

SELF-ORGANIZED CRITICALITY IN MARINE CONSERVATION ECOLOGY

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In the past decade, the concept of self-organized criticality (SOC) has generated considerable interest, in fields ranging from physics to finance. The implications of self-organization and critical states have the potential to revolutionize our models of many natural systems and reshape our intuition. This paper reviews the fairly limited treatment that SOC has been given in marine ecology within the deeper literatures on complex systems and fractals in marine environments. It also identifies some under-explored potential that SOC has for informing research on conservation in marine ecosystems.

Self-organized criticality is a kind of emergent behavior found in a wide range of complex, spacial, and historical systems.¹ These systems exhibit a kind of critical state between chaos and order, in which small changes can escalate to any size. Bak (1990) argues that

the large temporal fluctuations, and the spatial self-similarity are two sides of the same coin: “self-organized criticality”. The idea is that the systems operate persistently way out of equilibrium at or near a threshold of instability. The systems evolve automatically to this critical state without any fine-tuning of external fields; hence the criticality is self-organized.

Although the underlying mechanisms and structures that cause SOC are still unclear, most SOC systems exhibit a collection of interrelated characteristics. First, like most natural systems, these systems rely on structures in space or networks of connections, so their dynamics cannot be fully described with analytical expressions. Furthermore, the full state of the system is able to “build up” in time, historically and heterogeneously (Barabási and

¹Emergence in an ecosystem describes the process by which “properties of the ecosystem at large spatial scales result from feedback interactions between components occurring at smaller scales” (van de Koppel et al., 2005).

Albert, 1999). As it builds, driven by some force, the system approaches a kind of critical limit, beyond which it becomes locally and globally unstable. Instability leads to local collapses, which can avalanche by further destabilizing nearby regions. The distribution of the sizes of avalanches follow a power law, which suggests that there is no “normal” size of avalanches. As a result of this ongoing build-and-collapse dynamic, the SOC system maintains an emergent critical state. If the system is spacial, the critical state is characterized by fractal-shaped patches of order and disorder (Bak, 1990). If the system is on a network, the network shows the small world property and “hierarchical modularity”, in which a few nodes play a large role (Watts and Strogatz, 1998, Ravasz et al., 2002). In either case, the system exhibits heterogenous, scale-independent features both in time and space.

The classic sand pile example, developed by Bak (1990), remains among the most intuitive, and a brief overview is informative.² In this computational model, grains of sand fall on a plane, forming a pile. Sometimes, a grain of sand falls on an unstable area of the pile’s slope, causing an avalanche. A graph of the number of avalanches versus their size, measured in sand grains, conforms to a power law: for every doubling of avalanche size, the number of avalanches decreases by a consistent factor (see figure 1, a). This is a self-similar relationship, suggesting that the avalanches have no natural size or predictability. The continuous build-up of instability and avalanching process naturally organizes the pile into a critical state, where the next sand grain could produce an avalanche of any size. Furthermore, graphs of the stable and unstable regions of the pile have fractal properties, implying that there is no natural size to these spacial structures (see figure 1, b).

Models of self-organized criticality have been proposed for earthquakes, forest fires, market fluctuations, human conflicts, and many other systems (see table 1). If SOC is common, it has important implications for the role of history and local events, and the nature and predictability of catastrophic changes. As a tool for researchers, its main advantages include its departure from conventional (analytic or system dynamic) models, and the general applicability of its results.

²For other accessible examples, see Bak (1996) and Buchanan (2001).

Table 1: Some classic, ecological, and marine SOC studies, and the characteristics that they have identified. Traditionally, SOC systems are identified by a spacial and historical medium, a driving force which causes the system to self-organize, a critical variable at which it is balanced between order and chaos, and a kind of collapse which can build into an avalanche. As a result of this dynamic, a variety of scale-independent and self-similar properties emerge; some authors begin by identifying these properties and follow up with models of the process; others start with models. Table cells are left blank where authors do not discuss those elements. Turcotte and Rundle (2002) lists many others.

System	Medium	Driving Frc.	Critical Var.	Collapse	Scale-Independence	Reference
				Classic Examples		
sand piles	plane	sand drops	pile slope	avalanche	avalanche size	Bak (1990)
earthquakes	plane	tectonics	rock tension	earthquake	earthquake magnitude	Olami et al. (1992)
war	globe			conflict	casualties	Buchanan (2001)
academic papers	network				references	Buchanan (2001)
markets	line	competition		failures	fluctuation size	Stauffer and Sornette (1999)
				Ecological Studies		
forest fires	plane	tree growth	density	forest fire	area burned	Malamud et al. (1998)
species abundance					individuals per km ²	Peters (1986)
ecosystem variation	space	competition			variations by size	Jorgensen et al. (1998)
metabolic pathways	network	evolution			hierarchical mod.	Ravasz et al. (2002)
evolution	ecosystem	evolution		extinctions		Leroi (2000)
river braiding	plane	hydrology			spacial patterns	Sapozhnikov and Fofoula-Georgiou (1999)
				Marine Ecosystems		
marine fossil record	ecosystem	evolution		extinctions		see below
brittlestar beds	time	predation			predator-prey dynamic	Aronson (1992)
microphytobenthos	space	competition			patch shapes	Seuront and Spilmont (2002)
colonial organisms	networks		branch ratio		branch pattern	Sánchez et al. (2004)
salt marshes	plane	wave action		erosion		van de Koppel et al. (2005)
bioluminescence	space	turbulence		flashing		Noever and Cronise (1994)
seagrasses	plane					van der Heide et al. (2010)

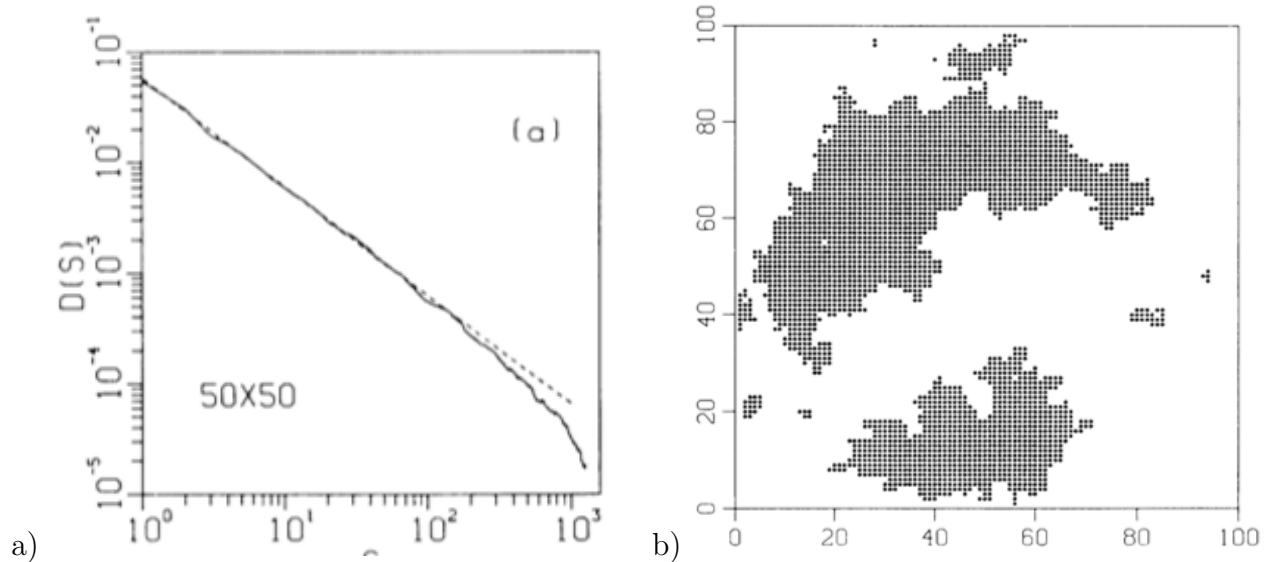


FIGURE 1. Example power law relationship and fractal clusters, from Bak et al. (1987). The power law in (a) applies to the sizes of cluster, such as the (b), which denote the shifts produced by sand grains.

Ecosystems are perfect candidates for SOC, because of their spacial complexity and nonlinearity, and their intense evolutionary forces and competitive limits. Jorgensen et al. (1998) suggests that “ecosystems strive towards moving as much as possible from thermodynamic equilibrium,” placing them in the out-of-equilibrium domain of self-organized criticality. Studies have identified SOC features in insect populations (Lockwood and Lockwood, 1997), pelican populations (Milne et al., 1997), forest canopies (Kizaki and Katori, 1999), river systems (Sapozhnikov and Foufoula-Georgiou, 1999), and many others.

Despite this work, there appear to be plenty of opportunities to integrate the insights from self-organized criticality more deeply into ecological studies. Theoretical work has focused on simplified ecosystem SOC modeling, while empirical studies seem satisfied to identify power laws. In particular, the implications of scale-independence in ecosystems; the community-wide relationships suggested by SOC; and the use of SOC metrics to gauge ecosystem health warrant additional research.

1. EXTINCTION IN THE MARINE FOSSIL RECORD

Self-organized criticality has long been suggested as an underlying factor of extinction in the fossil record. Evolution exhibits the “punctuated equilibria” characteristic of self-organized systems (Gould and Eldredge, 1977). Punctuated equilibrium also shows some scale-independent properties, applying both to ecological (microevolution) and geological (macroevolutionary) timescales (Carson, 1975).

Bak and Sneppen (1993) proposed a simple self-organizing model of coevolution, in which incremental evolutionary mutations organize the biosphere into a critical state of trophic relationships, which then “collapse” into a cascade of extinctions and macroevolutionary changes. In particular, the size of extinction events is predicted to follow a power law relationship, which suggests that species evolve into such a tightly knit complex that one extinction can start a chain of extinctions that can grow to any size.

This work set off a long empirical debate. Solé et al. (1997) found a strong power law in family extinction records. However, other authors have suggested that this is an artifact of the statistical methods used (Kirchner and Weil, 1998, Alroy, 2008). Further analysis showed that two distinct power law relationships may better explain the fossil record (Newman and Eble, 1999). Eble (1999) found no support for SOC in the timing of species origination for marine species, but did find evidence for SOC among land species.

Plotnick and Sepkoski Jr (2001) have attempted to move beyond this debate by applying some elements of SOC while discarding the rest. They propose a generalization of SOC properties called multifractal self-similarity:³

We also believe that the underlying assumptions of SOC are incompatible with our understanding of the processes controlling macroevolutionary patterns.

Statistical analyses of the data sets are compatible, however, with the presence

³Multifractals are distributions of a variable that show some spatiotemporal self-similarity. They have also been proposed for spacial patterns of species abundance (Harte et al., 1999)

of multifractal self-similarity in both records, consistent with a hierarchical and multiplicative generating process.

It appears that some kind of deeper structure underlies extinction— that it is not a simple matter of exogenous catastrophic events— but the nature of this structure remains unclear.

2. SCALE INDEPENDENCE

Scale, applied to ecology, refers to both the spatiotemporal extent and resolution used in an analysis (Wiens, 1989). Unlike some contexts and models studied for self-organized criticality, marine environments have strong scale dependence. Aronson (1992) emphasizes that “variables such as abundance and diversity often behave unpredictably at one level of resolution but produce predictable patterns at another”. For example, fish species distribution in the Great Barrier Reef is fairly random at the scale of a single patch or atoll reef, but show predictable patterns at the scale of reef systems. Phytoplankton distribution shows a complicated set of patterns, dominated by local turbulence at the scale of kilometers, ecosystem effects on a wider scale, and oceanic flows on a still wider scale (Wiens, 1989).

Although some authors have argued for scale dependence in opposition to the simplicity of SOC, ecological scales are neither surprising nor in opposition to the existence of scale independent properties. Organisms work in very scale-dependent ways, because they have a natural scale, and have evolved to exploit dynamics at particular scales. On a fine enough scale, they can be considered a substrate for other organisms; at another scale, all but the autotrophs act as predators; and on a yet wider scale, most organisms are prey. This cycle repeats itself in a self-similar way at all scales. Azam et al. (1983) argues that the marine food web spans seven orders of magnitude, from cyanobacteria and other bacteria (the smallest of which are $.2 \mu\text{m}$) feeding nanoplanktonic flagellates, which feed microzooplankton (such as ciliates), which feed a hierarchy of zooplankton topped by the ocean’s macrofauna. (The much larger phytoplankton compete with bacteria and support the conventional zooplankton trophic pyramid directly).

The biosphere as a whole can be scale independent precisely because of this succession of scale-dependences. At any scale, species have filled all appropriate niches, often configuring themselves vis a vis other species into common arrangements (such as the predator/prey dynamic, symbiotic relationships, and competition). The self-organized criticality of these relationships is evident in temporal studies of species (even though scale dependence dominates spatial studies). The population dynamics of brittlestar beds show self-similar predator-prey dynamics on the scale of days, decades, and eons (Aronson, 1992). Temporal self-similarities have also been identified in the effects of predators on gastropods and marine algae (refs in Aronson, 1992).

Spacial self-similarity is also present in a wide range of marine ecosystems. Studying the branching patterns in gorgonian corals, Sánchez et al. (2004) finds the fingerprints of a self-organized, self-similar critical state, which helps maintain the colony shape. Similar fractal properties are present in spacial patterns of the diverse and competitive ecosystems in intertidal sediment (Seuront and Spilmont, 2002). Fractals have been identified in a wide range of elements in the marine world: in the structures of coral reefs, marine snow, mussel beds, intertidal benthic communities, invertebrate and vertebrate behavior, species diversity, zooplankton, and phytoplankton (Seuront, 2009).

Simultaneously, the scale-independent process of evolution seems to abhor simplicity: every level of the biosphere is (fractally) filled with niches for other species. This is evident in the “patchiness” of marine ecosystems: the distribution of species in the marine biosphere is spatially heterogenous at all scales (Downing, 1991). This patchiness is both a result of the critical self-organization of marine ecosystems, and beneficial to those ecosystems by providing living environments for species on all trophic levels.

3. RELATIONSHIPS IN MARINE ECOLOGY

Most researchers studying the intersection of ecology and SOC appear to focus on identifying SOC features and extrapolating the implications of self-organizing forces. In particular, the

power law is taken to be the arbiter of self-organization: where it is absent, SOC is shown to not apply, and where it acts, its characterization is often taken to be the complete story. One contribution self-organized criticality models have that is missing from the ecological literature is the new relationships that it formally defines.

Ecologists model ecosystems largely as collections of species and nutrients, and the relationships between them. Direct relationships between species generally fall into the classes of symbiosis, competition, and predation. Where nutrients are involved, species are commonly identified as producers, decomposers, or consumers. Most of these roles and relationships are trophic; less frequently, relationships describe how species support or undermine other life functions.

These relationships reflect the simplistic view of ecosystem interaction that remains prevalent in marine ecology, which can be called the “organism bias”. In essence, this view is that a species plays the roles of its individual organisms (see figure 2). This is exemplified in the trophic map (see figure 3). The organism bias is a reflection of the implicit organism scaling problem above: the most natural scale for studying a species is the scale of its individual organisms. However, this need not be the only scale on which a species acts, as shown by the global effects of local changes in critical systems.

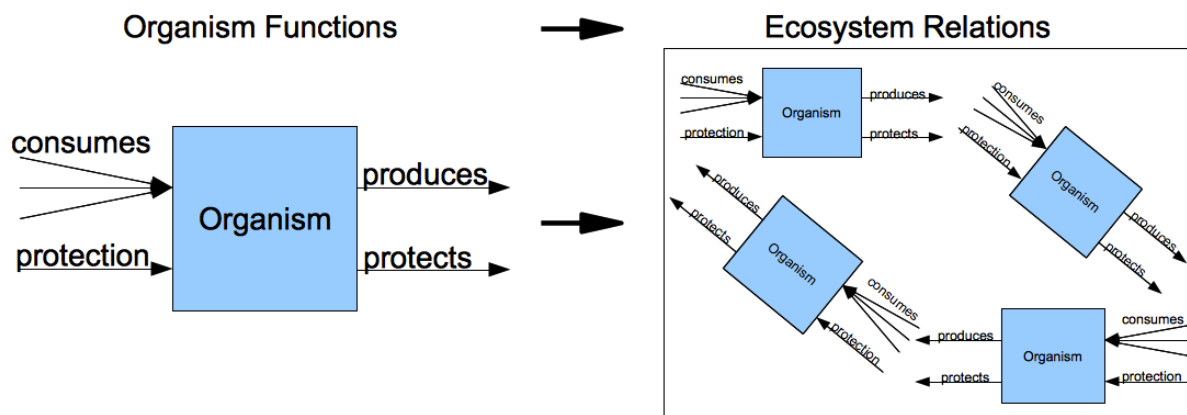
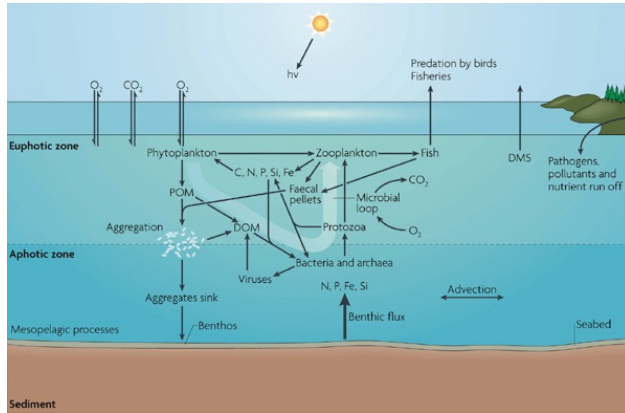
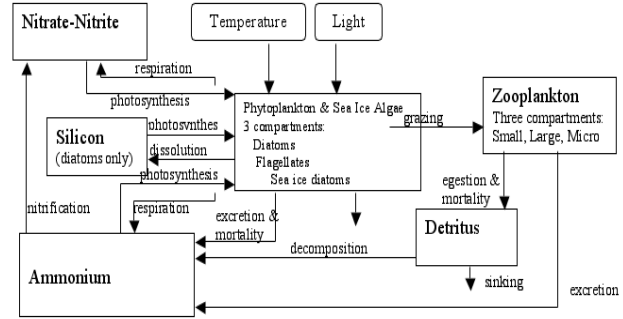


FIGURE 2. Diagram of the organism bias. Organisms have a collection of functions, which can thought of as instantaneous relationships between two organisms when they interact. The organism bias prescribes enduring relationships between two species based on the individual relationships found between their representative organisms.



http://www.nature.com/nrmicro/journal/v5/n10/fig_tab/nrmicro1747_F1.html



Interactions among variables in the 1-Dimensional marine ecosystem model

http://www.inis.iarc.uaf.edu/highlights/2005/coupled_marine_ecosystem/index.php

FIGURE 3. Examples of ecosystem diagrams, showing the fundamental organism bias. These diagrams are representative of marine ecosystem models, but all of the relationships they describe are exactly the actions of individual organisms.

SOC provides a suite of new relationships, based on species-wide and community-wide effects. These include:

Self-Organization Support: when one species provides material or behavioral support for another’s self-organization. For example, coralline algae supports coral recruitment (Harrington et al., 2004), which is necessary for coral to self-organize into fractal forms.

Critical Value Support: when the actions of one species affect the magnitude of the critical value about which another species is organizing. Salt-marsh vegetation organizes into a critical state which improves plant growth, but if the relevant critical value is too low, vegetation collapse leads to pervasive erosion (van de Koppel et al., 2005).

Collapse Facilitation: when one species plays a role in the collapse dynamic of another species. The effect of predation by fish and crabs on brittlestar beds supports its natural population collapse dynamic, which help its ecosystem maintain its critical population states (Aronson, 1992).

Critical Competition: when the competition between species produces critical state spatiotemporal patterns. One result of competition between diatoms of several species is the creation of self-organized, fractal patch patterns in intertidal soils (Seuront and Spilmont, 2002).

In general, these are not relationships between individual organisms, and cannot be observed at the individual level; they appear only between species, with respect to their environments. With the exception of colonial animals, it is not the organisms themselves that are self-organizing into a critical state, but their collective community.

A focus on the relationships present in SOC also emphasizes that power laws can apply locally. Just as there are limits on all SOC systems (for example, sand pile avalanches cannot exceed the size of the sand pile), scale-invariant properties can be confined to a collection of scales without losing their validity.

4. CONTRIBUTIONS TO CONSERVATION

Self-organized criticality has important implications for conservation and resilience. Complexity is omnipresent in ecosystems, making them unpredictable through nonlinearity, feedback, and chaos (Scheffer et al., 2001). Our capacity to predict the effects of human interference on marine ecosystems underlies much of the work of marine conservation ecology. Conservation is also greatly concerned with resilience, because it both is a natural consequence of health and biodiversity, and counteracts the conditions that result in catastrophic shifts. However, SOC simultaneously undermines predictive capacity and supports resilience. If SOC is prevalent in marine ecosystems, it may suggest the need to reconsider complex uncertainty as a friend to conservation.

Healthy ecosystems are characterized by a high level of self-organization, suggesting that SOC metrics might be useful in measuring the overall health of an ecosystem. van der Heide et al. (2010) argue that the self-organized, spacial patterns of intertidal seagrasses are reliable indicators of the multiple stressors acting on them. Kolasa (2006) investigates the use of

SOC power spectrum exponents as measures of self-organization and ecological integration. Higher exponents correspond to both ecosystem stability and species richness. Metrics of self-organization are significant because they reflect both ecosystem-wide dynamics, and signatures of local processes (Solé et al., 1999).

Further buttressing this association, decreases in ecosystem complexity often correspond to decreases in health. The overgrowth of macroalgae, a species that undermines the ability of coral reefs to self-organize, is a robust indicator of overall reef health (Bahartan et al., 2010). Lohrer et al. (2004) find that a decrease in the complexity of marine fractal structures through thin sediment deposits causes a decrease in ecosystem biomass and diversity. The dangerous effects of invasive species can also be understood in this light: these species have not evolved to fill critical state niches, so their propagation decreases ecosystem complexity (Bax et al., 2003).

Beyond reflecting ecosystem health, changes in the frequency relationships that characterize SOC systems can directly interfere with their functioning. Lohrer et al. (2004) notes,

Most likely, species evolve to cope with minor disturbances that occur relatively often, particularly when those disturbances occur at frequencies greater than the generation time of the species, as this would be adaptive. However, with increasing disturbance intensity, the response of the community may shift from negligible to catastrophic, with an intermediate domain consisting of sub-lethal effects and/or mortalities of selected individuals and taxa.

Self-organization is also an important factor in marine reserve design. Reserve design is greatly impacted by scaling effects of organisms (Wiens, 1989), which SOC informs. In addition, sites for marine reserves are currently selected under the assumption that physical features determine the distribution of species. However, new models suggest that large-scale and metapopulation patterns are self-organized, challenging that assumption and the reserve boundaries based on it (Guichard et al., 2004).

Based on these results, self-organized criticality has three major implications for marine conservation ecology. The research on SOC systems provides a framework for recognizing more complex relationships and coming up with ecosystem models that apply to many scales. Critical states point to the need for a new way of understanding and managing sustainability and catastrophic events, by working with and through complex uncertainty. Finally, self-organization is in no small way the very process of ecological restoration, and can be used as a metric for gauging the health of ecosystems.

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