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Dynamics of a food chain model from an arthropod-dominated lotic community

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Abstract

A simulation model, based on a series of Holling type II differential equations, was used to assess the effects of omnivory on the dynamics of individual populations at different trophic levels, as well as on the stability and persistence of food chains. Initial population densities were equal to actual field estimates, whereas predation rates and population growth rates were obtained from the literature for the top predator (*Corydalus cornutus*), secondary consumer (*Ambrysus circumcinctus*), and primary consumer (*Petrophila* sp.). Fluctuations in population density depended on the trophic level at which each population feeds. Demographic trajectories of primary and secondary consumers was similar to those produced by Lotka–Volterra models; the pattern of fluctuation in both populations resembled a sine function, with the predator population lagging behind the prey population. In the model without omnivory (minimal connectance), the range of fluctuation in population density was the greatest for the secondary consumer, followed by the primary, and then tertiary consumers. Low levels of consumption of the primary consumer by the top predator (between 1% and 4%) increased the minimum population density point of all consumer populations. Higher consumption rates produced wider oscillations and populations quickly became extinct. Sensitivity analysis revealed that the model was highly sensitive to initial conditions. A 5% increase in the initial population density of the primary consumer produced an output that diverged exponentially from the original output ($\lambda = 0.012$), confirming that the system behaved chaotically. This suggests that pervasive fluctuations in population density that are characteristic of many aquatic insects could be the product of deterministic rather than stochastic processes.

Keywords: Population dynamics; Prey–predator relationships

1. Introduction

In an attempt to quantify relationships and transform ecology into an “exact science,” many

investigators have forced data to adhere to linear models, or vice versa, thereby missing interesting and perhaps more realistic aspects of population and community dynamics (Schaffer and Kot, 1986; Morris, 1990). Ecological processes are frequently complex and often non-linear or stochastic (May, 1974; O’Neill et al., 1986). The behavior of even the most simple non-linear equations can pro-

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duce chaos (Gleick, 1986; Logan and Allen, 1992). In chaotic systems, the equations used for defining ecological relationships are deterministic, but the variables do not attain equilibrium values or produce stable oscillations; moreover, such systems are extremely sensitive to initial conditions (Schaffer, 1985). Chaos in ecological systems can occur because resources are limited, populations have intrinsic positive feedbacks, and energy transfers from one trophic level to the next are usually tied by feedbacks (Allen, 1990a; Hastings and Powell, 1991; Stone, 1991). Some ecological systems are predisposed to chaotic dynamics because they comprise large numbers of trophic interactions, which in turn, imply higher order interactions with time lags. Time series analysis illustrates how the effects of a predator on its prey diffuse like ripples through the community as time progresses (Turchin, 1990; Turchin and Taylor, 1992). As the number of trophic interactions among species (i.e., connectance) increases, so does the ripple effect within the community. This is exemplified by lotic invertebrate communities, where a large proportion of aquatic insect taxa are omnivores (Cummins and Klug, 1979).

At the population level, May (1974) noted that increases in the intrinsic growth rates in the discrete “logistic” analog equation increased the pathological behavior of the system, thus becoming chaotic. Insects are among the organisms with the highest reproductive potential, and some species have been shown to exhibit chaotic population dynamics (Turchin and Taylor, 1992). At the community level, several predator–prey models that exhibit chaotic behavior have been proposed to account for demographic patterns in field studies (Allen, 1990a,b, 1991; Hassell et al., 1991; Stone, 1991; Logan and Allen, 1992). In a food chain model involving three species (1° producer, 1° and 2° consumers), the system was chaotic and never attained a stable equilibrium, although it persisted over a long time periods (Hastings and Powell, 1991).

Some systems that are unstable are still capable of resisting “extinction” or transition to more stable neighborhoods (Auerbach, 1984). This phenomenon is known as persistence (DeAngelis et al., 1989). Variables may never approach equi-

librium, but they may oscillate above a constant positive value. This phenomenon produces local instability, but not extinction. In ecology, a community persists if none of the component species that compose it go extinct, and new species are unable to invade during ecological time. In reality, no community persists over large time scales (Pimm, 1991) because populations become extinct, new species invade, or the habitat changes. Species with low population densities are more prone to extinction by demographic stochasticity (May, 1974). In real communities, which are subjected to environmental stochasticity, top predators are usually the taxa with the lowest population densities and the highest risk of extinction (Gard, 1984).

Populations of many aquatic insects exhibit wide fluctuations in density over time (Coffman et al., 1971; Fisher and Grimm, 1988; Palmer et al., 1992). Several models, both stochastic and deterministic, that incorporate a suite of factors (e.g., hydraulics, disturbance, predation, and refugia) and their interactive effects have been proposed to account for such variation. However, these fluctuations in population density cannot be explained completely by availability of energy in the system (Coffman et al., 1971; Smock et al., 1992) or by the stochasticity of the environment (Fisher et al., 1982; Resh et al., 1988). A possible alternative is that the observed fluctuations in density are chaotic rather than stochastic.

The structure of the macroinvertebrate riffle community in the South Llano River has been examined in detail (Camilo, 1992; Camilo and Willig, 1993, 1995). This community is characterized by prevalent omnivory at most trophic levels. If the hypothesis of Moore et al. (1988) is true, and omnivory increases stability by reducing predation pressure on adjacent trophic levels, then chains with omnivores should persist for longer times and have populations characterized by narrower fluctuations in density than those without. Herein, we developed two system models, one with and one without an omnivore. Our objectives were: (1) to determine the dynamics (i.e., amount and periodicity of population change over time) of species feeding at different trophic levels; (2) to determine the dynamic behavior of the

Table 1
Value of variables and initial densities used in the equations for simulating food chains and source of information. Units of all variables are per cents of the respective absolute abundance. We followed the conversion procedure of Hastings and Powell (1991) (1 = *Petrophila* sp.; 2 = *Ambrysus circumcinctus*; 3 = *Corydalus cornutus*)

Variable	Value	Source
<i>a</i>		
<i>i</i> = 1,2	5.0	Peckarsky (1984)
<i>i</i> = 2,3	6.2	Peckarsky (1984)
<i>b</i>		
<i>i</i> = 1	6.8	Tuskes (1981), Lange (1984)
<i>i</i> = 2	4.2	Sites and Nichols (1990)
<i>i</i> = 3	2.3	Brown and Fitzpatrick (1978)
<i>d</i>		
<i>i</i> = 1	10.1	Tuskes (1981), Lange (1984)
<i>i</i> = 2	4	Sites and Nichols (1990)
<i>i</i> = 3	1.1	Brown and Fitzpatrick (1978)
<i>N</i>		
<i>i</i> = 1	87/m ²	unpublished data
<i>i</i> = 2	18/m ²	unpublished data
<i>i</i> = 3	7/m ²	unpublished data

overall system; and (3) to determine the persistence of food chains with different topologies.

2. Methods

Ecologists rarely can gather the large quantities of data required to determine the amount

and quality of periodicity in a system (Turchin and Taylor, 1992). An alternative approach uses simulation models to generate approximations of the process through iteration (Stone, 1991). The conceptual basis of the model was a series of Holling Type II equations, with the flux of prey numbers as the currency of the system (Hastings and Powell, 1991). Similar equations have been used to simulate food chain dynamics in various ecosystems and have proven to approximate ecological processes (DeAngelis et al., 1989a,b). Equations of Hastings and Powell (1991) were modified to correspond with the observed food chains (Fig. 1) of the South Llano River. The general demographic relation is:

$$dN_i/dt = [a_i N_i / (1 + b_i N_i)] - [a_{i+1} N_{i+1} / (1 + b_{i+1} N_{i+1})] - d_i N_i$$

where N_i is the relative density (see Table 1), b_i is the growth rate, d_i is the death rate, and a_i is the consumption rate of a species at the i th consumer trophic level ($i = 1$ to 3). The parameters for this equation were adapted from those published for the top predator, *Corydalus cornutus*, the most abundant intermediate predator *Ambrysus circumcinctus*, and the most abundant primary consumer, *Petrophila* sp. (Table 1). The producer level was not included in the simulation.

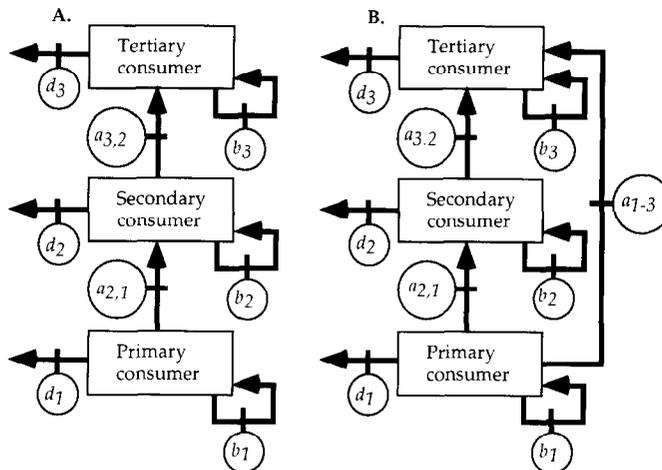


Fig. 1. Flow diagrams representing the two general models of food chains used in the simulations. A, without omnivore (connectance = 0.33); and B, with omnivore (connectance = 0.5). Parameters are: $a_{j,i}$, consumption rate of consumer j on consumer i ; b_i , birth rate of consumer i ; d_i , death rate of consumer i .

Two sets of connectedness models were developed in this study. In the first, no omnivory was permitted (Fig. 1A). The top predator fed on the intermediate consumer, which in turn fed on the primary consumer. In the second (Fig. 1B), the top predator was an omnivore, consuming between 1 to 50% of the primary consumer population in each simulation. For both models, simulations were conducted for 1500 iterations, with one iteration equivalent to a day, or until the system collapsed (≥ 1 species goes extinct).

Sensitivity analysis involves testing the effects of changes in values of the model's parameters, or initial state variables, on the output (Kitching, 1983). We performed a sensitivity test by changing the initial density of the primary consumer, *Petrophila* sp., by $\pm 5\%$. Absolute densities estimated from field measurements were equated with 100% of the relative densities for each corresponding species (Table 1), and used as the initial state variables.

The periodicity and behavior of the different trophic levels, as well as the total system, can be evaluated with time series analysis of the model output. The Lyapunov coefficient (λ) is a measure of the degree of chaos in the system (Schaffer, 1985; Logan and Allen, 1992) and can

be calculated from model output by the relationship:

$$\epsilon(t) = \epsilon(0)2(\lambda^t)$$

where $\epsilon(0)$ is the initial deviation between two outputs (i.e., time step one) from the same model which differ solely in the initial value of a state variable; $\epsilon(t)$ is the difference between two outputs at time t . A positive value for λ indicates that as time progresses the outputs of the model diverge in an exponential fashion, characteristic of chaotic systems.

3. Results

This system exhibited chaotic behavior. During the first 200 iterations, the system exhibited transient behavior (Logan and Allen, 1992). Primary and secondary consumer trophic levels exhibited fluctuations like those in classical predator–prey models. Patterns in the densities of the predator lagged behind those of the prey. In contrast, the demographic response of the top predator was unpredictable, with wide fluctuations in density that infrequently lagged behind those of its prey (Fig. 2). The dynamic behavior of the top preda-

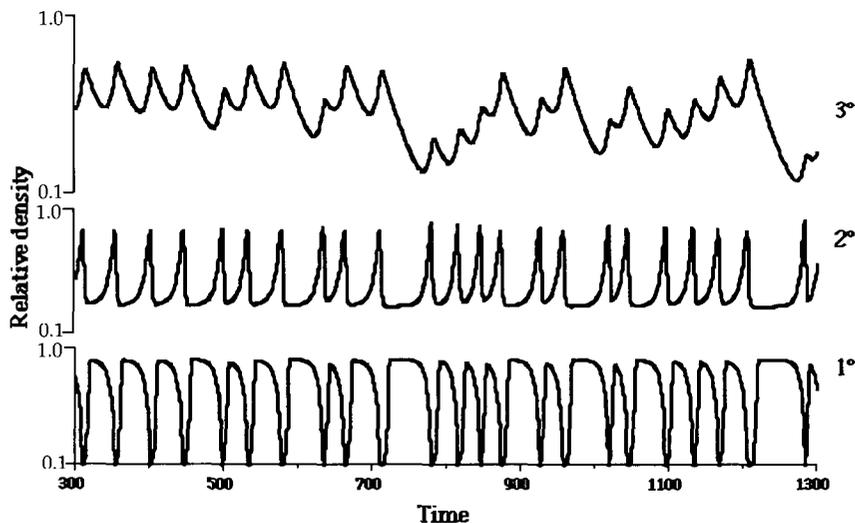


Fig. 2. Relative densities of the primary (1°), secondary (2°), and tertiary (3°) consumer trophic levels based on time series output of the model without omnivory. Iteration period was one day.

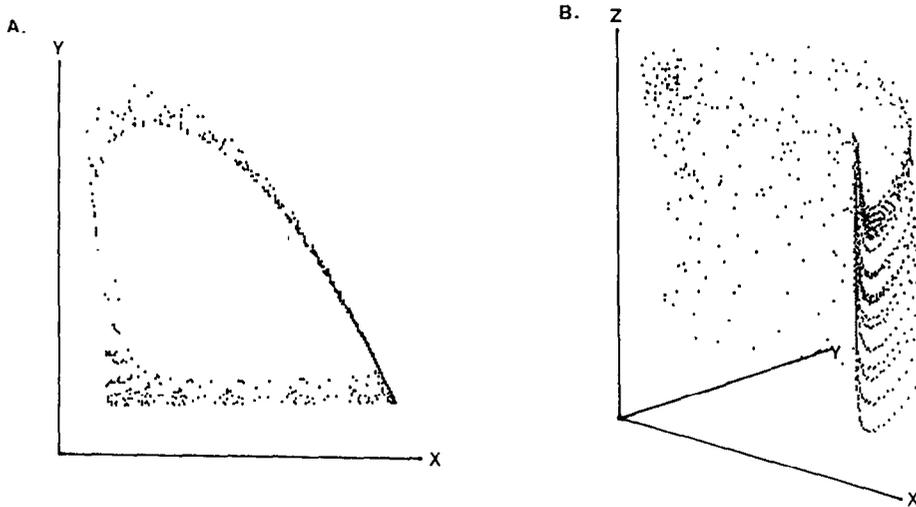


Fig. 3. Phase plot of the time series data generated by the simulation model without omnivory. Each axis represents relative densities of a trophic level (X-axis, primary consumer; Y-axis, secondary consumer; Z-axis, top predator). The Lyapunov exponent (λ) for the model output was 0.012. A. Top view; B. Side view.

tor was less predictable, with decreased correspondence with the primary producer (Fig. 2). Time series analysis of the model's output (auto-correlation, ARIMA Procedure, SAS Institute

Inc., 1989) failed to detect any periodicity in this system ($r_{\max} = 0.19$; $r_{\min} = 0.14$; average = 0).

Model output generated a phase space graph, in which system variables are plotted against each

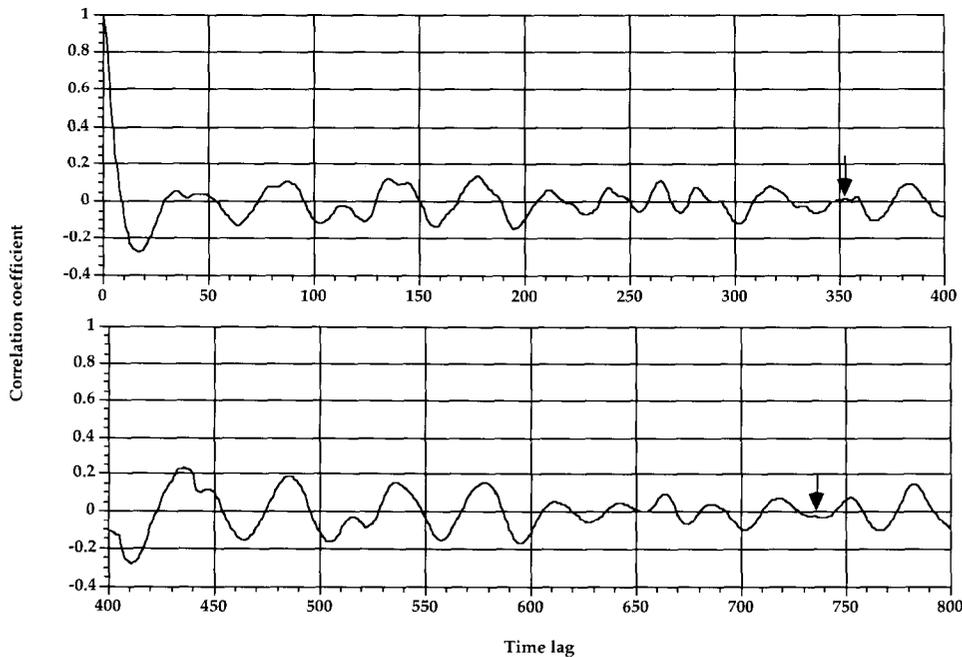


Fig. 4. Correlogram between relative densities of primary consumer and top predator in a food chain with omnivore (4% consumption rate). The system exhibited quasi-periodicity of ca. 1 yr. Arrows represent transition between cycles.

other, independent of time (Fig. 3). The surface of the strange attractor, a set of points in phase space around which the system rotates (Gleick, 1987), can be seen clearly from top view (Fig. 3A). This surface represents the interaction between primary and secondary consumers, but the dynamics of the entire system are better perceived in phase space (Fig. 3B).

Sensitivity analysis revealed that the model is hypersensitive to initial conditions. The Lyapunov coefficient was 0.012; indicating that as time progresses, output generated by the model with a 5% increase in initial population density of the primary consumer will deviate exponentially from the original output as a power of 0.012. A 5% decrease in initial density produced an exponential deviation of 0.0119. The positive λ corroborates system chaos, whereas zero or negative values refute chaos.

When consumption rates of the top predator on the primary consumer were 1%, 2%, 3%, and 4%, the model persisted. Primary and secondary consumer trophic levels exhibited stable limit cycles with a 4- and 6-month periodicity, respectively. Similarly, the top predator exhibited stable limit oscillations, but its periodicity was about two years. The entire system exhibited quasiperiodicity, with a cycle of approximately one year (Fig. 4). When consumption rate was increased to 5%, the system became unstable, and eventually, the primary consumer became extinct. Higher consumption rates (10%, 20%, 30%, 40%, and 50%) resulted in similar outcomes. Above the 4% consumption rate, the higher the amount of consumption of the primary consumer by the top predator (omnivory), the shorter the persistence; in fact, none of the models endured for more than 250 days when consumption rates exceeded 4%.

4. Discussion

The biological interpretation of the analyses are straightforward in some cases. First, the system without omnivory persisted despite wide fluctuations in population densities at all trophic levels (Fig. 2). Second, in the system with om-

nivory, the periodicity exhibited by each consumer is characteristic of the level at which it feeds, thus making demographics more unstable at higher positions in the food chain. Third, for both models (Fig. 1), we could not predict the behavior of the whole system, based on the behavior of the different consumers, even knowing all the different parameters in the model. This is an emergent property of the system. Species in the simulated communities persisted within stable limit cycles (model with omnivory, $C = 0.5$) or chaotic dynamics (model without omnivory, $C = 0.33$), depending on the amount of connectance in each system. The widespread occurrence of omnivory, especially in aquatic systems (Cummins and Klug, 1979), suggests that this phenomenon may not be a destabilizing factor of food chains. Moreover, a review of insect-dominated food webs showed that omnivory is prevalent in arthropod-rich communities (Schoenly and Cohen, 1991).

As predation by the top predator on the primary consumer was increased from 4% to 5%, oscillations in population densities increased; extinction was the ultimate fate of the system, usually within 200 iterations. If reliance by the top predator on the primary consumer was low, then the former could regulate density of the secondary consumer. On the other hand, if the top predator consumed more primary and fewer secondary consumers, the secondary consumer increased to densities that the primary consumer could not support, resulting in the extinction of the primary consumer. Our results corroborate the hypothesis of Moore et al. (1988) to the extent that limited omnivory (between 1% and 4%) decreased oscillations in population density, and did not produce chaos. In contrast to their predictions, increased omnivory resulted in greater oscillations in density and the eventual extinction of the primary consumer population.

Species that feed near the top of a food chain generally exhibit more unstable population dynamics and have longer return times (Pimm, 1982). Long return times occur because demographic parameters in Lotka–Volterra equations become “too restricted” by the population dynamics of species in lower levels of the food chain (Pimm and Kitching, 1987). Consequently, long

food chains also will have longer return times (the amount of time required for populations of species in a particular chain to return to equilibrium; Pimm, 1982).

The population dynamics question, i.e., whether the predictions of Pimm's model are applicable to real communities or not, has two facets. First, the actual population might be unstable because too many restrictions are imposed by population dynamics of species which occur lower in the food chain. Second, the output generated by the Lotka-Volterra equations used by Pimm and colleagues (Pimm and Lawton, 1977, 1978; Pimm, 1982) may become unrealistic when four or more predator-prey interactions are included in a food chain. In a recent paper by Law and Blackford (1992), communities were modeled with Lotka-Volterra equations that incorporated various levels of omnivory. As omnivory increased in the system, local stability of the component populations decreased and populations became extinct. On the other hand, communities with higher connectance (i.e., higher omnivory) could re-assemble more easily than those with lower connectance when re-colonization was allowed in the model.

Real communities, like the epimacro-benthic riffle community of the South Llano River, are much more complex than the models used in this work. Nonetheless, about 30% of the food chains from the empirical web were similar to those modeled herein (Camilo, 1992; Camilo and Willig, 1995). Caution must be exerted when trying to extrapolate the effects of omnivory from models to a real community. However, such constructs provide a way for ecologists to dissect the complex structure of food webs. Food webs incorporate a wide assortment of trophic interactions, energy avenues (Moore et al., 1988), and higher level interactions. This makes predictions about webs, based on simple food chain models somewhat controvertible. Still, even this simple model is able to capture a wide range of complex behaviors.

The role of chaos in ecology is controversial (Hansson, 1991; Sandell et al., 1991; Scheffer, 1991), with some authors even questioning if chaos occurs in nature (Berryman and Millstein,

1989a,b; Lomnicki, 1989; Mani, 1989; Nisbet, 1989). Nonetheless, the emerging consensus is that ecological systems are predisposed to chaos and that natural selection does not select against it (Allen, 1989; Logan and Allen, 1992). If oscillations are weak (Ellner, 1991) or the region of the strange attractor does not include areas of probable extinction (Allen, 1989), then chaos could persist despite natural selection. Our results indicate that the system without omnivory persisted because no region of high extinction probability was near the strange attractor surface, although fluctuations in population densities were of great amplitude (Fig. 2).

In the South Llano River, creeping water bugs (Naucoridae) maintain high population densities (Sites and Willig, 1991; Herrmann, 1992) and are the most abundant predators in the macrobenthic riffle community. Each of these predacious bugs (*Ambrysus circumcinctus*, *Cryphocricos hungerfordi*, and *Limnocoris lutzi*) is considered to be omnivorous, feeding at several trophic levels and on a wide variety of prey taxa (Camilo, 1992; Camilo and Willig, 1993). Monthly population surveys of benthic macroinvertebrates over the last three years have shown that abundances of all three species of creeping water bugs fluctuate widely, even in the absence of natural disturbance (Willig and Sites, unpublished data). The top predator in this system is the hellgrammite, *Corydalus cornutus*, which also is an omnivore (Camilo 1992; Camilo and Willig, 1993). For a top predator, this species can sustain large population densities (Brown and Fitzpatrick, 1978), although fluctuations have great amplitude (Bowles, 1990). An explanation for the persistent, wide fluctuations observed in the field for these insects may be the large connectance within the system and chaotic nature of the predator-prey interactions.

5. Conclusions

The pervasive fluctuation of population densities exhibited by many aquatic insects has long been attributed to stochastic events (Resh et al., 1988). Chaotic explanations were dismissed be-

cause of the view that natural selection should select against chaos (Berryman and Millstein, 1989a,b). On the other hand, if density fluctuations are not extreme, or the surface of the strange attractor is distant from areas of high extinction probability, then perhaps natural selection does not operate against chaotic population dynamics.

For more than a decade the prevalent opinion about omnivory was that it was a destabilizing force in community food webs (Pimm, 1982). Our empirical evidence (Camilo, 1992; Camilo and Willig, 1994) and modeling efforts, combined with the recent work of others (Moore et al., 1988; Schoenly and Cohen, 1991; Law and Blackford, 1992), indicates that omnivory is not necessarily a detrimental phenomenon, but can be an important stabilizing factor in food webs.

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