

COMPARING RESOURCE PULSES IN AQUATIC AND TERRESTRIAL ECOSYSTEMS

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Abstract. Resource pulses affect productivity and dynamics in a diversity of ecosystems, including islands, forests, streams, and lakes. Terrestrial and aquatic systems differ in food web structure and biogeochemistry; thus they may also differ in their responses to resource pulses. However, there has been a limited attempt to compare responses across ecosystem types. Here, we identify similarities and differences in the causes and consequences of resource pulses in terrestrial and aquatic systems. We propose that different patterns of food web and ecosystem structure in terrestrial and aquatic systems lead to different responses to resource pulses. Two predictions emerge from a comparison of resource pulses in the literature: (1) the bottom-up effects of resource pulses should transmit through aquatic food webs faster because of differences in the growth rates, life history, and stoichiometry of organisms in aquatic vs. terrestrial systems, and (2) the impacts of resource pulses should also persist longer in terrestrial systems because of longer generation times, the long-lived nature of many terrestrial resource pulses, and reduced top-down effects of consumers in terrestrial systems compared to aquatic systems. To examine these predictions, we use a case study of a resource pulse that affects both terrestrial and aquatic systems: the synchronous emergence of periodical cicadas (*Magicicada* spp.) in eastern North American forests. In general, studies that have examined the effects of periodical cicadas on terrestrial and aquatic systems support the prediction that resource pulses transmit more rapidly in aquatic systems; however, support for the prediction that resource pulse effects persist longer in terrestrial systems is equivocal. We conclude that there is a need to elucidate the indirect effects and long-term implications of resource pulses in both terrestrial and aquatic ecosystems.

Key words: allochthonous subsidies; bottom-up and top-down effects; ecosystem retention; *Magicicada* spp.; periodical cicadas; resource pulses; terrestrial and aquatic food webs; transient effects.

INTRODUCTION

The structure and dynamics of ecological systems are controlled, in part, through resource availability. Ecologists have long recognized that both bottom-up and top-down forces affect the relative abundance of populations in ecological networks (Hairston et al. 1960, Carpenter et al. 1985, Polis and Strong 1996, Brett and Goldman 1997), but ultimately basal resources limit the productivity of communities (Hunter and Price 1992, Power 1992, Strong 1992). In this context, a resource is generally defined as a commodity required by an organism for maintenance, growth, and reproduction (Ricklefs 2000). Because resource availability plays a primary role in determining consumer densities, biomass, and growth rates, the timing and availability of resources will influence both community structure and ecosystem function; however, the role of heterogeneity in resource supply has figured less prominently in

ecological research than the role of bottom-up and top-down forces.

Many communities and ecosystems experience infrequent, large magnitude, and short duration events of greatly increased resource availability that affect the dynamics of populations at multiple trophic levels (Ostfeld and Keesing 2000, Yang et al. 2008). Such resource pulses can elicit both bottom-up effects and subsequent top-down effects (Ostfeld and Keesing 2000, Yang et al. 2008). These studies have examined the impacts of infrequent, large magnitude pulses of limiting resources or resources that strongly influence consumers. Despite the far-reaching effects of resource pulse events, there have been few attempts to compare resource pulses in different ecosystems or to construct conceptual or theoretical frameworks for understanding population and community responses to resource pulses (Ostfeld and Keesing 2000, Reynolds et al. 2004, Holmgren et al. 2006).

In a number of recent reviews, ecologists have compared many characteristics of terrestrial and aquatic systems, including biogeochemistry (Grimm et al. 2003), herbivory and decomposition (Cyr and Pace 1993, Cebrian and Lartigue 2004), population density and

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TABLE 1. Examples of several well-known resource pulses in terrestrial and aquatic systems, including the pulse driver (or triggering event), specific ecosystem type, kind of resource pulse, primary consumer of the resource pulse, frequency of the pulse, and source of the pulse (autochthonously or allochthonously generated).

Pulse driver	System	Resource type
Terrestrial pulses		
ENSO	arid and semiarid environments	increased rainfall leading to increased seeds and vegetation biomass
Climatic or unknown cause	temperate forests	seed/mast production
Hurricane	tropical/subtropical forests	greenfall and light gaps
Insect outbreak/emergence	temperate forests	insect carcasses, frass
Anadromous fish reproduction	riparian forests	animal carcasses
Aquatic pulses		
ENSO	ocean pelagia	upwelling of deeper nutrient rich water
Hurricane	oceans, estuaries, coastal freshwater lakes	upwelling of nutrient rich water; increased terrestrial runoff, nutrient release from sediments
Anadromous fish reproduction	coastal streams and lakes	animal carcasses, nutrients
Migrating waterbirds	wetlands	guano deposition and release of nutrients
Insect outbreak/emergence	lakes and ponds	deposition of swarming insect carcasses, nutrient release

Notes: Representative publications are presented for each pulse type. The complete list of studies examining the food web and ecosystem-level effects of resource pulses is given in Appendix A: Table A1 and Appendix B. ENSO = El Niño Southern Oscillation.

size structure (Cyr et al. 1997, Brose et al. 2006), stoichiometry (Elser et al. 2000), and food web structure and function, including the strength of top-down and bottom-up forces (Strong 1992, Hairston and Hairston 1993, Polis and Strong 1996, Chase 2000, Shurin et al. 2002, 2006). These reviews suggest that terrestrial and aquatic systems differ in several fundamental ways, including food web structure and complexity, and the magnitude of energy flows through different trophic pathways (Cyr and Pace 1993, Cebrian and Lartigue 2004, Shurin et al. 2006). Many of these reviews also identify several characteristics of terrestrial and aquatic systems that are similar, implying universality in some ecological patterns and processes. For example, the range of net primary production rates is similar in terrestrial and aquatic systems (Cyr and Pace 1993, Cebrian 1999). Although both terrestrial and aquatic ecosystems experience resource pulses (Ostfeld and Keesing 2000, Stapp and Polis 2003, Babin et al. 2004, Yang 2004, Holmgren et al. 2006, Nowlin et al. 2007), reviews of resource pulses have focused primarily on terrestrial ecosystems (Ostfeld and Keesing 2000, Holmgren et al. 2006).

Here, we examine the similarities and differences in the causes, types, timing, and consequences of resources pulses in terrestrial and aquatic systems, and propose that different patterns of community structure and dynamics in terrestrial and aquatic systems are likely to yield different responses to resource pulses. Finally, as a case study of how aquatic and terrestrial systems respond to resource pulses, we compare the effects of periodical cicadas on aquatic and terrestrial systems in eastern North American forests.

DO RESOURCE PULSES IN TERRESTRIAL AND AQUATIC SYSTEMS DIFFER?

We examined studies that investigated the effects of resource pulses and compiled information on four specific aspects of these studies. First, we examined the causes or triggering mechanisms of each resource pulse. Second, we categorized what type of resource was pulsed in each study (i.e., seeds, inorganic nutrients, water, prey, detritus) and examined whether the pulse was generated from within the system (autochthonous origin) or from outside the system (allochthonous origin). Third, we examined the frequency of resource pulse events (i.e., amount of time between pulses). Last, we determined the consumers or utilizers of the resource pulse. We compiled 81 studies from the primary literature that examine the food-web-level and ecosystem-level effects of resource pulses (Table 1, Appendix A: Table A1, Appendix B). We present a list of several well-known and representative pulses in both terrestrial and aquatic systems in Table 1; the complete list of studies is provided in Table A1. We do not attempt to perform a quantitative literature review; rather, we assess these studies qualitatively to discern general patterns between ecosystem types.

As with most ecological phenomena, a gradient exists in terms of the timing and magnitude of resource availability in ecosystems. Thus, in almost all circumstances, resource supply to consumers in ecological networks is in some sense "pulsed"; resource supply is rarely constant. However, we here define a resource pulse as an infrequent, large magnitude, and short-duration occurrence of limiting resource superabundance (Yang et al. 2008). Use of this definition excludes

TABLE 1. Extended.

Primary pulse consumers	Pulse frequency	Pulse source	Representative references
vegetation; mammals and birds	2–7 years	autochthonous	Polis et al. (1997), Lima et al. (1999), Letnic et al. (2005)
rodents, large mammals	2–8 years	autochthonous	Ostfeld et al. (1996), Jędrzejewska and Jędrzejewski (1998)
soil microbes, vegetation	unpredictable seasonal	autochthonous	Tanner et al. (1991), Bloch and Willig (2006)
soil microbes, mammals, birds, plants	unpredictable seasonal or regular 13–17 year intervals	autochthonous	Lovett et al. (2002), Yang (2004)
soil microbes, vegetation, mammals and birds	1–5 years	allochthonous	Helfield and Naiman (2001), Naiman et al. (2002)
phytoplankton and microbes	2–7 years	autochthonous	Longhurst (2001), Wang and Fielder (2006)
phytoplankton and microbes	unpredictable seasonal	autochthonous and allochthonous	Paerl et al. (2001), Shumate et al. (2002), Babin et al. (2004)
algae and microbes	1–5 years	allochthonous	Naiman et al. (2002), Claeson et al. (2006)
algae and microbes	annual	allochthonous	Kitchell et al. (1999)
microbes, algae, fish	unpredictable seasonal or regular 13–17 year intervals	allochthonous	Carlton and Goldman (1984), Nowlin et al. (2007)

some well-studied examples of systems that are often associated with consistently recurring resource inputs. The persistence of some ecosystem types, such as mangrove forests, salt marsh tidal creeks, river floodplains, and ephemeral ponds, is highly dependent upon regular inputs of water and/or nutrients (Brinson et al. 1981, Bonner et al. 1997, Dudek et al. 1998, Krauss et al. 2006). In addition, many systems experience resource inputs as regular seasonal events, such as terrestrial leaf litter inputs to headwater streams and woodland ponds (Wallace et al. 1997, Rubbo and Kiesecker 2004), deposition of terrestrial insects to streams (Nakano et al. 1999), emergence of aquatic insects to riparian forests (Nakano and Murakami 2001), and inundation of floodplains (Brinson et al. 1981, Dudek et al. 1998). While these inputs undoubtedly play a vital role in these ecosystems, they do not represent brief and infrequent events of extremely high resource availability for most consumers. Using our definition of a resource pulse, however, we include extreme examples of regularly occurring seasonal events (i.e., 100-year flood event in a riparian forest) in our review. We also consider regularly occurring events of synchronous mass animal movements and/or reproduction to be resource pulse events when interannual variation in animal numbers is great (Watt et al. 2000, Greene et al. 2005). In addition, resource inputs that exhibit substantial spatial variation within an ecosystem, such as the deposition of semelparous animal carcasses or excreta by large groups of animals (Anderson and Polis 2004, Yang 2004, Nowlin et al. 2007) can result in pulsed resource availability for local populations.

To compile studies of resource pulses, we used studies cited in recent reviews of resource pulses (Ostfeld and Keesing 2000, Reynolds et al. 2004, Holmgren et al. 2006) and searched the *ISI Web of Science*, *Biological*

Abstracts, and *Aquatic Sciences and Fisheries Abstracts* databases for studies that examined the effects of resource pulses. Studies were included if an individual paper or a combination of papers about a specific system showed that (1) the resource pulse was of extraordinary magnitude, (2) the event was infrequent and brief relative to the perspective of the potential pulse consumers, and (3) the resource pulse affected community- or ecosystem-level properties such as population densities, taxon diversity, primary production, decomposition, or nutrient cycling rates. We excluded studies that examined anthropogenically generated pulses. Despite the large number of studies in Table A1, we acknowledge that our compilation is not comprehensive and we likely excluded a number of relevant examples.

Resource pulses occur in most types of terrestrial and aquatic ecosystems, including arid and semiarid environments, temperate forests, tropical forests, coastal oceans, lakes, reservoirs, streams, ephemeral ponds, and wetlands (Table 1, Table A1, and Appendix B). Most of the examples in Table 1 and Table A1 are associated with large-scale disturbance events (e.g., floods or hurricanes) or mass reproduction events. Climatic or environmental conditions appear to be the most common drivers of resource pulses in both terrestrial and aquatic systems (Table 1 and Table A1). Although many of the events contributing to resource pulses occur in both terrestrial and aquatic systems (e.g., El Niño Southern Oscillation [ENSO], hurricanes, periodical cicadas, and anadromous salmon), some pulse types are system specific. For example, seed pulses by primary producers in terrestrial systems do not have a direct analog in aquatic systems, and pulses of dissolved nutrients are more common in aquatic systems (e.g., pulsed runoff containing nutrients and sediments, deep water entrainment, atmospheric deposition).

Synchronous propagule production by primary producers is a type of resource pulse with far-reaching effects in several terrestrial systems (Ostfeld and Keesing 2000, Holmgren et al. 2006). Compared to their terrestrial counterparts, pelagic primary producers such as unicellular and colonial algae are small and do not produce large edible seeds or propagules. Although some aquatic organisms, such as scleractinian corals, exhibit synchronous propagule production that affects consumers in aquatic communities (McCormick 2003), synchronous seed production is not common among aquatic primary producers.

Both system types experience autochthonously and allochthonously generated resource pulses (Table 1 and Table A1), but autochthonous pulses are more common in terrestrial systems, whereas allochthonous pulses are more commonly delivered to aquatic systems, especially freshwater systems. Many essential nutrients required by primary producers are soluble in water (i.e., PO_4^{3-} , NO_3^- , NH_4^+) so that organisms in lakes and coastal oceans are likely to experience nutrient pulses associated with the movement of water, such as extreme stream flow events or infrequent events of upwelling of deep nutrient-rich water into surface strata. In general, aquatic systems more frequently receive dissolved nutrient pulses from terrestrial systems because of their “downhill” and “downstream” positions in landscapes (Shurin et al. 2006). Even open ocean pelagic zones, while very far from terrestrial systems, can receive aeolian dust and nutrients transported from mainland terrestrial sites (Table A1). Thus, the physiochemical characteristics of aquatic systems and their location within landscapes contribute to the higher frequency of dissolved nutrient pulse events in aquatic systems. While some terrestrial systems also receive inorganic nutrient pulses (e.g., riparian forests during extreme riverine flood pulses), these ecosystems often occupy “downhill” landscape positions and the nutrient pulses into these systems are often associated with pulses of water.

As with dissolved nutrient pulses, landscape position and gravity suggest that aquatic systems should receive detritus inputs from terrestrial systems more frequently than vice-versa. Our assembled studies generally support this prediction (Table 1 and Table A1). These pulses include both plant and animal detritus, such as hurricane-driven greenfalls in tropical forests (Lin et al. 2003) or swarms of terrestrial insects that fall into aquatic systems (Carlton and Goldman 1984, Nowlin et al. 2007). However, aquatic systems can also be important donors of pulsed detrital resources to terrestrial systems; for example, large inputs of marine detritus, such as algal wrack or animal carcasses, periodically wash up on beaches and can be utilized by a variety of terrestrial consumers (Polis et al. 1997, Rose and Polis 1998).

Many well-studied examples of pulsed resources in aquatic and terrestrial systems occur at time scales >1 year (Tables 1 and A1). While the majority of studies in

Tables 1 and A1 explore pulses that occur at annual and multi-annual scales, resource inputs that occur on more frequent timescales can also create pulsed dynamics in short-lived consumers (Table A1). For example, pulses of inorganic nutrients associated with the entrainment of deeper, nutrient-rich lake water into illuminated surface waters can occur multiple times over the course of a single growing season, providing resources for pelagic algae and bacteria (Soranno et al. 1997). The dominance of annual or multi-annual pulses in Tables 1 and A1 may be a function of the seasonal or annual temporal scales of study typical of many ecological investigations. Thus, we conclude that most well-studied examples of resource pulses occur at annual or multi-annual time scales in both aquatic and terrestrial systems, but this conclusion is likely to be at least partially biased by common scales of ecological observation.

DO TERRESTRIAL AND AQUATIC SYSTEMS DIFFER IN THEIR RESPONSES TO RESOURCE PULSES?

We utilized several reviews which compare and contrast terrestrial and aquatic food webs (Strong 1992, Cyr and Pace 1993, Hairston and Hairston 1993, Polis and Strong 1996, Cyr et al. 1997, Chase 2000, Elser et al. 2000, Shurin et al. 2002, 2006, Grimm et al. 2003, Cebrian and Lartigue 2004) and numerous empirical studies to generate predictions. Terrestrial and aquatic systems differ in several fundamental ways, including the type of resources that limit primary producers and consumers. These differences may cause difficulties when comparing the responses of aquatic and terrestrial systems to pulses of specific resources (e.g., nitrogen or phosphorus). Instead of examining the responses of each system type to any one particular resource, we attempt to predict patterns in the general responses of these systems to pulses of limiting resources based upon well-established differences in the size and physiology of organisms (Hairston and Hairston 1993, Chase 2000, Elser et al. 2000, Shurin et al. 2006). In particular, we are interested in how fundamental differences in physiology, life history, and size of aquatic and terrestrial consumers affect the rate at which the effects of pulses of limiting resources propagate through food webs and the amount of time these effects persist. We largely focus on numerical or biomass responses of consumers in food webs in relation to changes in reproductive rates. As with most previous comparisons of terrestrial and aquatic systems, we focus on pelagic systems within the aquatic realm, but also consider benthic macrophyte-dominated food webs in some cases. We predict that (1) the bottom-up effects of resource pulses should transfer through aquatic systems at faster rates because of differences in consumer strategies, growth rates, sizes, and stoichiometry of organisms in aquatic and terrestrial systems, and (2) the impacts of resource pulses should persist longer in terrestrial systems because of longer organism generation times, the more persistent nature of many terrestrial resource pulses, and the

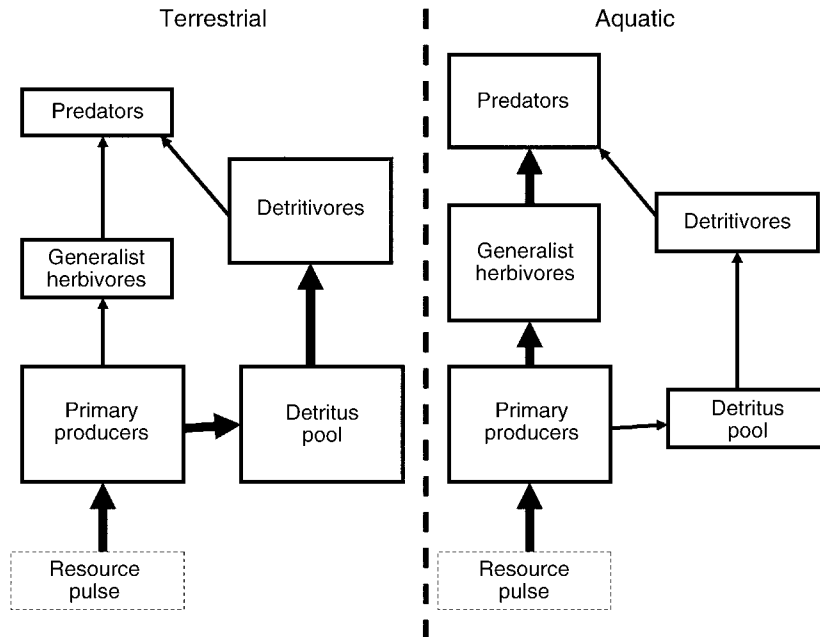


FIG. 1. Diagram of predicted responses of terrestrial and aquatic systems to a resource pulse event, such as water or dissolved labile nutrients, that affects the biomass and productivity of primary producers. Pathways of nutrients and energy between trophic levels are illustrated with arrows. The thickness of the arrows indicates the relative rapidity and magnitude of nutrient and energy flows through food webs between the specific ecosystem type (i.e., the thicker the line, the faster and/or greater the effect).

reduced intensity of top-down consumer effects in terrestrial systems relative to aquatic systems.

Predicting the speed and persistence of aquatic and terrestrial responses to resource pulses

Ostfeld and Keesing (2000) suggest that community-level responses to resource pulses depend on three interrelated characteristics of consumers in food webs receiving the resource pulse: (1) the degree of specialization on the pulsed resource, (2) the rate of consumer population increase in response to the pulse, and (3) the mobility of consumers in response to the pulse. Are these features also important in mediating the response of aquatic food webs to resource pulses? Here, we consider how differences in the size structure and growth rates of organisms, nutrient stoichiometry and chemical composition of primary producers, and the sensitivity of each system type to bottom-up and top-down forces may mediate community responses to pulsed resources.

Generation times and tissue turnover rates of aquatic organisms are more rapid than their terrestrial counterparts (Persson et al. 1999, Chase 2000, Shurin et al. 2006). Nutrient pulses can lead to increased nutrient content per unit biomass in both aquatic (Dickman et al. 2006) and terrestrial (Gratton and Denno 2003, Yang 2004) food webs, creating higher quality food for herbivores. However, pelagic phytoplankton have higher productivity and nutrient content per unit biomass than land plants (Enriquez et al. 1993, Elser et al. 2000, Niklas and Enquist 2001, Cebrian and Lartigue 2004, Kerkhoff and Enquist 2006), thus increases in algal

populations in response to resource pulses may translate into new biomass for herbivores more rapidly than terrestrial plants. Pelagic food webs are also highly size structured; in general, body size increases with trophic level (Brose et al. 2006, Shurin et al. 2006) and this size structure may contribute to more efficient energy transfer in pelagic systems (Hairston and Hairston 1993). In contrast, terrestrial herbivores can be smaller than plants (e.g., phytophagous insects vs. trees) or larger than plants (e.g., ungulate grazers vs. grasses and forbs) (Shurin et al. 2006). Benthic primary producers in aquatic systems typically exhibit traits intermediate of those in pelagic and terrestrial systems, in terms of size, growth, and stoichiometry (Shurin et al. 2006).

Due to these energetic, stoichiometric, and size-related differences, the proportion of primary production consumed by herbivores is approximately three times greater in pelagic than in terrestrial and macrophyte-dominated systems (Cyr and Pace 1993, Cebrian and Lartigue 2004). Thus, it is likely that primary producers in pelagic and terrestrial food webs respond differently to pulses of limiting abiotic resources, such as nutrients or light (Fig. 1). Specifically, we predict that responses of primary producer biomass or abundance to pulses of limiting resources should lead to larger magnitude and faster reproductive responses of aquatic herbivores due to the more efficient transmission of energy and nutrients in aquatic systems (Fig. 1). Part of the reason why responses to pulses may be more rapid in aquatic systems is because of the shorter generation times of aquatic organisms. However, even when scaled to

generation times, the overall community responses of pelagic ecosystems may be more rapid because (1) pelagic primary producers invest relatively fewer resources in structural tissues, which allows them to allocate more resources to growth and reproduction, and (2) the higher nutrient content of algae (Elser et al. 2000) and the reduced prevalence of structural and chemical herbivore defenses in pelagic primary producers (Koricheva et al. 2004, Shurin et al. 2006).

Because a smaller portion of primary production is conveyed to herbivores in terrestrial systems than in pelagic systems, a larger fraction of terrestrial primary production is transferred to the detritus pool (Cebrian and Lartigue 2004, Shurin et al. 2006). This difference between terrestrial and aquatic systems leads to generally larger detritus pools and more well-developed detrital food chains in terrestrial systems (Shurin et al. 2006). Exceptions to this generalization in aquatic systems, however, are headwater streams and woodland ponds that receive inputs of terrestrially derived leaf litter. Due to the difference in the development of pelagic and terrestrial detrital compartments, we predict that resource pulses may have a comparatively smaller impact on herbivore populations in terrestrial systems, but may have a larger impact on detritivore populations (Fig. 1). Thus, pulses of inorganic nutrients, light, or other factors that greatly stimulate primary production may increase the input of plant organic matter to detritus pools, leading to increased detritivore populations.

Heterotrophic microbial decomposers (bacteria and fungi) are generally of similar size and exhibit similar generation times in both systems. Thus, these organisms may respond to resource pulses at similar time scales in aquatic and terrestrial systems. This suggests that pulses transmitted through the autotrophic or "green world" channel (primary producers to herbivores) will propagate faster in aquatic systems than in terrestrial systems; however, pulses transmitted through the detrital or "brown world" channel (detritus to decomposers) may elicit responses that are similar in rapidity in the two system types. Because aquatic and terrestrial systems differ in the relative amounts of energy traveling through these channels, the overall rate at which resource pulses are propagated in the two system types may depend on the nature of the pulse. For example, pulses of inorganic nutrients that stimulate primary producers, and consequently herbivores, may be transmitted faster in aquatic systems, while detritus pulses may elicit responses that are similar in time scale in aquatic and terrestrial systems, at least in terms of the initial microbial response. However, detrital quality may affect the relative speed of microbial responses to detrital pulses. For some terrestrial detritus pulses, microbial responses could be relatively slower if the quality of the detritus is low compared to aquatic detritus (e.g., leaf litter vs. dead algae). In addition, after microbes remineralize nutrients in detritus to inorganic

primary producer-available forms, autotroph responses may be faster in aquatic systems. Thus, the rate at which entire food webs respond in aquatic vs. terrestrial systems may depend on the nature of the pulse, the quality of the pulse, organism size structure, the relative energy and nutrient flows through decomposer and herbivore channels, and the cycling of nutrients within the food web.

The effects of pulsed primary production on upper trophic levels may vary in their magnitude and rapidity both within and between aquatic and terrestrial systems. In both system types, some consumer taxa may be better suited than others to take advantage of these pulses. Ostfeld and Keesing (2000) suggest that generalist consumers in terrestrial systems are particularly adept at utilizing resource pulses. For example, consumers that can easily switch to feeding on seeds commonly capitalize on synchronous seed production events, often showing large numerical responses (e.g., Stapp and Polis 2003). However, some groups of terrestrial consumers exhibit extreme resource specialization (e.g., Novotný and Basset 2005), compared to aquatic consumers (Shurin et al. 2006). If a lower degree of resource specialization exists in aquatic systems, then pelagic food webs may have a greater capacity to opportunistically utilize resource pulses (Fig. 1). Indeed, *Daphnia* is a dominant generalist herbivore in many freshwater zooplankton communities and consumes a wide range of phytoplankton taxa and sizes (Cyr and Curtis 1999). *Daphnia* can show rapid numerical responses; in fact, when *Daphnia* dominate the herbivore assemblage, the biomass response of phytoplankton to nutrient pulses is considerably dampened compared to when other herbivores dominate, because new primary production is rapidly converted into *Daphnia* biomass (Cottingham and Schindler 2000, Cottingham et al. 2004).

Vertebrate and invertebrate poikilotherm consumers dominate pelagic food webs, whereas many terrestrial herbivores are homeothermic (Shurin et al. 2006). In many terrestrial systems, poikilothermic phytophagous arthropods do not typically consume a large portion of terrestrial production, except during periods of outbreak dynamics (e.g., larval lepidopterans or locusts [Lovett et al. 2002, Coupe and Cahill 2003, Whiles and Charlton 2006]). Poikilotherms exhibit higher biomass production efficiency, thus herbivore and carnivore biomass production may be higher in aquatic ecosystems (Shurin et al. 2006). These differences lead to the prediction that the initial bottom-up numerical response of plants, herbivores, and carnivores to pulses of limiting resources should be larger and more rapid in aquatic systems, even when scaled to consumer generation times. In addition, these population responses in pelagic consumers should exhibit shorter lag times between population responses of adjacent trophic groups than in terrestrial systems.

While initial reproductive and numerical responses may be larger and more rapid in aquatic systems, we predict that the effects of resource pulses are likely to be

more persistent in terrestrial systems, while aquatic primary producer and consumer populations return to pre-pulse levels more rapidly, in terms of the absolute amount of time after a pulse event. In part, this is because of longer generation times in terrestrial organisms. For example, terrestrial seed-eating consumers usually have generation times that are longer than the duration of a synchronous seed production event, thus numerical population responses of seed-eating consumers may show substantial time lags and persistence (Ostfeld and Keesing 2000). In addition, when pulsed terrestrial resources are stored in persistent community components such as long-lived aboveground biomass, roots, or soil, effects can persist for years (Gratton and Denno 2003, Holmgren et al. 2006). In contrast, when resource pulses increase densities of planktonic aquatic primary producers, their biomass may return to pre-pulse levels within weeks to months (Cottingham and Schindler 2000, Cottingham et al. 2004, Nowlin et al. 2007). Certainly, some pelagic consumers can exhibit generation times more comparable to some terrestrial consumers (e.g., long-lived fishes and cetaceans), and their long-term reproductive responses to resource pulses may be difficult to predict.

The effects of resource pulses may persist longer in terrestrial systems because terrestrial resource pulses themselves may persist for longer than pulses from aquatic systems. Many terrestrial resource inputs are of low quality and may persist for extended time periods. For example, terrestrial phyto-detritus is less labile and more persistent than aquatic detritus (Cebrian and Lartigue 2004). Indeed, terrestrially-derived detritus transported to aquatic systems (e.g., leaf fall into streams and ponds) can sustain aquatic food webs for months to years (Wallace et al. 1997, Hall et al. 2000). Because of their persistence in the environment, these resource inputs probably do not represent a pulsed perturbation for many consumers. Conversely, some terrestrial systems receive pulses of labile aquatic-derived detritus, such as algal wrack on beaches or river sediments deposited in flood plains during extreme flood events. These pulses are of high quality when compared to terrestrial phyto-detritus and may have strong ephemeral effects on recipient terrestrial food webs (Polis et al. 1997).

Finally, the effects of resource pulses in terrestrial systems may be more persistent due to the generally weaker top-down consumer effects in terrestrial systems (Chase 2000, Shurin et al. 2002, 2006, Halpern et al. 2005). The size structure, edibility of primary producers, and short generation times of consumers in aquatic systems suggest that the top-down regulation of populations by consumers may occur faster and with greater intensity in aquatic systems, so that predators rapidly reduce consumer populations to pre-pulse levels. It has also been suggested that terrestrial food webs are more reticulate than their aquatic counterparts, which may dampen top-down effects (Strong 1992, Polis and

Strong 1996). Differences in the susceptibility of aquatic and terrestrial food webs to top-down control suggest that consumer increases in response to a resource pulse may be longer-lived in terrestrial systems. The complex and reticulate interaction networks characteristic of some terrestrial ecosystems may also make it difficult to assess the persistence of resource pulse effects in terrestrial systems. For example, terrestrial consumers that migrate to take advantage of resource pulses may soon leave the area producing the pulse, rendering it difficult to assess the long-term effects of pulses. In addition, some consumers can move across the aquatic-terrestrial boundary to harvest resource pulses, thus integrating pulses across multiple ecosystem types (e.g., Kitchell et al. 1999).

Differences in the role of consumer mobility in mediating the effects of resource pulses in terrestrial and aquatic food webs are unclear. In terrestrial ecosystems, consumers with low population growth rates are unlikely to exhibit reproductive responses to pulses but may migrate into areas with pulsed resources (i.e., behavioral aggregative responses) and exert rapid and strong food web effects (Ostfeld and Keesing 2000). In comparison, pulsed primary production in well-mixed pelagic systems is more likely to be dispersed within the habitat, rendering consumer mobility less important for the propagation of pulse effects. On the other hand, mobile aquatic consumers such as fish readily move between benthic and pelagic areas, and can switch between consumption of benthic and pelagic prey (Schindler and Scheuerell 2002). Thus, a resource pulse in one of these aquatic habitats could cause a change in the spatial distribution of some consumers, with considerable implications for energy flow and nutrient flux between benthic and pelagic habitats (Vanni 1996, Schindler and Scheuerell 2002). In addition, consumers subsidized by resource pulses in one habitat (benthic or pelagic) could exert increased top-down effects in another habitat, perhaps with a time lag. In lakes, many “zooplanktivorous” fish actually obtain much of their energy from benthic food items (Vander Zanden et al. 2005), and this benthic subsidy can increase the top-down effects of fish on pelagic organisms (Schindler and Scheuerell 2002). The particular effects of pulsed vs. constant subsidies on this predator “spillover” effect remain unknown.

Influence of spatial processes in community responses to resource pulses

The dynamics of terrestrial and aquatic systems are not independent, and the effects of resource pulses in one ecosystem are not decoupled from surrounding ecosystems. In addition to the direct transport of pulsed resources across aquatic-terrestrial boundaries (allochthonous pulses; Tables 1 and A1), the food web and ecosystem effects of resource pulses in one ecosystem may indirectly affect communities in adjacent ecosystems. For instance, the frass produced by severe

outbreaks of gypsy moth caterpillars (*Lymantria dispar* L.) can be quickly utilized by soil organisms (Lovett et al. 2002), and pupae are consumed by generalist rodents (Jones et al. 1998). Severe defoliation during gypsy moth outbreaks can lead to increased stream nitrate concentrations through decreased uptake by terrestrial plants and leaching into ground water (Lovett et al. 2002). Increased stream water nutrient concentrations and greater exposure to light via overstory defoliation could lead to greater primary and secondary production in forest streams, and "excess" N not retained within streams would be transported to downstream lakes or estuaries (Lovett et al. 2002). In short, terrestrial and aquatic systems are often spatially coupled; thus, the effects of resource pulses in one ecosystem may have considerable indirect implications for the dynamics of adjacent ecosystems. Because the general pattern in cross-system pulses indicates that resources tend to move from terrestrial to aquatic systems, the propagation of indirect effects from resource pulses may follow the same general pattern; however, little data are available to examine this prediction.

*Predictions of ecosystem-scale differences
in pulse retention and export*

At the ecosystem scale, nutrient pulses may be more likely to be retained within terrestrial systems than within aquatic systems. In large part, this is because soil and its biota have a great capacity to retain nutrients with minimal loss when in the absence of widespread disturbance (Vitousek and Reiners 1975, Grimm et al. 2003). At the opposite end of this continuum, stream ecosystems often receive nutrient pulses that far exceed the uptake capacity of the biota, and thus a large fraction of the nutrients may pass through the system without being taken up by resident organisms. For example, Mitchell and Lamberti (2005) found that approximately 60% of the N from a pulse of senesced anadromous salmon carcasses in streams was exported back downstream to estuarine habitats, while Drake et al. (2006) determined that riparian forests adjacent to salmon-bearing streams can retain $\geq 80\%$ of N from the deposition of salmon carcasses for up to one year after a spawning event.

Pulsed resources that are not retained in an ecosystem may become pulsed inputs to other ecosystems positioned downstream or downhill, and both aquatic and terrestrial ecosystems modify the magnitude and quality of pulses experienced by subsequent ecosystems. For example, large precipitation events quickly deliver pulses of water and nutrients to consumers in terrestrial ecosystems, which in turn moderate the intensity of the pulse entering streams through biotic uptake and abiotic immobilization in soils. Similarly, lakes have longer hydrological retention times than streams, thus water and nutrient pulses flowing into a lake from a stream are likely to be more pulsed than those flowing out of a lake into a stream. Mature unperturbed forests often receive

N pulses primarily as inorganic N from bulk precipitation and throughfall (Likens et al. 1985), but export a much greater fraction of N in the organic form, due to transformations within the ecosystem (Hedin et al. 1995). Similarly, lakes may receive a large fraction of N and P in dissolved forms from streams. Within a lake, dissolved nutrients are often quickly converted to particulate forms because residence times are longer in lakes than streams, allowing more time for organisms to convert dissolved nutrients into biomass. These particulate forms, which are less available to microbes and algae, are subsequently exported to outlet streams (Kling et al. 2000).

*Periodical cicada pulses in aquatic
and terrestrial ecosystems*

We suggest that bottom-up effects of resource pulses should transfer at faster rates through aquatic systems, while effects of resource pulses should be more persistent in terrestrial systems. Here, we examine these predictions using a case study of periodical cicadas (see Plate 1). Periodical cicadas represent a high-quality resource pulse (i.e., cicada bodies contain large amounts of nitrogen, protein and lipids [Brown and Chippendale 1973]) in both terrestrial and aquatic systems; thus, we can compare responses of terrestrial and aquatic systems to the same resource pulse.

Periodical cicadas are one of the most abundant herbivores in eastern North American forests, exhibiting peak densities of >350 individuals/m² (Dybas and Davis 1962, Williams et al. 1993, Rodenhouse et al. 1997, Whiles et al. 2001). After feeding on root xylem fluid as nymphs for 13 or 17 years, cicadas emerge synchronously from belowground to reproduce. Cicada broods may cover thousands of hectares, with local densities commonly ranging from 10^4 to 10^6 cicadas per ha (Dybas and Davis 1962, Williams et al. 1993, Yang 2004, Nowlin et al. 2007).

During the emergence, cicadas are consumed by both aquatic and terrestrial consumers (Steward et al. 1988, Williams and Simon 1995). In general, ecologists have explored periodical cicadas as prey pulses for consumers to a much greater extent in terrestrial systems. For example, Koenig and Liebhold (2005) found that the demography of 15 North American bird species is correlated with occurrences of periodical cicada emergence, with some population responses lasting up to three years after an emergence event. In addition, periodical cicadas can constitute a substantial portion of small mammal diets during the few weeks they are above ground (Hahus and Smith 1990, Krohne et al. 1991). Live periodical cicadas can also fall into aquatic systems and may be consumed by fish, turtles and other consumers (Williams and Simon 1995, Vokoun 2000), but effects on these consumers are largely unknown.

Most adult cicadas escape predation due to predator satiation (Williams et al. 1993), leaving the vast majority of cicada biomass to be deposited as detritus. This

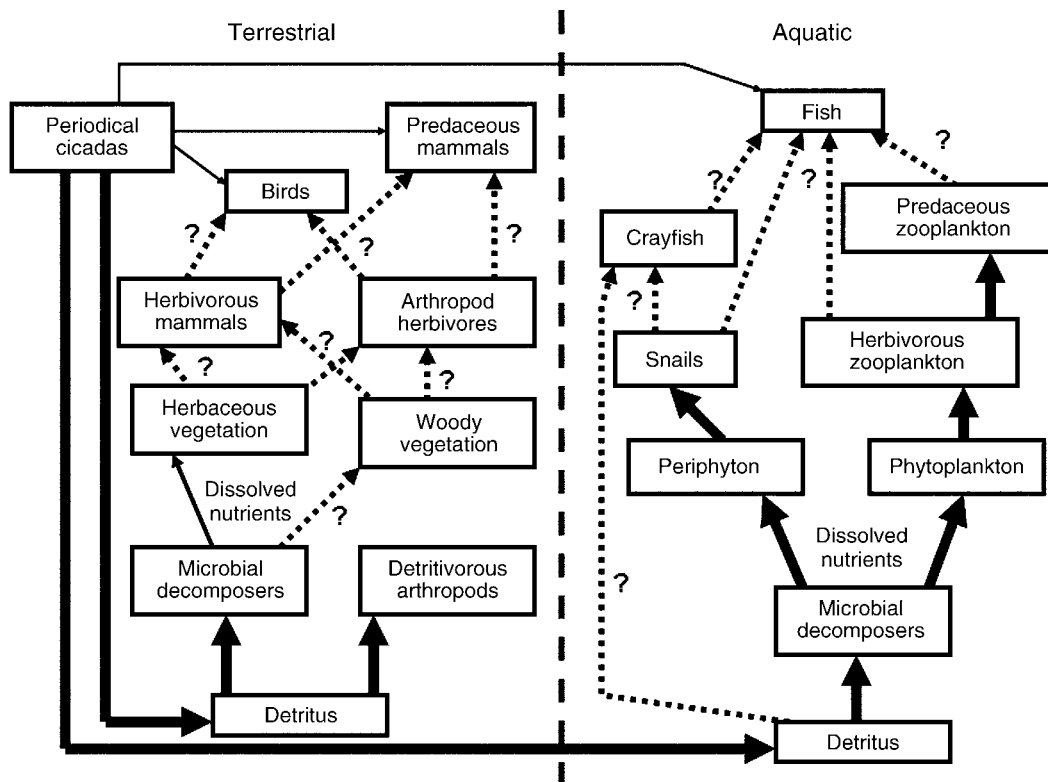


FIG. 2. Diagrammatic summary of the responses of terrestrial (forest-floor communities) and aquatic (woodland ponds) systems to deposition of periodical cicada detritus. Effects highlighted in the figure only indicate the responses of food web components during the year of cicada emergence. Pathways of nutrients and energy are illustrated with arrows. The thickness of the solid arrows indicates the relative rapidity and magnitude of nutrient and energy flows within the food web in the specific ecosystem type (i.e., the thicker the line, the faster or greater the effect). Dashed arrows accompanied by a question mark indicate that a likely interaction exists, but the numerical or biomass responses are unknown.

infrequent detritus pulse can represent a substantial input of nutrients and energy for forest ecosystems (Whiles et al. 2001, Yang 2004, Nowlin et al. 2007). In forests, senesced cicada biomass is deposited on the forest floor, as well as in headwater streams and small woodland ponds. Thus, the periodical cicada resource pulse (both live individuals and detritus) is autochthonous in terrestrial systems and allochthonous in aquatic systems (Fig. 2).

The food web effects of periodical cicada carcass deposition have been explored experimentally in both terrestrial (Wheeler et al. 1992, Yang 2004, 2006) and aquatic ecosystems (Nowlin et al. 2007). Food webs in both ecosystems exhibit pronounced bottom-up responses to this resource pulse; however, there are substantial differences in the timing and scale of the responses to the pulse. Deposition of periodical cicada detritus during an emergence event is spatially variable, but terrestrial (forest floor) and aquatic systems (small woodland ponds and low-order streams) commonly receive cicada detritus pulses of similar magnitude (Yang 2004, Nowlin et al. 2007).

The prediction that the bottom-up effects of resource pulses should propagate more quickly in aquatic systems

is generally supported in this comparison. Both systems showed rapid responses to cicada detrital pulses, though population increases and the attenuation of these effects were markedly faster in the aquatic system. Pelagic bacterial biomass in pond systems exhibited a strong positive response to deposition of cicada detritus, and showed significantly elevated densities in only three to four days; PO_4^{3-} and NH_4^+ concentrations increased and reached maximum levels within this same time span, but quickly returned to pre-deposition levels within approximately 30 days (Nowlin et al. 2007). Primary producer biomass in woodland ponds (pelagic phytoplankton and benthic periphyton) responded within a few days of the deposition of cicada material, and herbivorous and carnivorous zooplankton biomasses were substantially larger within two weeks of the deposition of cicada carcasses (Nowlin et al. 2007; Fig. 2). Approximately two months after the deposition of cicada detritus, herbivorous snail populations were also significantly greater in ponds receiving cicada pulses. In contrast, terrestrial forest communities generally exhibited less rapid food web responses (Fig. 2). Cicada detritus deposition did not increase bacterial and fungal biomasses in forest soils within 7 days, but significant



PLATE 1. Images of periodical cicadas in eastern North American forests. The larger photo shows periodical cicadas basking in the morning sun after their emergence at the University of Virginia Blandy Experimental Farm, Virginia, USA. The smaller inset photo shows *Formica* sp. ants consuming a dead periodical cicada carcass in Green Ridge State Forest, Maryland, USA. Photo credits: L. H. Yang.

increases were observed after 28 days (Yang 2004). Soil NH_4^+ and NO_3^- concentrations increased substantially during the first 30 days after cicada deposition, and NO_3^- concentrations remained elevated during days 31–100. The behavioral aggregation responses of some detritivorous arthropods were relatively quick, occurring within seven days after cicada deposition, although the indirect effects of mobile consumers may diffuse over a larger spatial scale (Yang 2006). American bellflower (*Campanulastrum americanum*) plants receiving pulses of cicada detritus exhibited higher foliar N content and greater seed size and mass at the end of the growing season 75 days later (Yang 2004; Fig. 2).

These contrasting responses to periodical cicada pulses offer limited support for the prediction that terrestrial systems show greater potential for persistent resource pulse effects. The persistence of direct and indirect soil nutrient effects in forest systems remains unknown, though the production of larger bellflower seeds among plants receiving cicada pulses may influence germination success and densities in subsequent growing seasons. In contrast, responses of dissolved nutrients, algae, and herbivorous and carnivorous zooplankton in woodland pond systems to pulses of cicada detritus dissipated after approximately two

months (Fig. 2). Benthic algae and pelagic phytoplankton biomasses returned to pre-pulse levels as the biomass of herbivorous zooplankton and snails increased, supporting the prediction that aquatic systems return to pre-pulse levels quickly because the top-down suppression of primary producers is generally stronger in aquatic systems. Also as predicted, the response of heterotrophic decomposers (bacteria) to this high-quality detritus pulse was rapid and occurred at similar time scales (within days) in both systems, while the biomass response of primary producers to nutrients remineralized by microbes was faster in the pond food web. The persistence of numerical responses among longer-lived aquatic organisms such as macrophytes, crayfish, amphibians, and fish remains uncertain.

CONCLUSIONS

The causes and consequences of resource pulses show both similarities and differences between aquatic and terrestrial systems. Resource pulses appear to be widespread phenomena in both ecosystems, and many well-studied examples of these events share similar climatic drivers and multi-annual timescales. Resource pulses in aquatic and terrestrial systems differ in the material nature of pulsed inputs and the allochthonous

vs. autochthonous origins of these resource pulses. Fundamental differences in the structure and dynamics of aquatic and terrestrial systems suggest that the bottom-up effects of resource pulses should transfer through aquatic systems at faster rates, but these effects may be more persistent in terrestrial systems. Studies examining the effects of periodical cicada detritus deposition in terrestrial and aquatic systems indicate that resource pulses transmit at faster rates through aquatic systems, but there is insufficient evidence to examine if the effects of pulses persist for longer periods in terrestrial systems. Soil microbial communities and behaviorally aggregating arthropod detritivores showed the most rapid responses in terrestrial forest systems, while rapid community responses and resilience were observed more broadly among pulsed resource consumers in woodland ponds.

While the community and ecosystem-level effects of resource pulses have been explored in some terrestrial (Polis et al. 1997, Ostfeld and Keesing 2000, Meserve et al. 2003, Stapp and Polis 2003) and aquatic systems (Naiman et al. 2002, Nowlin et al. 2007), there is clearly a need to determine the longer-term implications of resource pulses in many ecosystems. In addition, future research on resource pulses should focus on examining the responses of upper-level consumers and the top-down and indirect effects of resource pulses in food webs, over spatial scales that account for the complex and long-term effects of pulses.

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APPENDIX A

Description of studies examining the food-web-level and ecosystem-level effects of resource pulses (*Ecological Archives* E089-037-A1).

APPENDIX B

List of citations of studies examining the food-web-level and ecosystem-level effects of resource pulses (as presented in Appendix A: Table A1) (*Ecological Archives* E089-037-A2).