Climate-Induced Evolution of the Behaviour and Life-History Strategies of Atlantic Cod (*Gadus morhua*)

A Modelling Approach

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Summary

Climate change influences the marine environment, with ocean warming being the foremost driving factor governing changes in the physiology and ecology of fish. At the individual level temperature can directly influence numerous physiology processes in marine fish as well as bioenergetics, having consequences for life-history processes and population level consequences. A primary mechanism through which temperature can affect fish is through respiratory physiology as it has consequences for performance and fitness. The difference between maximum metabolic rate and standard metabolic rate is referred to as aerobic scope, and is suggested to constitute a key limiting process prescribing how fish may cope with or adapt to climate warming.

Field data and experiments have demonstrated an array of effects and influences of temperature on Atlantic cod and other marine fish species. This PhD research explores how temperature can influence the life-history and behaviour of Atlantic cod through a theoretical modelling approach. A state-dependent energy allocation model was developed to predict temperature-induced adaptations for the life-histories and behaviour of Atlantic cod, in response to climate warming. The model was parameterised primarily for the North-East Arctic cod stock and then extended to facilitate parametrisation of a further 19 stocks, enabling intra-specific stock comparisons across the North-Atlantic. The model is based on life-history theory, which addresses how an individual should schedule its life to maximise its expected lifetime reproductive output. Energy allocation and investment into growth, maturation and reproduction depends on a number of physiological and ecological factors, such as respiratory physiology and aerobic scope, constraints on body size, environmental variability in prey availability, spawning migration distance, and mortality. These constraints and mechanisms are well justified to the physiology and ecology of the species. By using state-dependent dynamic programming techniques, a model can find optimal energy allocation between growth and reproduction at the individual level as well as simulate lifetime trajectories in a population model under the external driver of increasing temperature. The model predictions provide a number

of results important for conservation physiology and fisheries management of Atlantic cod and marine fish species more generally.

Firstly the model shows that when predicting the effects of climate change on fish, one should view the species physiology and ecology as a whole, being aware that organisms possess a suite of traits that have co-evolved. Some methods within the literature for predicting the effects of climate warming can be one-sided, focussing on purely physiological or ecological responses, omitting evolutionary considerations. The effects of climate warming on fish are complex, thus an integrated whole organism approach is needed.

Secondly, we find for the North-East Arctic cod stock, the effects of climate warming are positive. Increased temperatures were predicted to select for faster life-history strategies, increasing growth rates, larger size-at-age and higher reproductive output.

Thirdly, our model fills in the gap between respiratory physiology as described by the Oxygen- and capacity-limited-thermal tolerance theory (OCLTT) and how it may influence fitness. We find that optimal temperatures for growth and fitness lie well below that for aerobic scope; and agree in accordance with a recent literature debate, that aerobic scope is a poor predictor of fitness at high temperatures. This has implications for climate change effects, conservation physiology, and the OCLTT theory.

Fourthly, we have identified key mechanisms and potential drivers pertaining to the life-history variation across 20 cod stocks in the North-Atlantic. We find that the drivers of intra-specific variation in Atlantic cod could be explained by differences in temperature, seasonality and spawning migration distance between the stocks. Furthermore, when predicting the effects of climate warming on these stocks, the model illustrates how climate warming may influence the life-history strategies of cod in diverse ways. We find that cold-water stocks may fare better and be more resilient under increasing temperature scenarios than their warm-water counterparts.

Lastly this PhD research provides a unique life-history modelling tool that can be adapted and extended. Due to the mechanistic modelling framework, the model could be adapted to other marine teleosts, particularly other boreal or temperate

species. As we include an explicit respiratory physiology component, it also allows flexibility to include additional drivers, such as the effects of hypoxia on increased respiratory costs as well as the effects of fishing mortality. The integrating effects of multiple drivers are already prominent in the current literature and our mechanistic model could take this further to assess effects on life-history traits.

List of publications

PAPER I

Holt, R.E and Jørgensen, C. (2014)
Climate warming causes life-history evolution in a model for Atlantic cod (*Gadus morhua*)
Conservation Physiology. 2: cou050

PAPER II

Holt, R.E and Jørgensen, C. (2015)
Climate change in fish: effects of respiratory constraints on optimal life history and behaviour
Biology Letters. 11: 20141032

PAPER III

Holt, R.E and Jørgensen, C. (Submitted)
Temperature and respiratory physiology drives local adaptation in a life history model for Atlantic cod (*Gadus morhua*)
Submitted to *Canadian Journal of Fisheries and Aquatic Sciences*.

PAPER IV

Holt, R.E and Jørgensen, C.
Stock-specific impacts of climate change on Atlantic cod (*Gadus morhua*) within a life history model
Manuscript

Contents

1. Climate Change

Marine organisms are under pressure from several natural and anthropogenic stressors such as climate change, ocean acidification, species introductions, pollution, exploitation, pathogens and disease as well as intensive aquaculture practices. Among these, climate change has an uncontested influence on the marine environment, and is considered one of the principal threats to biodiversity and the functioning of marine ecosystems (Graham and Harrod, 2009). The effects of climate change can influence water temperature, sea level rise, pH, stratification of water systems (Brander, 2007), dissolved oxygen concentrations and expansion and intensification of hypoxic zones (Doney *et al*., 2012), storm intensity and frequency as well as changes in ocean circulation patterns (Graham and Harrod, 2009). Other consequences pertain to changes in ocean productivity and the structure and composition of the ecosystems themselves.

The effect of climate change will affect marine fish stocks at all levels of biological organisation: cellular, individual, population, species, community and ecosystem, influencing physiological and ecological processes in a number of direct, indirect and complex ways. Direct effects of climate change on marine fish can act on physiology and behaviour as well as alter growth, development, reproductive capacity, distribution and mortality. There is already evidence for example, of rapid poleward shifts in distribution and biogeographic ranges of fish species in regions such as the North-East Atlantic (Perry *et al*., 2005; Brander, 2007; Burrows *et al*., 2011; Cheung *et al*., 2015). Further changes in distribution and productivity are expected due to continuing warming and increased fresh water input within the Arctic (Brander, 2007). Changes are also expected to occur within fish production, some effects like increased growth rates are suggested to be positive but in other cases reproductive capacity may be reduced, making them vulnerable to levels of fishing that were previously thought sustainable (Brander and Mohr, 2004); further confounding the problem.

Indirect effects of climate change on the marine environment can pertain to biological interactions, such as changes in predation, competition and parasitism.

Predation and competition may constrain, or in some cases expand the spread of competitors, imposing on the realized niche of other species (Bruno *et al*., 2003). Changes in predation and competition can therefore alter the composition and function of marine communities. Furthermore these changes can cause trophic cascades within an ecosystem. In polar marine regions, the reduction of sea ice extent and seawater warming has impacted upon predator-prey interactions. A recent study by Kjesbu *et al*. (2014) states how increasing amounts of warm Atlantic waters have increased temperatures within the Barents Sea importing with it, zooplankton, benefiting juvenile cod in the area. Furthermore, numerous disease outbreaks, especially in marine organisms have been associated with temperature increase, for example red-sore disease in large-mouth bass (*Micropterus salmoides*) and blackspot disease in coho salmon (*Oncorhynchus* spp.; Marcogilese, 2008). Transmission rates of parasites and pathogens in general are expected to increase with increasing temperature (Marcogilese, 2008), with disease emergence linked directly to changes in the ecology of hosts or pathogens, or both.
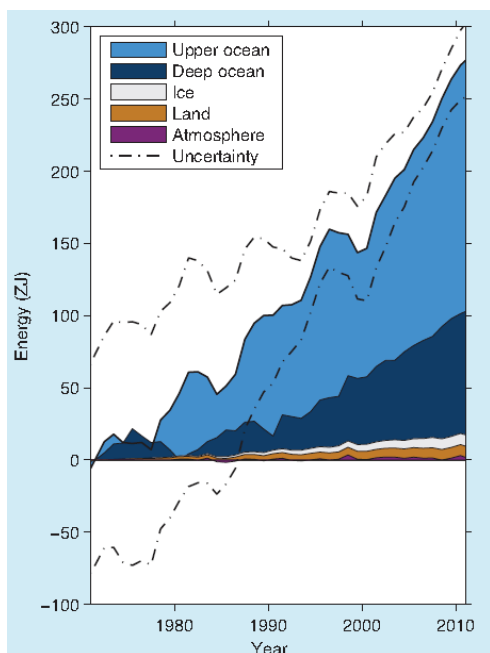
Figure 1. Plot of energy accumulation in ZJ (1 ZJ = 1021 J) within distinct components of the Earth's climate system relative to 1971 and from 1971 to 2010 unless otherwise indicated. Ocean warming (heat content change) dominates, with the upper ocean (light blue, above 700 m) contributing more than the mid-depth and deep ocean (dark blue, below 700 m; including below 2000 m estimates starting from 1992). Figure reproduced from IPCC (2013).

1.1 Temperature

Despite the many effects of climate change described above, temperature is considered the most important driver influencing the physiology and ecology of fish, and because of the pervasive effect on marine fish species, it is important in all ocean regions (Rjinsdorp *et al.,* 2009).

Many marine fish are ectotherms or thermal conformers, whereby their internal temperature is governed by the surrounding water; as such even small changes in temperature can directly influence biochemical rates and enzyme kinetics (Hochachka and Somero, 2001; Pörtner, 2001, 2010). Studies have documented that, climatic warming is causing changes in fish distribution, with species shifting northwards, changing their biogeographical ranges (Perry *et al*., 2005; Burrows *et al*., 2011; Cheung *et al*., 2015). Sprat, anchovy and horse mackerel have increased their range at the northern distribution of their range, whereas species such as cod and plaice have decreased at their southern limit and increased at their northern range (Rijnsdorp *et al*., 2009). Temperature increases have also been attributed to changes in phenology (Wiltshire and Manly, 2005), in particular migration phenology. Many pelagic species for example have exhibited clear changes in migration patterns related to climate-induced shifts in zooplankton productivity (Rijnsdorp *et al*., 2009), causing changes in arrival time of adults at the spawning grounds (Sims *et al*., 2004). The effect on fish production has been positive for cold-water fish species (Arctic Council, 2005; Kjesbu *et al*., 2014), as a result of warming and decreased sea-ice cover, but the opposite may be true for warm water regions due to shifting prey distribution, reduced vertical mixing in the water column and therefore reduced recycling of nutrients (Brander, 2007). These studies tend to focus on populations, communities and ecosystems. However, biological responses to climate warming will be ultimately driven by individual-level responses, such as physiology and behaviour and their effects on growth, survival and reproduction (Rijnsdorp *et al*., 2009; Jørgensen and Holt, 2013; Holt and Jørgensen, 2014).

Temperature can also directly affect metabolism within fish. If temperatures decrease, metabolic processes slow down and maximum food intake will decrease, regardless of prey availability (Michalsen *et al*., 1998). However, average global

temperatures have increased by ca. 0.6°C over the past century, warming both freshwater and marine environments. As a result, individual metabolism and energy demands increase, which can have consequences for energy allocation and bioenergetics, growth, reproduction, life-history considerations and population level responses. Besides food availability, temperature is the single most important factor governing fish growth rates (Fry, 1971; Brett, 1979). Fish activity is also strongly linked with temperature (Neuman *et al*., 1996), which can influence foraging behaviour and efficiency as well as escapement swimming behaviours (Webb, 1978; Johnson *et al*., 1993; Domenici and Blake, 1997). Time to completion of a fast start response in trout for example decreased with increasing temperature (Webb, 1978). An increase in temperature as well as an increase in juvenile growth rate may result in a decrease in the length and/or age of first maturation (Heino *et al*., 2002; Rijnsdorp *et al*., 2009) as well as reproductive success. If temperature conditions reach extreme values, mortality can result and is suggested to be high in some fish species (Rijnsdorp *et al*., 2009). Furthermore, changes in water temperature may cause changes in prey availability as well as interspecific interactions such as predation risk and competition; affecting the population and community levels of ecosystem structure.

2. Aerobic Scope

A primary mechanism through which temperature change is expected to affect marine fish is through respiratory physiology, because it has consequences for bioenergetics and for performance (Priede, 1985). Compared with air, breathing is energetically costly for marine fish, and individuals face the continual challenge of extracting water from their environment (Verberk *et al*., 2011). Water contains 300 times less oxygen and the diffusion rate is $3x10^5$ times lower than in air (Verberk *et al*., 2011). As temperatures increase the oxygen content of water decreases while metabolic costs rise. This dual challenge is particularly problematic as most of the heat associated with climate warming is taken up and stored within the world's oceans (IPCC, 2013; Figure 1).

Fry (1971) proposed how different environmental factors such as temperature can load metabolic costs and affect the metabolic scope of an organism. These ideas have since been built upon by Pörtner (2010) and his theory of Oxygen-and-capacity-limited thermal tolerance (OCLTT; Pörtner, 2010). The OCLTT theory is prominent in the biological literature describing how maximum oxygen uptake constrains overall metabolism in marine organisms, and how this varies in response to stressors such as temperature and hypoxia (Pörtner, 2010, 2012; for a terrestrial parallel please see Porter, (1973).
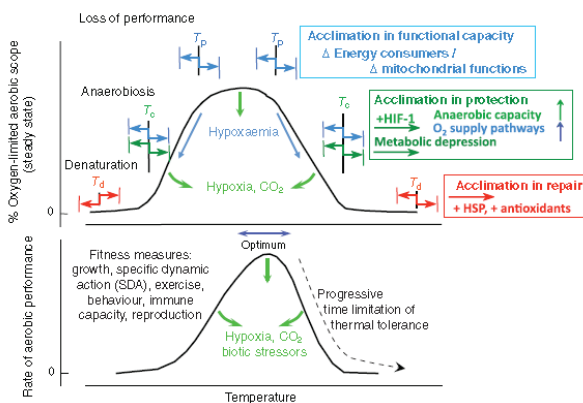

Figure 2. Conceptual model of oxygen- and capacity-limited thermal tolerance and the resulting thermal window of performance of a species, of one of its life stages or its population. Figure reproduced from Pörtner (2010).

Standard (resting) metabolic rate (SMR) represents the basic cost of existence, the minimum metabolic rate needed for an individual to survive. SMR increases

exponentially with increasing temperature (Pörtner, 2010). Maximum oxygen uptake is the ability of an individual to uptake oxygen from its environment. Maximum oxygen uptake also increases with temperature, and may reach an asymptote beyond which uptake declines. Aerobic scope is defined as the difference between maximum oxygen uptake and SMR, and all the activities that the organism needs to achieve must fit within this aerobic scope budget (Priede, 1985). The OCLTT theory assumes that an organisms' aerobic scope is directly proportional to performance and fitness, i.e. the temperature that maximises aerobic scope is also the temperature that will maximise fitness and performance; suggesting that aerobic scope is a central constraint that governs the performance and fitness of marine fish. These ideas have been challenged, and the suitability of the OCLTT theory in terms of its use in predictions of the effects of climate change on marine fish has come under scrutiny (Clark *et al*., 2013; Norin *et al*., 2014). It has been found for several species that aerobic scope increases continually up until lethal limits, suggesting that aerobic scope is not the central constraint on performance (Clark *et al*., 2013; Norin *et al*., 2014).

Often, respiratory physiology as described above is thought of on a short-term equilibrium basis, within experimental studies and/or in terms of immediate behavioural responses such as fast-start responses or burst swimming under the threat of predation. However, if organisms are to maintain energy balance in the longer term they also need to forage and digest, which incur additional oxygen demand beyond SMR, and can be thought of as overhead costs. The overhead costs of foraging and digestion also increase with temperature, taking up a great proportion of the free aerobic scope left for key processes such as growth and reproduction. If locomotion, digestion and growth were all running at a maximum rate, the oxygen requirement would greatly exceed aerobic scope (Priede, 1985). An organism's aerobic scope is finite, therefore some prioritisation or aerobic scope budgeting must take place (Killen *et al*., 2007), which can result in trade-offs mediated by oxygen availability having consequences for energy allocation and bioenergetics as well as life-history considerations and population-level responses.

3. Bioenergetics

The effect of temperature on marine fish respiratory physiology as described above has consequences for bioenergetics and performance. Respiratory physiological responses to increased temperature determine the proportion of how much energy must be used to support basal and active metabolism rather than be allocated to somatic growth and reproduction.

One bioenergetics framework or modelling approach is the metabolic theory of ecology (MTE; Brown *et al.*, 2004); which was developed to link the metabolic rate of an organism to its body mass and temperature, claiming universality across and within species (Brown *et al.*, 2004). It is reliant upon allometric scaling relationships and is designed to be general but does not easily allow for incorporation of species-specific parameters or relationships. Another approach is dynamic energy budgets (DEB; Kooijman, 2010). This approach does allow for incorporation of species-specific detail, but contains several assumptions that constrain the type of output a model can produce. For example, DEB assumes that allocation to reproduction happens over the entire lifetime, which may be the case for some organisms but not when studying a long-lived fish species like cod. (MTE, DEB and its assumptions are discussed in more detail in the model comparison section of this synthesis).

The framework we use in this thesis is based on a mechanistic modelling approach developed for Atlantic cod (Jørgensen and Fiksen, 2006), which is based upon the Wisconsin bioenergetics model (Hewett & Johnson, 1992). The Wisconsin bioenergetics model uses allometric scaling relationships as in MTE but allows for species-specificity as well as flexibility in the model design, which was needed in our approach to study evolution of maturation and reproduction as flexible traits that emerge from evolutionary optimisation. The next sections will review life history evolution, cod, existing modelling approaches for predicting climate change effects, and the potential for temperature-induced evolution in this species.

4. Life-History Theory

Life-history theory addresses the three most important areas of an organism's existence, survival, growth and reproduction (Stearns, 1992, Roff, 2002). There may be trade-offs among these that may be at work simultaneously across several dimensions. However, reproduction is the only facet of life-history theory that contributes to an organism's fitness. Reproduction and growth are inter-linked; growth can increase future reproduction at the cost of current reproduction. There are also tight links between reproduction and survival; an individual must survive until reproductive age, and reproduction itself is associated with mortality risk. There are several trade-offs associated with growth and survival, foraging behaviour and the threat the predation risk. Changing the allocation of time and energy between these compartments throughout a lifetime has interlinked consequences for fitness. The premise of natural selection and life-history theory is to maximise expected future reproduction, achieved through these trade-offs and selected life-history strategies.

4.1 Temperature causes evolution

Changes in temperature can have consequences for the life-history strategies and population level responses of fish. Observed phenotypic changes in the timing of migration and reproduction, age at maturity, age at juvenile migration, growth, survival and fecundity have been primarily attributed to changes in temperature in the marine environment (Rijnsdorp *et al*., 2009).

Higher mortality rates observed through fisheries exploitation for example can vary the scheduling of growth and maturation events in fish. To ensure survival at reproductive age, individuals should employ a faster life-history strategy, maturing earlier and at a smaller size. The same has been suggested for the effects of temperature (Crozier and Hutchings, 2014). Increasing temperature from resultant climate change can too cause higher rates of mortality; which may select for a faster life-history strategy for fish populations. Variations in the scheduling of growth and maturation events of the life-history strategy may therefore be employed. It has been suggested that evolutionary change arising from climate warming can be rapid in a

number of taxa, including marine teleosts (Hoffman and Sgrò, 2011). The effects can be both negative and positive and potentially enable species to counter stressful conditions and establish new ecological opportunities. The challenges are to understand when evolution will occur, as well as the underlying mechanisms and to identify potential evolutionary winners and losers; for example to identify those species which may lack resilience and adaptive capacity to climate warming (Hoffman and Sgrò, 2011).

4.2 Disentangling phenotypic plasticity and evolution

Fish geneticists, population biologists, ecologists and evolutionary biologists have made considerable advances in our knowledge of adaptation, selection responses as well as the rates of evolutionary change in fishes (Crozier & Hutchings, 2014). However, the complex mechanisms of phenotypic plasticity and evolution involved in climate-sensitive traits present a challenge for detecting adaptation to climate change in natural populations. Longitudinal studies of single populations can help determine whether traits have evolved or instead have occurred through plasticity (Hoffman and Sgrò, 2011). Common garden experiments have been carried out along environmental gradients, providing evidence for genetic adaptation to climatic conditions in space (Hoffman and Sgrò, 2011). Furthermore, reaction norm analyses are invaluable in the challenge of disentangling plastic versus genetic change; this method has been used within fisheries-induced evolution studies (Heino *et al*., 2002; Hutchings *et al*., 2007). Reaction norm estimations are critical for calibrating age and size structured population models as well as for understanding phenotypic plasticity and life-history changes in the presence of phenotypic plasticity. Quantitative genetic models have also been used to disentangle genetic effects of anthropogenic drivers (Enberg *et al*., 2010). As well as modelling techniques, experimental studies have contributed substantially to investigating temperature induced life-history evolution in fish.

4.3 Experimental temperature induced life-history evolution in fish

Work on fisheries-induced evolution generated numerous ways to evaluate the magnitude and likelihood that this anthropogenic driver would result in evolutionary change (Please see reviews by Dieckmann & Heino, 2007; Hutchings and Fraser, 2008). Methods such as reaction norm analyses, common garden experiments, literature on selection responses, trait heritability and genetic differentiation has enabled considerable advances in our knowledge of adaptation, selection, and rates of evolutionary change. A common garden experiment on Norwegian grayling (*Thymallus thymallus*) provides evidence that genetic changes in phenotypic, plastic responses to temperature can become adaptive (Haugen and Vøllestad, 2000). Populations of this species were reproductively isolated in freshwater lakes under different temperature conditions for 15 generations (Haugen and Vøllestad, 2000). Populations in colder environments developed a cold-adapted reaction norm for growth, exhibiting enhanced growth compared with populations in warmer environments. It is suggested that this observed response provides evidence for selection rather than genetic drift, and that these patterns correlated with temperature rather than physical distance (Haugen and Vøllestad, 2000).

Counter-gradient variation is prevalent in marine systems; it occurs when genetic differences counteract environmental effects, reducing phenotypic variation between populations and is expected when stabilising selection favours similar phenotypes in different environments (Conover and Schultz, 1995; Crozier and Hutchings, 2014). In fish, counter-current variation reflects adaptation to thermal environments, it has been found in Atlantic silversides, *Menidia menidia* (Conover and Present, 1990) and Atlantic cod (Marcil *et al*., 2006). Experiments have also looked at plastic responses to environmental stressors such as temperature, typically exposing individuals to a common rearing environment, controlling for acclimation responses (Johansen and Jones, 2011).

5. A role for modelling

The experimental field is sometimes limited in the study of the effects of climate warming on the life-history and behaviour of marine fish. One obvious way to try and assist with this problem is to use mathematical modelling. A modelled environment can be controlled to such a degree that one can ask and study large-scale complex questions in isolation of other potential causal mechanisms. To this end, mathematical models can be thought of as theoretical experiments that would not be otherwise possible in the lab or field. This is the approach used within this PhD research, which uses life-history theory and energy allocation to explore the effects of increased temperature on the life-history and behaviour of Atlantic cod alone. By using mathematical modelling to focus on one driver, one can explore the effects of climate-induced warming in isolation without confounding influences of hypoxia or fishing for example. The predictions from such a modelling technique will hopefully shed light on the effects of temperature within the complex real world setting. The model is of course a simplification of the complexity found in nature, but has a strong physiological and mechanistic basis. This ensures that constraints, which are very important for the evolutionary optimisation and life-history outcomes, are not introduced via convenient assumptions but based upon real species biology and ecology. In order to facilitate this type of modelling approach, one needs a flexible programming technique, which is detailed in the subsequent section.

5. State-Dependent Dynamic Programming

To design and build a model that sheds light on complex research questions such as those pertaining to climatic warming on marine fish is a balancing act. On the one hand, it is imperative to be as biologically and ecologically realistic as possible, including the processes that are necessary to understand the phenomena in question, while excluding additional complexity, as this can confound interpretation of the models predictions. State-dependent dynamic programming (Houston and McNamara, 1999; Clark and Mangel, 2000) is appropriate to use in this case as it enables a flexible construction to model design. This technique uses a backwards iterating algorithm through an individual's life-history starting at the maximum age, assuming that the individual acts optimally at every decision point in its future life. This modelling technique is particularly useful as it enables separation between the information available to the individual, i.e. the states, and other factors within the model such a foraging and temperature that may affect its success. Dynamic programming then finds the "best" or optimal response over several possible outcomes based on your optimisation criterion; which in this case is to maximise expected lifetime reproduction but could well be something like size. Emergent life-history strategies then result through evolutionary optimisation and these individual strategies can be simulated in a population. The optimal life-history strategy found by the backwards iteration is then simulated forward. This allows for visualisation of the individual and population characteristics emerging from the interaction between the life-history strategy and the environment.

The core idea behind the model within this PhD research is what combination of behaviour and energy allocation to growth and reproduction is optimal, depending on the individuals' states (age and length), and external factors of migration distance, food availability and external driver of temperature (climate variable).

6. Model Comparisons – Alternative Modelling Techniques

Predictions for the effects of climate warming on marine fishes, such as cod use a variety of different methods that range from statistical to mechanistic, from simple to complex, and from high-resolution oceanography to ignoring physics but with detailed biology. Each of the approaches has their own strengths and caveats.

A first and simple assumption is that species remain constant and when the environment changes they will move along with it. Species distribution models or bio-climate envelope models use a statistical approach to project distribution shifts under climate warming (Perry *et al*., 2005; Grebmeier *et al*., 2006; Bond *et al*., 2011; Jones *et al*., 2013). In the simplest versions, these models use presence-absence data in relation to temperature only to project changing distributions as function of climate change (Jones *et al*., 2013). Maxent and Aquamaps, for example, further estimate environmental co-variates conditioning species' presence, such as bathymetry, substrate, salinity etc. (Jones *et al*., 2013). These methods have for example been used to predict climate responses of several threatened and commercially important species around the U.K. (Jones *et al*., 2013). Being in principle statistical correlative modelling techniques, however, these methods fail to reveal a cause-and-effect understanding of the underlying mechanisms.

Just as the environment can be thought of as more complex, so too can the biology of a species. More complex statistical methodologies examine correlations between temperature and life-history traits such as growth and size-at-age (Pauly, 1980; Daufresne *et al*., 2009). Such studies may use a wealth of survey and experimental data together with e.g. meta-analyses or linear mixed-effects models to provide correlative, pattern-related predictions for geographical range shifts.

The use of classic models such as the von Bertalanffy growth model is also common in predicting the effects of climate change. For example, Baudron *et al*., (2011) test for a temperature effect on North Sea haddock (*Melanogrammus aeglefinus*) using the von Bertalanffy growth parameters to predict total length and mass-at-age responses to different temperature scenarios. Although this growth model

and similar alternatives are widely used, they are in principle phenomenological and not clearly tied to mechanisms (Roff, 1980; Day and Taylor, 1997; Czarnołęski and Kozłowski, 1998). As one growth trajectory can emerge from many different life-history strategies, it is a poor predictor for how performance of fitness may change in response to environmental change (Boukal *et al*., 2014).

In a similar vein, the metabolic theory of ecology (MTE) assumes that species biology is static and that temperature and mass drive the observed inter-species differences (Brown *et al*., 2004). Although a valuable null model (Harte, 2004), there is tremendous variation between and within species that MTE cannot account for and that likely covers up (Nee *et al*., 2005) important mechanisms (Cyr and Walker, 2004) through which species may be vulnerable or resilient to climate change. One avenue to seeing how MTE is too simple comes from high resolution oceanography models, where it becomes clear how species are intricately linked to their variable environments.

A relatively recent approach has been to predict changes in distribution and body size based on thermal preferences using more detailed bioclimate envelope modelling techniques in combination with life-history considerations (Cheung *et al*., 2009, 2012, 2015). These large scale population- or ecosystem-based studies statistically fit a species' thermal habitat based on observed presence-absence data, and then shift the species' distribution with the projected geographical displacement of the thermal habitat, incorporating a simple life-history model (Pauly, 2010) with explicit respiration mechanisms. With an ambitious scope, these models provide global predictions, but the mechanisms included in and the insights derived from our model suggest there might be more complexity in individual responses and a larger scope for adaptation and plasticity than they assume.

Individual-based models (IBM) focus on the individual mechanisms and rather let large-scale population or community effects emerge (Grimm and Railsback, 2012). Many IBMs incorporate physiology and estimate growth and survival using balanced bioenergetics and foraging potential (Grimm *et al*., 1996, 2005). A similar perspective, but more physiologically detailed, is taken by dynamic energy budget theory (DEB; Kooijman, 2010), which employs fundamental metabolic

considerations to allow for a range of different species from microbes to elephants to be studied. The use of DEB for predicting the effects of climate change is becoming more widespread within the literature (Teal *et al*., 2012; Kearney, 2013). Teal *et al*., (2012), for example, combined DEB models with temperature and food conditions as estimated by an ecosystem model to predict size-, season-, and area-specific growth potential of North Sea plaice (*Pleuronectes platessa*) and sole (*Solea solea*). Despite the generality of DEB, it incorporates several inflexible abstract assumptions, which may prevent predictions of ecological detail. Furthermore, DEB makes static assumptions that apply to all species, which may prevent evolutionary applications. Compared to DEB, our model allows allocation to be flexible and state-dependent whereas DEB assumes a fixed so-called kappa rule, we allow explicit foraging activity rather than being a constant within maintenance costs, and our mortality emerges from our model compared to DEB in which mortality is ignored.

Dynamic state-dependent modelling approaches have been used to study the effect of temperature on salmonid life-history strategies (Mangel, 1994) and steelhead trout (*Oncorhynchus mykiss*) (Satterthwaite *et al*., 2009). Dynamic state-variable approaches allow rich organism detail and inclusion of conditional strategies while using evolutionary methodologies to focus on adaptations to the environment. Our model follows the same framework and concepts, but is more explicit about physiological detail, in particular the oxygen budget component.

Our model belongs among the latter and more complex models mentioned above, where there is more emphasis on detailed biological mechanisms, local adaptation, and individual strategies that are optimal in given environments.

7.   Temperature and Cod

Atlantic cod (*Gadus morhua*) has a pan-Atlantic distribution and inhabits waters ranging from -2°C in Canadian waters to 12°C in the waters surrounding the British Isles. Their life-histories vary widely across their geographical range and are stock-specific, but in general this species is depicted as having a 'slow' life-history. Cod are long-lived; individuals can attain a large size, are late maturing and can perform extensive annual spawning migrations. Atlantic cod is also one of the most important commercial species in the North Atlantic, and has consequently been heavily exploited across its entire range and as such is sensitive to high mortality rates (Wiedmann *et al*., 2014). Atlantic cod was chosen as a focal species of my PhD research because it is one of the most studied species in the North Atlantic, our knowledge of its biology and life-history surpasses that of most other marine fish species to date (Drinkwater, 2005).

The influence of temperature on cod has been apparent in the literature for several years (Brett, 1956; Jobling, 1988); physiological studies have focused on oxygen uptake and metabolic rate (Claireaux *et al*., 2000; Tirsgaard *et al*., 2015) using respirometry. These studies have shown increasing temperatures cause an increase in both SMR and the rate of maximum oxygen uptake up until a peak or optimal temperature is reached, above which maximum oxygen uptake declines (Claireaux *et al*. 2000; Tirsgaard *et al*., 2015). Tirsgaard *et al*., 2015 show that cold water temperatures result in a reduction in metabolic scope across their entire body mass range studied (30-460 g). They however found that in warm waters a reduction in metabolic scope was only evident for larger individuals (200 and 450g), as a result of a plateauing rate of maximum oxygen uptake post 10°C. It is suggested therefore that warm temperatures are more favourable for smaller individuals rather than their larger counterparts (Tirsgaard *et al*., 2015). Optimum temperatures for growth (15°C; Claireaux *et al*., 2000) as well as respiratory physiological measurements of aerobic scope (15°C; Claireaux *et al*., 2000; Pörtner, 2010) as well as critical temperatures (21°C; Jobling, 1988) have also been found for Atlantic cod. Thermal windows and tolerance have also been heavily documented within the physiological literature for

this species (Pörtner, 2002; Pörtner & Knust, 2007; Pörtner, 2010; Pörtner & Peck, 2010; Tirsgaard *et al.*, 2015). Thermal windows are typically bell shaped curves with a peak temperature, representing an optimum for aerobic scope and performance of the organism. At either side of this optimum, performance is depicted to decline, termed pejus temperatures (Pörtner, 2002; Pörtner & Knust, 2007; Pörtner, 2010; Pörtner & Peck, 2010). These terms are often used to illustrate the degree of specialisation of a species such as cod to a particular thermal environment (Pörtner & Peck, 2010).

The effects of temperature on growth and feeding efficiency have also been studied extensively (Michalsen *et al.*, 1998), particularly with concerns to aquaculture application. Interest in cod farming has increased in recent years, especially in Norway, Iceland, Scotland, Faroes and Canada, to fill the gap between increasing demand and diminishing supply (Björnsson *et al.*, 2001, 2007). Growth rate has been found to increase with increasing temperature up until a maximum growth rate after which growth declines. The temperature that maximises growth rate is dependent on individual size and declines with increasing weight of cod (Björnsson *et al.*, 2001, 2007). Differences in weight were found across cod stocks, throughout their geographical range, with warm-water stocks generally larger than their warm-water counterparts at age 4 (Brander, 1995).

Variability in recruitment of Atlantic cod has been attributed to changes in environment for several years (Hjort, 1914; Sætersdal & Loeng, 1987; Ellertsen *et al.*, 1989), as well as to variation in the size of the reproductive stock (Planque & Frédou, 1999). Planque & Frédou, (1999) examined the relationship between recruitment variability and temperature in nine different cod stocks spanning the North Atlantic. Warm water stocks were found to exhibit a positive relationship with temperature, whereas cold water stocks showed the opposite relationship, for stocks located in the middle of the temperature range no relationship was found (Planque & Frédou, 1999). In addition to the important effects of temperature on early-life stages it has been found that temperature is equally important for the spawning stock biomass of Atlantic cod (Ottersen & Sundby, 1995; Ottersen *et al.*, 2006, 2013). Temperature has a direct effect on larval and juvenile growth. Furthermore in warm years, higher

temperatures cause a higher production of prey items for larval and juveniles facilitating higher growth rates and higher survival (Ottersen & Sundby, 1995).

The centres of distribution have shifted with increasing temperature for Atlantic cod and a number of other species including sole (*Solea solea*), with distances moved ranging from 43 to 403 km in latitude northwards (Perry *et al.*, 2005; Rose, 2005).

There is strong empirical evidence of fisheries-induced evolution in Atlantic cod (Jørgensen 1990; Swain 2011). Trends toward maturation at earlier age and/or a smaller size (Heino *et al.*, 2002; Yoneda & Wright 2004; Olsen *et al.*, 2005) are evident, as well as decreased size at age (Swain *et al.*, 2007) and increased reproductive effort (Yoneda & Wright 2004). Reviews by Planque *et al.*, (2010) and Perry *et al.*, (2005) provide anecdotal evidence of the combined effects of climate change and fisheries exploitation on fish populations, suggesting that those species that have been heavily exploited may be more sensitive and less resilient to climate change.

8. Thesis Approach and Aims

To this point I have discussed the physiological, ecological and life-history considerations pertaining to climatic warming, illustrating the complexity of the effects of increased temperature on Atlantic cod in the North Atlantic. Due to this complexity, there is a need for an integrated modelling approach that treats the organism as a whole, encompassing all of the aforementioned components. This "whole species approach" to modelling represents the underlying concept of the thesis. By encompassing physiology, together with ecology, life-history theory and evolution, the predictions of the effects of climate warming on cod and fish species as a whole may be improved.

The general research questions are:
1. What are the life-history implications of increased temperature on Atlantic cod?
2. Are purely physiological-based predictions for the effects of climate change on fish sufficient to help us tackle this global challenge?
3. Why do we see intra-specific life-history variation across the different cod stocks in the   North Atlantic? What are the key drivers?
4. Will the different cod stocks of Atlantic cod respond in the same way to the effects of increased temperature? Will some stocks be more resilient than others?

These questions evolved into the following specific aims:
1. To develop a flexible life-history modelling tool for the climate responses in fish (**Paper I, II, III, IV**)
2. To derive hypotheses for consequences of temperature-induced adaptations for life histories of North-East Arctic cod (*Gadus morhua*) (**Paper I, II**)
3. To identify key drivers and mechanisms underlying the intra-specific diversity observed within 20 North Atlantic cod stocks (**Paper III**)
4. To derive hypotheses for consequences of temperature-induced adaptations for life histories of Atlantic cod (*Gadus morhua*), providing intra-specific stock comparisons (**Paper IV**).

The first question focuses on the effects of temperature on the behaviour and life-history of Atlantic cod, with a focus on the North-East Arctic cod stock (**Paper I**) and an intra-specific stock comparison for 20 different cod stocks within a larger temperature increase range (**Paper IV**). The second question centres on the use of physiologically based studies such as those using the OCLTT for predictions on the effects of climate warming on fish. In particular the direct translation from physiological predictions of aerobic scope into predictions of performance and fitness, to which we discuss together with our modelling approach (**Paper II**). The last two questions focus on the life-history variation across Atlantic cod stocks (**Paper III**) and the potential for differences in response and resilience to climatic warming (**Paper IV**).

In **Paper I**, we provide a life-history modelling tool to derive predictions for the effects of increased temperature on the behaviour and life-history of the North-East Arctic stock of Atlantic cod. We use a state-dependent bioenergetics model to quantify changes in survival, growth, reproduction and fitness for this stock. Respiratory physiology is included as a key constraint. We focus on treating the organism as a whole, incorporating physiology, behaviour, life-history theory and evolutionary considerations. Organisms possess a suite of traits that have co-evolved and must be viewed as such when predicting the effects of climate warming on fish.

Paper II builds on the whole organism approach, and using North-East Arctic cod as a case study emphasises the need for an integrated view for predicting the effects of climatic warming. We suggest the need to move away from purely physiologically based methods for providing predictions towards the incorporation of behaviour and life-history evolutionary thinking. To do this we focus on respiratory physiology as a key constraint and compare predictions of performance and fitness from the theory of oxygen- and capacity-limited thermal tolerance to our model predictions. This enables us to ascertain the benefit of an evolutionary perspective to provide perhaps more realistic predictions for the effects of climatic warming on fish.

Paper III focuses on local adaptation and life-history variation of 20 cod stocks in the North-Atlantic. We focus on ecological differences between the stocks such as mean bottom temperature, annual temperature seasonality, spawning migration

distance and fisheries harvesting, keeping the physiological and ecological constraints constant. **Paper III** uses the tools developed in **Paper I** and whole-organism approach in **Paper I** and **II** to reveal the underlying mechanisms and drivers of the observed life-history differences found in these cod stocks.

Paper IV builds on **Paper III** and provides stock-specific predictions of the effects of climate warming. More often than not, predictions are provided generally for a species, where perhaps a stock-specific approach would be needed. The cod stocks of the North-Atlantic are so diverse (**Paper III**) and therefore need to be treated as separate entities to facilitate climate predictions as they are in management. **Paper IV** reveals the differences in life-history response to climate warming but also the potential resilience capability of North-Atlantic cod stocks if temperatures were to increase.

9. Discussion

Modelling Climate-Induced Evolution

The model presented in this PhD research extends beyond earlier models of the effects of climate warming on fish. A whole species approach is used, integrating physiology together with ecology, life-history considerations and evolutionary thinking; allowing for increased understanding of the potential for adaptation in response to climate warming as well as for improved predictions (Paper I, II, III, IV).

The model provides important insights into the underlying mechanisms and drivers of change in response to climatic warming. Respiratory physiology and in particular aerobic scope provide important constraints for the plasticity and evolution of behaviour and life-histories, and that natural selection may cause adaptations in a suite of traits that together determine fitness in new warmer environments (Paper I, II). We fill in the gap between physiological metrics often used for climate change predictions and fitness, illustrating that the use of pure physiology to predict the effects of climatic warming may not be the most suitable approach (Paper II).

Understanding the effects of climatic warming on fish is inherently complex, especially with concerns to a species such as cod which exhibits a plethora of life-history variation in several traits across its range in the Atlantic. Understanding the key drivers and underlying mechanisms of this variation is not only a key goal in ecology but has become increasingly important for conservation and management. We show that key features of locally adapted stocks can be predicted from a few central drivers and a common ecological and physiological template, which suggests that the mechanisms included in the model likely are central drivers also in the wild (Paper III). Model predictions suggest that temperature is a key driver in life-history variation. Aerobic scope is an important constraint in cold-water stocks, whereas ecological constraints related to foraging were more influential on the life-history strategies of intermediate and warm-water stocks.

Model predictions at the stock level suggest that the effects of climatic warming may be diverse and not all stocks will respond in the same way (Paper IV). For cold-water cod stocks climatic warming may be positive, increasing size- and

maturation-at-age as well as reproductive output. We show that temperature will not only accelerate physiological processes, but will also select for slower life-histories in the stocks at the coldest habitat temperatures and faster life-history strategies in warm-water stocks, implying that the effects of temperature depend on ecological parameters and that phenotypic plasticity and genetic adaptation together may influence the rate and extent of change (Paper I, II, IV). For warm-water stocks, climatic warming is predicted to be negative, reducing size-at-age and reproductive output as well as increasing rates of natural mortality. Stocks in the very warmest parts of the species range such as Irish and Celtic Sea cod stocks are predicted to be the least resilient to change.

Broad Implications of Climate-Induced Evolution

The predictions for the effects of climatic warming on cod provided within this PhD research have wider implications, not only for stock productivity but also for fisheries management. Many if not all of the cod stocks within this study have been heavily exploited by fishing, which may affect their capacity and resilience to withstand climate variability and change. Model predictions suggest positive responses in cold-water stocks to climate warming, and a decline in warm-water stocks. Fishing mortality must therefore be adjusted to take such climate-induced changes in life-history strategy and productivity into account to prevent local extirpations especially with concerns to warm-water stocks. If management of Atlantic cod stocks is to be successful, not only climate but fisheries stressors should be taken into account, through an ecosystem based management approach.

Model Evaluation and Application

The applied value of a model can be evaluated by how well it recreates typical patterns of the natural system in question (Grimm *et al*., 1996). The extent at which climate-induced evolution affects marine fish is still debated, and when providing predictions for the future, data are of course unavailable with which to compare. Model predictions can be compared with data at the stocks' current mean temperature; which well represents the current life-history strategy of most stocks

studied (Paper I, III). As this PhD research uses a modelling approach, it can never truly represent the vast complexity of the real world environment but can be thought of as a simple approach towards understanding how species may respond to the effects of climatic warming. The model represents a flexible life-history modelling tool and although focuses on cod could be readily applied to other gadoids as well as other temperate species. As a specific respiratory physiology component is incorporated within the model, the integration of multiple drivers could also be facilitated; such as hypoxia where data are already prominent in the literature (Pörtner, 2012) as well as the effects of fishing. Furthermore the model could also be applied to study the effects of climate warming on tropical species, although it is likely that additional trade-offs are also important in these environments.

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