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EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

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Resource waves: phenological diversity enhances foraging opportunities for mobile consumers

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Abstract. Time can be a limiting constraint for consumers, particularly when resource phenology mediates foraging opportunity. Though a large body of research has explored how resource phenology influences trophic interactions, this work has focused on the topics of trophic mismatch or predator swamping, which typically occur over short periods, at small spatial extents or coarse resolutions. In contrast many consumers integrate across landscape heterogeneity in resource phenology, moving to track ephemeral food sources that propagate across space as resource waves. Here we provide a conceptual framework to advance the study of phenological diversity and resource waves. We define resource waves, review evidence of their importance in recent case studies, and demonstrate their broader ecological significance with a simulation model. We found that consumers ranging from fig wasps (*Chalcidoidea)* to grizzly bears (*Ursus arctos*) exploit resource waves, integrating across phenological diversity to make resource aggregates available for much longer than their component parts. In model simulations, phenological diversity was often more important to consumer energy gain than resource abundance per se. Current ecosystem-based management assumes that species abundance mediates the strength of trophic interactions. Our results challenge this assumption and highlight new opportunities for conservation and management. Resource waves are an emergent property of consumer–resource interactions and are broadly significant in ecology and conservation.

Key words: ecosystem-based management; foraging; landscape heterogeneity; model; movement; phenological diversity; phenological tracking; resource wave; time-constraint; trophic interaction.

Introduction

A basic goal of ecology is to understand how the abundance of different resources affects biological productivity. For example, a large body of work has debated whether levels of trace nutrients, water, or food can limit species abundance and structure communities (Hairston et al. 1960, Sinclair 1975). A challenge in understanding resource limitation is that resources may appear abundant when averaged across time, yet prove limiting in light of temporal variation (Sinclair 1975). For example, food availability may vary strongly within or among seasons, generating periods of scarcity punctuated by periods of superabundance (Yang et al. 2008). This variability interacts with the functional response of consumers to generate time constraints on energy budgets; animals must process and store large amounts of energy over short periods of time, during which levels of food abundance are likely to exceed digestive capacity (Armstrong and Schindler 2011). In a world of feast and famine, time itself may limit consumers as much as

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resource abundance. Indeed, study of resource pulses has shown that the temporal characteristics of food availability strongly mediate consumer energy budgets, population productivity, and even community structure (Yang et al. 2008). Further, consumers exhibit an array of behavioral and physiological adaptations to maximize energy intake during pulsed foraging opportunities; evidence of their evolutionary response to severe time constraints on foraging opportunities (Piersma and Lindstrom 1997, Armstrong and Schindler 2011).

Time is particularly limiting for consumers in seasonal environments where phenology may have strong effects on trophic interactions. Many trophic resources exhibit ephemeral peaks in quantity, quality, or accessibility during specific stages in their ontogeny, in turn producing pulsed foraging opportunities for consumers (Werner and Gilliam 1984, Wilmshurst et al. 1999, Yang et al. 2008). An ongoing effort in ecology seeks to understand how the timing of resource ontogeny mediates consumer foraging opportunities. The vast majority of this work falls into two categories. Trophic match/mismatch studies explore how the central tendency of resource phenology (e.g., the timing of prey emergence), relative to that of consumers, mediates trophic interactions (Cushing 1969, Visser et al. 1998, Winder and Schindler 2004). In contrast, studies of resource synchrony explore how variation in resource phenology mediates trophic interactions by influencing the degree to which consumers are temporally constrained (Darling 1938, Ims 1990). Most of the work on reproductive synchrony and trophic match/mismatch has explored the consequences of prey phenology at relatively small spatial extents (Visser et al. 1998) or coarse spatial resolutions (Edwards and Richardson 2004, Winder and Schindler 2004). While it is recognized that resource phenology often varies across landscapes, this phenological variation is often regarded as noise when considering effects on consumers (Diez et al. 2012); here we demonstrate the ecological significance of phenological diversity, which we define as variation in phenology expressed across space or levels of biological organization. We show that the spatial and temporal patterning of resources across landscapes (i.e., phenological diversity) can influence foraging opportunities more than resource abundance alone. This realization challenges the assumptions in many food web models (i.e., that resources largely control predator consumption rates via functional responses) and provides critical but underappreciated perspectives on the conservation and management of mobile animals that forage widely across landscapes (Runge et al. 2014).

Mobile consumers can integrate across spatial variation in resource phenology, sampling a variety of temporally distinct resource stocks arranged across heterogeneous landscapes. This phenomenon is beyond the scope of existing conceptual frameworks; trophic mismatch and predator swamping are phenomena that mediate consumer foraging opportunities on a single resource stock at short time scales (typically hours to weeks). The ecological implications of variation in prey phenology across larger spatiotemporal extents remains poorly appreciated and understood. While it has been long appreciated that mobile consumers track spatial variation in resources (Drent et al. 1978, Dingle 1996), there has been little formal theory developed to explore its significance to ecological processes and their application to conservation and management. Here we propose a conceptual framework that describes how landscape heterogeneity in resource phenology mediates the seasonal foraging opportunities of mobile consumers. We provide empirical evidence that mobile consumers often integrate across substantial spatial variation in resource phenology, thereby relaxing time constraints that would otherwise limit their energy budgets. We develop a simple simulation to test whether the phenological variation of resources can be as significant to consumers as resource abundance itself, and under what ecological contexts this result could occur. Taken together, these results suggest that resource waves are broadly important in many ecosystems and for a wide variety of consumers.

RESOURCE WAVES: A DEFINITION AND EMPIRICAL EXAMPLES

Numerous studies illustrate how spatial variation in the phenology of trophic resources can stabilize and enhance the seasonal energy intake of wide-ranging consumers. In these empirical examples, consumers rely on trophic resources that are distributed heterogeneously across landscapes and provide ephemeral foraging opportunities at specific stages of development. Spatial heterogeneity in habitat conditions causes resources to develop asynchronously and reach profitable life-stages (for the consumer) at different times in different places (Fig. 1). As a result, consumer foraging opportunities do not occur as a spatially synchronized pulse, but instead as a series of pulses that propagate across the landscape through time, generating a resource wave (Fig. 1). If consumers can track the shifting mosaic of foraging opportunity (i.e., surf the wave), they can forage for long periods of time on a resource aggregate comprised of short-lasting components.

We define a resource wave as an aggregate of trophic resources that (1) offer ephemeral foraging opportunities at fixed points in space, (2) exhibit spatial variation in phenology across landscapes, and (3) protract foraging opportunities for consumers that can track phenological variation across space and time. The emergent property of resource waves is that they provide mobile consumers sustained energy intake from food items that are ephemerally available at small spatial extents. Although they share these defining attributes, resource waves may differ in their underlying causes, spatiotemporal patterning, and the foraging opportunities they present to different consumers in different ecosystems. For illustrative purposes, resource waves are often named after the color of

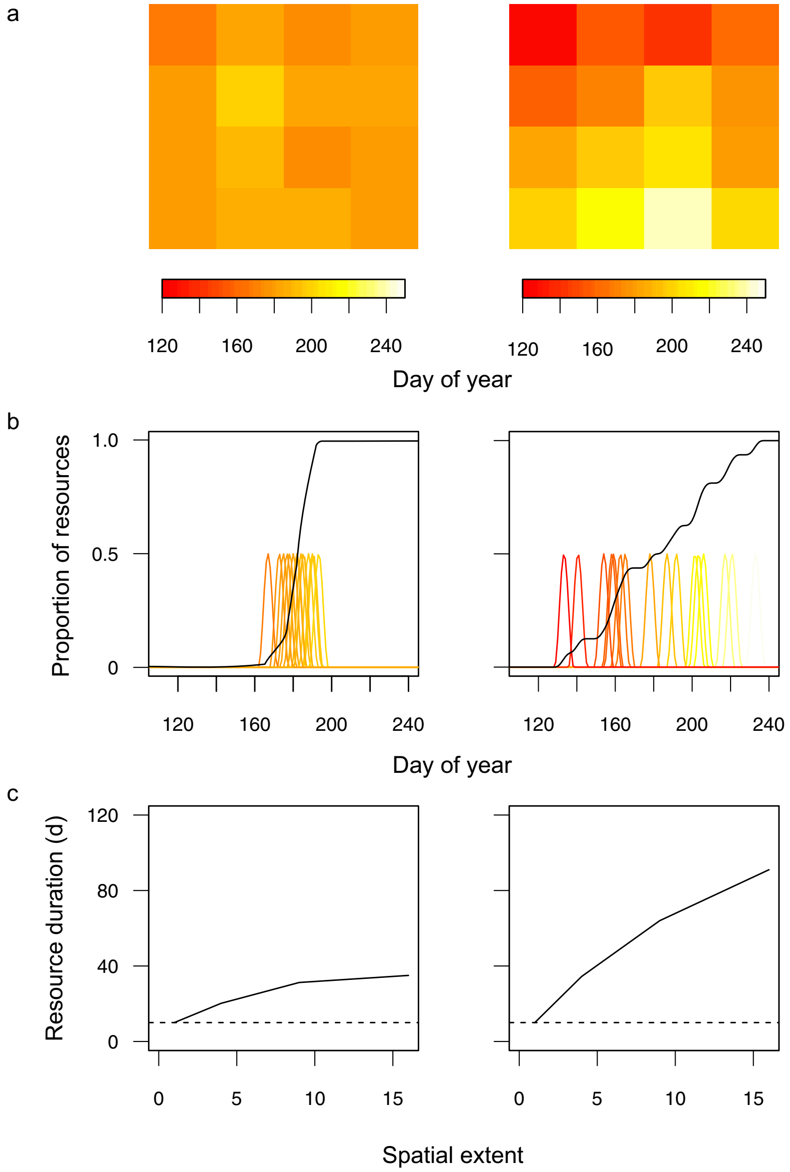


FIG. 1. Conceptual example of a resource wave. Columns consider two contrasting levels of spatial variation in resource phenology: left; low variation (standard deviation [SD] of phenology = 7 d), right; high variation (SD = 30 d). (a) Maps of resource phenology, indicating the day-of-year when resources in each cell reach the developmental stage conferring peak foraging opportunities for consumers. (b) Temporal dynamics of resource abundance: Black line shows cumulative resource availability over time, at the landscape-level. Superimposed lines show time-series of resource abundance in each cell from the map above. (c) The relationship between spatial extent (number of cells) and the duration of resource availability. Dashed line shows duration of resource availability in a single cell (10 d). Spatial variation in resource phenology protracts resource availability across landscapes, creating the potential for mobile consumers to surf resource waves.

the resource taxa (e.g., green waves of vegetation); note that these names have no relation to the color terms used in time-series analysis.

Below we summarize recent case studies that exemplify new understanding of resource waves across diverse taxa (Appendix S3: Table S1). We then develop a general simulation model to evaluate the potential significance of phenological diversity across the range of ecological contexts revealed in the case studies.

Green waves: Spatial gradients in vegetative growth entrain the seasonal migrations of ungulates, geese, and other herbivores

Though grasses and plant foliage are present for much of the year, the foraging opportunities they present to herbivores often vary substantially throughout the growing season. Plant growth initially increases herbivore energy gain by supporting higher foraging rates on high quality food. However, as plant biomass increases, it becomes increasingly dominated by structural compounds that are low in quality (e.g., fibrous cell walls) and causes herbivore energy intake to be constrained by digestion. Most plants offer high quality forage at early or intermediate stages of development, which may be quite ephemeral (Fryxell 1991, Wilmshurst et al. 1999). For example, the crude protein content in graminoids and herbs available to red deer (*Cervus elaphus*) declines exponentially after first emergence and may decrease by a third or more in the first month of plant growth (Albon and Langvatn 1992).

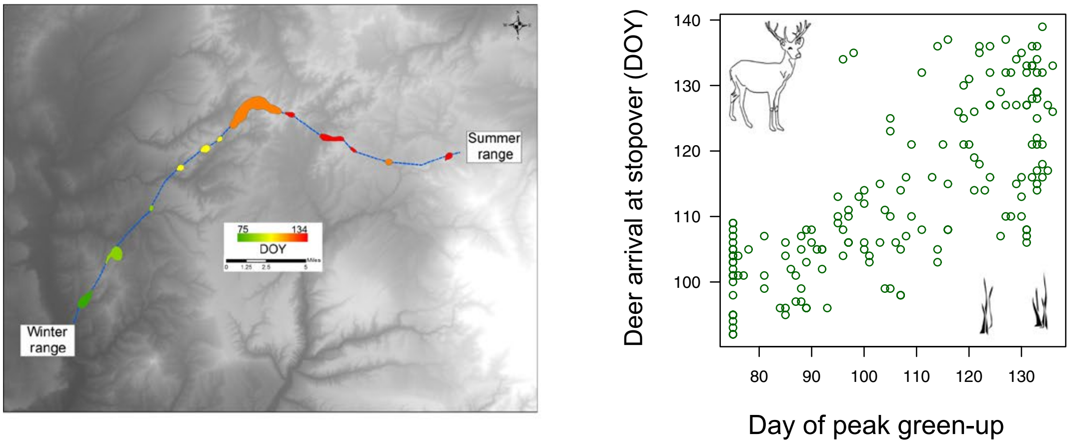
If plants developed synchronously across landscapes, the growing season for herbivores would be quite short and defined by the duration of high quality food at a single site. In contrast, spatial variation in habitat conditions generates variable plant phenologies, creating a shifting mosaic of foraging opportunity (Fryxell et al. 2004). Spatial heterogeneity in plant phenology is nested among spatial scales. Gradients in latitude or inland distance generate phenological diversity at regional scales (Albon and Langvatn 1992, van Wijk et al. 2012, Kölzsch et al. 2015). Within regions, elevation gradients have strong effects on plant phenology. For example, across migratory elk (*C. canadensis*) ranges in Alberta, Canada, vegetation exhibited a 5-d delay in green-up for every 100-m gain in elevation (Hebblewhite et al. 2008). Within elevational strata, topography creates fine-scale variation in phenology; for example, south-facing aspects exhibit earlier plant phenologies, as do areas where landscape features reduce the accumulation of snowpack (Hebblewhite et al. 2008). Habitat variation within patches of similar topography may also have strong effects on plant phenology, sometimes obscuring the effects of coarser-scale influences on phenology (Iversen et al. 2009). Spatial variation in rainfall and soil attributes can also generate phenological variation at a variety of spatial scales (McNaughton 1988, Fryxell et al. 2005).

Accumulating evidence supports the notion that herbivore migrations track spatial variation in plant phenology across landscapes. While it is widely recognized that the seasonal migrations of herbivores track phenological variation at coarse spatiotemporal scales (i.e., long-distance migrations between summer and winter habitats; Dingle 1996), recent work reveals that animals also track finer-scale variation along their migration routes via stopover sites assembled along phenological gradients. For example, migrating mule deer (*Odocoileus hemionus)* "stopped over" at foraging patches to stay in pace with spring green-up as it moved from low elevation winter range to high elevation summer range (Fig. 2a; Sawyer and Kauffman 2011). Mule deer occupied stopover sites during a narrow phenological range, 46 ± 7 d (mean ± 1 standard deviation) prior to peak green-up as measured by normalized difference vegetation index (NDVI) time series. The median day of occupancy at a stopover tracked the date of its peak forage quality, indicating that the migrating deer were surfing a green wave (Fig. 2a). Similarly, Greater White-fronted Geese (*Anser albifrons*), which migrate from the Netherlands to Northern Russia, track green-up by arriving at stopover sites at peaks in the third derivative of seasonal cumulative air temperature (van Wijk et al. 2012), which correspond to intermediate levels of plant development (~50% of maximum NDVI levels; Najafabadi et al. 2015).

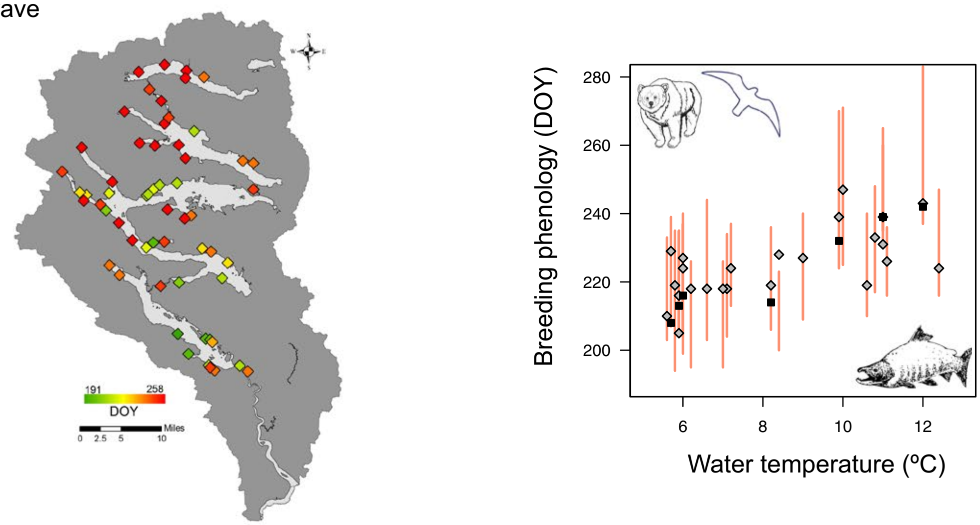
In addition to stopovers during directed migration, intra-seasonal foraging movements may function to track shifting mosaics of plant phenology (Van Moorter et al. 2013). For example, spatiotemporal patterns of Thompson's gazelle *(Eudorcas thomsonii*) abundance in the Serengeti reflect grazing quality as it shifts across the landscape (Fryxell et al. 2004). Moose (*Alces alces*) in Norway appear to track both fine-scale and coarse-scale gradients in plant phenology, exhibiting high frequency, short movements in response to "ripples" of change in the NDVI, and low frequency, long movements in response to "waves" of change across broader expanses of the landscape (Van Moorter et al. 2013).

The degree to which migrants surf green waves may vary substantial both among and within species. Migratory red deer in Norway tracked spatial variation in plant phenology, but many individuals "jumped" up to summer range, arriving ahead of peak forage quality (few animals were true surfers; Bischof et al. 2012). Plains Zebras (*Equus quagga*) in Botswana appear to exhibit both tactics within the same migration, initially surfing the green wave but then accelerating to jump to destination habitats (Bartlam-Brooks et al. 2013). Barnacle Geese (*Branta leucopsis*) surf green waves, but arrive slightly behind the onset of spring at early stopovers, and slightly ahead at later stopovers (Kölzsch et al. 2015). While fully tracking resource waves may maximize energy intake, constraints such as reproduction and predation risk may select for behavioral strategies that only partially track resource phenology. For example, Barnacle Geese surpass the latter portion of the green wave in order to reproduce earlier at their destination, fueling reproduction with energy derived from their earlier surfing of the green wave (Van Der Jeugd et al. 2009). A key point is that consumers can exploit the emergent property of resource waves, protracted foraging opportunity, without having to perfectly track spatial variation in phenology. Further, the NDVI data typically used to characterize green waves is an indirect measure of plant phenology that is far coarser than the actual resolution at which herbivores sample their environment, and thus may underestimate the degree to which herbivores track plant phenology.

Several studies have evaluated the influence of factors contributing to phenological diversity on herbivore nutrition or demographic performance (Pettorelli et al. 2005, Wang et al. 2006). For example, the body mass of red deer were positively associated with the topographic diversity of the habitats they occupied (Mysterud et al. 2001). Similarly migratory elk (that exploit a Green wave



b Red wave



c Silver wave

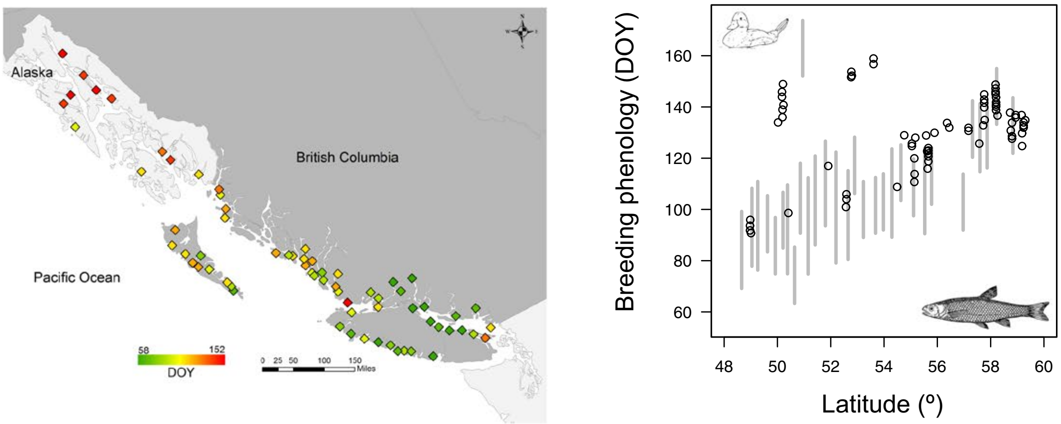


FIG. 2. Examples of resource waves. (a) Map showing the migration route and stopover sites (colored by date of peak green-up) for a mule deer in Wyoming, USA (1 mile = 1.6 km). The plot shows the timing of deer arrival at stopover sites, as a function of the site's plant phenology (pooled data from 18 individuals in Sawyer et al. 2010). (b) Map showing breeding sites for different sockeye salmon populations, colored by the day that spawning initiates. The plot shows salmon presence at different spawning sites (bars), as a function of water temperature. Overlaid symbols show peak consumer activity at each site (grizzly bears, black squares [monitored at 7 of 24 sites]; Glaucous-winged Gulls, gray triangles). Data from Schindler et al. 2013. (c) Map showing mean spawn timing of herring at discrete breeding sites. The plot shows occurrence of herring spawning (gray bars) and Scoter migratory stopovers (black circles), across space (*x*-axis: latitude) and time (*y*-axis: day-of-year). Data from Lok et al. 2012.

variation in elevation and topography) had diets that were 6% higher in digestible energy than their resident, nonmigratory, counterparts (Hebblewhite et al. 2008). Arctic-breeding populations of Barnacle Geese that surf portions of green waves had higher post-fledging survival than temperate-breeding populations that did not (Van Der Jeugd et al. 2009). The existing evidence to date shows that phenology tracking is clearly important to the overall foraging benefits that migrating herbivores receive. The factors influencing the ability of migrating animals to track phenology, and the relationship to nutritional gain and demographic performance, have yet to be fully explored or quantified and provide important topics for future research.

Red waves: Salmon biocomplexity generates a shifting mosaic of high quality foraging opportunities for bears, trout, and birds

Pacific salmon (*Oncorhynchus* spp.) generate pulsed marine subsidies in freshwater and terrestrial ecosystems when they spawn in streams and along lake shores (Gende et al. 2002). Over 50 species of inland consumers prey on spawning salmon, consume salmon eggs, or scavenge carcasses. These consumers range in size from bacteria and benthic invertebrates to grizzly bears (*Ursus arctos*) (Gende et al. 2002), and may achieve the majority of their annual energy intake seasonally feeding on salmon (Scheuerell et al. 2007, Armstrong and Bond 2013). Paradoxically, the lifespan of a spawning salmon at its breeding habitat is only about 1–3 weeks (Carlson et al. 2007).

The aggregate of salmon resources across a watershed persists for much longer than its component parts due to diversity in breeding phenology, which is hierarchically structured among biological levels (Schindler et al. 2010). Intra-population variation in spawn-timing protracts the duration of sockeye salmon (*O. nerka*) spawning from about 1–3 weeks for an individual to 3–6 weeks for single populations in their respective breeding habitats (Carlson et al. 2007). Across a watershed, which may be comprised of dozens of hydrologically distinct spawning areas, the spawn-timings of populations are locally adapted to ambient thermal regimes and range from early summer to autumn (Lisi et al. 2013). This inter-population phenological diversity protracts the foraging opportunities of mobile consumers, enabling them to feed on salmon for three months or longer as they move across the landscape to sequentially exploit individual salmon populations (Fig. 2b; Schindler et al. 2010, 2013).

Different species of salmon spawn at different times due to intrinsic physiological differences (e.g., rates of embryo development) and extrinsic ecological differences (e.g., conditions in spawning and rearing habitats). In watersheds where multiple species exist, spawning salmon may be present for six months or longer (Quinn 2011). Thus, the phenological diversity of salmon substantially protracts the foraging opportunities for mobile consumers. A multispecies portfolio of salmon distributed across a watershed may persist for six times longer than an individual population at a single breeding site.

The effect of salmon phenology on consumer foraging opportunity depends on a consumer's capacity to integrate across the hierarchy of salmon biodiversity. A relatively sessile scavenger such as a caddisfly (*Trichoptera*) larva is most likely to respond to intra-population attributes of salmon phenology, which influence phenomena such as trophic mismatch and swamping. However, for wider ranging fishes, birds, and mammals, seasonal energy budgets may be more influenced by the phenological diversity among populations and species of salmon, and how this diversity is spatially arranged across watersheds relative to the spatial scales over which these consumers can move. Rainbow trout (*Oncorhynchus mykiss*), which accumulate most of their seasonal growth by feeding on salmon eggs, moved within a stream network to track population-level variation in salmon phenology (Ruff et al. 2011). Individual trout moved roughly 3 km between sockeye salmon spawning sites and protracted the duration over which they could feed on salmon eggs from about 30 d to longer than 45 d. Trout that tracked the salmon resource wave exhibited growth rates that were 2.5 times higher those of sedentary individuals. Glaucous-winged Gulls (*Larus glaucescens*) and grizzly bears also appear to track population-level variation in salmon spawn timing (Schindler et al. 2013). The spatial distributions of both consumers tracked the spawn timing of sockeye salmon populations across tributary streams of the Wood River watershed in coastal Alaska (Fig. 2b). These studies occurred in a region where sockeye salmon comprise >95% of the total salmon available to consumers. Further study is needed to understand how consumers integrate across species-level phenological diversity. Preliminary data and local knowledge suggest wolves (*Canis lupus*) and grizzly bears on the Copper River Delta (Alaska, USA) track resource waves that change in composition from sockeye salmon to coho salmon (*O. kisutch*) and persist from late-spring to early winter (J. Armstrong, *unpublished data*).

Silver waves: Spatial variation in the spawn timing of herring protracts foraging opportunities for marine consumers

Pacific herring (*Clupea pallasii*) spawning events generate resource pulses of energy-rich eggs. Spawning activity persists for 3–6 weeks at single breeding sites and attracts more than 25 species of consumers including a variety of fishes, birds, and marine mammals (Willson and Womble 2006). Ocean water temperature mediates the spawning phenology of herring (Haegele and Schweigert 1985). Due to geographic variation in marine thermal regimes, Pacific herring exhibit latitudinal variation in breeding phenology; spawning begins as early as December in California, and occurs later with increasing latitude, commencing as late as June in northwestern Alaska (Willson and Womble 2006, Anderson et al. 2009, 2009) (Fig. 2c).

Many consumers of herring eggs are highly mobile and capable of surfing portions of the silver wave (Willson and Womble 2006). The Surf Scoter (*Melanitta perspicillata*, a species of sea duck) exhibits long distance migrations from wintering sites in coastal areas to summer breeding sites in Northern boreal forests (De La Cruz et al. 2009). Some Surf Scoter populations migrate along a Northern coastal route that parallels the latter portion of the silver wave, from Puget Sound to Alaska. Individual Scoters make about three to five stopovers along this migration route, and proximity to herring spawning sites is a strong predictor of stopover location (De La Cruz et al. 2009, Lok et al. 2011). Though not all Scoters stopped over at herring spawning sites (40% did not), Scoters generally tracked the Northward progression of herring spawning events, surfing the silver wave and protracting their foraging opportunities on high-quality herring eggs (Lok et al. 2012).

Additional examples of resource waves for mobile consumers

In addition to surfing red waves of salmon, bears may also surf brown waves, tracking spatiotemporal variation in the crude protein content of plant roots. Plants often store energy overwinter in their roots, and then transfer this energy to aboveground tissues over the course of the growing season. Landscape heterogeneity generates spatial variation in plant phenology, prolonging the period of profitable foraging opportunities on roots (Coogan et al. 2012). Grizzly bears appear to track the brown wave by moving to areas of delayed plant development (higher elevations and North facing slopes) as the growing season progresses (Hamer et al. 1991).

Fruiting events provide an ephemeral, energy-rich food source for consumers ranging from insects to large mammals. Plants exhibit both inter- and intraspecific diversity in fruiting phenology, which may vary spatially in association with precipitation, elevation, or other habitat variables (Loiselle and Blake 1991). Though spatial variation in fruiting phenology certainly protracts the *potential* foraging opportunities of mobile frugivores and nectivores, the degree to which mobile consumers realize these benefits is unclear. As indirect evidence, frugivorous birds typically exhibit elevational migrations (Levey and Stiles 1992), and the spatiotemporal patterns of bird and fruit abundance have been shown to shift in concert across elevational gradients (Loiselle and Blake 1991). More direct evidence can be seen in the fruit eating behavior of bears. Asiatic black bears target a narrow stage of *Prunus* fruit development, such that 63% of foraging marks left on trees occur during a 4-d window when fruits peak in sugar content, but have yet to decrease in abundance. By tracking altitudinal gradients in fruit phenology, bears are able to find fruit at this optimal stage of development for an entire month (Koike et al. 2008). Black bears in North America also appear to track spatial variation fruiting phenology; the phenological stage of trophic resources (composed largely of multiple berry species) was the strongest predictor of site selection for GPS-collared individuals (Davis et al. 2006).

In addition to fruits, the flowers of plants provide ephemeral foraging opportunities for consumers, particularly pollinators that consumer nectar or pollen. Flowering events occur synchronously within individual fig trees (*Ficus* spp.) and last roughly 5 weeks (Bronstein et al. 1990). Flowering provides a burst of foraging opportunity for wasps (*Agaonidae*) that specialize on single species of fig trees. Fig-specializing wasps can only survive about 2 d without access to flowering fig trees (Kjellberg et al. 1988). Phenological diversity is so important in this system that if fig trees exhibited population-wide synchrony in flowering phenology, they would be unable to support a population of fig-specific pollinators. However, fig trees exhibit extreme asynchrony among neighboring individuals, such that only about 100 trees are needed to provide year-round flowering at the population-level, providing continuous foraging opportunity for their mutualistic wasps (Bronstein et al. 1990).

Resource waves delivered to consumers: Stream networks and animal migration funnel phenologically diverse resources to stream-dwelling fishes and other consumers

Streams and rivers are branched networks that transport materials downstream towards the trunk of the system. The trophic resources available at a given location in a stream network include not only local in situ production, but also resources that drift downstream from upper portions of the watershed (Wipfli and Baxter 2010), fall from adjacent terrestrial vegetation (Nakano and Murakami 2001) or travel upstream from marine ecosystems (Gende et al. 2002). Resource subsidies to streams typically occur as pulses (Kawaguchi and Nakano 2001). Asynchrony among pulsed resource subsidies can protract high quality foraging opportunities for consumers. In contrast to the previous examples, stream-dwelling consumers may not need to move to exploit spatial variation in the phenology of resource subsidies; the hydrologic characteristics of streams integrate across spatial variation such that even sessile organisms can sample resources derived from a large spatial extent (Nakano and Murakami 2001).

In addition to the physical transport of downstream flow, fish migrations can funnel trophic resources down branched stream networks, and analogous phenomena occur as landscape morphology and ocean currents constrain the migration routes of terrestrial and marine animals, respectively (Hebblewhite and Merrill 2007).

For example, population- and species-level variation in the migration phenology of seaward-bound juvenile salmon protracts their availability to avian and aquatic predators that ambush them at the trunk of river networks (McBride 1980, Scheuerell et al. 2009, McGlauflin et al. 2011). Similarly, salmon shark (*Lamna ditropis*) reside in the migration pathways of adult salmon along the Alaska coastline and likely benefit from asynchrony in salmon migration timing (Weng et al. 2008). These examples of funneled resource waves illustrate that phenological diversity can benefit a wide variety of consumers, not just those that are highly mobile.

Key questions not addressed by existing case studies

The body of work on resource waves currently exists as independent case studies spread across a diverse array of taxa and ecosystems (Appendix S3: Table S1). These studies demonstrate both the generality of the resource wave phenomenon, as well as its significance: consumers were documented to prolong their access to ephemeral resources by anywhere from 50% (Ruff et al. 2011) to roughly 1000% (Bronstein et al. 1990) by tracking resource waves across space. A remaining challenge for empirical work is to understand how the ability to surf resource waves affects consumer fitness and demography. While many case studies document how surfing resource waves affected the duration of high quality foraging, few have estimated effects on growth (Mysterud et al. 2001, Ruff et al. 2011), population productivity (Pettorelli et al. 2005, Wang et al. 2006, Van Der Jeugd et al. 2009), or population viability (Fryxell et al. 2005).

Though these empirical examples share common underlying dynamics, they differ substantially in the ecological attributes of their focal consumers and resource waves. A key challenge for advancing the study of resource waves is to understand how this ecological context mediates the functional significance of phenological diversity across landscapes, and its implications for the conservation and management of specific consumers. We identified three key questions that identify the information needed for a more synthetic understanding of resource waves and their significance to conservation and management.

(1) How strongly can spatial variation in resource phenology mediate consumer foraging opportunities relative to total resource abundance?
(2) How do attributes of consumer behavior interact with attributes of the resource wave to mediate consumer foraging opportunities?
(3) How do habitat loss and homogenization affect resource waves and the benefits they confer to consumers?

These broad questions are difficult to address with single case studies, and meta-analysis is not yet practical given the early development of the field. Instead, we used a consumer-resource simulation model to explore a range of ecological scenarios and provide tangible answers to our three key questions.

ASSESSING THE ECOLOGICAL SIGNIFICANCE OF RESOURCE WAVES THROUGH A CONSUMER–RESOURCE SIMULATION MODEL

To simulate consumers foraging across landscapes, we developed an individual-based foraging simulation, with time and space represented discretely (Berec 2002). Our landscape was a 20 × 20 cell grid in which each cell provided a single resource pulse, modeled by a sinusoidal function with amplitude representative of resource abundance. The phenology of resources in each cell was defined by the date when the resource pulse peaked. We used random fields to generate spatial heterogeneity in phenology across the grid, given different levels of variation and spatial autocorrelation. We modeled consumer behavior based on the concepts of perceptual extent and resolution (Lima and Zollner 1996, Fryxell et al. 2004). Specifically, we varied both the spatial extent over which consumers could access resources (neighborhood size) and their ability to move to cells in relation to relative resource abundance (perceptual resolution). We related the resource abundance in an occupied cell to consumer energy intake using either a linear or type II functional response. To maintain a broad conceptual scope and avoid unwarranted complexity, we did not include resource depletion or interference competition in the model. Each simulation tracked 100 consumers over 365 time steps. The response variable was the average cumulative energy intake across consumers. We assume that energy intake positively affects population productivity. However, because this relationship is context dependent and involves many additional ecological variables, simulating numerical responses at the population level was beyond the scope of our general model.

To address questions 1 and 2 above, we simulated across six parameters: resource abundance (i.e., amplitude of resource pulse), phenological variation across the landscape, phenological spatial autocorrelation, consumer neighborhood size, consumer perceptual extent, and the type of consumer functional response. To address question 3, we removed 75% of each landscape and recorded how this affected consumer energy gain, as a function of spatial autocorrelation in resource phenology and consumer neighborhood size. A full description of the model, and its source code in R (R Core Team 2015), are provided in Appendix S1 and Data S1, respectively.

MODEL RESULTS

Relative importance of phenological diversity compared to resource abundance

Spatial variation in resource phenology can have a stronger effect on consumer energy gain than that of total resource abundance, across a broad range of consumer behavioral attributes (Fig. 3, Appendix S2: Fig. S3).

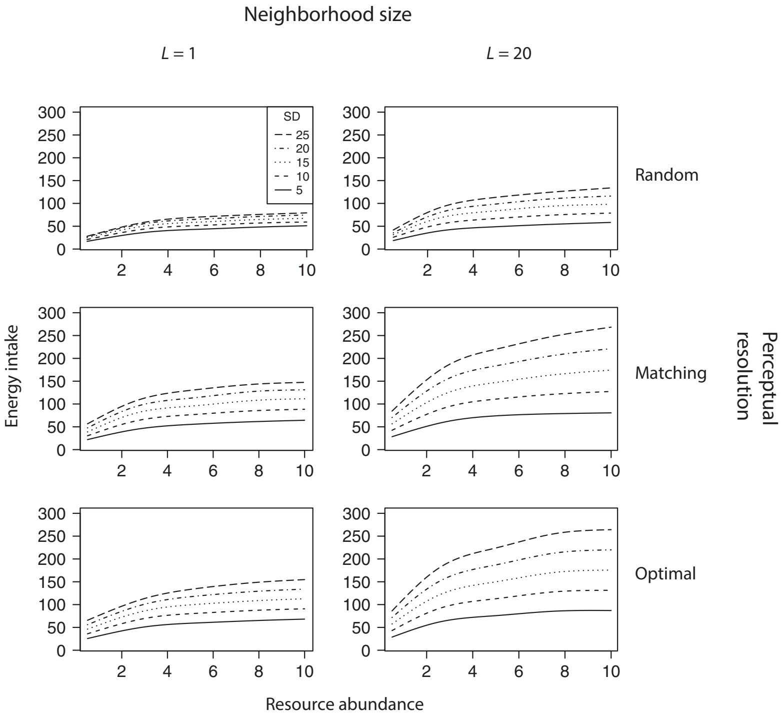


FIG. 3. Results from model simulations exploring the effect of resource abundance and phenological variation on consumer energy gain. Each panel shows results for five different levels of phenological variation, represented by different line types (legend in top-left panel, SD denotes standard deviation of peak resource dates across the landscape). Each panel shows results for different combinations of two consumer behavioral parameters: neighborhood size and perceptual resolution. Neighborhood size extends *L* cells vertically and horizontally and defines the area over which the consumer can move at each time-step (on the 20 × 20 cell lattice). Perceptual resolution describes the ability of the consumer to select cells according to their relative resource abundance (random, all cells have equal probability of selection; matching, probability of selection proportional to relative resource abundance; optimal, cells with highest resource abundance always selected).

Resource abundance influenced maximum rates of energy gain per time step, whereas phenological variation influenced the duration of foraging opportunity. Phenological variation had the strongest effect on consumer energy gain when resource abundance was high relative to the asymptote of the consumer's functional response. However, even under the unrealistic assumption of a linear, non-saturating functional response, phenological variation still had positive effects on consumer energy gain (Appendix S2: Fig. S3). While it is difficult to make direct quantitative comparisons between resource abundance and phenological variation, our results provide two clear messages: (1) reduced phenological diversity in trophic resources can substantially alter consumer foraging opportunities even if levels of resource abundance remain constant (Post 2013); and (2) if resource phenologies are synchronized at the landscape scale, the negative effects on consumer foraging opportunities are unlikely to be mitigated by increasing resource abundance.

Interactions between attributes of resource waves and consumer behavior

The neighborhood size and perceptual resolution of the consumer both had positive, saturating effects on energy intake (Fig. 3, Appendix S2: Fig. S1). However, even for animals with small neighborhoods and low perceptual resolution, phenological heterogeneity could increase energy intake by >50% over course of the year (Fig. 3, Appendix S2: Fig. S3).

Neighborhood size interacted with attributes of the resource wave to influence consumer energy gain. The positive effect of phenological variation on consumer energy gain was amplified when the consumer neighborhood size was large (Fig. 3). Spatial autocorrelation in resource phenology had negative effects on consumer energy gain, which were magnified when neighborhood size was small (Appendix S2: Fig. S1). Increasing spatial autocorrelation reduces the proportion of landscape-level variation that is expressed locally, so it reduces the amount of phenological variation accessible to consumers with limited mobility or perceptual extent.

Implications for habitat loss

Habitat loss always reduced consumer energy gain, but the effect was stronger when consumer neighborhood size was large or resource phenologies were spatially autocorrelated (Appendix S2: Fig. S2). An applied model of gazelles tracking phenological variation in grass growth found similar interactions (Fryxell et al. 2005). The virtual gazelles in that model always had large neighborhood sizes relative to the extent of the landscape (neighborhood area 36–100% of landscape area). We found that, when consumers had small neighborhood sizes relative to the extent of the landscape (e.g., neighborhood area = 0.5% landscape area), the interaction between habitat size and spatial autocorrelation disappeared (Appendix S2: Fig. S2).

We observed negative effects of habitat loss on consumer energy gain in the absence of confounding factors that often accompany habitat degradation such as increased competition, reduced landscape permeability, or decreased resource density. This shows that habitat alteration can have strong effects on consumers solely by mediating the duration of foraging opportunities at the landscape scale (Searle et al. 2010). We believe this is an underappreciated effect of human development: constraining animals spatially can in turn constrain them temporally, by truncating foraging opportunities.

General insights

The overarching result of our model is that resource waves offer large benefits to mobile consumers, and these benefits are generally robust to specific attributes of the resource wave and consumer behavior (Fig. 3). While the degree to which consumers can exploit resource waves is sensitive to their perceptual extent and resolution, across the vast majority of parameter space we explored, spatial variation in phenology translated into strong benefits to consumers. Prior work has suggested that a relatively small number of specialized consumers track resource waves (Yang et al. 2008), but our model suggests that most mobile consumers have the potential to capitalize on spatial variation in resource phenology (i.e., they do not need to track resource waves precisely to benefit from them) and thus may be more susceptible than previously recognized to habitat alterations that influence resource phenology or landscape connectivity.

Threats to Resource Waves

One of the most ubiquitous effects of human development is biotic and abiotic homogenization (Vitousek 1997). Habitat homogenization can dampen the physical mechanisms underlying spatial variation in phenology (Poff et al. 2007), whereas loss of biodiversity reduces the capacity for biological systems to express phenological variation. Ecologists typically study biodiversity among species, yet the studies reviewed here show that individual- and population-level diversity in phenology are important components of many resource waves. Alarmingly, losses of diversity occur much more rapidly at these finer levels of biological organization than at the species level. For example, populations go extinct roughly 1000 times faster than species do (Hughes et al. 1997). The population diversity that generates red waves of salmon is still intact at high latitudes of the Pacific Rim (Schindler et al. 2010, Griffiths et al. 2014) but is severely degraded elsewhere. In the continental United States, roughly one-third of 14000 historical Pacific salmon populations have been lost, and in inland regions, this proportion exceeds one-half (Gustafson et al. 2007). Further, in many areas, the remaining salmon portfolio is dominated by genetically homogenous hatchery stocks (Moore et al. 2010, Carlson and Satterthwaite 2011), which are often bred to exhibit synchronous phenologies (McLean et al. 2005).

Even the loss of phenotypes within a population may affect resource waves. Body size is associated with spawn timing in marine fishes (Lambert 1987, Secor 2000) and migration timing in juvenile salmon (Zabel and Achord 2004). This suggests that the size structure of a population can mediate its phenological diversity. Human actions that selectively remove large fish, homogenize age structures, or reduce the scope for fish growth may reduce individual variation in body size, and in turn, diminish the resource waves that fish generate for predators at the top of the food web (Willson and Womble 2006, Wright and Trippel 2009).

Climate change has the potential to change the characteristics of resource waves by affecting the distribution of abiotic conditions (e.g., precipitation and temperature) that modulate the development rates of plants and animals, and thus the duration of life stages that offer consumers high quality foraging opportunities. Additionally climate can mediate the level of phenological variation among components of the resource aggregate. For example if snow cover is responsible for delayed development in plants, reduced snowpack may homogenize plant phenologies and diminish late-season herbivory opportunities. Indeed, winter drought and spring/summer warming was associated with reduced phenological variability of plants in the Greater Yellowstone ecosystem, resulting in a narrower window of time for migratory herbivores to target plants at their optimal stage of development (Middleton et al. 2013). Migratory elk showed a decrease in fecundity following the climate-induced attenuation of the resource wave. Importantly, this demographic response in the herbivore came about in the absence of any change in the average timing of green up; instead, change in the rate of green up across the landscape (likely due to reduced spatial variation in phenology) was the important driver. Climate-induced shifts in salmon migration phenology were recorded in a small Alaska watershed, such that the period during which spawning adults are available to consumers has decreased by about 30% over four decades (Kovach et al. 2013). However, the period during which seaward-migrating juveniles are available to consumers has actually increased by approximately the same percentage (Kovach et al. 2013). An important challenge for ecologists will be to understand not only how climate change affects resource phenology, but also how direct human influences (e.g., via changing land-use) interact with changing climate to affect the seasonal progression of foraging opportunities across landscapes.

THREATS TO CONSUMERS THAT SURF WAVES

For consumers to capitalize on spatiotemporal variation in prey resources, they must be able to move across landscapes to arrive in particular habitats at specific points in time. Human development has reduced habitat connectivity worldwide and is particularly devastating in river systems, where point features in a watershed, such as dams, can render entire river networks impermeable to consumer movements (Fausch et al. 2002). Many terrestrial barriers still allow connectivity among discrete habitats (Sawyer et al. 2013). However, these semipermeable barriers may interfere with the ability of migrants to surf resource waves, in essence reducing their neighborhood size and perceptual resolution, which had strong affects on foraging potential in our simulations (Fig. 3, Appendix S2: Figs S1–S3). For example, migratory mule deer and pronghorn (*Antilocapra americana*) that surf green waves in the Western United States are increasingly likely to encounter fossil fuel extraction infrastructure during their seasonal migrations. Though they do not completely block movement, drilling sites cause mule deer to make detours, travel faster, and spend less time foraging at stopover sites (Sawyer et al. 2013, Seidler et al. 2015). This illustrates the concepts of connectivity and functionality in migration routes. If migrants can still travel between discrete seasonal habitats, yet can no longer exploit stopover feeding sites along the way, then their migration route is connective, yet not functional (Sawyer et al. 2013). Although movement ecologists have long recognized that migration may be as much about foraging as it is traveling (Dingle 1996), the significance of consumer access to resource waves has been largely neglected in conservation. As humans expand their development of landscapes across the globe, encroaching on the habitat of culturally important consumers, there is a strong need for research that quantifies how access to resource waves affects the population productivity of wide-ranging animals, especially those that are migratory (Bolger et al. 2008, Holdo et al. 2011).

BEYOND ABUNDANCE

A core assumption of many ecological models or frameworks for ecosystem-based management is that the magnitude of energy flow between consumers and their prey is mediated by resource abundance or productivity (Christensen and Pauly 1992). Our model, along with empirical study of resource waves, demonstrates that the spatiotemporal patterning of species abundance may have more influence on trophic interactions than resource abundance per se (Fig. 3). This result has broad implications for conservation issues involving the allocation of prey resources between humans and other consumers. For example, there is recent concern that commercial salmon fisheries are diminishing the foraging opportunities of grizzly bears and other inland salmon consumers (Darimont et al. 2010, Levi et al. 2012). However, existing analyses consider watershed-level estimates of salmon abundance as the metric of consumer foraging opportunities, ignoring the significance of resource waves. Though commercial fisheries may harvest >50% of the many North American salmon runs, many consumer species are digestively constrained when feeding on salmon (Gende et al. 2002, Bentley et al. 2012, Armstrong et al. 2013). This suggests that where salmon abundance is still relatively high, salmon-consumers are more limited by the duration, rather than the magnitude, of salmon feeding opportunities. Thus, instead of encouraging managers to reduce harvest rates, which has economic consequences for regional economies, conservation scientists may be better off working with managers to ensure that harvest policies do not reduce the life-history diversity of salmon and diminish the red wave.

A fundamental challenge in conservation is to prioritize the allocation of limited resources, for example, prioritizing specific locations for protection. Our results stress the potential importance of prioritizing sites to maintain phenological diversity. Resource stocks with unique phenology may be disproportionately important to consumers, yet their significance is rarely accounted for in current conservation models. For example, small snowmelt-dominated streams harbor early-spawning salmon populations in coastal watersheds of Alaska (Lisi et al. 2013). Though these populations make up a small fraction of salmon abundance across a watershed, they may be the only populations available to consumers for the first third of the salmon run. Many conservation strategies would not assign value to these phenologically unique populations due to their low abundance. Similarly, low elevation sites along mule deer migration routes typically have lower plant productivity compared to high elevation sites (Hebblewhite et al. 2008, Middleton et al. 2013). However, plants at these low elevation sites are the first to green up, providing critically important foraging when herbivores are near starvation and high elevations sites remain snow covered.

SUMMARY

The case studies reviewed here, in addition to our modeling results, demonstrate that spatial variation in resource phenology can strongly mediate the foraging opportunities of wide-ranging consumers. While the body of literature on phenology has grown exponentially in recent decades, research has primarily focused on characterizing the central tendency of phenology and range shifts (e.g., the arrival of spring), and how these have responded to changing environmental conditions (Parmesan and Yohe 2003). Variation has been studied primarily at the intra-population level and is often treated as statistical noise rather than as an ecologically significant attribute worthy of direct study (Diez et al. 2012). Spatial variation in resource phenology, which occurs at multiple levels of biological organization, protracts foraging opportunities for animals ranging from grasshoppers (*Caelifera*; Searle et al. 2010) to grizzly bears (Coogan et al. 2012, Schindler et al. 2013). The consumers that surf resource waves are often commercially and culturally important, yet existing management frameworks are typically inadequate for conserving either the underlying mechanisms of resource waves or the spatiotemporal aspects of habitat connectivity that enable consumers to surf them. Ecosystem-based models rely on abundance as proxies for the strength of trophic interactions, assuming that ecosystems are well-mixed reactors, yet our results suggest phenological diversity may be just as important in determining how energy flows to upper levels of food webs, particularly in seasonally dynamic ecosystems. The case studies presented here are just a small sample of the resource waves that propagate through ecosystems across the globe. We suggest that resource waves are an emergent property of consumer–resource interactions, and are critical to the stability and productivity of many ecosystems.

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