Life history variability in maturity and the influence of environment in Atlantic Salmon, *Salmo salar*, and Bullethead Parrotfish, *Chlorurus sordidus* and *C. spilurus*, under climate change

by

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Dedication

I would like to dedicate this thesis to my mentor Aaron MacNeil and the iFisheries research group at Dalhousie University, Jeffrey Hutchings, Brett Taylor, my partner, and my family. Thank you for your support and guidance throughout these two years.

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Abstract

Life history transitions are periods between lifecycle stages defined by physiological, morphological, or spatial change. By assessing the timing of transitions, we increase our understanding of the trade-offs in traits to maximize fitness. One such transition is maturity, which we study because it is required for successful reproduction. In this thesis, we explore maturation strategies and the drivers of their plasticity in two fish taxa. Here we show evidence of (1) inter- and intra- population variability in mature male parr age at maturity driven by intrinsic population-level differences and thermal experience in Atlantic Salmon and (2) population demography as a driver of size at phase change in protogynous Bullethead parrotfish. Identifying the drivers of plasticity in maturity traits and how maturation timing may change with environmental variability in fish taxa can provide ecological predictions of population dynamics and inform fisheries management.

Chapter 1. Introduction

Transitions in life history

The field of life history describes how individuals pass through their life cycle and how selective pressures may change an individual's passage. To develop a mechanistic understanding of life history it is useful to break down a species' life cycle into discrete periods so we can analyze the regular features present in each stage and understand how periods in a life cycle differ from each other. The regular features of life cycle stages include traits such as mortality, survival, or fitness, that are not independent in their function, but vary in relative importance depending on what aspect of life history is being studied. Since there exist differences in regular features between stages there is, therefore, a transitional stage that connects the two periods. It is within this transitional stage that individuals undergo transformations in order to fit the new features of the next stage. When and in what stage an individual makes critical life history transitions will inform our understanding of what changes are required and how these traits play a role in the overall persistence of species. These transitional life cycle stages are defined as periods in an individuals' life where they undergo a change other than regular growth. This change can be either reversible or irreversible and result in physiological, morphological, or spatial differences between stages (Taborsky et al. 2008). Physiological and morphological transitions often operate together and result in the development or degeneration of somatic or gonadal tissue (Mobley et al. 2021).

New tissue often serves a new purpose at a new stage in an individual's or animal's life marking a change in an individual's development. Therefore, by assessing the difference in observable features such as tissue we can question why transitions occur, how transitions serve new life stages, and what mechanisms control their timing. The most common assumption is that transitional changes are necessitated by new requirements, defined by an individual's fitness. Imagine the broad differences between a juvenile and adult individual; for example, primary development in juvenile stages is characterized with higher mortality and adult life stages are characterized by lower mortality (Metcalfe and Monaghan 2003). It is assumed that the overall fitness of the individual may not have changed and that the method to maximize fitness does not work from one stage to another; juvenile individuals can improve fitness by reducing mortality through rapid early growth (Metcalfe and Monaghan 2003), while rapid growth as an adult does not have the same effect on fitness, meaning adults must improve fitness through other means. Therefore, the energy dedicated towards growth changes between life stages, characteristic of a life history transition. Another example of this is the absence of development of gonadal tissue in juveniles since reproduction is not a priority and energy going towards gonads means reduced energy towards body size growth. There are, however, some cases where the development of gonadal tissue can supplement body size (Klemetsen et al. 2003). In adults, gonadal health and development is a priority and therefore energy input is high. Another example of transitions – spatial transitions, or migrations (Mobley et al. 2021) – are defined by a change in habitat. Migrations such as for annual breeding can be considered life history transitions because they represent a tradeoff of energy investment to reproduction. Changing habitats requires both behavioral adjustment to new potential food sources or predators and physiological changes, for instance a transition between fresh water and salt water. A new habitat may offer competitive advantages, but there is a trade-off between the requirements to transition and the relative gains. This trade-off determines when an individual transitions, therefore it is important to understand the differences between individuals that transition sooner rather than later. These fitness trade-offs between life history stages are also relevant to understanding how an individual's role may change and how this influences their survival. The first step to understanding this trade-off is to understand what drives the timing of an individuals' transition.

Fitness has an inherent environmental component. The environment in this case is not only natural conditions, but also includes social, and demographic conditions. The result of this is that environment influences the timing of transitions, allowing us a direct pathway to assessing changes to transition timing and the ability to ask questions such as: if an individual's fitness is influenced by its environment, and therefore subject to change, what is the result of changing fitness, changing environment, on the timing of transitions? Since changes in phenotype are based on the genotype of an individual or population, it follows that a change to fitness can have a corresponding change in the genotypic composition of a population. This means that life history transitions can change between generations. The heritable characteristic of life history transitions is important to understanding the rate and mode by which changes to transition timing may occur in a population. For this reason, one can imagine life history transitions not as specific points but instead as a window of opportunity. The size of this window has inherent plasticity that can complicate predictions and requires further study to obtain mechanistic understanding.

Maturity as a transition

One of the most studied transitions is that of sexual maturity because it is necessary for reproduction, and a good example of fitness trade-offs between reproductive success and survival. Sexual maturity has several definitions ranging from the development of reproductive organs and gonadal tissue, histology, morphological features, or the activation of oocytes, all of which are necessary to reproductive success. The definition of sexual maturity does not always include reproductive success, and for this reason some fields in ecology utilize definitions such as time at first maternity to signify the first offspring and successful reproduction (Baremore and Hale 2012). The difference between these concepts is important for understanding the relationship between maturity and fitness. To improve fitness one requires reproduction, however reaching maturity is a necessity for reproduction and is often assumed to be correlated with increases to fitness (Metcalfe and Monaghan 2003). Without reproductive success, there is no population persistence, and without a successful transition into maturity, there is no reproduction. So, while maturity is not in the same as fitness, it is part of it.

Maturity, as the transition into reproduction, is also relevant for its indirect role in important life history characteristics such as fecundity and the quantity of offspring (Quinn et al. 1995). Fecundity typically decreases with older maturing species, given that there is limited energy to invest into future generations (Metcalfe and Monaghan 2003). Limited energy can affect the quality of parental investment, for example in the trait of egg size (Kinnison et al. 1998). A larger egg, at the cost of higher parental energetic investment, is assumed to have a higher probability of early life growth, reduced mortality at early stages, and reach subsequent life stages faster. This is not always the case as Rollinson and Hutchings (2010) found that

Atlantic salmon with larger eggs emerged later and at earlier developmental stages, indicating that the fitness trade-off between size-at-emergence and the time of emergence does not always correlate between egg size and fitness. Therefore, the transition of maturation is an important component to understanding how the fitness of individuals changes both at the individual scale, but also through the indirect effect of parental condition and changing fecundity in populations.

Here I define sexual maturity as the first development of gonadal tissue also referred to as age at onset of sexual maturation, given the frequent usage of this definition in fisheries ecology and management (Barot et al. 2004). Reaching maturity, in many species, represents only one stage in the life cycle transitions from juvenile to adult stages. Maturity is a highly flexible transition and can occur either once or at several instances throughout an individual's lifespan (Taborsky et al. 2008; Nilsson-Ortman and Rowe 2021; Klemetsen et al. 2003). Depending on the species and reproductive method, the energy requirement to reach maturity and develop the necessary gonadal tissue requires re-allocation of energy from somatic tissue to gonadal, slowing growth and limiting the body size gains of the individual (Jokela 1997; Mobley et al. 2021). Since decreased body size is related to higher mortality, any process that effects body size attainment could also reduce fitness. Therefore, maturity strategies have been driven by adaptive pressures to diversify reaching maturity earlier or later in life, making the timing of maturity a useful metric to understand how the transition of maturity is related to fitness.

In thinking about the timing of maturity, imagine a distribution of maturation times with a mean and a variance created by the interactions of some series of terms. The mean and variance terms must be a combination of an genotypes, their environment, and their life history traits or ecology (Hutchings 2011). The distribution of maturation timing contains the probability of moving between two unique and separate life history stages in time, immaturity, and maturity. The quantification and prediction of the mean can be approached through several methods, most often in ecology with reference to the size or age at maturity. These methods are designed to calculate point estimates for the average age or size that an individual from a population will reach maturity, typically the age (A50) or size (L50) at 50% maturity and are among the most used metrics for fisheries management (Heino et al. 2004). A50 and L50 are maturation indices (Wheeler et al. 2009) often used to estimate harvestable yield while ensuring that at least half of a population had reproduced at least once. This definition has three major assumptions; first, that there is constant mortality across all ages, second, that individuals that reach maturity will successfully reproduce, and third, that fish will reproduce as many times as to replace themselves thereby accounting for mortality and spawning success. These assumptions were made due to the goal of general fishing theory being population replacement.

Within maturity indices are two characteristics age and size, which are most often used together as age-at-size a measure of growth rate as size per unit time given the relationship of growth rate to timing of maturity. Outside of growth rate, age and size when studied together they are useful in understanding the processes behind maturity. Size, a component of growth, is by itself an integral of growth over time. Size is related to growth as prior to maturity most energy allocation goes into somatic tissue and an increase to body size (Barot et al. 2004). Age is an explicit measurement of time representative of survival and longevity (Barot et al. 2004).

We may assume that while size is also related to time – the longer an individual is alive the higher the probability is that it will feed and grow – it is not the main process. The assumption that growth continues through time does not hold, while growth and time are related in juvenile stages, the relationship between growth and time is not constant over a complete lifespan. Considering that the methods of estimation of A50 and L50 are specific to the time at gonadal development or initial age-at-maturity post juvenile stages, it is worth keeping in mind that the relationship of size and age varies and represents different elements of maturity, growth, and survival (de Roos et al. 2006 and Barot et al. 2004). As defined, both size and age each contribute different life history information and combined, age and size give a more complete picture as to what influences the timing of maturity and its plasticity.

Maturity in fish

The range of variability in life history transitions, such as maturity, is well documented in fish. Two such examples of maturity transitions are migration in anadromous salmonids (Klemetsen et al. 2003; Hutchings 2011; Myers and Hutchings 1986), and protogynous sex change at maturity in some species of parrotfish (Taylor etc. 2018). Despite their differences, both examples are maturity responses that feature a complete range of transitional changes including physiological and spatial. Fish life history transitions have additional considerations than the previous generalized examples. Fish fecundity relative to body size is high, and the parental effort post spawning low. This combination means that reproduction often occurs in specific time windows and can happen either once or many times over the course of a single individual's sexually mature lifespan. The energy allocation towards spawning, gonad development, and the trade-off for growth is therefore considered a driver in timing of maturity, evident in the timing of returns in anadromous salmonids driven by energy requirements for gonadal development (Mobley et al. 2021). In addition, the social structures present in fish assemblages often generate competition between individuals over a harem or breeding territory. The result of increased competition and large egg production is that energy allocation (and by proxy growth) is the dominant factor in the timing of maturity. Survival can be difficult to assess in fish as it is difficult to sample effectively. Therefore, estimates of natural mortality are not well developed. However, age is easily obtainable from otoliths, allowing for maturity models to be controlled for the effects of survival. Survival and age are related through longevity, where proportions of older individuals are related to overall survival. For these reasons, fish represent a useful group with which to study the plasticity of maturity timing between individuals, populations, and different maturation strategies.

The study of maturation timing is critical for fisheries management, where the timing of transitions, such as sexual maturation or migration, are used to set harvesting periods or size cutoffs. A50 and L50 are particularly relevant in a population context as they include information of maturation timing and size, and the time between generations. A change in the timing of maturity can be indicative of changing environmental conditions or size-selective harvesting. Since fisheries have size cut-offs, by removing larger individuals there is a selection for earlier and smaller maturing phenotypes (Hutchings and Myers 1994b and Olsen et al. 2004). This size selectivity has recently been shown to vary by age and sex such that further to appropriate capture the complete ecological effects of size-selection multi-year studies are required (Kendall et al. 2009). The size selective pressure can disrupt the active reproductive population, which can in turn negatively affect demographic characteristics such as sex ratio (Coleman et al. 1996; Hutchings and Myers 1994b; Olsen et al. 2004). For these reasons A50 and L50 metrics have persisted for their usage in diagnosing phenotypic changes within populations.

Maturation Strategies and Alternative Strategies

Variability in maturity timing is not solely due to natural and genetic plasticity but is also a product of maturation strategies. Maturation strategies are defined as a combination of physiological and morphological characteristics arising from a genotype that develop upon reaching maturity for the purpose of increasing fitness (Hutchings 2011, Munday et al. 2006). Maturation strategy characteristics, at either the individual or population scale, include differences in the timing of reproduction, size at reproduction, social role, morphology, or fecundity. Maturation strategies are also referred to as reproductive strategies, however it is best to keep these ideas separate as reproductive and maturation strategies can have separate traits and while maturation strategies exist because of fitness, maturity does not guarantee reproduction. As an example of possible strategies consider two scenarios summarized by Metcalfe and Monaghan (2003): (1) earlier maturation at a small size; and (2) late maturation at a larger size. In the first scenario, individuals may increase their fitness by reducing the amount of time spent subject to predation and increase the likelihood of initial reproduction (Richner 1992, Ludsin and DeVries 1997). In the second scenario individuals take longer to mature but reach larger overall body size, increasing their fitness as a more competitive mate and may increase the probability of their success in repeat reproduction with a longer lifespan. The hypothesis that faster juvenile growth holds a fitness advantage is recent (Metcalfe and Monaghan 2003; Roff 1984; Richner 1992). Previous theory on the pace of life history held that longevity, and therefore the possibility of repeat reproduction, was the main mechanism for fitness (Arendt 1997). What was left out of this theory were the cases with minimal growth in adult phases, thus the time to reach the adult phase held a higher advantage regardless of lifespan. The current assumption is that the optimal rate of growth is dependent on the trade-offs of mortality, lifespan, population condition, and reproductive success between life history stages (Metcalfe and Monaghan 2003). Faster growth rates lead to higher survival when young and decreased mortality initially, however faster growing individuals typically have shorter lifespans (Metcalfe and Monaghan 2003). In this regard, it is likely that populations that reproduce once in a short lifespan versus many times in a long lifespan have comparable fitness and therefore reproductive successes per individual. As described, growth rate is highly plastic and contributes to the variability of a maturation strategy.

Maturation strategies are themselves variable, so much so that many species also exhibit one or more alternative strategies. A common example of such a strategy is the “sneaker male”, where individuals, typically males, successfully fertilize eggs ideally with minimal direct competition with physically larger males. By not competing with larger males, there is no investment into the physiological development for the adult morphotype in the sneaker males. The strategy of the sneaker male has been documented across many taxa including salmonids (Myers and Hutchings 1986, Hindar and L’Abée-Lund 1992, Klemetsen et al. 2003) and earwigs, *Forficula auricularia* (Tomkins and Brown 2004). These alternative strategies are defined as methods of increasing the fitness and likelihood of fertilization through a different set of traits than the prevalent maturation strategy. Different trait sets can include color polymorphism, morphological structures, allocation and acquisition of resources, territorial behavior, and social behavior. A critical part of this definition is that the phenotypic traits of each strategy can be differentiated (Taborsky et al. 2008). Taborsky goes on to state that reproductive strategies, and by extension maturation strategies, can result from both phenotypic plasticity and fixed life history patterns. The latter is the hypothesis that reproductive traits can be a result of divergent trait patterns persisting in a population.

For example, the prevailing strategy in salmonids is for males to reach sexual maturity during their at-sea migration. The amount of time spent in the river prior to leaving, and the amount of time spent at-sea is subject to environmental variation and other factors (Myers and Hutchings 1986, Jonsson and Jonsson 2009). The alternative strategy in this context is for male parr to mature in-river without under-going the necessary at-sea morphological changes to survive in salt water, and to then preform satellite “sneaker” fertilization (Myers and Hutchings 1986). Both strategies are successful and remain present in populations and are therefore likely equivalent in fitness, per location or population (Myers and Hutchings 1986). It is important to understand the presence of alternative life history strategies because they represent alternative fitness paths. This is particularly relevant in fish, where alternative maturation strategies are more prevalent than other taxonomic groups (Taborsky et al. 2008). Key to understanding the persistence of maturity strategies is to understand why one phenotype occurs over another. In this regard, the timing of maturity can be a metric by which to differentiate between strategies and study their occurrence.

Reaction norms and maturity ogives

Based on the concept that maturity, characterized by traits such as timing of maturity, exists as a distribution defined by the interaction of environment and genotype, we can begin to identify and estimate the dominant drivers for maturity. The mean point of maturity is believed to be a heritable trait (Hutchings 2011) that varies both within and among populations, representing the influence of environment on a specific phenotypic trait, in this case maturity. Therefore, maturity is an additive process of the interactions of genotype, and phenotype and environmental influence, each of whose components can be estimated. This function of variability is referred to as a reaction norm and is the foundation for current hypotheses on the processes governing maturity (Heino et al. 2001; Barot et al. 2004; Hutchings 2011).

Reaction norms, originally described by Woltereck (1909), are functions describing the patterns of phenotypic change, per genotype, in response to environmental change. This is best visualized as the distribution in response across a gradient, where the response is the presentation of a particular phenotype for example, the probability of maturing (Heino et al. 2001; Barot et al. 2004, Hutchings 2011). The probability of maturing is different from the earlier maturation indices in that A50 and L50 relate to the proportion of a population at maturity, where probabilistic maturation norms define the probability that an individual will mature at a given age or size. Reaction norms are used to estimate the magnitude of phenotypic plasticity, in traits such as maturity timing. Reaction norms can also be used to develop hypotheses on the degree to which individuals, populations and species respond to climate change, both human-induced and natural. Reaction norms can be further specialized into maturity reaction norms, where the probability of maturing is a function of both age and size. This is typically done by taking the L50 at age. Maturity reaction norms, however, do not account for environmental variables by assuming that environmental influence is the cause behind all variation (Stearns and Koella 1986; Stearns 1989). This assumes that environmental variability can be observed in growth rates. To estimate the impact of specific environmental influences another method is required.

Maturity ogives are the proportion of individuals across a trait, typically age or length. Reaction norms can be difficult to estimate and calibrate, but can be derived from maturity ogives (Heino et al. 2001). Ogives are the principal method used to estimate A50 and L50. The maturity reaction norm of the L50 by age is therefore a combination of the information of both L50 and A50 (Barot et al. 2004). Barot et al. (2004) states that by controlling for both age and size, one can effectively control for the processes of both growth and survival. On the other hand, the ogive approach describes the maturation process in-directly since maturity is dependent on both age and size, and that the probability of maturing depends on both the process of maturity and the survival and growth before and after maturation (Barot et al. 2004). Maturity ogives and reaction norms are closely related and are important methods for describing the processes behind maturity and how it may change. It may be concluded that both methods can identify differences between populations in terms of environmental influence and genetic difference. There are two additional considerations between methods. First, reaction norms are per specific year classes, where maturity ogives are population wide; and second, reaction norms are useful for understanding the changes to survival before and after maturity, where maturity ogives are useful for understanding initial maturation only.

Here, I use maturity ogives to describe the timing of maturity, represented as probabilistic hierarchical Bayesian models.

Threshold-trait hypothesis

A current hypothesis of the mechanism for fish maturity is the threshold-trait hypothesis (Atlantic salmon, *Salmo salar,* Hutchings 2011, earwigs, *Forficula auricularia*; Tomkins and Brown 2004, dung beetles, *Onthophagus acuminatus*, Emlen 1996), which asserts that maturity, regardless of strategy, depends on the attainment of a threshold point in a trait. Exceeding the trait threshold leads to the adoption of a particular phenotype at maturity. Examples of such traits include body size, growth rate, social status, or a combination (Hutchings 2011). This hypothesis is more flexible than the previously held assumption that absolute body size, believed to maximize reproductive potential, was the criterion for maturation (Thorpe 1986). The expanded definition of the threshold for maturity makes sense, since fitness, a direct measure of maximum reproductive potential, is not wholly dependent on body size. Current evidence (Hutchings 2011) shows that body size and growth rate thresholds exist in species such as Atlantic Salmon, in both natural and laboratory populations. It is unknown how the thresholds present in natural populations are influenced by changing environmental conditions.

Environmental influence on maturity

The plasticity of response in maturity phenotypes to the environment is related to trade-offs in fitness that may occur through direct and in-direct processes such as temperature and growth. We can define plasticity by how widely different phenotypes respond to environmental conditions differently as a function of their genotype. Individual growth occurs within an optimum function of temperature as a direct effect of increased metabolism and indirect effects such as increased access to food sources. In fisheries, environmental factors are often classified as those relevant to concepts of yield, growth, and the maintenance of a reproductive population. Estimation of key effects is further complicated by the fact that most environmental processes are not mutually exclusive and are instead functions of each other, for example food quality and population density, or temperature and precipitation. It is important to have clear model assumptions regarding what mechanistic connections are believed to exist between trait process and environmental conditions. With appropriate models, it is possible to estimate the conditional effects of environmental parameters on maturity. There are however limits, for example statistical models effectively mop up variability, but cannot distinguish between processes. Thankfully, it is not an either-or situation, and both statistical and mechanistic models are useful in understanding life history processes. For this reason, it is difficult to study the development of strategies without long-term monitoring of populations.

The plasticity of maturity is a function of environmental variability and genotype. The presence and inheritance of the genetic component of maturation traits and alternative maturation strategies can be approached through two methods outlined by Lepais et al. (2017). The first is that maturation is a genetic component and is heritable, and the second is that there are no genetic effects on maturation but instead an epigenetic effect. The epigenetic effect is defined as the process by which an individual’s environment may change how genes are expressed in a non-heritable way. Taking the hypothesis of Taborsky (2008), that maturity response is both plastic and a divergent trait, it could be possible that both processes occur. Both hypotheses by Lepais et al. (2017) point to a relationship between environment and genetics. The genetic and epigenetic methods of describing maturation processes can both determine if populations hold genetic differences, however, would not be able to distinguish between heritable and epigenetic effects. With known genetic and environmental influences, it is expected the populations should vary in the timing and requirements for maturity. The degree to which populations may vary is a function of their differences in environment and the plasticity of their phenotypic response.

For marine and freshwater fish, fisheries ecologists focus on the conditions necessary for early growth or growth opportunity, such as body size, or weight. These traits can be studied through many proxies, for example in Baum et al. (2004), variations in growth rate were explained by altitude among river sites of Atlantic salmon parr and argued that the size threshold for maturity also depended on altitude. Altitude by itself is related to many things like temperature, precipitation, vegetation, fishing pressure, predation, and discharge and water velocity. This illustrates how quantifying the environmental influence of maturity requires a directed approach specific to the condition or mechanism of interest.

Fish have evolved within specific water conditions that are often characterized by factors such as temperature, pH, habitat complexity and diversity, currents, water velocity, discharge, pigment-presence such as chlorophyll-a, or sediment load. The importance of these factors will vary by context, so when making comparisons of environmental influence between marine and aquatic environments it is important to critically consider what factors are relevant. In fisheries, where sampling can be limited, it is often the case that available environmental data are limited. For this reason, assessments typically only include a select series of factors, often temperature or a temperature proxy such as day-length or latitude, since temperature for fish is historically highly positively correlated with growth, body size, and overall condition, with exceptions at high temperatures (Killen et al. 2013, Boltana et al. 2017).

Changing environments and the implications of climate change

Environmental variation falls into two broad categories: natural and human induced climate change. The former includes seasonal differences and oscillations such as the North Atlantic Oscillation (NAO) (Brander and Mohn 2004). Natural oscillations are a result of the earth's orbital patterns and eccentricity, and their effects can change in magnitude across time and space. Natural oscillations are expected and are typically encompassed in the plasticity of traits per species as a result of selection. For example, the age of migration in salmonids is related to the length of the growing season (Klemetsen et al. 2003 and Power 1981), which vary year to year. With this information a reaction norm can be built, based on the gradient of possible growing season lengths and the corresponding age of migration. Human induced climate change is defined as environmental variability either outside of the natural oscillations, that creates extreme conditions for longer than normal, or at a larger spatial scale. The result is conditions outside of the reaction norm for a species, which can result in a change in behaviour (Nussey et al. 2005). Therefore, to calibrate reaction norms and our understanding of life history processes such as maturity, requires predictions of life history traits under future climate scenarios.

Human influence on maturity

Previously described environmental influence on the process of maturation in fish has been limited to natural conditions and human induced climate change. Human influence over the environment is not limited to climate warming as fisheries exert substantial pressure in many contexts and fishery selectivity holds a direct relationship with the survival, mortality, and age-based demographic of fish species (Heino and Godo 2002). Since maturity, and the presence of alternative maturation life histories are heritable responses, size-selective fisheries can create an artificial selection and either increase or decrease mortality for a specific phenotype. Without management, size selectivity can result in a change in the proportions of traits within a population visible as younger ages and smaller sizes at maturity (Pinca et al. 2012; Hutchings and Myers 1994b; Olsen et al. 2004). Due to the long-standing presence of fisheries on most fish populations, it is difficult to determine the extent to which fisheries pressure plays a role in life history characteristics outside of current sampling periods.

The implications of changes to maturation timing

In the context of changing environmental conditions outside of prevailing reaction norms combined with fisheries pressure, the implications of changing maturity schedules could include direct impacts to population demographics, depending on the relative influence from the environment and the length of generational turnover. Whether natural or human based size selection, a removal of larger individuals selecting for those earlier maturing will also impact mortality rates in adults and could reduce lifespan. By reducing lifespan and the gap between generations the population age structure will also be truncated. Shorter lifespans, and a resulting smaller window of potential reduction, can also lead to a reduction of overall population reproductive success (Wright and Trippel 2009) making populations increasingly susceptible to fisheries pressure. The impact of changing population age structures are complicated by alternative maturation strategies, especially since they are prevalent in fish taxa (Taborsky et al. 2008). Therefore, understanding how human induced changes to environmental variability and human pressures affect the timing of maturity will be important to reducing fisheries impacts.

Modelling approaches

To estimate the plasticity in maturity, we require one or more metrics with which to model maturity. Maturity reaction norms and maturity ogives are two such methods discussed which can represent the probability of maturing over a specified gradient such as age, length, or temperature. The utility of maturity ogives has been shown through the estimates of A50 and L50, parameters that represent population wide differences in the timing of maturity. By using appropriate analytical methods, we can test the theorized plasticity in maturity response in natural populations.

Maturity models in ecology often use growth equations to develop relationships between body size and the probability of maturity. The basic assumption of all the previously presented methods is that maturity a binary and only occurs once, therefore it can be represented as the probability of transitioning per unit. Once individuals are divided into a binary of immature or mature, we can begin to isolate what changes over the course of the transition. There are several equations used to derive the shape of a population's per age class sexual maturity response for example the von Bertalanffy, linear regression, and Lysack's formula (Trippel and Harvey 1991). These methods are similar in that they are developed for the purpose of estimating point values. While each method results in a similar growth curve function, there can be significant variation between them even on the same population (Trippel and Harvey 1991) making comparisons between populations of studies difficult. In addition, comparisons between method point estimates or model variances are made difficult due to different parameterization. Further difficulties with traditional maturity models can be the grouping of lengths discarding its continuous nature. Therefore, maturity modelling is presented with a series of issues namely how to estimate plasticity in response outside of a single point estimate, how to best to assess the information provided by covariates, and how to deal with the binomial nature of maturity data explicitly. Traditional maturity models included either age or size, however, Barot et al. (2004) concluded that models that condition on both age and length are more informative as they allow for evaluation of maturity processes independent of survival and growth rate.

Maturity ogive models are often formulated as logistic regressions (Barot et al. 2004; Vainikka et al. 2009; Heino et al. 2002). By producing maturity ogives conditional on both age and size, these may be directly integrated into probabilistic maturity reaction norms. This counteracts the problem of traditional A50 and L50 methods of estimation where the effects of survival and growth are made independent of the process of maturity described by Barot et al. (2004). The next stage of maturity models is the inclusion environmental covariates such as temperature to quantify the relationship between environment and size or age at phase. We may then use these relationships to predict changes under predicted environmental regimes. In this way, we can use maturity models to test theory on natural populations.

Bayesian hierarchical models present a one way to create flexible, mechanistic maturity models. One of the advantages of Bayesian modelling is the ability to explicitly include prior information. For example, it is currently hypothesized that temperature affects the rate of growth, therefore we may set a prior estimate of temperature's influence on the rate of maturit (Smart and Grammer 2021). Prior information can also be used in simpler cases, take for example, age, where age cannot go in reverse, therefore we can set the prior of the age parameter to ensure that it cannot be negative. Prior selection takes careful thought, particularly with smaller datasets where priors can overwhelm the model and reduce the information provided by the data. For this reason, it is important to explicitly state what assumptions are made during prior selection. What should also be emphasized is the ability to calculate distributions of probability, including intervals around estimates that are directly interpretable regarding the plasticity response of maturity. Bayesian models also readily incorporate nesting or hierarchies (Helser and Lai 2004). When faced with multiple populations over a large spatial scale of varying sample sizes, it can be useful to allow for the means of each group to inform each other. This phenomenon can lead to parameter shrinkage towards a global mean. Furthermore, the development of directed acyclic graphs (DAGs) which define the assumed causal flows among parameters, can help clarify how parameters interact and avoid biased estimates through backdoor information pathways (Pearl 2009), which is particularly important during model development. If our goal is to develop a mechanistic understanding of maturity, having a firm understanding of our assumptions is essential.

Statement of major aims

Based on the current literature and research on the plasticity of maturity timing in fish populations and the development of maturity modelling approaches, this project focused on the following goals: (1) the estimation and quantification of the plasticity of response in maturation timing in fish populations across spatial scales and differing maturation strategies, (2) the estimation of the relationships between environment and timing of maturity, (3) the prediction of how timing of maturity may change over forecasted climate warming.

These goals are addressed by two separate papers, presented here as Chapters 2 and 3. Both chapters discuss the plasticity of responses in maturation timing between populations. Chapter 2 focuses on two specific populations of Atlantic Salmon (*Salmo salar*), while Chapter 3 focuses on large spatial differences covering the complete species habitat range of bullethead parrotfish (*Chlorurs sordidus* and *spilurus*). Similarly, both chapters discuss the relationship between environment and maturity response. Chapter 2 specifically targets maturity in the alternative maturation strategy of Atlantic salmon and predicts how the timing of maturity may change with forecasted climate warming. Chapter 3 then targets the estimation of environmental and human influence in protogynous maturing bullethead parrotfish populations across a large scale.

Chapter 2: Thermal control of male parr maturity in Atlantic Salmon, *Salmo salar*, under climate change

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Introduction

Alternative life histories are reflected by within-population differences in individual age-specific rates of survival and fecundity (Hutchings 2021). These differences are often manifest in reproductive or mating phenotypes, particularly among males (Shuster and Wade 2003). Much of the literature on alternative mating strategies has focused on their conditional nature, such that the probability that an individual will express the phenotype is conditional on the attainment of a threshold (Roff 1996) associated with some element of intrinsic condition or the extrinsic environment (Shuster and Wade 2003; Oliveira et al. 2008). One example is a size-based threshold that must be attained before individuals are able to switch from alternative life history to another, evident across a broad taxonomic range, e.g., earwigs (*Forficula auricularia*; Tomkins and Brown 2004), dung beetles (*Onthophagus acuminatus*; Emlen 1996), and Atlantic salmon (*Salmo salar*; Hutchings 2011).

Body size and the rate at which it is attained with age (i.e., growth) are influenced by prevailing environmental conditions, particularly among ectotherms. This raises the fundamental question as to how climate change, and its concomitant increase in temperature, will affect the incidence or frequency of alternative life-history strategies.

Aquatic ecosystems have been among the first to be impacted by climate change, developing warmer environmental regimes that are adversely affecting a wide range of aquatic species (IPCC 2018) and the livelihood of coastal peoples (Renzi et al. 2019; Pecl et al. 2017).

The effects on individual fitness, population viability, trophic cycling, and habitat (Mattocks et al. 2017) are likely to be particularly acute for species that migrate between fresh and salt water (Jonsson and Jonsson 2009). For example, for a key life-history trait such as age at maturity, the expressed phenotype of smolt age (the age at which salmonid fishes migrate from fresh water to the sea) is related to length of growing season (Klemetsen et al. 2003 and Power 1981). What remains unknown is how variable maturation timing is in response to changing environmental conditions.

In male Atlantic salmon (*Salmo salar*), the alternative life history strategy of mature male parr (MMP) is a compelling example of life history and maturation strategy variability (Hutchings 2011). MMP occur when parr (the developmental stage that precedes potentially subsequent smoltification) attain maturity in fresh water prior to a potential seaward migration. Atlantic salmon, widely distributed throughout the northeast and northwest Atlantic, have well-documented occurrences of MMP (Hutchings 2011). The physiological impacts of life as a MMP include small size at maturity and a ‘sneaker’ breeding behaviour that leads to successful fertilization of eggs, ideally with minimal engagement with physically larger migratory males (Hutchings and Myers 1994a, Rowe and Thorpe 1990). There are fitness trade-offs for males that mature as parr and for those that postpone maturity until after they have completed a migration to and from the sea (Thorpe et al. 1992). By maturing in the absence of a seaward migration, parr have a considerably higher probability of surviving to maturity than their anadromous counterparts (Hutchings and Myers 1994a). Countering this benefit is the observation that individual reproductive successful among parr is relatively low and highly variable (Jones and Hutchings 2002). Several studies have documented a genetic component to male parr maturity (e.g., Piché al. 2008; Páez et al. 2011; Debes and Hutchings 2014; Lepais et al. 2017).

Current hypotheses for the presence and persistence of MMP are based on the concept of threshold traits and reaction norm theory (Hutchings 2011, Heino, Diekmann, and Godø 2002). A reaction norm is a function that describes phenotypic responses to environmental change by tracking trait expression across an environmental gradient (Woltereck 1909). The threshold trait hypothesis states that above a threshold of growth rate, individuals will attain sexual maturity in fresh water as MMP. The growth-rate threshold for male parr maturity is a heritable trait that is expected to vary between populations and cohorts (Piché et al. 2008). All else being equal, the more rapid the growth rate, the higher the incidence of male parr maturity (Myers et al. 1986, Myers and Hutchings 1986), however, the degree to which differences in environmental regime may account for intra-group variability is unknown (Nordwall, Naslünd, and Degerman 2001). The persistence of MMP in Atlantic salmon is indicative of a fitness equality with the anadromous male strategy; the two strategies are hypothesized to persist through time as a result of negative frequency dependent selection (Hutchings and Myers 1994b). Climate-change scenario simulations by Hedger et al. (2013) and Morita et al. (2014) suggest earlier swim-up date and earlier maturation (during the first year of life), respectively, with increasing temperature, based on indirect growth rate measures, such as time of egg-deposition. However, it is unknown how the rate of parr maturity across age classes will respond to climate warming scenarios.

Age-at-maturity models provide a template to study growth rate via rate of maturation of Atlantic salmon populations and understand how the rate of maturity can vary between populations, cohorts, and environmental regimes in response to climate change. Rate of maturity can be assessed by the steepness of the maturity ogive, i.e., the cumulative frequency of mature or immature individuals, given its relation to the average growth rate. Size-at-maturity models describe the physiological threshold required to attain maturity, and can be used to understand the genetic component of maturity (Larsen et al. 2021). It is important to compare these model approaches when approaching a complex system of multiple environments and populations.

One interpretation of the possible scenarios of age-at-maturity and size-at-maturity is presented in Figure 1. Comparisons of the two models can be used to clarify the relationship between growth rate and the maturation threshold. Warmer temperatures typically lead to faster growth rates due to decreased metabolic demand (Elliot and Hurley 1997 and Forseth et al. 2001) and thus the effects on growth are expected to scale additively as temperature increases within tolerant and below critical temperatures (Parmesan and Yohe 2003, Reist et al. 2006, Elliott 1994, and Jonsson and Jonsson 2009). Cumulative growing degrees (CGD) is a metric that captures the accumulated or total temperature experienced by an individual over their lifetime and holds a strong relationship to length-at-age (Neuheimer and Taggart 2007 and Chezik et al. 2014). Longer CGD regimes are therefore expected to lead to an increased rate of growth and faster transitions through maturity stages, suggesting proportions of MMP may increase with CGD.

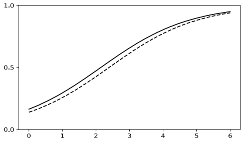
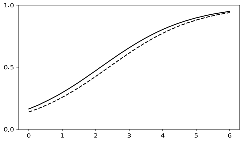
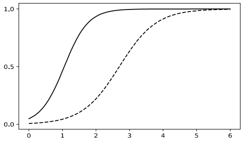
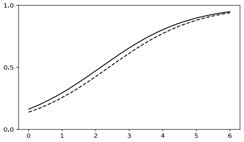
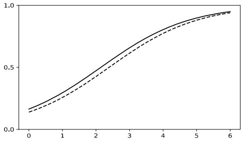
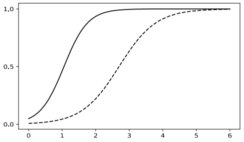
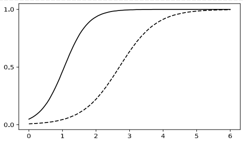
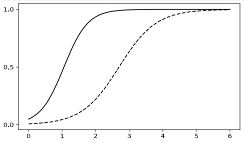
Age-at-maturity	Age Interpretation	Size-at-maturity	Size Interpretation	Combined Interpretation
	Growth rate is not affected by environment.		The threshold for maturity is deterministic, and/or populations are genetically similar and therefore have a similar threshold.	Either similar maturation thresholds between populations, or neither populations' threshold is determined by the environment and not related to growth rate.
	Growth rate is affected by environment.		The threshold for maturity is deterministic, and/or populations are genetically similar and therefore have a similar threshold.	Similar maturation thresholds between populations but differ in maturation timing due to growth rate differences between environments.
	Growth rate is not affected by environment.		Distinct maturation thresholds between populations.	Process behind maturation threshold independent of growth rate. May indicate presence of a factor controlling the threshold outside of the effects of growth rate, or distinct genetic populations.
	Growth rate is affected by the environment.		Distinct maturation thresholds between populations.	Populations with different thresholds experience different growth rates. May indicate presence of a factor controlling the threshold outside of the effects of growth rate, or distinct genetic populations.

Figure 1. Chapter 2 Figure 1.

Figure 1. Age at maturity and size at maturity, where maturity is the probability of attaining maturity (0-1), for two example populations with different environmental conditions. The interpretation of the age and size models is provided to the right of their respective plot. The fifth and final column is the combined interpretation of each row's models.

Warming temperatures lead to changes in precipitation and overall hydrology, resulting in shifts in river discharge and, in northern climates, glacial runoff. River discharge plays a role in defining river ecology through its influence on factors such as nutrient delivery, oxygen balance, and habitat availability (Gillson et al. 2020 and Heggenes 1999). High discharge regimes have been found to negatively affect juvenile salmonid densities and are believed to be linked with spawning site availability and lower egg-to-fry survival (Gillson et al. 2020 and Heggenes 1999). Therefore, if discharge is related to juvenile density and survival, lower rates of maturity should be present under higher discharge regimes (Hutchings and Jones 1998). Salmonid response to discharge is believed to be highly plastic (Milner, Cowx, and Whelan

2012), and we expect to see discharge moderate the effects of temperature. However, the effects of the interaction between discharge and temperature on rate of maturity is unknown.

Here, based on the longest available time series (~15 years) for mature parr in wild Atlantic salmon populations, we quantify the relationship between CGD, river discharge, and male parr maturity at age from two thermally distinct rivers in Norway, using Bayesian age-at-maturity models, and predict how forecasted warming will impact maturation timing over a 50-year timeframe, assuming all other conditions are invariant to temperature.

Methods

Study Populations

Atlantic salmon parr from the Os and Flåm rivers in Norway were monitored for 16 and 14 years, respectively, between 1996 and 2016 (Figure 2). The Os river is a relatively warm coastal river, with a mean annual temperature of 8.4˚C (Figure 3), located between 60.2357° N and 60.2508° N and 5.4396° E and 5.4610° E. It is separated into three stretches by lakes. Summer discharge is largely determined by precipitation. Smoltification most commonly occurs at age two; the adult population is dominated by 1-sea-winter fish (Harald Sægrov, Rådgivende Biologer AS, Bergen, Norway; unpublished data).

The Flåm river is located further north and inland between 60.8652 °N and 60.7928° N, and 7.1052° E and 5.1235° E with no lowland lakes along its path. Temperatures remain colder, with a. mean annual temperature of 5.6˚C, than in the Os and summer discharge is determined primarily by snow melt (Figure 3). Smoltification generally occurs between ages three and five years. Multi-sea-winter adults are more common in the Flåm than in the Os population (Harald Sægrov, Rådgivende Biologer AS, Bergen, Norway; unpublished data).

Data Collection

Sampling was carried out as part of an environmental monitoring program to understand the potential life-history changes following the possible impact from escape farmed salmon and infestations from lice. This program is maintained, run, and mainly financed by the Norwegian consulting company Rådgivende Biologer AS. Electrofishing was conducted in sweeps of 75-220 m^2 stretches annually at six sampling sites in each river, which were selected as representative habitats. It is unknown if the size distribution of the sampled population is representative of the river-wide population; however, there is no evidence to the contrary. Most sites had cobble or gravel substrates and a 5-80 cm depth. Deep pools and sandy areas were avoided to maintain a consistent sampling protocol, as outlined by Sægrov et al. (2001). Sampling took place between November and April in the Os from 1997 to 2016, and between October and December in the Flåm from 1996 to 2013, when temperatures were below 8°C.

For every parr caught, the length (nearest mm) and weight (nearest g) were measured, and age (years) was estimated, using otoliths and/or scales. No distinction between methods was made available in the biological data such that no method testing was performed. Otolith and scale age dating are expected to vary in estimates. Gonadal stage was necessary to classify individuals into a binary classification of ‘mature’ or ‘immature’. Maturity stages after maturity, for example spawning, resting, or spent individuals, were not assessed separately as the timing of later stages was not assumed to control maturation timing. Based on the timing of sampling, the measurement of individual age denotes time from emergence i.e., an individual aged +1 refers to an individual caught in November that hatched 1.5 years earlier in April/May. We also identified individual cohorts according to year class at emergence and differentiated between rivers, i.e., the same year-cohorts between rivers were given unique codes.

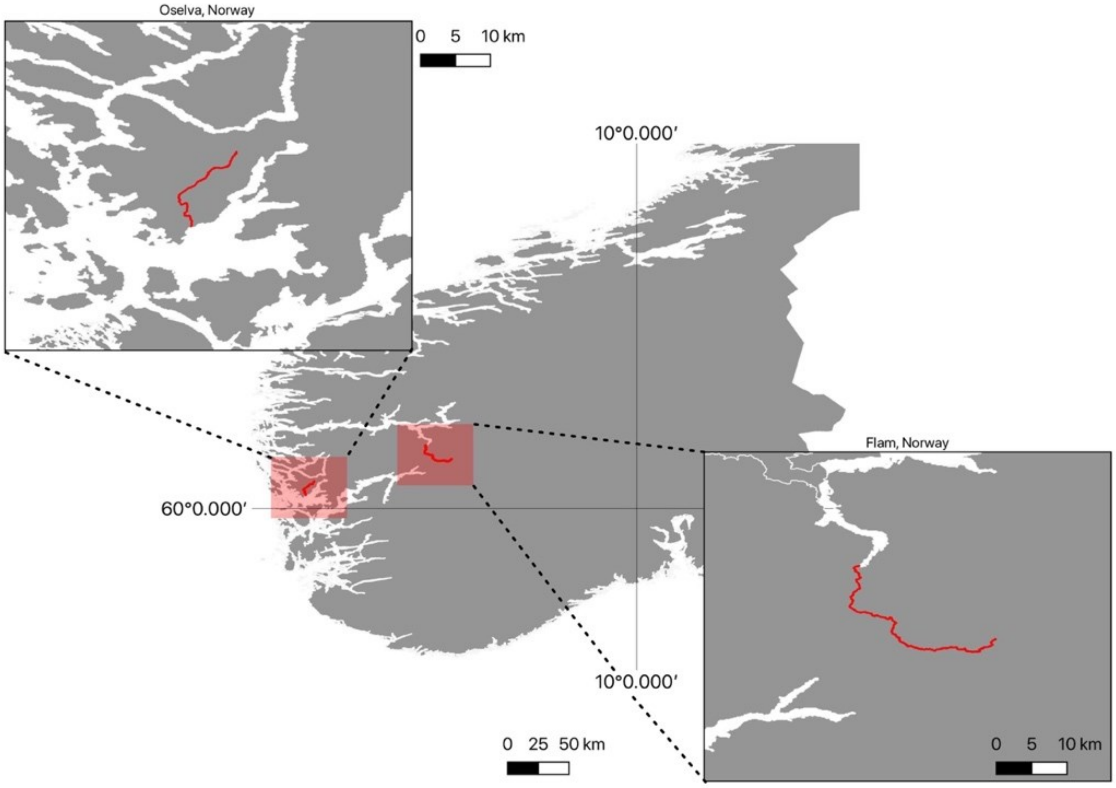


Figure 2. Chapter 2. Figure 2

Figure 2. Juvenile parr monitoring rivers Flåm and Os in Vestland, Norway.

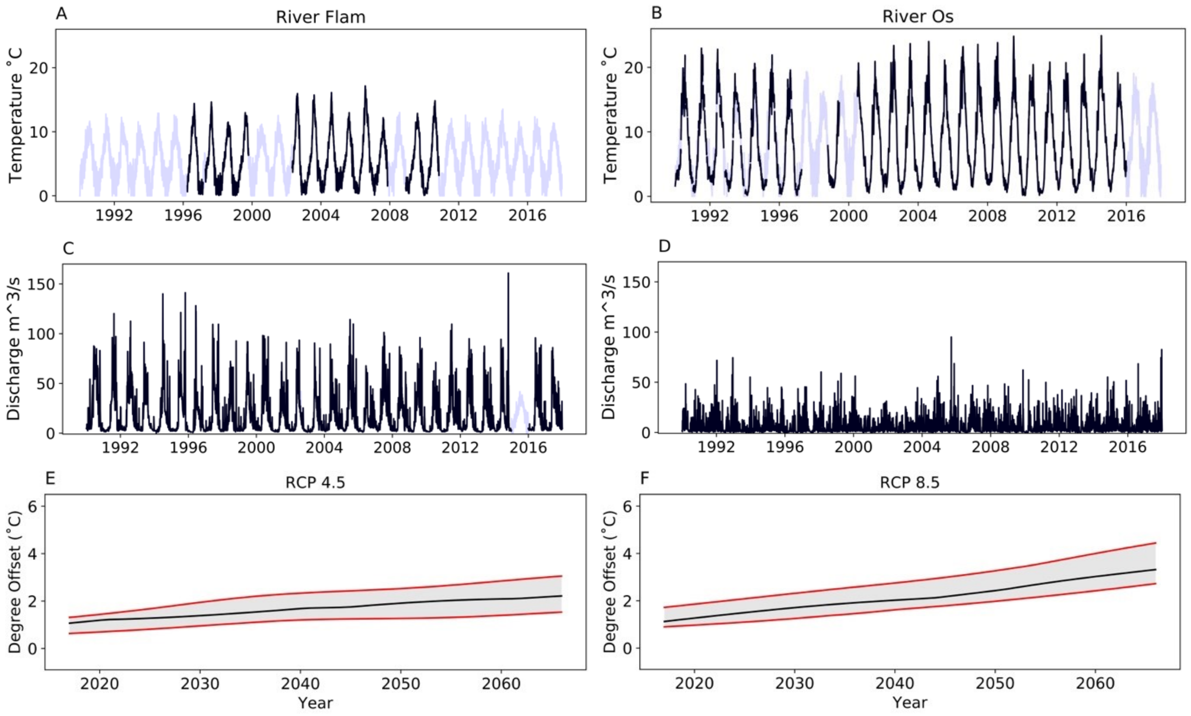


Figure 3. Chapter 2. Figure 3: Panels A-D

Figure 3. Daily monitoring river-temperature (˚C) timeseries for Rivers Flåm (Panel A) and Os (Panel B) spanning 1990 to 2017. (Black solid line). Daily imputed and modelled temperature timeseries of river-temperature (˚C) for Rivers Flåm and Os (Blue solid line). Daily monitoring river-discharge (m^3/s) timeseries for Rivers Flåm (Panel B) and Os (Panel D) spanning 1990 to 2017. (Black solid line). Daily imputed and modelled temperature timeseries of river-temperature (˚C) for Rivers Flåm and Os (Blue solid line). Norsk Klima Service Senter RCP 4.5 (Panel E) and 8.5 (Panel F) Climate Projection scenarios as degree offsets with 10th and 90th percentiles (red), spanning 1900 to 2011.

We excluded data on female parr, as they have not been observed to mature in fresh water as parr (Jones 1959) and exhibit different maturation timing from males (Birt and Green 1985). Data were excluded from one site (Site 6) in river Os, because of an anomalously cold temperature regime, and for year-zero (+0) individuals, which were too small to assess the gonadal stage. After these exclusions, the sample sizes of male parr for Flåm and Os were N = 1114 and N = 984, respectively.

Temperature and Discharge

We used cumulative growing degrees (CGD) as our metric of individual temperature experience to quantify river temperature's effect on maturation timing. To supplement existing gaps in the river temperature timeseries, daily mean air temperatures from the FROST API (Meterologisk Institutt av Norge) were used to calculate a per-river relationship between air temperature and river temperature (Figure 3b, 3c). CGDs were calculated as the difference between the average daily temperature degrees, T_d, and a predetermined basal temperature, T_0, (Equation 1) (Chezik et al. 2014):

(eq 1.)

$$CGD = \frac{\sum_{n=1}^{Year} T_d - T_0}{Number\ of\ years\ alive}$$

For each individual, the average yearly sum of CGD was calculated to produce the accumulated CGD, based on emergence and sampling year. Because CGD is calculated based on year of emergence, CGD is a cohort-based parameter. While individuals may vary in longevity, they will be bounded by cohort experience. We standardized CGD by taking the difference of each log yearly value and the mean log CGD across both rivers. The basal temperature was initially defined as 1˚C, based on a minimum physiological growth capacity (Chezik et al. 2014), and because observed river temperatures never reached below zero. To confirm that our choice of basal temperature had no undue effect on our model, a range of basal temperatures from 0˚ to 10˚C was tested (Supplement Figure 4). We found that an increase in basal temperature led to a change in the CGD model parameter scale, but without a change in the Widely Applicable Information Criterion (WAIC) score and therefore no difference in out of sample prediction. WAIC is an information criterion used to assess model differences in out of sample expectation based on the log pointwise posterior predictive density and a correction for effective number of parameters. Therefore, the shrinkage was not due to a reduction in information, but because overall CGD values were smaller. Accordingly, a basal temperature of 1˚C was used for our model to include the maximum posterior variability and to assess our initial assumptions behind the mechanistic relationship of temperature and growth.

To capture the effects of river discharge over an individual's life span, we calculated the average total discharge per year per individual and standardized by taking the difference of each log yearly value and the mean log total yearly discharge across both rivers. Average total discharge was calculated at the scale of the individual as it was expected that experience to environmental variability would vary by individual rather than by cohort. Within cohort variability is likely due to the existence of multiple sites per river. Standardization was necessary for model convergence. Then, we created a directed acyclic graph (DAG) to confirm that there were no causal backdoors created by allowing for two covariates to affect age within the model (Supplemental Figure 1).

Model

We began our analysis with a set of null models with a basic hierarchy of river and used them to test subsequent models' performance via WAIC (Supplemental Figure 2). A lower log-scale WAIC score and smaller δ was evidence that the model structure and covariates had less explanatory power than simply pooling by population (Supplemental Table 1). Model structure changed regarding how river, cohort, CGD, and discharge influenced the intercept and/or slope. Our full model was constructed hierarchically by river and included a random-effects term for cohorts (Figure 4a). Based on the hypothesis that CGD and discharge affect growth rate, we assumed that CGD and discharge only influenced rate of maturation, and that only the intercept varied between rivers. By pooling the intercept by river, we assumed that there were population-based differences in the timing of maturity that were either heritable or could not be captured by the covariates. The variability per cohort was not assumed to be affected by CGD and discharge but was driven solely by differences between individuals within each river and random effects.

The full model assumed a Bernoulli distribution to describe the probability of maturation, p, using a logit link:

$$
\begin{gathered}
y \sim Bernoulli(p) \\
p = invlogit(\beta_r + \beta_1 * Age) \\
\beta_r \sim Normal(0,2) \\
\beta_1 = \beta_2 + \beta_3 * CGD + \beta_4 * Discharge \\
\beta_3, \beta_4 \sim Normal(0,2) \\
\\
\beta_2 = \beta_5 + \beta_{6,c} * \sigma \\
\beta_5 \sim Normal(0,2) \\
\beta_{6,c} \sim Normal(0,1) \\
\sigma \sim Exponential(1)
\end{gathered}
$$

where the probability of maturation, p, is the inverse logit of a linear equation with β_r as the river-pooled intercept and β_1 the slope effect of age-at-maturity. β_1 is determined by the relationship of three slope-effects: β_3 is the slope of the CGD-effect on age, β_4 is the slope of the average total yearly discharge effect on age, β_5 is the random-effects component of the cohort pooled slope, and β_{6c} is the cohort pooled slope (Figure 4b). Variability by CGD, discharge and cohort was allocated within the slope effect of age-at-maturity given the goal of understanding plasticity in timing.

The model was built using a non-centered parameterization a method to increase model effective sample size and improve model convergence. The full model may be subject to over-control bias due to the effects of temperature and discharge (Supplemental Figure 1). Over-control bias is a product of conditioning the model on a variable between the treatment and outcome, and can result in a biased estimate of the treatment parameter effect size.

Size-at-maturity is modelled, by substituting age with size, as individual length (mm) (Supplemental Figure 3). We standardized size by taking the difference of each log individual value and the mean log size across rivers. No other model parameter or nesting was changed.

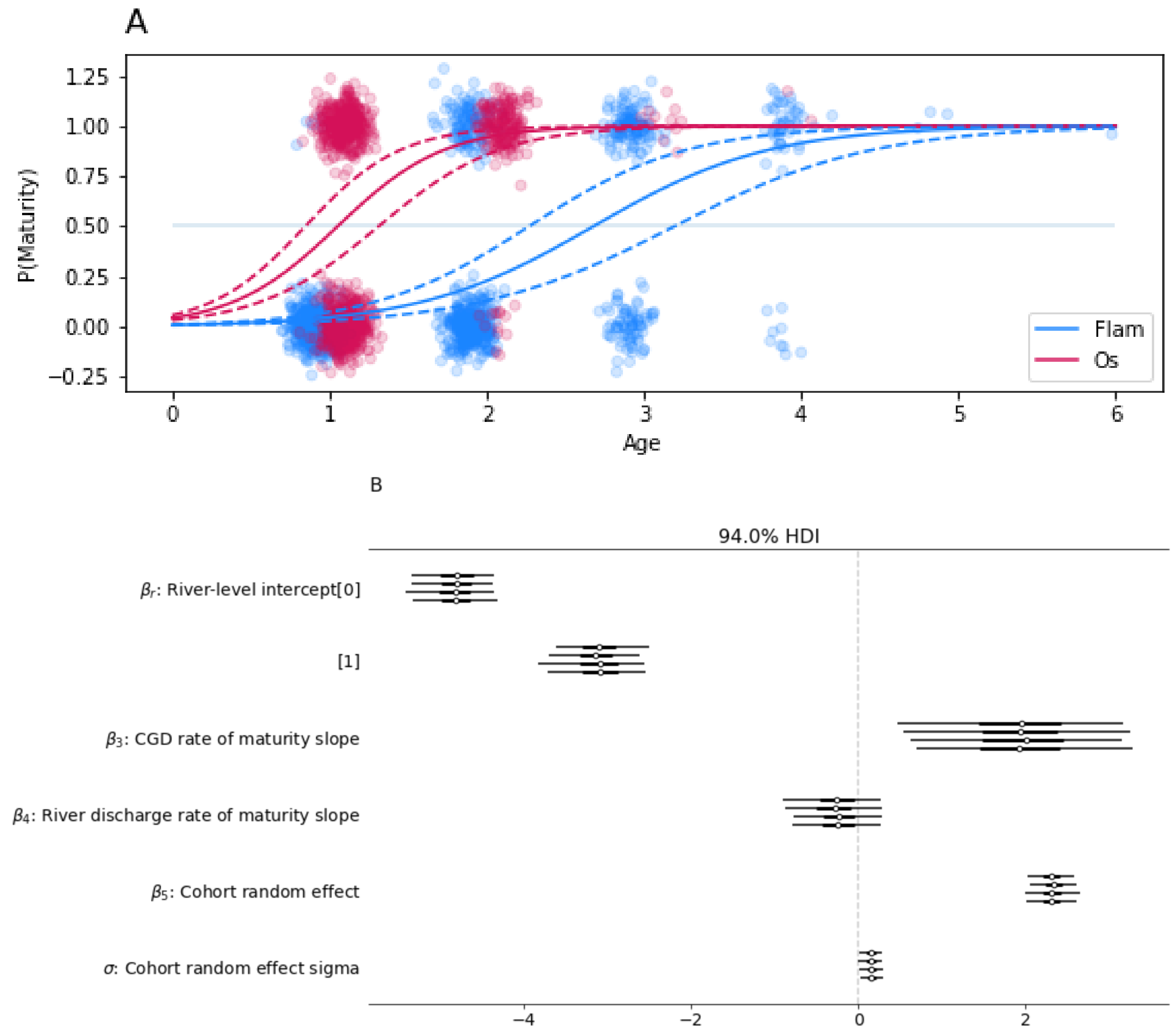


Figure 4. Chapter 2. Figure 4: Panel A, B

Figure 4. Panel A: Age-at-maturity curves (solid) for Flåm (River 0) (Purple) and Os (River 1) (Blue) with standard deviation (dashed), where all ages are +, e.g. 0+. Jittered points represent individuals pooled within the rivers Os (N = 984) and Flåm (N = 1114). Panel B: Forest plot of four-chain sampling for model parameters: $\beta_{r,0}$ (Flåm river level intercept), $\beta_{r,1}$ (Os river level intercept), β_3 (CGD rate of maturity slope), β_4 (River discharge rate of maturity slope), β_5 (Cohort random effect), σ (Cohort random effect sigma).

Projections and predictions

To predict how age-at-maturity may change in the context of a warming climate, IPCC Representative Concentration Pathway (RCP) temperature projections supplied by the Norsk

Klima Service Senter were used to simulate warming river-temperatures. Two climate scenarios were used; RCP 4.5 (moderate) and RCP 8.5 (severe), showing a respective temperature increase in Norwegian air temperatures of ~3 and ~5 ˚C over a 100-year period. The projections were created based on a reference period from 1971 to 2000 with observations from 1900 to 2014, however, we constrained our predictions to 50 years from the final sampling year of parr data (Figure 3d). River discharge was assumed to be constant because future discharge projections were unavailable.

Temperature offsets were converted to total accumulated CGD per year, added to the total CGDs of the final year of sampling (2017), and standardized by taking the log CGD then centering each value by the log mean CGD across rivers. No air-to-river temperature correction was applied as the simulated CGDs were based on offsets from a reference, not true degrees. 50-year predictions of age-at-maturity were calculated by re-sampling the full model posteriors 1000 times, now with CGD projections. For each new year of the simulation, per iteration, that corresponded to the year's offset mean, 10th and 90th percentiles were used to create a random normal distribution. From this distribution an offset was drawn and used to calculate the corresponding CGD, thus accounting for the variability within the projected offsets.

Results

The model parameters are divided between those that affect the model intercept, and those that affect the age-at-maturity. Age at maturity, described by β_r, showed strong evidence for between-river differences, with a mean of -4.797 ± 0.273 years for Flåm and a mean of -3.103 ± 0.316 years for Os. Rate of maturity, β_1, determined by the relationship of three slope-effects, CGD, river-discharge, and cohort random-effect, had a positive logistic slope consistent with our initial hypothesis of that temperature increase growth rate and therefore earlier time of maturity. The combination of these slopes showed a similar river-based divide as the river-level intercept, such that individuals from Flåm and individuals from Os had non-overlapping effect sizes, and Flåm more negative than Os (Figure 4). Therefore, individuals from Flåm experienced slower rates of maturity than Os. CGD had a non-zero, positive relationship with rate of maturity, meaning that an increase in CGD led to a higher likelihood of early maturation in both rivers.

River-discharge had a negative relationship with rate of maturity, meaning that an increase in discharge led to a higher likelihood of delayed maturation. Differences in CGD and river-discharge regimes between rivers drive the river-level differences in rate of maturity in our models. The river-discharge effect does encompass zero, possibly due to over control bias because of the presence of temperature in the same model (Supplemental Figure 1). This is also the case for Supplemental Figure 3. The cohort specific random-effect slope showed a non-zero positive effect size, with evidence for between-cohort differences in rate of maturity.

50-year climate projections were used to predict the impacts of future warming scenarios on timing of maturity in different populations and across different environmental regimes. Since the predicted probability of maturity is calculated with simulated temperature increases, the intervals between predicted ages-at-maturity year to year are not equidistant as the temperature simulations are themselves stochastic and do not show a constant increase over time. The current historical mean A50, based on the full model, are 2.68 years in Flåm and 1.05 years in Os. With a temperature change of 1.775˚C from 2017, the RCP 4.5 50-year projections showed a decrease in A50 by 5.5 [4, 7] (80% highest posterior density) months (0.46 years) in Flåm and 1.44 [0.98, 2.5] months (0.12 years) in Os (Figure 5a, top panel). The shift towards earlier maturation is more rapid in the RCP 8.5 scenario, a total temperature change of 3.859˚C, showing a change in 9 [8.4, 9.6] months (0.75 years) in Flåm and 2.64 [1.8, 2.4] months (0.22 years) in Os (Figure 5a, bottom panel).

The change in age at 50% maturity (A50) by CGD, in average degrees per day per year, is further evidence of a difference in the timing of maturity between river temperature regimes. A50 by CGD showed both a more negative slope and a larger total decrease in Flåm than in Os (Figure 5b). In Flåm, there was a total change in A50 of 0.746 years (~9 months) between 4 and 5˚C, and in Os there was a total change of 0.09 years (~1 month) between 6.78 and 8˚C (Figure 5b). Both rivers experience a relatively constant trend towards earlier maturation with no evidence of a temperature threshold in age-at-maturity.

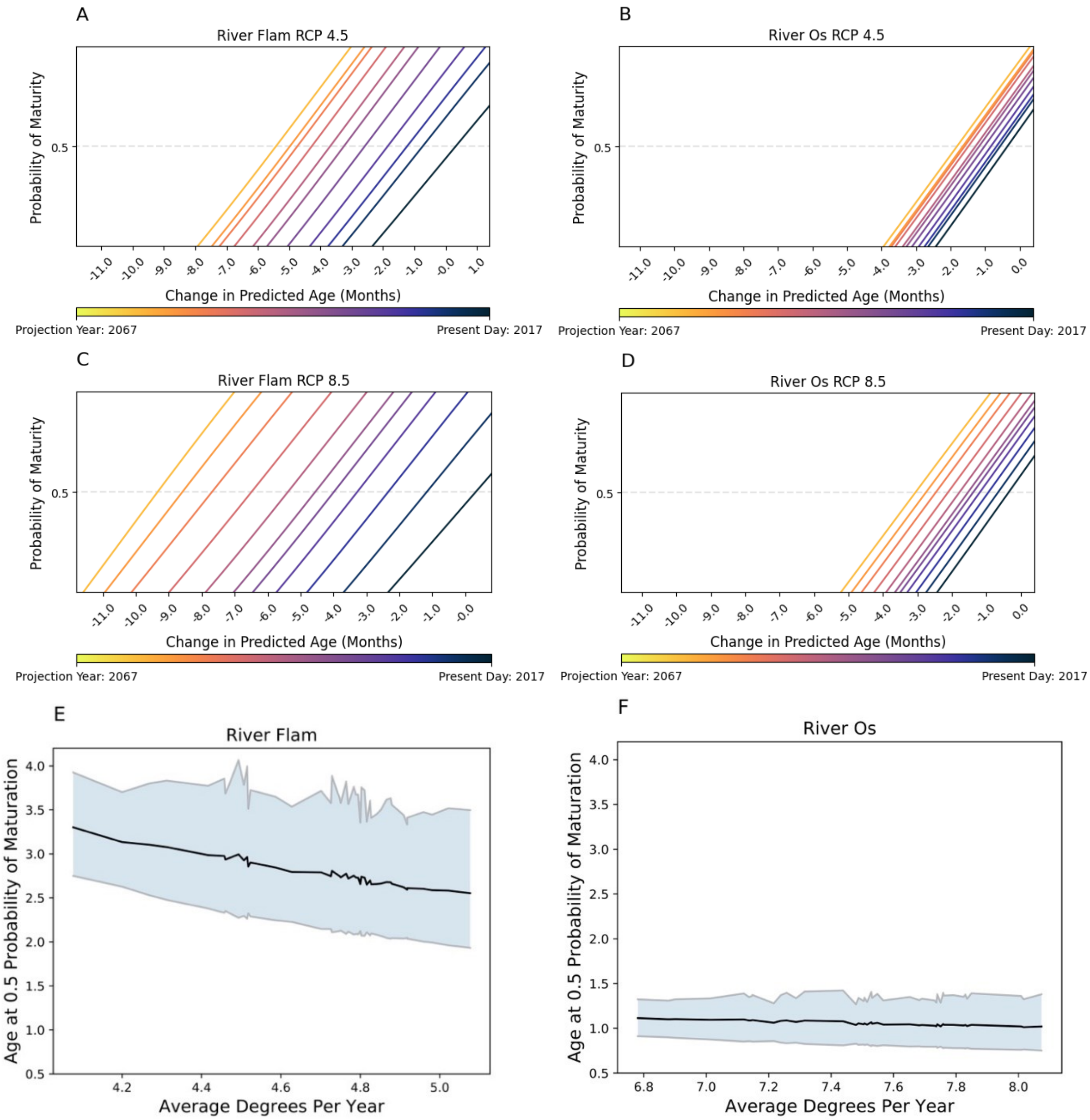


Figure 5. Chapter 2. Figure 5: Panels A-D

Figure 5. Prediction scenarios for RCP scenarios 4.5 (Panels A and B) and 8.5 (Panels C and D) for rivers Flåm (Panels A and C) and Os (Panels B and D), 50 years into the observable future from 2017. Flåm age in offset months 31.2 months (~2.6 years), and Os age in offset months 13.8 months (1.15 years). Every 5 years from initial start year 2017 indicated in color gradient. Age at 50% Maturity by average degrees per year for rivers Flåm (Panel E) and Os (Panel F). Blue shading denotes 5th and 95th quantile ranges.

Discussion

The relationship between temperature and male parr maturity in salmonids has previously been approached through factors such as ovulation timing, embryonic development, food availability, and body size (Nevoux et al. 2019, Hedger et al. 2013, and Morita et al. 2014). Our results show that the total thermal history of Atlantic salmon parr cohorts, expressed as average yearly total CGD, directly impacts rates of male parr maturity, such that higher total CGD per year results in faster maturation. This finding supports the use of CGD in assessing phenotypic trait expression, as it provides a mechanistic link between temperature and maturity via growth (Metcalfe and Thorpe 1990). Rate of maturity is negatively related to river-discharge, such that higher discharge regimes lead to slower rates of maturity. Higher discharge, a product of glacial runoff prevalent in Arctic and sub-Arctic rivers, may increase metabolic strain on parr thus slowing their growth (Gillson et al. 2020). The size-threshold for maturity was found to have a weak relationship with CGD and discharge, and did not vary between populations (Supplemental Figure). This combination of age-at-maturity and size-at-maturity is illustrated by the second row of Figure 1 and can be interpreted as follows: similar maturation size thresholds between populations due to genetic closeness, but a difference in maturation timing due to the relationship between growth rate and the environment. In this regard, we can tease apart the two major aspects of maturation present, namely genetic and physiological. Between cohort variability indicates that independent of environmental variability there exists differences between distinct hereditary groups. Further evidence for the genetic component of size-at-maturity lies in the strength of cohort random effect and identification in the size-at-maturity model. The scenario presented here is like the second row of Figure 1, where similar maturation thresholds exist between populations however differ in timing due to environmental variability. Therefore, the population-level variability is likely a signature of their inherent plasticity.

We estimated that the effect of increasing CGD on A50 is greater at lower temperatures, as fish in warmer rivers are already closer to the upper limit of their maturation rate. This suggests that colder rivers are more responsive to changes in temperature and are more likely to see increased rates of male parr maturity. Previously created reaction norms for temperature and early life history traits in parr such as length-at-emergence have been shown to vary both within and between populations (Hutchings 2011), findings that were also evident here. The relationship between temperature and maturation traits may suggest that populations habiting colder rivers may be more susceptible to trait changes as the climate warm.

At the individual level, previous work has found that growth rate in juvenile salmon varies significantly as a function of environmental conditions (Metcalfe and Thorpe 1992). We found that, while inter-individual variation is present, there is evidence for differences among cohorts once CGD and discharge have been accounted for. Salmonid cohorts are typically used to track heritable changes in populations by treating them as separate breeding groups within the total population. Therefore, changes in the rate of maturity are environmentally and genotype driven. While our model accounted for the effects of temperature and discharge, clear differences in maturity schedules between rivers suggest other un-measured factors are present.

Our RCP 4.5 and 8.5 climate warming simulations predicted earlier maturation of 5.5 and 9.0 months in Flåm and 1.4 and 2.64 months in Os, respectively. For some individuals in each population (especially Flåm), these differences have potential to reduce age at maturity in mature male parr. Early maturation has important population-wide impacts, particularly with respect to how it affects life-history strategies, individual fitness, and population viability. Hutchings (2011) hypothesized that faster average rates of growth will increase the probability that the growth-rate threshold for male parr maturity will be attained, thus increasing the proportion of males in the population that mature as parr. Hedger et al. (2013) and Morita et al. (2014) found that increased temperatures led to higher proportions of MMP. While we did not look at proportions of MMP here, we expect that with projected increases in rate of maturity, the threshold may be reached by a larger proportion of male parr leading to increased incidence of the MMP strategy.

Both Hedger et al. (2013) and Morita et al. (2014) describe maturation timing through indirect relationships of early growth conditions or time of egg-deposition. Therefore, by relating CGD and rate of maturity, we can add a direct mechanism for the predicted increase in MMP incidence. This is possible because CGD is additive over an individual's lifespan and can therefore capture periods of strong growth conditions, and control for cold over-wintering periods. In this regard, our model supports the idea that temperature history is relevant, across age-classes and cohorts, to understand rate of maturity in a population and ultimately the incidence of MMP. Faster maturing individuals will have experienced higher growth rates, and therefore would be expected to have a higher likelihood of attaining the maturity threshold (Myers et al. 1986). We believe that simulating populations by proportion of MMP to anadromous males and incorporating population density controls on the two life-history strategies could yield strong ecological predictions such as predictions of changing population dynamics by Morita et al. (2014). These predictions will depend on the relationship between rate of maturation and incidence of MMP.

The temperature regimes of both rivers represent divergent examples of northern riverine systems due in part to latitude and glacial runoff. River Flåm is one of the coldest salmon breeding rivers in Norway, and river Os is among the warmer rivers, spanning a range of temperature and discharge experiences. River temperatures in Os are near upper incipient lethal temperatures (Elliott 1994). With no physiological temperature limit within the model, there remains the possibility that continued warming conditions could lead to reduced growth or lethal conditions beyond thermal optima. Therefore, the growth threshold for increased proportions of MMP may itself have an upper bound. The model has its own probabilistic limit, due to the logit link, where extreme values in rate of maturity are unlikely and the probabilities become infinite. While this does not provide a hard cap as described, it does limit the possibility that model will reach exceptional temperatures. While we found some evidence for a negative effect of discharge, in some instances discharge could lead to increases in maturation rate. Discharge has also been shown to positively or negatively affect salmon survival depending on the timing of spring melt (Gillson et al. 2020). Annual river discharge may therefore be too coarse a metric to accurately describe changes to discharge between periods of spawning or emergence. Our age-at-maturity predictions were made under warming climate regimes assuming constant discharge, an assumption that remains to be addressed.

Future climate scenarios include many unknowns, which are not limited to the interactions between temperature, discharge, and rate of maturity (Hedger et al. 2013). Our study has shown that rates of maturity in Atlantic Salmon are capable of increasing into future decades. This appears likely independently of whether male parr maturity represents a genetically based alternative strategy or not, given the well-established correlation between growth and probability of parr maturity. Based on the described relationship between growth rate threshold and incidence of MMP, this may lead to increased incidence of MMP. Changing population demographics can have major consequences for conservation and management practices, as higher proportions of MMP are predicted to reduce the male at-sea population, making female salmon populations increasingly vulnerable to at-sea fisheries pressures (Morita et al. 2014). Proportion of MMP per river can range up to 60% of the male population (Myers 1984). Therefore, decreased Atlantic salmon abundance via higher incidence of MMP in Arctic and sub-Arctic populations may contribute to the ongoing decline of Atlantic salmon (Hedger et al. 2013; Jonsson and Jonsson 2009; Todd et al. 2008; Todd et al. 2021), increasing the importance of climate-linked conservation and fisheries resource management. What remains unknown is the relative fitness between the strategies of MMP and anadromous males, and what may limit their proportions per population. While both strategies are persistent, the question may be raised as to under what conditions their fitness may differ. On-going research on the migration of MMP will be important to understanding the implications to mortality and at-sea populations.

More generally, our work provides an empirically based predictive framework for exploring how the frequency of alternative mating strategies within populations might be affected by climate change. The potential ramifications for population viability may be profound for some species, depending on the extent to which their alternative life histories are influenced by thresholds for which the probability of attainment is partially influenced by temperature.

Given the influence that the environment can have on phenotypic traits, such as individual growth and body size, the question can be raised as to how climate change, and its concomitant increase in temperature, will affect the incidence or frequency of alternative life-history strategies. This question, largely unexplored to date, is the primary one that we address here, based on time series of alternative strategies of unprecedented length in two populations of Atlantic salmon.

Given the influence that the environment can have on phenotypic traits, such as individual growth, the question can be raised as to how climate change, and therefore an increase in temperature, will affect the plasticity of alternative life-history strategies. This question, largely unexplored to date, is the primary one that we address here, based on time series of alternative strategies of unprecedented length in two populations of Atlantic salmon.

Supplement: Methods

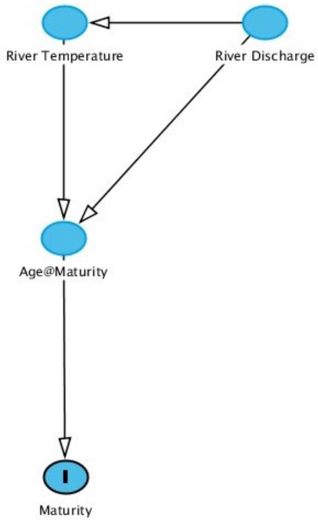


Figure 6. Chapter 2. Supplemental Figure 1.

Supplemental Figure 1. Directed acyclic graph for age-at-maturity modelling, including predictors of river temperature, river discharge, age-at-maturity, and the outcome of maturity. Produced using Dagitty.net.

Supplemental Table 1. multiple regression table of WAIC value comparisons

Table 1. Chapter 2. Supplementary Table 1.

Model Title	Model Rank	WAIC score	p_waic	d_waic	Weight	Standard Error	dse	Warning	WAIC Scale
Full Model	0	-1042.892	17.201413	0	0.920801	21.521043	0	FALSE	log
Null 4	1	-1052.676	3.94581	9.784502	0	21.431609	4.338301	FALSE	log
Null 2	2	-1057.032	3.001018	14.140458	0.079199	21.248395	5.704485	FALSE	log
Null 3	3	-1061.114	3.186285	18.222235	0	22.145891	5.811061	FALSE	log
Null 1	4	-1342.829	1.898105	299.93675	0	14.48643	19.73815	FALSE	log

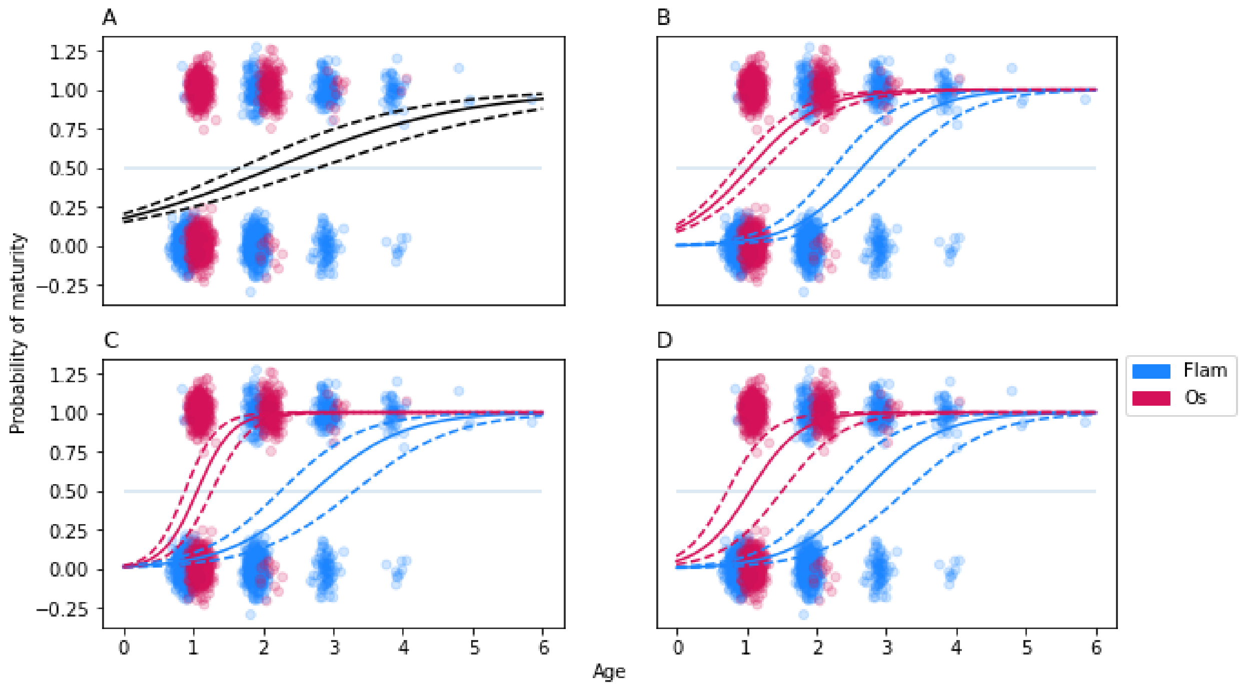


Figure 7. Chapter 2. Supplementary Figure 2: Panels A-D

Supplemental Figure 2 (A, B, C, D). Probability of maturity at age for null models specificed in table 1: Null 1: A, Null 2: B, Null 3: C, Null 4: D. Age-at-maturity curves (solid) for Flåm (Purple) and Os (Blue) with 5th and 95th percentiles (dashed), where all ages are + i.e. +0. Jittered points representing individuals pooled between the rivers Os (N = 984) and Flåm (N = 1114).

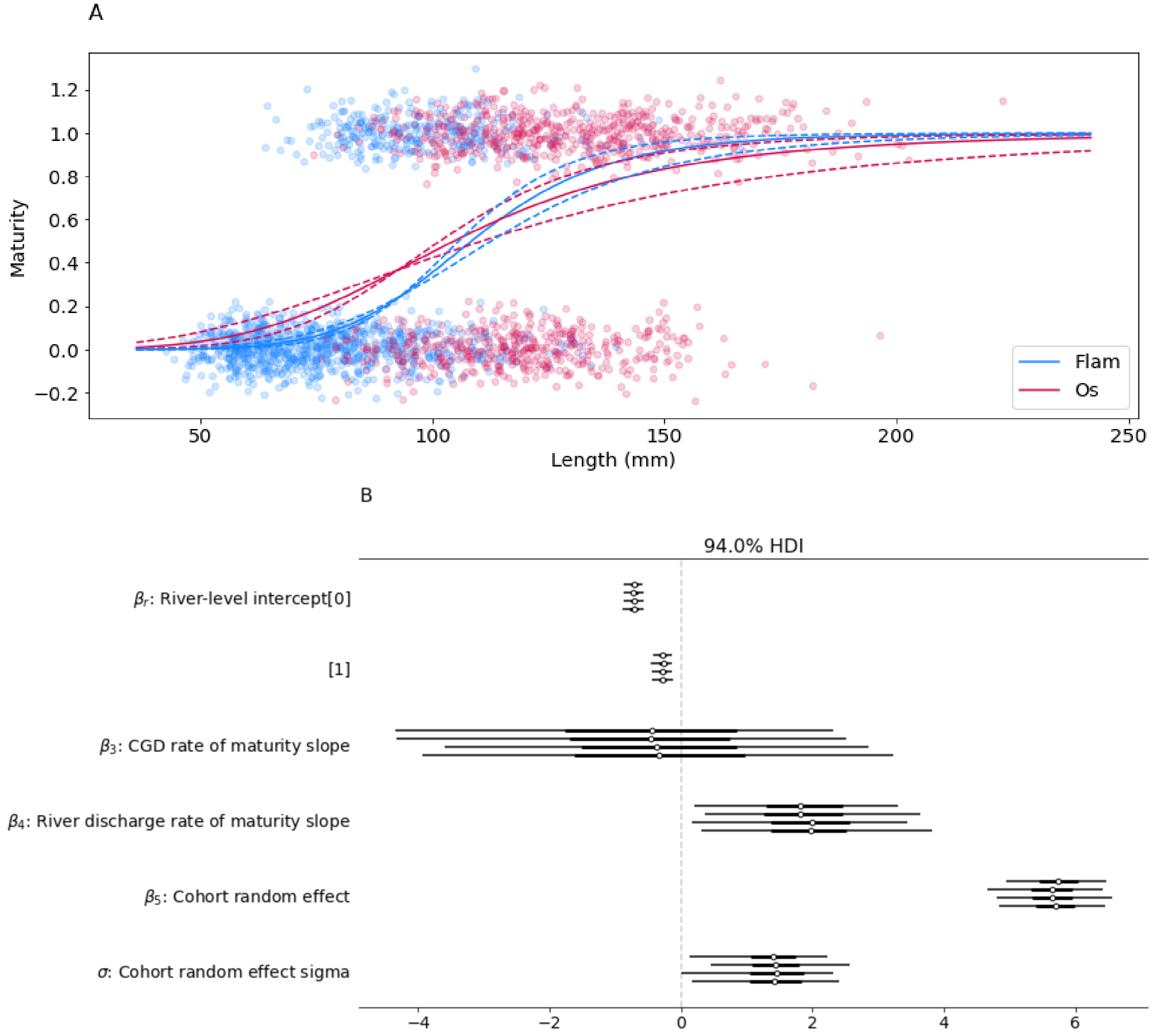


Figure 8. Chapter 2. Supplementary Figure 3: Panel A, B

Supplemental Figure 3. Panel A: Size-at-maturity curves (solid) for Flåm (River 0) (Purple) and Os (River 1) (Blue) with standard deviation (dashed), where size is measured as length (mm). Jittered points representing individuals pooled between the rivers Os (N = 984) and Flåm (N = 1114). Panel B: Forest plot of four chain sampling for model parameters: $\beta_{r,0}$ (Flåm river level intercept), $\beta_{r,1}$ (Os river level intercept), β_3 (CGD rate of maturity slope), β_4 (River discharge rate of maturity slope), β_5 (Cohort random effect), σ (Cohort random effect sigma).

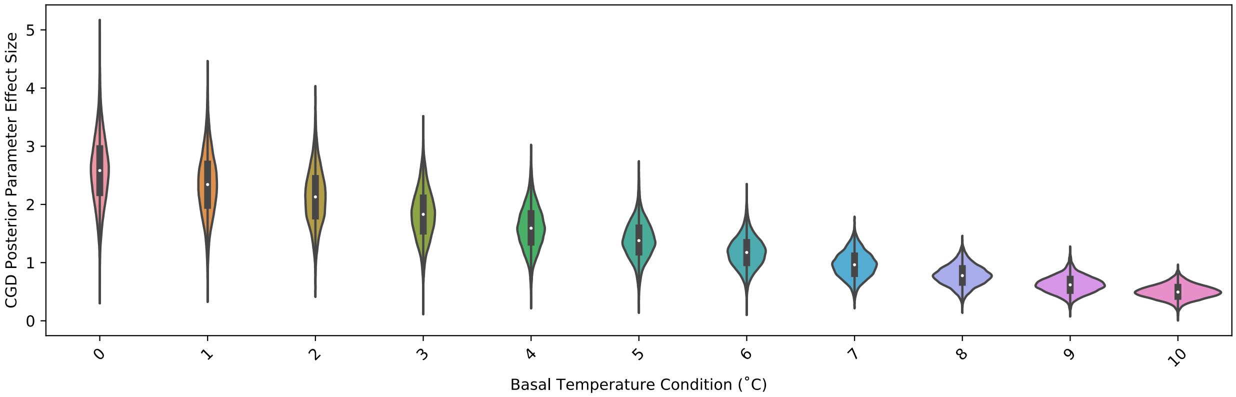


Figure 9. Chapter 2. Supplementary Figure 4.

Supplemental Figure 4. Changing T0 (basal temperature condition (C), see equation 1) by posterior 'CGD' parameter effect size. Each poster parameter was calculated with the full model, described in Methods, while discharge was assumed constant to replicate the condition of the predictive stage.

Supplement: Results

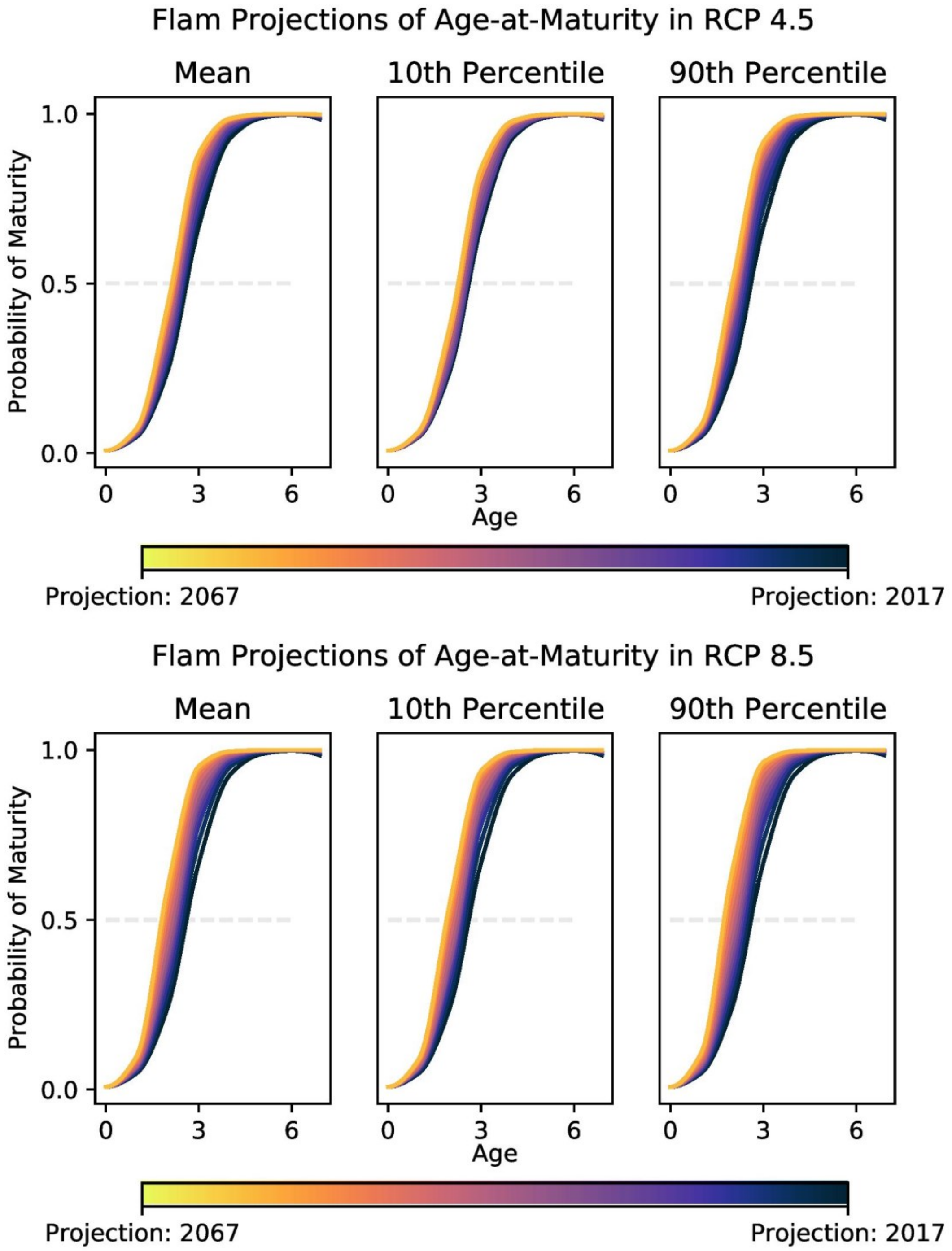


Figure 10. Chapter 2. Supplementary Figure 5

Supplemental Figure 5. Flam probability of maturity by age predictions under climate scenario (Top) RCP 4.5, and (Bottom) 8.5 temperature projections. (Left) mean, (Middle) 10th percentile, (Right) 90th percentile of the projected age-at-maturity logistic parameters. Colour-bar gradient represents predictions in 5 year intervals over a 50 year period from 2017 to 2067.

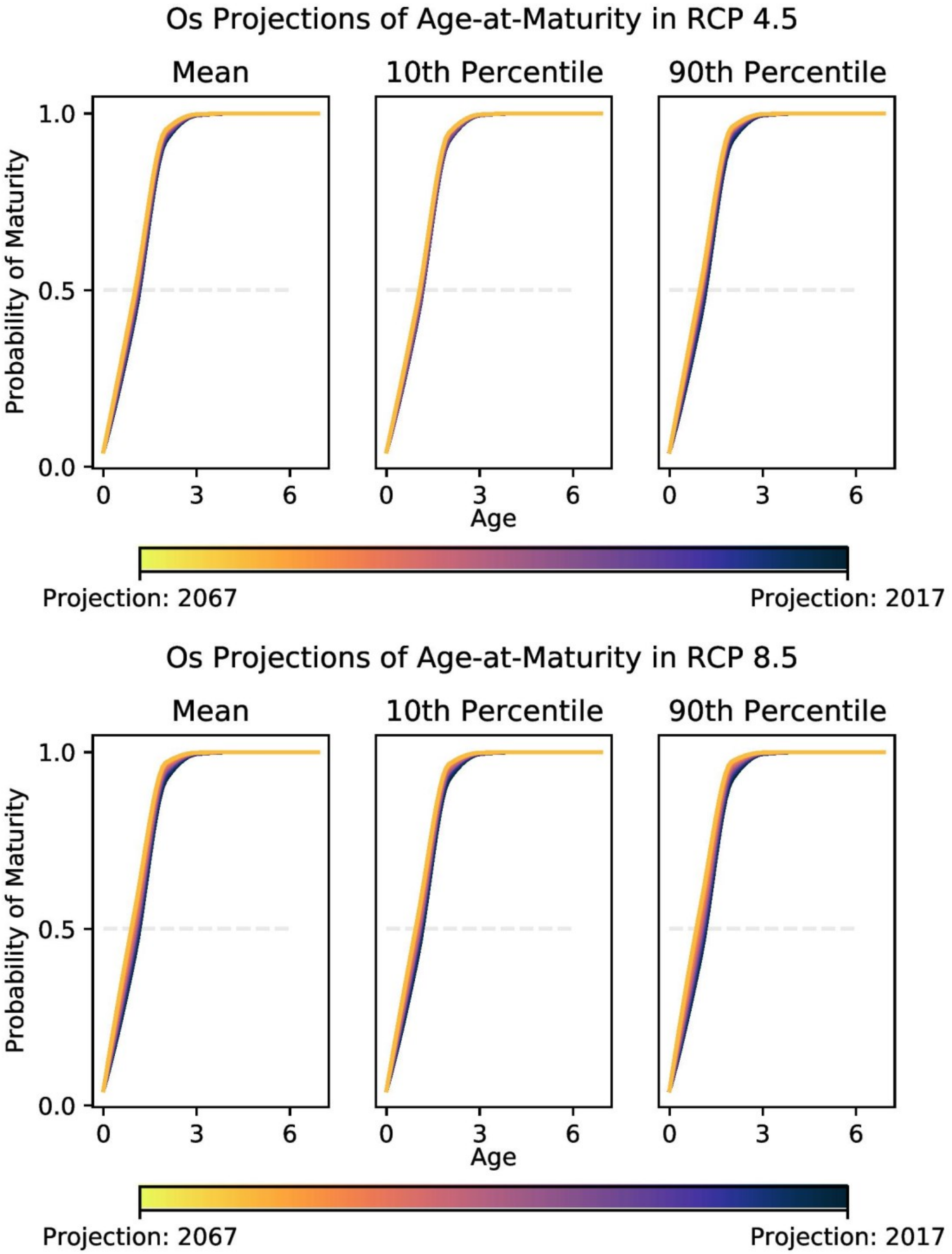


Figure 11. Chapter 2. Supplementary Figure 6

Supplemental Figure 6. Os probability of maturity by age predictions under climate scenario (Top) RCP 4.5, and (Bottom) 8.5 temperature projections. (Left) mean, (Middle) 10th percentile, (Right) 90th percentile of the projected age-at-maturity logistic parameters. Colour-bar gradient represents predictions in 5 year intervals over a 50 year period from 2017 to 2067.

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Chapter 3. Environmental and demographic drivers in the timing of phase-change in *Chlororus sordidus* and *Chlorurus spilurus*

Tor Kitching, Brett Taylor, Matt Mclean, Chris Mull, Aaron MacNeil

Introduction

Life history trait plasticity is a result of adaptation by species to different environments (Barot et al. 2004; Stearns 1989). Many fish species, such as members of the Scaridae family, occupy large spatial ranges over a spectrum of environmental regimes. Adaptation to these different regimes requires different strategies to improve fitness, including the tradeoffs required to survive and succeed in each environment. To assess fitness related to the probability of successful reproduction, we can utilize the probability of sexual maturation. Maturity, a function of growth, survival, and environmental variability, is necessary for reproduction but remains understudied in most species. For most fishes, maturity can only be determined through physiological examination; however, for a subset, such as wide-ranging protogynous coral reef parrotfish, morphological changes make maturity status obvious.

Protogynous hermaphrodites exhibit female to male sex change often represented by three phases; initial phase (IP), transitional phase (TC), and terminal phase (TP) (Taylor et al. 2018; Robertson and Choat 1974). Protogynous phases are classified by morphological changes, such as color. Male and female dimorphism exists and is evident in body size where males are larger than females at a given age. Individual variability in the timing of phase is driven in part by growth and mortality rates, and environmental condition (Gust 2004; Taylor et al. 2018). The rate of growth in individuals is a major factor in determining the timing of maturity for fishes and is believed to operate via a growth threshold or size threshold (Hutchings 2011), where individuals must reach a specific size before they can mature. It is, therefore, likely that similar growth thresholds may be present for sex-change transitions, due to the similar presence of fitness tradeoffs between reproductive strategies. Sexual transformation, sex reversal, or, phase-change, is not solely dependent on the individual (Shapiro 1991, Gust 2004) but instead also involves population hierarchy and demographic pressure. While individuals may mature and undergo reproduction without undergoing sex-change (Choat et al. 1996), sex-change is more often used in reference to life history transitions in protogynous fishes than sexual maturity (Van Rooij et al. 1995). The driver behind sex-change is the improvement of reproductive success or value of the individual dependent on the size and social structure of the population (Taylor et al. 2014), which assumes that there is a difference in energetic requirements between sexes.

For parrotfish social hierarchies, phase-change functions as a trade-off of reproductive reward and energy output (Van Rooij et al. 1995), depending on the density of the population, presence of dominant males in harems, and the reproductive strategy of the males. In the case of a harem, unless the male were to die or leave, other individuals are unlikely to phase-change. There is evidence in some members of Scaridae (Van Rooij et al. 1995) that earlier phase-changes hold a fitness advantage due to lower lifespan costs of life as a male and higher potential reproductive success per individual. The presence and absence of these grouping effects is believed to be strongly driven by local population densities where dominant males hold greater influence in lower density populations (Hoffman 1985, Gust 2004).

Variability in phase-change timing and size plays an important role in the demographic composition of parrotfish populations. Taylor et al. (2014) showed that depending on reef position and fisheries pressure, the size-at-phase changes. Reef location and fisheries pressure are associated, as fishery pressure increases with proximity to human settlements, therefore reefs that are further offshore can be more sheltered from fishing. Fisheries induce change on phase-change through size selection; however in protogynous fish, size selection is also a male selective pressure. In addition, if individuals' phase-change at a smaller size or experience more rapid growth rates, it is likely that they will also experience different patterns in mortality, for example in *Naso unicornis* (Taylor et al. 2019), where more rapid growth results in higher mortality and abruptly decreases across age classes. Therefore, if older age-classes are reduced by both size selection and a change to natural mortality, the overall reproductive success of a population may decline. It is in this way that a change in size-selection can affect the size-at-phase and result in a change to population demographic composition. Demographic composition can be studied through their sex ratio where, if phase-change is driven by an increase in individual reproductive success, populations with a higher proportion of males will likely see an earlier phase-change compared to other populations conditional on density. The effect of different sex ratio compositions on parrotfish fecundity is currently unknown.

While demographic characteristics are important, phase-change plasticity is also driven by environmental conditions (Taylor et al. 2014). Environmental conditions are related to maturity through growth, a relationship commonly described by temperature or habitat quality. Higher growth rates are related to warmer temperatures, driving rates of maturity faster and earlier. For example, temperature plays both an important metabolic role in growth in fish and is also a proxy for latitudinal differences and habitat quality. In coral reefs, environmental characteristics can be highly variable at small scales due to the complexity of reef structures;

however, this work will be focused on both inter and intra-population wide differences in phase-change and will therefore utilize broad scale measurements.

Bullethead parrotfish (*Chlorurus sordidus* and *Chlorurus spilurus*) are coral reef associated species targeted by fishing across the equatorial Indo-Pacific and into the Red Sea. Bulletheads play a role in the maintenance and structure of coral benthic communities through grazing and bioerosion (Campbell and Pardede 2006), most notably in the prevention of macroalgal dominance (Carpenter 1986, Mumby et al. 2006). As bio-eroders, body size is related to their rate of grazing and therefore their impact on reef function. Given the known size-selective impacts of fishing, it is important to have accurate estimates of life history characteristics such as growth, maturity, and sex-change. The dominant fisheries engaged with parrotfish, and specifically bulletheads, are spearfishing and netting (Taylor 2014). Bullethead parrotfish are frequently present in high densities, representing a widespread, protogynous species to understand how life history characteristics such as sex change may vary in response to environmental and demographic differences.

Assessments of life history traits such as time and size sex-change have been explored in some species of Parrotfish (DeMartini et al. 2018, Pardee et al. 2020) in near-shore fisheries management. To-date these analyses have been focused on estimating growth rates, age and size at sexual maturity, and lifespan since together they can describe the demographic structure of a population. This is particularly relevant for parrotfish, where demographics can vary at both the reef and basin scale (Pinca et al. 2012; Taylor and Choat 2014; Taylor 2014; Heenen et al. 2016). While the influence of environment and human pressure has been explored in similar species across their full habitat range (Taylor et al. 2018), no work to date has been done on *C. sordidus* and *C. spilurus*.

Maturity is typically approached through the commonly used fisheries metrics of age and size at 50% maturity, also referred to as A50 and L50 respectively. A50 and L50 indicate the age or size at which half the population has likely reached maturity; they are commonly used in fisheries management to evaluate the timing and quantities of yields. A50 and L50 are informative from a life history perspective as they can be used to differentiate between populations since they contain underlying information of growth rate and survival. Here, A50 and L50 will be referred to as A50P and L50P, given that estimates will be the probability of phase change, not sexual maturity. Due to the high expected variability between populations, hierarchical models will be used to facilitate partial pooling, which allows for information from each level of the model to inform each other level such that data-sparse populations will be informed by the entire dataset. This is particularly relevant to coral reef systems that are hierarchically structured (MacNeil et al. 2009) and where sampling effort can vary greatly.

Here we identify the spatial patterns, and relationships of environmental, human, and demographic covariates over the complete range of *C. sordidus* and *spilurus* parrotfish, with estimation of between nation and reef level variability, to the timing of phase change using a hierarchical model framework. It is expected that size at phase will show a relationship to environmental condition, fisheries pressure, and demographic characteristic to be modelled using temperature, chlorophyll-a, human gravity, sex ratio, and population density.

Methods

Study Populations

Chlorurus sordidus and *C. spirulus* were surveyed across the Indo-Pacific in 29 nations and 84 reef sites, spanning their range from -175˚ to 158˚ longitude, from 1993 to 2019. Across all sampling sites, biological data was collected including species, population density, fork length, age measurements using cross-sections of sagittal otoliths, and body color-phase, from 2391 individuals.

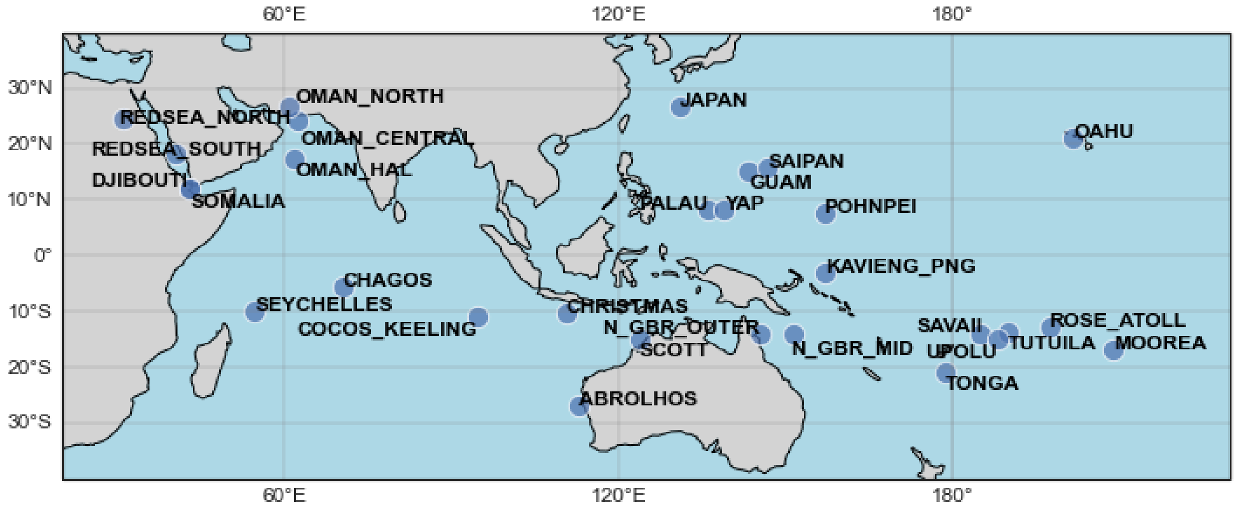

Figure 12. Chapter 3. Figure 1

Figure 1. Map of all nations surveyed for *Chlorurus sordidus* and *C. spirulus* from 1993 to 2019.

Collection Methods

To cover the range of size and age-based reproductive traits, samples were collected from the field via spear-fishing at all locations except Oahu, where samples were predominantly derived from local fish markets. All fished samples were processed fresh dead, or at least on the same day of collection. Size was measured as fork length, to the nearest mm. Otoliths were recovered where skulls were intact for all sampled individuals, dried and preserved for later study. Age was determined from sectioned sagittal otoliths, whereby annuli were counted until

2 or more equal counts were attained via blind reading 1-2 weeks apart (following Taylor and Choat 2014). *C. sordidus* and *spilurus* are closely related sister species that were only recently confirmed as separate (Parenti and Randall 2011) based on mitochondrial 16S rRNA gene sequencing. Morphological and trait-based differences are minimal between the species.

Color-phase represents a morphological transition during the sexual transition from female to mature male or from primary (sneaker) male to secondary male, which is generally associated with changes in reproductive behaviour (Choat and Robertson 1975). Color-phase was always recorded for each individual where gonadal processing was only done on a subset where sampling allowed following work by Taylor et al. (2018). The determination of sexual maturity between histology and color-phase differs by 6% (Taylor et al. 2018). The color-phase present in the data were grouped by sex into inital phase (IP), terminal phase (TP), transitional individuals (TC). The IP category includes both sneaker males and females and the terminal phase is exclusively males. IP males have been demonstrated to occur at a low proportions low enough to have little effect on estimates of phase-change timing (Taylor et al. 2018). Un-detected phase individuals were likely resulting from errors in surveying and were excluded from analysis. Transitional individuals were included in the terminal phase grouping, as these individuals were undergoing the transitional process that was under investigation.

Population demography

Bullethead population demography was captured using two variables: population density and sex ratio per unit length at year of sampling per site. Reef sites were surveyed by transect to calculate population density in addition to biological sampling. *Chlorurus sordidus* and *C. spirulus* were grouped together for estimates of density and sex ratios at the one sampling location where they overlapped (Christmas Island, Indian Ocean). Transects densities were then used to calculate density per hectare. Sex ratio, based on samples from the biological data set, was calculated dividing the number of individuals at the IP phase over the sum of the number of individuals in the IP and TP color-phases per site per year of sampling. Sex ratio per reef was then divided by mean length per reef to produce sex ratio per unit length, referred to as sex ratio hereafter. Both population density and sex ratio were z-scored for model fitting and ease of comparison.

Temperature and Chlorophyll-a

Sea surface temperature (SST) and Chlorophyll-a (Chl-a) measurements were taken from the Hadley Centre Global Monthly Average Sea Surface Temperature (HADSST) and AQUA Moderate Resolution Imaging Spectroradiometer (MODIS) satellite databases respectively. These databases were chosen based on their resolution, 0.0417˚ (HADSST, 1870 to 2020) and 0.025˚ (AQUA, 2003 to 2021), and time frame to match the desired reef-specific resolution. Per site measurements were used to calculate 3-year averages. For Chl-a values in sample years earlier than available measurements, the earliest 3-year average value was estimated as the 2004 3-year average. We assume that there was little significant change between 1993 and 2004. 3-year averages were used to allow for long-term variability but reduce noise between years caused by anomalous events. In the case of non-exact position matches, the nearest pixel to the site latitude and longitude was taken. SST and Chl-a were standardized by z-score, subtracting their mean and dividing by their standard deviation.

Human Gravity

Human gravity was calculated following the work of Cinner et al. (2016) and represents the potential interactions between reef habitats and either major urban markets or the nearest human settlement. Human gravity is based on estimates of population and travel time between to the reef from the population center. The final gravity value is calculated by dividing the nearest population by the squared travel time between settlement and reef site. For the model, we used total gravity, although other variants include gravity of nearest city, settlement, or population. Total gravity is also referred to as cumulative gravity as it is the combined gravity of all human settlements within a 500 km radius of the location. Total human gravity was standardized by z-score.

Model

The model was developed to examine the hierarchical influence of environmental and biological factors on the length at phase change of the bullethead parrotfish clade. Initial modelling used null (intercept-only) models to understand and build the basic hierarchy of nation, and reef site. These model sets were compared using WAIC, looCV and manual checking of pareto-k values. Lower log-scale WAIC scores were indicative of better out-of-sample predictive performance. Pareto-k values from point-wise Loo testing were assessed via criteria from (Vehtari, Gelman, Gabry 2015), with values >0.5 indicative of high-leverage data points.

A full model was structured with nation level (29), and site level (84) intercepts based on the null model results, since in a logistic curve the intercept controls where the 0.5 probability point lies or in life history terms, the L50 or in this case the length at 50% phase-change. There was no hierarchy on the slope of the inverse logit equation, as the slope influences the steepness around the L50 or the rate of phase change. Finally, the model was conditioned on age according to Barot et al. (2004) to account for both variations between age-classes and for differences in survival.

The full model assumed a Bernoulli distribution to describe the probability of phase-change at size (fork length (cm)), using a logit link:

$$y \sim Bernoulli(p)$$
$$p = invlogit(\beta_i + \mu_i * SIZE)$$
$$\mu_i = Lognormal(0, 0.25)$$
$$\beta_i = \beta_S + \beta_6 * AGE + \beta_7 * SPECIE$$
$$\beta_S = \beta_N + \beta_{Reef} * \sigma_{Reef} + \beta_1 * SST + \beta_2 * CHLA + \beta_3 * GRAV + \beta_4 * DENSITY + \beta_5 * SRS$$
$$\beta_{1,2,3,4,5,6,7} \sim N(0, 1)$$
$$\beta_{Reef} \sim N(0, 1)$$
$$\sigma_{Reef} \sim Exp(1)$$
$$\beta_N = \mu_N + \beta_{Nation} * \sigma_{Nation}$$
$$\beta_{Nation} \sim N(0, 1)$$
$$\sigma_{Nation} \sim Exp(1)$$
$$\mu_N \sim N(0, 1)$$

Where the probability of phase-change a size, p, is the inverse logit of a linear equation. Within the intercept of the base function, the slopes of the covariate effects are β_1 for SST, β_2 for CHL-A, $\beta_3$for human gravity (GRAV), β_4 for fish population density (DENSITY), β_5 for sex ratio (SRS), β_6 for age, and β_7 as an offset for *C. spilurus*. β_s is the site-level intercept and β_N is the nation-level intercept. A lognormal slope was chosen for mu to restrict the model to positive slopes, as growth can only be positive and there is no evidence of backwards transitions from TP to IP.

To identify possible spurious correlations in the model construction, a directed acyclic graph (DAG) was created. DAG's include the conditional independence relationships between all model parameters and are created based on current expectations of information flow (Textor et al. 2017). According to the DAG of the full model (Supplemental Figure 1), sex ratio is a collider for human gravity and density. When the model excluded sex ratio, to cutoff the causal backdoor, there was no effect on the parameter estimates of human gravity and density. Therefore, there did not appear to be evidence that sex ratio was biasing the estimates of gravity and density, and sex ratio per size remained in the full model.

Model convergence was assessed using R-hat, posterior traces, and estimates of effective sample sizes. Large R-hat values paired, low effective sample sizes, and poor traces are all signs of poor to model convergence. To prevent divergences, non-centered parameterization was employed in model development. Finally model fit was checked using both prior and posterior checks.

Results

The full model produced a global mean logistic curve with an estimated a global L50 phase-change of 21.8 +/- 3.8 cm at average conditions across all covariates (Figure 3). Variability both within and between nations and sites were captured by the nation and site-level random effects, and while nation had a negative effect size across all nations, the effect size of the site level random effect changed sign (Supplemental Figure 2 and 3).

The remaining six covariate effect sizes will be broken down into three categories: environmental, human, and demographic (Figure 4, Table 1). All covariates presented were at the level of site, and therefore explain the degree of variability between sites in addition to the random site effect. Due to the relationship of terms within the inverse logit, parameters nested within the intercept have an inverse relationship to that of a linear equation. The first of the environmental covariates, SST, was found to have a weak positive effect size that bounded zero resulting in a decrease in size-at-phase with higher temperatures. Conversely, CHL-A was found to have a weak near-zero negative effect size that bounded zero. Given that the effect size bounds zero, the effect is of CHL-A do not have explanatory power conditional on the model. The sole human covariate of human gravity, a proxy for fisheries pressure, had a weak near-zero negative effect that bounded zero. Finally, both demographic covariates had stronger positive effects, with the strongest effect of sex ratio per unit size and population density, where sex ratio per unit size showed the strongest effect size of estimated covariates. Therefore, both demographic characteristics were found to decrease the size-at-phase through the model intercept in instances of high density and a high proportion of males per size. The second individual level fixed variable was age which was found to have a strong negative effect on L50P, Table 1. In this regard, higher ages were found in individuals at smaller size-at-phase, which may be an indication of increased survival and subsequent improvements to lifespan. Finally, the intercept fixed effect for species, at the level of the individual, was a dummy variable for species identity, at average conditions, the mean L50P per species was 20.8 +/- 4.12 cm for *C. sordidus*, and 21.0 +/- 4.20 cm for *C. spilurus*.

All r-hat values were between 1.0 and 1.01 indicating convergence (Table 1, Figure 5). Effective sample size bulk and tail histograms (Figure 5) also indicate that the model converged without issue and retained large effective sample sizes relative to an N = 2391. Pointwise loo testing on the full model showed 15 points over the threshold of 0.5, however as less than 1% of the sample size, the model was assumed to have converged.

Figure 6 shows the global map of L50P per nation. It can be observed that there are more instances of large size-at-phase at higher latitudes, with the smallest L50P near the equator. There also appears to be smaller overall L50P in the Indian Basin versus the Arabian and Pacific Basins. Finally, as is evident in the islands of Micronesia, there is strong variance between nations despite being close geographically.

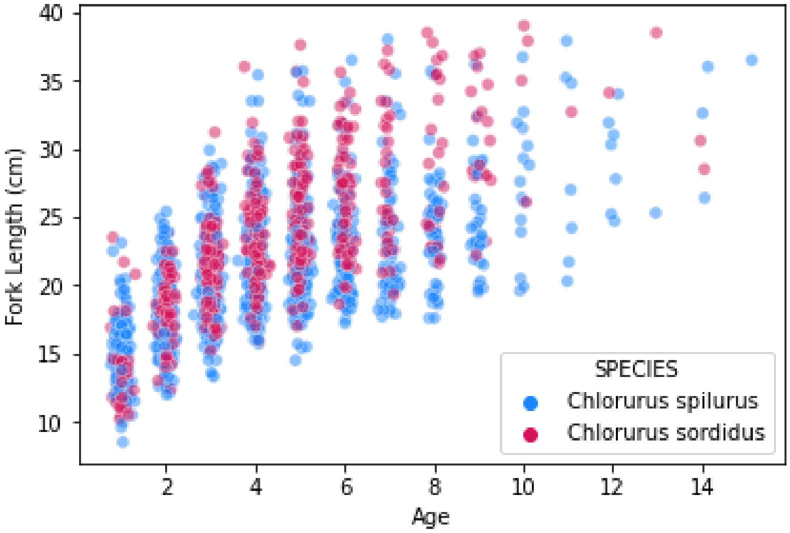

Figure 13. Chapter 3. Figure 2

Figure 2. Fork length (cm) at age for *C. sordidus* (red) and *C. spilurus* (blue), N = 2391.

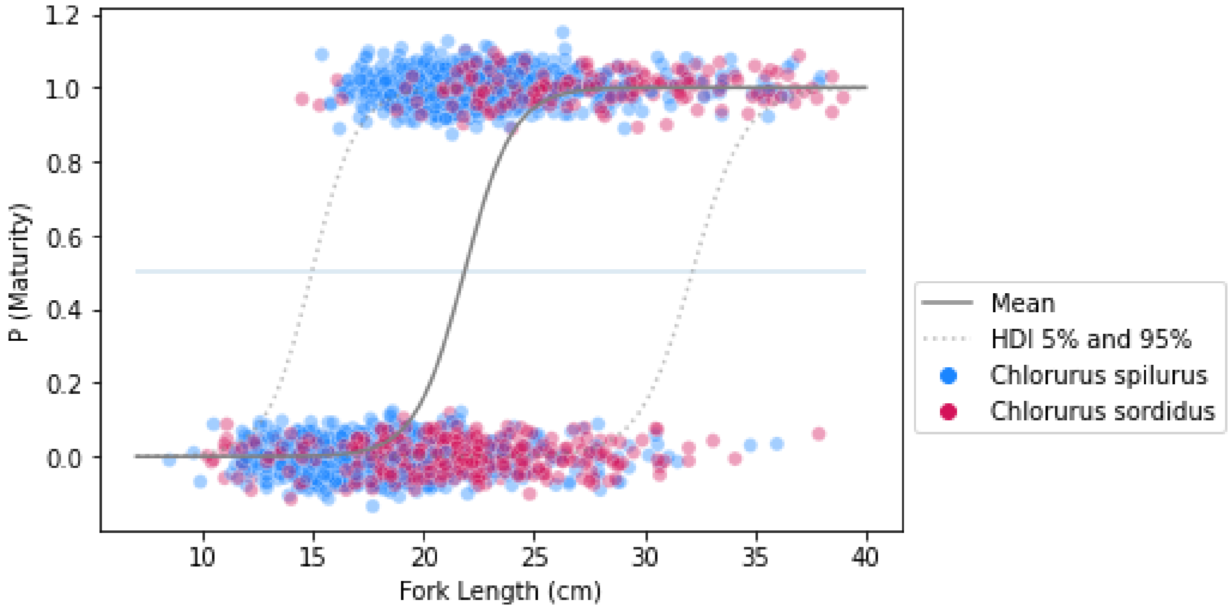

Figure 14. Chapter 3. Figure 3

Figure 3. Length (Fork length (cm)) at phase change ogive for the global mean line (grey) with 5th and 95th percentile estimates (dotted), N = 2932. Jittered points colored by species: *C. sordidus* (red) and *C. spilurus* (blue), N = 2391.

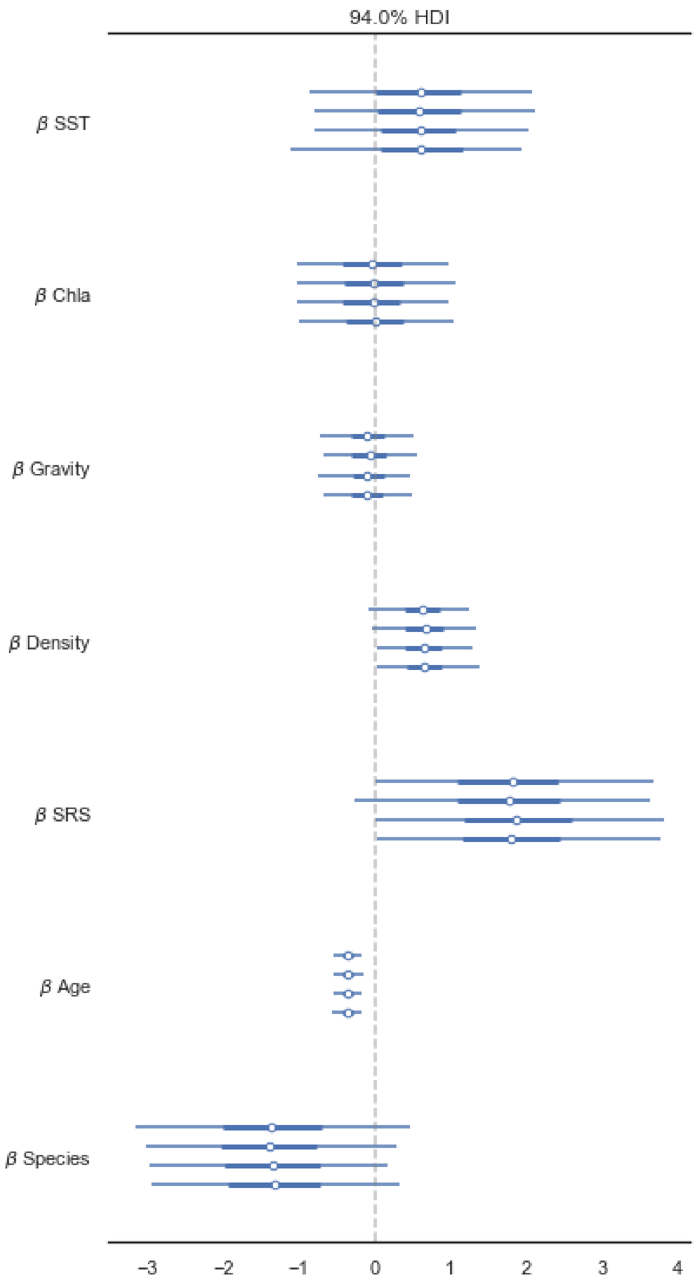

Figure 15. Chapter 3. Figure 4

Figure 4. Forest plot of 4-chain sampling of covariate model parameters at the reef level hierarchy from the full model: SST, Chl-a, Human Gravity, Bullethead Density, and sex ratio of mature individuals (males) per unit size, with 94% high density intervals.

Table 1. Summary table with mean, standard deviation, HDI 3 and 97% bounds, bulk effective sample size (Ess_bulk), tail effective sample size (Ess_tail), and Rhat for the model β parameters of SST, Chl-a, human gravity, fish population density, sex ratio per unit size, age, and species random effect.

Table 2. Chapter 3. Table 1

Parameter	Mean	Std.	Hdi_3%	Hdi_97%	Ess_bulk	Ess_tail	R_hat
β **SST**	0.591	0.791	-0.849	2.142	2012.0	2679.0	1.0
β **Chl-a**	-0.028	0.554	-1.030	1.024	3014.0	3114.0	1.0
β **Gravity**	-0.093	0.324	-0.680	0.539	3015.0	2839.0	1.0
β **Density**	0.645	0.360	-0.013	1.345	3285.0	3010.0	1.0
β **SRS**	1.810	1.016	0.038	3.862	3780.0	2691.0	1.0
β **Age**	-0.356	0.102	-0.541	-0.158	5761.0	3289.0	1.0
β **Species**	-1.351	0.914	-3.049	0.302	3531.0	2791.0	1.0

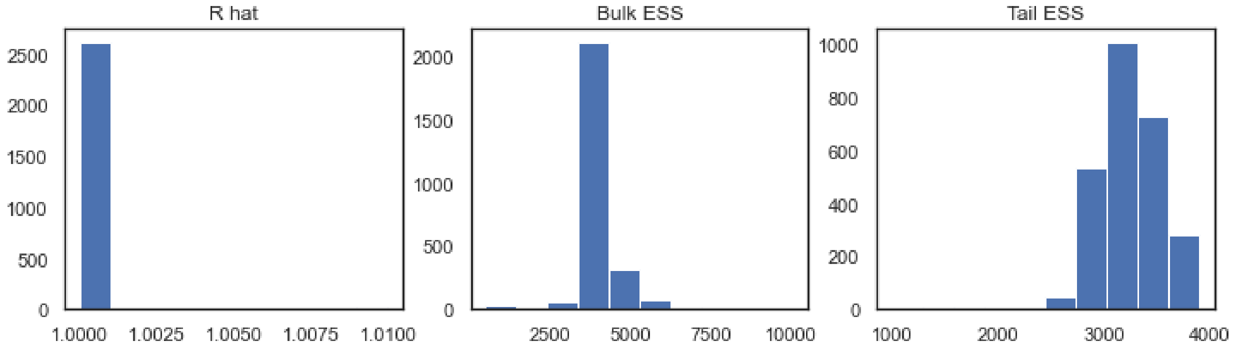

Figure 16. Chapter 3. Figure 5

Figure 5. Distribution of mean R hat, bulk effective sample size, and tail effective sample size for all model parameter estimates.

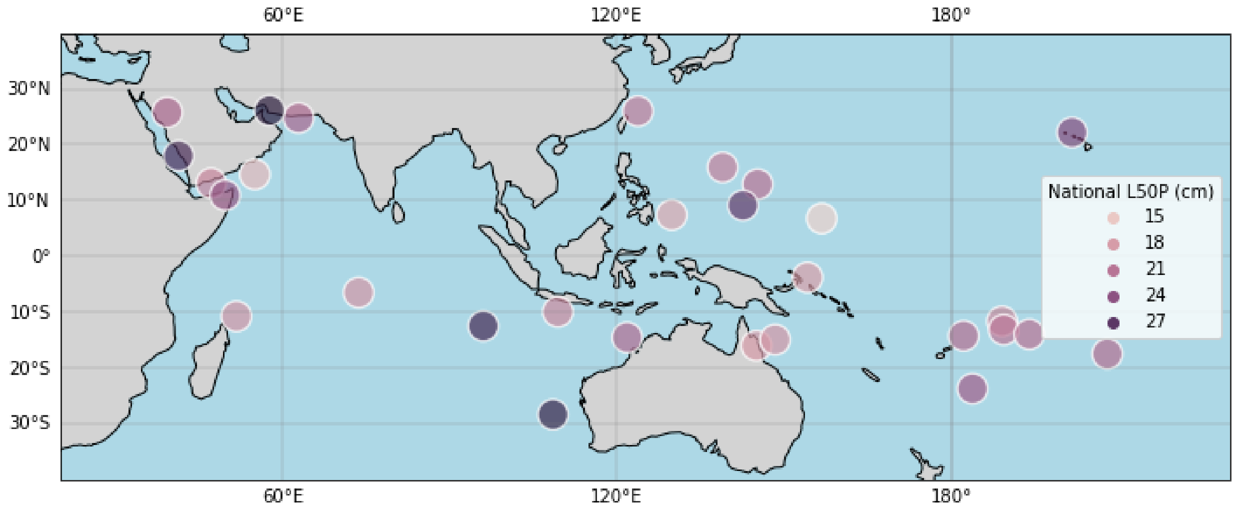

Figure 17. Chapter 3. Figure 6

Figure 6. Map of length at 50% phase change (L50P) per nation. L50P (cm) was described by five 3 cm bins to create a color gradient from white (15 cm) to dark purple (27 cm).

Discussion

Few studies have presented hierarchical estimates of environmental, human, and demographic effects on the timing of maturity at across the entire range of a fish species, particularly those that exhibit protogynous sex change (Taylor 2014; Munday et al. 2006). Here results clearly show the importance of demographic drivers to size at phase-change across the full spatial range of both *C. sordidus* and *C. spilurus*.

The first environmental covariate, 3-year average SST per site, had a weak negative relationship to length at maturity such that higher SST leads to smaller size at maturity. This is due to higher temperatures increasing individual growth rate. Increased growth rate will decrease the length at maturity since the requirements in size or body condition, such as a size threshold, will be reached earlier in life. The variations in L50P across the Bullethead's habitat range are likely a result of temperatures driving size differences. The relationship of temperature and sex-change was expected based on life history research to date and has been observed across multiple fish taxa (Taborsky 2008). Taylor et al. 2019 also found site level variations in lifespans relative to temperature and concluded that differences in growth likely lead to different mortality regimes between fast and slow growing individuals. Therefore, it may be hypothesized that smaller size at maturity may be driven by a trade-off for reproductive success and mortality. Earlier maturation, and faster growth, may increase mortality but increase the change of successful reproduction. However, since the model was conditioned on age, we may assume that the effect of temperature is independent of survival. It is possible that increasingly high temperatures may reach past an optimum, given that coral reefs experience the highest marine water temperatures, and therefore result in deteriorating conditions and reduce growth.

Chl-a had a weak negative relationship to length at maturity where higher concentrations of Chl-a were related to small size at maturity. Chl-a in coral reef context is a proxy for marine oligotrophy, such that at higher Chl-a concentrations, it is likely that higher Chl-a concentrations indicate poor growing conditions due to higher algal content and larger sizes at maturity. As bioeroders, in the event of high Chl-a content, it is likely that coral cover and condition is lower, therefore a lower food quality for parrotfish feeding. The relationship between Chl-a and phase-change is weak, and conditional on the model, and little variability is explained by Chl-a's presence in the model. Chl-a and productivity more generally, are likely not strongly linked to differences between populations in sex-change, a finding that confirms work by Taylor et al. (2019). It should be noted that regardless of conditioning on the human and population demographic covariates, the effect size of both SST and Chl-a did not change, see Supplemental Figure 1.

The human influence on size at maturity was represented through the metric of human gravity, a description of the proximity and size of the nearest human settlement and associated with fisheries pressure. Human gravity had a weak negative relationship to length at maturity such that larger and closer human populations were related to larger sizes at maturity. This is unexpected, given the expected size selective pressure of near-shore fisheries (Taylor 2014). If the larger individuals are removed from the population through size-selection, there is a resulting advantage to attaining maturity earlier to increase fitness and the likelihood of reproduction. Taylor (2014) found a decrease in sex change by size selection from fisheries pressure in *C. spilurus*. Taylor (2014) goes on to conclude that both density and sex ratio play a role in the degree to which fisheries pressure impacts size at phase, and that depending on the combination of pressures, the social dynamics of maturity are subject to plasticity. Despite no effect size conditional on the model, the effect of fisheries pressure is likely to present in the system. It can be hypothesized that both sex ratio and density are affected by fisheries pressure, however, if both parameters are removed the direct effect of gravity does not change in either magnitude or sign. Therefore, we assume that fisheries induced size-selection likely exists within the site and nation level random effects.

Parrotfish population demographics were described by density, and sex ratio per unit length. Population density showed a strong negative relationship with size at maturity such that dense populations show smaller sizes at maturity. Interpretation of protogynous sex-change timing is difficult as there are many strategies individuals can use to maximize reproductive potential (Munday et al. 2006; Taylor et al. 2018). Therefore, if size at phase decreases, we may then assume that higher density populations offer more success for males. This advantage could manifest either as preparations for taking over a harem, or that while there is no immediate success it may reduce mortality. An alternative strategy in the event of an already dominant male may be a delay in sex-change, however Munday et al. (2006) points out that it is not always the case that the largest female in a harem undergoes sex-change, and that it is dependent on the relative reproductive potential between individuals. Regardless of strategy, these results point towards an inter-population trend of smaller sex-change with higher densities.

The second demographic covariate of sex ratio per unit length had a strong negative relationship with size at maturity such that with a higher proportion of males it is more likely for individuals to mature at smaller sizes. This is likely a similar effect to that described by population density such that the fitness advantage to phase change, maturity, is advantageous when there are already males present. Munday et al. (2006) states that the timing of sex-change covaries between genetically connected populations such that the timing of sex-change per individual results in a change at the population level. This trend was also found by Taylor (2014) and is further evidence that sex-change dynamics are driven by the fitness advantage of individuals. Here, we present evidence that, while the relationship of population sex-ratio is similar across reefs, it does exhibit plasticity. Finally, given that sex ratio per size was found to have the largest effect size, it is further evidence that population demographics play a strong role in driving sex-change dynamics. This will however depend on the social hierarchy present (Van Rooij et al. 1995). To further understand the role of demographics, identification of social grouping by association to a dominant male would allow for further estimation of social group interactions.

As mentioned earlier, sex ratio can also be related to human pressures, due to the size selection of fisheries. Since sex ratio was scaled by size, we can effectively control for populations that have more males having also larger average size, given the size differences in males and females. Males, as the mature phase, are larger and should therefore be selected out by fisheries. If fishery pressure is high, then there should be selection for smaller males. However, as described earlier, there did not appear to be a confounding effect between human gravity and sex ratio, therefore we may assume that while fisheries pressure is likely existent, sex ratio per length holds a strong relationship to size at phase change. While sex ratio was found to have the largest effect size conditional on the model, it should be noted that sex ratio as a measurement is limited by sampling bias. In the event of high proportions of females, it is likely that sampling will seek out males to ensure that an adequate number of individuals per sex and phase are recorded. For this reason, it is likely that there is a skew of higher proportions of males present in the dataset.

Based on the presented evidence here for the relationship of environment, human pressure, and population demographics on size at phase change, it is worth recognizing that these covariates describe between site variability. All described covariates within the model can influence change at scales both larger and smaller than at a site. For this reason, it is important to recognize that the evidence presented here points towards trends across all sites in addition to within site variance. Nation and site level variability are therefore unlikely to be explained by the available covariates. This is also relevant when discussing the differences between species, *C. sordidus* and *C. spilurus*. Studies by Allsop and West (2003) have suggested that traits such as size at sex-change are invariant across taxa, however Munday et al. (2006) explains that while size at sex-change divided by maximum size may be invariant it is likely that this is not the case for populations with distinct breeding groups such as parrotfish. One would therefore expect to see between group variances. Both of these concepts appear evident in the model outcomes where, between nation estimates of A50 (Figure 6) and between reef and nation-level random effect estimates (Supplemental Figure 2, 3) show between group estimates, and the overlapping global mean L50P between species and in the length at age relationship between species (Figure 2) may represent broad scale trait invariance. Conditional on the model, there was a strong effect of species, such that *C. spilurus* showed a larger size at maturity that *C. sordidus*. While little physiological differences have been yet observed between these two species, we find evidence that there likely exists a driver behind phase-change per species outside of the modelled covariates.

The timing of sex-change in protogynous coral reef fish is an important priority in managing changing near-shore fisheries (Pinca et al. 2011). The time at phase-change is important to fisheries because it involves both size and sex, and can therefore have larger impacts on protogynous species and other maturation strategies. Here we have given evidence that the timing of phase change is a function of both environmental and demographic characteristics. Under climate change conditions, coral ecosystems are changing be it their diversity, chemistry or simply SST. With environmental forced changes to maturity timing, it is likely that there may be a greater negative effects of fisheries on already stressed populations. For this reason, it is important to provide both life history trait baselines for fisheries monitoring, but to also predict how changes outside of fisheries pressure may impact population structures. It is through this application of life history research that it is possible to prevent excessive yields.

This study demonstrates that the plasticity in the timing of sex-change between populations is driven both by physiological conditions and changes in the environment, and by demographics. These drivers are relevant across the complete spatial scale of both *C. sordidus* and *C. spilurus*. Due to the complexities of social interactions, it is increasingly important to understand how sex-change decisions are made, to appropriately manage populations in the context of size and sex selective fisheries.

Supplemental Figures and Tables

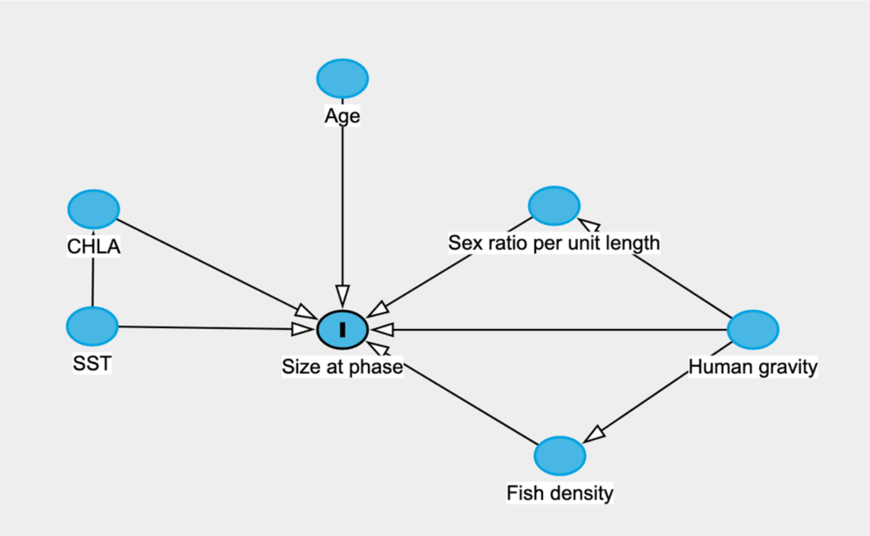

Figure 18. Chapter 3. Supplementary Figure 1

Supplemental Figure 1. DAG of full model including conditional independence relationships of the following covariates: SST, Chl-a, age, sex ratio per unit length, human gravity, fish density, and size at phase. Created using Daggitty (Textor et al. 2017).

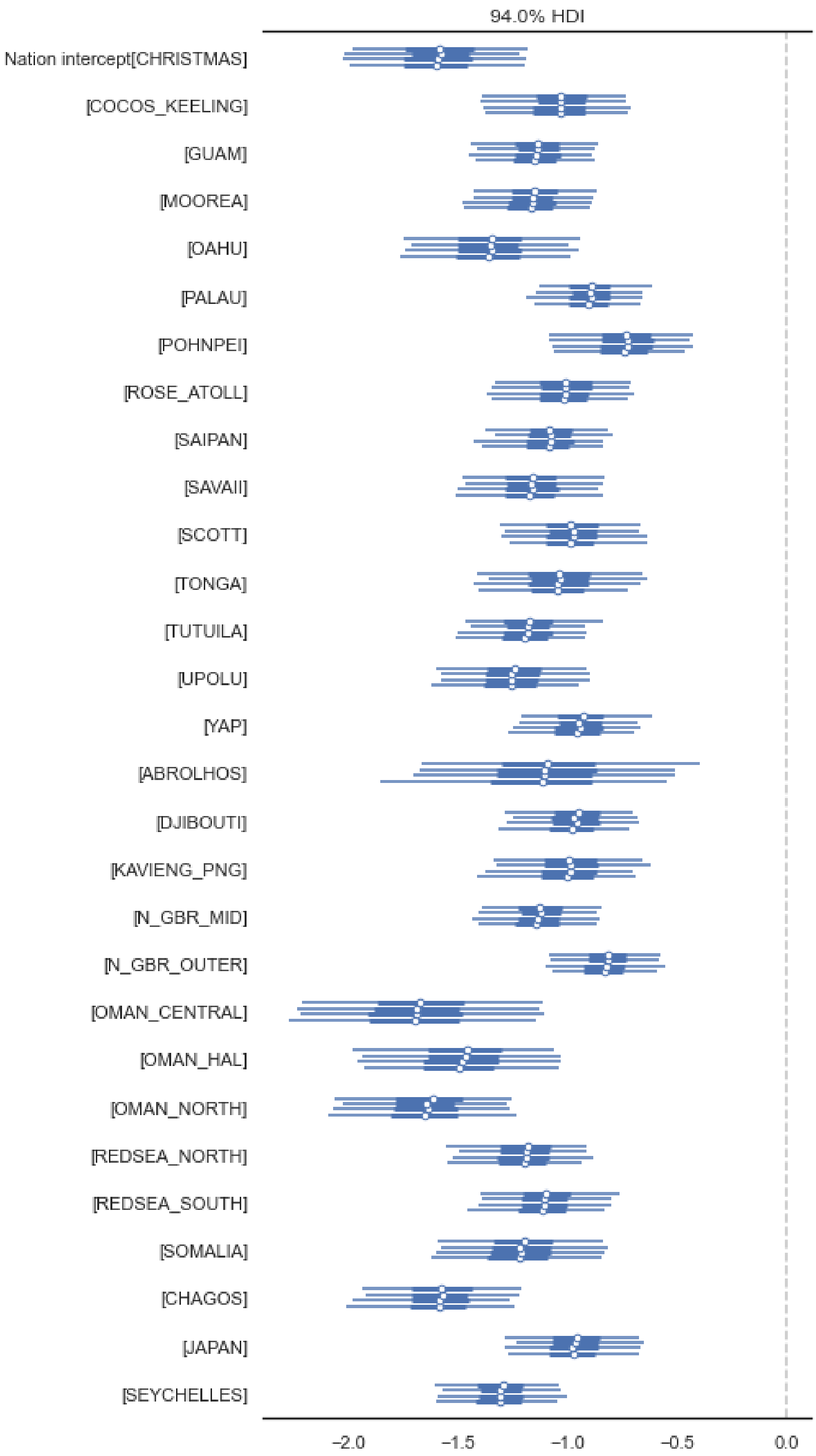

Figure 19. Chapter 3. Supplementary Figure 2

Supplementary Figure 2. 4-chain sampling of the nation level slope parameters with 94% high density intervals.

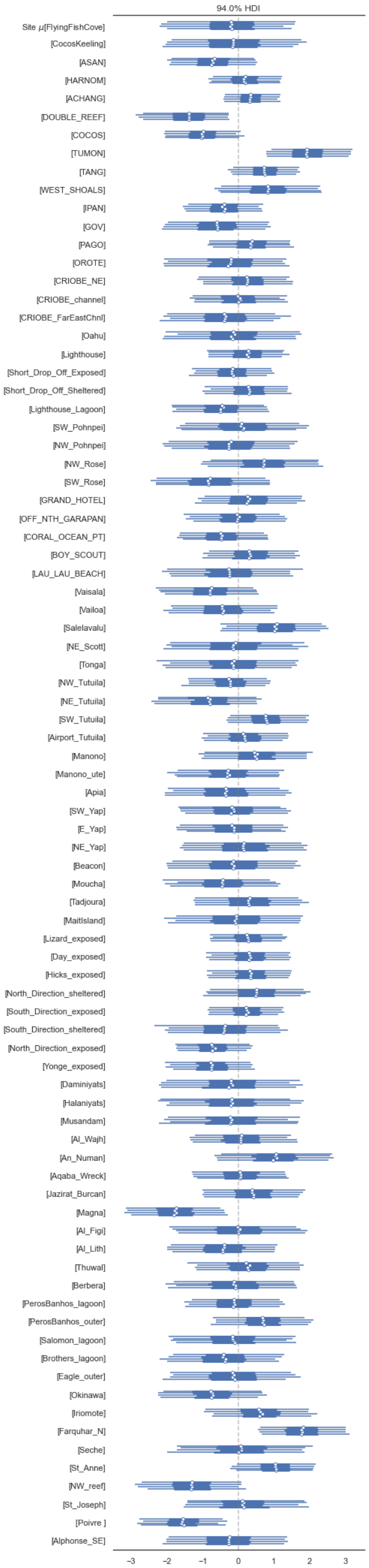

Figure 20. Chapter 3. Supplementary Figure 3

Supplementary Figure 3. 4-chain sampling of the site level slope parameters with 94% high density intervals.

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Chapter 4. Discussion

This research has characterized the plasticity of maturity in three different species across broad environmental conditions at a global and local scale. The plasticity of maturity has been shown to be related to environmental, demographic, and human factors; plasticity of maturity has also been shown to vary between both generations and genetically distinct populations. Finally, this research has shown that probabilistic maturity ogives can be used to predict, under climate warming scenarios, changes to maturation timing. The Bayesian modelling approaches used offer an explicit mode of expressing assumptions on maturation process and relationships, that can accommodate for multiple levels of hierarchical data pooling and data-sparse events. These forms of mechanistic modelling approaches are important to life history study as they can be used to investigate the processes behind traits.

Atlantic salmon exhibit one of the more extreme examples of alternative maturation strategies where some male parr mature in-river rather than under-go the morphological transformation of smolting to migrate to sea. Chapter 2 estimated the plasticity of the alternative maturation strategy in response to environmental differences between two distinct Atlantic salmon populations in Norway and predicted earlier maturation timing under climate warming scenarios. In addition, Chapter 2 found between cohort variability which is further evidence for the genetic component of male parr maturity (Lepais et al. 2017, Hutchings 2011). To capture the timing of maturity a logistic maturity ogive model was constructed as a function of age specific to parr. Previous maturity modelling in the field of Atlantic salmon has been focused on maturity at sea for returning at-sea males. Otero et al. (2012) found a relationship between proportions of returners to both marine and river temperature conditions, indicating impacts to growth at both at multiple life stages. To-date, there has been little directed study towards the conditions of male parr maturity in wild populations and the relationship between male parr maturity and environmental conditions.

In Chapter 2, to understand the mechanism of maturity, the maturity ogives of age and size were estimated individually. This method was assisted by use of a DAG to understand the conditional nature of inclusion of age and size. In this regard, DAGs are a useful tool to help build mechanistic models to understand what drivers maturity by identifying the causal assumptions of the model. To estimate the effect of age, the model should not condition on size because of a causal backdoor where size influences both age and the probability of maturity. Barot et al.'s (2004) definition of the maturation reaction norm as a combination of both age and size does not consider this casual pathway. Instead, it is shown that by comparing the maturity ogives of age and size, there is information as to how two populations may vary with respect to maturation thresholds and relationship to the environment (Chapter 2 Figure 1).

The second maturation strategy, discussed in Chapter 3, of protogynous sex-change was found to be driven by environmental and demographic characteristics. By using a hierarchical partial pooling modelling approach, chapter 3 presented evidence that the relationship between size at sex-change was found to be similar across species and across the complete habitat range of *C. sordidus* and *C. spilurus*. Following work by Barot et al. (2004), maturity ogives were constructed conditional on both age and size, thereby making estimates independent of growth and survival. The characterization of life history traits for coral reef parrotfish has been explored in few species to-date (DeMartini et al. 2018, Pardee et al. 2020), and is of direct relevance to the management of near-shore fisheries. Due to the relationship of sex and size, fisheries selection has been observed to reduce the size at sex-change (Taylor 2014), however conditional on the model human gravity was not found to have an effect. This stands out from previous literature and can be interpreted two ways. The first is that fisheries pressure, in the context of the model, was not appropriately attributed, or second, that fisheries pressure plays a smaller role in average density populations where demographics are the larger forcing. Previous work Taylor (2014) has identified highly variable timing of sex-change in and between local populations, which enforces the importance of hierarchical partial pooling techniques. The ability to estimate the variance between different levels and estimate covariate effects per levels will be important when try to distinguish between small population groupings such as those in Bullethead parrotfish. In this way it is possible to leverage as much information regarding trait change as possible.

Alternative maturation strategies are common across fish taxa (Taborsky et al. 2008) and therefore represent an important component of life history analysis. The first goal of the two chapters presented here was the estimation and quantification of the plasticity in maturity as a life history trait between populations and maturation strategies. Two maturation strategies were targeted: male parr maturity in Atlantic salmon, and protogynous sex-change in Bullethead parrotfish. For both maturation strategies, there was evidence of growth driving the timing of maturity as a function of environmental condition. This agrees with current life history theory, and the theory presented by Hutchings 2011 regarding size-threshold reaction norms.

Maturity modelling through maturity ogives is frequently used in fisheries science. Maturity ogives are flexible, and can provide both important characteristics such as L50, but also be used to estimate reaction norms. Maturity ogive modelling is often performed separately between age and size, however recent works by Barot et al. (2004) have conditioned models on both age and size for the purpose of utilization in reaction norm calculation. It should be noted that the age and size reaction norms were not calculated in either case, and the marriage between partial pooled hierarchical models and reaction norm calculation will be of high priority. The work presented in these chapters has built upon these methods by incorporating hierarchical structures in Bayesian framework. Hierarchical modelling techniques are becoming increasingly important in life history studies as they allow for estimates to be made that incorporate information across many populations at large spatial scales. In addition, hierarchical model structures are useful in data-sparse scenarios. Hierarchical modelling techniques will likely be useful when handling datasets of combined sampling methods particularly with cryptic fish species with few to no dedicated monitoring programs. Both chapters also utilize DAGS to state the assumptions of the mechanistic models used. Through the use of DAGs it is possible to estimate causal interactions and ultimately provide insight into how life history processes work.

The ability to build mechanistic models and estimate the process involved in life history transitions has direct implications to marine and freshwater fisheries. Human fisheries pressure and human induced climate change are compounding factors that threaten to change how species interact with their environments. Predicting changes to the timing of maturity is important to both our understanding of how life history traits may change over time, but also how populations may vary regarding population structure and overall reproductive potential. It is therefore critical to understand how species have adapted to their current conditions, and how individuals improve fitness through different reproductive strategies.

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