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Short-term dynamics of processing chain systems

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Abstract

A processing chain results when a single resource passes through a sequence of changes in condition and two (or more) consumer species specialize on resource in different stages of transformation. Each consumer species removes some resource from the total pool and may also accelerate processing of resource to the next condition in the sequence. As a result of the tradeoff between processing and consumption, interactions in processing chains may be either amensal or commensal at equilibrium.

In this paper I examine short-term (transient) dynamics of processing chains, by considering population growth through time in a simple two-species processing chain model. I address interspecific interactions by comparing the performance of one species, to a given time horizon, in patches with and without the second. I examine the dependence of short-term interactions on various model parameters. The three parameters with the most influence on short-term interactions are those which largely determine interactions at equilibrium: the consumer-independent processing rate, upstream consumer sloppiness, and upstream resource loss rate.

More generally, and regardless of the details of the model, short-term processing chain interactions are often commensal even when the equilibrium interaction in the same system is amensal. The tendency towards commensalism is most pronounced with the shortest time horizons: all processing chain interactions are commensal for at least an infinitesimal interval. This tendency to short-term commensalism, combined with the non-equilibrium nature of many ecological systems and the limited duration of many experiments, may explain why literature examples of processing chains are nearly all commensal. I discuss the importance of temporal scale in planning and interpreting field experiments with processing chain systems.

Keywords: Amensalism; Commensalism; Interactions, interspecific; Resource dynamics

1. Introduction

Many ecological systems involve resources that pass through a temporal sequence of changes in condition. Such sequences may include physical and chemical changes in detritus during decomposition, changes in plant tissue quality with ripening, maturation, or herbivore damage, release of nutrients from animal tissues by predation, and many others. When such resource transformations exist, and when different consumer species specialize on resource in different conditions, the consumers' dynamics may be coupled through their effects on the resource. Such a system may be termed a *processing chain*. In an

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earlier paper (Heard, 1994) I developed compartment models of simple, two-species processing chain systems and examined their equilibrial properties. I now extend this analysis to consider shorter-term behavior, emphasizing the time-dependence of the signs and strengths of interspecific interactions.

A two-species processing chain is illustrated, and some terms are defined, in Fig. 1 (see also Heard, 1994). In this simplest case, resource exists in the system in two conditions: it is supplied in the "upstream" condition, and some is transformed to the "downstream" condition. The choice of terms emphasizes the unidirectional flow of resource (which results in unidirectional interactions). Each consumer species specializes on, and consumes, resource in only one condition: for instance, in temperate streams some detritivores (shredders) feed on intact leaves while others (collectors) feed on particles derived from leaf breakdown.

The interspecific interaction in a processing chain will depend on the net effect of the "upstream" consumer on resource availability for the "downstream" consumer. The upstream consumer will remove some of the resource, which is therefore unavailable to the "downstream" consumer; however, it may also accelerate resource processing. For instance, if particle size is the relevant aspect of resource condition, the upstream consumer may consume some material which might otherwise have been mechanically fragmented, but may also produce particles in fecal pellets or allow particles to escape while feeding.

As a result of this tradeoff between processing

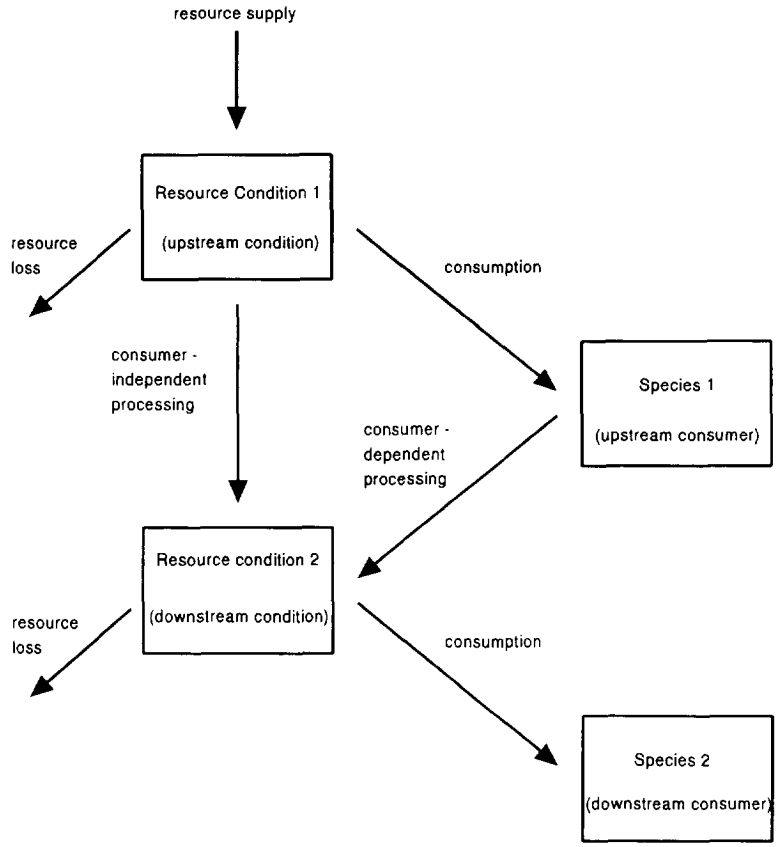

Fig. 1. A general two-species processing chain. The left-hand boxes, or compartments, represent pools of resource in a sequence of two conditions. The right-hand boxes represent populations of two consumer species, one specializing on each resource condition. Arrows represent flow of resources between compartments.

and consumption, interactions between upstream and downstream consumers may be either commensal (downstream consumer population larger in presence of upstream, but no reciprocal effect) or amensal (downstream consumer population smaller in presence of upstream, but again no reciprocal effect) when evaluated at equilibrium (Heard, 1994). However, shorter-term dynamics are also of interest if natural systems do not always reach equilibria. This may be so, for instance, when disturbance or seasonality prevent the attainment of equilibrium (e.g. Denslow, 1985; Pickett and White, 1985), or in ephemeral patches of resource where only short-term consumer growth is possible and consumers survive by dispersing to new patches (e.g. Beaver, 1984; Lacy, 1984; Schoenly and Reid, 1987; Shorrocks, 1990, 1991; Marino, 1991). Furthermore, short-term dynamics may be the relevant concern in interpreting many ecological experiments, which are typically of relatively short duration (Schoener, 1983, his table 1; Tilman, 1989; Gurevitch et al., 1992).

In this paper I examine the short-term dynamics of the processing chain models introduced earlier (Heard, 1994), with emphasis on the outcome of interspecific interactions evaluated at different time horizons. I define a measure of interaction strength, and I describe its time-dependence and its dependence on the parameters of the model. Because the analysis shows that cases which are amensal at equilibrium may be commensal at shorter time horizons, I also ask whether the time-dependence of interactions can help account for the fact that, of literature studies of probable processing chain systems, the overwhelming majority are commensal (Heard, 1994).

2. The model

The compartment model in Fig. 1 can be represented by the system of differential equations

$$\frac{dR_1}{dt} = p(t) - h(R_1) - w_1(R_1) - f_1(R_1,S_1) \tag{1a}$$

$$\frac{dR_2}{dt} = h(R_1) - w_2(R_2) + s[f_1(R_1,S_1)] - f_2(R_2,S_2) \tag{1b}$$

$$\frac{dS_1}{dt} = g_1\{(1-s)[f_1(R_1,S_1)]\} - m_1(S_1) \tag{1c}$$

$$\frac{dS_2}{dt} = g_2\{f_2(R_2,S_2)\} - m_2(S_2) \tag{1d}$$

R_1 and R_2 denote the instantaneous quantities of resource in the upstream and downstream conditions, respectively; S_1 and S_2 denote the instantaneous densities of the upstream and downstream consumers. Resource is supplied to the system at a rate $p(t)$. Resource lost from the system, from condition i, is $w_i(R_i)$. Total resource removal by consumer i, including assimilated and non-assimilated fractions, is $f_i(R_i,S_i)$. For the upstream consumer, a portion $s[f_1(R_1,S_1)]$ of this represents consumer-dependent processing of resource (to condition 2). I refer to this as "sloppiness", as it represents resource taken by the upstream consumer but not assimilated by it; however, I do not mean to restrict the physical or chemical means by which this processing may occur. Consumer-independent processing (again, by any means) is $h(R_1)$. Finally, each species has a metabolic cost, expressed in population units as $m_i(S_i)$, and converts some fraction of the resource it removes to population growth: $g_1\{(1-s)[f_1(R_1,S_1)]\}$ for the upstream consumer and $g_2[f_2(R_2,S_2)]$ for the downstream consumer.

A more explicit model is necessary for further analysis. Letting each consumer species have a type II functional response (using the exponential formulation of Watt, 1959), and making all other functions linear, we have

$$\frac{dR_1}{dt} = p - h \cdot R_1 - w_1 \cdot R_1 - k_1 \cdot S_1 \cdot (1 - e^{-R_1}) \tag{2a}$$

$$\frac{dR_2}{dt} = h \cdot R_1 - w_2 \cdot R_2 + s \cdot k_1 \cdot S_1 \cdot (1 - e^{-R_1}) - k_2 \cdot S_2 \cdot (1 - e^{-R_2}) \tag{2b}$$

$$\frac{dS_1}{dt} = g_1 \cdot (1-s) \cdot k_1 \cdot S_1 \cdot (1 - e^{-R_1}) - m_1 \cdot S_1 \tag{2c}$$

$$\frac{dS_2}{dt} = g_2 \cdot k_2 \cdot S_2 \cdot (1 - e^{-R_2}) - m_2 \cdot S_2 \tag{2d}$$

This is a simple and biologically reasonable choice with which to begin. All quantities are scaled in arbitrary units, because I am interested in examining general, qualitative behavior rather than reproducing any particular system precisely. I previously (Heard, 1994) derived the equilibrium resource levels (R_1^* and R_2^*) and population densities (S_1^* and S_2^*) for Eqs. 2a--2d, and compared S_2^* for two cases: $S_1(0) = 0$, and $S_1(0) > 0$. When $S_2^*(t)|^{S_1>0} > S_2^*(t)|^{S_1=0}$, the interaction is commensal at equilibrium; when $S_2^*(t)|^{S_1>0} = S_2^*(t)|^{S_1=0}$, it is neutral; and otherwise it is amensal. I showed (Heard, 1994) that an approximate condition for equilibrium commensalism is

$$s > \frac{h}{h + w_1} \tag{3}$$

This is valid when $m_1 \ll g_1 \cdot k_1 \cdot (1-s)$: that is, when the upstream consumer (when not food limited) is capable of consuming much more resource than needed to meet metabolic costs. It also requires $p > 0$; when $p = 0$ (an ephemeral resource patch), both equilibrium population sizes are 0 and the interaction is always (and trivially) equilibrium-neutral.

3. Methods

In what follows, I examine short-term dynamics of the processing chain model of Eqs. 2a–2d. Other formulations are possible, with different forms given to the functions in Eqs. 1a–1d. While their dynamics will doubtless differ in detail, they also share important features (e.g. Appendix).

I used a computer program, written in QUICK BASIC, to provide numerical solutions of the differential equations. Given parameter values and initial conditions, the program steps through time using the difference equation analogs to Eqs. 2a–2d (i.e. with $d(\bullet)/dt$ replaced by $\Delta(\bullet)/\Delta t$) to determine changes in R_1, R_2, S_1, and S_2. One simple adjustment is needed, because with the difference equation analogs it is possible for ΔR_i to exceed the available pool R_i when this pool is small and consumers are numerous. Therefore, at each iteration, the "demand" on R_i by all fluxes (Fig. 1) is calculated, and if total demand exceeds R_i, each flux is adjusted proportionately. Error introduced by the numerical method may be assessed by iterating the computer model close to equilibrium, for which exact solutions are available (Heard, 1994). In what follows, I use a Δt at least a factor of 2 smaller than that required to give accurate equilibrium values. Further reduction of Δt did not appreciably change results at any time horizon.

Since I am primarily interested in assessing interspecific interactions, I compare the population trajectories of S_2 with and without S_1 present, given a set of parameters, by setting $S_1(0) > 0$ or $S_1(0) = 0$. (The converse case, S_1 with and without S_2, is uninteresting because S_2 has no effect on S_1). An interaction is commensal, evaluated at time horizon t, if $S_2(t)|^{S_1>0} > S_2(t)|^{S_1=0}$; it is neutral when $S_2(t)|^{S_1>0} = S_2(t)|^{S_1=0}$, and it is amensal otherwise.

Several further definitions will be useful. First, calculate $I = (S_2(t)|^{S_1>0} - S_2(t)|^{S_1=0})/S_2(t)|^{S_1=0})$; this quantity is the *interaction strength* at time horizon t. This definition of interaction strength is analogous to the measure of competition intensity described by Wilson and Tilman (1991), except that the order of subtraction is reversed so that negative interactions will have negatively signed interaction strengths. An interaction strength of -0.5, for instance, indicates that the downstream consumer attains by time t, in the presence of the upstream, only half the population size it would reach alone. Notice that this definition of interaction strength is a cumulative one: it measures the interaction measured after a time t, not the instantaneous interaction at time t. Equivalently, it is the interaction one would measure in an experiment running from time 0 to time t.

Next, because interactions which are amensal for large t are commensal for some smaller val-

ues of t (see below and Appendix), define the *switchpoint* (t_{sw}) as the non-zero time horizon at which the interaction is exactly neutral. Equilibrium-commensal interactions have infinite switchpoints. Third, define the *maximum interaction* (I_{max}) as the highest value of I attained during iteration; this is the strongest commensalism possible given the particular set of parameter values. I_{max} and t_{sw} are useful measures because the likelihood of observing a commensal result in an experiment of arbitrary power and length is directly proportional to the magnitudes of I_{max} and t_{sw}. Finally, the *equilibrium interaction* (I_{eq}) is just the interaction strength at equilibrium, approximated here by $I(t = 1000)$. See Fig. 3 for an illustration of these measures.

The short-term dynamics of any system are, of course, strongly dependent on the initial conditions $R_1(0)$, $R_2(0)$, $S_1(0)$, and $S_2(0)$. Here I examine the biologically interesting case where the initial resource pool is small ($R_1(0) = R_2(0) = 0$), but there is a non-zero resource supply rate. This represents a system with ongoing resource input, such as detritus in a stream. I use $S_1(0)$ and $S_2(0)$ small ($= 1$); that is, iteration begins when colonization of a site has just occurred. In such systems, short time horizons would be externally imposed, for instance by disturbance or short-term experiments. Ephemeral patches, to which short time horizons are intrinsic, would be represented by models with $R_1(0)$ substantial and $p = 0$; these show similar but not identical dynamics (Heard, unpublished simulations) and I will not examine them further here.

I examine the dependence of the maximum interaction (I_{max}), the switchpoint (t_{sw}), and the equilibrium interaction (I_{eq}) on the values of the parameters of model 2a–2d. There are 11 parameters in the model, and therefore a full characterization of the model's behavior would require mapping an 11-dimensional hypersurface. This is clearly impractical; instead I examine the dependence of interactions on one parameter at a time, in slices across the hypersurface. For each parameter I examined several such slices; that is, I examined the effect of that parameter for several different reasonable combinations of the others. Different "slices" were qualitatively similar, except that behavior often differed across the equilibrium-commensalism condition 3. I show here only representative plots.

3.1. Parameter values

Of the 11 parameters in the model, eight (g_1, g_2, h, m_1, m_2, s, w_1, and w_2) can in the difference formulation range from 0 to 1 (while h, w_i, and m_i could theoretically exceed 1 in the differential formulation, such large values are biologically uninteresting). The remaining three parameters (k_1, k_2, and p) can take any non-negative value. I chose to restrict k_1 and k_2, the saturation feeding rates, to values less than 1 in my simulations. In doing so, I did not allow an organism to consume more than its body mass of resource during one time unit. Because the saturation feeding rates can be reduced by reducing the length of the time unit, this does not sacrifice any biological realism.

I made one further set of restrictions to the parameter values. I did not consider combinations of parameters for which one species or the other was unable to grow even when resource was available – that is, combinations of parameters representing consumers too inefficient to live. This meant disallowing very low growth efficiencies (g_1 and g_2), very low saturation feeding rates (k_1 and k_2), very high metabolic rates (m_1 and m_2), and very high sloppinesses (s). Specifically, I required $g_1 \cdot k_1 \cdot (1 - s) > m_1$ and $g_2 \cdot k_2 > m_2$.

4. Results

How do populations grow and interspecific interactions change through time in processing chain systems? The answers, of course, depend somewhat on which explicit forms are chosen for the functions in the model 1a–1d; therefore, I will not emphasize quantitative details here.

For systems with ongoing resource input, the equilibrium result may be either commensalism or amensalism (see condition 3 above). A typical set of population growth curves for an equilibrium-commensal case is shown in Fig. 2a. Each population increases monotonically to the equi-

librium, which is approximated closely by the population sizes at $t = 1000$. The important comparison is of the growth curves for the downstream consumer (species 2), with and without the upstream consumer. In this case, the biomass of the downstream consumer when the upstream is present exceeds the biomass of the downstream consumer when alone, for all time horizons: the interaction is always commensal (Fig. 2b).

In contrast, the behavior of equilibrium-amensal cases is more complex. A typical result is shown in Fig. 3. The population growth curves (Fig. 3a) still show monotonic increases, but now the curves for the downstream consumer alone and together with the upstream cross (here when $t = 33.7$; the switchpoint, t_{sw}, as defined above). As a result, the interaction is commensal (Fig. 3b) for short time horizons, with the interaction

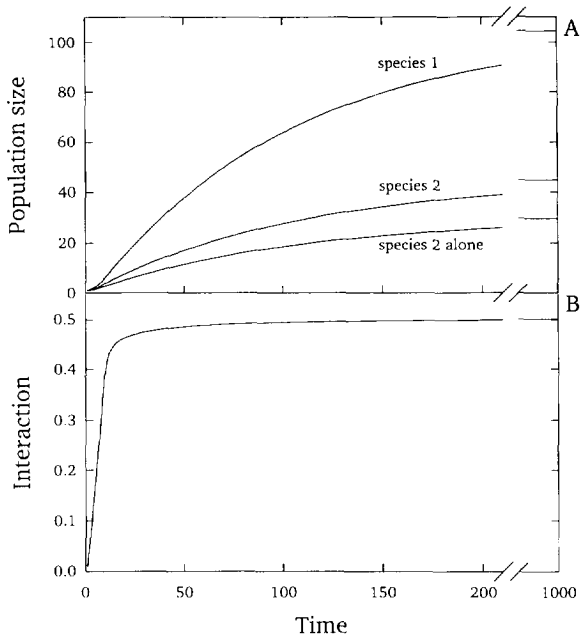

Fig. 2. Typical population growth curves (A) and interaction strength plot (B) for an equilbrium-commensal case. "Species 1" is the upstream consumer; "species 2" is the downstream consumer. Time and population units are arbitrary; interaction strength is defined in the text (see "Methods: short-term dynamics"). Initial conditions (for all figures): $R_1(0) = R_2(0) = 0$, $S_1(0) = 1$ or 0, $S_2(0) = 1$ Parameter values (see Eqs. 2a–2d): $g_1 = g_2 = 0.3$, $h = 0.1$, $k_1 = k_2 = 1$, $m_1 = m_2 = 0.01$, $p = 5$, $s = 0.3$, $w_1 = 0.4$, $w_2 = 0.2$.

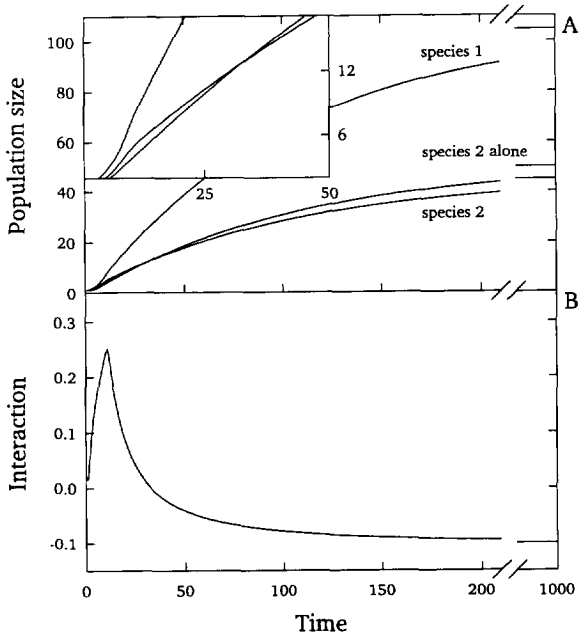

Fig. 3. Typical population growth curves (A) and interaction strength plot (B) for an equilibrium-amensal case. Here $I_{max} = 0.252$, $t_{sw} = 33.7$, and $I_{eq} = -0.10$. Parameter values as in Fig. 2, except $w_1 = 0.2$. Inset: blowup of curves around region of the switchpoint, showing the population trajectories for the downstream consumer with and without the upstream (lower two curves) crossing at $t = 33.7$.

strength peaking (here at $t = 10.8$) and then declining. Past t_{sw}, the interaction is amensal, with strength approaching the equilibrium value. In fact, barring the trivial case where there is no consumer-dependent processing, all equilibrium-amensal interactions (regardless of initial conditions, of parameter values, or even of the particular form given to the functions in model 1a–1d) behave this way, with short-term commensalism for some time interval (for a simple proof, see Appendix). Both the strength and the duration of the short-term commensal interaction can be significant. For instance, in Fig. 3 at its peak the commensal interaction results in a 25% higher population density in patches with the upstream consumer, and the interaction remains commensal for nearly 5 half-lives for consumer-independent resource processing ($t_{1/2} = \ln(2)/h$), during which the downstream consumer population increases 12-fold.

How does the short-term behavior depend on the value of the parameters of model 2a–2d? In particular, what influences the strength and duration of short-term commensal interactions, and how do different parameters compare in their influence?

Higher resource supply rates (p) produced larger populations, but did so proportionately so that interspecific interactions were unaffected; I discuss p no further here. All other parameters did influence the interactions, although not equally strongly. Of the 10 remaining parameters, three (h, s, and w_1) largely determine the nature of the equilibrium interaction (condition 3). They also have strong effects on the short-term dynamics, and I examine them first.

Effects of the consumer-independent processing rate (h) are shown in Fig. 4. When consumer-independent processing is slow, interactions are equilibrium-commensal (Fig. 4a) and therefore have infinite switchpoints (Fig. 4b). For larger values of h, interactions become equilibrium-amensal and show earlier switchpoints. However, a non-zero switchpoint always exists; that is, the interaction is always commensal for at least some time horizons. Furthermore, for all non-zero h, I_{max} exceeds I_{eq}, which means that the interaction strength peaks at some shorter-than-equilibrium time horizon. Finally, notice that very small values of h give extraordinarily strong interactions. This is because when the consumer-independent processing rate is negligible, downstream consumers must rely completely on upstream consumers to produce resource in the appropriate condition (Fig. 1) and the result is an obligate association.

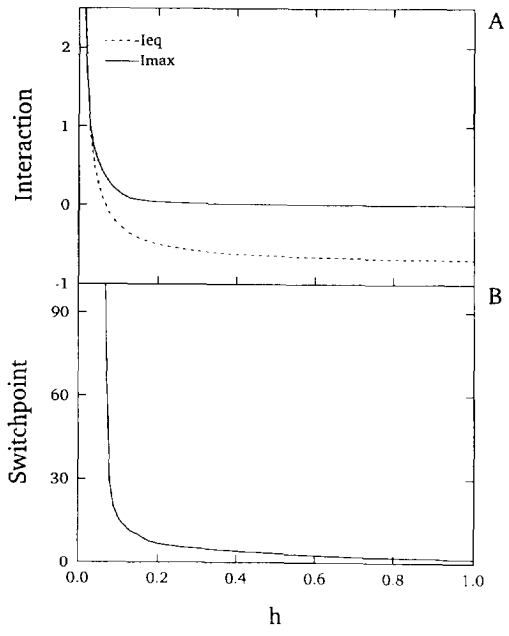

Fig. 4. Effect of consumer-independent processing rate (h) on interspecific interaction strength (A) and switchpoint (B). I_{eq}, I_{max}, and switchpoint are as defined in the text (see Methods). Parameter values as in Fig. 2, except $w_1 = 0.2$ and h as plotted.

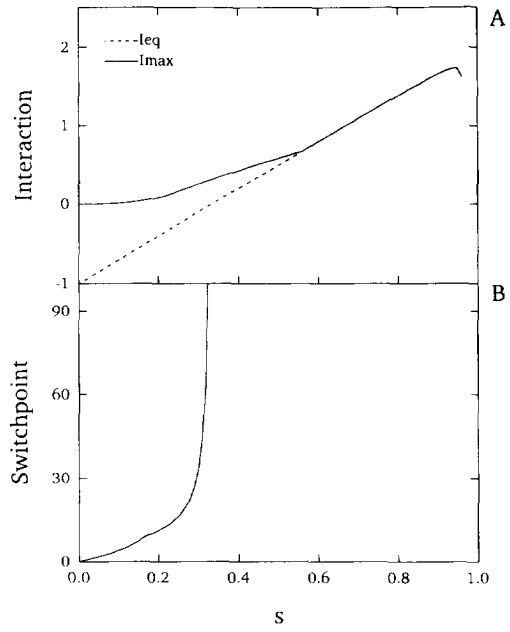

Fig. 5. Effect of upstream consumer sloppiness (s) on interspecific interaction strength (A) and switchpoint (B). Parameter values as in Fig. 2, except $w_1 = 0.2$ and s as plotted.

Effects of the upstream consumer's sloppiness (s) are generally opposite to those of the consumer-independent processing rate (Fig. 5). For large s, interactions are equilibrium-commensal with infinite switchpoints (Fig. 5a), while for smaller s, interactions are equilibrium-amensal with earlier switchpoints. For equilibrium-amensal and some equilibrium commensal interactions (for intermediate values of s; Fig. 5a), interaction strength peaks for short time horizons

and then declines ($I_{max} > I_{eq}$). Both equilibrium and maximum interaction strengths increase with s, except for extremely high values, representing upstream consumers nearly too inefficient to live. The switchpoint vanishes as s approaches 0, because when there is no consumer-dependent processing commensalism at any time horizon is impossible. Upstream resource loss rate (w_1) affects interactions in a very similar way, except that strengths do not show the downturn for very large values (Fig. 6), and the switchpoint does not vanish as w_1 goes to 0.

The remaining parameters have generally more moderate effects on interaction strengths and switchpoints (summarized in Table 1; for more detailed results see Heard, 1993). These effects can differ across the equilibrium-commensalism condition 3; most conspicuously, only equilibrium-amensal systems have finite switchpoints. In general, switchpoints for the equilibrium-amensal case are long when upstream consumers are neither too fast- nor too slow-growing (intermediate g_1 and k_1, low m_1; from the point of view of downstream consumers, upstream consumers that reach high density very fast outstay their welcome sooner.) Switchpoints are, of course, longest when downstream consumers cannot quickly exhaust their resources (low g_2 and k_2, high m_2). However, this relationship is very strong only for very small m_2 and for very small k_2, both of which represent downstream consumers nearly too inefficient to live. Effects on maximum interaction strengths are mild, except for moderate effects of m_1 and m_2: strong interactions were more likely for small m_1 (upstream consumers delivering the most benefit to downstream consumers) and for very large m_2 (downstream consumers nearly too inefficient to live).

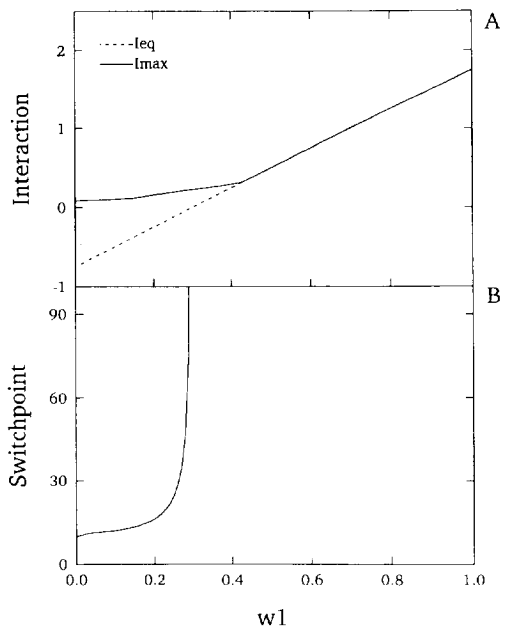

Fig. 6. EFfect of upstream resource loss rate (w_1) on interspecific interaction strength (A) and switchpoint (B). Parameter values as in Fig. 2, except w_1 as plotted.

Table 1
Effects of less influential parameters on system dynamics. For each parameter I show effects for both equilibrium-amensal and equilibrium-commensal systems (combinations of h, s, and w_1); the most conspicuous difference is that only the former have switchpoints. For more detailed results see Heard (1993)

Parameter	Equilibrium-amensal		Equilibrium-commensal
	switchpoint	I_{max}	I_{max}
g_1	peaked	increasing	increasing
k_1	peaked	increasing	increasing
m_1	decreasing	decreasing	decreasing [a]
g_2	decreasing	increasing	increasing
k_2	decreasing [b]	increasing	increasing
m_2	increasing [a]	increasing	increasing [a]
w_2	–	–	–

[a] moderate effect.
[b] strong effect.

5. Discussion

Temporal scale is clearly an important consideration in studies of processing chain dynamics, as the magnitude and even the sign of interspecific interactions can depend on the time horizon at which those effects are evaluated. Short-term interactions depend particularly strongly on the consumer-independent processing rate (h), the upstream resource loss rate (w_1) and the upstream consumer's sloppiness (s), mirroring the importance of these parameters in determining the equilibrium interaction. In general, switchpoints increase sharply as model parameters ap-

proach the threshold for equilibrium commensalism (condition 3 above); however, substantial switchpoints and maximum interaction strengths are not restricted to such cases.

Although the general models I consider here establish that processing chain interactions are time-sensitive, they are less informative about the time scales at which this sensitivity is expressed (steep portions of figures like Figs. 2b, 3b). Either more detailed modelling or (preferably) experiments considering time horizon as a factor would be necessary to establish the relevant time scales for any particular system. However, in at least some cases it would appear that the duration of time-sensitivity can be biologically significant. For instance, the parameter set of Fig. 3 shows a switchpoint equal to several half-lives of consumer-independent processing. The relevant parameters are very rarely measured in nature, but for leaves in temperate streams (where processing has been best documented) the half-life for shredder-independent processing can be very long (e.g. for Augusta Creek, Michigan, in excess of 60 days; Cummins et al., 1980).

The asymmetry in behavior between equilibrium-commensal and equilibrium-amensal interactions is a particularly striking feature of processing chains. The former type are commensal for all time horizons (although they may peak and decline in strength), while the latter show commensalism at short time horizons before switching to the equilibrium amensalism (Figs. 2–3). This is a particularly important result, because it is a very general feature of processing chain models: it is not peculiar to the specific model (2a–2d), nor to the choice of initial conditions (new patch colonization) I make here (see Appendix).

This asymmetry may contribute to a conspicuous pattern observed in a set of (probable) examples of processing chains I recently collected from the literature (Heard, 1994). Condition 3 indicates that at equilibrium both commensal and amensal interactions are possible, and it does not imply that either should predominate. However, of those examples including some information about the interspecific interaction, the overwhelming majority (39 of 40) showed commensalism. The results of the short-term modelling suggest at least a partial explanation for this incongruity. If ecological experiments are of short duration, or if the systems under study rarely reach equilibria, then commensal results should predominate.

These two reasons for seeing predominantly commensalisms have quite different implications. If we see short-term commensalisms because the natural systems are non-equilibrial, the phenomenon is real. In contrast, if we see short-term commensalisms because our experiments are short, we are misinterpreting nature: with more appropriate methods, we might discover many amensal interactions.

It is unfortunately difficult to attribute the pattern in literature processing chain studies (Heard, 1994) to one or the other of these possibilities; most likely, both make contributions. First, biologically relevant time horizons may often be fairly short. Many processing chain studies have dealt with consumers for which only part of the life cycle is involved in the processing chain. For instance, shredder and collector insect larvae in streams participate in processing chains (e.g. Short and Maslin, 1977; Wallace et al., 1982; Richardson and Neill, 1991), but as adults they leave the stream and either cease to feed (e.g. mayflies) or exploit different food resources (e.g. blackflies). Consumers like these, then, have time horizons dictated by the timing of the life cycle shift, and equilibrium dynamics are not necessarily relevant.

Second, most processing chain studies have used relatively short-term experiments (if any), and studies of processing chain systems have generally not acknowledged the possible sensitivity of results to temporal scale (but see Wallace et al., 1982). For instance, Short and Maslin (1977) reported increased food uptake rates by stream collectors (caddisflies and blackflies) in artificial streams with shredders (stoneflies). However, the experiment lasted only seven days (much less than one generation), and over longer time intervals the cost of shredder consumption might well have outweighed the benefit of shredder-mediated processing.

Without some justification of the time horizon considered, an observation of a commensal inter-

action in a processing chain system is not very informative. A short-term experiment might suggest a commensal interaction between two consumers in a processing chain system, even though the interaction is amensal at a longer and more biologically relevant time horizon. Of course, an experiment which runs too long might make the opposite error, although one is much less likely to encounter this problem. Extrapolations of commensal results to *shorter* time horizons, on the other hand, are valid for the sign (if not the strength) of interactions, and the same is likely to be true for extrapolating amensal results to longer time horizons.

It is important for ecologists in general to match the time scale of experiments to the relevant time scale for the system (Wiens et al., 1986; Abrams, 1987; Bazzaz and Sipe, 1987; Giller and Gee, 1987; Franklin, 1989; Allen and Hoekstra, 1992, p. 11; Ginzburg and Akçakaya, 1992) – for instance, the lifespan or the interval between reproductive bouts of an organism. The fact that all processing chain interactions will be commensal for sufficiently short time horizons means that this need is particularly acute in field studies of processing chain systems. Such studies to date have not paid sufficient attention to temporal scale. Experiments conducted with carefully justified time horizons, or better still with time horizon as a manipulated variable, are clearly called for.

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Appendix 1

Here I demonstrate that except for the trivial case where there is no consumer-dependent processing ($s = 0$), all processing chain interactions are commensal for at least an infinitesimal interval, regardless of the equilibrium interaction type. Consider a processing chain interaction over an interval from $t = 0$ to $t = \varepsilon$. Effects of upstream (S_1) on downstream (S_2) consumers in processing chain models are mediated only through changes in available downstream-condition resource (R_2); downstream consumer growth rate increases with R_2. Therefore, if we compare cases initially differing only in the presence or absence of the upstream consumer (especially, $R_2(0)|^{S_1>0} = R_2(0)|^{S_1=0}$), a sufficient (although not necessary) condition for commensalism at time $t = \varepsilon$ is that

$$R_2(\varepsilon)|^{S_1>0} > R_2(\varepsilon)|^{S_1=0}, \quad \forall t < \varepsilon \tag{A1}$$

Now, beginning with the model of equations 2a–2d (see text), we have

$$\left.\frac{\mathrm{d}R_2}{\mathrm{d}t}\right|^{S_1>0} = h \cdot R_1 - w_2 \cdot R_2 + s \cdot k_1 \cdot S_1 \cdot (1 - \mathrm{e}^{-R_1}) - k_2 \cdot S_2 \cdot (1 - \mathrm{e}^{-R_2}) \tag{A2}$$

and

$$\left.\frac{\mathrm{d}R_2}{\mathrm{d}t}\right|^{S_1=0} = h \cdot R_1 - w_2 \cdot R_2 - k_2 \cdot S_2(1 - \mathrm{e}^{-R_2}). \tag{A3}$$

Now let the interval ε become very short. In the limit as ε approaches 0,

$$R_2(\varepsilon) = R_2(0) + \frac{\mathrm{d}R_2}{\mathrm{d}t}(0) \cdot \varepsilon.$$

Comparing cases with and without the upstream consumer, we must have commensalism if (but not only if) $R_2(\varepsilon)|^{S_1>0} > R_2(\varepsilon)|^{S_1=0}$; since we are dealing with the limit as ε approaches 0, we do not need to worry about $t < \varepsilon$. Using Eqs. A2 and A3, then we have commensalism if

$$\left[R_2(0) + \frac{\mathrm{d}R_2}{\mathrm{d}t}(0) \cdot \varepsilon\right]^{S_1>0} > \left[R_2(0) + \frac{\mathrm{d}R_2}{\mathrm{d}t}(0) \cdot \varepsilon\right]^{S_1=0} \tag{A4}$$

or if

$$\frac{\mathrm{d}R_2}{\mathrm{d}t}(0)\bigg|^{S_1>0} > \frac{\mathrm{d}R_2}{\mathrm{d}t}(0)\bigg|^{S_1=0}, \qquad \text{(A5)}$$

which is true when

$$s \cdot k_1 \cdot S_1 \cdot (1 - \mathrm{e}^{-R_1}) > 0. \qquad \text{(A6)}$$

But this is true for any positive non-zero values of s and k_1; in particular, it is true regardless of the equilibrium interaction determined by condition 3 (see text). It does not require that $R_1(0)$, $R_2(0)$ or $S_2(0)$ be small, as I used in my simulations, as long as we compare cases with $R_1(0)$, $R_2(0)$ and $S_2(0)$ equal in the two cases ($S_1 > 0$ and $S_1 = 0$). Furthermore, this result (condition A6) does not depend on the specific mathematical form of the terms in Eqs. A2 and A3. In the general processing chain model 1a–1d, the same logic can be applied to find the condition analagous to Eq. A6: $s[f_1(R_1,S_1)] > 0$, which is true whenever the upstream consumer plays a processing role (Fig. 1). Therefore, all processing chain interactions are commensal at sufficiently short time scales (as long as there is some consumer dependent processing), regardless of the details of the model or of their equilibrium signs.

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