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# Plasticity masks and mediates evolution in warming environments

Lyndsie S. Wszola, lyndsie.wszola@huskers.unl.edu

Mikko Heino, mikko.heino@uib.no

Ulf Dieckmann, dieckman@iiasa.ac.at

## Approved by

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**Supervisor:** Mikko Heino and Ulf Dieckmann

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## **ABSTRACT**

Harvest-induced evolution has been linked to many documented declines in fish size at maturity, size-at-age, and harvest yields. Predicting the course of harvest-induced evolution to address scientific questions and design policy interventions is complicated by plastic relationships between temperature and growth in many species. We built an individual-based eco-genetic model incorporating growth plasticity in response to harvest via a temperature-inclusive biphasic growth model to ask how plastic responses to temperature affect the evolution of fish life-histories in response to harvest. We found that intensive harvest resulted in rapid evolution; catch rate of vulnerable fish was associated with increasingly rapid evolution of reduced genetic length at maturity and increased gonadal-somatic index. We additionally found that plasticity masked and mediated evolution. Populations subjected to the hot temperature regime evolved increased growth capacity whereas cool populations evolved reduced growth capacity, with the consequence that hot populations exhibited relatively little phenotypic response to harvest. Though hot populations exhibited marked genotypic changes, complementary trait evolution resulted in little decline in length at maturity or emergent patterns of growth compared to the cool populations. However, hot populations did experience declining harvest rates relative to cool populations, demonstrating that the application of evolutionary models to management on a warming planet demands an examination of how plasticity affects the strength of evolution and our ability to observe it.

## **INTRODUCTION**

Harvested fish populations and the human social structures that rely on them are facing a rapidly changing environment that demands novel policy innovations. As growing human

populations and complex supply chains increase the need for fish protein, global water temperatures are increasing and becoming more variable (Hoegh-Guldberg et al. 2019). Designing fisheries policy solutions for a warming planet therefore demands that we understand not only the basic biology of harvested fish species and the social dynamics of fishers, but how they interact to shape the social, ecological, and evolutionary dynamics of warming fisheries.

Fishing shapes not only relationships between fish and fishers but also eco-evolutionary dynamics of harvested fishes and their relationships with their ecological communities. Over the course of their lives, fish allocate energy exceeding their maintenance needs to growth and reproduction (Beverton and Holt 1957). This heritable division of energy interacts with environmental factors like temperature and food availability to shape a fish's life-history: the sequence of important events that a fish does or experiences in its life. As gape-limited foragers in size-structured aquatic food webs, fish with life-history strategies that prioritize somatic growth gain the dual benefits of increasing their own range of prey options while escaping predation (Graeb et al. 2004; Urban 2007a, 2007b; Magnhagen and Borcherting 2008). Larger individuals, especially those from species with a broadcast spawning reproductive strategy, can also enjoy a fitness advantage from large somatic mass because gonad size scales with body size (Barneche et al. 2018; Shaw et al. 2018). However, fish that devote most of their energy to somatic growth generally reproduce later and are therefore more likely to die before reproducing in high-mortality environments (Reznick 1983; Roff 1983; Werner and Hall 1988; Jensen 1996; Rosenfeld et al. 2020). Commercial, subsistence, and even recreational fisheries harvest mortality can equal or exceed natural mortality for many populations (Russell 1931; Mertz et al. 1998; Zhou et al. 2012; Byrne et al. 2017; Rudd and Thorson 2018). A wealth of theoretical and empirical evidence suggests that the increased mortality imposed by fishing can induce

evolutionary changes in fish life-history, reducing the selective advantage of maturing late at large sizes and encouraging early maturation at smaller sizes (Jennings et al. 1998; Law 2000, 2007; Heino and Dieckmann 2008; Allendorf and Hard 2009; Enberg et al. 2012; Heino et al. 2015; Kuparinen and Festa-Bianchet 2017). In addition to raising the overall rate of mortality in harvested populations, fishing changes the relationship between fish size and likelihood of mortality. Unlike other predators, humans exhibit a preference for harvesting larger species and individuals, either through active selection of individual fish or through passive selection via gear choice (Jørgensen et al. 2009; Claireaux et al. 2018; Kaemingk et al. 2020). Imposing additional mortality on large fish should further favor life-history strategies where fish mature at smaller sizes below the harvest threshold (Kuparinen and Merilä 2007; Hutchings and Fraser 2008). Selective fisheries harvest thus creates a grand and deeply policy-relevant natural experiment into the effects of mortality on the eco-evolutionary dynamics of growth and reproduction (Rijnsdorp 1993; Jensen et al. 2012).

If all changes in fish size and life-history could be attributed to evolutionary effects of fishing, policy interventions would be readily identifiable if not easily implemented. Identifying causes of variation in fish life-history and thus recommending appropriate policy responses is complicated by the fact that fish are ectothermic, indeterminately growing organisms that often express a high degree of phenotypic plasticity. Warming waters make it extremely difficult to isolate factors affecting fish growth and reproduction in the field because temperature, the “ecological master factor,” can affect the growth, reproduction, and yields of harvested fish species in diverse, non-linear ways (Brett 1971; Angilletta 2004; Deane and Woo 2009). Some fish exhibit “thermal aging” that results in plastically faster growth and earlier reproduction in warmer environments because warmer waters enable them to forage longer or speed up

metabolism (Neuheimer and Taggart 2007; Chezik et al. 2014a, 2014b). Conversely, warming waters and attendant conditions like hypoxia may force fish to divert energy from growth and reproduction to maintenance, plastically inducing later reproduction or stunting (Madeira et al. 2017; Chadwick and McCormick 2017; Hamel et al. 2020). Temperature and harvest can also affect fish growth and reproduction by changing community structure. Thermally-induced changes in the distribution and abundance of food resources may limit growth and reproduction or shift the competitive balance between species (Poletto et al. 2018; Koenker et al. 2018).

To craft fisheries policies that address the interaction of harvest and temperature, we first need to understand how temperature and harvest affect fish life-history through the joint mechanisms of plasticity and evolution. Though much work has been conducted on the interaction of warming and harvest patterns in marine environments, freshwater species have received much less attention outside of iconic systems like the Laurentian Great Lakes (Dunlop et al. 2015, 2018; Morbey and Mema 2018). This is a missed opportunity both to study the emerging eco-evolutionary dynamics of human-dominated aquatic systems in the wild and to develop conservation strategies for a significant portion of the world's fish supply.

This objective is extremely difficult to accomplish in the field where patterns of harvest and warming often covary. Freshwater systems are spatially smaller and simpler in food web structure than marine systems, but are facing mounting conservation concerns. Smaller water bodies warm faster than huge marine systems and may be profoundly restructured by anthropogenic forces like nutrient runoff and invasive species introduction (Hansen et al. 2017; Maberly et al. 2020; Jenny et al. 2020; Manjarrés-Hernández et al. 2021). They also offer rich and well-documented variation in governance structures and water temperatures across geographic boundaries, allowing us to swap space for time in our quest to model the joint effects

of evolution and plasticity (Song et al. 2017; Jørgensen et al. 2019). Freshwater fisheries have furthermore been foundational to the study of social-ecological systems, providing a deep well of social science theory from which to form hypotheses about the interactions between people and nature (Folke et al. 2005, 2006; Arlinghaus et al. 2016, 2017; Noble et al. 2016). They have also provided some of the most experimentally robust examples of fishing-induced evolution and the first real-world examples of evolutionary recovery of fish maturation schedules following release from harvest (Haugen and Vøllestad 2001; Feiner et al. 2015).

Freshwater fisheries monitoring practices also create exactly the kinds of replicated life-history datasets that are essential to forming a robust understanding of fish response to temperature and harvest. North American state, federal, and provincial fisheries agencies have systematically monitored the abundance and size structure of harvested freshwater fish populations for decades, creating a rich source of fishing-independent data that we can use to evaluate the selective impact of fishing (Bonar et al. 2009). Increasingly, states and provinces are also surveying anglers about themselves and their harvest during and after fishing trips (Pollock et al. 1994). These “creel” surveys evaluate angler motivations, demographics, catch, and harvest behavior, illuminating the connections between human social structures, basic ecology and evolutionary questions, and applied conservation.

Herein, we leverage a large freshwater fisheries dataset to ask how plastic responses to temperature affect the evolution of fish life-history in response to harvest. Walleye (*Sander vitreus*) are a popular food fish for recreational, subsistence, and even commercial anglers in their native and introduced ranges across northern North America (Barton 2011). Broadcast spawners that need cool water over fine gravel to breed, walleye exhibit a remarkable example of thermal aging, growing more slowly and maturing later at northern latitudes than in the southern

part of their range (Venturelli et al. 2010; Bozek et al. 2011; Hansen et al. 2015). Emerging evidence also suggests that walleye may respond to intensive harvest by evolving reduced size and age at maturity (Bowles et al. 2020). The popularity of walleye fisheries combined with their well-documented plastic response to temperature creates a fascinating opportunity to combine theoretical and empirical approaches to ask how temperature and harvest interact to shape fish eco-evolutionary dynamics.

We built an agent-based model to test two contrasting hypotheses about how temperature could affect the evolutionary effects of harvest. Evolution of reduced size and age at maturity results in part from a tradeoff between survival and fecundity: typically fish that mature earlier and at smaller sizes ultimately reach smaller adult sizes and die sooner. However, if warmer temperatures allow fish to plastically grow faster, the size cost of early maturation could be diminished, lessening the selective advantage of genetically-determined early maturation. We therefore test the hypothesis that rising temperatures may reduce the evolutionary effects of harvest by removing selective advantage to genetically determined early/small maturation. Conversely, the pace of evolution depends in part on fish generation length. If warming facilitates faster maturation due to plasticity, generations may become plastically shorter, allowing faster evolution and also faster recovery. We therefore evaluate the contrasting hypothesis that rising temperatures may exacerbate harvest-induced evolution but also facilitate recovery by shortening generation times.

## **METHODS**

### *Study system*

Walleye are large freshwater predatory fish with asymptotic lengths reaching 60–90 cm inhabiting lakes and rivers throughout northern North America. Their native range, which

stretches from Northern Quebec and Ontario, Canada, to Nebraska and Iowa, USA, is largely defined by the distribution of lakes and rivers formed by glacial till and outwash during the last ice age. Due to their high food quality and recreational value, they have also been introduced to many natural and artificial water bodies outside of their native range. As sexually dimorphic broadcast spawners, walleye fecundity is highly influenced by body size (Shaw et al. 2018). Males mature earlier than females, reaching smaller sizes and living shorter lives (Bade et al. 2019). Walleye managers therefore often strive to implement policies that allow anglers to fulfill harvest and non-harvest objectives while conserving large adult female walleye to promote recruitment (Drewes et al. 2015). Walleye have long been commercially harvested in large water systems like the Laurentian Great Lakes (on the border between the USA, Canada, and Tribal lands) and Lake Winnipeg (Manitoba, Canada). Although many walleye fisheries have been closed to commercial harvest due to fisheries-induced population collapse, recreational walleye anglers are often highly harvest-oriented, and even recreational walleye harvests can be considerable.

In addition to their social, ecological, and economic importance as a heavily harvested fish species, walleye present an ideal study system in which to evaluate the effects of thermal growth plasticity on evolutionary responses to harvest. Walleye exhibit a striking example of thermal aging; annual walleye growth and mortality are highly positively correlated with the annual mean number of growing degree days above 5°C (Venturelli et al. 2010). At the northern edge of their range in Northern Quebec, Canada, walleye may not mature until they reach 12 years of age and can live up to 40 years. In contrast, walleye at the southern edge of their range in Nebraska may mature as young as two years old and live only for a maximum of 5–10 years (Bozek et al. 2011). When walleye growth is considered as a function of growing degree days



above 5°C, however, walleye exhibit a remarkably consistent growth pattern across their entire range, creating a well-documented backdrop of thermal growth plasticity against which to evaluate the effects of selective harvest in a warming world.

### *Modelling approach*

We model interacting effects of temperature and size-selective harvest on growth, maturation, and reproduction using an individual-based eco-genetic model (Dunlop et al. 2009) that builds on models of biphasic growth (Lester et al. 2004, 2014, Quince et al. 2008, Boukal et al. 2014), probabilistic maturation dynamics (Heino et al. 2002), and quantitative genetics (Law 2000, Tables 1-2). Biphasic growth models improve on older models by explicitly accounting for differences in energy allocation between adults and juveniles, facilitating the examination of tradeoffs between growth and reproduction in species with high phenotypic plasticity. Eco-genetic models improve on older models by allowing selection to arise via the interaction of individuals' traits with the simulated environment.

### *Adaptive traits*

Individual patterns of growth, reproduction, harvest, and natural mortality are determined by the interaction of individual phenotypes with their environment. Phenotypes, in turn, vary among individuals as a function of genotype, heritability, environment, age, and sex. Individuals are characterized by genotypic and phenotypic values of their juvenile growth rate (also called growth capacity;  $h_g$  = genotypic juvenile growth rate,  $h_p$  = phenotypic juvenile growth rate), gonadosomatic index (gonadal mass as a fraction of somatic mass;  $g_g$  = genotypic gonadosomatic index,  $g_p$  = phenotypic gonadosomatic index), and length at 50% maturation

probability ( $L_g$  = genotypic length at 50% maturation probability,  $L_p$  = phenotypic length at 50% maturation probability).

### *Initial population*

All model runs are initiated with a population whose abundance  $N_s$  and age distribution corresponds to the abundance and age distribution resulting from cohorts at ages  $a = 0$  to the maximum considered age  $a_{\max}$ . initiated with  $N_0$  individuals per cohort dying at an instantaneous mortality rate  $\mu_0$ ,

$$N_s = N_0 \sum_{a=0}^{a_{\max}} \exp(-\mu_0 a).$$

We partition the observed phenotypic variance  $\sigma_p^2$  for each trait into an initial genetic variance  $\sigma_g^2$  and an initial environmental variance  $\sigma_e^2$  according to the initial heritability  $h^2 = \sigma_g^2 / \sigma_p^2$  with  $\sigma_p^2 = \sigma_g^2 + \sigma_e^2$ . All individuals in the initial population are assigned genotypic values  $L_g$ ,  $h_g$ , and  $g_g$  randomly drawn from normal distributions with means equal to the initial phenotypic means of each trait and variances equal to the initial genotypic variances  $\sigma_g^2$  of each trait. The corresponding phenotypic values  $L_p$ ,  $h_p$ , and  $g_p$  are assigned by adding to the genotypic values environmental effects randomly drawn from normal distributions with zero means and variances equal to the initial environmental variances  $\sigma_e^2$  of each trait.

### *Growth and maturation*

Individual length  $l(t)$  at age  $t$  is modeled as a biphasic function of an initial length  $l_0$  and an annual juvenile length increment  $h_p$  (Lester et al. 2004, 2014; Dunlop et al. 2009). Juvenile length  $l_j(t)$  is a linear function of age  $t$ ,

$$l_j(t) = l_0 + h_p t,$$

while adult length is a recursive function of the annual juvenile length increment  $h_p$ , the phenotypic gonadosomatic index  $g_p$ , and a correction factor  $\gamma$  reflecting the higher cost of gonadal tissue relative to somatic tissue,

$$l_A(t + \Delta t) = (l_A(t) + h_p \Delta t) \frac{3}{3 + \gamma g_p}.$$

Each juvenile's probability  $p_m$  of maturation is a logistic function of its length  $l_j$ , phenotypic length at reproduction  $L_p$ , and the steepness parameter  $d_a$  (Dunlop et al. 2009).

$$p_m(l_j) = \frac{1}{1 + \exp(-(l_j - L_p)/d_a)}.$$

Each new adult is assigned a phenotypic gonadosomatic index  $g_p$  randomly drawn from a normal distribution with a mean equal to its genotypic gonadosomatic index  $g_g$  and a variance equal to the initial environmental variance of  $g_p$ , truncated to avoid negative growth rates at the maximum gonadosomatic index  $3\Delta t/(T_p + l_0/h_p)$ , where  $T_p$  is the individual's age at maturation (Lester et al. 2004).

Each individual's somatic mass  $M$  is an allometric function of its length  $l$ , with allometric coefficient  $a_m$  and allometric exponent  $b_m$ ,

$$M = a_m l^{b_m}.$$

### *Reproduction and inheritance*

Each female's realized fecundity  $f_i$  at the end of the spawning season is the product of her somatic mass  $M_s$ , her phenotypic gonadosomatic index  $g_p$ , and the density-independent mortality probability  $\mu_e$  of eggs between deposition and first fall, divided by the dry mass  $M_e$  of eggs

$$f_i = \frac{M_s g_p}{M_e} (1 - \mu_e).$$

The number  $R$  of new recruits added to the population in each year is determined by a recruitment function in which the sum of the realized fecundities  $f_i$  of the current  $N_f$  adult females is multiplied by a density-dependent survival probability to recruitment that decreases exponentially with the current number  $J$  of juveniles according to a coefficient  $b_r$ ,

$$R = e^{-b_r J} \sum_{i=1}^{N_f} f_i.$$

Each new individual is assigned genotypic values  $h_g$ ,  $g_g$ , and  $L_g$  based on randomly drawn male and female adults as its parents. Female adults are drawn with a probability proportional to their realized fecundity  $f_i$ , while male adults are drawn with a probability proportional to their somatic mass. On this basis, the new juvenile's genotypic values  $h_g$ ,  $g_g$ , and  $L_g$  are randomly drawn from normal distributions with means equal to the mid-parental values (arithmetic means) of its parents' corresponding genotypic values and variances equal to half the corresponding initial genetic variances  $\sigma_g^2$  of each trait. The corresponding phenotypic values  $L_p$  and  $h_p$  are assigned by adding to the genotypic values environmental effects randomly drawn

from normal distributions with zero means and variances equal to the initial environmental variances  $\sigma_e^2$  of each trait.

### *Natural and harvest mortality*

Annual survival probability ( $S$ ) is determined by an instantaneous rate combining fishing mortality ( $z_f$ ) and natural mortality ( $z_n$ ),

$$S = e^{-\Delta t(z_f + z_n)} .$$

Natural mortality  $z_n$  combines the mortality effects of temperature and a growth-survival tradeoff. Baseline walleye instantaneous natural mortality rate increases relative to a temperature mortality coefficient  $m_t$  and the number of growing degree days  $t_t$  fish experience (Bozek et al. 2011). Walleye also experience increased mortality as a cost of increased growth capacity  $h_p$ , expressed as a fraction of a maximum growth capacity  $h_m$  relative to natural mortality at equilibrium trait value  $z_{h*}$ ,

$$z_n = m_t t_t + \left( -\frac{1}{\Delta t} \ln \left( 1 - \frac{h_p}{h_m} \right) - z_{h*} \right)$$

Harvest in the model is based on a freshwater recreational fishing system where fish are caught, evaluated on an individual basis for harvest legality and desirability, then either harvested or returned to the water. The per-capita instantaneous fishing mortality rate at length  $l$  is therefore a function of maximum instantaneous catch rate across all lengths ( $c_v$ ; the instantaneous rate at which vulnerable fish were caught by anglers), probability of being vulnerable to capture at length  $l$  ( $v(l)$ ), probability of being assessed legal to harvest at length  $l$  ( $l_k(l)$ ), probability of harvest given legal capture at length  $l$  ( $k(l)$ ), and probability of discard mortality of released fish ( $z_d$ ),

$$z_f(l) = c_v v(l) [l_k(l)(k(l) + z_d l_k(l)(1 - k(l)) + (1 - l_k(l))].$$

For the purposes of estimating harvest, we also calculated the expected harvest rate excluding discard mortality:

$$z_{fk}(l) = c_v v(l) [l_k(l)(k(l))].$$

Natural and fishing mortality were assumed to occur simultaneously with total catch ( $C$ ) tracked via the Baranov catch equation,

$$C = N \frac{z_{fk}}{z_{fk} + z_n} (1 - e^{-(z_{fk} + z_n)\Delta t}).$$

### *Implementation*

The model was implemented in a discrete yearly-cycle framework. In each simulation run, individuals were initiated once, then grew and reproduced each year. Individuals' ages were recorded in years and growing degree days, and growth at each timestep was calculated as a function of increased age in growing degree days. In each timestep, age in years was updated by one year and age in growing degree days was updated by the chosen number of simulated growing degree days ( $t_t$ ), for each scenario. Updated length was calculated for adults per the adult asymptotic growth function, individuals' growth capacity and GSI phenotypes, and ages in growing degree days. All population models were built using the tidyverse group of packages in the R programming language (R Core Team 2016, Wickham et al. 2020).

### *Parameterization*

We evaluated the interacting effects of harvest and temperature by modeling two temperatures: 1800 growing degree days per year as found in Northern Minnesota and Wisconsin, USA, and Southern Ontario, Canada, the core of the walleye range, and 3000

growing degree days per year, typifying the extreme southern edge of the range in Nebraska, Kansas, and Missouri, USA. By using real temperature values from across the walleye range, we can swap space for time to ask how a phenotypically plastic fish copes with the dual pressures of climate and harvest. All starting parameter values were taken from a walleye population in Leech Lake, Minnesota, which experiences an average of 1793 growing degree days per year (Wszola et al. in review). We additionally modeled four catch rates: 0, 30%, and 60% of vulnerable individuals caught and all legal caught fish harvested. For each temperature-harvest combination, we modeled the ecological and evolutionary dynamics of simulated walleye populations under 100 years of fishing at the reference temperature and warm temperature. We ran 100 replicates of each scenario and tracked means and standard deviations of each trait value, as well as the number of individuals in each age and stage group and the harvest yield in each timestep.

## **RESULTS**

### *Intensive harvest resulted in rapid evolution*

Patterns of evolution and phenotypic expression of length at reproduction, growth capacity, and reproductive investment varied by exploitation level. Across both cool and hot temperature regimes, exploited populations evolved reduced genetic length at reproduction and increased GSI relative to their starting values and unexploited counterparts (Figure 1, Table 2). The magnitude of the declines in genetic length at reproduction and the increase in GSI was associated with increasing catch rates. The highest catch rate was associated with the most rapid decline in genetic length at reproduction and increase in GSI, amounting to a 6.25% decline in genetic length at reproduction in the cool populations and a 7.7% decline in the hot populations in 100 years. The highest catch rate was likewise associated with a 6% increase in GSI in the cool populations and an 8% increase in GSI in the hot populations.

### *Plasticity mediated evolution of multiple traits*

Populations subjected to the warm temperature exhibited diverging genotypic and phenotypic outcomes from populations that experienced the reference cool temperature. Despite exhibiting similar trends in evolution of genetic length at reproduction, the hot and cool populations diverged in their evolution of growth capacity. The hot populations evolved increased growth capacity, whereas cool populations evolved decreased growth capacity (Table 1, Figure 2). The pace of growth capacity evolution correlated with harvest intensity at both temperatures; growth capacity increased most rapidly in warm populations at the highest catch rate and minimally in the no-harvest populations. Likewise, growth capacity declined most rapidly in the cool populations harvested at the highest catch rate, at an intermediate rate in populations harvested at the intermediate catch rate, and minimally in the no-harvest populations.

### *Plasticity masked evolution*

Because both hot and cool populations evolved reduced genetic length at reproduction, hot and cool populations ultimately expressed different relationships between growth capacity and genetic length at reproduction. In the cool populations, increasing harvest rate was associated with an increasingly strong positive relationship between growth capacity and genetic length at reproduction, both of which declined (Figure 2). In contrast, hot populations displayed an increasingly strong negative relationship between growth capacity and genetic length at reproduction (Figure 2). The complementary evolution of genetic length at reproduction and growth capacity in the hot populations, coupled with plastically faster growth in the hot populations meant that hot populations expressed relatively little phenotypic change despite experiencing similar degrees of genotypic change to the cool populations (Figure 3).



### *Increased temperature changed demographic structure and decreased harvest*

The contrasting pattern of growth capacity evolution in cool and hot temperature regimes, coupled with plastically faster growth in the hot populations, meant that the hot populations experienced less emergent decline in phenotypic length at reproduction than cool populations despite experiencing similar declines in genetic length at reproduction. Despite exhibiting apparently less phenotypic difference in growth and maturation, populations in the hot temperature regime exhibited lower catch numbers relative to the same catch rate at the reference cool temperature regime (Figure 4). Increased catch rates were also associated with changes in the population's demographic structure: increasing catch rates caused stark declines in the numbers of adult fish but only small declines in the numbers of juveniles relative to unexploited populations (Figure 4). Unsurprisingly, increased exploitation rates were also associated with higher numbers of harvested fish (Figure 4).

## **DISCUSSION**

We set out to ask how plastic responses to temperature affected evolutionary responses to harvest. We replicated the classic finding that intensive harvest results in rapid evolution, but the addition of temperature-driven growth plasticity showed that plasticity can both mask and mediate evolution, resulting in disconnects between growth and harvest outcomes. Simulated fish populations allowed to evolve under different harvest and temperature regimes experienced varying magnitudes, and in some cases directions, of evolutionary charge. In keeping with the classical expectations of fishing-induced evolution (Allendorf and Hard 2009; Kuparinen et al. 2017), increased harvest intensity selected for reduced length at reproduction and increased allocation of adult energy to reproduction across both temperature regimes. Life-history strategies that facilitate reproducing at large sizes and advanced ages with significant energy

allocated to somatic growth in the adult life stage are generally adaptive in low-mortality environments (Charnov 1993; Grégoir et al. 2018). The shift to earlier and smaller maturation, coupled with increased adult energy allocation to reproduction, is a widely-documented evolutionary response to increased mortality risk that often leads emergent size reductions in indeterminately-growing organisms (Heino et al. 2015; Feiner et al. 2015). While populations simulated at their reference “cool” temperatures of 1800 growing degree days largely conformed to the traditional fishing-induced evolution pattern by exhibiting declining genotypic and phenotypic length at reproduction, increasing GSI, declining growth capacity, and ultimately smaller sizes, the “hot” populations simulated at 3000 growing degree days diverged in several important respects. Like the cool populations, the hot populations exhibited declining genotypic length at maturation and increased GSI in response to harvest. In contrast to the cool populations, however, the hot populations evolved increased growth capacity. When added to the existing plastic growth advantage granted by the hot environment, the increased growth capacity created life histories with significantly less phenotypic loss of length at maturity compared to the cold populations and resulted in relatively little change in patterns of lifetime growth. Though hot populations appeared to exhibit less phenotypic change in growth and maturation than their cool counterparts at similar exploitation levels, they also exhibited declines in harvest and a demographic structure more biased toward juveniles.

The genotypic and phenotypic divergence between hot and cool populations demonstrates that temperature-driven plasticity may both induce and mask evolutionary change. The evolution of increased growth capacity in hot populations suggests that plastically allowing faster growth changed the relative advantage of growth capacity in a fishing context. In the cool populations, faster growth increased the risk that fish would be harvested before reproducing, causing growth

capacity and length at reproduction to decline in tandem. In the hot populations, however, faster growth allowed individuals to reach maturity quickly but still at relatively large sizes, granting fish the timing advantage of early maturation without the size cost. Even if larger fish were still harvested faster in the hot populations, they received the benefits of having reached a large size, achieving reproductive success by producing more eggs in fewer reproductive attempts.

This effect is only perceptible because we monitored both genotypes and phenotypes with an explicit mechanism for plasticity. If we had merely monitored phenotypes, it would appear that the hot populations changed very little because the decline in genotypic length at reproduction was largely offset by the increase in growth capacity. This dynamic highlights the challenge of observing fishing-induced evolution in empirical systems. What appears to be a lack of evolutionary change may in fact result from plasticity facilitating the complementary evolution of multiple traits to suit a complex environment. Additionally, the lower catch numbers found in hot populations relative to cool populations at the same catch rate suggests that the mechanistic links between evolution, growth, and applied outcomes may be substantively altered by the inclusion of plasticity. Though there are some caveats to our characterization of temperature and its effects — we did not, for example, account for oxygen depletion or increased competition among faster-growing fish — our finding that temperature affects both the trajectory of evolution and our ability to observe it demonstrates that investigations of fishing induced evolution in a changing world must consider the relationship between evolution and plasticity.

Our findings furthermore demonstrate the importance of carefully considering the mathematical form of a model when seeking to apply modeling for conservation decision-making. Our modeling framework included an explicit energetic difference between adults and juveniles, a dynamic universally present in real fish but often lacking in models. By including

energetic complexity across life stages, we were able to observe that increased temperature created a life-history where juveniles grew quickly then dedicated much of their energy to reproduction as adults, striking a balance between reproduction and survival across stages. Insights such as we have made here demonstrate the utility of emerging growth modeling approaches that directly capture temperature-induced energetic differences and their consequences for growth and evolution (e.g., Clark et al. 2017). Though models cannot and should not be expanded ad nauseum in an attempt to capture all the complexity of the real world, our findings demonstrate that judicious inclusion of energetic realism can facilitate the detection of qualitatively different evolutionary outcomes.

Empirical investigations of fishing-induced evolution have demonstrated that fish populations may respond to fishing by growing faster or more slowly across their lifespans, by maturing earlier or later, and by appearing to do nothing at all (Enberg et al. 2012). We built an individual-based biphasic growth model to ask how thermally-induced plasticity in growth affected evolutionary responses to size-selective harvest. We found that while populations simulated under hot and cool conditions both evolved reduced genotypic size at maturity and increased GSI, they diverged in the trajectory of their growth capacity evolution. The divergence between the hot and cool populations in our model, and the resulting change in emergent patterns of lifelong fish growth, suggest that some of apparently divergent evolutionary patterns attributed to fishing may be reconciled by considering the interaction of fish and fishing with the larger environment. Our results demonstrate that temperature can both induce and mask evolution and that the mathematical forms we choose influence our ability to detect certain patterns. Perhaps most importantly, our findings demonstrate the importance of understanding plasticity when seeking to apply the findings of eco-genetic models in a dynamic environment.

Models that do not account for the ways that genetic change is expressed in a dynamic environment may miss the signs of an evolutionary change or fail to distinguish the effects of evolution from those of plastic responses to a directional environmental shift. Applying evolutionary theory to conservation policy in a changing world demands that we expand our questions and our methods to capture the interplay between evolution and plasticity.

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## TABLES AND FIGURES

Table 1: Model variable symbols, descriptions, and units

Description	Symbol	Unit
Genotypic growth capacity	$h_g$	cm/year
Phenotypic growth capacity	$h_p$	cm/year
Maximum growth capacity	$h_m$	cm/year
Genotypic gonadal somatic index	$g_g$	Unitless
Phenotypic gonadal somatic index	$g_p$	Unitless
Genotypic length at 50% probability of maturity	$L_g$	cm
Phenotypic length at 50% probability of maturity	$L_p$	cm
Size of starting population	$N_s$	Individuals
Maximum age of starting population	$a_{max}$	Years
Cohort size for starting population	$N_0$	Individuals
Instantaneous mortality rate of starting population	$\mu_0$	Deaths/year
Phenotypic variance	$\sigma_p^2$	Depends on trait
Environmental variance	$\sigma_e^2$	Depends on trait
Genotypic variance	$\sigma_g^2$	Depends on trait
Heritability	$h^2$	Unitless
Juvenile length at time t	$l_j(t)$	cm
Length at age 0	$l_0$	cm
Age	$t$	GDD-adjusted years
Adult length at time t	$l_A(t)$	Unitless
GSI correction factor	$\gamma$	Unitless
Probability of maturation	$p_m(l_j)$	
Maturation steepness parameter	$d_a$	
Mass	$M$	g
Allometric coefficient	$a_m$	
Allometric exponent	$b_m$	
Fecundity	$f_i$	Eggs
Somatic mass	$M_s$	g
Egg mass	$M_e$	g
Egg mortality rate	$\mu_e$	Deaths/time
Number of recruits	$R$	Individuals
Density-dependent coefficient	$b_r$	Recruit mortality rate/Juvenile
Number of adult females	$N_f$	Individuals
Annual survival probability	$S$	Survival/time
Fishing mortality rate	$z_f$	Deaths/time
Natural mortality rate	$z_n$	Deaths/time
Mortality rate/GDD	$m_t$	1/time <sup>2</sup>
Time	$t_t$	Growing degree days
Mortality rate at equilibrium h	$z_{h*}$	Deaths/time
Fishing mortality rate	$z_f(l)$	Deaths/time
Catch rate of vulnerable fish	$c_v$	Catch/individuals
Probability of vulnerability to capture	$v(l)$	
Probability of legality to harvest	$l_k(l)$	
Discard mortality rate	$z_d$	Deaths/discards
Probability of harvest given capture	$k(l)$	Harvests/captures
Harvest mortality rate excluding discard	$z_{fk}(l)$	Harvests/individuals
Number of fish harvested	$C$	Individuals

Table 2: Parameter descriptions, values, and symbols and citations where relevant

Description	Symbol	Value	Citation
Cohort size for starting population	$N_0$	1000	
Instantaneous mortality rate of starting population	$\mu_0$	0.24	
Maximum age of starting population	$a_{\max}$	30	Bozek et al. 2011
Sex ratio		0.5	Bozek et al. 2011
Mean starting growth capacity		6	Wszola et al. in review
SD starting growth capacity		1	Wszola et al. in review
	$m_t$	0.00013	Bozek et al. 2011
Mean starting GSI		0.1	Wszola et al. in review
SD starting GSI		0.02	Wszola et al. in review
Mean starting length at 50% probability of maturation		40	Wszola et al. in review
SD starting length at 50% probability of maturation		4	Wszola et al. in review
Sexual dimorphism modifier		0.8	Wszola et al. in review
Trait heritability	$h^2$	0.3	
Length at age 0	$l_0$	10	Wszola et al. in review
Allometric coefficient	$a_m$	0.0057 Female 0.0047 Male	Wszola et al. in review
Allometric exponent	$b_m$	3.1139 Female 3.1678 Male	Wszola et al. in review
GSI correction factor	$\gamma$	1.74	Lester et al. 2014
Reference/cool GDD		1800	Wszola et al. in review
Warm GDD		3000	Wszola et al. in review
Egg mass	$M_e$	0.001	Bozek et al. 2011
Egg mortality rate	$z_e$	0.999	Bozek et al. 2011
Density-dependent coefficient	$b_r$	0.005	
Catch rate	$c_v$	0 No harvest 0.3 Intermediate harvest 0.6 high harvest	
Discard mortality rate	$z_d$	0.1	Hoffman et al. 1996
Maximum growth capacity	$h_m$	20	Bozek et al. 2011
Mortality rate at equilibrium h	$z_{h^*}$	0.25	Bozek et al. 2011

Table 3: Catch rate of vulnerable fish and temperature interacted to drive the evolution of age at reproduction (T), length at 50% probability of maturation (L), growth capacity (h), and GSI.

Catch rate	Timestep	Temperature	Mean T (years)	Mean L50 (cm)	Mean L (cm)	Mean h	Mean GSI	Number harvested
0	1	1800 GDD	2.727	40.005	41.578	5.732	0.100	0
0	50	1800 GDD	3.810	40.032	29.571	5.425	0.098	0
0	100	1800 GDD	4.011	39.993	29.266	5.101	0.095	0
0.3	1	1800 GDD	2.737	39.996	40.443	5.690	0.100	511
0.3	50	1800 GDD	3.285	39.315	26.706	5.401	0.101	259
0.3	100	1800 GDD	3.468	38.541	26.226	5.015	0.102	261
0.6	1	1800 GDD	2.787	40.001	39.118	5.645	0.100	712
0.6	50	1800 GDD	3.036	38.774	25.305	5.375	0.103	391
0.6	100	1800 GDD	3.213	37.501	24.774	4.970	0.106	390
0	1	3000 GDD	2.698	40.003	44.215	5.835	0.100	0
0	50	3000 GDD	2.596	39.977	34.429	5.835	0.099	0
0	100	3000 GDD	2.604	39.919	34.481	5.841	0.098	0
0.3	1	3000 GDD	2.703	40.003	43.921	5.838	0.100	363
0.3	50	3000 GDD	2.274	39.289	31.834	5.937	0.102	230
0.3	100	3000 GDD	2.195	38.457	31.707	6.111	0.103	222
0.6	1	3000 GDD	2.680	40.011	43.650	5.850	0.100	551
0.6	50	3000 GDD	2.082	38.512	30.027	5.969	0.104	349
0.6	100	3000 GDD	1.987	36.921	29.886	6.189	0.108	329

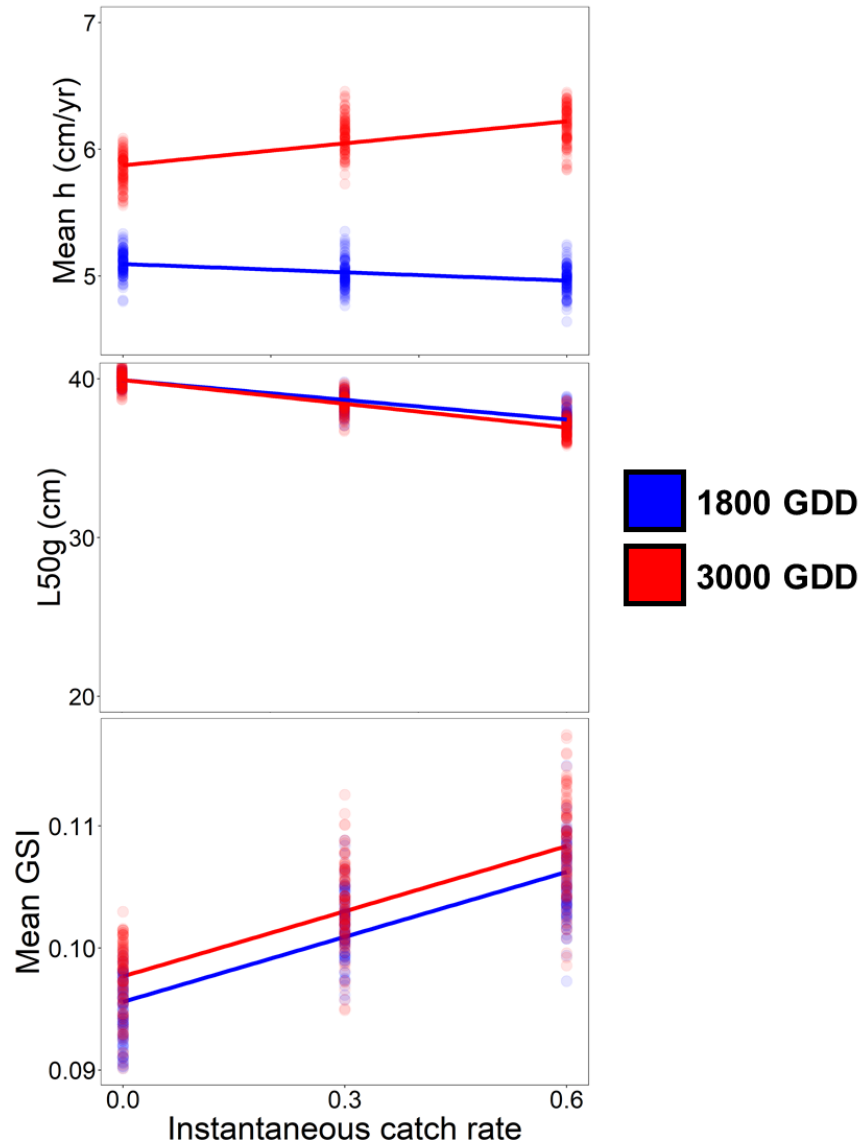


Figure 1: Intensive harvest resulted in rapid evolution. Endpoints at  $t = 100$  of length at reproduction (L50g),  $h$ , and GSI genotypes declined the fastest under the high harvest scenarios and slowest under the no-harvest scenarios. GSI likewise increased under the intermediate and high harvest scenarios but not under the no-harvest scenarios. Temperature affected the magnitude of the phenotypic shifts. Populations in the 3000-GDD environment, though they evolved reduced genotypic length at maturity, also evolved greater growth capacity. Similarly, the magnitude of GSI increase was positively correlated with instantaneous catch rate.



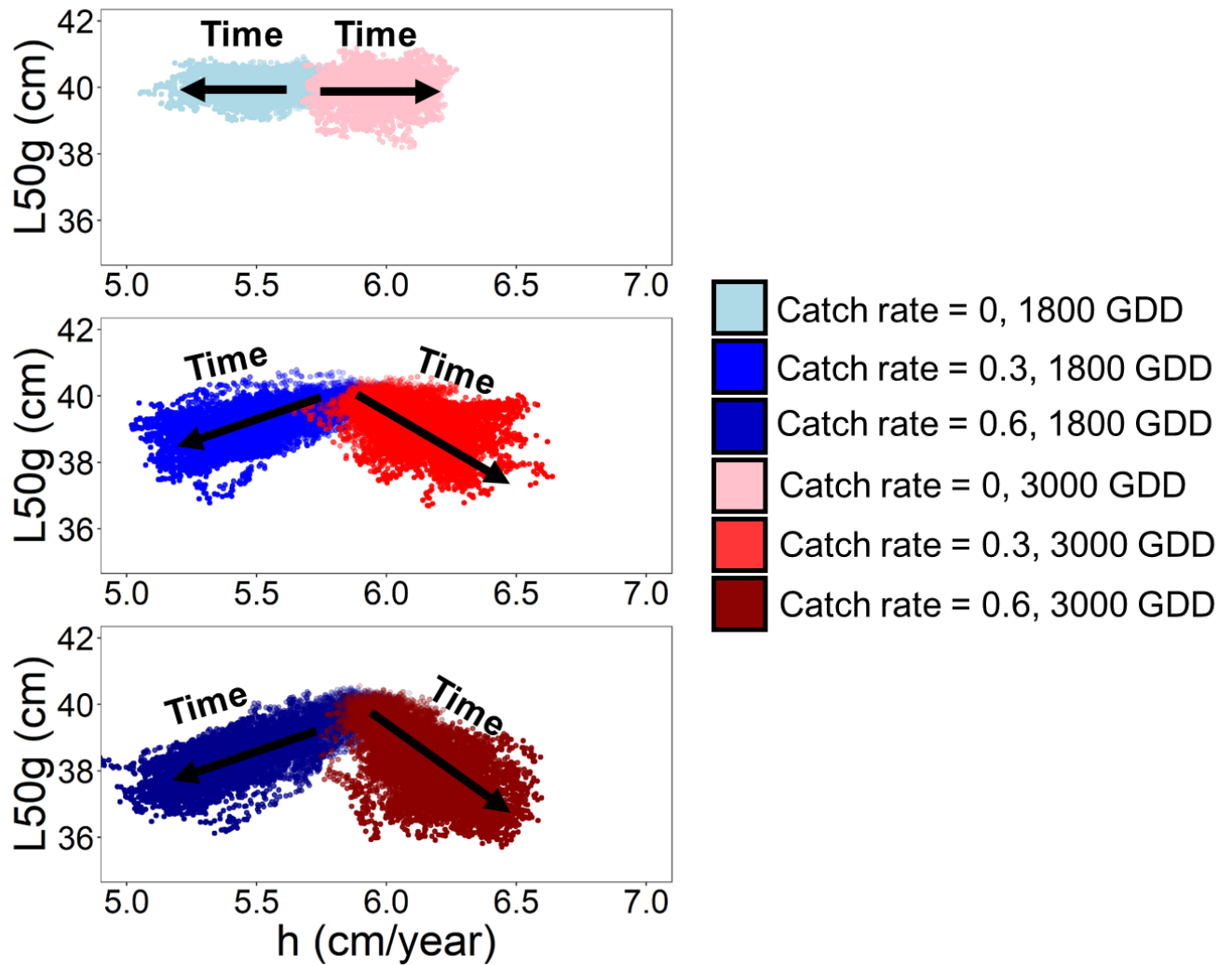


Figure 2: Plasticity mediated evolution of multiple traits. The relationship between growth capacity ( $h$ ) and genotypic length at reproduction ( $L_{50g}$ ) in no harvest (top), intermediate harvest (middle) and high harvest (bottom) scenarios became increasingly apparent with increasing harvest, but diverged by temperature. Though both populations evolved decreasing genetic length at reproduction, warm populations evolved increased growth capacity while cool populations evolved decreased growth capacity.

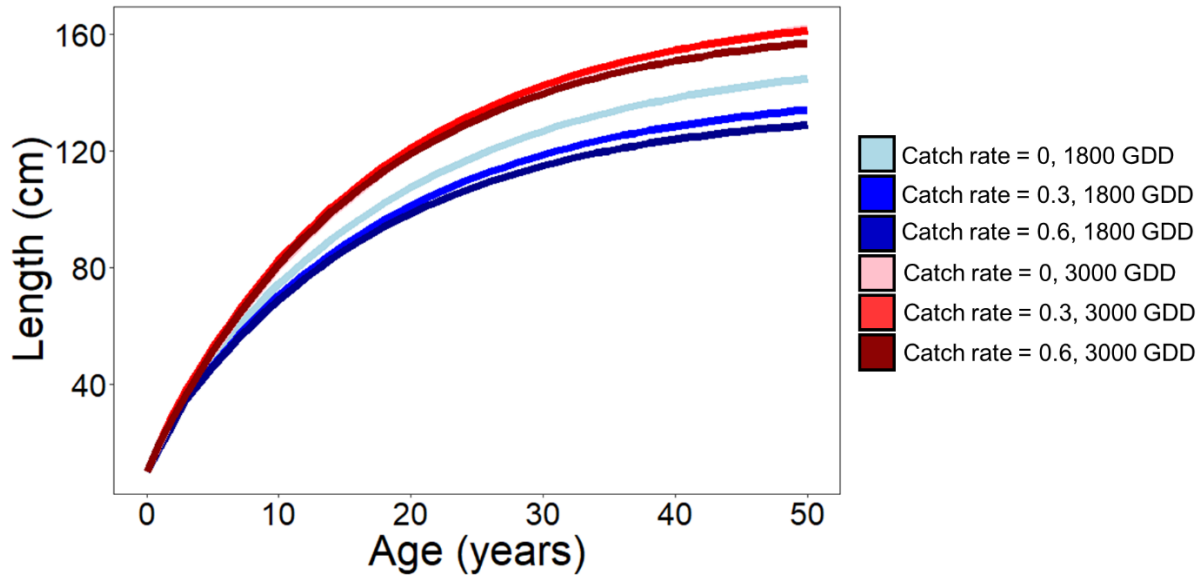


Figure 3: Plasticity masked evolution. Differences in growth emerged as a result of evolutionary and plastic changes in length at reproduction, growth capacity, and reproductive investment (growth trajectory expanded to 50 years at  $t = 100$  to show differences). Populations in the hot temperatures displayed less difference overall in growth patterns. Populations harvested according to the high harvest regime (dark) evolved a larger difference in growth trajectory compared to the intermediate (middle) and no-harvest (light) scenarios.

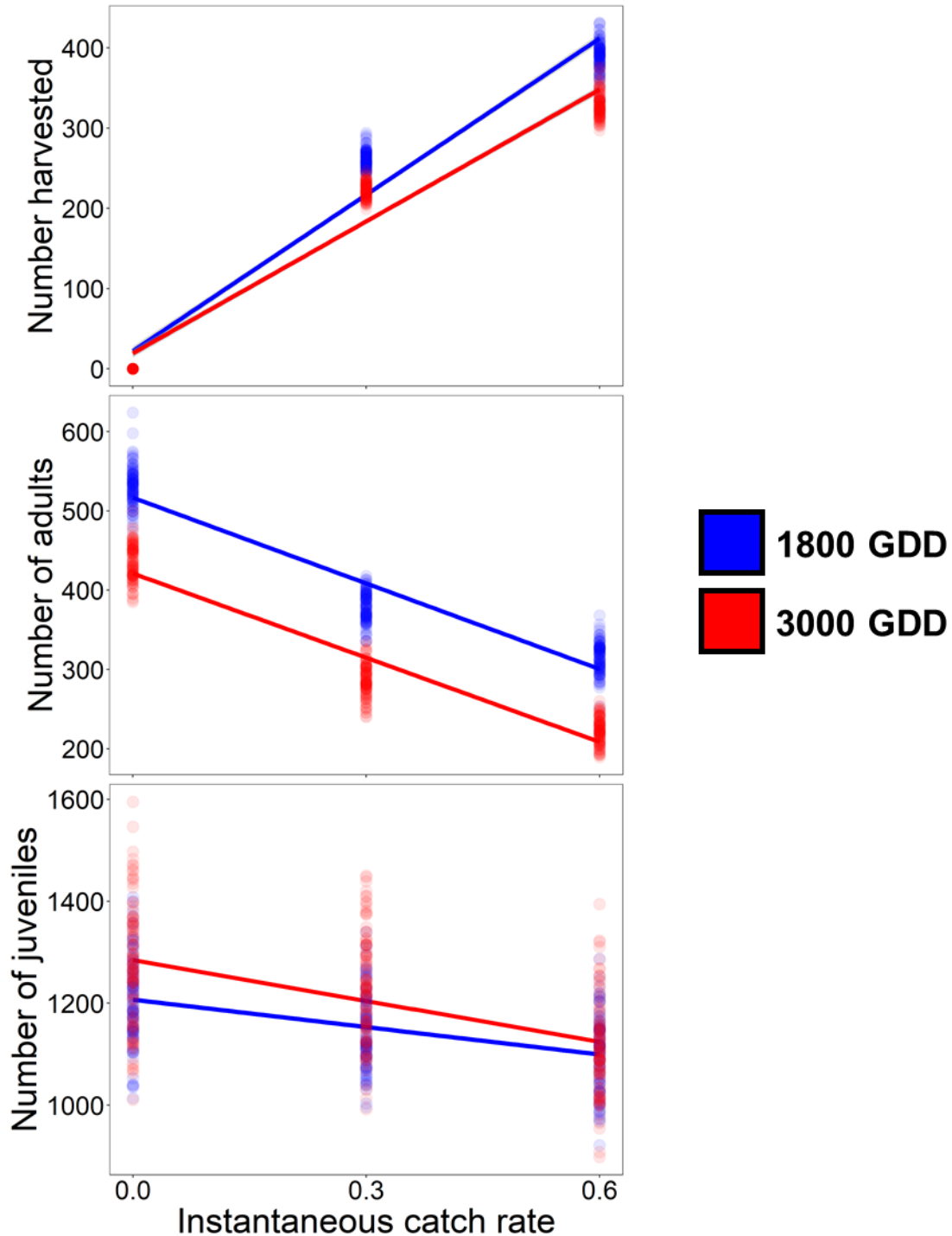


Figure 4: Increased temperature changed demographic structure and decreased harvest. Populations subjected to hot temperatures in addition to harvest experienced a decline in harvest relative to cool populations. They also had slightly different demographic structure, with a similar number of juveniles but a lower number of adults.