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Quality over quantity: Trophic cascades in a warming world

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Climate change threatens all ecosystems and the organisms within them. Freshwater habitats, in particular, appear to be experiencing rapid environmental change (Almond et al., 2020; Knouft & Ficklin, 2017). Over the last decade, there has been a growing interest in the effects of warming on freshwater populations, which includes changes in abundance, body size, reproductive success and survival of a range of organisms (e.g. Hovel et al., 2017; Ledger et al., 2013; Velthuis et al., 2017; Yvon-Durocher et al., 2011). For instance, research in a natural warming experiment in Iceland has found that elevated temperatures increase the abundance of diatoms, with implications for secondary production (Junker et al. 2020; O'Gorman et al. 2017). All of this research has contributed to our knowledge that the effects of warming can be both direct and indirect. Even if there are no direct consequences of warming on a consumer population, they may suffer cascading consequences due to a change in resource availability. These '*trophic cascades*' have been documented in the ecological literature for decades, from Stephen Carpenter's seminal work on fish–zooplankton–algal cascades in lakes (Carpenter et al., 1985), to more recent work on how they are altered under global change (Jackson et al., 2017; Murphy et al., 2020). For instance, warming can enhance the cascading effects of fish on zooplankton (and, subsequently, phytoplankton) by elevating feeding rates (Kratina et al., 2012). Alternatively, warming can also result in phenological mismatch, where fish fry emerges earlier in spring before zooplankton prey peaks, causing a bottom-up trophic cascade where loss of prey reduces consumer survival (Jonsson & Setzer, 2015).

Importantly, research investigating the effects of warming on trophic cascades usually quantifies changes in abundance or biomass, rarely considering more subtle effects. For instance, warming can alter individual respiration rates (Cloyed et al., 2019), feeding selectivity (Gordon et al., 2018), behaviour (Kua et al., 2020) and food quality—all with consequences for other trophic levels. For instance, algae often produce less polyunsaturated fatty acids (PUFAs) in warmer conditions (Fuschino et al., 2011; Von Elert & Fink, 2018), which can have implications for consumers, such as the herbivorous grazer *Daphnia*. This filter-feeding crustacean is incapable of de novo synthesis of long-chained PUFAs, like most other arthropods (Harrison, 1990; but see Kabeya et al., 2018), and therefore such PUFAs must be derived directly from diet. PUFAs have two main functions: they help maintain membrane fluidity, especially at low temperatures (homeoviscous adaptation; Hazel, 1995) while the long-chain PUFAs eicosapentaenoic acid (EPA, 20:5ω3) and arachidonic acid (ARA, 20:4ω6) serve as precursors for eicosanoids, a family of hormone-like substances which play an important role in animal reproduction (Heckmann et al., 2008; Stanley-Samuelson, 1994). Therefore, at low PUFA availability, *Daphnia* can experience performance limitations in terms of decreased growth and reproduction (Müller-Navarra, 1995; Ravet et al., 2003; Wacker & Von Elert, 2001). In other words, resource quality can be just as, or more, important than resource quantity for *Daphnia* and other arthropods.

In this current issue of Functional Ecology, Tseng et al., investigated if changes in resource quality due to warming had consequences for higher trophic levels through trophic interactions. The authors discovered that, although algae produced more total PUFAs under warming, due to declines in cell size there was no net difference with the ambient treatment. However, the cold-reared algae produced more neutral lipids (i.e. fat content) than warm-reared algae. Somewhat surprisingly, these changes in lipid content had little cascading consequences for higher trophic levels. While *Daphnia* at ambient temperatures and fed cold-reared algae had higher abundance than those fed warm-reared algae, this positive effect was lost when *Daphnia* were kept at higher temperatures, and there were no cascading effects on the next trophic level (*Chaoborus*).

One of the explanations Tseng et al. give for this finding is that *Daphnia* require less PUFAs at warmer temperatures because their role in the maintenance of membrane fluidity declines with warming (Hazel, 1995). Similar results have been observed in several other studies (Masclaux et al., 2009; Schlechtriem et al., 2006). For instance, Martin-Creuzburg et al. (2012) showed that the effect of food quality (i.e. PUFA availability) on population growth of *Daphnia magna* was strongest at low temperatures. Addition of single PUFAs (ARA, EPA) had a consistent positive effect on the number of viable offspring, which showed a hump-shaped temperature dependency. However, juvenile somatic growth was less affected by food quality, indicating an important role of life stage.

In response to warming, food quality is not only expected to change due to altered PUFA content per algal cell but also due to changes in community composition (Ahlgren et al., 1997), as the content of essential PUFAs is taxon-specific (Ahlgren et al., 1990; Lang et al., 2011). At high temperatures and nutrient availability, bloom-forming cyanobacteria are favoured (Lürling et al., 2017; Pearl & Hiusman, 2008), which are a low-quality food as they lack essential PUFAs and sterols (Martin-Creuzburg et al., 2005; Von Elert et al., 2003). Furthermore, intraspecific and interspecific variation in consumer physiological and life-history traits might further shape their overall response to warming (Geerts et al., 2015; Vanvelk et al., 2020). For example, naturally coexisting *Daphnia longispina* genotypes were shown to differ in their susceptibility to PUFA limitations (Ilić et al., 2021) while Werner et al. (2019) found pronounced differences in heat tolerance within a natural population of *Daphnia magna*. Therefore, future studies should investigate the effects of temperature on natural communities, and monitor population dynamics and compositional changes (and thus potential food quality alterations in the phytoplankton) over time periods long enough to allow for potential evolutionary changes.

Other factors not considered by Tseng et al., such as encounter rate, body size and development time of the prey, play an important role in prey–predator interactions (Pastorok, 1981). These factors are expected to be affected by warming, either directly via changes in metabolic rates, or indirectly via changes in food quality (Giebelhausen & Lampert, 2001; Lampert, 2006). Tseng et al., found that the population size of *Daphnia* decreased with temperature, indicating that food quantity and encounter rate for *Chaoborus* will also decline while neckteeth induction is expected to increase, potentially increasing handling time (Tollrian et al., 2015). Additionally, *Chaoborus* is a gape-limited predator (Tollrian, 1995), and therefore lower growth rates in *Daphnia* will result in longer time spent in the vulnerable size spectrum (Pastorok, 1981).

Tseng et al.'s work highlights the need to consider quality, as well as quantity, in trophic interactions in a warming world. Moving forward, network approaches should be used to understand how stressor effects on resource quality ripple through the food web. In our rapid changing world, it is also important to consider how warming will interact with other stressors (Jackson et al., 2016), which may mitigate or amplify one another's effects on food quality with implications for cascading interactions.

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