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Fathers modify thermal reaction norms for hatching success in Atlantic cod, *Gadus morhua*

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ABSTRACT

Climate-driven warming is altering marine ecosystems at an unprecedented rate and evolutionary adaptation may represent the last resort for many ectothermic organisms to avoid local extinction. The first step to elucidate the potential for adaptation to unfavorable thermal conditions is to assess the degree of genotype-based variation in thermal reaction norms of vital fitness traits. Marine broadcast spawning fishes experience extremely high rates of mortality during early life stages. Paternally derived (genetic) variation underlying offspring fitness in adverse environmental conditions may therefore hold important implications for resilience. This study examined how males differ in their ability to sire viable offspring and whether the paternal contribution modified thermal reaction norms for hatching success in two replicated trials with cod *Gadus morhua* from the Northwest Atlantic (trial 1) and Baltic Sea (trial 2). Each trial included five temperature treatments (2.0, 4.0, 6.0, 8.0, 10.0 °C in trial 1, and 6.5, 8.0, 9.5, 11.0, 12.5 °C in trial 2) encompassing optimum conditions as well as the amount of warming projected in various future pathways for the year 2100. In both trials, mean hatching success significantly decreased towards thermal extremes. However, half-sibling families varied in their response to different incubation temperatures as indicated by significant paternity × temperature interactions and crossing of reaction norms. The influence of paternity itself was highly significant and explained 56% and 44% of the observed variation in hatching success in trials 1 and 2, respectively. Early embryogenesis represented the most crucial developmental period in terms of thermal tolerance and paternally mediated variation in hatching success. High variation in daily embryo survival among half-sibling families and temperature treatments was observed during blastula and gastrulation stages (until 100% epiboly), while almost no mortality occurred during subsequent development and throughout the hatching period. The observed magnitude of genetic variation underlying thermal reaction norms for embryo viability represents a relevant resource for adaptive responses (favorable selection) of cod populations exposed to environmental variability and/or directional changes, such as ongoing ocean warming.

1. Introduction

In light of projected climate-driven ocean warming, there is renewed interest in assessing the ability of individuals, populations, and eventually species to adapt to directional changes in their environment (Pörtner et al., 2014). In ectothermic organisms such as fish, reproductive success and population abundance will decline under unfavorable thermal conditions if vital life history traits are rigid in response to changing temperatures (Hoffmann and Sgrò, 2011). In this context, phenotypic plasticity describes the ability of a genotype to adjust the expression of certain phenotypic traits across an environmental gradient, which allows individuals to persist under unfavorable conditions (Chevin et al., 2010). However, the capacity of genotypes to produce viable phenotypes under stressful conditions is limited and, with regard to global warming, it is expected that long-term persistence will require rapid evolutionary adaptation, especially if populations already exist close to their upper thermal tolerance limit (Visser, 2008; Reusch, 2014). Accordingly, it is critical to understand the mechanisms driving adaptive differences in plasticity for managing valuable aquatic resources effectively and to mitigate potential socioeconomic consequences of population decline and biodiversity loss (Gattuso et al., 2015).

Among marine and freshwater fishes, the parental contribution to offspring fitness is increasingly recognized as a potential mechanism through which wild populations might buffer against natural environmental variability and facilitate adaptation to anthropogenic climate change (Hutchings, 2011; Munday et al., 2013). Previous breeding experiments show that parental effects can shape offspring fitness traits

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through both genetic and non-genetic pathways. Despite the predominant role of maternal effects via differences in egg size and composition (Kamler, 2005; Green, 2008), there is compelling evidence for the importance of paternal (genetic) effects on embryo viability and larval fitness traits in salmonids (e.g. Burt et al., 2012; Eilertsen et al., 2009; Nadeau et al., 2009; Wedekind et al., 2001) as well as in marine species such as Atlantic herring *Clupea harengus* (Panagiotaki and Geffen, 1992), haddock *Melanogrammus aeglefinus* (Probst et al., 2006; Rideout et al., 2004), winter flounder *Pseudopleuronectes americanus* (Butts and Litvak, 2007a, b), and Atlantic cod *Gadus morhua* (Kroll et al., 2013; Politis et al., 2014; Rudolfsen et al., 2005; Trippel et al., 2005). However, most of these studies were conducted under optimal rearing conditions, and less is known about the extent to which the genetic contribution of male spawners modifies the expression of offspring responses to different thermal regimes (Burt et al., 2011).

A basic approach to elucidate the potential of populations to respond adaptively to directional changes in their environment is to assess the degree of genotype-based variation in phenotypic plasticity (Munday et al., 2013). Herein, reaction norms use linear or non-linear functions to illustrate genotype- and environment-based differences in the expression of a trait (Schlichting and Pigliucci, 1998) and can, in combination with quantitative analysis of parental effects and genotype by environment interactions, illustrate genetic variation underlying plastic trait expressions across environmental gradients (Kruuk et al., 2008).

Climate-driven changes in the genetic architecture shaping physiological performance and life-history traits of fishes were primarily observed at the population-level (e.g., Baumann and Conover, 2011; Haugen and Vøllestad, 2000; Hutchings et al., 2007; Jensen et al., 2008; Oomen and Hutchings, 2015). Empirical evidence for individual variation in thermal reaction norms is comparatively rare and the majority of studies to date have focused on Pacific salmon *Oncorhynchus* sp. For example, significant family-level differences in the shape, intercept or slope of thermal reactions norms for offspring performance and survival have been demonstrated in pink salmon *Oncorhynchus gorbuscha* (Beacham and Murray, 1990), Chinook salmon *Oncorhynchus tshawytscha* (Heath et al., 1993; Munoz et al., 2015) and sockeye salmon *Oncorhynchus nerka* (Burt et al., 2012) but also in marine sticklebacks, *Gasterosteus aculeatus* (Shama et al., 2014) and Atlantic cod (Purchase et al., 2010). Recently, a companion study, Politis et al. (2014) demonstrated that paternal effects and genotype-by-temperature interactions significantly affected size-at-hatch as well as the incidence of deformities in larval cod.

The early life history of cod and other broadcast spawning species is characterized by extremely high rates of mortality and considered as an ontogenetic bottleneck with respect to adverse environmental conditions (Llopiz et al., 2014; Pörtner and Peck, 2010). Tolerance limits to abiotic stressors such as salinity, hypoxia and temperature are particularly narrow during early embryogenesis (Bunn et al., 2000; Geffen et al., 2006). At this stage, the activation of the zygotic genome occurs and organ systems arise, which facilitate physiological resilience and homeostasis during subsequent development (Hall et al., 2004). Differences in male quality and paternally derived variation in thermal sensitivity are therefore expected to represent an important factor during this critical period.

The objective of this study was to assess the impact of paternity on hatching success and whether the paternal contribution modifies offspring responses to potentially stressful temperatures during embryonic development of cod. We use a maternal half-sibling breeding design to assess the magnitude of genetic variation (via paternal effects) and genotype-based variation in thermal reaction norms for hatching success in cod from the Northwest Atlantic (trial 1) and the Baltic Sea (trial 2). Both trials included five temperature treatments (2 to 10 °C in trial 1 and 6.5 to 12.5 °C in trial 2) encompassing optimum conditions as well as the amount of warming projected in various future pathways for the year 2100 (+2 to 4 °C; IPCC, 2014). Specifically, we aimed to test the hypotheses that (1) ocean warming has a negative impact of hatching success, (2) a significant portion of variation in hatching success is attributable to paternal effects (elevation of reaction norms), that (3) half-sibling families vary in their response to different incubation temperatures (crossing of reaction norms) and (4) that paternally mediated differences arise during early embryogenesis.

2. Material and methods

2.1. General experimental design

Two independent experimental trials were conducted to examine the influence of paternal effects on thermal reaction norms for hatching success by using cod from the Northwest Atlantic, (January to May 2009) and central Baltic Sea (June to August 2009). Both populations reside close to the southern limit of the species' latitudinal range at each side of the North Atlantic and projected ocean warming is likely to have negative consequences for early life survival. In both regions, spawning temperatures range from 2 to 8 °C, while developing embryos are normally found at 4 to 6 °C (Brander, 1994; MacKenzie et al., 1996; Nissling, 2004). Temperature treatments in the Atlantic cod trial (2.0, 4.0, 6.0, 8.0, 10 °C) were selected to cover the entire range of ambient spawning conditions, laboratory-based optima (6 to 6.5 °C, Rombough, 1997) as well as projected ocean warming by the end of this century (+2 to 4 °C; IPCC, 2014). Due to logistical limitations, a different range without supra-optimal temperatures had to be used in the Baltic cod trial (6.5, 8.0, 9.5, 11.0, 12.5 °C).

For each trial, a maternal half-sib crossing design was applied to study the influence of paternal effects on embryo survival in relation to temperature. Initially, the eggs of a single female were fertilized with the milt of several males (Atlantic cod: $n = 4$; Baltic cod: $n = 5$) to create a total of nine maternally linked half-sibling families (labeled Ac1, Ac2, Ac3, and Ac4 for Atlantic cod and Bc1, Bc2, Bc3, Bc4, and Bc5 for Baltic cod). Subsequently, equal numbers of progeny from each cross were randomly assigned into four technical replicates within each of five temperature controlled incubation units (80 replicates for Atlantic and 100 replicates for Baltic cod). By partitioning variance components (VCs) into proportions of variation in hatching success that are associated with temperature, paternity and the interaction of both factors, this breeding design allows to evaluate the extent to which males influence embryo survivorship and how differently paternal effects correspond with different temperature treatments. In cod, males provide nothing but sperm to the next generation; hence the variation in hatching success attributable to paternity indicates genetic variation and the interaction of paternity × temperature can be used to determine whether there is significant genotype-based variability in phenotypic plasticity (Schlichting and Pigliucci, 1998).

2.2. Broodstock management

2.2.1. Atlantic cod

Between 2004 and 2006 wild cod were caught by longline off Nova Scotia (near Cape Sable Island) as well as in the Gulf of Maine and transported to the Department of Fisheries and Oceans Biological Station in St. Andrews, N.B., Canada. All broodfish were held in outdoor tanks and received ambient light conditions. Water temperatures during the spawning season ranged from 3 to 5 °C and salinity was 31 ± 1.

2.2.2. Baltic cod

Male and female broodfish were caught by trawl in the area of the Bornholm Basin in 2007 and held at the Bornholms Lakseklækkeri (Technical University of Denmark) in Nexø, Denmark. Upon capture, these fishes experienced a constant light regime (12 h day/night) and the indoor tanks were supplied with temperature-controlled seawater (6 ± 1 °C), which had an ambient salinity of 15 (Nissling and Vallin, 1996). Further details about broodstock rearing and husbandry at both locations are presented in Politis et al. (2014).