Evolutionary responses of Atlantic cod (*Gadus morhua*) to concurrent fisheries and climate stressors

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Thesis for the degree of Philosophiae Doctor (PhD)
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Scientific environment

The work was carried out primarely at the Department of Biological Sciences, Faculty of Mathematics and Natural Sciences, at the University of Bergen, within the Theoretical Ecology Group. It began in May 2019 and ended in December 2023. While no official stays with other institutions were conducted, a large part of this work was done remotely, not in the least due to the COVID-19 pandemic spanning the majority of the project timeline.

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To say that the last $4\frac{1}{2}$ years have been life-altering, massively eventful and overall tumultuous feels like an understatement, owing in no small part to experiencing everything from a global pandemic and a cancer diagnosis all in such a short time. Life never quite works out the way you intented, and I suppose the same is true for science - but at least I have had good company for the ride.

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Tak for alt!
Tønsberg, 2023

Henrik H. Jessen

Summary

Evolutionary changes in fish have by now become a generally accepted truth, in large part due to research into fisheries-induced evolution since the 1970's. We especially see these changes as adaptive alterations to individual life-histories, such as shorter lives with higher growth rates, faster maturation and smaller asymptotic body sizes. In addition to fisheries, adaptive responses to climate warming has also been studied both theoretically and empirically, with results depending on current temperature regime of the population in question. Given the prevalence of smaller individuals with faster paces of life at warmer regions, the Temperature Size Rule would predict uni-directional changes to both increased fishing pressure and warming oceans. However, recent studies on Northeast Arctic Cod have demonstrated that individuals inhabiting the colder ranges of their thermal tolerance may actually see increased sizes in a warming climate. Additionally, research into fisheries selectivity seem to indicate that different gear types may also have different consequences for life-history evolution.

This thesis explores life-history evolution, as well as emergent population level responses, using Individual-Based Modelling of the Northeast Arctic Cod stock. Throughout the three chapters contained within, I aim to mechanistically examine the interacting effects of warming and fishing on evolutionary adaptation.

In **Paper 1** the groundwork is laid for the newly introduced 'Appetite' parameter, which places our research into the context of behavioural evolution and personality. We find that a key point of optimisation for life-history evolution, is the desire to reach larger sizes, counterbalanced by the risk of dying before reproducing. Larger fish are safer from predation, and have significantly increased relative fecundity, both of which are desirable. As mortality increases, the probability of reaching these sizes decrease, making earlier maturation at smaller sizes more optimal.

The following chapters, **Papers 2&3**, then gets to the matter at hand, and introduces

warming and temperature as external stressors on the population. Fisheries typically select for faster life-histories with earlier maturation, but opting for gillnets rather than trawling nets is shown to potentially select for later maturation at larger sizes, depending on intensity and targeted sizes. Notably, fisheries consistently result in increased foraging effort and faster growth. For the Northeast Arctic Cod, temperature is found to increase aerobic scope, reducing mortality. This resulted in increased growth, later maturation at larger sizes as well as larger populations overall.

Similarly to **Paper 1**, the balancing of expected benefits at larger sizes measured against probability of reaching the sizes appear to be the central tradeoff. Warming motivates foraging, which increases growth in order to reach these sizes faster; fisheries can lessen the benefit of reaching larger sizes by selectively targeting large fish, while simultaneously reducing probability of surviving to reach these sizes as well. Gillnets appear to be an exception, by providing a size-refugium, provided it is feasible to grow through the targeted size range.

In conclusion, it was found that increasing temperatures had the potential to (at least partially) compensate for fisheries-induced evolution, though this greatly depend on intensity and method of fishing as well as the level of warming expected. Evolutionary studies would benefit from considering both stressors in unison, as to not overlook potential interactions.

Sammendrag

Evolutionære ændringer i fisk er efterhånden en anderkendt sandhed, især på grund af forskning i fiskeri-induceret evolution siden 1970'erne. Vi ser især disse ændringer påvirke individuelle livshistorier, resulterende i kortere liv med hurtigere vækst, tidligere modning og mindre asymptotiske størrelser. I tillæg til fiskeri er adaptive ændringer i respons til klimaopvarmning også studeret både teoretisk og empirisk, og responsen hertil afhænger af hvilke temperatur-regimer og populationer der undersøges. Eftersom vi ser en tendens til at arter i varme områder er mindre, og har hurtigere livshistorier, ville vi typisk forvente at øget intensitet af fiskerier samt varmende have ville føre til ensrettede ændringer. Mere nylige studier på den Nordøstartiske Torsk har dog demonstreret at arter som befinder sig i den kolde ende af deres temperatur-niche faktisk bliver større som temperaturen stiger. Hertil kommer at effekten af forskellige typer fiskegrej også kan have vidt forskellige konsekvenser for evolution af livshistorie.

Denne tese udforsker evolution af livshistorier, samt de deraf fremkommende konsekvenser på populationsniveau, ved at bruge Individ-Baseret Modellering af Nordøstarktisk Torsk. Gennem de 3 kapitler heri undersøger jeg mekanistisk de interagerende effekter af varmning samt fiskeri på evolutionær tilpasning.

I **Artikel 1** lægger vi en grundlinje for vores nyligt introducerede 'Appetit' parameter, som skal placere denne forskning i kontekst med henhold til evolution af adfærd og personlighed. Vi finder frem til at omdrejningspunktet for evolution af livshistorie i denne model er at fisk søger at nå til store størrelser, modbalanceret af risikoen for at dø inden de gør det. Større fisk er både mere sikre fra predation, og har langt højere relativ fekunditet, og begge disse er eftertragtelige. Som dødelighed stiger, falder sandsynligheden for at vokse sig stor, hvilket gør det mere optimalt at modnes tidligere.

I de efterfølgende kapitler, **Artikel 2&3**, kommer vi så til sagen, og introducerer varmn-

ing og fiskeri som eksterne stressorer. Fiskeri selekterer typisk for hurtigere livshistorier med tidligere modning, men at vælge garnfiskeri (også kendt som gællenet) kan dog selektere for senere modning ved større længde, afhængig af intensitet samt maskestørrelse. Fiskeri resulterer konsistent i en øgning i fodersøgende adfærd og hurtigere vækst. For Nordøstarktisk Torsk øger temperatur også fiskens aerobe kapacitet, hvilket reducerer dødelighed. Dette resulterer i øget vækst, senere modning, større fisk og en generelt større bestand.

Ligesom i **Artikel 1** er omdrejningspunktet balancen mellem fordelene ved at være stor, vejet mod chancen for at kunne blive stor. Varmning motiverer fodersøgning, hvilket øger vækst så fiskene kan blive store hurtigere; fiskeri derimod reducerer fordelen ved at være stor, da vi typisk fanger store fisk, og reducerer samtidig også chancen for at fiskene kan nå at blive store. Garnfiskeri lader til at være en mulig undtagelse, da de ikke fanger de helt store fisk, og dermed bibeholder fordelen ved at være stor, såfremt det er muligt at vokse sig op til en sikker størrelse.

Samlet fandt vi at øgende temperaturer har potentiale til at modvirke de evolutionære konsekvenser af fiskeri, men at dette kommer strengt an på hvor intenst der fiskes, hvilket grej der benyttet samt hvor meget varmning der forventes. Evolutionære studier bør betragte begge disse stressorer samlet, da de ellers risikerer at overse interaktioner mellem dem.

Publications

Publications included in the thesis

PAPER 1

Jessen, H. H., Opdal, A. F., Enberg, K. (2023). Life-history evolution in response to foraging risk, modelled for Northeast Arctic Cod (*Gadus morhua*). Ecological Modelling, **482**, 110378. https://doi.org/10.1016/j.ecolmodel.2023.110378

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PAPER 2

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PAPER 3

Jessen, H. H., Opdal, A. F., Enberg, K. Warming climate impacts optimal fisheries strategy in model for Northeast Arctic Cod (*Gadus morhua*).

(*manuscript*)

Contents

Synthesis

1.1 Introduction

1.1.1 Variation and evolution

General evolutionary theory

Evolutionary theory as we know it today was most notably defined when Charles Darwin published his "On the Origin of Species" in 1859, positing a natural mechanism capable of explaining the vast variety we see various related taxa of organisms. The essence of the theory is that variation exist among individuals, and provided that this variation is heritable, we would expect the trait combinations that best allow for survival and reproduction to increase in prominence over time - or as it has famously been put since, "survival of the fittest".

Since this conceptualisation, the theory has been refined. We now understand that observable differences between individuals stem from a combination of individual genotype and expressed phenotype (Johannsen, 1911; Wojczynski & Tiwari, 2008). Genotype refers to the heritable genetic information encoded by DNA, while phenotype is the measurable and realised expression of this. An intuitive example of this would be height in humans: while there is definitely a genetic component to height, even genetically similar individuals may exhibit differences in height (McEvoy & Visscher, 2009). This observable variation is referred to as phenotypic variation, and may or may not imply genetic variation. Natural selection, the proposed driver of evolution, acts on phenotypes, as any gene must be expressed in order to affect reproductive success.

This non-linear coupling between genotype and phenotype presents a challenge to the study of evolution, as it becomes uncertain whether changes in phenotype really do imply changes in genotype. Several charasteristics have been found to exhibit what's called 'phenotypic plasticity', where some organisms have demonstrated the ability to alter their phenotype slightly without changes in genotype (DeWitt et al., 1998; West-Eberhard, 1989), though the extent of this is not universal, and capacity for plasticity is likely also subject to evolutionary selection (Pigliucci, 2005). An example of plasticity is acclimatization to warm temperatures, where phenotype is altered by exposure to increased temperatures within the lifespan of an individual organism (Beitinger & Bennett, 2000; Johnston & Dunn, 1987; Roots & Prosser, 1962).

Given the relatively high cost and labor intensivity of mapping genetic changes compared to e.g. morphometric measurements, most studies of evolution focus on changes in average phenotypes over time. Typically these phenotypic responses are also the point of interest: for instance we may wish to know if a fish species is evolving to have higher growth rates - a change in phenotype. This focus is particularly prominent within conservation and management, while a focus on changes in genome is of more interest to those who study speciation and genetic diversity.

Life history & behavioral evolution

Within fisheries science, life histories refer to how fish forage, age, grow and reproduce over the course of their lives, and often studied parameters include metrics such as maturation age, asymptotic size, natural mortality and individual growth rates (Thorson et al., 2017). All of these metrics are of direct interest to both managers and conservationists, as individual life histories come together to form population averages of productivity, recruitment, growth and death.

Life histories are frequently organised into different 'strategies'. Terrestrial ecologists developed a classification of animals as either r-strategists or K-strategists (MacArthur & Wilson, 1967; Pianka, 1970): r-strategists are those with typically shorter life-cycles, smaller sizes and earlier maturation; K-strategists are those with longer lives, larger sizes, slower growth and later maturation.

These strategies are more commonly, at least for fish, summarised by the Pace of Life Syndrome (POLS) hypothesis (King & McFarlane, 2003; Stearns, 1983), stating common strategies around the tradeoff between current and future reproduction tend to lead to covariance of life-history, behavioral traits and physiological traits (Montiglio et al., 2018). 'Fast' pace of life indicates that organisms prioritize reproduction and growth over current survival, resulting in shorter lives with higher rates of turnover. Contrarily, 'slow' pace of life involves slower life-histories, longer life spans and larger asymptotic sizes.

Relatedly, individuals not only differ in life-histories, but also exhibit differences in behaviour. The term personality might to some seem anthropomorphising, but individual differences in e.g. willingness to undertake risk has been demonstrated in a wide range of species (Harcourt et al., 2009; Polverino, 2017; Ward et al., 2004; Wilson et al., 1994), particularly in regards to foraging behaviour (Dammhahn & Almeling, 2012). These differences remain consistent within individuals, and have been found to correlate well with genetic differences, indicating heritability (Dochtermann et al., 2015; Wilson et al., 1994). Given that these personalities are intrinsic, affect behaviour such as foraging, and have a degree of heritability, they should be included in evolutionary considerations.

For fish, most studies on personality categorise individuals on a spectrum ranging from 'bold' to 'shy' (Harcourt et al., 2009; Toms et al., 2010). Bold individuals are typically defined by willingness for risk-taking behaviour, with shy individuals being more averse. Alternate frameworks describe motivation by fear or hunger (Budaev et al., 2018), but irrespective of terminology, individual differences in personality are well documented in fish.

Relating personality back to the POLS hypothesis, bolder behaviour is more commonly seen alongside faster paces of life, and bold/aggresive individuals are expected to have higher rates of mortality (Damsgård et al., 2019; Montiglio et al., 2018; Réale et al., 2010), leading to shorter life spans. Behaviour is similarly found to covary with physiological traits (Wikelski & Ricklefs, 2001), with bolder individuals having higher maximum metabolic rates in bluegill sunfish (Binder et al., 2016).

1.1.2 Climate warming and ocean ecology

Warming oceans

The term "climate change" has been receiving increased attention for the past decades, and covers a host of consequences of human expansion and industrialization. For ocean scientists, the increase of CO_2 in the atmosphere due to fossil fuel consumption and land degration has been a point of focus, due to the causal relationship between atmospheric CO_2, climate warming (Anderson et al., 2016; Arrhenius, 1896; Joos et al., 1999) and ocean acidification (Cao & Caldeira, 2008; Doney et al., 2009; Zeebe, 2012).

The Intergovernmental Panel on Climate Change (IPCC) was established in 1988, with the aim of summarising and communicating scientific information to governmental institutions. The role of the IPCC is to compile and review key findings, which they publish as assessment reports available to both policymakers, scientists and the general public. It is in these reports that we find the most commonly accepted projections of future climate warming (Anderson et al., 2016), pending various emission scenarios (IPCC, 2021, 2022a, 2022b). The scenarios are included in the Shared Socioeconomic Pathways (SSPs). They range from anticipating global shifts towards reducing emissions (SSP1) to anticipating global acceleration in emissions (SSP5). It should be noted that the SSPs embed a lot more information than only emission scenarios, but for the purpose of this thesis, those will be the focus. When applying the SSP emission scenarios, it's difficult to determine the realism of these, but present policy likely has us headed towards the intermediate scenarios (SSP2-SSP3) (Ho et al., 2019; Rogelj et al., 2016), with SSP5 in particular becoming "increasingly implausible with every passing year" (Hausfather & Peters, 2020).

Most discussion regarding climate warming has focused on atmospheric warming, but the IPCC also publishes expected increases in Sea Surface Temperature (SST) in their 6th assessment report (IPCC, 2021), noting that it is "virtually certain" that SST will continue increasing. The report does include regional differences in SST warming, but omits the Arctic Ocean from this comparison, though recent research by Chen et al. (2019) found that oceanic temperature anomalies in the arctic resemble global averages.

Increasing ocean temperature is of great importance to ocean scientists due to its strong influence on both biotic (Brown & Sibly, 2012; Brown et al., 2004; Gillooly et al., 2001; Peters, 1986) and abiotic factors (Goschen & Schumann, 1988; Killen et al., 2013; McPhaden & Zhang, 2002; Polyakov et al., 2010; Zacher et al., 2009). According to NOAA data from 2022, the oceans have so far absorbed 90% of the increased warming (NASA Global Climate Change, 2022). The vast majority of oceanic animal life is ectothermic, meaning that unlike endotherms such as humans, they typically lack internal temperature regulation. Because of this, they are more directly affected by changes in their ambient temperature.

Responses to warming

Given the impact of temperature, organisms already inhabiting areas with temperatures optimal for them will have to adapt as temperature changes. Commonly these adaptations might be one of three common universal ecological responses: **1)** Shifting species range (Burrows et al., 2019; Pinsky et al., 2013). **2)** Seasonal shift of life-cycle events (Petitgas et al., 2013; Wedekind & Küng, 2010). **3)** reducing body size (Atkinson, 1994; Daufresne et al., 2009). The motivation behind adaptations **1** and **2** is simple - follow your temperature preference. This is possible by shifting distribution, such as by moving poleward (Kortsch et al., 2015; Langbehn et al., 2022; Pinsky et al., 2013; Roessig et al., 2004) or into deeper waters (Burrows et al., 2019; Freitas et al., 2015; Pinsky et al., 2013; Tirsgaard et al., 2014). In seasonal regions, it may also be done by changing the timing of life-cycles, for instance by spawning later in warmer waters (Petitgas et al., 2013), though timing changes are also tied to food availability (Drinkwater, 2005; Ferreira et al., 2020; Petitgas et al., 2013).

The last adaptation, adaptive reduction in body size, is less intuitive. Nonetheless, the trend has been noticed and defined as a rule in several iterations. Bergmann's rule (Bergmann, 1847) states that within taxonomic clades, larger sizes are found in colder environments, assuming that the relatively lower surface-to-volume ratio of larger animals better preserves heat, while the inverse is true for smaller organisms. James' rule (James, 1970) expands, stating that within a given species, the populations in warmer environments tend to have smaller body sizes. For ectotherms, the Temperature Size Rule (TSR) was proposed (Atkinson, 1994, 1996), positing slower growth and larger asymptotic sizes in colder environments.

Given the definition of ectotherms, the mechanism posited by Bergmann (1847), namely heat dissipation, cannot explain this rule. Early attempts tried to reason a tradeoff using the Von Bertalanffy growth model (von Bertalanffy, 1957), reasoning a tradeoff between the growth parameter and the asymptotic size (Berrigan & Charnov, 1994; Perrin, 1995), but this was ultimately found to have little explanatory power (Angilletta & Dunham, 2003).

It is still uncertain what mechanism is responsible for the trend, or indeed if there are several possible mechanisms, which may explain apparent exceptions to the rule (Angilletta & Dunham, 2003; Walters & Hassall, 2006). It has been suggested by Kozłowski et al. (2004) that optimal resource allocation favors TSR growth patterns if increasing temperature results in increased mortality (elevated mortality resulting in smaller individuals is also discussed in **Paper 1**) or if the size-dependant trade off between resource acquisition and metabolism change with temperature.

Another suggestion has been that a reduction in aerobic scope or oxygen limitation with increasing temperatures favors smaller body sizes (Baudron et al., 2014; Pörtner, 2001), which is another mechanism that cannot be universally assumed (Audzijonyte et al., 2016, 2019). Populations in cold climates may even see an increase in aerobic scope with warming temperatures (Holt & Jørgensen, 2015), and increased baseline metabolism cannot be assumed as a general response (Wootton et al., 2022).

1.1.3 Fisheries and their management

Capture fisheries

Fisheries, or more specifically capture fisheries, is the activity of removing wild animals, usually fish, from aquatic environments. This includes a large swathe of different means of doing so, ranging from angling and spearfishing all the way to industrial fleets of trawlers or purse-seiners. Naturally, these activities have very different levels of impact and efficiency, leading to different classifications, from recreational to industrial fishing. In developed, western nations such as Norway, industrial-scale fishing undoubtedly has the greatest impact.

Typical industrial catch methods include trawling nets, gillnets, purse seines and longlines, the relative importance of which depend on the targeted stock and management goals. For the Northeast Arctic Cod, a stock of Atlantic cod (*Gadus morhua*), which is the focus of this dissertation, approximately 70% of landings come from trawling, and the majority of the remaining 30% come from gillnets (ICES, 2021). As such, these gears will be the focus of this section.

Trawling nets are large cone-shaped nets that are dragged behind fishing vessels. They may be suited for either dragging along the seafloor (bottom trawling) or through the open water masses (pelagic trawling). In either case, the intention is for fish to enter the wide opening, and subsequently be funneled into the 'cod-end'. The mesh size of the net and cod-end determine what is retained after entering the net - small fish may pass through, while in theory everything that is too big to slip through is retained.

Gillnets are nettings that are left suspended in the water column. The mesh sizes are intended to allow fish to get their head through, while the body cannot pass. As the fish attempt to back out, their gills get caught in the net, and they are retained. As such, the nets target certain size ranges - small fish pass through, and larger fish cannot get their head through enough to get entangled.

It is hard to accurately assess the cumulative ecosystem impacts of fisheries. Even a conceptually perfect fishery, catching only intended individuals of a target species, would be a major source of mortality - fisheries are likely the primary source of mortality for adult fish in industrially exploited populations (ICES, 2021). Such large-scale mortality will inevitably impact population size and demography (Hamilton & Otterstad, 1998), with potential impacts reaching throughout the food web (Eliasen et al., 2011; Hjermann et al., 2007). Coupled with concerns over bycatch, the capture of unintended animals (Davies et al., 2009; Glass, 2000); and ghost gear, lost gears that continue to impact marine life (FAO, 2016; Richardson et al., 2019), the sustainability of fisheries have come into focus as part of the sustainable development agenda (United Nations, 2016). In this thesis, I will focus on the effects of fisheries on their targeted stocks.

Evolutionary consequences of fisheries

Given that fisheries are a source of mortality, they have the capacity to induce evolutionary changes. This idea goes back to the late 1970's (Handford et al., 1977; Ricker, 1981), and constitutes a form of artificial selection. As has since been documented, heavily exploited populations tend to decrease age- and length at maturity as well as asymptotic sizes (Law, 2007), which is now considered indicative of fisheries-induced evolution.

The theoretical foundation for fisheries-induced evolution is strong, and indeed we see phenotypic changes in fish stocks across the world (Andersen et al., 2007; Arlinghaus et al., 2017; Claireaux et al., 2018; Diaz Pauli & Sih, 2017; Heino et al., 2015; Law, 2007; Reznick & Ghalambor, 2005), consistent with expected responses to fisheries. However, the relative importance of genetic changes is hard to disentangle from phenotypic plasticity and mere demographic responses. More recently it has been suggested by Eikeset et al. (2016) that accounting for density-dependent processes, at least for Northeast Arctic Cod, explains maturation trends well enough as to require very little evolution. While their model has since been criticised for inadequate parametrization (Enberg & Jørgensen, 2017), it does still indicate that evolutionary and ecological processes should be considered jointly, as we might otherwise overestimate relative contributions of both ecology and evolution, and neglect potential interactions (Kuparinen et al., 2014).

To say with any certainty that fisheries-induced evolution is driving observed changes, genomic data is needed both before and after periods of intensive fishing. For cod, such data was analysed by Pinsky et al. (2021), focusing on 2 stocks: the Newfoundland stock, and the Northeast Arctic stock. They did not discover significant loss of genetic diversity, or signals of selective sweeps; though their methodology cannot capture polygenic evolution and also suffers from a small sample size (Hutchings & Kuparinen, 2021), despite life-history traits often being polygenic in nature (Conner & Hartl, 2004; Roff, 1993). Indeed, upon revisiting the data, evidence of polygenic evolution was found (Reid et al., 2023), further supporting the importance of considering evolution and ecology jointly, and being cautious when making sweeping statements about exploited populations.

While the genetic basis for phenotypic changes might not yet be resolved, it is at this point readily apparent that fisheries do indeed cause changes in fished population. Since evolution operates through favouring specific phenotypes, a logical next step is to look at the selectivity of various fishing gears. While it has been shown that even unselective fishing can lead to adaptive changes (Claireaux et al., 2018), as it is still a source of mortality, most fisheries are highly selective (Hamley, 1975; Handford et al., 1977; Huse & Soldal, 2000). Fisheries are economically incentivized, and size/type of fish greatly influence earnings (Asche et al., 2015; Lee, 2014; Sjöberg, 2015; Sogn-Grundvåg et al., 2021). This motivates fisheries to target larger individuals when fishing for species such as cod, that are typically eaten as fillets.

As described above, trawling nets and gillnets target different size ranges, and are typically simplified thus: trawling catches all fish above a certain size, and catch probability goes down as fish get smaller than this target. Gillnets target a specific size, and catch probability decreases as fish get either smaller or larger than this targeted size. This is typically described as sigmoidal selectivity and bell-shaped selectivity, and while conceptualizations that might alter selectivity exist (e.g. Stepputtis et al. (2016)), we will assume these simplified curves in this thesis.

Given this difference in selectivity curves, the evolutionary adaptations to fishing depends on gear type (Jørgensen et al., 2009). A typical trend seen for fish is the disproportionately larger fecundity of large individuals (Hixon et al., 2014; Morita et al., 1999), meaning that if individuals can survive to reach large sizes, they are rewarded by notably larger reproductive output. However, as fisheries are introduced and mortality is increased, the probablity of reaching these sizes is decreased, even in the abscence of selective harvest (Claireaux et al., 2018).

When fishing with trawling nets, this increase in mortality remains constant for larger individuals - this universally lessens the benefit of delayed maturation and faster growth (Huse & Soldal, 2000; Jørgensen et al., 2009). However, when fishing with gillnets, a 'size refugium' is introduced - provided the individuals can survive long enough to grow through the size range targeted by the fisheries, they can make use of the higher relative fecundity at these larger sizes. As such, while trawling should always select for faster pace of life, gillnets can theoretically select for later maturation, and an emphasis on somatic growth (Fig. 1.1).

1.1.4 Atlantic cod

General eco-physiology and temperature range

Atlantic cod (*Gadus morhua*) is a species of demersal teleost fish with a long history of exploitation and historical importance to humans (Rose, 2019), going all the way back to the Mesolithic Stone Age (7000-3900 BC)(Enghoff et al., 2007). It is a relatively large and long-lived species of fish, growing up to 2 metres in length over their 25-year lifespan, though typically they are found around 1 metre of length (Cohen et al., 1990; Muus, 1974). Cod has a wide geographic range throughout the Northern Atlantic Ocean, in areas with average bottom temperatures ranging from 0 °C at Labrador and Newfoundland (Myers et al., 2001) to 11 °C in the English channel, Celtic Sea and central Baltic (Brander, 1994; Myers et al.,

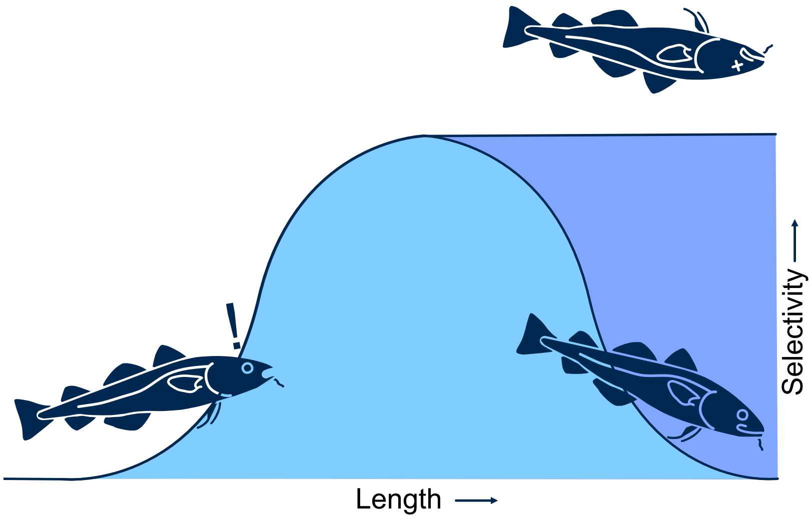

Figure 1.1: Conceptualisation of the effect gear type has on selectivity. As fish grow in length, they reach a size where both gillnets and trawl can catch them, with probability increasing until they reach the size of maximum selectivity. For trawls the selectivity remains high for all larger sizes, while for gillnets it decreases with further growth.

2001). Experienced daily temperature ranges may be as much as 10 °C (Le Bris et al., 2013).

Spawning is typically timed as multiple batches of broadcast spawning in late winter or early spring, aiming to time hatching 10-12 days later with the phytoplankton bloom (Drinkwater, 2005; Petitgas et al., 2013). As a cold-water species, cod typically spawn in waters between 2-7 °C, but show a preference for 5-7 °C (González-Irusta & Wright, 2016). Temperatures above 9.6 °C appear to reduce fertilization success, even when populations are acclimated to up to 13 °C (van der Meeren & Ivannikov, 2006).

Important fisheries have been centered around cod on both the Western- (Brander, 2007; Brander, 2018) and Eastern Atlantic (Beaugrand et al., 2003; Rijnsdorp et al., 2009). While the cod fisheries in the Eastern Atlantic are still yielding good catches (FAO, 2022; ICES, 2021), the Western Atlantic fisheries suffered large-scale collapse between the years 1990-1995, both in the Gulf of Maine (Brander, 2018; Pershing et al., 2015) and the Newfoundland/Labrador region (Bavington, 2011; Mason, 2002; Schijns et al., 2021), which has largely been credited to overfishing (e.g. Pershing et al. (2015)).

The Northeast Arctic Cod

The largest present-day stock of Atlantic cod, and the focus of this thesis, is the Northeast Arctic Cod (NEAC) stock (Øiestad, 1994). Of the annual cod catches between 1.0 and 1.3 million tonnes between 2017-2020 (FAO, 2022), the NEAC stock alone has provided annual catches of approximately 800,000 tonnes in the decade 2010-2020 (ICES, 2021). Primarily residing in the Barents Sea, NEAC feed mostly on macrozooplankton (Orlova et al., 2005) and capelin (Denechaud et al., 2020; Dolgov, 2002; Hjermann et al., 2007). In early spring (February-April) mature individuals undertake spawning migrations to the main spawning areas around Lofoten and Vesterålen in Northern Norway (Opdal & Jørgensen, 2015, 2016; Opdal et al., 2011).

The NEAC stock, known to the Norwegians as 'Skrei', has been caught by fishers in Northern Norway since the 1100's (Nielssen, 2009), where they were airdried for preservation, becoming what is known as 'stockfish'. It was also around this time that cod became an important trade good (Barrett et al., 2008; Christensen & Nielssen, 1996). Catches of NEAC have, like most other stocks, varied greatly throughout the years (Godø, 2003; Øiestad, 1994), but peaked around the same time as the Labrador/Newfoundland fisheries in the middle of the 20th century. Trawlers were introduced as the primary gear type around the 1930's, followed by what we now consider to be unsustainable levels of fishing (Hylen et al., 2008), culminating in major catch declines up to the early 1990's (around the same time as the cod fishery collapsed in the Western Atlantic). Since then, the NEAC stock has recovered well, and catches now again are near their previous record levels (ICES, 2021).

Atlantic cod, specifically NEAC, was chosen as the model organism for this thesis for two reasons: firstly, the rich historical, cultural and economic importance described above. Secondly, Atlantic cod (likely because of this history) is one of the most well researched species of fish, leading to extensive knowledge on responses to both warming (Björnsson et al., 2007; Brander, 2018; Neuheimer & Grønkjær, 2012; Opdal & Jørgensen, 2015, 2016) and fisheries (Huse & Soldal, 2000; Hutchings, 1996; Hutchings, 2022; Jørgensen et al., 2009; Rose & Rowe, 2015).

Additionally, the NEAC stock specifically has been a common model organism for evolutionary responses to both warming (Holt & Jørgensen, 2014, 2015) and fisheries (Enberg et al., 2009, 2010), making it an ideal candidate for exploring the as of yet unknown interactions of these stressors might have on evolutionary change (Calosi et al., 2016).

1.2 Thesis aim and research questions

The previous sections are intended to present relevant concepts for the thesis - both climate warming and fisheries are stressors that are expected to cause adaptive evolution in exploited fish populations. Evolutionary responses to both stressors are discussed, and we find both have a solid theoretical foundation as well as empirical examples supporting these. What is still missing in extension of this, is a mechanistic understanding of how fisheries and climate might interact to change populations, particularly on evolutionary timescales.

Typical studies on interactions between climate and fisheries take one of several forms: those focused on changing catch potential (Cheung et al., 2013; Cheung et al., 2008) or potential yield (Brander, 2015); and those focused on how these stressors might amplify each other (Gaines et al., 2018; Griffith et al., 2012; Morrongiello et al., 2019; Schindler et al., 1996). Evolution is understudied in relation to climate/fisheries interactions, and that is the gap that this thesis aims to help fill.

To synthesise this kind of knowledge, I have throughout the thesis employed mechanistic, individual-based modelling methods which is described in detail, along with the rationale for various components, in section 1.3. The overarching goal has been to study **how the interacting effects of climate warming and fisheries cause evolution in a cold-water fish, and what the population-level consequences of this are**. The chosen model organism, Northeast Arctic Cod (NEAC), a stock of Atlantic cod (*Gadus morhua*), was chosen because its rich history of both cultural and economical importance has led to it being one of the most well-studied fish species available. Included in these studies, are previous modelling efforts (e.g. Enberg et al. (2009), Holt and Jørgensen (2014), and Jørgensen and Fiksen (2006)), providing my thesis model with a starting framework as well as parameterization of many key variables. At the same time, the NEAC stock resides primarily North of the Arctic Circle, an area commonly hypothesized to be particularly vulnerable to climate warming.

During the construction of the model, parameterization was lacking for foraging risk, relating to mortality resulting from energy acquisition. This led to what might be considered a 'detour' in relation to the main goal of the thesis, which is the warming/fisheries interaction, where the effect of foraging risk on life-history evolution and population size was studied (**Paper 1**). This study sought to increase understanding of life-history might change as a result of behavioural evolution, while at the same time providing an estimate of risk parameterization by comparing results to catch data (ICES, 2021).

Throughout the three papers, I will attempt to answer the following questions:

1. How does life-history evolve in response to variable risk associated with energy acquisition? What are the mechanisms driving these changes? (**Paper 1**)
2. What are the effects of different levels of fishing under select warming scenarios? Will the stressors act antagonistically or synergistically, and why? (**Paper 2**)
3. Do different fisheries strategies interact differently with climate warming, and could appropriate management help mitigate potential effects of warming? (**Paper 3**)
4. What are the consequences of warming/fisheries on yield? Is there a tradeoff between managing for yield, and managing to mitigate evolutionary change? (**Paper 3**)

Section 1.3 will describe the model in detail, including rationale behind decisions, while section 1.4 will present short summaries of all papers and their findings.

1.3 Methodology

The central methodology applied throughout all three papers is mechanistic modelling, which allows us to explore complex interactions that cannot be tested in conventional laboratory- or field studies. The model used is based on the framework published by Enberg et al. (2009), which was built to model evolutionary effects of fisheries, but add explicit modelling of energy and oxygen budgets, with parametrisation drawn from the optimisation model published by Holt and Jørgensen (2014) and from Claireaux et al. (2000), to simulate the effects of increasing temperatures.

The model is written in the FORTRAN programming language, which is a good language for computationally intensive operations due to its speed and efficiency. In the

spirit of transparency, the source code used in the model is hosted on my GitHub here: https://github.com/henrikhjessen/NEAC_ibm/tree/main
Here I will also host a .pdf of the complete thesis, which will contain high-resolution zoomable versions of figures for those who find the printed versions lacking.

1.3.1 Why use an IBM?

The method chosen for this project was to implement an Individual Based Model (IBM), sometimes also referred to as an Agent Based Model (ABM) (DeAngelis & Mooij, 2005). They are characterised by simulating a model organism on the individual level, and letting population-level patterns emerge from the responses of the individuals.

The reasoning behind using an IBM is that: **1)** It is mechanistically based, meaning that we don't restrain the direction of change, such as by assuming that warming leads to smaller sizes. **2)** Keeping individuals separate allows us to not only find the mechanisms directing responses, but to examine variation between various individuals, instead of solely determining optimum values. **3)** By having not only life-histories but also demography respond to external changes, we can also model the effects of density dependence, which is notably absent from optimization models. **4)** IBMs better approximate the mechanism behind evolution, compared to optimization models - heritable individual variation that impact lifetime reproductive output is passed on in incremental time steps. This allows IBMs to simulate not only the direction of evolution, but also the expected rate of change.

1.3.2 Model description

The model employed in this thesis is divided into modular compartments carried out in sequence, in annual time steps. Evolution is simulated by allowing individuals to pass on the two inherited traits - Appetite and PMRN Intercept, both of which are described below.

Every year, temperature and food environment is determined, and are used as universal parameters for all individuals in that year. Baseline temperature is normally distributed around 4 °C, which is the annual mean temperature in the Barents Sea, as measured along the Kola hydrographical transect (Boitsov et al., 2012). Warming scenarios maintains this distribution, but increases mean temperature as prescribed by the IPCC warming scenarios

SSP1, SSP2 and SSP3 (IPCC, 2021). These scenarios stabilise around mean sea surface temperatures of 4.8 °C, 7.0 °C and 12.4 °C respectively.

Food environment is simplified as a unitless number, normally distributed around 1, with higher values indicating years of abundant food and lower values indicating scarce food. The food environment is uncoupled from temperature, and is only affected by total population biomass, in order to mimic density dependence. Larger total biomasses reduce the food environment coefficient, simulating increased competition for food, and the subsequent increase in foraging effort required to forage a given amount of energy.

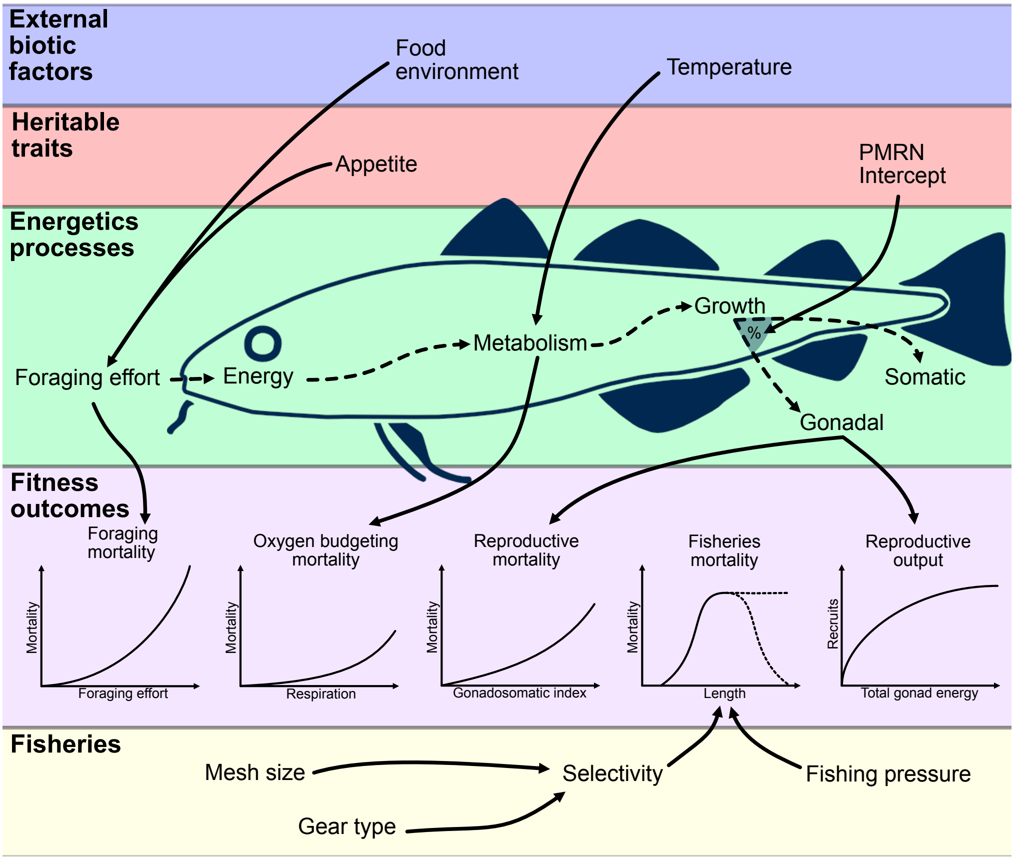

Figure 1.2: Conceptual overview of critical processes. Solid arrows indicate direct influence, and dashed arrows indicate the energy flow. The shaded "%" area represents the proportion of energy dedicated to somatic/gonadal growth. Figure is reproduced from **Paper 2**.

Maturation

Maturation is modelled using a Probabilistic Maturation Reaction Norm (PMRN) (Dieckmann & Heino, 2007). As individuals increase in length and/or age, so too does the likelihood of maturing. While there are several components to a PMRN, such as intercept, slope and width, our model focuses on the intercept. The width of the PMRN governs how 'sharply' maturation occurs, and was calibrated to match catch data from ICES (2021). Both intercept and slope affect maturation schedule, and both were previously allowed to evolve by Enberg et al. (2009), but this was found to add little explanatory power, and so our model focuses on PMRN intercept, which was judged to be a more intuitive variable, and is one of our two evolving traits. Higher intercept values correspond to later maturation at larger sizes, and vice versa.

Energetics

The energetics section could be considered the 'core' of the model, describing the acquisition of energy, and how that energy is used. It is a modified version of the Wisconsin Bioenergetics Framework (Hewett & Johnson, 1992), which was parameterised for NEAC by Holt and Jørgensen (2014). Individuals possess the inherited/evolving trait 'Appetite' (Jy^{-1}), which is a measure of desired energy intake. Individuals will match their foraging effort to reach this desired energy intake, provided it is possible, with required effort increasing as total population biomass increases, in order to simulate density dependence. To calculate energy available for growth, we subtract standard metabolic rate, foraging cost and specific dynamic action from ingested energy. This metabolic rate increases with temperature, and is the primary point of influence for warming (Brown et al., 2004; Gillooly et al., 2001). The second point is an oxygen budget adapted from Claireaux et al. (2000), which is included to account for respiratory capacity, corresponding to aerobic scope.

Remaining energy for growth can be invested into either somatic growth or gonad growth (reproductive investment). For immature individuals, all the energy is allocated to somatic growth. After individuals mature, they start dedicating an increasing proportion of their available energy to reproduction. This increasing reproductive investment follows the rate described in the Biphasic Growth Model by Quince et al. (2008), with values of initial investment and somatic investment decay calibrated to match NEAC catch data (ICES, 2021). For mature individuals, energy allocated to gonads will be used to calculate egg production (see section 1.3.2), but energy used for the NEAC spawning migration (Opdal et al., 2011) is calculated based on swimming speed (Ware, 1978). Individuals with insufficient energy for both migrating and spawning instead skip spawning, and re-allocate all energy to somatic growth.

Mortality

The model calculates mortality risk based on 6 sources of mortality: **1)** Fixed mortality, from size-independent sources such as illness and disease. **2)** Predation mortality, which is the likelihood of getting eaten, decreases with individual length (Sogard, 1997). Since this is assumed to be the primary cause of death, this is also used to scale the remaining sources of natural mortality. **3)** Foraging mortality, likelihood of dying increases with foraging effort as individuals are exposed when foraging, corresponding to a reduction in sheltering behaviour (Stephens, 2008; Townsend & Winfield, 1985). **4)** Reproductive mortality, increasing with gonadosomatic index, reflects morphological changes and courtship behaviour from increased gonadal investment. **5)** Respiration mortality, corresponding to exhaustion, scales inversely with aerobic scope. **6)** Fisheries mortality, death resulting from extraction by fishing vessels.

These sources of mortality are the primary drivers of evolution in the model, and the scaling of these drive evolutionary trade-offs. An example, and arguably the most important, is the tradeoff between growing fast and staying alive, which is discussed in all three papers included in this thesis.

Recruitment

The number of recruits to add to the population is calculated using a Beverton-Holt recruitment function (Beverton & Holt, 1993), based on total population gonadal investment as in Enberg et al. (2009). To simulate evolution, the model allows for inheritance of traits using a simplified framework, due to the typical polygenic nature of life-history traits (Conner & Hartl, 2004; Roff, 1993). Every recruit has two parents selected among mature individuals, chosen by random selection weighted by individual reproductive investment, so that individuals with a higher level of reproductive investment are more likely to be chosen as parents. For inherited traits, midparental values are used with a measure of stochasticity resulting in an emergent heritability of approximately 0.2, in line with typical heritability of life-history traits (Carlson & Seamons, 2008; Enberg & Jørgensen, 2017; Gjedrem, 1983; Law, 2000). Another simplification made, is that the model does not distinguish between male and female individuals. This is assumed to be a suitable simplification for populations with similar life-histories and demographies for males and females (Dunlop et al., 2009), as is believed to be the case for NEAC.

Phenotypic variation and stochasticity

The model contains 9 sources of stochasticity, or non-deterministic processes. These can be roughly categorised into two categories - the ones resolving chance occurrences, and the ones accounting for noise around various processes.

Chance occurrences are: **1)** When resolving maturation, PMRNs are used to estimate probability of maturing, which is calculated and resolved for every fish. **2)** Determining which gear type is encountered, expressed as probability of encountering trawling nets. This is calculated on an individual basis, and every individual will be exposed to the selectivity curve for either trawling nets or gillnets. **3)** Resolving mortality - the sum of all sources of mortality is used to calculate probability of surviving. Individuals who do not survive are flagged for death, and subsequently removed from the population. **4)** Parental selection, which is based on weighted random selection as described above.

Sources of noise are simulated as normal distributions around otherwise deterministic variables or processes: **5)** Recruitment noise, added to the number of recruits added by the Beverton-Holt function, aims to simulate environmental variability not otherwise considered in the model. **6)** Phenotypic expression of genomic traits, which are 'Appetite' and 'PMRN intercept' (also initial gonadal allocation in Paper 1). Noise is added to the inherited values to simulate phenotypic variation. **7)** Food environment, simulating 'good' or 'bad' years in terms of food availability. **8)** Temperature, simulating annual fluctuations around average temperature. **9)** Inheritance, noise around midparental values aimed at producing realistic emergent heritabilities.

The intention of these sources of stochasticity, in particular numbers 5-9, is to account

Table 1.1: Overview of values considered for tested variables across all three papers.

Variable	Values	Paper		
		1	2	3
Foraging risk exponent	1.0	x	-	-
	1.4	x	-	-
	1.8	x	x	x
	2.2	x	-	-
	2.6	x	-	-
Max fishing mortality, F_{max} (y^{-1})	0.0	-	x	-
	0.1	-	x	-
	0.2	-	x	x
	0.3	-	x	-
Proportion trawled (%)	0	-	-	x
	30	-	-	x
	50	-	-	x
	70	-	x	x
	100	-	-	x
Target length, L_{max} (cm)	90	-	-	x
	100	-	-	x
	110	-	x	x
	120	-	-	x
	130	-	-	x

for at least some of the variability inherent to natural systems, given the impossibility of mechanistically accounting for every single process within an ecosystem. This comes with the tradeoff that effects of explanatory variables on these processes, for instance temperature effects on food availability, are not considered, which must be remembered when drawing conclusions.

1.4 Summary of papers

This thesis includes three papers, all implementing variations of the model described in the previous section, testing the variables of foraging risk, maximum fisheries mortality, trawling proportion and target length. For an overview of which values are considered in which papers, refer to Table 1.1.

In **Paper 1** we implement the model, albeit a simplified version with no fisheries and no climate warming, to clarify the evolution of foraging behavior at various levels of simulated foraging risk. In ecological terms, changes in foraging risk might result from changes in community structure or physical environment that change predation-pressure or make foraging more/less time consuming. Our model simplifies this, by simulating risk as the relation between foraging effort and the associated foraging mortality. It is assumed that individuals differ in their willingness to undertake risk, as previously categorized in the bold/shy spectrum (Toms et al., 2010) or the fear/hunger framework (Budaev et al., 2018), which our model collects into the inherited trait 'appetite'. As risk increases, the chance of dying to acquire a given amount of energy goes up - this especially impact individuals with larger appetites, who spend more time foraging. We found that increased levels of risk select for lower appetites and earlier maturation, resulting in reduced growth and smaller sizes. Given the direct link in the model between appetite and foraging behaviour, a reduction in appetite in order to decrease foraging effort appear to be the best way to minimize the increased mortality associated with higher risks. However, total mortality still increases despite the reduction in appetite. Given the disproportionately higher mortality of smaller individuals, growing fast to reach safer sizes would be optimal, which becomes a key trade-off as increasing risk selects against higher levels of foraging. Increased risk thus results in increased mortality, either from spending more time at vulnerable sizes or from foraging despite the increased risk, in order to grow faster. The increase in mortality subsequently select for earlier maturation, which is a common trend in fish (e.g. Claireaux et al. (2018) and Law (2000)).

With the inclusion of warming and fisheries, the model now allows us to consider the interactions of these in **Paper 2**. We did this by exposing the individuals in the model to 3 different warming scenarios, based on IPCC scenarios: SSP1, SSP2 and SSP3 (IPCC, 2021). In addition, a no-warming baseline was included. For each of these scenarios, increasing levels of fisheries mortality was applied, ranging from no fishing to a maximum fisheries mortality of $F = 0.3$. We found that increasing fishing pressure selects for earlier maturation, in line with earlier research (Claireaux et al., 2018; Law, 2007), but that rising temperatures counteracted this by selecting for later maturation. For other (especially temperate and tropical) populations temperature is expected to drive evolution for smaller sizes, fast life-histories and earlier maturation in line with the Temperature Size Rule (Daufresne et al., 2009; Pörtner, 2001). For the Northeast Arctic Cod, however, increasing temperatures appear to increase aerobic scope and reduce mortality. This decreased mortality subsequently favors faster growth and later maturation. Similar to the evolutionary consequences, our results also indicate that while increased fishing reduces population size measured as both biomass and number of individuals, the reduced mortality resulting from increasing temperatures increase population size. While model assumptions are questionable at the highest level of warming (discussed in **Papers 2&3**), these results still provide mechanistic reasons for expecting positive effects of warming on Northeast Arctic Cod.

While **Paper 2** focused on the effect of variable fishing pressure while not changing fisheries strategy, **Paper 3** focuses on the effect of strategy while maintaining constant fisheries pressure. The selectivity of fisheries is mostly determined by the gear type and the mesh size. Northeast Arctic Cod is fished predominantly by trawling (with sigmoidal selectivity) and gill nets (with bell-shaped selectivity), with targeted sizes controlled by mesh size. In **Paper 3** we implement five different target lengths across five different gear type selections for all the same temperature scenarios tested in **Paper 2**. Temperature once again seem beneficial, leading to increased population size, larger individual sizes and increased fisheries yield, while simultaneously mitigating the selectivity for earlier maturation from the fisheries. We further find that while trawling fisheries typically select for earlier maturation, gillnets might potentially select for later maturation depending on mesh size - and that this mesh size threshold in turn depends on temperature. This highlights the key mechanistic difference between the gear types: while trawling adds a constant mortality increase for larger individuals, gillnets provide a size refugium if fish can grow beyond the targeted sizes. If individuals cannot realistically grow beyond this range (e.g. because the target size is too big), this gear difference is diminished. In our model, temperature affects this relationship by allowing higher growth rates and larger asymptotic sizes. Population biomass mostly responded to gear choice, while number of individuals responded more strongly to target length: biomass was higher when favoring gillnets and number of individuals increased when targeting larger individuals. More interestingly, average yield and average size of caught fish responded non-linearly to fisheries strategy. Maximum yield seems to occur at intermediate mesh sizes with a slight preference for trawling, though this relationship shifts toward larger sizes and a larger prevalence of trawling as temperature increases, likely due to the increased growth and larger sizes seen in response to temperature.

Considering all the papers together, our model highlights the importance of considering evolution in the management of living resources. We provide a mechanistic basis for expecting changes in behaviour as well as life history in Northeast Arctic Cod. Furthermore, we show that while both climate warming and fisheries have the potential to cause evolution and change population size, they should be considered simultaneously in order to account for interactions that would otherwise lead to suboptimal management and conservation efforts.

1.5 General discussion & future perspective

Throughout the preceding papers, this thesis has provided a mechanistic basis for expecting interacting effects of climate warming and fisheries on life-history evolution of Northeast Arctic Cod (NEAC). Furthermore, we have shown how population size and demography can change as a result of individual differences in foraging behaviour and maturation schedule adapting to anthropogenic stressors. These findings build on previous modelling efforts by combining the framework published by Enberg et al. (2009) with the physiology and oxygen budgeting of Claireaux et al. (2000) and Holt and Jørgensen (2014), in a way that allows accounting for density dependence, given the recent uncertainty surrounding the importance of density dependence (Eikeset et al., 2016; Enberg & Jørgensen, 2017).

The model does rely on certain assumptions that are not strictly realistic. **First** and foremost is the assumption that temperature and fisheries strategy are the only changing external factors - in the real world temperature changes such as the ones modelled would likely bring changes in both physical/chemical environment (salinity, pH and O_2) as well as distribution of marine-related fauna (Ottersen et al., 2023). **Secondly**, temperature responses in the model relies on the accuracy of the modelled physiology, the parameterization of which was conducted for the NEAC stock under current conditions. The further temperatures move from present ranges, the less reliable this assumption becomes. While internal testing included comparisons to cod populations from warmer waters, it will never be a 1:1 comparison given the inherent differences in ecosystems outside of temperature. **Thirdly**, fisheries strategy was modelled statically. This means that strategy did not change from year-to-year in the model, but rather remained constant throughout the models runtime.

In real systems, fisheries strategy is continually assessed from year to year, based on stock indices in an attempt to manage for sustainable harvest.

Despite these caveats, I believe that the underlying mechanisms are sound. The results can be considered as an "all else being equal" situation, and do indicate important interactions between warming and fisheries on adaptive evolution of the NEAC stock. These interactions appear largely driven by how they change mortality throughout the life of individuals; fisheries are a source of mortality and warming reduce mortality in this stock (**Papers 2&3**). This reduced mortality appear to stem from the increased aerobic scope (Holt & Jørgensen, 2014).

Interestingly, rather than simply accepting this decrease in mortality, adaptation seems to then favor an increase in the inherited 'appetite' parameter, increasing foraging and energy acquisition until total natural mortality is largely indistinguishable between temperature scenarios. In other words, it seems that there is a optimal threshold of natural mortality favored by the evolutionary mechanisms in the model, and individuals will increase foraging effort until they reach this. The result of this is increased growth and larger sizes at maturation with warming temperatures - the opposite of what would be expected when considering the temperature-size rule (Atkinson, 1994).

On the other hand, effects of fisheries-induced evolution were much as anticipated, generally reducing asymptotic sizes age/length at maturation (gillnet selectivity was able to select for later maturation, see **Paper 3**)(Law, 2007). As such, the cumulative impact on maturation schedule depends on the relative strengths of warming and fisheries, with warming being able to counteract the effects of fisheries, at least to some extent. In **Paper 2**, we see this as the fisheries selecting for smaller PMRN intercept, and warming selecting for larger PMRN intercept.

While the effects of fisheries and warming on PMRN intercept are opposed, both warming and fisheries select for larger appetites, but in this case the mechanisms differ. As mentioned above, warming temperatures result in increased foraging and faster growth by reducing natural mortality, which the fish then respond to by scaling up appetite. It might seem counterintuitive then, that an *increase* in mortality from fisheries would then cause the same type of response as the *decrease* in natural mortality. The reason for this is two-fold:

first of all fisheries are size-selective, and as the benefit of being large is decreased, adaptive evolution would favor a faster pace-of-life. However, even unselective fisheries cause a similar effect (Claireaux et al., 2018), so there must be more to the mechanism.

The rationale has to do with the probability of surviving to reach maturity. The mortality introduced by fisheries is strictly detrimental to the fish, whereas the mortality from foraging comes with an increase in growth. What we see when we introduce fisheries mortality on a population, is typically a willingness to accept increased natural mortality as well (Jørgensen & Holt, 2013). Putting yourself in the mind of a fish, if you will pardon my anthropomorphising departure from scientific terms, if you were less likely to reach maturity despite living cautiously, would you not throw caution to the wind and choose to risk more in an attempt to grow faster so you might reach fertile sizes? In more direct terms, if you are likely to die anyways, why not at least attempt to grow faster? This is of course a metaphor, as the fish in the model do not have cognition, but I believe it serves to conceptualise why evolution would favour such responses. Evolutionary adaptation to this might take two forms: selecting for earlier maturation to reproduce before dying (selection for smaller PMRN) or selecting for increased foraging effort to reach a size capable of maturing (selection for increased appetite).

This leads to the key point of interaction for fisheries and warming on evolution in the model. The optimal threshold for 'acceptable' natural mortality mentioned earlier is subject to change as fishing mortality is introduced. As the proportion of total mortality coming from fisheries increases, adaptive evolution favour behaviours that increase natural mortality, as discussed by Jørgensen and Holt (2013).

1.5.1 Where do we go from here?

In extension of the results presented in these papers, I see several potential avenues for future research building on the findings in this thesis, and filling in gaps not covered within:

1. **How might these results change if fisheries employed adaptive management?** Given that fisheries were not able to change or adapt their capture strategies in response to changes in the population, resulting catches were likely not maximised. In terms of the figurative "evolutionary arms race", we allowed only one side to adapt.

In **Paper 3** we found that extensive warming might theoretically even allow fish to grow well beyond the target sizes considered in the study, which inevitably impacts the relative effectiveness of gillnet vs. trawl. In extension, using exclusively gillnets with smaller target sizes in high-warming scenarios results in significantly diminished catches. Adaptive management, with annualy updating target sizes based on stock indices, could result in more suitable ranges being tested.

2. **How might retreating ice caps affect results?**
   As outlined previously, the model does not include ecological changes in response to warming. One such expected change is the shrinking of polar ice cover (Polyakov et al., 2010). Retreating ice results in more open water, and potentially larger area with increased productivity for NEAC (Kjesbu et al., 2014), but would need to be considered in relation to the annual spawning migration (Opdal, 2010).

3. **The introduction of new species?**
   Given the expected polewards migration (Roessig et al., 2004) the Barents Sea could see the introduction of new species, which might alter the food web (Kortsch et al., 2015). The introduction of generalist species might increase food-web connectivity, increasing energy transfer to upper trophic levels, but might also lead to more competition for resources. The type of model presented in this thesis is ill suited for considering this type of changes, but output from end-to-end models such as Atlantis (Fulton et al., 2011; Hansen et al., 2016) or Ecopath with Ecosim (Christensen & Walters, 2004) could serve as input for further scenarios to consider using individual based evolutionary modelling.

4. **Could this model be adapted to other stocks or even species?**
   The model in its current form is only suitable for testing responses of the NEAC stock, but given the general mechanistic framework it could theoretically be applied to other stocks of Atlantic cod, given proper re-parameterization. The key tradeoff between fisheries and warming in the model centers on optimal natural mortality and maturation timing, and provided realistic responses of mortality in other species could be parameterized, this framework should be applicable to any exploited fish population.

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Paper 1: Life-history evolution in response to foraging risk, modelled for Northeast Arctic cod (*Gadus morhua*)

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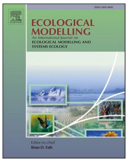

Life-history evolution in response to foraging risk, modelled for Northeast Arctic cod (*Gadus morhua*)

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ABSTRACT

Foraging behaviour is known to be a key element in ecology and evolution. Increased foraging intensity increases energy intake, which is useful for growth and reproduction but comes at the cost of higher mortality risk due to increased exposure to predators. Here, we investigate these trade-offs through an individual-based, mechanistic modelling framework adapted to the Northeast Arctic Cod. The model incorporates a series of life-history traits, survival trade-offs, and heritability, which allow evolution to occur and optimal strategies to emerge due to individual trait combinations and their fitness consequences. By altering the relationship between foraging intensity and mortality risk, we find that increased risk causes evolution towards lower foraging effort leading to lower growth and in turn, earlier maturation and a faster pace of life. These results build on previous studies by demonstrating behavioural evolution without direct anthropogenic stressors. Natural mortality among fish is poorly understood, and these results highlight an interesting point of further research that could help future modelling approaches make more accurate assumptions about natural mortality and its components.

1. Introduction

1.1. The ecology of foraging

All animals require energy to survive and reproduce, as energy is used in a multitude of processes ranging from basal metabolism to tissue repair and synthesis. While some animals can passively acquire energy even when stationary, most animals will need to actively seek out food, an activity known as foraging. Foraging provides an interesting behavioural framework to consider the cost/benefit of performing an activity (Emlen, 1966; MacArthur and Pianka, 1966).

On one hand, the more time spent foraging, the more energy an individual could feasibly obtain - energy that could be used for faster growth, stores, or reproduction, likely leading to more offspring. This makes the benefit of foraging clear, and had there been no downsides, one would expect individuals to forage continuously, barring other limitations such as digestive capacity (Fall and Fiksen, 2020).

However, there are costs associated with foraging, which take on two primary forms: first off, foraging is active and requires energy. The energy gained must exceed the energy cost to be worth foraging. Secondly, foraging individuals are more exposed to predation since they must venture away from potential hiding spots to find food. This leads to an increase in mortality with an increase in foraging effort (Toms et al., 2010).

Individual differences in willingness to engage in risky behaviour have been found in a wide variety of species (Harcourt et al., 2009; Ward et al., 2004; Wilson et al., 1994). This risk-taking also includes a willingness to accept greater risks when foraging (Dammhahn and Almeling, 2012), which can remain consistent within individuals, suggesting that this is an intrinsic trait. Furthermore, studies have highlighted interactions between these behavioural patterns and environmental factors such as temperature (Biro et al., 2010; Killen et al., 2013), making understanding these behaviours increasingly relevant in our warming climate.

Such traits have been linked to personality, often categorised as being either ’shy’ or ’bold’ (Toms et al., 2010), with risk-averse individuals generally categorised as ’shy’ and risk-accepting individuals being categorised as ’bold.’ Alternative frameworks have also been suggested, such as risk-taking being characterised by a fear/hunger trade-off (Budaev et al., 2018). Regardless of terminology, personality differences are well documented within fish, and there is good reason to suspect at least partial heritability of personality traits (Dochtermann et al., 2015; Wilson et al., 1994).

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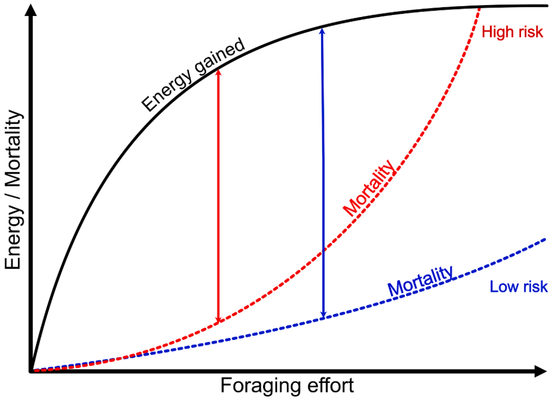

Fig. 1. Conceptual illustration of the survival trade-off when foraging. Increased foraging effort increases both energy intake and mortality, but since energy intake experiences diminishing returns various risk scenarios will have different optimal foraging efforts, here assumed to be where the energy gained in relation to mortality experienced is largest.

1.2. Anticipating evolution

Fish evolve in response to stressors, and the evolution of various life-history traits has the potential to not only alter demographic parameters such as growth (Crozier and Hutchings, 2014; Enberg et al., 2012; Holt and Jørgensen, 2014) and age-at-maturity (Dieckmann and Heino, 2007; Heino et al., 2002b), but these changes may, in turn, affect the relationship between recruitment and indices such as spawning stock biomass (Enberg et al., 2010), which in turn can lead to mismanagement if not accounted for. It becomes apparent then that proper consideration of evolution should be included in management and conservation efforts (Jørgensen et al., 2007).

Given that individuals will differ in willingness to forage under varying degrees of risk and that these differences are heritable, we have reason to suspect that time spent foraging (and subsequent energy acquisition) would evolve in response to varying foraging risk (Stephens, 2008; Fig. 1), which might vary due to changing community structure or physical environment. Building on this, changes in energy intake might in turn lead to shifts in optimal life history.

Mechanistic models are tools that aim to simulate the natural processes and trade-offs that impact survival and subsequent lifetime fecundity. When properly calibrated, this allows us to calculate optimal strategies for any scenario we wish to test by assuming that strategies maximising lifetime fecundity will be favoured by evolution.

When changing input parameters (such as temperature or foraging risk), new optimal strategies might emerge, indicating the direction we can expect evolution to drive the population.

Among mechanistic models, Individual Based Models (IBMs, sometimes referred to as Agent-Based Models) are particularly suited to studying evolution, as they can simulate evolution by including inter-individual variability in inherited traits that influence fitness, allowing individuals to reproduce and die according to their life histories (e.g., Enberg et al., 2009). However, to our knowledge, no evolutionary IBMs for fish have been created that include realistic physiology with oxygen limitation. Such physiological frameworks have been included in other types of models, for instance, dynamic optimization (Holt and Jørgensen, 2014), but including it in an IBM will allow us to more

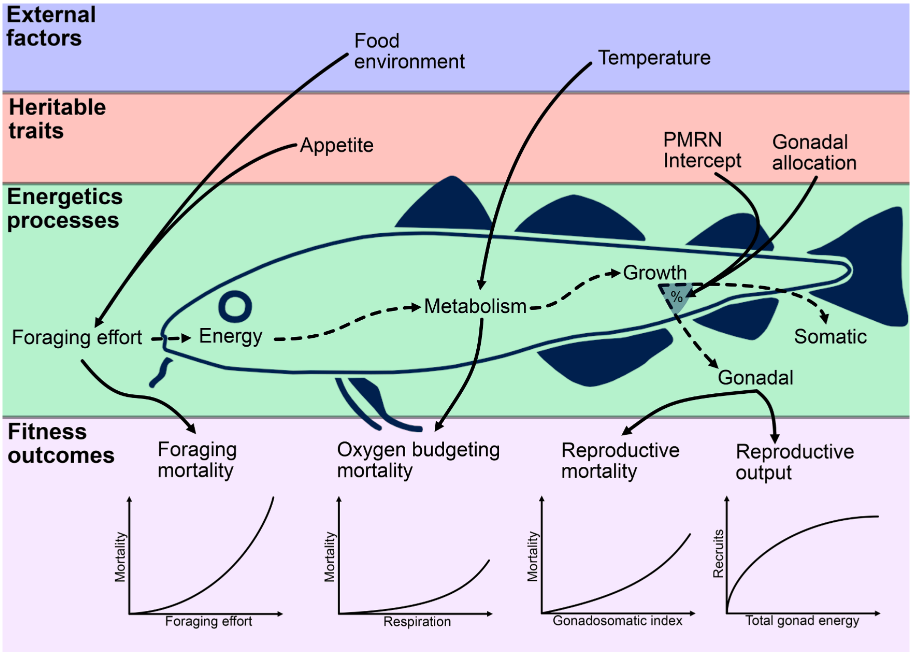

Fig. 2. Conceptual schematic highlighting critical processes in the model relating external factors and heritable traits to fitness outcomes through energetics. Solid arrows indicate direct influence, and dashed arrows indicate the energy flow. The shaded '%' area represents the proportion of energy dedicated to somatic/ gonadal growth.

Table 1
Model parameters.

Variable	Description	Value	Unit	Source
Energetics				
β	Allometric scaling exponent	0.7	–	Holt and Jørgensen, 2014
c_R	Efficiency of converting energy to tissue	0.5	–	–
c_{SDA}	Energetic cost of digestion	0.17	$Jkg^{-1}y^{-1}$	–
c_{SMR}	Standard metabolic rate coefficient	$4.67 * 10^6$	$Jkg^{-1}y^{-1}$	–
c_ϕ	Foraging cost coefficient	0.15	Jy^{-1}	Holt and Jørgensen, 2014
c_{T1}	Unit conversion coefficient	6.63	–	–
c_{T2}	Arrhenius function constant	15.7	K	Claireaux et al., 2000
c_{T3}	Arrhenius function constant	5020	K	Claireaux et al., 2000
c_{D2}	Rate of somatic investment decay	0.5	–	–
ρ_s	Energy density of somatic tissue	$4.62 * 10^6$	$J\ kg^{-1}$	Holdway and Beamish, 1984
ρ_g	Energy density of gonad tissue	$6.93 * 10^6$	$J\ kg^{-1}$	Holdway and Beamish, 1984
D_M	Distance to migrate, one way	780	km	Jørgensen and Fiksen, 2006
c_{COT}	Cost of transport coefficient	41.8	$J\ km^{-1}$	Ware, 1978
c_u	Optimal swimming speed coefficient	0.138	s^{-1}	Ware, 1978
b_2	Optimal swimming speed exponent	0.43	–	Ware, 1978
b_3	Length scaling factor for c_M	1.02	–	Ware, 1978
b_4	Swimming speed scaling factor for c_M	2.42	–	Ware, 1978
K	Length-weight relationship coefficient	0.01	$kg\ cm^{-3}$	–
V_1	Maximal oxygen uptake parameter	$4.11 * 10^6$	$J\ y^{-1}$	Claireaux et al., 2000
V_2	Maximal oxygen uptake parameter	0.015	°C	Claireaux et al., 2000
V_3	Maximal oxygen uptake parameter	1.062	°C	Claireaux et al., 2000
V_4	Maximal oxygen uptake parameter	$7.13 * 10^6$	$J\ y^{-1}$	Claireaux et al., 2000
c_{DD1}	Foraging density dependence parameter	0.15	–	–
c_{DD2}	Foraging density dependence parameter	$3.6 * 10^{-5}$	–	–
c_{F1}	Foraging diminishing returns parameter	2.4	–	–
c_{F2}	Foraging diminishing returns parameter	0.29	–	–
Maturation				
W	PMRN width	40	cm	–
L_S	PMRN slope	2	cm year^{-1}	–
Mortality				
$c_{predation}$	Predation mortality coefficient	0.66	y^{-1}	Holt and Jørgensen, 2014
c_ϕ	Foraging mortality coefficient	0.03	y^{-1}	Holt and Jørgensen, 2014
$c_{respiration}$	Respiration mortality coefficient	11	y^{-1}	Holt and Jørgensen, 2014
e_1	Predation mortality exponent	0.75	–	McGurk, 1986
e_2	Foraging mortality exponent	Varies	–	Holt and Jørgensen, 2014
e_3	Reproductive mortality exponent	2.5	–	Holt and Jørgensen, 2014
e_4	Respiration mortality exponent	3	–	Holt and Jørgensen, 2014
M_{fixed}	Size-independent mortality	0.07	y^{-1}	Holt and Jørgensen, 2014
GSI_{ref}	GSI at which $Mreproduction = Mpredation$	0.10	–	Holt and Jørgensen, 2014
Recruitment				
c_{R1}	Stock-recruitment constant	$1.877 * 10^{-6}$	–	Enberg et al., 2009
c_{R2}	Stock-recruitment constant	$2.346 * 10^{-11}$	–	Enberg et al., 2009
$Wegg$	Weight of a single egg	$4 * 10^{-4}$	g	Enberg et al., 2009
Evolving traits				
ζ	Appetite	–	$J\ kg^{-1}$	–
L_I	PMRN Intercept	–	cm	–
c_{D1}	Initial rate of somatic investment	–	–	–

realistically simulate actual population responses to stressors rather than describing optimal behaviour. Additionally, few evolutionary models have included costs associated with foraging, leading to a lack of mechanistic understanding of how risk might impact optimal life history.

1.3. Aim of the study

This study aims to build on previous evolutionary modelling efforts using Atlantic cod (*Gadus morhua*), specifically the Northeast Arctic (NEA) cod stock, as the focal population. The NEA cod stock is not only commercially important, accounting for 796,000 tonnes of catches annually between 2010 and 2020 (ICES, 2021), but is also well-researched, with a large body of literature available on maturation schedule (Heino et al., 2002b), temperature-growth response (Björnsson et al., 2007; Brander, 1995), behaviour (Freitas et al., 2015) as well as expected evolution in response to both climate (Holt and Jørgensen, 2014) and fisheries (Heino et al., 2002b; Jørgensen et al., 2007, 2009) to name a few.

Through the lens of NEA cod, we explore the relationship between foraging risk and the evolution of foraging effort and maturation schedule, as well as the emerging life histories. In doing so, we develop an IBM that includes explicit energy budgeting sensitive to temperature, suitable for studying evolutionary responses to fisheries and climate. As such, the model does include complexity that is not strictly necessary to study the effects of foraging risk but is useful for increased versatility in future model applications.

2. Model description

We introduce an individual-based model based on the framework previously published by Enberg et al. (2009), adding explicit energetics and oxygen budget for NEA cod within a stochastic food environment, drawn mainly from Holt and Jørgensen (2014). The inclusion of explicit energetics and oxygen budget allows for better accounting of what effect temperature can be expected to have on the population for use in future

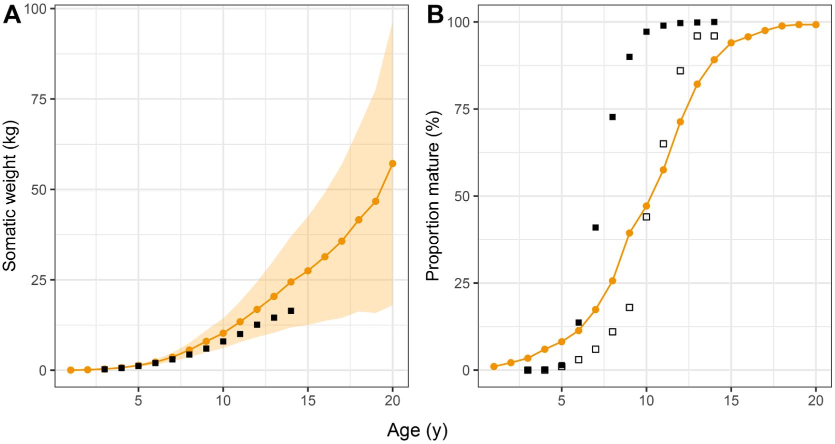

Fig. 3. Initial population compared to ICES data (squares). (A) Average weight-at-age ±SD of the final population compared to ICES averages from 2014 to 2021. (B) Average proportion mature-at-age ±SD of the last 200 years of stabilisation (Appendix B), compared to both ICES averages from 2014 to 2021 (black squares) and ICES values from 1946 (hollow squares). 1946 values were not available for weight-at-age.

applications of the model. Each individual carries traits that impact their life history through maturation, growth, reproductive investment, and mortality, while population dynamics and fitness are allowed to emerge from the interactions of all these individuals (Fig. 2). Each of these sections are described in more detail below, and a full list of parameters can be found in Table 1.

2.1. Purpose

The model aims to simulate the evolution of the maturation scheme and somatic energy allocation (life history) by including genetic traits that influence the phenotypic expression, with a measure of stochasticity to mimic environmental variability, which impacts survival. The model also introduces the inherited trait ”Appetite,” which takes the form of desired energy intake, in turn governing foraging activity. As such, individuals with high appetites are comparable to bold individuals on the bold/shy spectrum (Toms et al., 2010) or hungry individuals in the fear/hunger framework (Budaev et al., 2018), while the inverse is true for individuals with low appetites.

Surviving individuals reproduce, passing on their genetic traits to the next generation. This method allows for evolutionary patterns to emerge over time, as individuals with favourable traits will survive and produce more offspring over their lifetimes, simulating natural selection.

Using this model, we will test evolutionary responses to varying degrees of foraging risk, represented by the variable ‘foraging risk exponent,’ e_2, as explained below.

2.2. Process overview

The model simulates 2000 years in annual time steps. Every year, individuals are first faced with the possibility of maturing, after which energetics are calculated. Based on trade-offs in these sections, mortality/survival probability is determined. Recruitment (and inheritance) is then performed based on gonadal energy allocation, followed by model upkeep, removing dead individuals and ageing the remaining ones. Individuals are allowed to live for 20 years, after which they are removed, and recruits are added as 1-year-olds.

2.3. Initializing the model

To initialize the model, we first ran it for 5000 years to let the population stabilize using a foraging risk exponent $e_2 = 1.8$ (explained in more detail below). 5000 years is used to make sure that the initial population is evolutionarily stable and does not carry trends into the simulation experiments. The risk exponent value ($e_2 = 1.8$) was chosen because it best replicated observed growth patterns and proportion mature-at-age when comparing the model against observed data (ICES, 2021; Fig. 3) from the Barents Sea and Lofoten between 2004 and 2018. While the fit is not perfect, it should be noted that the NEA cod has been fished for many generations, likely explaining this small discrepancy, as the proportion of mature individuals better fit with the data from 1946, before fisheries were intensified (Fig. 3, B). The resulting population (305,470 individuals) was used as a starting point for all future runs. For every value of e_2 tested, the model was run for 2000 years, and each run was done 20 times with different random seeds to act as replicates. Two thousand years was chosen because that was the earliest point in which inherited traits were stabilised, and evolutionary trends were visible.

2.4. Input

The model includes several sources of stochasticity: phenotypic expression of genetic traits, variability in the food environment, temperature and recruitment, and offspring variability compared to mid-parental values. For simplicity, all of these are assumed to be normally distributed around their respective values with a standard deviation of 5%, except for offspring variability (described below), as sensitivity analysis showed that none of them were driving results. Temperature is centred around 4 °C, which is the average annual temperature in the Barents Sea as measured along the Kola hydrographical transect (0 – 200 m, 1900–2020, Boitzov et al. 2012).

2.5. Full process description

2.5.1. Maturation

The maturation scheme is based on a Probabilistic Maturation Reaction Norm (PMRN) Heino et al., 2002b), shown in Eqs. (1)–((3). The probability of maturation for individual i, $p_{mat}(i)$ within year y is dependent on the intercept and slope of the maturation reaction norm,

$$p_{mat_y}(i) = \frac{1}{1 + \exp\left(\frac{-L_y(i) - L_{p50}(i)}{\theta}\right)} \tag{1}$$

where L_y is the length of individual i in year y, L_{p50} is the length at 50% maturity (Eq. (3)), and θ is based on reaction norm width as follows,

$$\theta = \frac{w}{logit(p_u) - logit(p_l)} \tag{2}$$

where w is the PMRN width, p_u and p_l being the upper and lower probability bonds, respectively (generally set to 0.75 and 0.25). The length at 50% maturity, L_{p50}, is calculated as,

$$L_{p50}(i) = L_I(i) + Age_{y-1}(i)^{*}L_S \tag{3}$$

where L_I and L_S are the intercept and slope of the reaction norm, respectively, and Age_{y-1} is the age prior to year y. While Enberg et al. (2009) allowed both intercept (L_I) and slope (L_S) to evolve, they also found that the evolution of slope added little explanatory value. Hence, in this study, only the L_1 is an inherited trait. Slope (L_S) is set to 2 cm year^{-1}, and width (w)¸is set to 40 cm, as this resulted in a reasonable maturation schedule when compared to available data (ICES, 2021). When interpreting results, higher L_I means late maturation at a larger size, while low L_I means earlier maturation at a smaller size. The slope parameter L_S influences how dependant the maturation process is on length and age relatively: if slope is 0, it is only the size that impacts maturation probability, whereas increasingly negative slope values mean that age start playing increasingly important role in the maturation probability. For more information on PMRNs, please refer to Heino et al. (2002b).

2.6. Energetics

All individuals (i) forage until they reach their predetermined energy intake, ϕ, determined as follows,

$$\phi(i) = \zeta(i)^{*}W^{\beta}(i) \tag{4}$$

where ζ is the appetite described earlier for individual i, W is weight, and β is an allometric exponent.

This model then includes a modified energetics framework based on the Wisconsin Bioenergetics Framework Hewett and Johnson, 1992), previously parametrized for NEA cod by Holt and Jørgensen (2014), Eqs. (5)–((12) (Eq. (6) modified to account for density dependence).

For every year, a food environment ω_y is set,

$$\omega_y = \chi_1 + [c_{DD1} * c_{DD2} * \Sigma(W(i))] \tag{5}$$

where χ_1 is a stochastic function normally distributed around 1 with a standard deviation of 0.05, and $\Sigma(W)$ is the total population biomass to simulate competition for food (density dependence). The total energy intake for individual i in any year, $\phi_y(i)$, is then determined by,

$$\phi_y(i) = \omega_y{}^{*}\frac{c_{F1}{}^{*}f_{int}(i)}{1 + c_{F2}{}^{*}f_{int}(i)}{}^{*}B_{SMR}(i) \tag{6}$$

where f_{int} is the foraging intensity, which individuals scale to reach the desired energy intake set by ζ, and c_{F1} and c_{F2} are constants. For ease of interpretation, f_{int} is given in units of standard metabolic rate, B_{SMR}. Based on the food intake we can construct an energy budget for individual i,

$$N_y(i) = [\phi_y(i) - B_{SDA}(i) - B_{SMR}(i) - B_{\phi}(i)]c_R \tag{7}$$

where N_y is the net available energy for growth in year y, B_{SDA} is the energy lost by specific dynamic action (digestion, etc.), B_{SMR} is the standard metabolic rate based on weight and temperature, B_{ϕ} is the energetic cost associated with foraging, and c_R is the efficiency of converting energy to new tissue. B_{SDA}, B_{SMR} and B_{ϕ} are calculated as follows,

$$BSDA(i) = c_{SDA}{}^{*}\phi_y(i) \tag{8}$$

$$BSMR(i) = c_{SMR}{}^{*}f(T)^{*}W^{\beta}(i) \tag{9}$$

$$B_{\phi}(i) = c_{\phi}{}^{*}f_{int}(i)^{*}B_{SMR}(i) \tag{10}$$

where c_{SDA}, c_{SMR} and c_{ϕ} are constants (Table 1) and $f(T)$ is an Arrhenius function of temperature,

$$f(T) = c_{T1}{}^{*}\exp\left(c_{T2} - \frac{c_{T3}}{T + 273.15}\right) \tag{11}$$

c_{T1}, c_{T2} and c_{T3} are constants (Table 1).

The available energy, N_y, is then divided based on the maturity status of the fish; for immature fish, all the energy is allocated to somatic growth G_s,

$$G_s(i) = \frac{N_y(i)}{\rho_s} \tag{12}$$

where ρ_s is the energy density of somatic tissue.

For mature individuals, a somatic growth allocation function, p_t, is used to describe the decreasing allocation to somatic growth as the fish ages (Quince et al., 2008), resulting in increased gonadal allocation,

$$p_t = c_{D1}(i)^{*}c_{D2}^{A(i) - A_m(i)} \tag{13}$$

where c_{D1} is the initial investment to somatic growth, c_{D2} is the rate of somatic growth allocation decay, A is the current age and A_m is the age at maturation. Initial investment, c_{D1}, is an evolving trait in the model. Energy is then divided between somatic growth, G_s, and gonad growth, G_g, as in Holt and Jørgensen (2014),

$$G_s(i) = \frac{N_y(i)^{*}p_t}{\rho_s} \tag{14}$$

$$G_g(i) = \frac{N_y(i)^{*}(1 - p_t) - B_M(i)}{\rho_g} \tag{15}$$

where B_M is the energy used for spawning migration and ρ_g is the energy density of gonadal tissue.

Mature individuals of NEA cod undertake annual spawning migrations of 780 km each way to spawn near the Lofoten islands (Opdal et al., 2011). B_M is modelled based on the swimming speed bioenergetics published by Ware et al. (1978), where optimal swimming speed is a function of length (body lengths per second), $U_{opt}(i) = c_u * L^{b2}(i)$, where c_u and b_2 are constants. The cost of transport is then calculated as a function of length and optimal swimming speed, $c_M(i) = c_{COT} * L^{b3}(i) * U_{opt}^{b4}(i)$, where c_{COT}, b_3 and b_4 are constants (Table 1). The total energetic cost of spawning migration then becomes,

$$B_M(i) = c_M(i)^{*}2^{*}D_M \tag{16}$$

where D_M is the migratory distance, undertaken twice for the round-trip. A minimum amount of energy allocated to gonads, $N_y * (1 - p_t)$, is required for the fish to undertake the spawning migration, here calculated as having enough energy to reach a gonadosomatic index of at least 0.1 post-migration. This value was chosen in order to achieve a realistic number of spawning-skippers, based on personal experience. If an individual does not meet this energy threshold, it instead allocates all energy to somatic growth and skips spawning for the year.

Growth in length is derived from the growth in weight by allometric scaling,

$$W(i) = k^{*}L^{3}(i) \tag{17}$$

where k is a constant (Table 1).

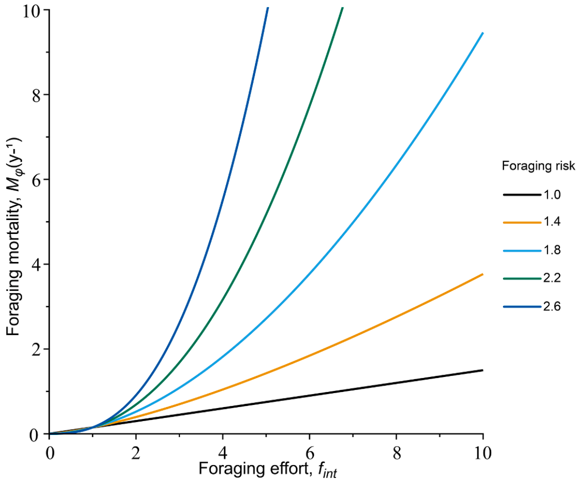

Fig. 4. Changes in base foraging mortality in response to increasing foraging effort, shown for several values of foraging risk. Note that the mortality values on the y-axis does not yet include the scaling by predation mortality, $M_{predation}$ (see Eq. (24)), in order to make the figure general.

In addition to this energy budget, the model includes a budget for oxygen adapted from Claireaux et al. (2000), Eqs. (18)–(20).

The maximum oxygen uptake V_{max} of individual i is calculated as,

$$V_{max}(i) = \left(V_1 T^{-V_2 T + V_3} + V_4\right) W_{som}^{b}(i) \tag{18}$$

where V_{1-4} are all constants, and W_{som} is the somatic weight (excluding gonad weight). Oxygen consumption V_y is defined as the sum of the metabolic processes,

$$V_y(i) = B_{SDA}(i) + B_{SMR}(i) + B_{\phi}(i) + B_{growth}(i) \tag{19}$$

where B_{growth} is metabolic work associated with converting energy, c_R,

$$V_y(i) = B_{SDA}(i) + B_{SMR}(i) + B_{\phi}(i) + B_{growth}(i) \tag{20}$$

2.7. Mortality

Since many of the activities accounted for in the energetics section above impact mortality, the trade-offs must be included in the model. As such, mortality in the model is split into several compartments, based on previous modelling efforts by Holt and Jørgensen (2014), Eqs. (21)–(26),

$$Z(i) = M_{predation}(i) + M_{\phi}(i) + M_{reproduction}(i) + M_{respiration}(i) + M_{fixed} \tag{21}$$

where M_{fixed} is a fixed rate of size-independent natural mortality, and the remaining factors are the mortalities associated with predation, foraging, reproduction and respiration, respectively. For any given individual i, the probability of surviving, $S(i)$, in a given year is,

$$S(i) = exp(-Z(i)) \tag{22}$$

Predation mortality is the primary size-dependant mortality, in the form of the increased risk of being preyed upon as smaller individuals.

$$M_{predation}(i) = c_{predation} * L^{-e_1}(i) \tag{23}$$

where $c_{predation}$ and e_1 are constants (Table 1), and L is the length of the fish in cm. Foraging mortality comes primarily in the form of increased risk of being preyed upon when increasing foraging intensity (f_{int}), and is therefore related directly to $M_{predation}$,

$$M_{\phi} = c_{\phi} * f_{int}^{e2}(i) * M_{predation}(i) \tag{24}$$

where c_{ϕ} and e_2 are constants. The risk associated with foraging is governed by e_2, the foraging risk exponent, which is the focus of this paper. By changing $e2$ we alter the relationship between foraging effort and mortality as seen in Fig. 4.

Reproductive mortality relates to decreased swimming capacity due to the change in form factor and additional risk-taking behaviour during courtship and mating.

$$M_{reproduction}(i) = \left(\frac{GSI(i)}{GSI_{ref}(i)}\right)^{e3} * M_{predation}(i) \tag{25}$$

where $GSIref$ is the GSI at which $Mreproduction = Mpredation$, and $e3$ is a constant. Respiration mortality is the result of limited respiratory capacity in relation to respiratory demand (essentially exhaustion),

$$M_{respiration}(i) = c_{respiration} * \left(\frac{V(i)}{V_{max}(i)}\right)^{c4} * M_{predation}(i) \tag{26}$$

where $c_{respiration}$ and e_4 are constants (Table 1).

2.8. Recruitment

The number of recruits in year t is calculated using Beverton-Holt recruitment Beverton and Holt, 1993) based on total fecundity, ΣQ(i, t), adapted for Atlantic cod by Enberg et al. (2009), Eqs. (27) & ((28), as follows,

$$N_0(t) = \frac{c_{R1}\sum Q(i,t)}{1 + c_{R2}\sum Q(i,t)} e^{\lambda_R(t)} \tag{27}$$

where c_{R1} and c_{R2} are constants (Table 1) determining survival at low fecundity and strength of density dependence, respectively, and $e^{\lambda R(t)}$ describes inter-annual environmental variability. In practice larger individuals are expected to dedicate more energy to gonads, making individual fecundity weight-dependant.

Inheritance of traits is simplified in the model, as it is in Enberg et al., 2009, due to the often highly polygenic nature of life-history traits (Roff, 1993; Conner and Hartl 2004). For every recruit, two parents are

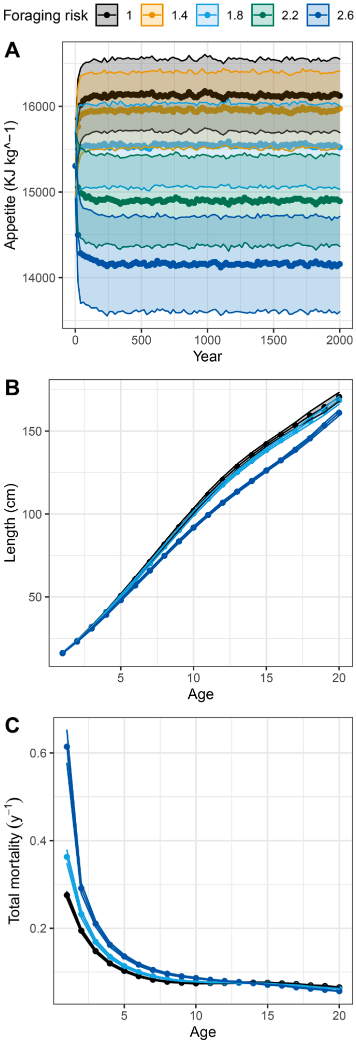

Fig. 5. Changes in energy acquisition and resulting growth/mortality differences. (A) Average genetic appetite ±SD over the model's runtime. (B) Average length ±SD as a function of age at the end of the 2000-year runtime. (C) Total mortality ±SE ($n = 20$) at the end of the 2000-year runtime. For plots B and C, values for foraging risks of 1.4 and 2.2 are omitted, as they didn't fall outside visible trends, but the dense clustering made the plots difficult to read.

chosen from mature individuals by random sampling, weighted by gonad growth, $G_g(i)$. This makes a fish more likely to be chosen as a parent the more it contributed to the total fecundity of the population. Evolving traits are then calculated based on mid-parental values as shown here for appetite, ζ

$$\zeta(i) = \frac{1}{2}[\zeta_{Parent1} + \zeta_{Parent2}]^{*}\chi_2 \tag{28}$$

where χ_2 is a stochastic function normally distributed around 1 with a standard deviation of 0.14. This stochastic function aims to simulate the effects of mutation, segregation and recombination, generating heterogeneity in offspring for selection to act upon. The standard deviation of 0.14 was chosen as it yielded emergent heritability of approximately 0.2 calculated as the linear correlation between mid-parental values and offspring values for both length- and age at maturation, which is within the range typically seen for life history traits (Gjedrem 1983; Law 2000; Carlson and Seamons 2008).

Note that the model does not separate between males and females, but only has a single sex. This is considered to be an acceptable simplification when male and female life-histories and demography are similar (Dunlop et al., 2009) – which we believe is the case for NEA cod.

3. Results

We found that an increase in foraging risk leads to evolution towards lower appetite and, thereby lower growth (Fig. 5, A). Comparing the runs over time (2000 years), appetite rapidly (within 250 years) diverged and stabilised around new means, indicating strong selection. The highest mean appetites were found for the lowest risks (~ 16,100 $kJ\ kg^{-1}$) while increasing risk decreased mean appetite up to 12% (~ 14,200 $kJ\ kg^{-1}$) in the highest risk scenario. A consistent trend for all results was that values of foraging risk (e_2) between 1.0 and 1.8 were more similar than the highest values ($e_2 = 2.2$ and 2.6). This is likely because foraging risk increases exponentially with increasing e_2. Increasing the foraging risk even higher leads to the population crashing due to too high mortality in the early years (results not shown).

In extension of the reduced appetite, growth was consistently lower in the higher-risk scenarios, as seen by the lower size-at-age (Fig. 5, B). Individuals in the lowest risk scenario grow to reach 100 cm in length by age 10, while individuals in the highest risk scenario reached 9 cm. There were no clear differences between the three lowest risk scenarios, implying that growth is not significantly impacted until risk reaches a certain threshold.

Mortality increased notably in the two high-risk scenarios, a trend that is particularly apparent for the younger fish (Fig. 5, C), likely due to mortality being scaled by length-dependant predation mortality (Eq. (23)). For the one-year-old fish, the rate of mortality was 0.28 y^{-1} in the lowest risk scenario, but 0.61 y^{-1} in the highest risk - more than a twofold increase. While this difference diminishes as the fish ages it doesn't disappear until the fish reaches 14 years of age, at which point the fish have already matured and reproduced (Fig. 6). This also translates to a smaller population size, measured both as total biomass and as the number of individuals (Appendix C).

The changes in energy acquisition and mortality lead to changes in life history, specifically by favouring a reduction in PMRN intercept after stabilization (Fig. 6, A). In this case, the clustering of low-risk scenarios compared to high-risk scenarios is even more pronounced than for appetite. The average intercept for low-risk scenarios ranges from 113 to 107 cm, while the highest-risk scenario leads to an intercept of 95 cm.

Unlike the other evolving traits (appetite and PMRN intercept), the initial gonadal allocation c_{D1} did not seem to change significantly with increasing risk (e_2) (Fig. 6, B). While the higher e_2 values did at first lead to an increase in the initial allocation, allocation started decreasing again once PMRN intercept and appetite had stabilised (around year 4–500) (Appendix B), and even when the difference between risks is largest, average allocation only differs by 1 percentage point. After stabilization, differences appear negligible. The initial increase in gonadal allocation in high-risk scenarios is likely driven by the sudden increase in mortality, making investing in reproduction over growth more beneficial. Once appetite stabilises, this pressure is relaxed, and allocation once again decreases.

To see how these changes in PMRN intercept translated into changes in the actual life histories, we considered age and length at maturation, which follows the same trend (Fig. 6, C&D). As risk increases, mean length and age at maturation decrease, with this effect being more

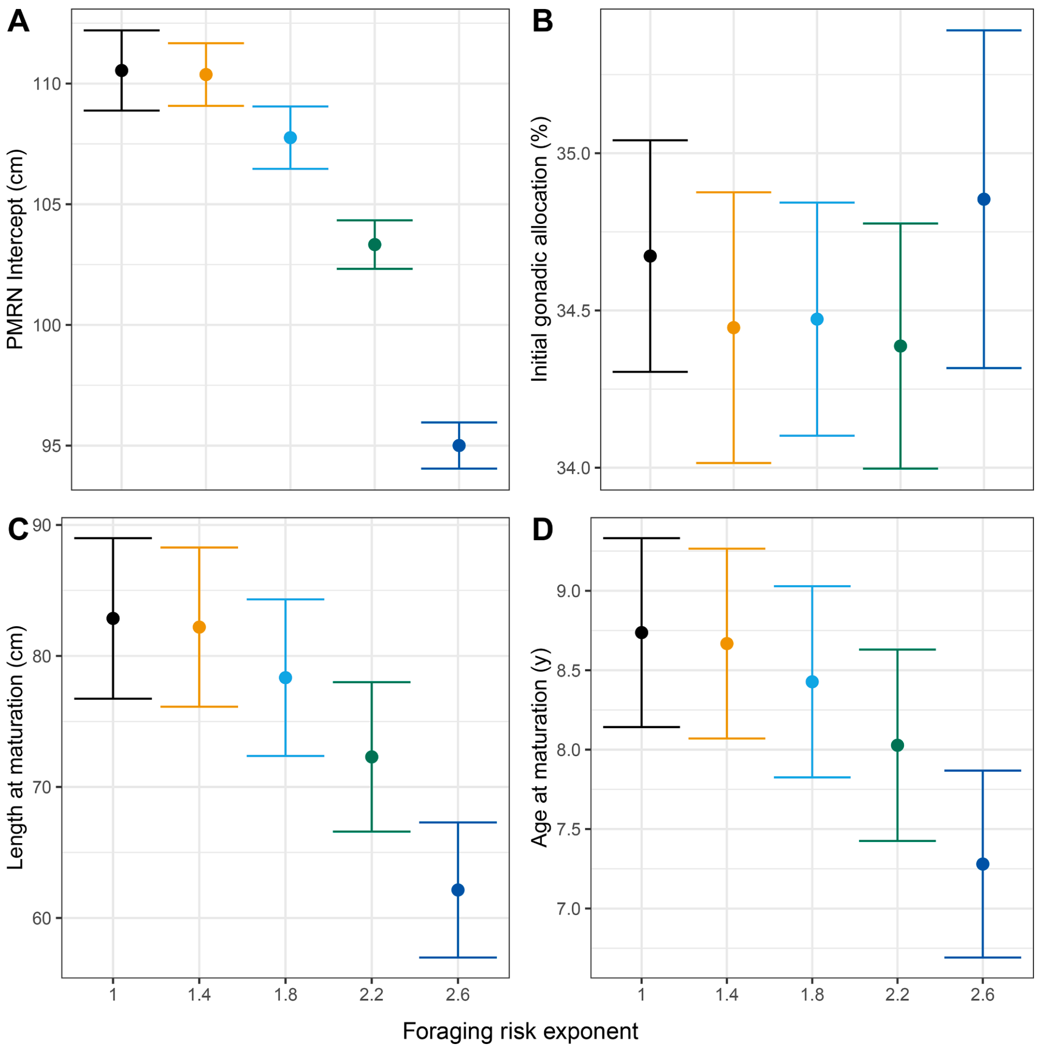

Fig. 6. Changes in maturation schedule in response to varying foraging risk. Values shown are all stabilised averages at the end of the 20 model runs. (A) Average PMRN intercept ±SD. (B) Average genetic initial gonadic allocation ±SD. (C) Average length at maturation ±SE. (D) Average age at maturation ±SE. Time trajectories of changes in these traits are shown in Appendix B.

pronounced for higher risks. However, while the overall trend is similar, the variability of length and age at maturation is notably higher than for the PMRN intercept, implying that other processes also influence the maturation schedule. This can happen because the PMRN intercept is directly inherited, while the emergent traits (such as length/age at maturation) result from more processes and traits also involving stochasticity. This is the case for e.g. age-at-maturation, which is not directly controlled by the PMRN intercept but is also influenced by appetite that controls energy acquisition, which drives growth and in turn, maturation.

4. Discussion

We found that with increasing foraging risk, evolution selected for lower appetite and earlier maturation, both leading to lower growth. This is expected, as higher mortality associated with energy acquisition should select for individuals with lower appetite, which forage less. Further, the fitness benefit associated with late maturation is offset by lower overall survival due to higher foraging risk, causing a selection towards earlier maturation.

While it seems intuitive that an increase in foraging risk and a decrease in energy intake would lead to reduced growth and higher mortality, respectively, these points still warrant further consideration. Since we are not enforcing a lower limit for appetite, the fish can theoretically maintain lower mortalities even in high-risk scenarios by foraging less and accepting slower growth. Similarly, they could have accepted higher mortality risks to maintain growth, but it seems that the optimal strategy is a combination of the two.

These results highlight a critical life-history trade-off related to optimal foraging behaviour. Given that overall mortality is higher for smaller individuals, a selection towards fast growth early in life (McGurk, 1986; Shepherd and Cushing, 1980; Ware, 1975) motivates foraging. However, foraging is a risky activity, so high foraging effort will lead to higher mortality risk - this dissuades foraging (Stephens, 2008). This is further complicated by larger individuals having higher relative fecundity (Hixon et al., 2014; Morita et al., 1999), further motivating foraging. However, fisheries may nullify this factor by targeting larger individuals (Jørgensen et al., 2009).

A similar trade-off has been considered by Claireaux et al. (2018), who used a dynamic optimization to simulate evolutionary endpoints when fisheries target certain behaviours on the bold/shy spectrum. They found that any increase in fishing mortality, even unselective, caused evolution towards reduced growth and age/length-at-maturity. However, when explicitly targeting bold/hungry individuals, the selection became stronger, and also selected for reduced foraging effort.

This is an interesting comparison to our study. While the sources of mortality (predators vs fisheries) and the modelling framework (IBM vs dynamic optimization) differ, the experiments are quite analogous - increasing mortality disproportionately for foraging individuals. In both studies, this leads to lower foraging rates and a faster pace of life. As such, our study expands on Claireaux et al. (2018) by using an IBM to simulate actual life histories and by showing that this sensitivity to foraging risk is not limited to fisheries but is fundamental to optimal foraging theory.

It is a commonly found trend that higher mortality leads to earlier maturation (e.g., Heino et al., 2002a; Law, 2000, 2007; Jørgensen et al., 2009; Claireaux et al., 2018; Andersen et al., 2018). When life expectancy is reduced, the associated benefits of large body size and late maturation diminish (Heino et al., 2015). This aligns with our findings that high-risk scenarios and increased mortality select for earlier maturation life histories.

Adaptation to an increase in external mortality, like fishing mortality, has been shown to lead to increased natural mortality (Jørgensen and Fiksen 2010; Jørgensen and Holt 2013), and even though in our study, the increase in natural mortality is due to adaptation to higher foraging risk, which could be caused by for example increased predator population, the bottom line is that while a population is adapting to increased external mortality, it can lead to an increase in total natural mortality rates.

Our results (along with those of Claireaux et al., 2018) highlight the need to consider the coupling between energy acquisition and mortality. It becomes clear that when mortality is coupled with foraging, attempts to decrease mortality risk associated with being small comes at the cost of increased mortality risk from foraging. Other studies have found that increased selection pressure for small or intermediate sizes (e.g., gillnet fishing) can favour later maturation since late-maturing fish will more quickly grow out of the vulnerable size range (Huse, 2000; Jørgensen et al., 2009; Stepputtis et al., 2016). This trend, however, is only found at moderate fishing pressure, allowing fish to grow past the vulnerable size range.

In the past couple of decades, fisheries selection for behavioural patterns has been getting more attention, as different gear types have been shown to select for bold/shy behaviour (Cooke et al., 2007; Uusi-Heikkilä et al., 2008; Biro and Stamps, 2008; Diaz Pauli and Sih, 2017; Arlinghaus et al., 2017; Claireaux et al., 2018). As such, changes in behavioural patterns and the effects they have on life history evolution are becoming known. Our results further build on this by showing that the evolution of behaviour (e.g., foraging activity) is not limited to direct anthropogenic stressors such as fisheries but can also result from other changes to the ecosystem. For instance, foraging risk might change due to new species altering community structure, or changes in the physical environment that either reduce opportunities for seeking shelter or make foraging more time-consuming. Knowledge of what behavioural phenotype is favoured by natural selection would allow managers to make better-informed decisions about which gears to use.

The current model is an amalgamation of two earlier models: an eco-evolutionary individual-based model with rich population dynamics including density dependence, several evolving life history traits, but no explicitly physiological relationship climate (Enberg et al., 2009), and an optimization model with detailed physiological mechanisms including oxygen budget (Holt and Jørgensen 2014). Even though not fully taken advantage of in the current study, this model is a powerful tool for modelling the concurrent contemporary evolution and eco-evolutionary dynamics of the NEA cod in relation to fishing and climate warming. Future studies should include investigations of the relative importance of these anthropogenic drivers and which harvest strategies might be most suitable and least harmful for the long-term sustainability of the fished population.

In summary, this study shows that increasing foraging risk leads to a decrease in appetite, foraging activity and energy acquisition. These changes in turn, lead to an increase in mortality and subsequent selection for faster life histories. This builds on previous studies showing that foraging behaviour is subject to evolution in response to stressors and expands the field by demonstrating that even without direct anthropogenic influence (such as fisheries), ecological factors may select for bold or shy foraging strategies. For fisheries and their managers, this avenue of potential evolution should be addressed, as knowing which behavioural phenotype is most favoured locally allow for more informed decision-making.

CRediT authorship contribution statement

Henrik H. Jessen: Methodology, Software, Formal analysis, Writing – original draft, Writing – review & editing, Conceptualization. **Anders F. Opdal:** Conceptualization, Methodology, Writing – review & editing. **Katja Enberg:** Conceptualization, Methodology, Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Initial population equilibrium

Fig. A1.

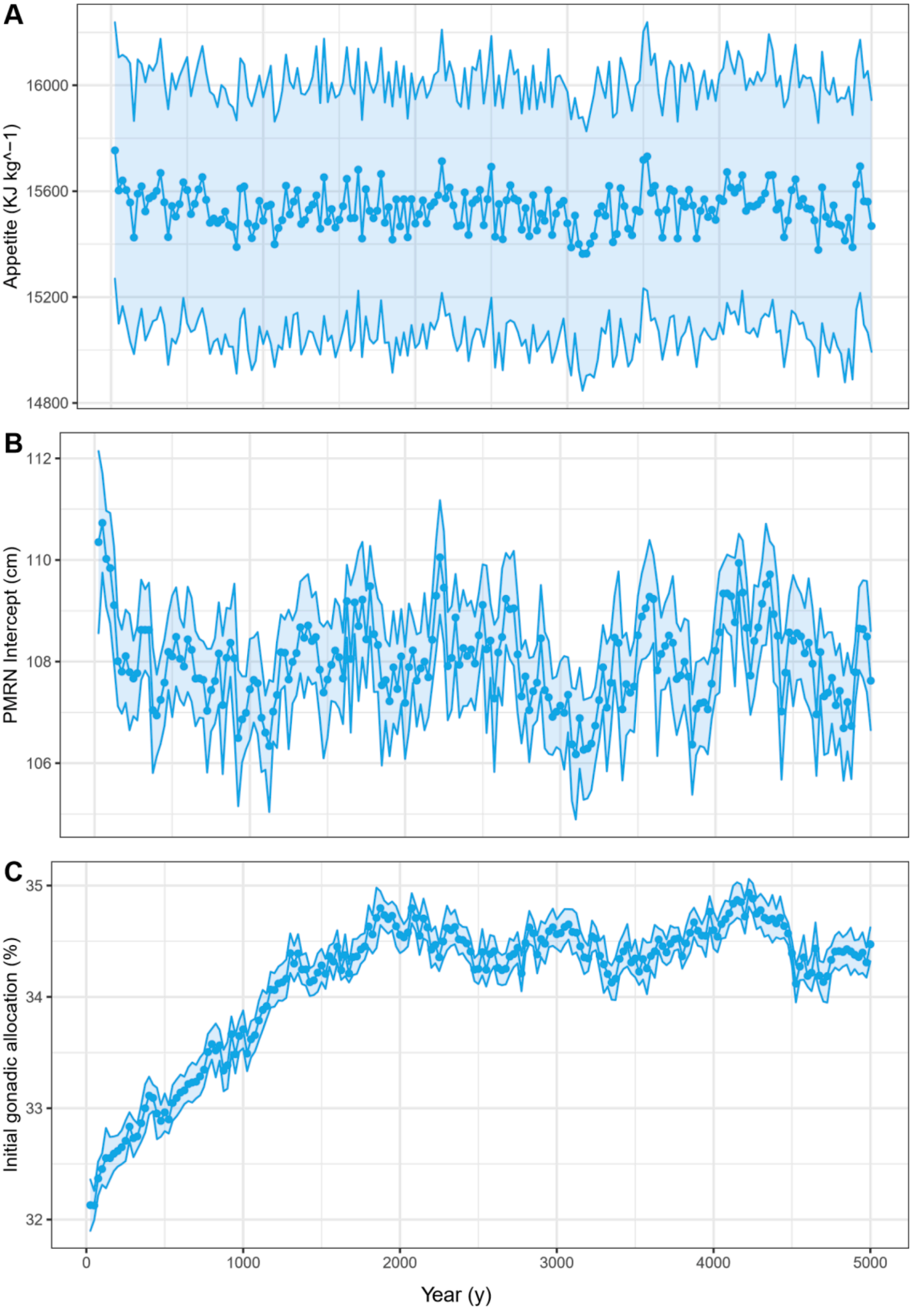

Fig. A1. Average values ±SD for evolving traits over the years of running the initial population to equilibrium prior to actual model runs.

Appendix B. Maturation schedule evolution

Fig. B1.

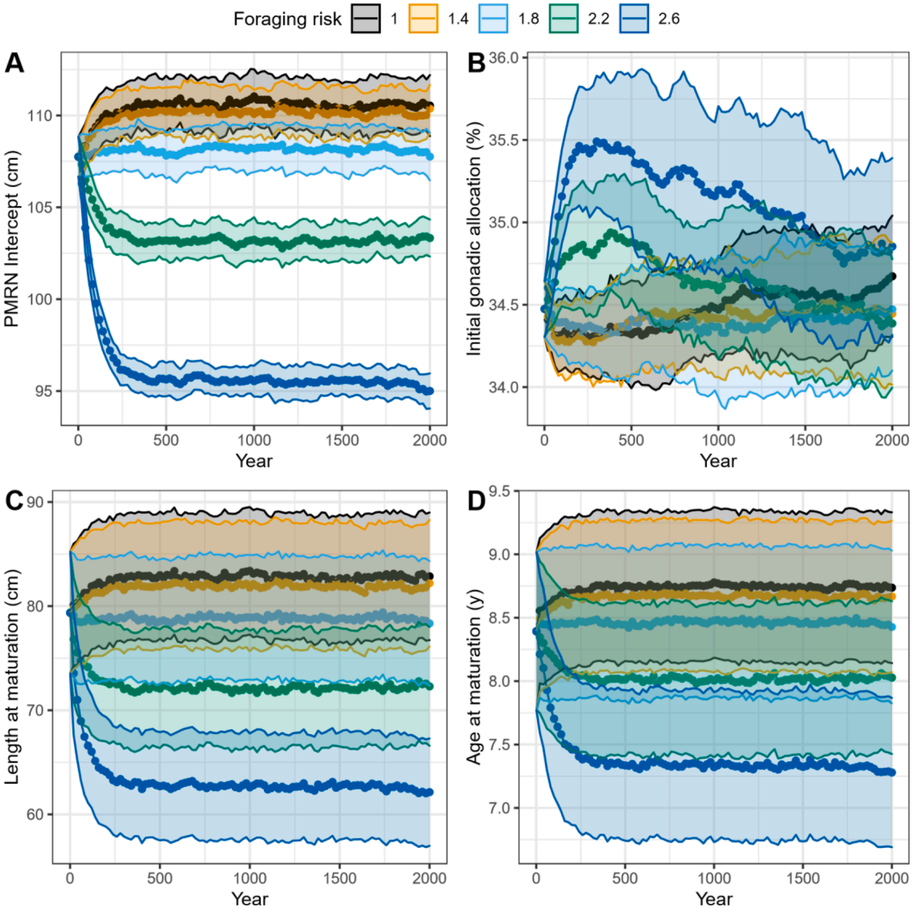

Fig. B1. Changes in maturation schedule over the years of running the model. All plots show averages of the 20 runs for each value of *e*2. (A) Average PMRN intercept ±SD. (B) Average initial gonadic allocation ±SD. (C) Average length at maturation ±SE. (D) Average age at maturation ±SE. Values in final year (2000) corresponds to Fig. 6.

Appendix C. Population demography

Fig. C1.

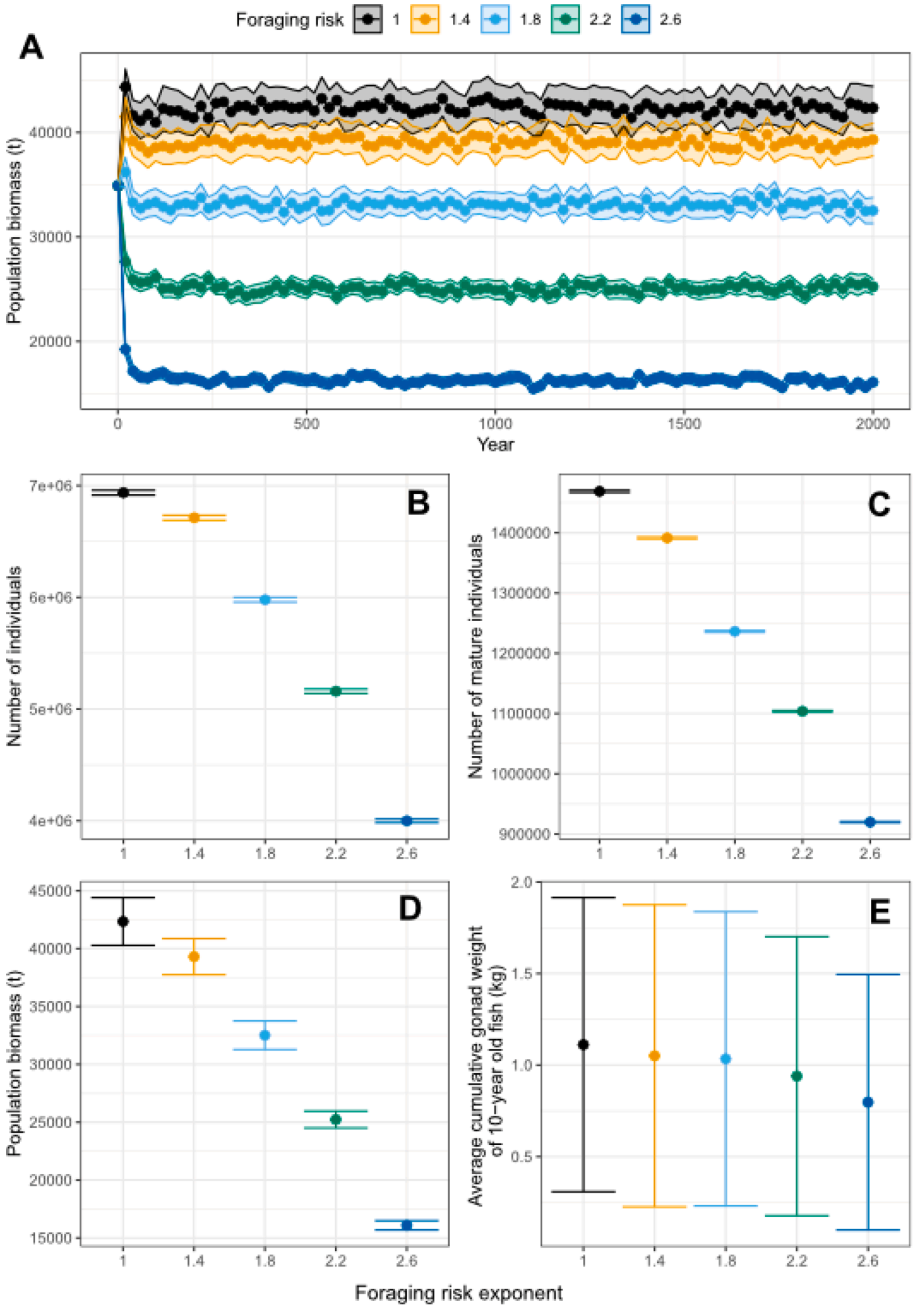

Fig. C1. Population demographic responses to varying foraging risk. (A) Change in population biomass ±SD throughout the model's runtime. Plots B – E show mean values ±SD at the end of the 2000-year runtime. (B) Total number of individuals. (C) Total number of mature individuals. (C) Population biomass. (D) Average cumulative gonad weight of a 10-year-old fish.

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Paper 2: Increasing temperatures counteract the evolutionary consequences of fishing in model of Northeast Arctic Cod (*Gadus morhua*)

Paper 3: Warming climate impacts optimal fisheries strategy in model for Northeast arctic cod (*Gadus morhua*)

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