to a new concern is in relation to fisheries on schooling fish, as is typical for many pelagic species. A typical gear used is the purse seine, which our model predicted would lead to evolution of higher foraging rates. This is because individual fish seek safety in the school (Hamilton, 1971), and we assume that is where they are more vulnerable to purse seines. To avoid the purse seine, fish could spend more time outside the schools, where foraging is more efficient (Eggers, 1976). Exploitation could thus favor individuals with a higher activity and growth rate, which in turn also leads to elevated natural mortality due to predation. However, even though they are expected to capture shyer fish, it is not yet clear how strong their behavioral selectivity is (Diaz Pauli & Sih, 2017). Our expectations are therefore qualitative, and we cannot infer about how strong the changes in response to this fishing gear will be.

The predicted evolutionary effect of purse seining on behavior could not explain why the Norwegian spring-spawning herring population (*Clupea harengus*), although extensively monitored and with 80-year-long time series of maturation age, shows few signs of earlier maturation (Engelhard & Heino, 2004) in contrast to almost all other stock with a similar exploitation history (Heino et al., 2015). We need to adapt our model precisely to herring before trying to make further conclusions. It is also possible that the behavioral selectivity of the purse seine is, in reality, very low (close to $\gamma = 0$) and the changes in response to this fishing gear are not detectable in the wild.

As it is, the life-history modeled is closer to a long-lived, cod-like species. Qualitatively, we believe that the general expectations drawn from our model could apply to a wide range of other life histories. However, it is more difficult to predict how our results would change if we decided to model species with a specific ecology inducing additional costs (e.g., extensive migrations, large investments into reproductive behavior). A parameterization of the model specifically for these species would therefore be required before drawing further conclusions on this question. Adaptation toward more risk-taking phenotypes may also be induced by other active gears such as trawls (Diaz Pauli et al., 2015; guppies; Leclerc et al., 2017).

4.3 | Similarities and differences with the Andersen et al. (2018) model

Our model is largely similar to that by Andersen et al. (2018) except for four important differences: (a) we focus on finding the optimal values for a set of jointly evolving traits, whereas Andersen et al. (2018) focus on selection responses and selection trajectories; (b) in our model, the behavioral and life-history traits are varying with age, whereas in the model of Andersen et al. (2018), the trait values are independent of age or size; (c) treat the different types of fishing gears as a continuum rather than specific cases, allowing us to fill a broader canvas; and (d) we ignore the size dependence of fishing gear, in order to favor interpretation and analysis even though it makes the model less applicable to real-world fisheries. Below we discuss how the approaches differ, and how the contrasting findings can be interpreted.

Our state-dependent model allows foraging behavior and reproductive investment to be optimized for each age, whereas those traits are assumed fixed to one lifelong trait in Andersen et al. (2018), resulting in a compromise between the optimal trait combinations in different phases of life. In the absence of fishing, we find a slight increase in foraging activity with age. This is because individuals at larger sizes have lower length-dependent mortality and can afford to forage more, although it makes them more exposed to predators. The shortening of life span caused by fishing leads to decreased age at maturation and increased investment into reproduction. The consequences of these changes are two-fold: reproduction starts earlier and, consequently, adult fish are smaller, leading to increased size-dependent predation mortality. When fishing is not selective for behavior ($\gamma = 0$), the increase in predation mortality due to smaller size prohibits further risk-taking through elevated foraging, and our model predicts no change in boldness with increasing fishing pressure.

Overall, the age-dependent changes in foraging activity are rather small in our model, except when resting/hiding individuals are vulnerable to fishing. However, our preliminary runs with size-selective fishing show that the foraging behavior can vary substantially with age/length when size selectivity is included. This is because adaptations of foraging behavior allow the fish to stay under the target size. For example, with relatively high minimum size, the optimal strategy seems to be foraging less when young in order to stay at smaller size and avoid the fishing mortality, regardless of the behavioral type the fishing is targeting. However, when the size at which fishing starts is reached, the foraging activity will change depending on which behavior is targeted. These preliminary results highlight the importance of including state dependence, especially when introducing a fishery selecting on length, weight, or age.

Different fishing gear can target a range of behavioral as well as physiological traits: Hungry individuals (potentially with high metabolic rate) are more vulnerable to baited hooks (Stoner, 2003), angling is selecting individuals with elevated activity levels and aggressive behavior (Cooke et al., 2007; Suski & Philipp, 2004), and trawls are more efficient in catching fish with a low swimming capacity (Huse, Løkkeborg, & Soldal, 2000), low metabolic rate, and low maximum aerobic swim speed (Killen, Nati, & Suski, 2015). The selection pressures caused by different fishing gears are thus likely to favor different behavioral, physiological, and life-history strategies, even within the same species. We simplified this into a single continuum describing the strength of correlation between energy acquisition rate (foraging) and vulnerability to fishing mortality. An important difference between Andersen et al. (2018) and our study is that we included the possibility that fishing could target satiated or hiding/sheltering fish, as might be the case with schooling, pelagic fish. It is for these types of fisheries we predict the strongest increases in boldness and, consequently, the most dramatic increases in natural mortality rate.

We excluded size selectivity from our model (fish have the same probability of being caught regardless of size) to avoid confusing the effects of size-selective harvesting with the ones of behavior-selective harvesting. The different components of selectivity obviously interact and lead to different trait combinations being optimal under different selectivity combinations. Andersen et al. (2018) analyze this to some degree, but a full treatment of the evolutionary effects of size selectivity is complicated (for cases without behavior, see, e.g., Jørgensen et al., 2009; Zimmermann & Jørgensen, 2017). Comparing the joint effects of size- and behavior-selective fishing is a natural extension of this model but beyond the scope of the current study. We expect the optimal foraging behavior to depend on the type and shape of size selectivity and an additional study dedicated to this specific point is needed.

5 | MANAGEMENT IMPLICATIONS

Modern fisheries management relies on up-to-date estimates of population parameters as an input for realistic stock assessments, and ignoring the evolutionary consequences of fishing might lead to suboptimal management (Biro & Post, 2008; Enberg, Jørgensen, & Mangel, 2010; Heino et al., 2013; Laugen et al., 2014; Uusi-Heikkilä, Wolter, Klefoth, & Arlinghaus, 2008). Length-at-age, reproductive investment, and age at maturity are prone to evolve due to fishery selection, but we showed that the predicted changes are largely independent of behavioral selectivity. At the same time, these are also the most common traits scientists have used to detect fishing-induced evolution (Heino & Godø, 2002; Law, 2000; Sharp & Hendry, 2009). However, traits crucial for understanding stock dynamics such as behavior and natural mortality are difficult to estimate, and often not estimated at all but out of convenience assumed to be constant, even though notable variations in the latter has been observed in several stocks (Cadigan, 2016; Swain, 2011; Swain & Benoit, 2015; Swain, Jonsen, Simon, & Davies, 2013; Thorley & Andrusak, 2017). Our and previous (Jørgensen & Fiksen, 2010) results suggest that regardless of the behavioral selectivity, natural mortality will increase due to fishing-induced adaptations, but even more so when fishing targets hiding/resting individuals. Ignoring such increase would lead to underestimation of stock size, even though the fishing mortality maximizing long-term yield (F_{MSY}) might not drastically change. Given that in most stock assessment models, the reported catch is the most important entity defining the stock level, while survey time series are used as relative indices, a discrepancy between the observed stock size in the field and the perceived stock estimated by the assessment model might arise. Such discrepancy, where fishermen observe larger amounts of fish than stock assessments estimate, can erode trust, complicate stakeholder dialogue, and in the long run be detrimental for successful management.

Incorporating the effects of behavioral selectivity through different gear types adds to the tool box available for sustainably managing fish stocks in an evolutionarily enlightened manner and potentially mitigating detrimental changes for future fisheries yields as well as population viability. Regardless of the differences in methodology and some differing results when comparing with Andersen et al. (2018), our main findings coincide and make a strong case that behavioral-selective fishing can induce changes in exploited populations.

ACKNOWLEDGMENTS

MC, JC, and KE acknowledge the Research Council of Norway for funding (ConEvolHer, project No 243735). CJ and KE also acknowledge funding from MARmaED funded by the European Union's

Horizon 2020 research and innovation program under the Marie Skłodowska Curie grant agreement No 675997. The results of this study reflect only the authors' views, and the Commission is not responsible for any use that may be made of the information it contains.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

MC, CJ, and KE contributed to building the model, interpreting the results, as well as writing and reviewing the article before submission. All authors have approved the final, submitted version.

DATA ACCESSIBILITY STATEMENT

Script: https://doi.org/10.5281/zenodo.1307394.

ORCID

Marion Claireaux http://orcid.org/0000-0002-0395-7954

Christian Jørgensen http://orcid.org/0000-0001-7087-4625

Katja Enberg http://orcid.org/0000-0002-0045-7604

REFERENCES

Andersen, K. H., Marty, L., & Arlinghaus, R. (2018). Evolution of boldness and life history in response to selective harvesting. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*(2), 271–281, https://doi.org/10.1139/cjfas-2016-0350.

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

Biro, P. A., & Sampson, P. (2015). Fishing directly selects on growth rate via behaviour: Implications of growth-selection that is independent of size. *Proceedings of the Royal Society of London B: Biological Sciences*, *282*(1802), 20142283. https://doi.org/10.1098/rspb.2014.2283

Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution*, *23*(7), 361–368. https://doi.org/10.1016/j.tree.2008.04.003

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*, *105*(8), 2919–2922.

Budaev, S. V. (1997). Alternative styles in the European wrasse, *Symphodus ocellatus*: Boldness-related schooling tendency. *Environmental Biology of Fishes*, *49*(1), 71–78. https://doi.org/10.1023/A:1007380212475

Cadigan, N. G. (2016). A state-space stock assessment model for northern cod, including under-reported catches and variable natural mortality rates. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(2), 296–308. https://doi.org/10.1139/cjfas-2015-0047

Clark, C. W., & Mangel, M. (2000). *Dynamic state variable models in ecology: Methods and applications*. New York, NY: Oxford University Press on Demand.

Cochrane, K. L., & Garcia, S. M. (Eds). (2009). *A fishery manager's guidebook*. 2nd edn. , Oxford, UK: Wiley-Blackwell. pp. 544. https://doi.org/10.1002/9781444316315

Cooke, S. J., Suski, C. D., Ostrand, K. G., Wahl, D. H., & Philipp, D. P. (2007). Physiological and behavioral consequences of long-term artificial selection for vulnerability to recreational angling in a teleost fish. *Physiological and Biochemical Zoology*, *80*(5), 480–490. https://doi.org/10.1086/520618

Cutts, C. J., Metcalfe, N. B., & Taylor, A. C. (2002). Fish may fight rather than feed in a novel environment: Metabolic rate and feeding motivation in juvenile Atlantic salmon. *Journal of Fish Biology*, *61*(6), 1540–1548. https://doi.org/10.1111/j.1095-8649.2002.tb02496.x

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

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

Dochtermann, N. A., Schwab, T., & Sih, A. (2015). The contribution of additive genetic variation to personality variation: Heritability of personality. *Proceedings of the Royal Society of London B: Biological Sciences*, *282*(1798), 20142201.

Dunlop, E. S., Enberg, K., Jørgensen, C., & Heino, M. (2009). Toward Darwinian fisheries management. *Evolutionary Applications*, *2*(3), 245–259. https://doi.org/10.1111/j.1752-4571.2009.00087.x

Eggers, D. M. (1976). Theoretical effect of schooling by planktivorous fish predators on the rate of prey consumption. *Journal of the Fisheries Research Board of Canada*, *33*, 1964–1971. https://doi.org/10.1139/f76-250

Enberg, K., Jørgensen, C., Dunlop, E. S., Heino, M., & Dieckmann, U. (2009). Implications of fisheries-induced evolution for stock rebuilding and recovery. *Evolutionary Applications*, *2*(3), 394–414. https://doi.org/10.1111/j.1752-4571.2009.00077.x

Enberg, K., Jørgensen, C., Dunlop, E. S., Varpe, Ø., Boukal, D. S., Baulier, L., ... Heino, M. (2012). Fishing-induced evolution of growth: Concepts, mechanisms and the empirical evidence. *Marine Ecology*, *33*(1), 1–25. https://doi.org/10.1111/j.1439-0485.2011.00460.x

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

Engelhard, G. H., & Heino, M. (2004). Maturity changes in Norwegian spring-spawning herring *Clupea harengus*: Compensatory or evolutionary responses? *Marine Ecology Progress Series*, *272*, 245–256. https://doi.org/10.3354/meps272245

Fraser, D. F., & Gilliam, J. F. (1987). Feeding under predation hazard: Response of the guppy and Hart's rivulus from sites with contrasting predation hazard. *Behavioral Ecology and Sociobiology*, *21*(4), 203–209. https://doi.org/10.1007/BF00292500

Gislason, H., Daan, N., Rice, J. C., & Pope, J. G. (2010). Size, growth, temperature and the natural mortality of marine fish. *Fish and Fisheries*, *11*(2), 149–158. https://doi.org/10.1111/j.1467-2979.2009.00350.x

Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, *31*(2), 295–311. https://doi.org/10.1016/0022-5193(71)90189-5

Heino, M., Baulier, L., Boukal, D. S., Ernande, B., Johnston, F. D., Mollet, F. M., ... Arlinghaus, R. (2013). Can fisheries-induced evolution shift reference points for fisheries management? *ICES Journal of Marine Science*, *70*(4), 707–721. https://doi.org/10.1093/icesjms/fst077

Heino, M., Díaz Pauli, B., & Dieckmann, U. (2015). Fisheries-induced evolution. *Annual Review of Ecology, Evolution, and Systematics*, *46*, 461–480. https://doi.org/10.1146/annurev-ecolsys-112414-054339

Heino, M., & Godø, O. R. (2002). Fisheries-induced selection pressures in the context of sustainable fisheries. *Bulletin of Marine Science*, *70*(2), 639–656.

Holt, R. E., & Jørgensen, C. (2014). Climate warming causes life-history evolution in a model for Atlantic cod (*Gadus morhua*). *Conservation Physiology*, *2*(1), cou050. https://doi.org/10.1093/conphys/cou050

Houston, A. I., & McNamara, J. M. (1999). *Models of adaptive behaviour: An approach based on state*. Cambridge: Cambridge University Press.

Huse, I., Løkkeborg, S., & Soldal, A. V. (2000). Relative selectivity in trawl, longline and gillnet fisheries for cod and haddock. *ICES Journal of Marine Science*, *57*(4), 1271–1282. https://doi.org/10.1006/jmsc.2000.0813

Jørgensen, C., Dunlop, E. S., Opdal, A. F., & Fiksen, Ø. (2009). The evolution of spawning migrations: State dependence and fishing-induced changes. *Ecology*, *89*(12), 3436–3448.

Jørgensen, C., & Fiksen, Ø. (2010). Modelling fishing-induced adaptations and consequences for natural mortality. *Canadian Journal of Fisheries and Aquatic Sciences*, *67*(7), 1086–1097. https://doi.org/10.1139/F10-049

Jørgensen, C., & Holt, R. E. (2013). Natural mortality: Its ecology, how it shapes fish life histories, and why it may be increased by fishing. *Journal of Sea Research*, *75*, 8–18. https://doi.org/10.1016/j.seares.2012.04.003

Killen, S. S., Nati, J. J., & Suski, C. D. (2015, August). Vulnerability of individual fish to capture by trawling is influenced by capacity for anaerobic metabolism. *Proceedings of the Royal Society of London B: Biological Sciences*, *282*(1813), 20150603. https://doi.org/10.1098/rspb.2015.0603

Krause, J., Bumann, D., & Todt, D. (1992). Relationship between the position preference and nutritional state of individuals in schools of juvenile roach (rutilus-rutilus). *Behavioral Ecology and Sociobiology*, *30*(3–4), 177–180. https://doi.org/10.1007/BF00166700

Laugen, A. T., Engelhard, G. H., Whitlock, R., Arlinghaus, R., Dankel, D. J., Dunlop, E. S., ... Nusslé, S. (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. (2000). Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science*, *57*(3), 659–668. https://doi.org/10.1006/jmsc.2000.0731

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

Leclerc, M., Zedrosser, A., & Pelletier, F. (2017). Harvesting as a potential selective pressure on behavioural traits. *Journal of Applied Ecology*, *54*(6), 1941–1945.

Mangel, M. (1994). Climate change and salmonid life history variation. *Deep Sea Research Part II: Topical Studies in Oceanography*, *41*(1), 75–106. https://doi.org/10.1016/0967-0645(94)90063-9

Mousseau, T. A., & Roff, D. A. (1987). Natural selection and the heritability of fitness components. *Heredity*, *59*(2), 181. https://doi.org/10.1038/hdy.1987.113

Nannini, M. A., Wahl, D. H., Philipp, D. P., & Cooke, S. J. (2011). The influence of selection for vulnerability to angling on foraging ecology in largemouth bass *Micropterus salmoides*. *Journal of Fish Biology*, *79*(4), 1017–1028. https://doi.org/10.1111/j.1095-8649.2011.03079.x

Philipp, D. P., Cooke, S. J., Claussen, J. E., Koppelman, J. B., Suski, C. D., & Burkett, D. P. (2009). Selection for vulnerability to angling in largemouth bass. *Transactions of the American Fisheries Society*, *138*(1), 189–199. https://doi.org/10.1577/T06-243.1

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P. O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *365*(1560), 4051–4063. https://doi.org/10.1098/rstb.2010.0208

Satterthwaite, W. H., Beakes, M. P., Collins, E. M., Swank, D. R., Merz, J. E., Titus, R. G., Sogard, S. M., ... Mangel, M. (2009). Steelhead life history on California's central coast: insights from a state-dependent model. *Transactions of the American Fisheries Society*, *138*(3), 532–548. https://doi.org/10.1073/pnas.1212536109

Sharp, D. M., & Hendry, A. P. (2009). SYNTHESIS: 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

Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral syndromes: An integrative overview. *The Quarterly Review of Biology*, *79*(3), 241–277. https://doi.org/10.1086/422893

Stoner, A. W. (2003). Hunger and light level alter response to bait by Pacific halibut: Laboratory analysis of detection, location and attack. *Journal of Fish Biology*, *62*(5), 1176–1193. https://doi.org/10.1046/j.1095-8649.2003.00117.x

Suski, C. D., & Philipp, D. P. (2004). Factors affecting the vulnerability to angling of nesting male largemouth and smallmouth bass. *Transactions of the American Fisheries Society*, *133*(5), 1100–1106. https://doi.org/10.1577/T03-079.1

Sutter, D. A., Suski, C. D., Philipp, D. P., Klefoth, T., Wahl, D. H., Kersten, P., ... Arlinghaus, R. (2012). Recreational fishing selectively captures individuals with the highest fitness potential. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(51), 20960–20965. https://doi.org/10.1073/pnas.1212536109

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

Swain, D. P., & Benoit, H. P. (2015). Extreme increases in natural mortality prevent recovery of collapsed fish populations in a Northwest Atlantic ecosystem. *Marine Ecology Progress Series*, *519*, 165–182. https://doi.org/10.3354/meps11012

Swain, D. P., Jonsen, I. D., Simon, J. E., & Davies, T. D. (2013). Contrasting decadal trends in mortality between large and small individuals in skate populations in Atlantic Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, *70*(1), 74–89. https://doi.org/10.1139/cjfas-2012-0179

Thorley, J. L., & Andrusak, G. F. (2017). The fishing and natural mortality of large, piscivorous Bull Trout and Rainbow Trout in Kootenay Lake, British Columbia (2008–2013). *PeerJ*, *5*, e2874. https://doi.org/10.7717/peerj.2874

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

Werner, E. E., & Anholt, B. R. (1993). Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *The American Naturalist*, *142*(2), 242–272. https://doi.org/10.1086/285537

Wilson, D. S. (1998). Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *353*(1366), 199–205. https://doi.org/10.1098/rstb.1998.0202

Wilson, D. S., Clark, A. B., Coleman, K., & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends in Ecology & Evolution*, *9*(11), 442–446. https://doi.org/10.1016/0169-5347(94)90134-1

Zimmermann, F., & Jørgensen, C. (2017). Taking animal breeding into the wild: Regulation of fishing gear can make fish stocks evolve higher productivity. *Marine Ecology Progress Series*, *563*, 185–195. https://doi.org/10.3354/meps11996

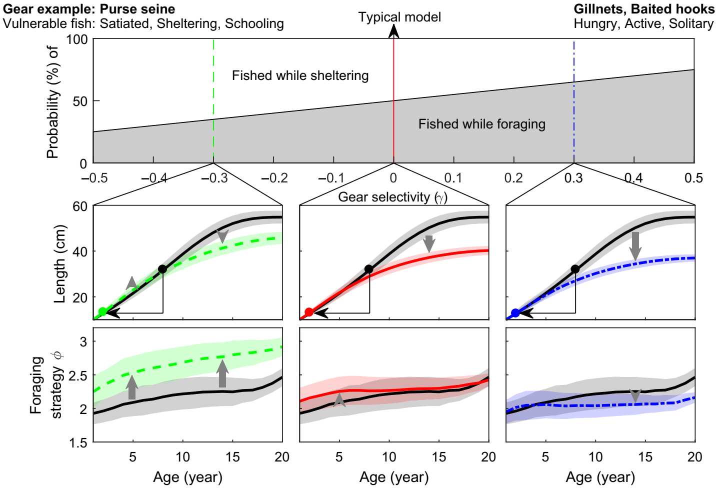
SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Claireaux M, Jørgensen C, Enberg K. Evolutionary effects of fishing gear on foraging behavior and life-history traits. *Ecol Evol*. 2018;00:1–11. https://doi.org/10.1002/ece3.4482

Graphical Abstract

The contents of this page will be used as part of the graphical abstract of html only.
It will not be published as part of main article.



Using a state-dependent dynamic programming model, we aimed at clarifying theoretical expectations about how behavior-selective fishing can shape the evolution of risk-taking behavior, life-history traits, and emergent natural mortality. First, our results are in line with earlier findings that an increased fishing mortality leads to increased natural mortality, earlier maturation, reduced size at age, and increased reproductive investment. Second, we found that the intensity of changes in natural mortality, length, and risk-taking behavior depends on whether fishing is targeting active, foraging ("bold") fish, or passive, sheltering ("timid") fish.

Paper II

Paper III

Paper IV

Graphic design: Communication Division, UiB / Print: Skipnes Kommunikasjon AS

uib.no

ISBN: 978-82-308-3573-9