Chaos-induced coherence in two independent food chains

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Coherence evolution of two food web models can be obtained under the stirring effect of chaotic advection. Each food web model sustains a three-level trophic system composed of interacting predators, consumers, and vegetation. These populations compete for a common limiting resource in open flows with chaotic advection dynamics. Here we show that two species (the top predators) of different colonies chaotically advected by a jetlike flow can synchronize their evolution even without migration interaction. The evolution is charaterized as a phase synchronization. The phase differences (determined through the Hilbert transform) of the variables representing those species show a coherent evolution.

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I. INTRODUCTION

When dealing with transport processes in complex fluid flows, the concept of turbulence comes to mind. In bidimensional flows, it is possible to obtain a situation where chaotic trajectories can be generated by a simple and regular velocity field. This situation is called chaotic advection [1,2]. Here we show that chaotic advection in an oceanic jet flow can induce coherence evolution in two chaotic systems. As an illustrative example, this simple and robust mechanism is examined using an ocean food chain advected by mesoscale eddies in the ocean.

In most natural habitats, numerous competing species are able to coexist, while in general these communities are limited by only a few resources (niches). This fact contradicts the classical theoretical and empirical studies predicting competitive exclusion of all but the most perfectly adapted species in relation to each limiting factor. Recent developments in the field of chaotic advection in hydrodynamical/environmental flows encourage us to revisit the population dynamics of competing species in open aquatic systems. A typical model that takes into account species interactions is a trophic web food chain [3–6]. Among them we choose a trophic web food chain with a complex behavior. The complex behavior, that is, a local disorder, is a requirement believed to be necessary for observing nontrivial collective behavior [7].

The article is organized as follows. In Sec. II, we introduce the ecological model used as well as the flow model along with the parameters chosen. The results of the coherent evolution of species inmersed in a chaotic flow are presented in Sec. III. The type of synchronized regime is also investigated in that section. Our main conclusions are summarized in Sec. IV.

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II. MODELS

Simple models for three-species food chains exhibit a broad range of nonequilibrium dynamics, from characteristic natural cycles to more complex chaotic oscillations [3,6,8–11]. Two chaotically oscillating food web models coupled diffusively may also synchronize [12,13]. This synchronization phenomenon in coupled chaotic systems has been extensively studied [14,15]. Those systems can display different degrees of synchronization, namely complete synchronization, phase synchronization, lag synchronization, and generalized synchronization [16]. Synchronization by periodic external actions in the presence of noise [15] or noise-induced synchronization [17] has also attracted considerable interest. Recently, the effect of stirring of chaotic advection in an inhomogeneous oscillatory medium was investigated [18]. In the present work, we study instead two chaotic oscillators coupled through the chaotic advection of the flow they are immersed in.

We use a simple model of two three-species food chains immersed in a meandering jet flow. The flow, which is laminar and unsteady, produces chaotic advection. One important consequence of chaotic advection is the exponential separation of initially nearby fluid elements. The spatiotemporal dynamics of the two colonies of food chains embedded in the time-dependent incompressible flow is described by the advection-reaction equations which, in a Lagrangian representation, take the form

$$\frac{d\hat{\mathbf{r}}}{dt} = \mathbf{V}(\hat{\mathbf{r}},t), \tag{1}$$

$$\frac{dU_i}{dt} = F_i(U_j, \mathbf{r}=\hat{\mathbf{r}}(t)), \quad i,j=1,2, \tag{2}$$

where the second set of equations describes the dynamics of the concentration or the amount of species $U_i=\{u_i,v_i,w_i\}$ contained in a fluid parcel that is being advected by the flow described by the first equation (1) [19]. The flow is assumed

to be imposed externally, so that the population dynamics has no influence on the velocity field. At scales large enough (i.e., like ocean currents of $\approx$100 km), diffusion effects can be neglected [20]. The coupling between the flow transport capacity and the population evolution appears through the spatial dependence of the $F_i(U_j,\mathbf{r})$ functions. F_i varies from point to point, in a fluid element that moves with the flow velocity. Those functions are evaluated at the position of the fluid element at time t, that is, at $\mathbf{r}(t)$.

The population dynamic represented by the function $F_i(U_j,\mathbf{r})$ is a metacommunity explicitly modeled by two trophic food chains. Standard three-level "vertical" food chains evolve in every parcel of a well-mixed fluid. The resources (i.e., nutrients) $u_{1,2}$ are consumed by $v_{1,2}$ (i.e., phytoplankton), which in turn are preyed upon by top predators $w_{1,2}$ (i.e., zooplankton). The coupled differential equations for the biomass of the different species are

$$\frac{du_1}{dt} = a[u_1 - u_0(\mathbf{r})] - \alpha_1 f_1(u_1,v_1), \tag{3}$$

$$\frac{dv_1}{dt} = -b_1 v_1 + \alpha_1 f_1(u_1,v_1) - \alpha_2 f_2(v_1,w_1), \tag{4}$$

$$\frac{dw_1}{dt} = -c(w_1 - w^*) + \alpha_2 f_2(v_1,w_1), \tag{5}$$

$$\frac{du_2}{dt} = a[u_2 - u_0(\mathbf{r})] - \alpha_1 f_1(u_2,v_2), \tag{6}$$

$$\frac{dv_2}{dt} = -b_2 v_2 + \alpha_1 f_1(u_2,v_2) - \alpha_2 f_2(v_2,w_2), \tag{7}$$

$$\frac{dw_2}{dt} = -c(w_2 - w^*) + \alpha_2 f_2(v_2,w_2). \tag{8}$$

The coefficients a, $b_{1,2}$, and c represent the respective net growth rates of each individual species in the absence of interactions among them ($\alpha_1=\alpha_2=0$). Each three-species model, in the absence of interactions among them, has equilibrium or steady-state populations $(u^*_{1,2},v^*_{1,2},w^*_{1,2})$ which are the solutions of $du_{1,2}/dt=0$, $dv_{1,2}/dt=0$, $dw_{1,2}/dt=0$ (respectively). A linear stability analysis yields that the steady state $(u^*_{1,2}=0,v^*_{1,2}=0,w^*_{1,2}=0)$ for the chosen parameters (after Blasius *et al.* [12]) is a saddle-node point. We set the origin of each of the three-species models as the steady state (in the absence of interactions among them and uncoupled with the flow) $u^*_{1,2}=0$, $v^*_{1,2}=0$, $w^*_{1,2}=w^*>0$. From the population dynamics point of view, this steady state means that the predator w is allowed to maintain a low equilibrium level even when the prey v is rare. In other words, there are alternative food sources available for the predator w. The two colonies can be distinguished by a parameter mismatch of $\Delta f \approx b_2 - b_1$. The functions f_i describe interactions among the species with strengths α_i. We use standard interactions of Holling type II $[f_1(u,v)=uv/(1+k_1u)]$ to describe the competition among species u and v. The interaction among species v and w is modeled by a Lotka-Volterra interactions $[f_2(v,w)=vw]$. Equations (3) and (6) describe the evolution of $(u_{1,2})$, with net rate a, toward a space-dependent value, $u_0(\mathbf{r})$. This term, $u_0(\mathbf{r})$, is the only explicitly nonhomogeneous term; it represents a spatially dependent resource (nutrient in a plankton model) input which could arise naturally from a variety of processes such as localized upwelling and river runoff, translated as a source or a sink in the flow model.

The two colonies are chaotically advected by a two-dimensional flow. The velocity field of the flow was assumed to be time-dependent, which ensures efficient mixing. Different flows have proven to produce good stirring effect in particles, chemical reactions, and plankton (see, for example, [21] and references therein). To illustrate this case, we choose a flow of geophysical relevance, a jet flowing eastward with meanders, of amplitude $B(t)$ and wave number k in the North-South direction with a phase velocity c_x [22]. The Cartesian components of the flow $\mathbf{V}=(-\partial\psi/\partial y,\partial\psi/\partial x)$ are expressed, in nondimensional units, in terms of the stream function ψ,

$$\psi(x,y) = 1 - \tanh \frac{y - B(t)\cos k(x - c_x t)}{[1 + k^2 B(t)^2 \sin^2 k(x - c_x t)]^{1/2}}. \tag{9}$$

The meander amplitude $B(t)$ is a time-dependent oscillation, $B(t)=B_0+\epsilon\cos(\omega t+\theta)$.

This flow, representing an open flow, advects eastward most of the fluid particles, all together with the species contained in each parcel. The source (or sink) of resources (nutrients) $u_0(\mathbf{r})$ is localized at the origin of coordinates, according to

$$u_0(x,y) = \begin{cases} 1 + A \sin\left(\dfrac{2\pi x}{L}\right)\sin\left(\dfrac{2\pi y}{L}\right) & \text{if } x,y \in (0,L), \\ 0 & \text{elsewhere}, \end{cases}$$

where the amplitude A is constant.

III. RESULTS

The evolution of the colonies in the flow is integrated numerically according to the method proposed by Ottino [2] and later used by others [19,23]. The two-dimensional physical space accessible to fluid particles is subdivided into regions characterized by different Lagrangian behaviors. The model we use, without the spatial dependence, was shown [13] to have synchronized behavior among the top predator species of the two colonies when migration of rate D is allowed. Actually in the absence of migration, $D=0$, Blasius *et al.* [12,13] showed that the two colonies would normally be nonsynchronized. This nonsynchronized behavior can be observed in most of the time evolution of the top predators, as can be seen in Fig. 1. In this figure, we show the temporal evolution of the $w_{1,2}$ for a fixed parcel in the Lagrangian point of view.

We observe in Fig. 1 that the two web chains are not synchronized at the beginning. Then, when the parcels enter into the region where the nutrients are spatially nonhomogeneous, the two colonies start to evolve synchronously. In the

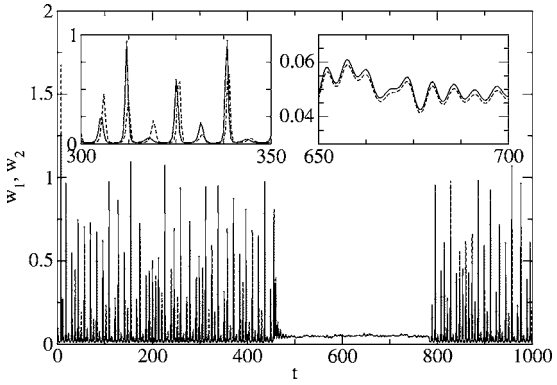

FIG. 1. Chaotic time series of top predators, w_1 and w_2 (dashed line), in the web model. The top images correspond to zooms of the main image. The image on the left shows the nonsynchronized evolution when the parcel goes through a region where the nutrients are homogeneous. On the contrary, when the parcel enters into a region where the nutrients are nonhomogeneous (right), the top predators evolve in synchronicity. Parameters for the web food model are $a=1$, $b_1=1.1$, $b_2=1.055$, $c=10$, $k_1=0.5$, $\alpha_1=0.2$, $\alpha_2=1.0$, $w^*=0.006$, $u_{1,2}(0)=5.0$, $v_{1,2}(0)=5.0$, and $w_{1,2}(0)=0.0$. For the flow $B_0=1.2$, $\epsilon=0.3$, $\omega=0.4$, $c_x=0.12$, and $A=0.2$.

top left corner, a zoom of the first time interval is shown. For this period of time, the fluid parcel goes through a region where the nutrients are homogeneous. A nonsynchronized evolution is observed, as was expected for these parameter values [13]. A zoom of the synchronous evolution can be seen in the top right corner. This inset corresponds to the interval when the spatial dependence, that is, the nonhomogeneous sources or sinks, advects the resources (nutrients). This figure shows also that the evolution of the two subsystems undergoes a transition to another chaotic attractor, adjusting their rhythm due to the interaction of the flow.

The coherent evolution of the top predators of the two colonies w_1 and w_2 can be explicitly shown plotting w_2 versus w_1 as in Fig. 2. In the top panel [Fig. 2(a)], w_2 versus w_1 is plotted during the time where the source is not forcing the system. The cloud of points clearly shows the uncorrelated behavior of the two variables. In Fig. 2(b), on the contrary, w_2 and w_1 display a coherent evolution.

It is well known that two chaotic systems could display different synchronized regimes [13,15,16]. Thus, we investigate the regime of synchronization of the two colonies, as well as the influence of the degree of mixing power of the flow.

A closer look at the synchronized evolution reveals that this is not a complete synchronization regime. In fact, $w_1-w_2\approx b_1-b_2$ (where … means a temporal average of …). Another possible scenario is that the two colonies are in a phase synchronization regime.

To describe the phase synchronization, we need to introduce corresponding quantities. The phase of the signal (the time evolution of the population density of one of the species) can be obtained in different ways. We calculate the phase, using the standard construction of the analytic signal [15,24]. Complex signals obtained from the real signals are rewritten as complex signals $z_{1,2}=w_{1,2}(t)+iH[w_{1,2}(t)]=|a_{1,2}(t)|e^{i\phi_{1,2}(t)}$, where $H[w_{1,2}(t)]$ is the Hilbert transform of $w_{1,2}(t)$.

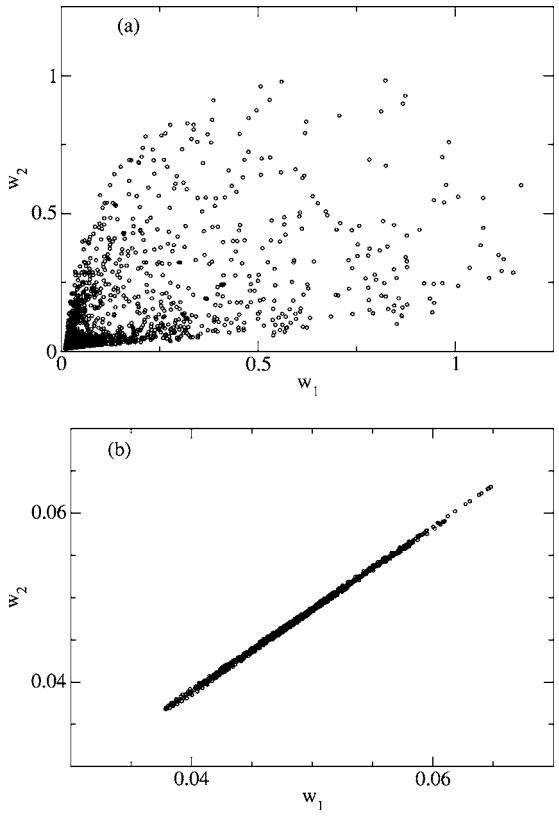

FIG. 2. Projections of the phase portrait on the (w_1,w_2) plane. Panels (a) and (b) correspond to the cases where the nutrients are homogeneous and inhomogeneous, respectively. Notice the perfect synchronization. Parameters for the web food model and the flow are the same as for Fig. 1.

In Fig. 3, we plot the relative phase difference $\Delta\omega(t)=\phi_1(t)-\phi_2(t)$ as a function of time. The method of phase estimation has several advantages and some drawbacks (for a more detailed discussion, see [24] and Chap. 6 and Appendix 2 of [15]). The evolution of the point in the complex $(w_{1,2}(t),H[w_{1,2}(t)])$ plane rotates around two different centers of the two chaotic attractors. The densities of population $w_{1,2}$ evolve in a chaotic attractor while nonsynchronized. Then after a transient time they fall into another chaotic attractor (with different signal mean value) and they synchronize in phase. After another transient time (where the mean value is neither of the previous ones), they rotate once again nonsynchronously in the first chaotic attractor. The transitions between the different attractors and the time spent in each attractor are clearly reflected in Fig. 3. The first region shows the two colonies not synchronized; the phase difference $\Delta\omega(t)$ grows with time. The next window time corresponds to the transient time when the colonies abandon the nonsynchronized chaotic attractor. The phase cannot be estimated with the above procedure. Once the parcel reaches the region where the source (or sink) of nutrients is located $[u_0(\mathbf{r})\neq 0]$, the phase difference between the two patches drops to a constant. The two species are synchronized. The two species evolve in another chaotic attractor with a well-defined mean value. Then, as the parcel leaves the upwelling region (or sink), there is a transient during which the signal

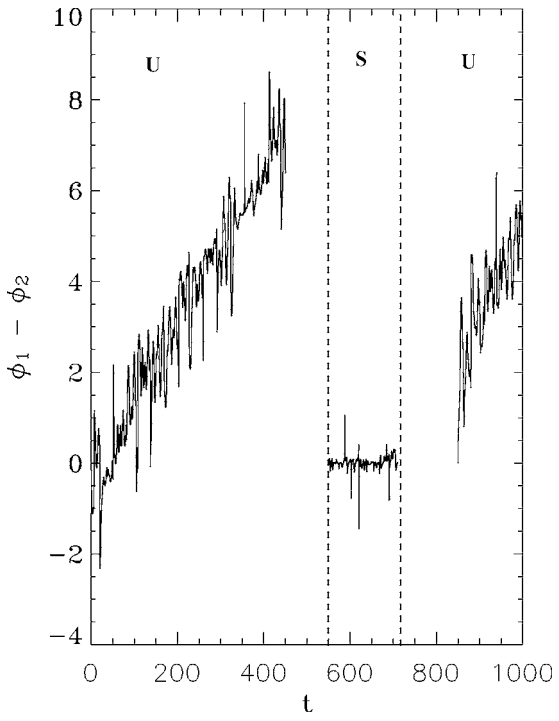

FIG. 3. Plot of the phase difference $\Delta\omega(t)=\phi_1(t)-\phi_2(t)$ as a function of time. The regions where the phase difference grows (meaning no synchronization) correspond to nonchaotic advection while the regions of constant phase difference are associated with synchronized evolution. Parameters for the web food model and the flow are the same as in Fig. 1.

leaves the attractor evolving to the nonsynchronized one. Once again, the phase difference in the transient time of the phase cannot be calculated. After that transient the evolution of the two species is once again nonsynchronized.

The flow can influence the coherence evolution of the two colonies. Neufeld and co-workers [18] have shown that oscillators advected chaotically by a flow can produce collective oscillations or oscillator death by controlling the mixing capacity of the flow, actually the stirring rate of flow. It has been shown [22] that the mixing capacity of the type of flow we are using in this work can be modified by three parameters that govern the time-dependent oscillation of the meander amplitude, namely B_0, ϵ, ω. We choose the values used by Cencini *et al.* [22] and later by López and co-workers [19] originally motivated mainly by observations in ocean jets. These are the critical values for obtaining "large-scale chaos." It is in this situation that exchange of particles between the north-south part is more favorable (more mixing). The parameters $B_0=1.2$, $\epsilon=0.3$, $\omega=0.4$ were chosen by Cencini *et al.* to be greater than the critical value in order to have great power of mixing. Different collective behaviors of the two colonies are expected when the mixing capacity is changed through any of the three parameters involved, as they will be changing the mean value, the amplitude, and the stirring rate of the inhomogeneity. Different situations may

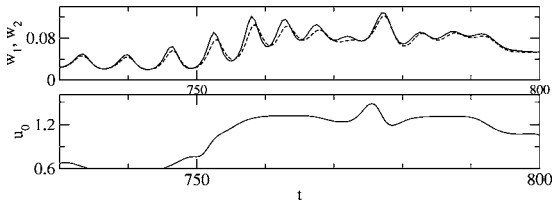

FIG. 4. The two top predators $w_{1,2}$ and the flow forcing $u_0(\mathbf{r})$ as functions of time are shown. Only the region where the nutrients are nonhomogeneous is shown. The two panels show the independent behavior of the variables $w_{1,2}$ of the dynamical system related to the forcing ($\omega=0.5$, $A=0.5$). Parameters for the web food model are the same as for Fig. 1.

arise though, changing the parameters of the flow (as well as the parameter of the colonies dynamic). These situations are discussed somewhere else [25].

We would like to remark that the two population (w_1, w_2) are in fact synchronized. That is, they are not just two (chaotic) oscillators passively following the same forcing. It can be observed in Fig. 4 that the top predators $w_{1,2}$ are not adiabatically following the forcing. Indeed, for the values where the flow remains constant (and different from zero) the variables $w_{1,2}$ are oscillating.

IV. CONCLUSIONS

In summary, we have addressed the evolution of two food web models immersed in a flow. The chaotic advection, a mixing mechanism present in the real ocean, was shown to induce a coherence evolution of two species of different colonies. In particular, we have considered two food web models of a three-species food chain, each advected by a jetlike flow. The population model considered here represents a quite general population dynamic, and the main issues found here, namely the possibility of finding coherence evolution of two species, may be present in biological transport situations. There still remain open questions in this issue, such as mapping in the phase parameter space all the possible collective behavior of the two colonies and the transition between the different attractors. A simpler dynamical model (although less ecologically plausible) may help to examine the influence of different flows. Finally, we stress that the coherence evolution of two species as a result of a mixing property of the flow they are immersed in is a powerful process. It has the potential to shape the distribution and abundance of aquatic species in a current flow with important implications for ecological dynamics in fluid flows.

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[1] H. Aref, Phys. Fluids **14**, 1315 (2002).
[2] J. M. Ottino, *The Kinematics of Mixing: Stretching, Chaos, and Transport* (Cambridge University Press, Cambridge, 1989).
[3] J. D. Murray, *Mathematical Biology*, 3rd ed. (Springer, New York, 2002), Vol. I.
[4] R. M. May, *Theoretical Ecology: Principles and Applicactions* (Blackwell Scientific Publications, Oxford, 1981).
[5] W. S. C. Gurney and R. N. Nisbet, *Ecological Dynamics* (Oxford University Press, Oxford, 1998).
[6] M. Kot, *Elements of Mathematical Ecology* (Cambridge University Press, Cambridge, 2001).
[7] L. G. Brunnet, H. Chaté, and P. Manneville, Physica D **78**, 141 (1994); L. G. Brunnet and H. Chaté, Physica A **257**, 347 (1998); H. Chaté, Int. J. Mod. Phys. B **12**, 299 (1998).
[8] R. M. May, *Stability and Complexity in Model Ecosystems* (Princeton University Press, Princeton, 1975).
[9] W. M. Schaffer, Ecology **66**, 93 (1985).
[10] A. Hastings and T. Powell, Ecology **72**, 896 (1991).
[11] A. Hasting, *Population Biology* (Springer-Verlag, New York, 2000).
[12] B. Blasius, A. Huppert, and L. Stone, Nature (London) **399**, 354 (1999).
[13] B. Blasius and L. Stone, Int. J. Bifurcation Chaos Appl. Sci. Eng. **10**, 2361 (2000).
[14] M. G. Rosenblum, A. S. Pikovsky, and J. Kurths, Phys. Rev. Lett. **76**, 1804 (1996).
[15] M. G. Rosenblum, A. S. Pikovsky, and J. Kurths, *Synchronization: A Universal Concept in Nonlinear Sciences*, Vol. 12 of Cambridge Nonlinear Sciences Series (Cambridge University Press, Cambridge, 2001).
[16] S. Boccaletti, J. Bragard, F. T. Arecchi, and H. Mancini, Phys. Rev. Lett. **83**, 536 (1999).
[17] R. Toral, C. Mirasso, E. Hernández-García, and O. Piro, Chaos **11**, 665 (2001).
[18] Z. Neufeld, I. Z. Kiss, C. Zhou, and J. Kurths, Phys. Rev. Lett. **91**, 084101 (2003).
[19] C. López, Z. Neufeld, E. Hernández-García, and P. H. Haynes, Phys. Chem. Earth, Part A Solid Earth Geod. **26**, 313 (2001).
[20] E. R. Abraham, Nature (London) **391**, 577 (1998).
[21] E. Hernández-García, C. López, and Z. Neufeld, in *Chaos in Geophysical Flows*, edited by G. Bofetta, G. Lacorata, G. Visconti, and A. Vulpiani, (OTTO Editore, Torino, Italy, 2003), p. 35.
[22] M. Cencini, G. Lacorata, A. Vulpiani, and E. Zambianchi, J. Phys. Oceanogr. **29**, 2578 (1999).
[23] A. Martí and F. Sagués, Physica A **295**, 77 (2001).
[24] B. Boashash, Proc. IEEE **80**, 520 (1992).
[25] A. Martí and R. Montagne (unpublished).