

**Directing the Fall of Darwin’s “Grain in the Balance”:
Manipulation of Hydraulic Flushing as a Potential Control
of Phytoplankton Dynamics**

by

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Abstract

Foodweb interactions, such as competition for limiting resources, are inherently non-linear. Consequently, they can give rise to chaotic, or undeterminable, population dynamics. Population dynamics are not always undeterminable, however, sometimes they are quite predictable. What conditions cause one behavior to prevail over the other? Here we focus on aquatic environments, specifically plankton ecosystems, and show numerically and experimentally that when the magnitude and periodicity of hydraulic flushing and nutrient loading are large chaotic behavior, as described by chaos theory, is replaced by determinable dynamics. In other words, the system only responded to manipulation in a predictable manor when the disturbance to the system was large. It may be that management efforts aimed at maintaining ecosystem health in aquatic systems, e.g., enhancing biodiversity, controlling eutrophication, preventing harmful algal blooms, etc., may require large-scale, controlled manipulations of flushing periodicity and magnitude.

Introduction

Chaos, as described by chaos theory, has been observed in many systems, including mechanical oscillators, electric circuits, lasers, chemical reactions, nerve cells, and heated fluids (Hilborn, 1994). These chaotic systems are completely deterministic, i.e., all external and internal forces acting on the system are understood, yet their behavior remains erratic and undeterminable. The behavior of ecosystems can also be undeterminable. Unlike the simple systems mention above, ecosystems are not deterministic, i.e., there are many external and internal forces acting on the system that are not understood. The relative contribution of chaos, which arises from non-linear interaction between foodweb constituents, and system-level noise, which arises from unknown complexity, to ecosystem stochasticity is not yet understood.

In theory, chaotic behavior stemming from non-linear dynamics occurs in biological systems ranging from the complex to the very simple (Rogers, 1981; Scheffer, 1991; Smale, 1976), and may be a prominent factor influencing biodiversity (Armstrong and McGehee, 1980; Huisman and Weissing, 2000; Koch, 1974). Much of

the non-linearity in ecosystems arises from interspecific competition for limiting resources (Arneodo, et al., 1982; May and Leonard, 1975; Smale, 1976). It is this non-linearity that contributes to chaotic behavior, which undermines our ability to forecast the outcome of competition and the succession of populations. This realization is not novel. Darwin (1859) captured the essence of this argument in his “grain in the balance” metaphor, where small variations in environmental condition “determine which individual shall live and which shall die”.

The idea of diminished predictability due to chaotic behavior is particularly troublesome in aquatic environments where the occurrence of harmful algal blooms appears to be increasing, and the need to protect human health and natural resources through proactive management is great (Anderson and Garrison, 1997; Paerl, 1988b; Roelke and Buyukates, 2001; 2002; VanDolah, et al., 2001). This concern is warranted because there is a growing body of evidence from numerical modeling studies (Ebenhoh, 1988; Huisman and Weissing, 2000; 2001a; Roelke, 2003; Scheffer, 1991), laboratory experiments (Buyukates and Roelke, 2002; Kersting, 1985; Roelke, et al., 2003), and field observations (Cottingham, 1996; Roelke, 2002; Scheffer, 1998; Sugihara and May, 1990) which support the notion that chaotic behavior occurs in phytoplankton succession. If dynamics are chaotic, then our ability to forecast blooms of nuisance species, and our ability to manipulate target systems to circumvent blooms, might be limited. In other words, the “balanced grain” could tumble in any number of directions in response to management efforts.

Yet at some level aquatic systems do behave determinably. For example, succession from rapidly growing, highly edible colonizing species to more specialized slower growing, less edible species often occurs following favorable disturbances (Reynolds, 1993; Roelke, et al., 1997; Sommer, et al., 1986). Similarly, community composition often shifts following changes in resource ratios towards dominance of species adapted for optimal performance under the new conditions (Kilham, et al., 1996; Paerl, 1988a; Scheffer, et al., 1997; Sommer, et al., 1993a). The predictability of some species’ behavior has even prompted the formation of functional classification schemes in which probability of group dominance is linked to environmental conditions (Reynolds, et al., 2002). Determinable behavior of this nature often arises from environmental change, where the magnitude and period of disturbance are important factors (Padisak, 1993; Reynolds, 1993; Reynolds, et al., 1993; Sommer, et al., 1993b). Returning to Darwin’s metaphor of the “grain in the balance”, it may be that the direction in which the grain tumbles is determinable, given that the grain is supplied a strong enough “push”.

In Roelke et al. (2003), we tested the hypothesis that disturbance results in more determinable behavior of plankton systems using a well-known numerical model that depicted five phytoplankton species competing for three growth-limiting resources (Grover, 1997; Leon and Tumpson, 1975; Tilman, 1982). Here we reiterate and expand upon those findings. For our application the only loss factor simulated was hydraulic flushing. We parameterized and initialized the model in a way that was known to produce chaotic behavior under continuous inflow conditions (Huisman and Weissing, 2001b). In addition, we confirmed some of our model

results with laboratory experiments using natural plankton assemblages that addressed the role of pulsed inflows on phytoplankton succession patterns.

Methods

Mathematical model and numerical procedure

The demographics of each of the five competing phytoplankton populations were simulated using equations of the form:

$$\frac{dN}{dt} = \mu N - \lambda N \quad (1)$$

where N was the population concentration, μ was the specific growth rate of the population, and λ was the total flushing rate.

The specific growth rates for each of the five phytoplankton populations were determined using the Monod equation and Liebig's "Law of the Minimum", and the equations had the form:

$$\mu = \mu_{\max} \left(\min \left[\frac{S_1}{S_1 + k_{S1}}, \frac{S_2}{S_2 + k_{S2}}, \frac{S_3}{S_3 + k_{S3}} \right] \right) \quad (2)$$

where μ_{\max} was the maximum specific growth rate for the population, S_1 , S_2 , and S_3 were the three growth-limiting substrates, and k_{S1} , k_{S2} , and k_{S3} were the half-saturation coefficients for substrate-limited population growth.

Total flushing was determined using the equation:

$$\lambda = \lambda_c + \lambda_p \quad (3)$$

where λ_c and λ_p were the flushing rates resulting from continuous and pulsed flows, respectively.

The concentrations of the three growth-limiting substrates were simulated using equations of the form:

$$\frac{dS}{dt} = \lambda(S_{in} - S) - \sum_{i=1}^5 Q_i \lambda_i N_i \quad (4)$$

where S_{in} was the fixed concentration of the source substrate, Q_i was the fixed cellular content of the substrate for each of the five phytoplankton populations, and other parameters were the same as previously described.

The mathematical equations were solved numerically using ordinary differential equation solving routines that were a part of a commercial software package (The Math Works, Inc.). The routines were based on fourth-order Runge-Kutta procedures, and used a variable time step that was based on a local error tolerance set at 10^{-15} . Each system-state boundary diagram depicted in this manuscript has a resolution of 80×80 , i.e., 6,400 simulations were required to construct each. The total number of simulations performed was 44,800. Simulations were performed using six Macintosh G4 computers.

Model initialization and parameter values

As in a previous study (Huisman and Weissing, 2001b), initial conditions for three of the competing species were the same for all simulations, i.e., $N_{1,3,5} = 0.1$ (biomass liter⁻¹). In addition, initial substrate concentrations were the same for all simulations, $S_{1,2,3} = 10$ (μM). Initial concentrations for species 2 and 4 varied between simulations as described in the figure captions.

Similar to previous work (Huisman and Weissing, 2001b), parameter constants included total flushing, maximum specific growth rate, half-saturation coefficient, substrate concentration of the source, and cellular substrate content. These values were: $\square = 0.25$ d⁻¹; $\mu_{\text{max}} = 1$ d⁻¹ for all five phytoplankton populations; and $S_{\text{in}} = 10$ μM for all three growth-limiting substrates. Values for k_s (μM) and Q ($\mu\text{mole-S biomass}^{-1}$) were:

$$k_s = \begin{bmatrix} 0.20 & 0.05 & 1.00 & 0.05 & 1.20; \\ 0.25 & 0.10 & 0.05 & 1.00 & 0.40; \\ 0.15 & 0.95 & 0.35 & 0.10 & 0.05 \end{bmatrix}$$

$$Q = \begin{bmatrix} 0.20 & 0.10 & 0.10 & 0.10 & 0.10; \\ 0.10 & 0.20 & 0.10 & 0.10 & 0.20; \\ 0.10 & 0.10 & 0.20 & 0.20 & 0.10 \end{bmatrix}$$

where values across columns represent the five competing phytoplankton species, and values down rows represent the three growth-limiting substrates.

Although the total flushing was held constant for all simulations (and consequently substrate loading), the proportion of continuous flow and the proportion of pulsed flow varied. Pulsed flows were delivered using a sine function over a period of one day. The magnitude of the pulse was a function of the pulsing period. For example, the magnitude of flow and substrate loading were three-fold greater on the day that a pulse occurred during the 3-day 100% pulsing simulations

compared to the 100% continuous flow simulations. But no flow occurred on the other two days, which resulted in equal flushing between simulations.

Laboratory flow-through experiments

Surface waters for the laboratory experiments were collected from the Rincon Delta, Texas, placed into 20-liter Nalgene carboys, and kept shaded and cool during the ~4 h transport to the laboratory located in College Station, Texas. Upon arrival, a portion of the water was filtered through 47 mm Whatman GF/F glass fiber filters, then autoclaved at 121°C and 15 PSI for 30 minutes. After the sterilized water cooled f/2 media was prepared by dissolving solid standards into the water. This process took ~2 h. Water to be used in the flow-through chambers was pre-filtered through a 200 μm mesh-size plankton net to avoid bias from large zooplankton (Sommer, 1985). Experiments began approximately 6 h after water was collected from the delta.

The flow-through chambers used in this experiment consisted of a vertical glass tube within a tube. A water temperature controller re-circulated water through the outer tube, a peristaltic pump delivered media to the inner tube, and an air pump supplied intermittent bubbling to the inner tube. Chambers were housed within closed light-cabinets (Figure 1).

Flow rate and nutrient loading were selected according to previous studies, and were meant to represent hydraulic conditions

in a tidal creek of the Rincon Delta (Roelke, 2000; Roelke, et al., 1997). They were controlled using peristaltic pumps. The volumes of the six flow-through chambers were 365 ml. Inflows were adjusted so that the hydraulic residence times were 0.11 d^{-1} in the three chambers receiving continuous inflow, and 0.33 d^{-1} in the three chambers receiving pulsed inflows, but only on one day out of three, the other two days there were no inflows. In this way, the magnitude of flushing and nutrient loading over the course of the experiment was the same for the continuous and pulsed-flow treatments. Only the mode of flushing and nutrient loading differed.

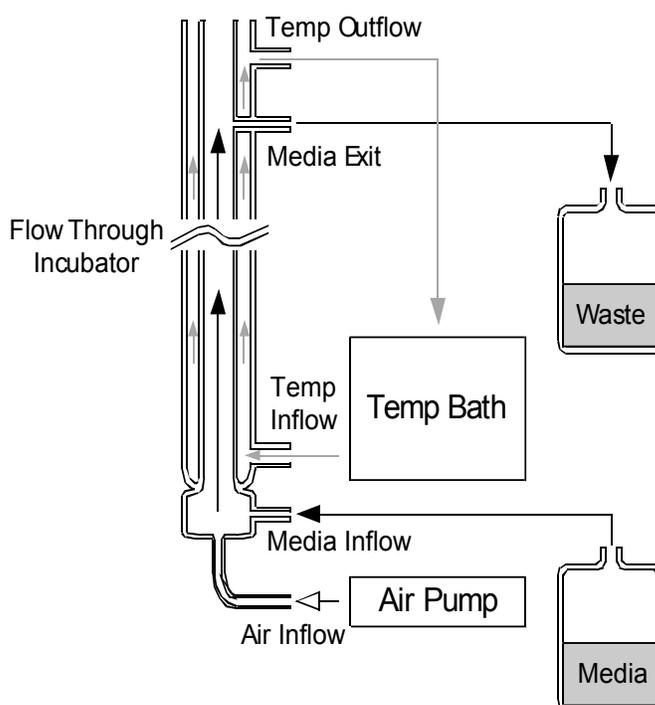


Figure 1. Incubator design for experiments using natural plankton assemblages

Temperature was held constant at 20°C and the photoperiod was 12-h light/dark cycle. Cool white fluorescent bulbs were used as a light source and irradiance was 200 $\mu\text{Em}^{-2}\text{s}^{-1}$. This value was in the range of typical light saturated photosynthesis rates of many phytoplankton (Kirk, 1994). Turbulence was controlled using an aerator powered through a time delay relay (5 seconds on/40 seconds off). This resulted in periods without disturbance, presumably reducing deleterious effects to zooplankton grazing (Boraas, 1980; Lampert, 1976), but still provided adequate mixing to maintain a homogeneous environment for sampling. Finally, the water used for the inoculum prior to each experiment was well mixed. Therefore, we assumed that the initial assemblage structure was very similar in each of the flow-through chambers in a given experiment.

Samples for microscopic analyses were collected every three days and preserved in 5% glutaraldehyde. Phytoplankton enumeration was achieved using inverted phase-contrast light microscopy, where samples were first concentrated using a standard settling technique (Utermohl, 1958). Phytoplankton identification was to the taxonomic level of genus. Cellular volumes for phytoplankton were estimated using common geometric shapes and measurements of appropriate dimensions (Wetzel and Likens, 1991).

Results and Discussion

As described previously (Huisman and Weissing, 2001b), under conditions of continuous flushing and nutrient loading simulated phytoplankton succession patterns were chaotic. Briefly, two possible states of the system existed, the first was characterized by coexistence of some combination of species 1, 2 and 3, and the second was characterized by coexistence of some combination of species 1, 4 and 5. Selection of a system community-state was very sensitive to the initial structure of the phytoplankton community, and at times appeared to be random, even though the modelled system was simple and fully deterministic (Figure 2A). Once a community-state was selected, repeating population shifts between coexisting species ensued.

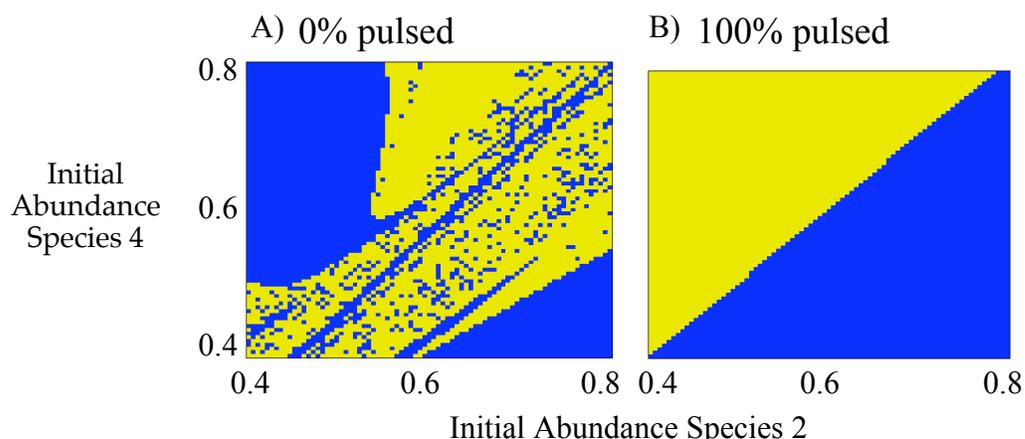


Figure 2 (adapted from Roelke et al., 2003). Community-state boundary diagram. Selection of community-states under conditions of A) continuous inflow and B) 100% pulsed inflow with a 3-day periodicity. The first community-state was characterized by coexistence of some combination of species 1, 2 and 3 (blue) and the second community-state was characterized by coexistence of some combination of species 1, 4 and 5 (yellow). Only the initial concentration of species 2 (x-axis) and species 4 (y-axis) varied during simulations.

Note that despite differences in the structure of the model and the numerical procedure used to solve it between our study and that of Huisman and Weissing (2001b), under continuous inflow conditions results were the same.

When inflow was delivered in a pulsed fashion with a three-day period, i.e., 100% of the inflow was delivered on the third day and no inflow during the previous two days, the same two community-states existed. But the behavior of the model was very different. For example, the selection of a community-state as a function of the initial phytoplankton community composition was now determinable (Figure 2B). The introduction of disturbances of this magnitude and period forced predictable behavior on this aspect of the system, i.e., chaos was completely removed! The mechanism that controlled which community-state was selected was the early sequestration of resources that limited competitors. For example, the first community-state was selected when species 2 was initially more abundant than its competitors because species 2 sequestered more of resource 2, which limited growth of species 4 and 5. Similarly, the second community-state was selected when species 4 was initially more abundant because it sequestered more of resource 3, which limited growth of species 2 and 3.

The introduction of pulsed inflows also changed the observed succession pattern. For example, aperiodic oscillations characterized succession within the first community-state. Species 1, 2 and 3 coexisted but the timing of population overturn, which was very slow, never repeated. A “dynamic” equilibrium now characterized the second community-state. Species 1, 4 and 5 coexisted, and population oscillations occurred solely as a function of the episodic inflows.

Our findings varied depending on the periodicity of inflow. In additional simulations, we increased the period of pulsing, and the behavior of the model was “pushed” away from succession trajectories that lead toward either of the previous two community-states, and toward a new state of the system (Figure 3). This third

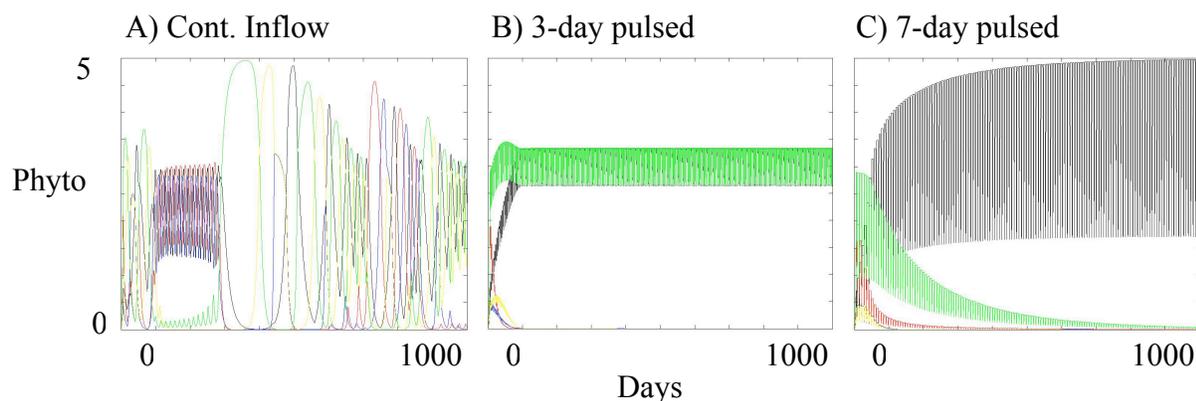


Figure 3. Succession dynamics of the plankton model showing A) transient chaos when inflow was continuous which eventually lead to the selection of the first community-state, B) classic competitive exclusion behavior leading to the second community-state when inflow was 100% pulsed with a 3-day periodicity, and C) classic competitive exclusion behavior leading to a new state of the system where only species 1 survives when inflow was 100% pulsed with a 9-day periodicity.

community-state was characterized by exclusion of all competitors by species 1, and was selected regardless of initial community composition over the same ranges tested in the previous simulations. Again, population oscillations occurred solely as a function of the episodic inflows, and the magnitude and timing of accumulated biomass was very similar. Again, chaos was totally removed from this aspect of the system!

Laboratory experiments on natural plankton assemblages showed a consistent trend with the model simulations. Under conditions of continuous flushing and nutrient loading the phytoplankton succession patterns from three incubators, each having very similar initial plankton composition and identical environmental conditions, were different in the timing of the peak phytoplankton biovolume, the magnitude of the peak biovolume, and the community composition at the taxonomic level of genera. In the first incubator phytoplankton bloomed late in the experiment and were dominated by *Nitzschia* sp. (Figure 4A), phytoplankton in the second

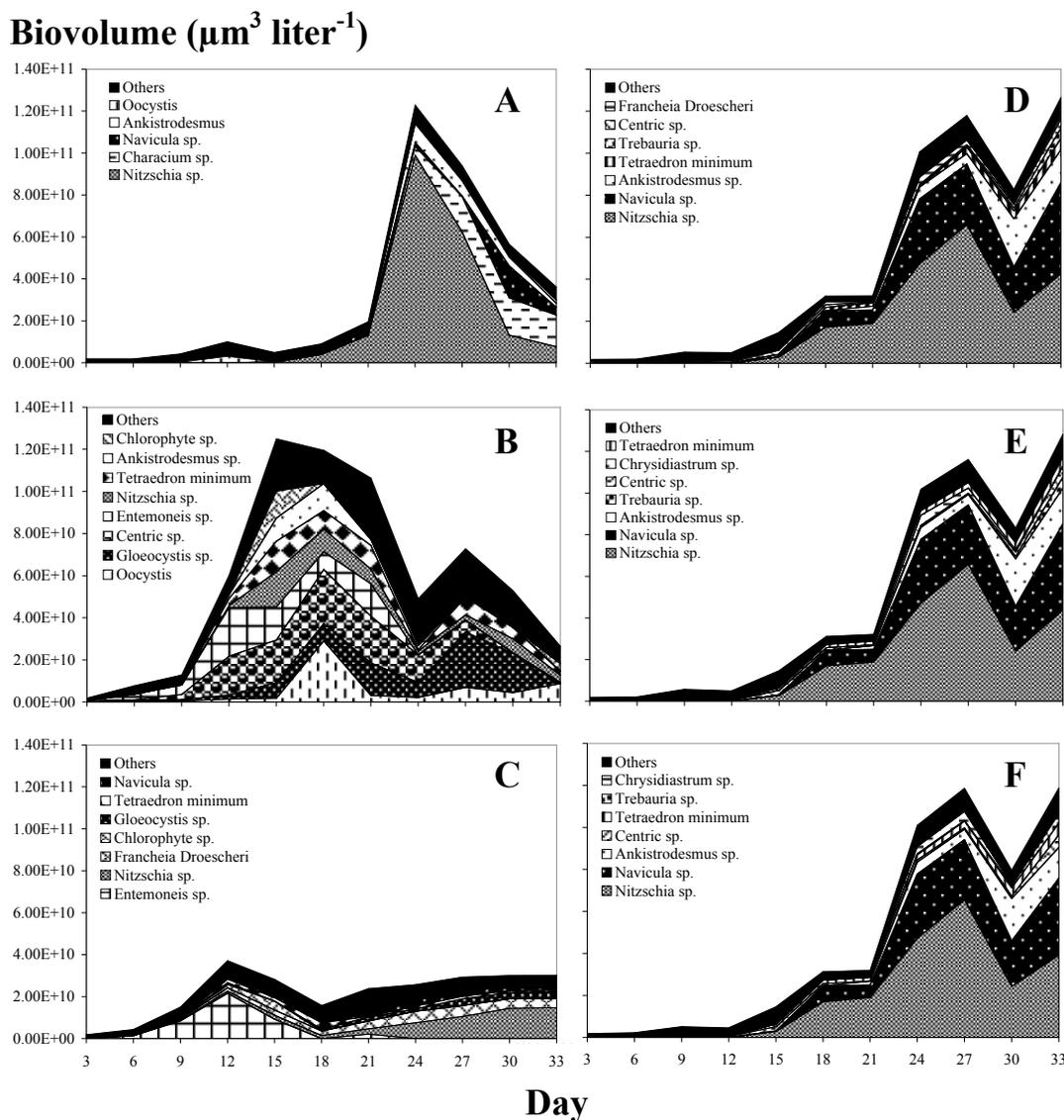


Figure 4 (adapted from Roelke et al., 2003). Seemingly random phytoplankton succession patterns in flow-through incubators receiving continuous inflow (A-C), while succession patterns in incubators receiving pulsed inflows (D-F) were near identical.

incubator bloomed mid-way through the experiment with shared dominance among eight genera (Figure 4B), and no bloom occurred in the third incubator with early dominance of *Entemoneis* sp. (Figure 4C). In other words, seemingly random, or chaotic, succession patterns were observed.

Contrastingly, under conditions of pulsed inflow with a three-day period, i.e., again 100% of the inflow delivered on the third day with no inflow during the previous two days, phytoplankton succession trajectories were remarkably similar. Phytoplankton bloomed late in all three incubators, the magnitude of accumulated biovolumes were near identical, and assemblage structures were very similar with *Nitzschia* sp., *Navicula* sp., and *Ankistrodesmus* sp. dominating (Figure 4D, E, F). As with the model simulations, the introduction of disturbance of this magnitude and periodicity forced determinable behavior on the system!

Chaotic succession patterns were not always observed in our experiments. For example, replicate continuous inflow treatments from some of our other experiments, where natural assemblages were collected from the same location but during different times of the year, were very similar to each other (Buyukates and Roelke, 2002). This reinforces previous findings wherein numerical models were used to demonstrate that chaotic behavior was confined to a narrow range of assemblage structures (Huisman and Weissing, 2001a; Scheffer, 1991; Schippers, et al., 2001), i.e., some assemblages are structured in such a way that chaotic behavior cannot occur regardless of the disturbance regime.

Finally, using this particular plankton model, we tested “how” fragile the likelihood of chaotic selection of community-states might be to the magnitude of pulsed inflow. Our simulations indicated that the occurrence of chaotic succession was fairly resistant to inflow disturbances at a period of three days (Figure 5). In fact, only when 85% of the total inflow was pulsed did the system become determinable. Chaotic succession patterns emerged when the proportion of pulsed flow was reduced to 80% (Roelke et al., 2003). Experimental verification of this trend is left for future research.

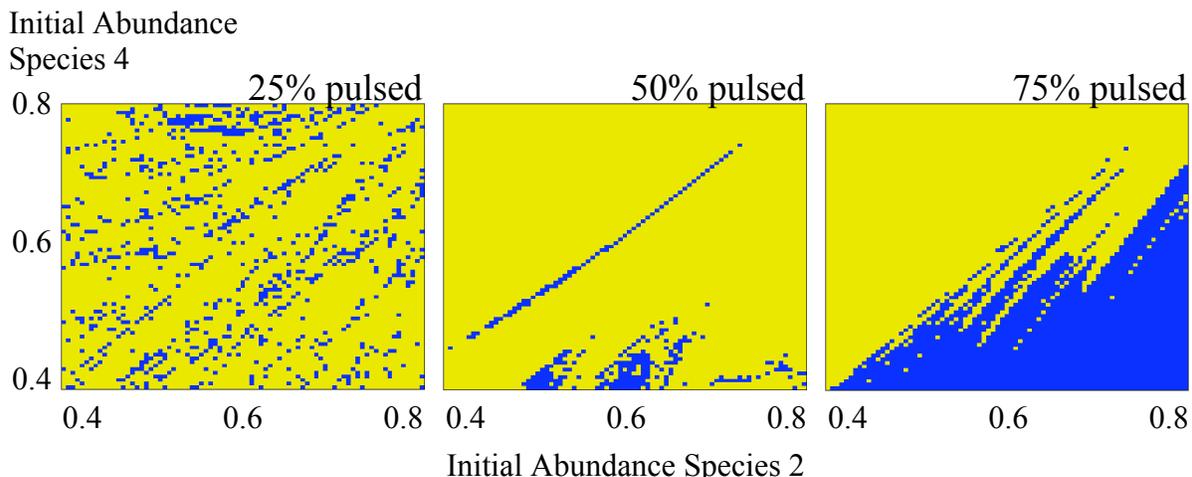


Figure 5 (adapted from Roelke et al., 2003). Community-state boundary diagrams. Chaotic selection of system community-states was robust in this plankton model, and was removed from the system only when the pulsed inflow reached very high percentages of the total inflow. In all simulations a 3-day pulsing periodicity was applied.

Conclusions

Water quality issues in coastal and inland water bodies, which include harmful algal blooms, fish kills, and extended periods of anoxia, will be paramount for many years to come. Consequently, proactive management efforts to circumvent these problems must be considered. Implementing and evaluating proactive management efforts, however, might be hindered by the very nature of foodweb interactions. Our findings indicate that plankton communities will only respond to manipulations in a predictable manner when the manipulation, or disturbance, to the system is large. Returning to Darwin's metaphor of the "grain in the balance", the grain can tumble in a predictable direction, but only if it is pushed hard enough. It may be that large-scale hydraulic manipulations, i.e., flushing periodicity and magnitude, or other large-scale manipulations, are required to circumvent deleterious water quality issues.

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