Demonstrating temperature induced phenological mismatch does not require negative effects on fitness or population growth: A comment on Samplonius et al.

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In a recent article Samplonius et al. (2020) argue that there are “systematic weaknesses in the evidence for temperature mediated phenological mismatch”. While we appreciate their review of the literature on this topic and their call for a broadening of the taxonomic and geographic scope of mismatch research, their conclusion that there is weak evidence for temperature mediated mismatches is, in our opinion, misleading. Our comments relate to two central issues.

First, Samplonius et al. (2020) define a set of five criteria that should be fulfilled to demonstrate temperature mediated phenological mismatches. In particular, they require that asynchrony between the phenology of a consumer and a resource should reduce consumer fitness (criteria 4) and negatively impact consumer population size or growth (criteria 5). The authors thus contend that fitness costs to the consumer should be part of the definition of phenological mismatch. However, these two criteria are not needed to demonstrate mismatch (Visser & Gienapp 2019) and are also not what Cushing intended when he introduced the match/mismatch hypothesis. For example, in Cushing (1990) he writes: “The degree of match and mismatch in the time of larval production and production of their food has been put forward *as an explanation* of part of the variability in recruitment to a stock of fish”. Note that the italics are ours.

Including the consequences of asynchrony within the definition of mismatch, as Samplonius et al. (2020) do, introduces confusion as this leads to subsuming multiple patterns under the one terminological banner of mismatch, which can obscure important and interesting underlying processes. We are all in agreement that fitness costs are *expected* and indeed are implicit in the *concept* that consumers strive to match resource demands with resource supply, but they are not a prerequisite to term a phenomenon as ‘mismatch’. To quantify the extent of the mismatch, alternative metrics than the commonly used number of days between the peak in consumer needs and resource supply could be used (Durant et al. 2007, Lindén 2018, Raemakers et al. 2020). But regardless of the chosen metric, the point is to represent match/mismatch by a single number at the individual or population level, which can then be related to individual- or population-level consequences in subsequent analyses. Including fitness consequences in the operational definition complicates things unnecessarily, as one cannot easily reduce the complex chain of events (from temperature change to asynchrony to individual level costs to population level outcomes) to a single number that is easily compared across studies. Thus, in our view, it is less confusing and more useful operationally to define phenological mismatch simply as the difference in the date of maximal resource availability and the date of maximal resource need (Cushing 1990, Stenseth & Mysterud 2002, Durant et al. 2007, Miller-Rushing et al. 2010, Visser & Gienapp 2019).

So, is this all just semantics? No, this is an important difference that can change the perception of what we know about the extent of documented cases of temperature mediated phenological mismatches. For example, in their literature review Samplonius et al (2020) find that few studies meet all of their defined criteria and thus conclude very few studies have found evidence for temperature mediated phenological mismatch. However, this is only true if requiring demonstration of negative fitness and population consequences. Thus, based on the studies reported in Samplonius et al, we would argue that there is limited evidence for consequences of temperature mediated mismatch on population size or growth but mounting evidence for “temperature mediated mismatch” *per se*.

A second comment is that Samplonius et al muddy the waters by not being clear about how fitness consequences of mismatches cascade through to demographic rates and population growth. It is important to keep in mind that reductions in the fitness of (some) individuals do not necessarily lead to reductions in population size or growth when there is density-dependent competition for limiting resources. For example, reductions in the annual production of juveniles as a result of mismatch may have little impact on adult population size in species that compete for limited breeding sites, so long as there are more potential breeders than sites. In this scenario, mean absolute fitness remains unaffected by mismatch, even though the relative fitness of some individuals decreases. In great tits, for instance, reductions in fledging output in years of large mismatch is compensated by increased subsequent recruitment probability, which buffers negative fitness consequences of temperature induced mismatch at the population level (Reed et al. 2013). This, however, does not mean that there is no temperature induced phenological mismatch in this system, nor that future climate change could not drive population decline via increased mismatch once the population becomes recruitment limited. Of course, not all populations are strongly density regulated, or trophic mismatch could impact the survivors of density dependence (e.g. adults), in which case stronger effects on population growth are expected. But immediate population-level impacts should not always be assumed, and lack of currently detectable population-level impacts does not mean that future increases in mismatch will not jeopardize population viability. Projection modelling based on an understanding of the underlying individual-level processes may be required to reveal such future impacts.

In conclusion, we appreciate the efforts by Samplonius et al (2020) to review the literature and their attempt to offer a clear definition of temperature mediated phenological mismatch. However, we believe that their explicit requirements of demonstrating negative individual and population level fitness consequences adds unnecessary complications to a simple idea behind phenological mismatch: that there is a difference in the date of maximal resource availability and the date of maximal resource need (Cushing 1990, Visser & Gienapp 2019). This phenology difference is expected to lead to negative consequences at the individual as well as population level, but it is not a requirement to observe these impacts in order to demonstrate temperature mediated phenological mismatch. Including the consequences of a phenomenon (such as phenological mismatch) as part of what defines the phenomenon, and then concluding that there is weak evidence for the phenomenon because of a lack of evidence for population-level impacts is not the way forward and has led, in our opinion, to an unnecessarily dismissive general tone and wording of the title of the Samplonius et al. paper.

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