

CHAPTER TWENTY-SIX

Climate change, phenology and the nature of consumer–resource interactions: advancing the match/mismatch hypothesis

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Introduction

Understanding how species cope with ecological and environmental variation is a fundamental concern of ecology. Over the course of their lives, many organisms alter their phenotypes in response to biotic and abiotic pressures (Miner *et al.* 2005), responses that cascade through the food web to, in turn, affect the dynamics of species interactions. These effects, called trait-mediated effects, are pervasive in ecological communities, and their study has offered new insights into community ecology, a subject previously dominated by a density-mediated understanding of species interactions (Werner and Peacor 2003). Most analyses of trait-mediated effects take a top-down perspective where variation in consumer traits causes phenotypic responses by prey species. These phenotypic responses include behavioural, morphological and/or physiological plasticity that have ramifying consequences for the food web by influencing how predators and prey interact (Werner and Peacor 2003). This top-down perspective on the influence of traits in communities suggests that it is consumers that determine the nature and strength of the mediated effects.

Climate change is an ongoing global perturbation that also affects the densities and traits of interacting species, although these effects are not necessarily related to food web trade-offs. Cohesive shifts in phenology – the timing of periodic biological events, such as migration, flowering or mating – reveal the global scale of climate change's influence on species' traits (Parmesan and Yohe 2003; Root *et al.* 2003). These phenological changes affect conditions that influence

the relative fitness contributions of life-history traits, traits such as age-structured growth, reproductive timing or developmental rates. For some species, these traits are plastic to fitness trade-offs created by phenological shifts. In this way, climate change can affect the expression of traits that have an overwhelming influence on species interactions. Unlike the top-down influence of consumers, this non-trophic forcing can affect food webs via bottom-up processes. Phenology not only affects the nature and timing of species interactions, but also influences the very likelihood that two species will interact at all. In this manner, it can conflate or confound prey trait responses to immediate food web trade-offs, like those mediated by predators. Climate-driven phenological variability provides new context for understanding the interaction between trophic and non-trophic traits and how this influences overall food web dynamics.

The consequences of phenological shifts for consumer-resource interactions have been most clearly documented when interacting species experience a differential response in time and/or space to a shared change in climate (Parmesan 2006). Phenological asynchrony related to climate change has been identified among trophic levels (Thackery *et al.* 2010), species (Visser and Both 2005) and even within species (Høye *et al.* 2007). These differential shifts reveal frequent changes in consumer-resource interactions that many communities are likely to experience (Walther *et al.* 2002; Post *et al.* 2009). Emergent inter-trophic asynchrony can trigger demographic changes that affect the entire food web by affecting interactions that structure communities (Costello *et al.* 2006; Borcherting *et al.* 2010). For example, differential climate-driven phenological shifts have been implicated in the collapse of avian population cycles at high latitudes (Ludwig *et al.* 2006). Traditionally, these population irruptions have provided periodic flushes of nutrients that support predator populations while simultaneously regulating plant successional dynamics (Ims *et al.* 2008).

Analyses of the consequences of climate-driven shifts in phenological traits trace their conceptual origins to the ‘match/mismatch hypothesis’ – a simple framework that links climate-driven trophic mismatch with population and community-level consequences.

Origins of the match/mismatch hypothesis

The match/mismatch hypothesis emerged in the 1970s from the marine fisheries literature to explain the extreme variation in population recruitment of economically important fish stocks of cod (*Gadus* spp.) and herring (*Clupea* spp.) in the North Atlantic (Cushing 1974). It proposes that in seasonal waters, fish recruitment is determined by the degree of temporal overlap between a ‘critical period’ of fish larval development, a period marked by high food- and predator-mediated mortality, and the timing of the peak abundance of their food resource, pelagic zooplankton. The magnitude of this overlap, conceptualized by two bell curves of species abundance resting on a temporal axis

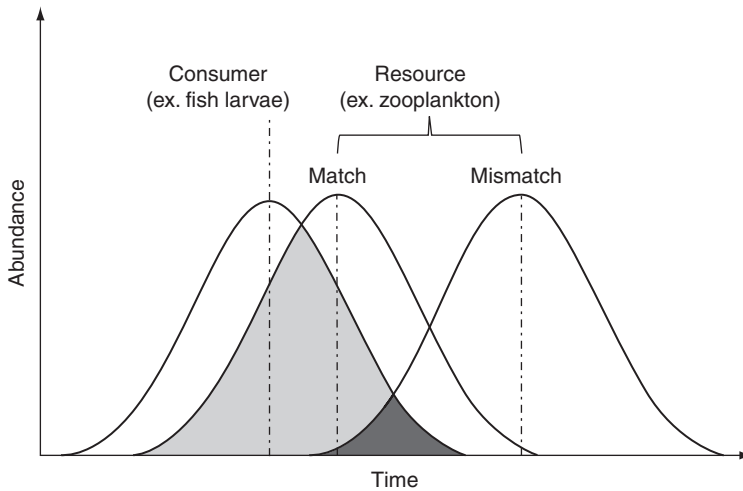


Figure 26.1 The temporal match/mismatch hypothesis. The abundances of consumers and resources are shown as distributions in time. The relative overlap between consumer and resources varies with resource phenology and results either in a match and high consumer population recruitment (light shading), or a mismatch with low consumer population recruitment (dark shading). Modified from Durant *et al.* (2007).

(Fig. 26.1), conceivably results in either a temporal overlap of resource demand and availability, a trophic match, and thus high fish population recruitment, or a temporal disjunction between resource demand and availability, a trophic mismatch, with low fish population recruitment.

Over the course of several decades, David Cushing, a British fisheries biologist, expanded on hypotheses proposed in the early twentieth century (Hjort 1914) and developed what he named the ‘match/mismatch hypothesis’ (Cushing 1974, 1982, 1990). Cushing observed that the mean timing of peak fish spawning and, by extension, the phenology of the critical period for the majority of fish larvae, was relatively fixed from year to year, whereas the appearance of zooplankton populations was regulated from the bottom-up by stochastic climatic processes (Cushing 1990). Earlier hypotheses had assumed that the critical period for these fishes was brief, lasting only from the time of hatching to first feeding (Hjort 1914). Cushing broadened the application of the critical period to include all of larval development and just beyond (Cushing 1990). By relaxing this assumption, Cushing’s hypothesis emphasized an outlook where the per capita effects of life-history stage transitions were regarded as processes rather than fixed events. Cushing’s match/mismatch hypothesis also emphasizes that climate variability plays a decisive, but indirect role in species interactions by affecting the expression of species’ life-history traits via its influence on their reproductive phenology. When generalized, the match/mismatch hypothesis proposes that nascent consumers

are unable to track consistently variability in the reproductive phenology of lower trophic levels, and that this failure has disproportionately large consequences on population recruitment relative to other instances of interspecific interaction throughout their ontogeny.

Empirical support for Cushing's match/mismatch hypothesis has been somewhat equivocal; however, this has often been the result of data limitations and the model's simplification of complex multitrophic dynamics (Leggett and DeBlois 1994; Durant *et al.* 2007). Despite this, in the fisheries literature alone, the match/mismatch hypothesis has spawned decades of research, numerous allied hypotheses, and encouraged ongoing debate about the mechanisms of bottom-up community regulation in marine systems (reviewed in Durant *et al.* 2007).

Climate change and the match/mismatch hypothesis

Cushing's simple framework is not conceptually bound to marine systems, and has proven readily adaptable for the study of the consequences of differential phenological responses to climate change across several systems. In recent decades, the scientific community has drawn increasing attention to the ecological consequences of climate change (Walther *et al.* 2002; Forchhammer and Post 2004, Fig. 2; IPCC 2007; Post *et al.* 2009). Phenological shifts relative to calendar dates (Fitter and Fitter 2002), and more recently phenological shifts relative to other species' phenologies (Visser and Both 2005), have emerged as foci for climate ecology research. Cushing himself perceived the relevance of his framework for addressing questions related to climate change (Cushing 1982); however, the first applications of this framework beyond the North Atlantic system focused on the mistimed reproduction in great tits (*Parus major*) in the Netherlands (Visser *et al.* 1998).

Since this advance in the late 1990s, population-level effects of trophic mismatch caused by differential phenological shifts among species have been documented in detail across diverse consumer-resource pairings, including interactions between birds and invertebrates (Visser *et al.* 1998; Hipfner 2008; Both *et al.* 2009), birds and fish (Durant *et al.* 2005; Gremillet *et al.* 2008), vertebrate herbivores and plants (Post and Forchhammer 2008; Post *et al.* 2008a), invertebrate herbivores and plants (Visser and Holleman 2001), pollinators and plants (Memmott *et al.* 2007; Hegeland *et al.* 2009) and marine and freshwater fishes and invertebrates (Edwards and Richardson 2004; Winder and Schindler 2004). Trophic mismatch may occur at any level in a food web, or even in multiple levels simultaneously, from primary producers to apex predators (Grebmeier *et al.* 2006; Both *et al.* 2009; Gremillet *et al.* 2008; Primack *et al.* 2009; Montes-Hugo *et al.* 2009; Thackeray *et al.* 2010). Cushing's match/mismatch hypothesis is the progenitor of these studies, but several key conceptual advances, some of which are discussed below, have granted this

framework broader relevance to the abovementioned and future investigations of the ecological consequences of climate change.

Accounting for abundance, temporal variance and adaptation

Resource and/or consumer abundance can influence the strength of a trophic match/mismatch by decreasing or increasing the likelihood that consumers will encounter resources at the ‘tails’ of their temporal distributions (Cushing 1982; Durant *et al.* 2005). While the original match/mismatch hypothesis focused on the mean timing of peak abundances, it is clear that the magnitude of either resource or consumer abundance, represented by a narrower or more highly dispersed distribution (Fig. 26.2a), can influence the degree of temporal matching during the critical period by increasing the area of potential overlap between the consumer and resource curves (Durant *et al.* 2005). The relative effects of resource timing versus resource abundance can be separated from one another using time series analyses (Durant *et al.* 2005); however, the prevalence and significance of these relationships across diverse systems remains relatively underreported and, at times, equivocal (Hipfner 2008).

The extent to which the abundance curves of interacting species overlap is also determined by their temporal variance (Fig. 26.2a, b). Warming manipulations of two Arctic shrub and one forb species in Greenland demonstrate that in addition to shifts in the timing of phenological events, the duration of phenological life-history periods, or phenophases, may also be sensitive to climatic factors (Post *et al.* 2008b). Most match/mismatch studies have focused on the timing of the first or mean date of phenological processes, whereas few have explored the prevalence and consequences of shifts in phenological duration (but see Both and Visser 2001, 2005). Despite this, differential shifts in the duration of phenophases in response to climate change could conceivably give rise to match/mismatch conditions similar to, but independent of, those linked with the mean date of peak abundance.

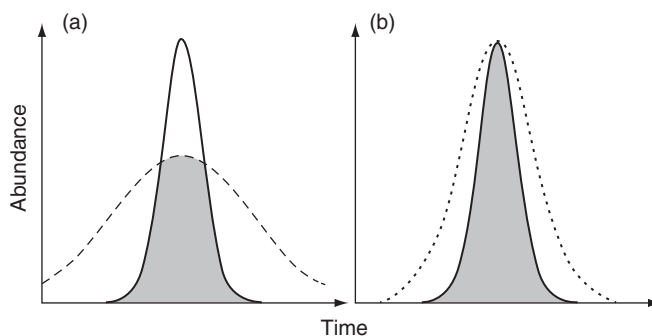


Figure 26.2 Factors which may affect the degree of match/mismatch independent of a shift in the peak timing of resource abundance. A shift in consumer or resource abundance (a), or temporal variance (a, b) about the peak can conceptually limit or magnify the effects of temporal trophic mismatch. Reproduced from Miller-Rushing *et al.* (2010).

To understand the consequences, both observed and expected, of phenological shifts requires, at the minimum, a coarse understanding of the evolutionary context of the development of each interacting species' phenological trait plasticity. For example, fish-zooplankton interactions in the North Atlantic, the focus of Cushing's original hypothesis, presumably coevolved in an environment that commonly experiences variable climatic conditions. In these fish populations, a mismatch between the timing of the peak in larval food requirements and the timing of peak food availability can clearly limit population recruitment. A complete mismatch between consumers and resources in these populations is, however, unlikely, because the duration of fish spawning throughout the season may occur for well over a month, albeit at low levels, before and after the 'fixed' peak date of spawning (Cushing 1982, 1990). This wide temporal variance about the peak spawning date ensures that at least some individuals of each year class will experience high-quality resource conditions and presumably thrive in 'mismatch' years (Cushing 1982, 1990). Such a prolonged period of spawning represents a bet-hedging strategy (Slatkin 1974); one that emerged from the evolutionary context of selective pressures that existed while this community was formed.

In many regions, climate is changing at rates that exceed those under which existing communities have been formed and maintained – a situation predicted to become increasingly commonplace in the coming decades (IPCC 2007). Without ecological precedent of such climatic pressures, species will not have evolved the adaptive plasticity necessary to hedge against emergent mismatches (Williams 1966). In some cases, species will have sufficiently plastic traits capable of tracking climatic and ecological shifts merely by chance, thus minimizing the potential for mismatches. Conversely, other species will be unable to respond at a sufficient rate to remain functional members of interaction webs under the selection pressures brought on by climate change (Visser 2010). This element of chance makes predicting future instances of mismatch more difficult.

Spatial mismatch

The spatial dimension of trophic mismatch (Post *et al.* 2008a) can also influence the magnitude and type of consumer-resource interactions in ecological communities. While many factors, including species interactions, combine with environmental conditions ultimately to determine spatial patterns of consumers and resources within and among trophic levels (Hutchinson 1957), the influence of climate change on these patterns has recently been the subject of increasing research and debate (Pearson and Dawson 2003; Levinsky *et al.* 2007). As with phenological trends, mean distributional shifts in response to climate change have been documented across numerous taxa around the globe (Parmesan and Yohe 2003; Root *et al.* 2003). Of particular significance to community ecology is how species' distributions covary in

response to shared climate change. The match/mismatch hypothesis can again act as a framework for this line of study, by focusing on the consequences of trophic asynchrony using new methods to overcome the complexities associated with spatial analyses.

Until recently, temporal mismatch, that which occurs at a single point in space, was the primary focus of research related to the match/mismatch hypothesis. Unlike temporal processes that occur in one ordinal dimension, spatial changes in the same processes can occur in three; these additional factors, combined with variable interpretations of the term 'spatial mismatch', complicate studies that seek to account for spatiotemporal components of trophic match or mismatch. The term 'spatial mismatch' has been used in several, often complementary, mechanistic explanations of trophic asynchrony that arise from spatiotemporal variability, some examples of which are discussed below.

One usage of 'spatial mismatch' refers to predicting how distributions of interaction-paired species will differentially respond to climate change, by using bioclimatic-niche models (Levinsky *et al.* 2007). The methodologies of these models are diverse, but their basic aim is to project a species' realized niche onto a map and explore how this niche space will respond in a geographic sense to predicted changes in niche-limiting variables. Comparisons between the predicted niche spaces of interacting species under various climate models often reveal niche divergence. For example, it has been suggested that climate-linked niche divergence may cause a spatial mismatch between a monophagous butterfly (*Boloria titania*) and its larval host plant (*Polygonum bistorta*) in Europe (Schweiger *et al.* 2008). Using a combination of climate, soil and land-cover variables, the authors of that study suggest that the potential northward expansion of these butterflies may outstrip the dispersal ability of their larval host plant over the next 70 years, resulting in a reduced and increasingly fragmented consumer niche-space (Schweiger *et al.* 2008). In some areas this could lead to a complete extirpation of this interaction pairing, and therefore, all components of the interaction web that stem from it. Interaction diversity is an essential component of biodiversity (Thompson 1996; Price 2002), and the loss of interactions to mismatch, potentially independent of immediate changes in taxonomic diversity, may presage future taxonomic losses, yet this area of research continues to be relatively under-emphasized by conservation scientists.

Despite predictions of complete niche divergence, there are few empirical examples of this that can be directly linked to climate change. This paucity of empirical evidence may be the result of many factors, including difficulties in defining niche space. To some extent, this difficulty may also owe to conflation of the concepts of 'niche' and 'habitat', which is one of the most easily quantified and described niche components. Beyond this conceptual hurdle are the empirical challenges of measuring dynamic changes in niche-limiting

factors across large geographic areas. Broad-scale phenological monitoring networks, such as the USA National Phenology Network (NPN) and the European Phenology Network (EPN), may be able to ease some of the data limitations that plague coarse-scale modelling approaches. Because many species traits that influence niche space are plastic with respect to both climatic and ecological influences, realistic parameterization of bioclimatic niche models is difficult. Furthermore, niche modelling studies are currently unable to incorporate the possibility of the emergence of new species interactions, which may be particularly important for so called 'specialist' species such as the butterflies described above. As a resource becomes rare or disappears, it is unclear whether or not 'specialist' consumers will express latent plasticity in their ability to respond to these pressures (Miller-Rushing *et al.* 2010), and if not, this raises questions about the evolutionary advantages for specialization in what are inherently dynamic environments. Future studies will need to clarify how species interactions emerge from rapidly changing community milieus across a continuum of spatial scales (see Araujo and Luoto 2007).

The term spatial mismatch is also used to describe how the *strength* of consumer-resource interactions is affected by climate-sensitive distance relationships (Durant *et al.* 2007; Gremillet *et al.* 2008). In this case, the effects of differential shifts of species distributions in space are analogous to the effects of phenological mismatch. A conceptually simple model of this scenario might arise for central place foragers if the mean distance between the forager and its resource varies with climate or other pressures (Durant *et al.* 2007). Greater distance between resources and reproductive sites can lead to trade-offs of increased travel and/or search time, which translate to decreased efficiency in provisioning young, a situation that could have serious repercussions during an energetically demanding 'critical period' around reproduction (Durant *et al.* 2007). For example, Cape gannets (*Morus capensis*) are central place foraging sea birds that have recently experienced this type of spatial mismatch with their primary prey – sardines and anchovies (Gremillet *et al.* 2008). These large seabirds nest along the Atlantic coastlines of South Africa and Namibia, but make long foraging flights out to marine regions of high primary productivity, regions that traditionally have been linked with abundant stocks of their preferred food (Gremillet *et al.* 2008). Spatial mismatch between the distributions of copepods and fish, potentially caused by a combination of climate factors and direct anthropogenic influences, has contributed to a strong decline in Cape gannet prey in these foraging regions, decreasing the efficiency with which Cape gannets can find and acquire resources needed to provision their chicks (Gremillet *et al.* 2008). This type of spatial mismatch, which arises from linear distance-time relationships between resources and consumers, may be widespread, although it is not

widely reported outside of the context of apex marine predators (Veit *et al.* 1997; Grebmeier *et al.* 2006; Montes-Hugo *et al.* 2009).

Many species rely on environmental cues to inform them of current or future ecological conditions and they respond to this information by altering their phenotype to address perceived trade-offs (Miner *et al.* 2005). If the relationship between a cue and an associated environmental factor changes, *and* if these changes occur at a rate that exceeds a species' ability to adapt their decision making to these changes, species' responses to these cues may be poorly informed and lead to trophic asynchrony or even ecological traps (Visser 2010). Climate change is capable of influencing the relationship between cues and environmental conditions in several ways. For example, photoperiod and mean expected temperature may diverge with climate change because only temperature is affected by current global climate forcings. If species were to make decisions that rely on one to inform about the other, they may experience a decoupling between the type of phenotypic trait plasticity they express and the type of phenotypic plasticity that might be best suited to actual conditions (Visser *et al.* 1998; Phillimore *et al.* 2010). A prominent spatial dimension to these decouplings can arise because climate change occurs unevenly in space (IPCC 2007). As distance increases between two ecosystems, they are increasingly unlikely to experience similar climatic change as the result of variability in regional biosphere-atmosphere interactions. The potential for trophic mismatch in migratory species is therefore heightened relative to residents. These animals experience this temporal variability across a spatial continuum, not just at a single point, and can be particularly vulnerable to mismatch if they rely upon cues in one location to inform about another. Said another way, match or mismatch may arise from differential species response at any one point in space, and/or from the influence of differential climate change at multiple locations. This forms the basis for another usage of the term 'spatial mismatch'.

In Europe, many long-distance migrant bird populations are in decline relative to non-migrants (Sanderson *et al.* 2006), part of which can be explained by the above type of spatial mismatch between wintering and breeding grounds (Both *et al.* 2010; Jones and Cresswell 2010). One study of Palearctic passerines found evidence to support the 'distance hypothesis' – that long-distance migrants are more likely to experience population declines associated with mismatch than shorter-distance migrants or range residents because the probability of mismatch occurring at any one location along the migration route increases with migratory distance. However, this was only supported by empirical evidence when distance was considered in context with the seasonality of the migrant's breeding ground, where seasonality was defined as the temporal variance about the mean peak in consumer resources (Both *et al.* 2010). Long-distance migrants that bred primarily in more seasonal forest

habitats, with a narrow window of food abundance, experienced significantly sharper population declines than long-distance migrants that bred in less seasonal marshy areas (Both *et al.* 2010). Irrespective of seasonality, resident and shorter-distance migratory species that lived in both areas were comparatively less affected than long-distance migrants (Both *et al.* 2010). Another study, that did not incorporate a seasonal variance component, but included migratory birds from both hemispheres, also found evidence that suggested absolute migration distance could be a factor in bird population declines, and that overall, migratory birds were more likely to experience mismatch conditions and population declines than were residents (Jones and Cresswell 2010). In both of these studies, the great distances between wintering and breeding grounds imply an increasingly likely probability that ineffective migratory cues will result from divergent climate regimes (Both *et al.* 2010; Jones and Cresswell 2010). Studies at these broad scales require simplified assumptions about abiotic influences on trait plasticity that inevitably accompany low-resolution phenological data. However, that these studies were still able to detect effects of migratory distance and divergent climates in spite of these limitations raises important questions about how spatiotemporal components of species interactions that occur over continental scales will be affected by climate change.

The pattern of resource distribution at the landscape scale may also vary with changing climate conditions. For example, by differentially affecting the timing of plant emergence – a phenophase with high nutrition and low digestive costs for herbivores – climate is capable of affecting spatial patterns of resource quality across a wide array of scales from thousands of kilometres to less than one metre (Chen *et al.* 2005; Post and Stenseth 1999; Post and Forchhammer 2008; Post *et al.* 2008b). This variation in spatial patterning can have repercussions for consumer foraging decisions and manifest itself as another type of spatial mismatch. At the landscape scale, a spatial continuum of temporal shifts in resource availability and/or quality is expressed as spatiotemporal resource heterogeneity, an important factor in population dynamics (Roughgarden 1974; Levin 1976). Consumers have evolved foraging strategies to cope with and even rely on heterogeneous distributions of high quality resources. In seasonal environments, migratory ungulates take advantage of spatiotemporal resource heterogeneity by following the early/mid phases of plant phenology through the landscape. This can effectively prolong their access to high quality resources (Senft *et al.* 1987). Because climate change alters the pattern of resource quality expressed in a landscape by affecting plant phenology, it can impact the efficiency of herbivore foraging strategies designed to maximize high quality forage intake required to offset the high costs of reproduction. For example, in highly seasonal West Greenland, reproductive success of

migratory caribou (*Rangifer tarandus*) depends on their ability to arrive and give birth at their calving site around the mean temporal peak in resource abundance (Post and Forchhammer 2008), but also on their ability to track spatial phenological heterogeneity along a local forage horizon during and around the calving period (Post *et al.* 2008b). These studies are an early step towards unifying the spatial match/mismatch hypothesis with landscape ecology concepts (e.g., Turner 2005), but future investigations will need to explore a more complete range of climatic effects on species interactions in relation to resource patterning, rather than just timing, across a hierarchy of spatial scales.

Migratory species may offer a clear insight into how differential spatio-temporal shifts in the distributional patterns of resources can be expected to influence trophic interactions. In some situations, migration itself may become an ineffective strategy as a result of what might be termed a spatial mismatch. This would be spatial mismatch in the sense that changes in the spatial patterning at one trophic level would negatively influence foraging success in higher trophic levels and result in a trophic mismatch, potentially independent of the mean timing of resource availability throughout the study area. Ungulate migration has been studied for decades and may provide a good starting point for these investigations. If migration is the result of spatial patterns of resource distribution, as is predicted by the forage maturation hypothesis (Fryxell 1991), spatial compression (i.e., homogeneity) of plant phenology along the migratory route, as has been observed at local scales in West Greenland (Post *et al.* 2008b), could conceivably alter selection coefficients between non-migratory and migratory members of populations. For instance, elk (*Cervus elaphus*) populations in the Canadian Rockies are composed of both migratory and non-migratory individuals (Hebblewhite *et al.* 2008). A 3-year observational study found that, on average, migrant individuals of these populations were exposed to more nutritious and digestible food resources than residents, owing to their strategy of exploiting heterogeneous spatial patterns of plant phenology during migration (Hebblewhite *et al.* 2008). The advantages that migration confers on individuals could diminish in this population should spatial compression of resource phenology occur here. In seasonal environments, even slight shifts in foraging efficiency can have dramatic impacts on reproductive success (White 1983). Large herbivores are often important interactors in ecological communities, and their removal from interaction networks has been shown to induce significant community restructuring (Pringle *et al.* 2007; Post and Pedersen 2008). While the potential for this type of spatial mismatch to influence migratory species' population dynamics is clear, future studies will be required to verify to what extent these concepts may apply to empirical situations.

Integrating match/mismatch with life-history strategies

Trophic mismatch is most widely documented in seasonal environments where food resources are limited throughout much of the year however, even within these environments, consumer sensitivity to temporal resource limitation will vary among species as a function of, among other factors, variation in their life-history strategies. Income breeders, for example, require a continuous influx of energy to offset the high costs of reproduction, and thus are likely to have a critical period clearly related to food acquisition around the timing of their reproductive efforts. Conversely, capital breeders build up an energy surplus throughout the year that they later expend during reproduction, giving their reproductive effort relatively more independence from immediate food resource conditions (Drent *et al.* 2006). Capital breeders may thus prove less sensitive, but by no means immune, to climate-driven fluctuations in resources.

Traditionally, infant or juvenile mortality associated with what is assumed to be a fixed and intuitively described critical period of breeding phenology has been the sole effect reported by match/mismatch investigations (Durant *et al.* 2007). While this may be the most tractable metric of mismatch, it has almost certainly drawn attention away from efforts to document other potential consequences of a mismatch. For some insect species, ecological and environmental conditions during an early critical stage of ontogeny may have a delayed influence on adult body size and fertility (Prout and McChesney 1985) – both of which are life-history linked traits that greatly contribute to fitness. These delayed effects on traits could also have ramifications for the strength and type of interactions species experience throughout their development (Yang and Rudolf 2010). Identifying a broader range of direct effects that trophic mismatch can have on populations is a pressing, but presently poorly documented component of the demographic consequences of mismatch (Miller-Rushing *et al.* 2010). This approach will, however, challenge the traditional interpretation of the ‘critical period’ concept.

In a general sense, a species’ ‘critical period’ is the product of interactions from within a hierarchy of biological sensitivities, integrating individual’s traits from embryology, neurobiology and/or behaviour (Browman 1989). Ecological or environmental factors can induce trait plasticity within each level of this hierarchy, and by extension, affect how biological sensitivities interact to be expressed as a critical period of the life history of an organism. In contrast to this perspective, most analyses treat the critical period of a species’ life history as an intrinsic property, i.e., as though it were a fixed trait (Visser and Both 2005). This assumption may limit our understanding of trophic decoupling in some species, whereby new critical periods will emerge as a consequence of novel ecological forcings associated with phenological shifts of life-history traits.

In many communities, species interact over their respective lifespans. These interactions can change in intensity or type depending on the timing of one or both interacting species' stage specific development and/or body size (Fig. 26.3a, b) (Werner and Gilliam 1984; Osenberg *et al.* 1988; Yang and Rudolf 2010). For example, fish eggs of one species may initially be prey items for fish or larvae of another, but once hatched, these larvae may compete with or even prey upon their former predators before eventually becoming generalist predators that consume prey from several trophic levels. When species interactions are stage structured in this manner, as might be expected in many invertebrate and/or aquatic ecosystems, the timing, duration and physical traits associated with life-history stages can determine the magnitude and type of interactions a species experiences (Werner and Gilliam 1984; Osenberg *et al.* 1988; Yang and Rudolf 2010). Similarly in plant-herbivore interactions, invertebrate herbivores may transition from predators to pollinators depending on the timing and duration of both species' ontogeny (Bronstein *et al.* 2009). Because shifts in the timing or duration of ontogeny may be variable in response to climate change (Werner and Gilliam 1984; Post *et al.* 2008b; Yang and Rudolf 2010), there is potential for species interactions to change, decouple or even strengthen over the entire span of their respective life histories. Instead of limiting focus to the differential shifts in phenological events to a traditionally critical period of development (Visser and Both 2005), some match/mismatch studies will benefit by focusing on stage-specific per capita effects of species interactions throughout the entire span of their trophic coupling (Yang and Rudolf 2010). A focus on per capita interactions throughout aggregate life history may clarify how trait plasticity and ecological sensitivity interact to affect population fitness, even via delayed responses to mismatch. This may be an effective approach better to understand a broader suite of the ecological consequences of climate change, even in less seasonal environments where sensitivities to resource limitation may be harder to predict and are certainly less well documented.

Conclusions

As empirical evidence of climate change's perturbing effects on ecological communities mounts, phenology has emerged as an essential component of species trait-responses to these emergent forcings. Trait-mediated ecological effects are increasingly the subject of community ecology research. However, the effects of non-trophic forcings on species traits must not be overlooked. Differential phenological shifts will continue to affect trophic interactions as climate regimes change by influencing not only the timing of species interactions, but also their very nature.

The match/mismatch hypothesis has been a popular framework for analyses documenting the immediate consequences of these climatic

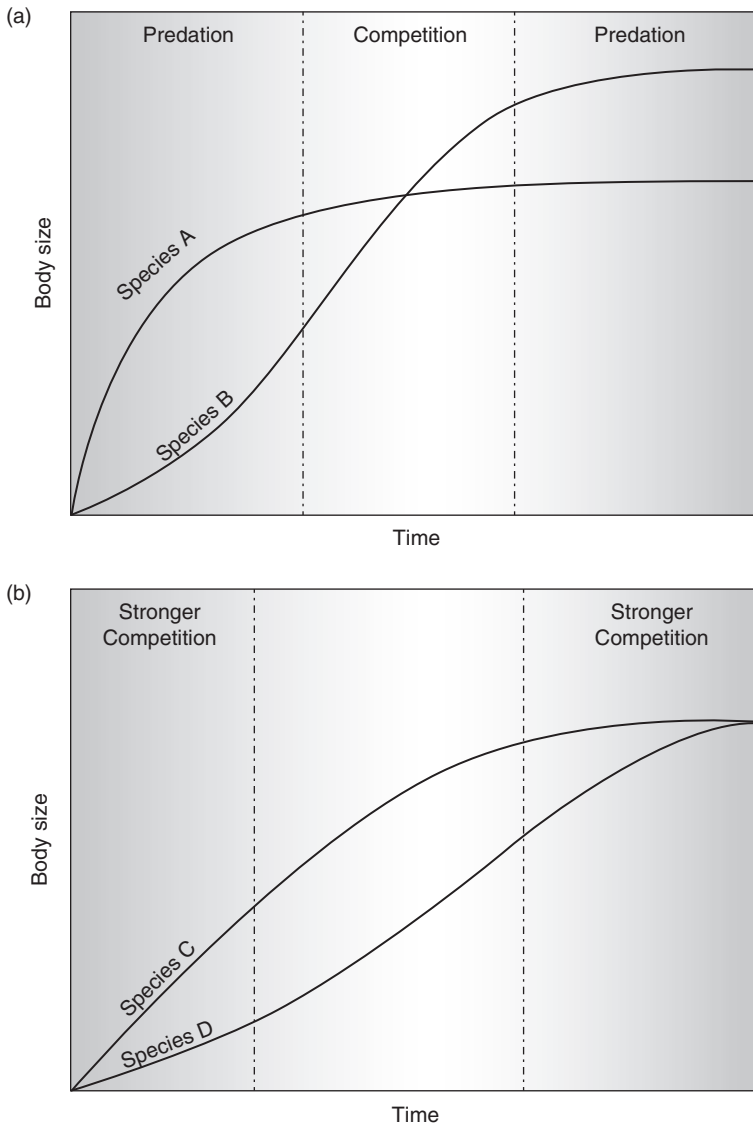


Figure 26.3 Conceptual diagram demonstrating how both the type (a) and strength (b) of species interactions may change over time as a consequence of differential shifts in the phenology of ontogeny. Shading represents the transition in type (a) or strength (b) of an interaction. For example, a hypothetical species A may switch from consumer of species B to its competitor, or even a prey item for species B as a function of the relative timing of growth between the two species (a). Similarly, a differential timing of growth between interacting species C and D can alternately ease or strengthen competition (b). Reproduced from Yang and Rudolf (2010).

perturbations, but future research will need to continue to clarify further spatial dimensions of these consequences. Spatial mismatch is currently a popular subject of study, but inconsistent use of terminology among studies has made a concise definition of the concept challenging. Integrating the study of trait- and density-mediated interactions with landscape ecology is a logical next step for community ecology research.

Furthermore, the spectrum of possible effects stemming from trophic mismatch is relatively unknown apart from recruitment failures. Future studies will benefit from an approach that links shifts in the life-history traits of interacting species with the delayed consequences of these shifts on species' traits. This will further clarify the interaction between trophic and non-trophic traits' influences on ecological communities.

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