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Nature's Pulsing Paradigm

WILLIAM E. ODUM[1]
Department of Environmental Science
University of Virginia
Charlottesville, Virginia 22903

EUGENE P. ODUM[2]
Institute of Ecology
University of Georgia
Athens, Georgia 30601

HOWARD T. ODUM
Environmental Engineering Sciences
University of Florida
Gainesville, Florida 32601

ABSTRACT: While the steady state is often seen as the final result of development in nature, a more realistic concept may be that nature pulses regularly to make a pulsing steady state—a new paradigm gaining acceptance in ecology and many other fields. In this paper we compare tidal salt marshes, tidal freshwater marshes, and seasonally flooded freshwater wetlands as examples of pulsed ecosystems. Despite marked differences in species composition, biodiversity, and community structure, these wetland types are functionally similar because of the common denominator of water flow pulses. Often a period of high production alternates with a period of rapid consumption in these fluctuating water-level systems, a biotic pulsing to which many life histories, such as that of the wood stork, are adapted. Pulsing of medium frequency and amplitude often provides an energy subsidy for the community thus enhancing its productivity. The energy of large-scale pulses such as storms are usually dissipated in natural ecosystems with little harm to the biotic network; however, when seawalls, dikes, or stabilized sand dunes are constructed to confront these strong pulses, the whole ecosystem (and associated human structures) may be severly damaged when the barriers fail because too much of the storm energy is concentrated on them. The relationship between biologically mediated internal pulsing, such as plant-herbivore or predator-prey cycles, and physical external pulsing is discussed not only in wetlands but in other ecosystem types as well. An intriguing hypothesis is that ecosystem performance and species survival are enhanced when external and internal pulses are coupled. We suggest that if pulsing is general, then what is sustainable in ecosystems, is a repeating oscillation that is often poised on the edge of chaos.

Introduction

The concepts by which we view nature are sometimes called paradigms. One of our comfortable concepts of nature visualizes growth followed by a leveling. In these days when society is beginning to recognize the limits of the biosphere, people, scientists, and governments talk of sustainability, that is, managing growth so that the life-support carrying capacity of the earth is not exceeded. The steady state is seen as a goal for such efforts as well as the final result of self-organization in nature. However, there may be a more realistic concept, that nature pulses even after carrying capacity or satuaration limits are reached (Fig. 1)—a new paradigm we define and present examples of in this paper.

First, we review pulsing in wetlands ecosystems as a background for a discussion and modelling of a general theory of the pulsing paradigm; special attention is given to the interaction of external and internal pulses.

It is generally accepted that the key to wetland function and structure is the pulsing water-flow regime, or the hydroperiod. Organisms not only adapt to the pulse but may also utilize the water-flow energy to enhance productivity as shown in Figs. 2 and 3. Tidal wetlands, especially the contrasting saline and freshwater marshes, provide excellent sites for the study of the interaction of physical and biotic components. Riverine swamp and floodplain forests display other aspects of the pulsing paradigm.

Comparison of Tidal Freshwater and Saltwater Wetlands

Ocean-driven lunar tides are not only a dominant physical factor in coastal estuaries but extend

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[1] Naturalists-ecologists are saddened by the untimely death of William E. Odum in April 1991.

[2] Corresponding author.

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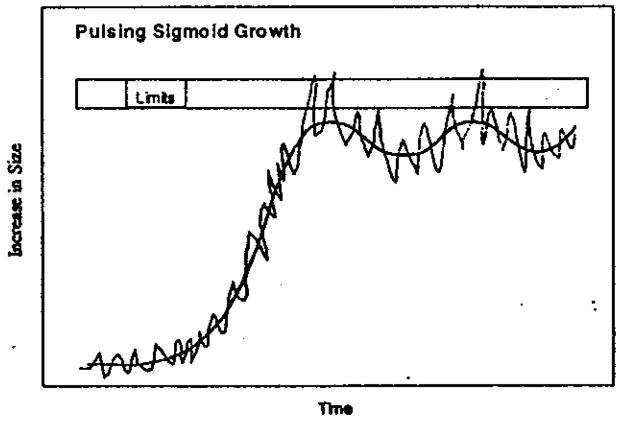


Fig. 1. The sigmoid growth model with pulses superimposed. Pulses are not trends, but very often are part of long-term trends.

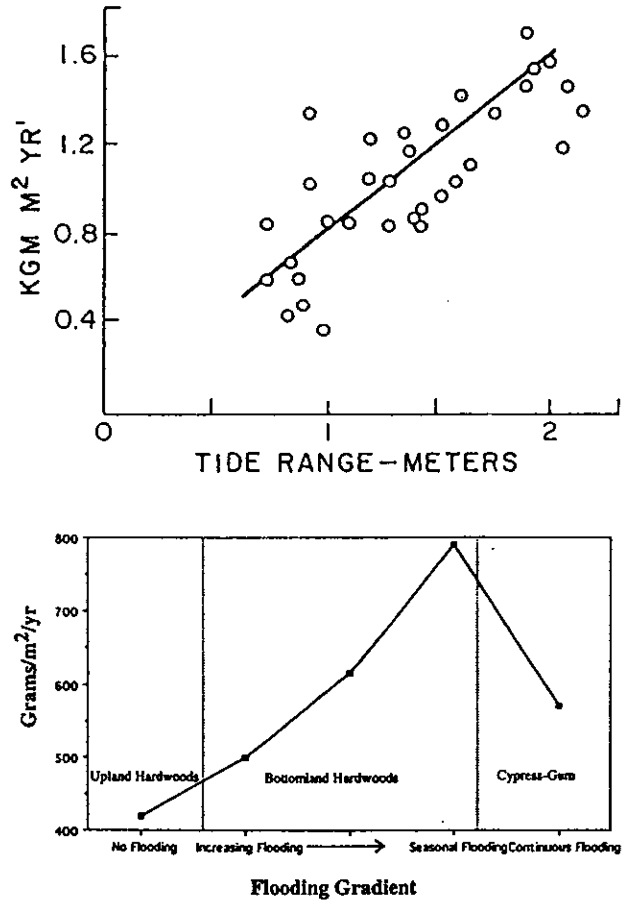


Fig. 2. Relationship between hydroperiod and productivity. The upper graph illustrates tidal amplitude as it varies with biomass production in *Spartina* salt marshes (from Steever et al. 1976). The lower graph illustrates the productivity of bottomland forests along a flooding gradient (from Birch and Cooley 1983).

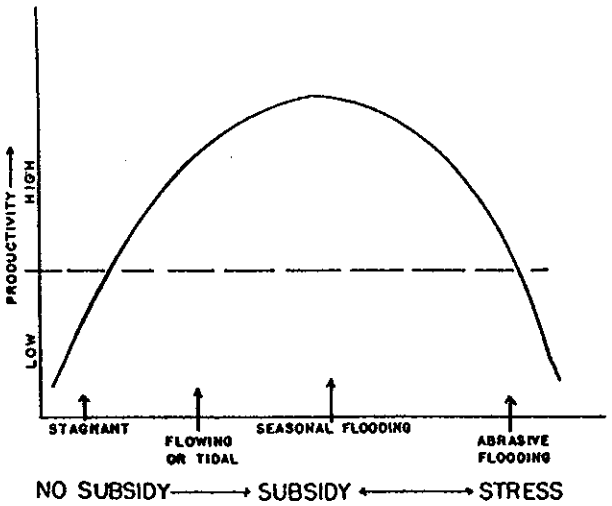


Fig. 3. Graphic model of the relationship between productivity and a flooding gradient in wetlands, shown as a subsidy-stress model.

many kilometers upstream in coastal plain rivers, creating tidal freshwater wetlands. It is not unusual to have a greater tidal range upstream than in the estuary. For example, at the mouth of the Potomac River the tidal range is approximately 70 cm while 100 km upstream in tidal freshwater marshes near Washington the tidal ranges exceed 1 m. This can be attributed largely to the constricting of the tidal water mass as it moves upstream in a continually narrowing river channel.

The presence or absence of salt in a tidal marsh makes a difference in the vegetative structure and the food web as well as in species composition, but perhaps not in overall productivity, which tends to be high in both ecosystem types. Salt reduces the net primary productivity of vascular plants since they must invest more energy to exclude salt and sulfides, but at the community level this reduction may be compensated for by the contribution to productivity by marine algae, greater areation of sediments due to burrowing of fiddler crabs, and the presence of more C_4 plants.

Salt-marsh plants, largely perennial graminoids and halophytic shrubs, are fibrous and remain standing throughout the year. In contrast, freshwater tidal herbaceous marsh plants are more fleshy and many decompose down to mud level in the winter (W. E. Odum and Hoover 1987). Colonization and dispersal of macrophytes in saline marshes is largely by vegetative growth of rhizomes; in freshwater marshes by seeds. The anaerobic microbial component is dominated by sulfate reducers in the salt marsh and methane producers in the freshwater marsh. Sediments in tidal freshwater marshes on average are higher in organic content and are less sandy than those in the estuaries. Food chains in the salt marsh tend to end up in aquatic organisms-shrimp, crabs and fish in salt marshes, while semi-aquatic vertebrates—for example, furbearers, amphibians, reptiles, ducks and avian waders, are more often at the end of food chains in the freshwater wetlands.

Species diversity of vascular plants (including emergent annual and perennial aquatic macrophytes, shrubs, and trees) is very much greater upstream, but diversity of fish and invertebrates can be very high in both tidal salt and freshwater ecosystems. Seasonal changes in species in salt marshes are mostly confined to the sediments where green mud-algae dominate in the summer and diatoms dominate in the winter. In contrast, there may be a pronouced seasonal succession of vascular plants in tidal freshwater marshes with perennials such as *Peltrandra* and *Acorus* dominating early and annuals such as *Zizannia, Polygonum,* and *Nidens* peaking later in the growing season. These and other contrasts between tidal salt and freshwater marshes are detailed in W. E. Odum's papers and monographs (W. E. Odum et al. 1984; W. E. Odum and Hoover 1987; W. E. Odum et al. 1987; W. E. Odum 1988).

Despite the many differences in the physical nature of the environment and in species composition, the two marsh-types are more similar than different in overall function because of the forcing function of tidal pulsing. High productivity resulting, in part at least, from the energy subsidy of the tides (E. P. Odum 1980), is a common denominator of both marsh types. Another common denominator is that a large part of the food web is detritus-based in these marshes and also in mangroves (W. E. Odum et al. 1972; W. E. Odum and Heald 1975; W. E. Odum and Heywood 1978; E. P. Odum 1980; W. E. Odum 1984).

The auxiliary energy of water flow may not only alter the rate of primary and/or secondary productivity but may also alter the course of ecological succession. Where the input is regular in occurrence, as in tidal systems, the ecosystem may be "pulse-stabilized" at a youthful stage characterized by high net community production, some of which may nourish an adjacent less productive system. The outwelling of organic matter and organisms from a productive estuary to adjacent coastal waters is an example of such a "source-sink" process (E. P. Odum 1980). Whether an estuary exports or imports may depend on geomorphology, especially whether the connection between estuary and the sea is narrow or broad (W. E. Odum et al. 1979).

Nontidal Wetlands

In nontidal wetlands such as inland marshes, floodplain, and swamp forests, the pulse is seasonal or periodic rather than daily. Water levels rise and fall one or more times a year. Of course, tidal wetlands are also subjected to seasonal flooding and storms. The amplitude of flooding in inland wetlands is often much greater and lasts longer, but they are less frequent than the tidal pulses. The interaction between pulse height and periodicity is complex, but neverless many species of plants and animals are especially adapted to the longer term periodicity and uncertainty. Cypress, for example, tolerate extensive or irregular flooding but must have a prolonged drawdown exposing the surface of sediments before seeds will germinate. Consequently, many stands are even-aged.

The wood stork (*Mycteria americana*) is an example of a species especially adapted to nontidal wetlands having a shallow, fluctuating water-level. As first worked out by Kahl (1964), this species breeds when small fishes are being concentrated in small pools as water levels are falling. Unlike many waders, this species is a "tactile-feeder" that waits for fish to actually touch the half-opened beak before grasping them. In the past the wood stork bred abundantly in south Florida during the winter dry season when water levels in the Everglades and elsewhere were lowest. But, this natural seasonal pulse has been so disrupted by human water diversions and impoundments that the stork has now moved north to breed in small undisturbed wetlands where the seasonal draw down in spring is more reliable.

Graphic Models of Productivity of Pulsed Wetlands

In general, increasing pulse amplitude increases net productivity in most types of wetlands up to an optimum point beyond which too much flooding reduces productivity. In coastal salt marshes, for example, productivity increases up to an average tidal range of 2 m or 3 m (Fig. 2, upper). This is why productivity of salt marshes in the Georgia-South Carolina Bight, where tidal amplitude is high, is greater than to the north or south where the amplitude is less. Tidal amplitude on the Gulf Coast is small, but frequent storms result in considerable water-level fluctuation to which the biota are adapted. Regular tides above 3 m or so may cause such severe erosion that productivity is reduced (Bay of Fundy, for example). In this case, the energy may go into geologic rather than biologic work. A similar pattern is seen in floodplain and swamp forests (Table 1 and Fig. 2, lower). Productivity is highest where flooding is moderate, especially where high water occurs in the dormant season. Too much flooding is a stress that reduces productivity and diversity, but interesting and valuable species may thrive in this environment. Cypress and tupelo

TABLE 1. Productivity estimates tidal and nontidal wetlands. All figures: g dry matter m^{-2} yr^{-1} in round numbers.

Tidal marshes	
Spartina alterniflora salt marshes, Sapelo. (Gallagher et al. 1981; Pomeroy and Wiegert 1982)	
Streamside marsh–strong daily tides	3,700
Middle marsh—less strongly inundated daily	2,400
High marsh—spring tide flooding only	1,200
Spartina cynosuroides brackish tidal marsh (E.P. Odum and Fanning 1973)	
Low elevation—daily tides	2,100
Higher elevation—periodic flooding	900
Zizaniopsis miliacea freshwater tidal marsh (E.P. Odum, Birch and Cooley 1983)	
Tidal	1,530
Impounded (diked)	1,172
Swamp and floodplain forests (nontidal)	
Florida cypress (Mitch and Ewell 1979; Brown 1981)	
Seasonal flooding (winter)	3,000
Flowing water	2,000
Stagnant (ponded)	1,000
Cypress-Gum-Louisiana (Conner et al. 1981)	
Seasonal flooding	1,200
Flowing water	700
Stagnant	200
Bottomland hardwood and Cypress-Gum-GA (Birch and Cooley 1983)	
Seasonal flooding	800
Occasional flooding	600
Continuous flooding (stagnant)	550
Upland—no flooding	450

gum, for example, may develop adventitous "water roots" (as well as "knees" and swollen buttresses) at the water-sediment interface that overcome the stress of an anaerobic root environment resulting from continuous flooding.

Figure 3 is a general graph of the relation between productivity and the pulsing gradient in wetlands, shown as a subsidy-stress model (E. P. Odum et al. 1979).

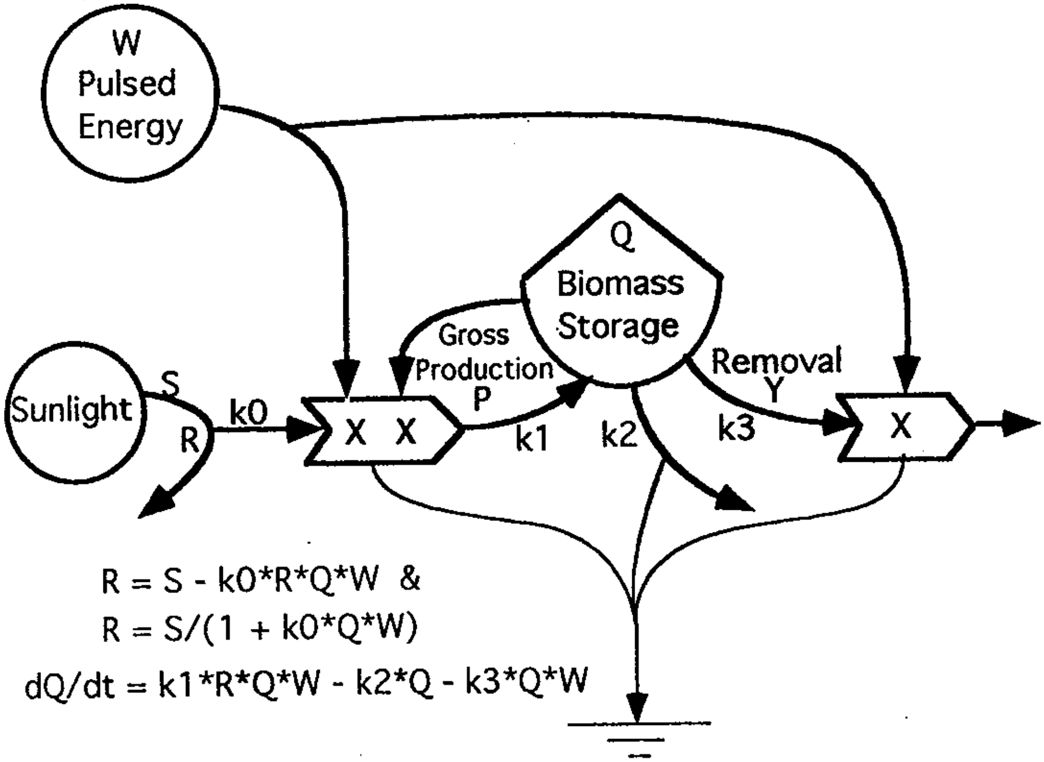
Biologically Mediated Internal Pulses

Since wetlands are true ecotones in that they have properties and species not found in the adjacent land and open water, it is important to note that internal structures and processes, such as tropic interactions, root masses, microbial and animal activity, play a role along with external forces in maintaining wetlands as pulsing ecotones (W. E. Odum 1990).

By no means are all pulsings directly related to the external physical environment. All ecosystems exhibit internal pulses, mostly biologically mediated, such as plant-herbivore, predator-prey, and parasite-host oscillations. For example, extensive study and experimentation has so far failed to link any environmental physical factor with the "boom and bust" cycles of tent caterpillars and budworms in northern forests. The latest findings are that special viruses are involved in the alternation of weak and strong generations. In a recent review, Meyers (1993) states that, "these insects seem to have been adapted by years of evolution to insure that outbreaks do not devastate the host trees." In fact, as a general rule, parasite-host and herbivore-plant interactions co-evolved for co-existence in a pulsing state so that despite the oscillating evolutionary "arms race" the parasite or herbivore does not eliminate its food supply and thereby itself (Alexander 1981; Anderson and May 1982). Such coevolution may involve what we can term reward feedback, where the parasite or herbivore does something to promote the welfare of the host (or to put it in more general terms, where a downstream component in a food web benefits an upstream component). For example, it has been shown that the saliva of grasshoppers and mammalian grazers contains growth hormones that stimulates the regrowth of the grass on which they feed (Dyer et al. 1986).

Interactions Between External and Internal Pulses

Suzane Painting describes, in a recent doctoral dissertation, an interesting case of "diet-switching" as a pulsing that results from the linking of different food chains with an external upwelling pulse. As reported by Pomeroy (1992), upwellings off the west coasts of North and South America and Africa are rich in nitrates that support a dense phytoplankton-zooplankton bloom. The phytoplankton quickly deplete the nitrogen and subside before the zooplankton have had time to complete their



$$R = S - k0*R*Q*W \ \&$$
$$R = S/(1 + k0*Q*W)$$
$$dQ/dt = k1*R*Q*W - k2*Q - k3*Q*W$$

Push-pull Model of Physical Energy Pulses

Fig. 4. Minimodel of the pulses of physical energy and the production and loss of biomass.

reproductive cycle. The zooplankton then switch to feeding on protozoa that thrive on the smaller phytoplankton and bacteria subsisting on the dissolved organic matter that has accumulated from the blooms. The oscillation of different food chains as a response to external pulses in this manner is probably of common occurence.

What is little understood is how internal pulses, such as plant-herbivore cycles, are related to external pulses, such as tides. An intriguing hypothesis, to be discussed later in this paper, is that synchronism of internal and external pulses enhances ecosystem performance as a whole.

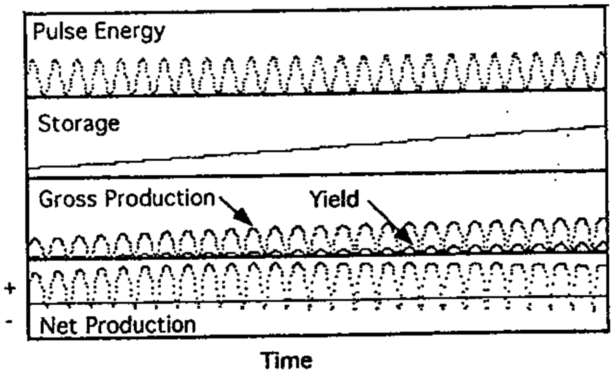


Fig. 5. Simulation of the model in Fig. 4 for an intermediate level of physical energy pulses.

Simulation Models

Minimodels are useful to isolate effects that are part of more complex systems, much as one does with controlled experiments. A push-pull model of physical energy effects on biomass production is shown in Fig. 4. The work that comes from pulses of physical energy such as water-level flucuations are shown amplifying production on the left and removing biomass on the right. Physical energies improve the necessary circulation of inputs and waste products. Very strong physical energies may remove more biomass than is produced and also divert energies in other ways.

A typical simulation with optimum levels of pulsed physical energy increases gross production and causes net production greater than the concurrent removal (Fig. 5). The average of several runs at different levels of physical energy are plotted in Fig. 6. At higher levels of energy, net production and biomass are diminished, even though

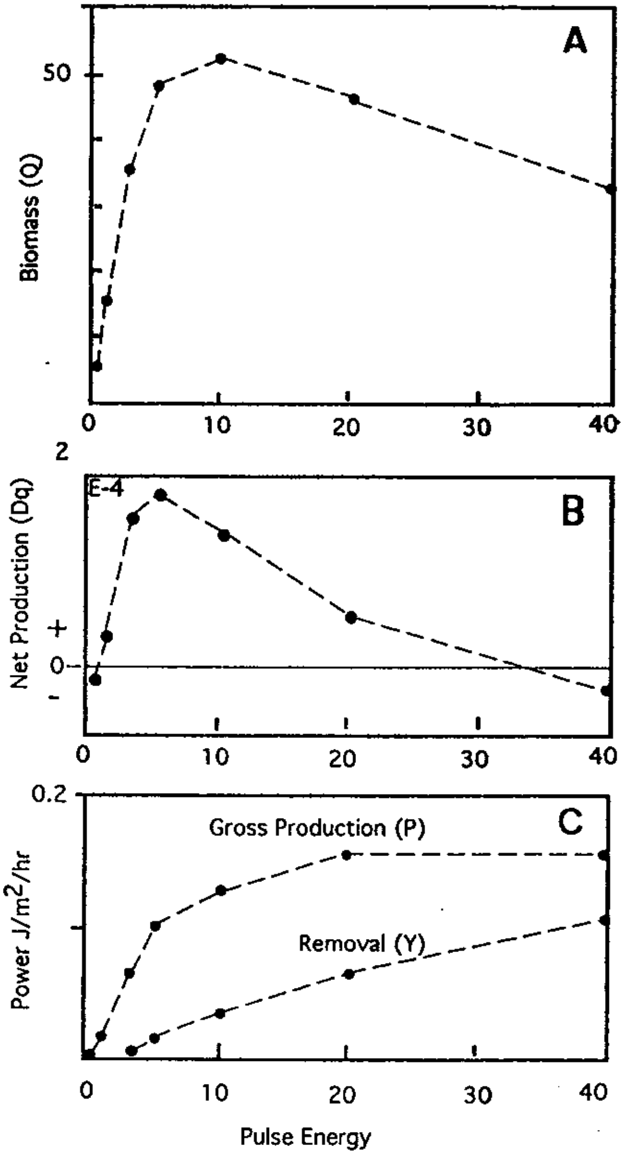


Fig. 6. Results of simulation of the model in Fig. 4 for different levels of energy pulses: (A) stored biomass as a function of pulsed energy; (B) net production as a function of pulsed energy; and (C) energy flow in gross production and removal processes as a function of pulsed energy.

the throughput of production and biomass does not diminish. Many kinds of stress produce this kind of effect, increasing turnover time and causing small, high turnover organisms to replace the larger ones that maximize productivity at lower stress levels.

Whereas the model does help account for the optima observed in many production data (Figs. 2 and 3), it is not sensitive enough to varying frequency nor to pulse alteration of production and consumption.

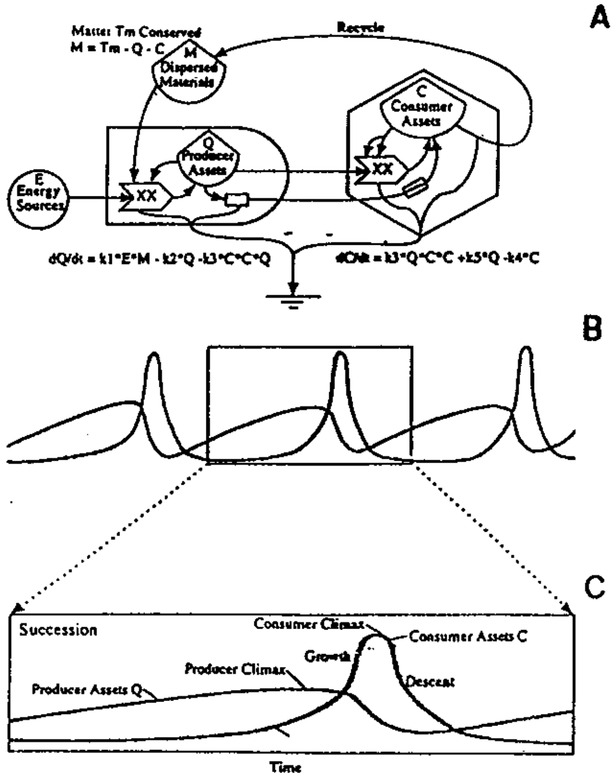


Fig. 7. Pulsing alteration of production, consumption and recycling in the internal oscillating Alexander model (H. T. Odum 1983): (A) systems diagram and equations; (B) typical oscillations; and (C) modified use of the classical names "succession" and "climax" suggested for regions of sustainable pulsing.

General Pulsing Theory

In all the scales of nature from tiny fast systems of biochemistry to the largest galaxies of the cosmos, we observe systems that pulse. Host-parasite and predator-prey cycles are examples. As Fig. 7 suggests, growth of one part of nature consumes and pulls down another part of nature temporarily. Then a cycle is completed with retrogression and regrowth (Fig. 7). Since pulses occur at all scales, the larger scales impose their bursts on the smaller scales. Each part of nature is composed of pulsing components and is occasionally impacted by a pulse from the larger scale. An ecosystem is driven by pulses of its energy inputs and also by oscillations from within its own network, as in the upwelling-diet switching case described earlier in this paper.

Pulsing in one place may be out of phase with that in another so that growth and retrogression, as well as source-sink exchanges of materials and organisms, makes a patchy landscape with each area in a different stage of pulsing. The diversity that comes from patches is thus a part of the pulsing of patches; it may increase the gross performance of the landscape as averaged over a longer scale.

The pulsing of nonliving systems of geology, meteorology, and oceanography is part of the pulsing of the ecosystems. One of the main ways that the earth participates in ecosystems and vice versa is through the pulsing of rains, tides, floods, etc. Wetlands are a good example of the way ecosystems organize to fit the pulses of resources and through their own cycles of growth impose pulses on the environment. The kind of wetland depends on the frequency of impacting oscillations.

The works of nature are governed by energy laws. Energy is part of all processes and is transformed from one form to another in food chains. According to one theory, which was first offered a century ago, systems develop relationships that mutually reinforce the efficient processing of energy. For example, energy of sun and water flows are transformed into the productivity of marsh vegetation. The rate of flow of energy is power. As Lotka (1924, 1925) stated, systems that maximize useful power in production tend to prevail. However, there is a tradeoff between efficiency and power (H. T. Odum and Pinkerton 1955). A system that is arranged to be very efficient may go too slowly, delivering less productivity. A system that is arranged to go faster at lower efficiency may be too wasteful of energy. The question for us here is how are power and efficiency related in pulsing systems that alternate periods of net production and times of net consumption.

It may be that systems in level steady state do not have the optimum efficiency for maximum power, whereas the pulsing systems do more production in the long run. All this is still theory, but there has to be some basic reasons why all systems have the periodic pulsing of their processes related to the level of their energy sources.

Pulsing, Energy, and Chaos

May (1974) showed that the spurts of change in iterative digital simulation could cause the logistic equation model for growth to go into a form of chaos. If the increments of adding stock were large relative to the stock stored, the stock would jump to a high value. This high value would cause the next iteration to decrease massively so the stock jumped to a lower level. The result was a jumping up and down of the stock with time.

In our modeling, we have always been careful to identify an energy source with any mathematical model, thus making the system realistic to energy contraints. The "r" (intrinsic rate of natural increase) is really the specific growth rate based on an unlimited energy source (i.e., a source that provides a constant input concentration regardless of demand). We write "r = k*E" so that the growth term is k*E*Q where Q is the stock, thus recognizing that the intrinsic rate is really proportional to the extrinsic energy source concentration E (H. T. Odum 1983, p. 144). If this energy source is increased, then the amount of flow involved for the same periods of growth and outflow is greater, the chaos becomes greater, involving more and more levels of jumping until the plot of points with time appears without pattern (hence the name chaos). Graphs of energy-driven logistic chaos are shown in Beyers and Odum (1993, p. 124). Since the iteration in this logistic example is in the digital computing and not in the real world, we call this "artificial chaos."

However, the principle that we draw from this illustration is that whenever an oscillation (pulsing) is causing a system to fill and discharge, the more chaos is caused and the larger and more complex are the oscillations.

As part of a review of Keith's book on the 10-yr cycle of wildlife in Canada (H. T. Odum 1964) it was suggested that the observed fact of shifting period of the wildlife oscillations might be accounted for by shifts in the rates without abandoning the general idea that predator-prey oscillations were the main cause. Later we simulated one predator-prey cycle with low frequency being driven by a smaller period of high frequency. The simulation result (Beyers and Odum 1993, p. 124–125) produces oscillations with shifting periods. On a phase plane plot (graph of one species as a function of another), the similation traces loops that change with each oscillation, but within an outer limiting loop, which in chaos terminology is the attractor. Hanski et al. (1993) has also related the predator-driven 4-yr arctic rodent cycles to chaos theory.

Since nearly all ecosystems are apparently hierchical and pulsing, at least some of the time, the pulses of the smaller, faster species being coupled to the larger slow-turnover species, produce chaotic oscillations. Therefore, we conclude that a corollary of the "pulsing paradigm" is that oscillations can be expected to become chaotic when energy levels are increased.

Let us now turn the reasoning around. Chaotic models such as those we have just discussed can be stabilized without oscillations by relatively minor adjustments in coefficients. Why then do systems self-organize with chaotic oscillations instead of developing properties and species that do not oscillate? It may be that chaotic dynamic mechanisms provide a better loading of ecosystem work to input energy, one that optimizes efficiency and maximizes power in the long run.

Kauffman (1993) using examples and simulations of molecular, organismal and population biology sought general systems principles about the evolution of life and its environmental basis. He proposes that life in ecosystems is adapted to, and more stable in the long run with, pulsing systems. On page 280 he writes: "Co-evolving systems whose members have tuned the structure of their fitness landscapes and couplings to other members such that the entire ecosystem is poised at the edge of chaos appear to sustain the highest fitness. Thus we may adopt the hypothesis that selection attains systems which are poised both internally and collectivity."

Frequency Modulation, Niches, and Resonance

Sometimes we compare wetlands to a frequency modulated radio. For different frequencies of pulsing and hydroperiod, different species may be best adapted to draw useful work. Different frequencies of input energy are different niches for species opportunity.

Campbell (1984) studied with a long series of computer simulations the transfer of energy from pulsing inputs to systems with internal oscillations, such as predator-prey cycles. Maximum contribution to the system's production was obtained when the frequency of inputs were similar to the frequency of internal oscillation. Reinforcement of production comes from coupling of external and internal pulses is sometimes called resonance. Systems with adapted harmonics are reinforced by resonance. Thus, during self-organization an ecosystem develops the components that maximize energy available from the pulsing. Campbell (1984) found a model calibrated for salt-marsh data had good properties of energy capture from energy-pulsed inputs.

Zwick (1985) studied the coupling of pulsed inputs to systems with inertial impedance (ones generated as a part of the process of storing input energy surges). By using general systems models, behavior long known for electrical and mechanical systems was extended to biological and social systems where pulses are actively resisted while energy of the pulse is transformed and stored.

Pulsing Enhancement of Ecosystem Performance

When ecosystems receive pulsing on a small scale of space and time (high frequency pulsing), the pulses are generally absorbed, their energy used adding small-scale variation and microdiversity. For example, microbial oscillations do not interfere with larger detritus consumers.

When an ecosystem receives pulsing on the same scale of space and time as its own oscillations (medium frequency pulsing), it can benefit if it has species that can resist the pulses enough to catch and use the pulsing energy. As we have noted earlier in this paper tidal pulses are used by many species to aid their feeding, behavior, life histories, and migration, thereby enhancing productivity of the whole system.

When ecosystems receive periodic pulsing of a much larger scale (low frequency pulsing) the energies may pass through without much absorption if the components don't resist the perturbations. For example, W. E. Odum et al. (1987b) found that natural coastal grassy dunes were able to survive infrequent storms by maintaining a loose structure that allows the wave energies to be dissipated over the whole dune system; in other words, sands erode and redeposit without destroying the biotic network. On the outer banks of North Carolina, shifting dunes periodically blocked traffic on a highway that was built through the dune system. Hoping to reduce this tendency, introduced grasses were planted on the fore dunes to form a more rigid and resistent turf that did indeed stabilize the dunes under condition of ordinary winds and waves. But, when the big storm came, the effect of the resistence was to catch too much of the energy so that the whole system was destroyed and the damage to the highway and other human structures was much more severe than before. The same situation is evident where seawalls on beaches and dikes on rivers are constructed; small storms and floods are contained but big ones break through the resisting structures, often doing more damage than would occur in the absence of such barriers (Kaufman and Pilkey 1983; W. E. Odum et al. 1987). In general, it pays to design with nature's pulses rather than to confront them!

Summary

The prevalence of pulsing in all scales of the earth and beyond and the widespread energy transfer through coupling of oscillators seems to be the general rule. Very steady steady-states are the exception, although they can be induced in microcosms by cutting off the outside pulses (Beyers and H. T. Odum 1993). The interaction of external and internal pulses often enhances, but sometime seems to detract from, the overall performance of the ecosystem. An attractive hypothesis is that by pulsing and appropriate coupling of external and internal pulsing, a higher performance is obtained, which generates more work, thus reinforcing the system's characteristics. If pulsing is general, then what is sustainable in ecosystems is a repeating oscillation.

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