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Processing chain ecology: resource condition and interspecific interactions

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Summary

1. When units of a resource pass through a sequence of condition changes over time, and when some consumers specialize on resource in each condition, consumer dynamics may be coupled through their effects on the resource even though they cannot directly compete. Consumers may also influence the rate at which resource is transformed between conditions (e.g. shredders processing leaf detritus in streams). I call such a system a processing chain.

2. Although examples in which consumers influence one another through resource processing have been recognized (if poorly documented), a general treatment of processing chain dynamics has not been available. I use simple compartment models to examine the population behaviour and interspecific interactions of consumers in two-species processing chains. I also compile literature examples of possible processing chain interactions.

3. A range of interactions, from amensal (−, 0) to commensal (+, 0), is possible in theory, and I address factors controlling the interaction type.

4. Despite the theoretical implication of a range of outcomes, literature examples of processing chains are largely commensal. I discuss several possible reasons for this incongruity, including guild- versus species-level effects and issues of temporal scale.

Key-words: amensalism, commensalism, resource quality, resource processing, species interactions.

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Introduction

Studies of interspecific interactions have often focused on effects mediated through the quantity of resources available to consumers. In competitive interactions, two species exploit and diminish a single limiting resource pool, while in predatory interactions the abundance of one species translates directly to resource quantity for the other. These two resource-quantity interactions have had a central place in the development of community ecology (reviews: e.g. Pimm 1982; Connell 1983; Schoener 1983; Kikkawa 1986; Cohen 1989; DeAngelis *et al.* 1989; Yodzis 1989; Goldberg & Barton 1992).

However, consumer population dynamics may also be affected by resource quality or condition. Resource condition may include a number of different properties, and these may vary more or less independently of resource quantity. For example, many browsing or grazing herbivores prefer younger, more nutrient-rich foliage, which may grow in the wake of browsing by other species (e.g. Thompson's gazelles, McNaughton 1976). Alternatively, herbivory early in the growing season may induce defensive responses which lower foliage quality for later herbivores (Faeth 1986). Among frugivorous *Drosophila*, *D. immigrans* survival is higher in citrus fruits infected by *Penicillium* moulds, while *D. melanogaster* survival is higher in uninfected fruits (Atkinson 1981). Different genera of scarab dung beetles are attracted to dung pats of different ages (Peck & Forsyth 1982). Mycophagous *Drosophila* prefer as oviposition sites mushrooms which have been partially browsed by slugs (Worthen 1988); similarly, a variety of mites and insects prefer acorns to which access is afforded by weevil exit holes (Winston 1956).

When units of a single resource pass through a temporal sequence of condition or quality changes, for example as fruit ripens or organic detritus decomposes, the dynamics of the pools of resource in each condition will be strongly coupled. If different con-

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sumer species specialize on resource in different conditions, their dynamics may in turn be coupled through their effects on resource levels, as resource removed while in one condition cannot be transformed to another. Furthermore, in addition to removing some of the resource, consumers may influence the rate at which resource is transformed between conditions. As a result, two consumer species can interact even though the same unit of resource is never simultaneously available to both (and they cannot, therefore, be said to compete). The interaction will be indirect *sensu* Strauss (1991), because the interaction is mediated by resource condition. Such a system may be termed a processing chain (Fig. 1).

Although resource processing has been widely recognized (if only implicitly) in the systems ecology literature (e.g. O'Neill 1976; Hunt 1977; Newbold *et al.* 1982; Odum & Biever 1984; Valiela 1984, p. 297; Hunt *et al.* 1987; Anderson 1988; Moore, Walter, & Hunt 1988; Day *et al.* 1989, p. 283; DeAngelis 1992), these workers have focused on ecosystem-level phenomena and on nutrient cycling rather than interspecific interactions. The population- and community-level implications of processing chains apparently have not been modelled or discussed in general terms (although for some related ideas see Reilly 1974; Kitchell *et al.* 1979; Richardson 1980). Therefore, in this paper I focus on population dynamics and interspecific interactions arising from processing chains. I discuss the nature of simple, two-species processing chains and develop basic theory to predict possible outcomes of interactions between the species. I also briefly review some literature examples of simple ecological systems which are likely to fit into a processing chain framework, and ask what broad patterns may be drawn from them.

Structure of processing chains

Processing chains may be analysed by tracing patterns of resource flow in compartment models. The two-species case is the simplest. A general two-species processing chain is illustrated and some terms are defined in Fig. 1. Resource exists in the system in two conditions: resource is supplied to the system in the 'upstream' (first) condition and some is transformed to the 'downstream' (second) condition. These terms emphasize the unidirectional flow of resource (I do not mean to suggest more than an analogy with the flow of water in a stream or the flow of materials carried by that water; processing chains occur in streams, but they also occur in many other systems (Table 1)). Each consumer species specializes on and consumes resource in only one condition, as in the case of one aquatic species feeding on coarse detritus and a second feeding on particulates derived from the same detritus.

The transformation or processing of resource from the upstream to the downstream condition may follow

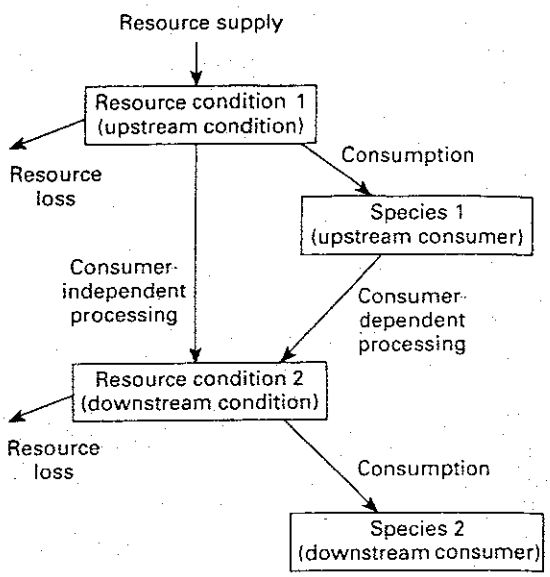

Fig. 1. A general two-species processing chain. The left-hand boxes or compartments represent pools of resource in a sequence of two conditions. The right-hand boxes represent populations of two consumer species, one specializing on each resource condition. Arrows represent flow of resources between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

two pathways (Fig. 1). In consumer-dependent processing, some resource is processed as a consequence of the activity (especially feeding activity) of the upstream consumer; for instance, faecal pellets might be a source of particulates. Consumer-independent processing, on the other hand, occurs even in the absence of the upstream consumer. If a particular upstream consumer species is of interest, then processing by other species might be included in this pathway (and a suitable form given to the function describing it); alternatively, abiotic agents, such as mechanical fragmentation of detritus, may be responsible for this processing. Finally, resource in each condition may leave the system (or equivalently, be transformed to a condition not available to consumers).

The processing chain depicted in Fig. 1, and the models I develop based on that compartment diagram, are simple in structure and will undoubtedly omit some features of many natural systems. More complicated models could, of course, be constructed for detailed simulations of any single system. For instance, the models could be elaborated by adding further resource conditions or consumers and the connecting processing pathways. Alternatively, consumer species might be replaced by consumer guilds, although perhaps with some loss of modelling precision. Non-trophic interactions, such as waste product toxicity or behavioural interference, might occur in addition to trophic interactions and introduce additional feedbacks. Finally, if one consumer can use resource in both conditions, another consumption arrow would be added and the interaction

Table 1. Literature p[illegible]sing chains

System	R_{up}	R_{down}	Mech*	S_{up}	S_{down}	Comp†	Outcome‡	Data§	Lab/field¶	Reference
Stream detritus	Alder leaves	FPOM : faeces, leaf fragments	PS	*Pteronarcys californica* (Plecoptera), *Simulium articum* (Diptera)	*Hydropsyche california* (Tricoptera)	—	(+, NR)	E(I) E(M)	L	Short & Maslin (1977)
Stream detritus	Alder leaves	FPOM : faeces, leaf fragments	PS	*Lepidostoma quercina* (Trichoptera)	Simuliidae (Diptera)	—	(+, NR)	E(M) N(I)	L	Grafius & Anderson (1979)
Stream detritus	Hickory leaves	FPOM : faeces, leaf fragments	PS	*Pteronarcys* (Plecoptera), *Pycnopsyche* (Tricoptera), *Tipula* (Diptera)	*Stenonema* (Ephemeroptera)	—	(+, 0)	E(I) N(I)	L	Cummins *et al.* (1973)
Steam detritus	Leaves	FPOM : faeces, leaf fragments	PS	Various shredders	Various collectors	m	(+, NR)	E(M) N(I)	L	Shepard & Minshall (1984)
Stream detritus	Leaves	FPOM : faeces, leaf fragments	PS	Various shredders	Various collectors	m	(NR, NR)	Ob(M) N(I)	F	Kirby, Webster & Benfield (1983)
Stream detritus	Alder, maple leaves	FPOM : faeces, leaf fragments	PS	Various shredders	Various collectors	—	(+, NR)	E(M) E(I)	F/A	Richardson & Neill (1991)
Stream detritus	White oak leaves	FPOM : faeces, leaf fragments	PS	*Goniobasis clavaeformis* (Gastropoda)	None considered	—	(NR, NR)	E(M) N(I)	L	Mulholland *et al.* (1985)
Stream detritus	Leaves	FPOM : faeces, leaf fragments	PS	Various shredders	Various collectors	—	(+, NR)	E(M) N(I)	F	Wallace *et al.* (1982)
Stream detritus	Leaves	DOM	PS	*Peltoperla*, *Pteronarcys* (Plecoptera) ; *Tipula* (Diptera)	Bacteria	—	(+, NR)	E(M) N(I)	L	Meyer & O'Hop (1983)
Soil detritus	Grass leaves	Organic particles	PS	Millipedes, insect larvae	Termites, oligochaetes, bacteria	—	(+, NR)	N(M) N(I)	—	Lamotte (1989)
Soil detritus	Coarse forest litter	Fine litter	PS	Millipedes	Bacteria	—	(+, NR)	Ob(M) N(I)	F	Nef (1957)
Soil detritus	Coarse litter	Faeces	PS	Soil arthopods	Bacteria, fungi	—	(+, NR)	Ref	—	Crossley (1976)
Phytotelm : *Heliconia* bracts	Bract tissue	Particles, bacteria	PS	*Cephaloleia* (Coleoptera)	*Wyeomyiia pseudopecten* (Diptera), copepods	—	(+, NR)	N(M) N(I)	—	Naeem (1990)
Phytotelm : Sulawesi treeholes	Coarse detritus	Fine detritus	PS	Scirtid beetle, *Tiputoidina* (Diptera)	*Dasyhelia*, *Megaselia* (Diptera)	—	(NR, NR)	N(M) N(I)	—	Kitching (1987)
Phytotelm : British treeholes	Coarse and buried detritus	Fine and suspended detritus	PS	*Metriocnemus* (Diptera), *Prionocyphon* (Coleoptera)	*Aedes geniculatus* (Diptera)	m	(+, NR)	N(M) E(I)	F	Bradshaw & Holzapfel (1992)
Phytotelm : various treeholes	Coarse detritus	Fine detritus	PS	Various Diptera, Coleoptera	Various Diptera, mites	—	(NR, NR)	N(M) N(I)	—	Kitching & Pimm (1985)
Phytotelm : *Nepenthes* pitchers	Intact carcasses	Older detritus	PS	Various Diptera	Other Diptera, mites	+	(NR, NR)	N(M) N(I)	—	Kitching & Pimm (1985) Beaver (1983, 1985)

Table 1 (*cont'd*)

System	R_{up}	R_{down}	Mech*	S_{up}	S_{down}	Comp†	Outcome‡	Data§	Lab/ field¶	Reference
Phytotelm: *Sarracenia* pitchers	Sunken carcasses	Particles (and bacteria)	PS	*Metriocnemus knabi* (Diptera)	*Wyeomyia smithii* (Diptera)		(+, 0)	E(M) E(I)	F	Heard (1993)
Wood	Interior wood (pine, oak logs)	Exposed wood	A	Beetles	Fungi, small invertebrates	+	(+, NR)	N(M) N(I)	—	Savely (1939) see also Maser *et al.* (1984)
Wood	Interior wood (pine logs)	Exposed wood	A	Buprestid and cerambycid beetles	Fungi	+	(+, NR)	Ob(M) E(I)	F/A	Leach, Orr & Christensen (1937) see also Kaarik (1974)
Oyster reefs	Suspended organic matter	Deposited detritus	A	Oysters, mussels	Benthic detritivores	—	(+, 0)	Ob(M) Mod(I)	F	Dame & Patten (1981)
Carrion	Intact carcasses	Exposed or tunnelled flesh	A	Ants, muscoid flies	Dermestid, trogid beetles	m	(+, NR)	N(M) N(I)	—	Schoenly & Reid (1987)
Carrion	Intact impala carcasses	Exposed flesh	A	Serval (Felidae)	Blowflies	+	(+, NR)	Ob(M) Ob(I)	F	Ellison (1990)
Carrion	Intact salmon carcasses	Torn carcasses	A	Bald eagles	Crows, glaucous-winged gulls	+	(+, NR)	N(M) N(I)	—	Skagen, Knight & Orians (1991)
Acorns	Intact acorns	Exposed cotyledons, faeces	A	*Curculia recrus* (Coleoptera)	*Valentinia glandulella* (Lepidoptera), dipteran larvae, mites	—	(+, NR)	Ob(M) N(I)	F	Winston (1956)
Acorns	Intact acorns	Exposed cotyledons, faeces	A	*Melissopus latiferreanus* (Lepidoptera)	*Valentinia glandulella* (Lepidoptera), dipteran larvae, mites	—	(−, NR)	Ob(M) N(I)	F	Winston (1956)
Mushrooms	Intact, fresh mushrooms	Exposed, roughened tissue (for oviposition)	A	*Arion* slugs	Drosophilid flies	+	(±, NR)	E(I) N(I)	F	Worthen (1988)
Dung	Intact cow pat	Exposed tunnelled faeces	A	*Aphodius*, *Sphaeridium*, *Cercyon* beetles	Dipteran larvae, mites	+	(+, NR)	Ob(M) N(I)	F	Valiela (1974)
Carrion	Live teleosts	Dead floating teleosts	RL	Human prawn trawlers	Gulls, terns, cormorants	—	(+, NR)	Ob(M) Ob(I)	F	Wassenberg & Hill (1990) Blaber & Wassenberg (1989)
Carrion	Live teleosts	Dead floating teleosts	RL	Human whitefish trawlers	Gulls, skuas, gannets	—	(+, NR)	Ob(M) Ob(I)	F	Hudson & Furness (1988)
Dung	Grass	Herbivore dung	RL	Herbivores	Coprophilous insects, fungi	—	(+, NR)	N(M) N(I)	—	Hanski & Cambefort (1991); see also McNaughton, Coughenour & Wallace (1982)

Table 1 (*cont'd*)

System	R_{up}	R_{down}	Mech*	S_{up}	S_{down}	Comp†	Outcome‡	Data§	Lab/field¶	Reference
Soil detritus	Live plant tissues	Detritus	RL	Herbivores	Detritivores	—	(+?, NR)	N(M) N(I)	—	Hunt *et al.* (1987)
Soil detritus	Detritus	Soil inorganic nitrogen	RL	Detritivores	Plants	—	(+, NR)	N(M) N(I)	—	Hunt *et al.* (1987)
Soil	Bacterial tissue N	Soil nitrogen	RL	Amoebae	Blue grama grass	—	(+, NR)	E(M) E(I)	L	Elliott, Coleman & Cole (1979)
Patch reefs	Sea grass nitrogen, phosphorus	Soluble, particulate N, P	RL	Grunts	Corals	—	(+, +)	Ob(M) E/Ob(I)	F	Meyer *et al.* (1983)
Lake plankton	Zooplankton phosphorus	Soluble P	RL	Yellow perch	Nanoplankton	—	(+, NR)	E(M) E(I)	F/A	Mazumder *et al.* (1988)
Lake plankton	Zooplankton phosphorus	Soluble P	RL	Yellow perch	Phytoplankton	—	(+, NR)	E(M) E(I)	F/A	Vanni & Findlay (1990)
Serengeti grassland	Mature, senescent grassland	Regrowth	O	Wildebeest	Thompson's gazelles	?	(+, NR)	E(M) Ob(I)	F	McNaughton (1976)
Soil detritus	*Pteridium* petiole cellulose	Sugars	CH**	Cellulose- and lignin-decomposing fungi	Phycomycete sugar fungi	—	(+, NR)	Ob(I) N(M)	F	Frankland (1966)
Soil detritus	Chitin nitrogen	Mineral nitrogen	CH	*Pseudomonas stutzeri*	Blue grama grass	—	(+, NR)	E(M) E(I)	L	Ingham *et al.* (1985)
Rumen	Carbohydrates	Lactate	CH	*Lactobacillus*, *Streptococcus*, others	*Veillonella alcalescens*, *Megasphaera elsdenii*	—	(+, NR)	E(M) N(I)	L	Hobson (1976)
Rumen	Carbohydrates	H_2, CO_2	CH	Various bacteria and protozoa	Methanogens	—	(+, NR)	E(M) N(I)	L	Wolin (1979) Hobson (1976)
Milk spoilage	Casein	Amino acids	CH	*Bacillus cereus*	*Bacterium fluorescens*	m	(+, NR)	—	L	Waksman & Lomanitz (1925)
'Detritus'	Potato starch	Maltose	CH	*Mucor rouxianus*	*Micrococcus* sp.	—	(+, NR)	E(M) E(I)	L	Vueillemin (1902)
Fermentation	Mannitol	Fructose	CH	*Acetobacter suboxydans*	*Saccharomyces carlsbergensis*	—?	(+, 0)	E(M) E(I)	L	Chao & Reilly (1972)
Vinegar production	Fruit sugars	Ethanol	CH	Yeasts	*Acetobacter*	—	(+, NR)	—	—	Brock (1966)

* Mechanism: A, access; CH, chemical; RL, release from living biomass; PS, particle size; O, other.
† +, Competitive element present because one consumer uses resource in both conditions; —, no competitive element; m, maybe (not clear from reference).
‡ Outcome: as posited, but not necessarily tested. NR, not reported.
§ Data: E, experimental; Ob, observational; Mod: mathematical modelling; N, none. In parentheses: I, pertaining to interaction; M, pertaining to the postulated mechanism of interaction. Ref, synthesized from referenced sources.
¶ Lab/field: F, mostly field data, natural communities; F/A, mostly field data, artificial communities (e.g. artificial streams); L, mostly laboratory data.
** These 'chemical' processing chains are probably widespread among micro-organisms; I give only a few representative examples here. For review, see for example Alexander (1971, Ch. 10).

could include an element of interspecific competition. The theoretical models I develop here deal with the basic processing chain of Fig. 1 and are, therefore, most appropriate as general, qualitative models or for systems where at least as a first approximation such elaborations are not necessary.

The effect of an upstream consumer on the population of a downstream consumer depends on its net effect on the availability of resource in the downstream condition (that is, neglecting non-trophic interactions). On the one hand, the upstream consumer removes resource which, if unconsumed, could eventually have entered the downstream condition. On the other hand, the upstream consumer may also increase the rate at which resource is processed to the downstream condition, the fraction of resource so processed, or both. This sets up a trade-off, from the point of view of the downstream consumer, between the upstream consumer's role as a consumer (reducing the ultimate resource supply) and its role as a processor (making the remaining resource available sooner).

In the absence of consumer-independent processing, the downstream consumer depends entirely on the upstream to provide resource in the appropriate condition ('resource dependence'; Fig. 2a). Clearly, this interaction is commensal [or (+, 0); because resource flow is unidirectional, the downstream consumer cannot affect the upstream via resources]. In contrast, when there is no consumer-dependent processing, the resource use of the upstream consumer only reduces the availability of resource in the downstream condition, and the interaction is amensal [or (−, 0); 'resource pre-emption'; (Fig. 2b)]. Intuitively, then, we might expect processing chain interactions to range from strongly amensal through strongly commensal, depending on the relative importance of the two processing pathways. A simple mathematical model will make this expectation more explicit.

Modelling processing chains

The compartment model of Fig. 1 can be described by a system of four differential equations:

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

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

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

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

In these general equations, no particular forms are given to the functions describing resource flow. 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 consumer (I consider units for these and other quantities after introducing a more specific model). The rate of resource supply to the system is $p(t)$. Resource lost from the system from condition i, as a function of the standing pool, is $w_i(R_i)$ (if this function is linear, these models resemble chemostat models). Total removal of resource by consumer i, including assimilated and non-assimilated portions, is $f_i(R_i, S_i)$; the functions f_i are functional responses (multiplied by the appropriate consumer densities). In the case of consumer 1, a fraction

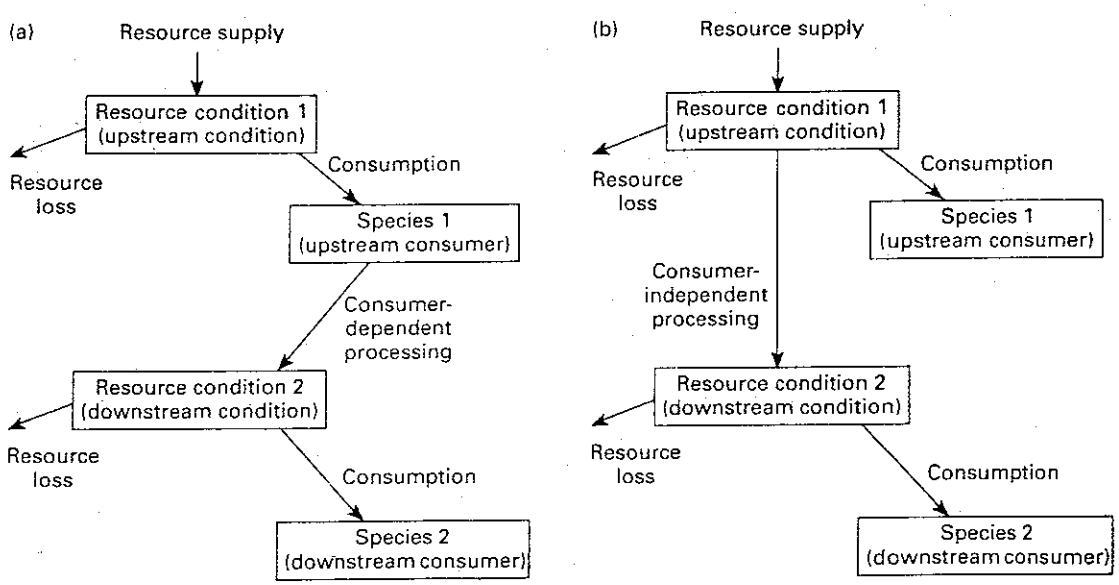

Fig. 2 Limiting cases for processing chain dynamics (a) Resource dependence: no consumer-independent processing (b) Resource pre-emption: no consumer-dependent processing.

$s[f_1(R_1, S_1)]$ of this removal represents consumer-dependent processing of resource to condition 2 (I refer to s as 'sloppiness', and include here all material processed by activity of the upstream consumer). Consumer-independent processing is a function $h(R_1)$. Finally, each consumer has a maintenance 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 consumer 1 and $g_2[f_2(R_2, S_2)]$ for consumer 2. I ignore non-metabolic losses such as predation.

To examine the interspecific interactions in a processing chain system, we must give more explicit forms to the functions in equation 1a–d. Since different resources will no doubt have different mechanisms of transformation and uptake, no single form will be fully appropriate for all systems; however, if we confine our interest to general, qualitative features it is appropriate to begin with a relatively simple set of equations. One reasonable possibility is to specify type II functional responses (Holling 1959; but using exponential formulation of Watt 1959) for both consumers, and let the remaining functions be linear:

$$\frac{dR_1}{dt} = p - h \cdot R_1 - u_1 \cdot R_1 - k_1 \cdot S_1 \cdot (1 - e^{-R_1}) \tag{2a}$$

$$\frac{dR_2}{dt} = h \cdot R_1 - u_2 \cdot R_2 + s \cdot k_1 \cdot S_1 \cdot (1 - e^{-R_1}) - k_2 \cdot S_2 \cdot (1 - e^{-R_2}) \tag{2b}$$

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

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

The assignment of units for parameters and state variables (R_i, S_i) is flexible: the most appropriate choices for a particular system will depend on the biology of that system. For my purposes in this paper, the exact choice of units is unimportant. It is convenient for book-keeping reasons to denote resource pools (R_i) and consumer densities (S_i) in the same units: mass is perhaps most intuitive, but depending on exactly what limits consumer growth in a particular system, both resources and consumers could be counted in other units such as nitrogen- or phosphorus-equivalents. Different state variables may be given different units if desired, but then appropriate conversion constants must be introduced. Any convenient time unit may be used, with parameters scaled to accommodate that choice. Of the parameters, p is a rate in (resource units)(time units)$^{-1}$; s and g_i are dimensionless fractions, and h, u_i, and m_i are exponential decay rates measured in (time units)$^{-1}$; s and g_i must range from 0 to 1. Finally, the saturation feeding rates (k_i) are also measured in (time units)$^{-1}$ (resource units per consumer unit per time unit, with resource and consumer units cancelling as suggested above). The k_is could theoretically exceed 1 if a consumer can take in more than its body equivalent in food in one time unit, although this situation might warrant the adoption of a finer time resolution.

Effects of one species on another may be evaluated at different temporal scales (equilibrium or transitory dynamics), depending on the questions of interest. Here, I will examine the nature of the equilibria and comment only briefly on shorter term behaviour. Two species, then, may be said to interact if the presence or absence of one in the system affects the equilibrium density of the other. Criteria other than population density are, of course, possible: for instance, individual fitnesses or population growth rates might be compared instead (Abrams 1987). However, here I examine only density, which is both ecologically important and relatively simple to measure in nature.

The system (2) has four different biologically meaningful equilibria: (i) $S_1^* > 0$, $S_2^* > 0$; (ii) $S_1^* = 0$, $S_2^* > 0$; (iii) $S_1^* > 0$, $S_2^* = 0$; and (iv) $S_1^* = 0$, $S_2^* = 0$. Of these, the last two are uninteresting (because the downstream consumer has no direct or indirect effect on resource in the upstream condition. S_1^* in case (iii) is the same as for case (i)).

For case (i), restricting $p > 0$, $g_i > 0$, $k_i > 0$, $m_i > 0$, and $s < 1$, we find from equation 2a–d that

$$R_1^* = -\ln\left[1 - \frac{m_1}{g_1 \cdot k_1 \cdot (1-s)}\right] \tag{3a}$$

$$R_2^* = -\ln\left[1 - \frac{m_2}{g_2 \cdot k_2}\right] \tag{3b}$$

$$S_1^* = \frac{g_1 \cdot (1-s)}{m_1} \cdot \left\{p + (h + u_1) \times \ln\left[1 - \frac{m_1}{g_1 \cdot k_1 \cdot (1-s)}\right]\right\} \tag{3c}$$

$$S_2^* = \frac{g_2}{m_2} \cdot \left\{s \cdot p + u_2 \cdot \ln\left[1 - \frac{m_2}{g_2 \cdot k_2}\right] + [(s-1) \cdot h + s \cdot u_1] \ln\left[1 - \frac{m_1}{g_1 \cdot k_1 \cdot (1-s)}\right]\right\} \tag{3d}$$

Notice that the presence and feeding biology of the upstream consumer influence the equilibrium density of the downstream consumer (S_2^*), but there is no converse influence (at least through the processes modelled here) of the downstream consumer on the upstream. The unidirectional flow of resource results in a unidirectional interaction.

Whether the interspecific interaction (evaluated at equilibrium) is commensal or amensal can be determined by comparing the performance (here I consider population density) of the downstream consumer in patches with and without the upstream consumer; this is equivalent to comparing S_2^* in the equilibria of

cases (i) and (ii) above. If $S_1^* = 0$ (case ii) then from equation 2:

$$S_2^*(S_1^* = 0) = \frac{g_2}{m_2}\left[\frac{h \cdot p}{h + w_1} + w_2 \cdot \ln\left(1 - \frac{m_2}{g_2 \cdot k_2}\right)\right] \tag{4}$$

Therefore $S_2^* > S_2^*(S_1^* = 0)$ (the interaction is commensal) if:

$$[(s-1) \cdot h + s \cdot w_1] \cdot \ln\left[1 - \frac{m_1}{g_1 \cdot k_1 \cdot (1-s)}\right] + s \cdot p > \frac{h \cdot p}{h + w_1} \tag{5}$$

When the upstream consumer can consume much more resource than needed to meet metabolic costs (if not food limited), $m_1 \ll g_1 \cdot k_1 \cdot (1-s)$. This is equivalent to having a large metabolic scope (*sensu* Yodzis & Innes 1992; McNab 1980 used a slightly different definition). Then, condition 5 reduces to:

$$s > \frac{h}{h + w_1} \tag{6}$$

This approximation should often be reasonable (especially for invertebrates; Yodzis & Innes 1992). The interaction is commensal when consumer-dependent processing is more 'effective' than consumer-independent processing: that is, when the fraction of resource removed by upstream consumers which is processed to the downstream condition (s) exceeds the fraction of resource not consumed which is so processed [$h/(h+w_1)$]. The interaction is amensal when the reverse is true, and neutral if consumer-independent and consumer-dependent processing are equally effective. The influence of the value of s on the interaction, for an illustrative set of parameter values, is depicted in Fig. 3a.

There is no *a priori* reason to expect either consumer-dependent or consumer-independent processing to be consistently more effective, and therefore a range of interaction types is to be expected. Note that if $h = 0$ (resource dependence), the interaction is always commensal, and if $s = 0$ (resource pre-emption) the interaction is always amensal; this confirms the intuitive assessment offered above. If $w_1 = 0$, so that all resource is eventually subject to consumer-independent processing, the interaction is always amensal because consumption (removal less processing) by the upstream consumer represents an uncompensated loss of resource. However, if some resource is lost from the system ($w_1 > 0$) this consumption can produce a net gain for the downstream consumer (e.g. stream insect shredders processing leaves otherwise lost by transport or during storms: Wallace, Webster & Cuffney 1982; Webster 1983).

The equilibrium density of the downstream consumer is influenced not only by the presence or absence of the upstream consumer, but also by its properties (s, k_1, m_1, and g_1; Fig. 3). The downstream consumer is better off with a sloppier (larger s) upstream consumer, except when s is very large (Fig. 3a). Very sloppy upstream consumers attain only small populations, and resource accumulates in the upstream condition (equation 3a), unavailable to the downstream consumer.

The sign of the influence of k_1, m_1, and g_1 on downstream consumer density depends (equation 3d) on the sign of the quantity $[(s-1) \cdot h + s \cdot w_1]$, which is positive if $s > h/(h+w_1)$, or (approximately) if the interaction is commensal (condition 6). In commensal cases, downstream consumers do better with upstream consumers that have larger saturation feeding rates (k_1; Fig. 3b), higher growth efficiencies (g_1; Fig. 3c), and smaller metabolic costs (m_1; Fig. 3d). All of these produce larger equilibrium upstream consumer populations which process more of the resource, leaving less for species-independent processing (which is less effective in commensal situations). Conversely, when the interaction is amensal and species-independent processing is the more effective, downstream consumers do better with upstream consumers having smaller saturation feeding rates (Fig. 3b), lower growth efficiencies (Fig. 3c), and larger metabolic costs (Fig. 3d). However, the curves are steep only for rather small saturation feeding rates and growth efficiencies and for rather large metabolic costs.

Two elaborations on the basic model deserve mention. First, if two (or more) upstream consumers can be present, indirect 'alternative processor' interactions become possible (S.B. Heard, unpublished). Somewhat more complicated models are required, because evaluating the interaction of each upstream consumer with the downstream consumer involves considering the other(s) as part of 'consumer-independent' processing, but the basic results are not hard to derive intuitively. Consider two competing upstream consumers, one a more effective processor (larger s) than the other, and their interaction with a downstream consumer in patches containing one or both. Either alone could affect the downstream consumer positively or negatively (with the more effective processor of the two more likely to be commensal). However, the net effect of each may depend on the presence or absence of the other. The presence of the more effective processor will benefit the downstream consumer if the less effective is also present—even if either upstream consumer alone, or the guild as a whole, has an amensal interaction with the downstream consumer. This might be called a 'best of a bad job' commensalism. Likewise, even if either upstream consumer alone benefits the downstream consumer, in competition with the more effective processor the less effective will have a negative effect on the downstream consumer. The magnitude and even the direction of the interaction between a particular pair of

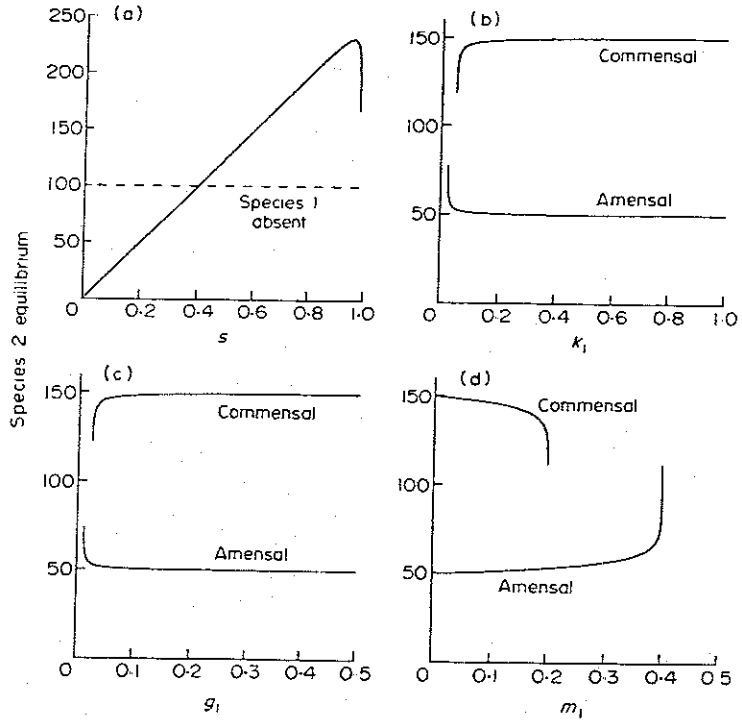

Fig. 3. Dependence of downstream consumer (species 2) equilibrium on upstream consumer properties for equation 2. Plotted values were calculated directly from the equilibrium equation 3d. Values of model parameters other than those plotted: $p = 5$, $u_1 = u_2 = 0.3$, $h = 0.2$, $k_1 = k_2 = 1$, $g_1 = g_2 = 0.5$, $m_1 = m_2 = 0.01$, and $s = 0.2$ ('amensal') or $s = 0.6$ ('commensal'). (a) Effect of varying upstream consumer sloppiness. Broken line: downstream consumer equilibrium in a patch without upstream consumer. (b) Effect of varying upstream consumer saturation feeding rate. (c) Effect of varying upstream consumer growth efficiency. (d) Effect of varying upstream consumer metabolic cost.

consumers are therefore likely to depend on which other consumers are also present.

Secondly, considering transitory dynamics rather than equilibria shows that the temporal scale considered is important (Heard 1993). The magnitude and even direction of the interspecific interaction can be strongly influenced by the time interval after which effects are evaluated (the time horizon). In particular, commensalism is more likely at short time horizons. In fact, all processing chain interactions, even those which show strongly amensal interactions at equilibrium, are initially commensal. This is because the upstream consumer influences the rate of processing as well as the fraction processed and the benefit of accelerated processing temporarily outweighs the cost of less effective processing.

The transitory dynamics may often be more relevant biologically than the equilibrium dynamics. This may be true, for instance, because seasonality imposes limits on time available for growth, because disturbances or predation prevent equilibrium from being attained (e.g. Sousa 1979; Paine & Levin 1981), or because patches of resource are ephemeral (e.g. Beaver 1984; if single-patch $p(t)$ peaks and then falls to 0, S_1^* and S_2^* will be 0, but the patch will support growth, in the shorter term, of consumers which can disperse to new patches). Commensal interactions may be more common in these situations.

Processing chains in nature

Although a general treatment of processing chain dynamics has not been previously attempted, many specific instances in which consumers may influence one another through resource processing have been recognized. A number of studies that have examined possible processing chain systems are listed in Table 1. I include here two-species systems that can be depicted in the format of Fig. 1, as well as a few systems where the upstream consumer may be able to use resource in both conditions, potentially competing with the downstream consumer for resource in the downstream condition. I exclude most cases where the upstream consumer also feeds directly on individuals of the downstream consumer, e.g. situations where arthropod comminution of litter facilitates bacterial growth, but the same arthropods prey on the bacteria (Fenchel 1970; Hanlon & Anderson 1979; see also Sterner 1986 for an analogous uation with plankton).

Although this list is surely not comprehensive, it should provide a general picture of the character of those processing chains which have received attention. Most of the examples in Table 1 fall into one of four classes, based on the sort of processing involved, although other sorts of processing are possible. First, there are many examples of probable processing

see Heard 1994 (Short-term dynamics of processing chain systems. *Ecological Modelling*, in press)

chains based on reductions in particle size of detritus, including that in streams, soils and various phytotelmata (plant-held water bodies). Secondly, processing often involves modifications arising from feeding by one consumer that make resource accessible to other consumers: for instance, large scavengers opening up carcasses to insect attack. Thirdly, a number of studies have pointed out that predators and herbivores, by leaving dead but unconsumed or egested organic material, can release nutrients otherwise bound up in the living tissues on which they feed. Abrams (1987, his example 4) briefly discussed a model of interactions among predators, prey and scavengers which belongs to this class, and which shares many features with the processing chain models above. Finally, among micro-organisms processing chains based on chemical transformations may be relatively common, often involving one species of bacteria metabolizing the waste products of another species.

Several further points arising from the compilation of examples in Table 1 bear discussion. These include the rarity of thorough documentation, the preponderance of decomposers, and the high frequency of commensal interactions.

DOCUMENTATION OF PROCESSING CHAIN INTERACTIONS

Although the phenomenon of processing is widely recognized, processing chain interactions are very poorly documented in the literature. For instance, it is a 'common assumption' (Richardson & Neill 1991; see also Richardson 1980; Vannote *et al.* 1980; Roeding & Smock 1989) in stream ecology that collectors (fine-particle feeders) benefit from particles produced by the feeding activity of shredders. However, few researchers have attempted to test this idea (Winterbourn, Rounick, & Cowie 1981; Table 1; Roeding & Smock 1989; Richardson & Neill 1991). Several studies have shown that shredders produce particulates (demonstrating $s > 0$ in equation 2b), but only two to my knowledge have also examined interactions between shredders and the collectors that might benefit from this processing: Short & Maslin (1977) in laboratory populations, and Richardson & Neill (1991) with indirect tests (manipulating resource supply rather than shredder densities). Simple experiments manipulating shredder densities in the field and measuring particulate levels and collector populations downstream are clearly needed. A similar situation holds for interactions among soil decomposers (Swift, Heal & Anderson 1979; Hassell, Turner & Rands 1987).

In many cases, processing interactions have been peripheral issues in studies whose foci lay elsewhere (often in natural history or in ecosystem-level nutrient cycling). Perhaps as a result, very few of the studies in Table 1 develop any explicit population- or community-level models or theory, or suggest that the dynamics dealt with might be of general interest. Similarly, few of the tabulated studies provide convincing documentation of both the interspecific interaction and its resource processing mechanism: in all cases the supporting data are either incomplete, indirect, or exclusively obtained in laboratory populations. Apparently, in only one case has both the outcome and the mechanism of a processing chain interaction been demonstrated experimentally in a natural population (Heard 1993).

see Heard 1994 (Pitcher-plant midges and mosquitoes: a processing chain commensalism. *Ecology* 75:1647-1660)

DECOMPOSERS AND PROCESSING CHAINS

Decomposer or detritivore systems are the subject of the overwhelming majority of studies in Table 1. Decomposition very often represents a unidirectional sequence of resource condition changes, and as a result processing chain interactions will no doubt be most common among decomposers (this is not to say that all decomposer systems are processing chains). Decomposer systems are, of course, of tremendous importance; at least 75% and very often in excess of 90% of net primary productivity enters the detritus pathway directly (figures for terrestrial systems; Swift *et al.* 1979), and only fossilized production escapes eventual passage through decomposers. Connell & Slatyer (1977; see also Richardson 1980) suggested that facilitation might be common in 'heterotrophic successions' among decomposers, citing examples which are clearly processing chains (e.g. Savely 1939; my Table 1). Connell & Slatyer (1977) were not, however, primarily concerned with resource processing and did not consider the possibility of amensal processing chains. Futhermore, they left unclear the relationship between these unidirectional interactions among decomposers and their other facilitative successions where later species displace earlier ones: the former are likely to be well described by processing chain models, but the latter are not.

Most of the decomposer studies involve physical or chemical transformation of dead organic matter (I would include such organisms as rumen, cheese-making and fermenting bacteria as chemical decomposers). Several related examples involve the production, by predators or grazers, of dead organic matter which then is used by decomposers (e.g. Meyer, Schultz & Helfman 1983; Vanni & Findlay 1989; Wassenberg & Hill 1990). Relationships between predators and carrion feeders in general should be well described by processing chain models.

COMMENSALISMS VS AMENSALISMS

It is clear from Table 1 that nearly all the literature examples (39 of the 40 that include a clear indication of the interaction type) suggest a positive effect of the upstream consumer on the downstream (the reciprocal effect is very rarely tested). The model treated

above, however, implies a range of interactions from commensalism to amensalism. Why are more amensal processing chain interactions not reported? There are a number of possibilities.

First, as discussed above, if a guild of two or more species compete for the upstream resource, the interaction of at least one with the downstream consumer will be amensal. It is worth noting that one of the two studies in Table 1 which may involve amensal interactions involves alternative processors: in Illinois, *Melissopus latiferreanus* moths afford entry to acorns by *Valentinia glandulella* moths, but in doing so consume much more of the endosperm than do the other processors, *Curculis rectus* weevils. The majority of studies in Table 1, however, either consider the entire upstream guild together (e.g. Valiela 1974; Shepard & Minshall 1984; Richardson & Neill 1991) or else isolate a single upstream consumer in the laboratory (e.g. Short & Maslin 1977; Grafius & Anderson 1979; Mulholland *et al.* 1985). In either case, alternative processor amensalisms cannot be detected. This cannot be the entire explanation, however; we can still ask why there are so few amensalisms with isolated consumers or at the guild level.

Secondly, (equilibrium) condition (6), $s > h/(h+w_1)$, may normally hold in natural processing chains; that is, that consumer-dependent processing may be generally more effective than consumer-independent processing. This proposition is difficult to evaluate, but there seems no compelling reason to suppose it true. Stream shredders, for example, vary considerably in s, the extent to which they are 'sloppy eaters' (e.g. Herbst 1982). Furthermore, both rates of resource loss (w_1) and consumer-independent processing (h) surely vary from system to system and with spatial and temporal changes in climate and other physical conditions (e.g. storms, Wallace *et al.* 1982; Newbold *et al.* 1983). Systems with $s < h/(h+w_1)$ would therefore seem quite possible.

Thirdly, condition 6 may not hold because some of the assumptions and choices involved in giving a specific form to condition 1, or the assumption necessary to derive condition 6 from the more complicated condition 5, do not hold. Certainly, it would be surprising if any real system were cooperative enough to behave entirely in such a simple fashion. The two limiting cases of resource pre-emption and resource dependence must obviously remain amensal and commensal, respectively, so at issue is only the position of the switch from commensalism to amensalism described by conditions 5 or 6. This switch must be influenced by the forms of the functions in condition 1 (although it is very insensitive to the choice of functional response). However, there is no reason to suspect that all other possible forms have analogs to condition 6 which are very easily met.

Fourthly, condition 6 applies when interactions are evaluated at equilibrium. As discussed above, shorter time scales may be equally important, and the shorter the time frame of interest, the more likely the interaction is to be commensal. The preponderance of commensal interactions in Table 1 may then, have much to do with the importance of non-equilibrium dynamics in nature, or the typically short time scale of ecological investigations. Of the studies in Table 1, only one (Wallace *et al.* 1982) considers the possible sensitivity of results to temporal scale.

Finally, the preponderance of commensalisms in the literature need not necessarily reflect preponderance of commensalism in nature. Perhaps researchers have not considered amensal processing chain interactions as interesting as commensal ones. More plausibly, some processing chain amensalisms may have been described instead as cases of asymmetric competition: an observed negative interaction need not do violence to a competition-centered paradigm, but a positive one cannot be so easily reconciled.

Conclusions

Interspecific interactions arising from resource processing may be quite common in nature, especially in decompositional systems. However, such interactions have received little theoretical attention, and even in systems such as streams where their existence has been discussed, empirical tests of the interactions and their mechanisms have been extremely limited.

Simple models of processing chains suggest that interactions may be either amensal or commensal, depending on a number of factors including temporal scale, guild composition, and relative processing rates and efficiencies. Literature examples, on the other hand, seem to be mainly commensal. More theoretical work, and empirical studies guided by this theory, will be necessary to resolve this apparent incongruity.

The realization that a system may be a processing chain suggests approaches for its study and aspects of particular interest, which may differ from those appropriate for other types of systems. If our goal as ecologists is to correctly understand and predict the behaviour of natural systems, it is important that processing chain systems be recognized and treated as such, and that appropriate empirical tests be applied.

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