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Modeling the impact of climate change on a rare color morph in fish

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ABSTRACT

Species are typically comprised of a large number of genotypes, some of which are rare. Rare genotypes that are temperature-sensitive will predictably be impacted by climate change more profoundly than common genotypes for which gene expression does not depend on temperature. Computer simulations were used in this study to analyze the impact of changing temperatures on a very rare melanic morph that expresses a temperature-sensitive phenotype and is found in an abundant fish species *(Gambusia holbrooki)*. This numerical model assesses the frequency of the two natural color morphs, silver and black-spotted, over time and iterates in each generation, incorporating survival estimates for different life stages based upon data collected during empirical experiments. Using the current projections for mean surface temperature increase, which are 2.5° F to 10.4° F by the year 2100, the impact of warming environment on the mosquitofish population was analyzed. Three different climate warming scenarios were used to address annual temperature fluctuations and incorporate predicted temperature rise at correspondingly minimal, mid, and maximum levels. Our results indicate that increasing temperatures will seriously affect the rare color morph and in some cases will result in extinction. The minimal climate-warming scenario produced lower extinction risks for the rare morph; however, it still decreased the frequency of the rare genotype to minimal values. The mid-range warming scenario produced a higher risk of extinction, while the maximum warming scenario resulted in the extinction of the rare color morph. The results of this study shed light on the possibility that the effects of climate change may have important ramifications for rare genotypes in nature and will likely drive some rare species genotypes to extinction.

1. Introduction

The Earth's climate has changed since the preindustrial era and is projected to continue to change throughout the 21 st century. Global mean surface temperature is projected to increase over the next 100 years by up to 10.4 °F, and it has already warmed by 1.3° F over the 20th century (IPCC, 2007). Correlations between observed changes in climate and many factors such as survival, population size and distribution, reproduction time, and migration have been documented (Thomas et al., 2004). Studies using mid-range climate-warming scenarios and sample regions covering about 20% of Earth's terrestrial surface indicate that an estimated 15–37% of species and taxa in the studied regions may go extinct by 2050. This impact is anticipated to be greater if changes in climate are more extreme (Thomas et al., 2004). Recently, the thermal sensitivity of 2960 ray-finned fishes to future climatic exposure was investigated to find that fish will either migrate, adapt, or die off as temperatures continue to warm; this demonstrates that global patterns of vulnerability differ substantially between freshwater and marine realms (Comte and Olden, 2017).

Despite a voluminous literature on the impact of climate change, freshwater ecosystems have been relatively poorly studied. Heino et al. (2009) have shown that freshwater biodiversity is highly vulnerable to climate change, with extinction rates and extirpations of freshwater species matching or exceeding those suggested for better-known terrestrial taxa. Some evidence shows that freshwater species have exhibited range shifts in response to climate change in the last millennia, centuries, and decades. The proportion of potential losers (taxa becoming extinct) ranged from zero species for snails to 33% of the regional species pool for dragonflies. The set of potential winners (taxa becoming colonizers) was much larger, ranging from 53% for amphibians to 61% for dragonflies (Rosset and Oertly, 2011). However, these effects are typically species-specific, with cold-water organisms being generally negatively affected and warm-water organisms positively affected (Heino et al., 2009). Recent studies of freshwater invertebrates experimentally assessed the impact of altered temperature regimes on the emerging adults in aquatic insect communities. Experiments showed that mean body size decreased under warming conditions; however, the degree to which an organism's size was affected by

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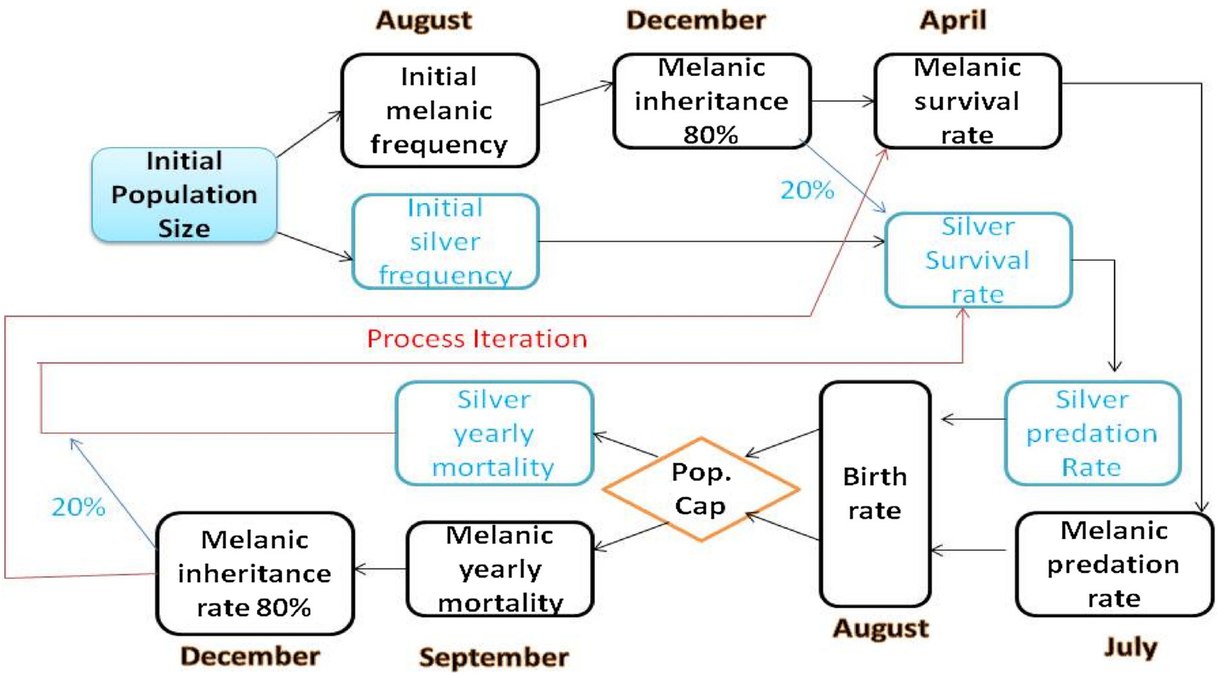

Fig. 1. The algorithm for the numerical model. The simulation begins with 'Initial Population Size' icon and the arrows point to the sequential changes affected in designated times (specific months) as the population ages and fitness changes occur for the color morphs.

temperature varied within and between taxa (Sardiña et al., 2017). These changes show the potential for changed temperature regimes to impact ecological systems at individual, population, and community levels, which in turn will affect the global biodiversity.

Long term preservation of biodiversity requires an understanding of the resistance of different species to environmental stress and particularly the impact of changing temperatures on ecological systems. The long time periods required to study the maintenance of rare genotypes in natural populations make numerical simulations an alluring option to field study when assessing long term changes in biological systems. Here we use numerical simulations to assess the impact of climate change on persistently rare genotypes in nature, as well as the populations that harbor them. We focus this study on Eastern Mosquitofish *(Gambusia holbrooki)*, which have a natural body color polymorphism wherein the rare morph is black-spotted and the common one is silver. Mosquitofish are small, live-bearing, freshwater fish that were commonly and widely introduced in US in early 1900s by the former U.S. Public Health Service, in large part because they were thought of as an effective and inexpensive way to control mosquitoes (Krumholz, 1948). More recent studies on mosquito control have not supported the view that *Gambusia* are particularly effective in reducing mosquito populations or in reducing the incidence of mosquito-borne diseases (Courtenay and Meffe, 1989; Arthington and Lloyd, 1989). Nevertheless, mosquitofish are widely spread in Atlantic and Gulf Slope drainages as far west as southern Alabama and as far north as Pennsylvania and New Jersey. Eastern Mosquitofish (*Gambusia holbrooki*) is native to the southeastern United States and shares a hybrid zone with *Gambusia affinis* (Western mosquitofish) around Mobile Bay, AL. The wild-type coloration of both species is silver, but small percentage of Eastern Mosquitofish express a rare but heritable melanic, black-spotted pattern that is not found in Western Mosquitofish.

The melanistic phenotype is almost entirely restricted to males and is inherited as a Y-chromosome-linked single-gene trait. Angus (1989) has shown that the Y-linked melanism allele (*M*) is temperature sensitive. It is dominant with high penetrance when fish are raised at 22 °C. Penetrance is much reduced, to about 42%, when fish are raised under warmer conditions (26 °C–29 °C) (Angus, 1989). Later Horth (2006) has shown that in some populations, 80% of males born to melanic sires turn melanic after at least 12 weeks of cold exposure. This expression pattern may result from the activation of a temperature-sensitive enzyme (e.g. tyrosine hydroxylase) (King et al., 1991). However, as Horth stated, "melanic inheritance is more complex than can be entirely resolved from the experimental design of this work…some populations have inducible melanism, others constitutive, therefore, more than one genotype produces the melanic phenotype" (Horth, 2006). In the short-term, genetic variability is often less critical than other determinants of population persistence (Lande, 1988). But over time, it can play the decisive role in allowing a population to persist and adapt in a changing environment (Lande and Shannon, 1996). As phenotypic expression of melanism in majority populations is directly affected by temperature and the consequence of loss of expression of melanism is the loss of fitness for the black male phenotype/genotype, the increasing temperatures as a result of climate change will directly affect melanic population.

Horth and Panayotova (2012) have shown that the persistence of the rare melanic morph is maintained through negative frequency dependent selection. Negative frequency dependent selection occurs when there is an advantage to being rare in a population, but this advantage decreases when the rare genotype increases in frequency (Cain and Sheppard, 1954; Ford, 1975; Sinervo and Lively, 1996). Although negative frequency dependence contributes to the persistence of melanic mosquitofish, as well as rare color morphs in other live-bearing fish, a rise in temperature will probably change the dynamics of this stable polymorphism (Rodd et al., 2002). The goal of this work is to use numerical simulations to study the long term effects of temperature changes predicted for the southeastern U.S. on the rare melanic morph and the mosquitofish population. Three different climate change scenarios were modeled: minimal (+4° F), mid-range (+8° F), and maximum climate-warming scenarios (+10° F). All relative fitness parameters for the two color morphs used in the simulations were obtained from empirical studies addressing natural selection (Horth and Travis, 2002; Horth et al., 2010).