Climate change creates nutritional phenological mismatches

Cornelia W. Twining[1], J. Ryan Shipley[1], and Blake Matthews[1]

[1]Eawag, Swiss Federal Institute of Aquatic Science and Technology, Department of Fish Ecology and Evolution, Seestrasse 79, CH-6057 Kastanienbaum, Switzerland

Corresponding author: Twining, C.W. (cornelia.twining@eawag.ch)

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Abstract

Climate change is creating phenological mismatches between consumers and their resources. However, while the importance of nutritional quality in ecological interactions is widely appreciated, most studies of phenological mismatch focus on energy content alone. We argue that mismatches in terms of phenology and nutrition will increase with climate change.

Nutritional phenological mismatch

Climate change is causing the advancement of **phenologies** (see Glossary) for many species, which often results in **phenological mismatches** between consumers and resources due to differential rates of advancement [1]. Consumers at energetically-demanding life history stages, such as reproduction, early development, and migration, are especially sensitive to phenological mismatches. For example, insects such as caterpillars are advancing faster than insectivorous bird breeding time, which causes a reduction in fitness when nestling food demands do not coincide with insect availability [2]. Migratory animals, including many birds and mammals, are especially likely to experience phenological mismatches because they rely on indirect information from their wintering and/or stopover sites. Unlike resident species, migrants are unable to readily anticipate resource conditions at breeding sites and adjust their life history events accordingly [2].

Most previous work about how climate change affects consumer-resource phenologies has focused on energy and biomass as the main currency underlying consumer demand, even though consumers can also be strongly limited by the nutritional composition of their resources [3]. Mismatches during critical life history stages associated with key nutrients, including both **elemental nutrients** (see Glossary) like phosphorus or calcium as well as **organic nutrients** (see

Glossary) like fatty acids, amino acids, and vitamins, can result in reductions in growth, energetic efficiency, reproductive success, and even survival [3]. **Nutritional**, rather than purely **energetic, mismatches** (see Glossary) are likely to be most pronounced during life history stages when demand for specific nutrients is greatest, such as during reproduction and early development or prior to hibernation or migration (e.g., 2). Because food resources vary widely not only in their seasonal availability, but also in their nutritional composition throughout the year (Figure 1), there is high potential for phenological mismatches based upon nutritional content. For example, while the biomass of primary producers typically peaks later in the season, their nutritional quality for herbivores, in terms of protein and nitrogen content as well as the **stoichiometric ratio** (see Glossary) of carbon to phosphorus (C:P), is typically higher earlier in the season (e.g., 4, 5, 6, 7). Importantly, the nutrient and energetic content of food resources may also respond to climate change at different rates. If the phenology of nutrients shifts independently of biomass, consumers may experience phenological mismatches in which nutrient-poor food is readily available, leading to nutritional limitation during times of apparent bounty (Figure 1).

The ecological context of consumers' nutritional phenological mismatches

Consumers vary in their likelihood to experience **nutritional phenological mismatches** (see Glossary), due largely to the consumers' 1) ability to advance its own phenology to match phenological variation of the nutrient, 2) degree of dietary specialization and ability to use alternative sources of a nutrient, and 3) ability to synthesize the nutrient.

Seasonal variation in nutrient availability present consumers with a moving target, especially when the nutrient content of resources changes independently of biomass or energy content. For instance, although total flying insect biomass is greatest later in the Tree Swallow (*Tachycineta bicolor*) breeding season, fluxes of key fatty acids, which are associated with increased chick growth, condition, and survival, and come from aquatic insects. Aquatic insect abundance is greatest earlier in their breeding season, suggesting that phenological variation in insects containing these key nutrients may be more relevant to swallow fitness than phenological variation in overall insect biomass [8, Figure 2). While few studies have formally considered the ability of consumers to track shifts in nutrient content due to climate change, such mismatches are likely to occur across a diversity of food webs when consumers do not match the rates of phenological advancement of specific nutrients (Figure 2). For example, nutritional phenological mismatches between pollinators like bees and flowering plants are highly likely because: pollen from different species varies in essential nutrients for bees, like amino acids and sterols (e.g., 9), and rates of phenological advancement vary between bees and different species of flowering plants [10].

A consumer's trophic ecology is also likely to influence its risks of nutritional phenological mismatch. More specialized species that are tied to a particular resource, foraging habitat, or foraging mode may be more likely to experience mismatches for nutrients than generalist species. Consumers that rely upon single resources may encounter mismatches if there is seasonal variation in the quality of the resource (Figure 1A) and the period of higher nutrient density advances more rapidly or more slowly than the consumer's demand for the nutrient (Figure 1B-C; Figure 2A). For example, while seston biomass can continue to increase throughout the summer, phytoplankton quality for zooplankton tends to decline later in the season as algal assemblages either become increasingly dominated by cyanobacteria or as the stoichiometric ratio of carbon to elemental nutrients like phosphorus increases (7, Figure 2D).

Multiresource mismatches are possible when consumers use multiple resources that vary in nutrient density (Figure 1D) and the higher quality resource advances more rapidly or more slowly than the consumer (Figure 1E-F). For example, a bear that relies upon migratory fish and local berries may encounter a mismatch if it keeps pace with berries but not salmon, the latter having higher fat content and quality to support hibernation (e.g., 11-12, Figure 2B). In contrast, consumers that switch between multiple high-quality resources may be less likely to encounter mismatches. For example, Dippers (Cinclidae) are able to switch between two alternate local sources of n-3 LCPUFA, namely larval aquatic insects and emergent aquatic insect adults, depending on their availability [13].

While **energetic phenological mismatches** depend largely upon timing and trophic ecology, the risk of nutritional mismatch also depends on the ability of consumers to synthesize the nutrient of interest, and the costs of meeting nutritional demands via **internal synthesis**. Elemental nutrients that vary in their availability seasonally, such as phosphorus in phytoplankton, are highly likely to create nutritional phenological mismatches because consumers cannot synthesize them. In the case of organic compounds, species with greater synthesis capacity are more likely to be able to cope with temporal variability in nutrient availability by shifting to using precursors to meet nutritional needs. For example, some animals may synthesize key fatty acids from precursors where they are locally scarce, but obtain them directly from diet where they are abundant, limiting their risk of nutritional phenological mismatch [14]. Animals lacking the synthesis capacity to meet their nutritional needs will likely face the greatest risk, because they must meet their demands from direct consumption.

The future of nutritional phenological mismatches

As anthropogenic climate change continues, phenological mismatches may arise from declining resource availability, shifts in resource composition, and consumer-resource range shifts. There is also growing risk that organisms will confront temporal mismatches in the supply and demand of nutrients. Future research programs examining nutritional phenological mismatches should characterize: 1) shifts in the quantity, quality, and phenology of resources, and 2) the capacity of species to adapt to such changes. Importantly, we need to better understand whether biomass, energy, and nutrients respond to climate change at similar or different rates (Figure 1), and what are the underlying mechanisms of adaptation to variation in nutritional quality [14]. Specifically, will we observe evolutionary shifts in 1) the timing of life-history events (i.e. phenology), 2) the degree of resource and nutrient specialization, and 3) the rates of internal nutrient synthesis? Answering these questions will help us to understand if consumers encountering mismatches have the adaptive capacity to keep pace with advancing nutrient phenology.

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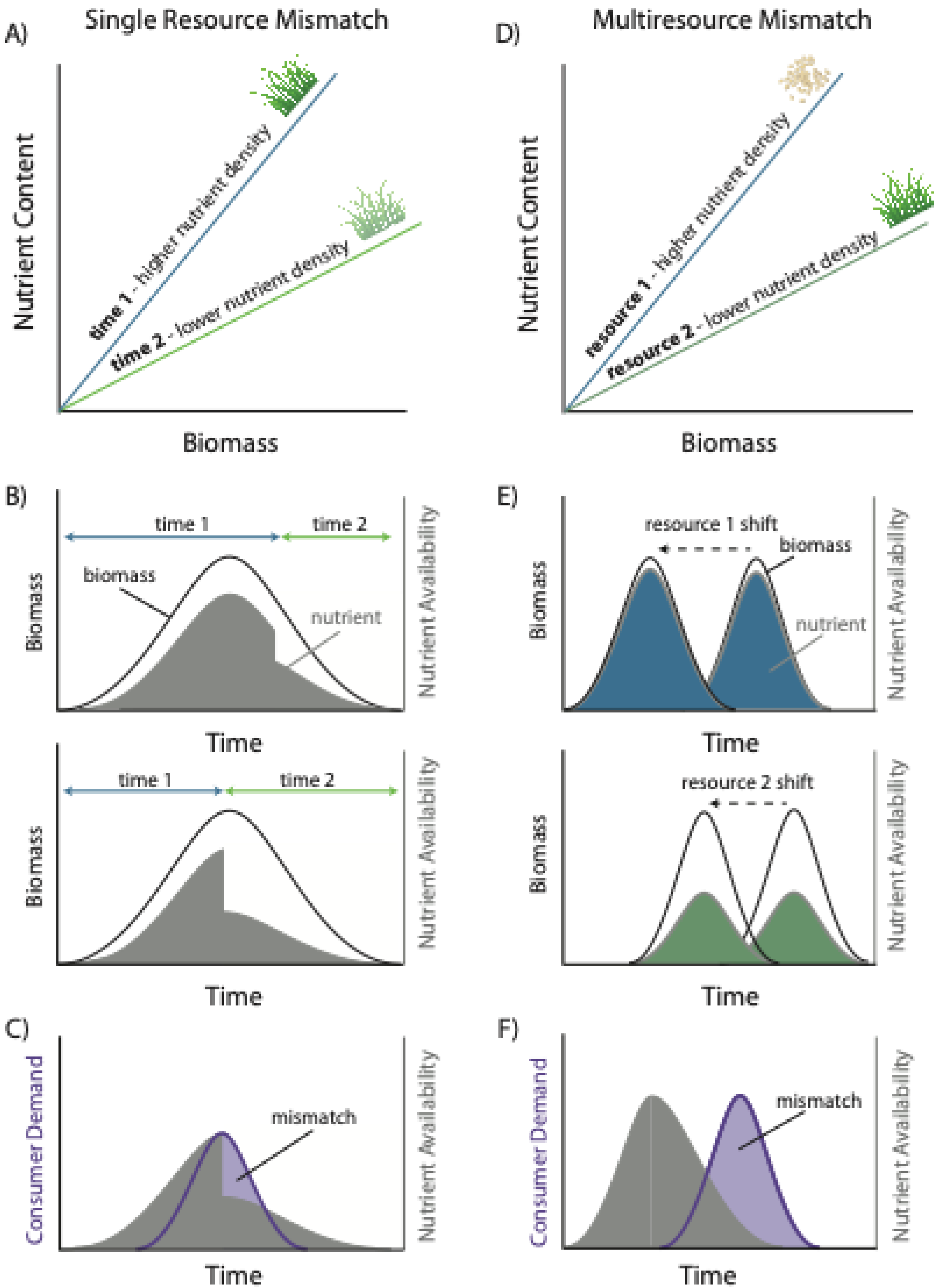
Figure 1: Nutritional phenological mismatches between single resources that vary in quality seasonally and multiple resources that vary in both quality and phenology

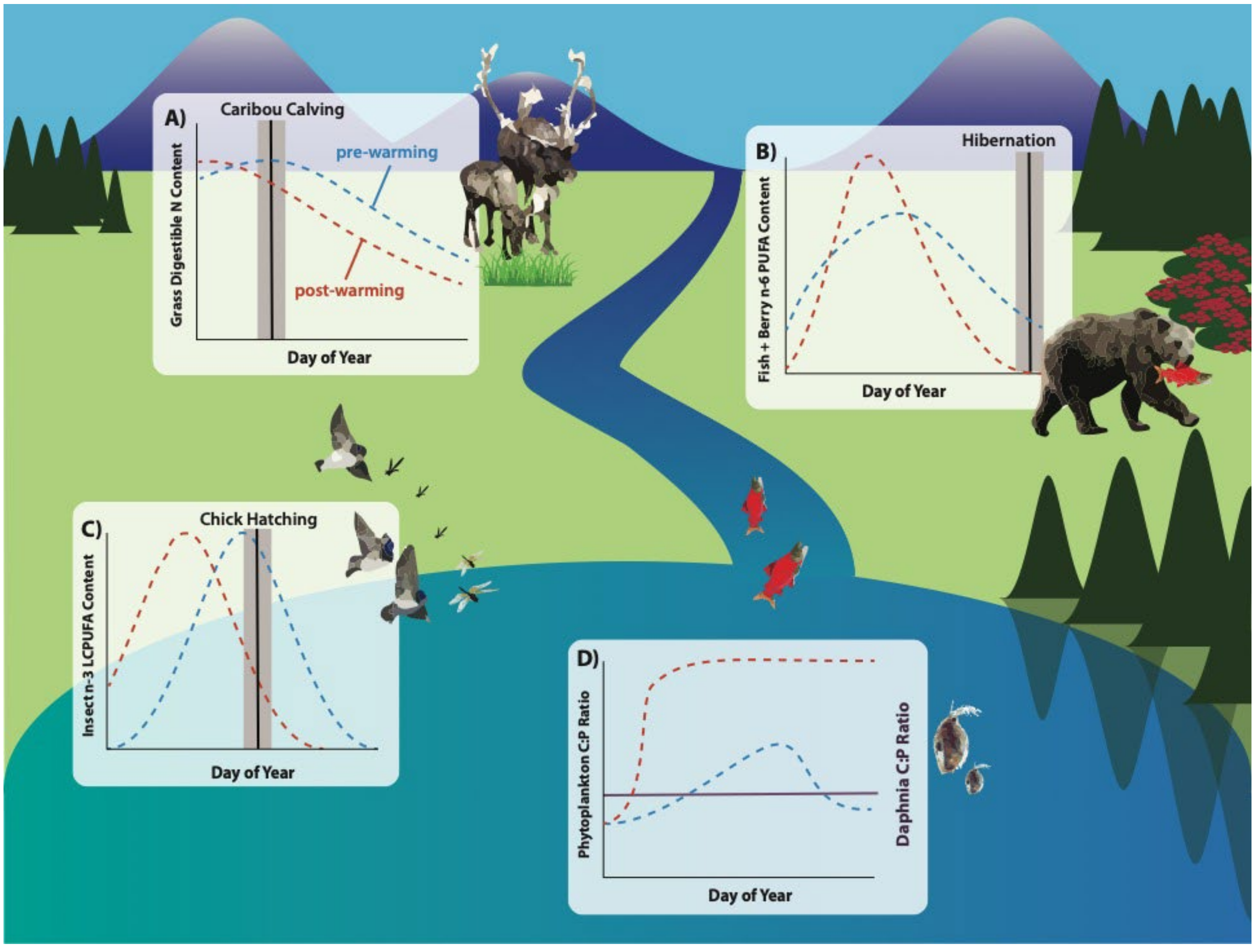
In the single resource scenario, (1A), the nutrient content per unit of biomass is greater during time 1 than time 2. With phenological advancement in the single resource scenario (1B), the period of lower nutrient density (i.e., time 2) begins earlier in the year even if biomass does not shift. A consumer may experience nutritional phenological mismatch in (1C) if its demand for the nutrient (dark purple line) does not advance as rapidly as the period of higher nutrient availability advances, resulting in unsatisfied demand (light purple filled area). In the multiresource scenario (1D), the nutrient content per unit of biomass is greater for resource 1 compared to resource 2. With phenological advancement in the multiresource mismatch scenario (1E), resource 1 is available earlier in the year than resource 2 and both advance. A consumer may experience nutritional phenological mismatch (1F) if its demand for the nutrient (dark purple line) does not advance as rapidly as the higher nutrient resource advances, resulting in unsatisfied demand (light purple filled area) when it is no longer matched with nutrient availability (shaded gray area = sum of nutrients from both resources).


A)
Single Resource Mismatch
Nutrient Content
time 1 - higher nutrient density
time 2 - lower nutrient density
Biomass
B)
time 1
time 2
biomass
nutrient
Biomass
Nutrient Availability
Time
time 1
time 2
Biomass
Nutrient Availability
Time
C)
mismatch
Consumer Demand
Nutrient Availability
Time
D)
Multiresource Mismatch
Nutrient Content
resource 1 - higher nutrient density
resource 2 - lower nutrient density
Biomass
E)
resource 1 shift
biomass
nutrient
Biomass
Nutrient Availability
Time
resource 2 shift
Biomass
Nutrient Availability
Time
F)
mismatch
Consumer Demand
Nutrient Availability
Time

1

2: Examples of likely phenological nutritional mismatches.

A) Digestible nitrogen (N) and protein are important components of grass quality for caribou (*Rangifer tarandus*), especially during calving. Digestible N content declines over the growing season and is likely to decline earlier in the year under climate change [6], presenting caribou with a mismatch if their calving time does not advance at the same rate. Caribou migrate to their summer calving grounds and thus may not use the same local cues to time their phenology as grasses on calving grounds. B) Omega-6 polyunsaturated fatty acids (n-6 PUFA) are important fats for mammals preparing for winter hibernation (ADD Arnold and Ruff). Climate change is shifting the timing of elderberry (*Sambucus racemosa*) availability for Kodiak brown bears (*Ursus arctos middendorffi*), such that the availability of n-6 PUFA, from berries and salmon are becoming more pulsed, resulting in lower nutrient availability prior to hibernation [11]. C) Omega-3 long-chain polyunsaturated fatty acids (n-3 LCPUFA) are important nutrients for Tree Swallow (*Tachycineta bicolor*) chicks. With climate change, insect n-3 LCPUFA content is advancing more rapidly than birds like Tree Swallows are advancing their breeding time [8]. D) The carbon to phosphorus ratio (C:P) of phytoplankton is a key determinant of food quality for zooplankton like Daphnia [7]. With earlier spring warming due to climate change, phytoplankton C:P ratios can quickly become higher than those of Daphnia (solid purple line).


A)
Caribou Calving
pre-warming
post-warming
Grass Digestible N Content
Day of Year
B)
Hibernation
Fish + Berry n-6 PUFA Content
Day of Year
C)
Chick Hatching
Insect n-3 LCPUFA Content
Day of Year
D)
Phytoplankton C:P Ratio
Daphnia C:P Ratio
Day of Year

Glossary

- Biomass Mismatch – occurs when the biomass of food resources does not meet consumer demands
- Elemental Nutrient – an element that organisms require for survival and life cycle completion
- Energetic Mismatch – occurs when the energetic content of food resources does not meet consumer energetic demands
- Energetic Phenological Mismatch – occurs when the energetic content of food resources does not meet consumer energetic demands due to seasonal mismatches between consumer demand and resource availability
- Internal Synthesis – the production of an organic compound by an organism
- Nutritional Mismatch – occurs when the nutritional content of food resources does not meet consumer nutritional demands even if energetic demands are satisfied
- Nutritional Phenological Mismatch – occurs when the nutritional content of food resources does not meet consumer demands for a nutrient due to seasonal mismatches between consumer demand and nutrient availability

- Organic Nutrient – a carbon compound that consumers require directly from diet and are unable satisfy their demands for through internal synthesis

- Phenology – the seasonal timing of life history events

- Phenological Mismatch – occurs when consumer and resource seasonality are mismatched

- Stoichiometric Ratio – the ratio of different elemental nutrients to one another