Predation, competition, and nutrient recycling: a stoichiometric approach with multiple nutrients

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Abstract

A model for two competing prey species and one predator is formulated in which three essential nutrients can limit growth of all populations. Prey take up dissolved nutrients and predators ingest prey, assimilating a portion of ingested nutrients and recycling or respiring the balance. For all species, the nutrient contents of individuals vary and growth is coupled to increasing content of the limiting nutrient. This model was parameterized to describe a flagellate preying on two bacterial species, with carbon (C), nitrogen (N), and phosphorus (P) as nutrients. Parameters were chosen so that the two prey species would stably coexist without predators under some nutrient supply conditions. Using numerical simulations, the long-term outcomes of competition and predation were explored for a gradient of N:P supply ratios, varying C supply, and varying preference of the predator for the two prey. Coexistence and competitive exclusion both occurred under some conditions of nutrient supply and predator preference. As in simpler models of competition and predation these outcomes were largely governed by apparent competition mediated by the predator, and resource competition for nutrients whose effective supply was partly governed by nutrient recycling also mediated by the predator. For relatively small regions of parameter space, more complex outcomes with multiple attractors or three-species limit cycles occurred. The multiple constraints posed by multiple nutrients held the amplitudes of these cycles in check, limiting the influence of complex dynamics on competitive outcomes for the parameter ranges explored.

Keywords: Predation; Resource competition; Apparent competition; Microbial ecology; Ecological stoichiometry

1. Introduction

The interaction between predation and interspecific competition continues to fascinate ecologists. Chase et al. (2002) recently reviewed this enduring topic, emphasizing that predation has diverse effects on coexistence of competitors. Some of these effects follow from niche theory sensu lato, with predators acting as limiting factors for competitors in addition to whatever resources are limiting (Leibold, 1995). This possibility has been extensively examined in models of competition for a single nutrient resource (Armstrong, 1979; Holt et al., 1994; Grover, 1994, 1995, 1997; Leibold, 1996; Grover and Holt, 1998). In these models, coexistence of competitors stems from a tradeoff between the ability to compete for the nutrient resource and susceptibility to predation. In simple cases, the outcomes of simultaneous competition and predation can be predicted by “R*-rules” extending the rules governing competition for a resource, and “P*-rules” extending the rules governing apparent competition (Holt et al., 1994). Realistic complications could render these rules inapplicable (Grover and Holt, 1998; Abrams, 1999), but the role of predators as limiting factor(s) is a robust principle.

Predators can also affect coexistence among competitors by altering the resource base for which competition occurs (Chase et al., 2002), through nutrient recycling, for example. When predators differentially recycle nutrients, they alter the effective supply ratio of nutrients and can change the identity of the resource for which competition occurs (Stern, 1990; Daufresne and Loreau, 2001). Although much more study is needed, dynamics and outcomes of competition appear strongly related to predators’ effects on nutrient supply (Andersen, 1997; Grover, 2002). This recent body of theory suggests that predator-mediated coexistence

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most likely in single-resource systems when resource supply is intermediate. Outcomes in two-resource systems can be more complex, with predator-mediated coexistence perhaps difficult.

Theory that examines the role of predators as limiting factors or modulators of the competitors’ resource base has relied heavily on models that reach a stable equilibrium. However, dynamics could complicate competitive outcomes under predation. Periodic dynamics are well known from predator–prey models, and with two competing prey species, chaotic dynamics are possible (e.g. Vandermeer and Maruca, 1998; Vayenas and Pavlou, 1999). Abrams (1999) suggested that predator-mediated coexistence was less likely under such dynamically complex circumstances, than in otherwise similar steady state situations. Multiple attractors can also exist for models with predators and two or more competitors (Vance, 1978; Vandermeer, 1991; Vayenas and Pavlou, 1999). Finally, if prey compete for three or more resources, then both chaotic dynamics and multiple attractors are possible even without predators, implying very complex competitive outcomes (Huisman and Weissing, 1999, 2001).

Existing theory that synthesizes predation, competition, and nutrient recycling typically assumes one or two limiting nutrients for the competing prey. Two factors motivate more complex models with three limiting nutrients. First, they fill a gap in existing theory and contribute to the emerging approach of ecological stoichiometry which has the potential to connect across levels of organization from cellular biochemistry to biogeochemistry (Elser et al., 1996). Second, natural communities of the aquatic microorganisms modeled here are frequently limited by the three nutrient elements C, N, and P.

Grover (2003) recently formulated a predator–prey model based on these three nutrient resources, with a flagellate predator population attacking a bacterial prey population—a situation found in virtually every aquatic ecosystem known (Sherr and Sherr, 1984; Fenchel, 1986; Sanders et al., 1992). Bacterial prey consume dissolved nutrients from their environment and predators obtain nutrients solely from ingesting bacterial prey. Both bacteria (prey) and flagellates (predators), the rate of population growth ($\mu_i$, d$^{-1}$) increases with the intracellular nutrient content or quota, $Q_{ij}$ (mol cell$^{-1}$), of the nutrient whose content is lowest relative to a subsistence minimum, $Q_{ij}^{min}$.

$$\mu_i = \mu_i^{max} \left[ 1 - j \max \left( \frac{Q_{ij}^{min}}{Q_{ij}} \right) \right].$$

The parameter $\mu_i^{max}$ is the “apparent” maximal growth rate reached asymptotically when nutrient quotas become infinite. Because quotas are bounded, the true maximal growth rate is lower, and is a complex function of many model parameters.

The rate of nutrient assimilation $V_{ij}$ (mol cell$^{-1}$ d$^{-1}$) differs between bacteria ($i = A$, $B$) and flagellates ($i = Z$), because it is assumed that the former obtain nutrients solely from the dissolved phase, while the latter obtain nutrients solely from ingesting bacterial prey. For bacteria, nutrient assimilation follows Michaelis–Menten uptake kinetics modulated by the current nutrient quota, so that assimilation vanishes when quota reaches an upper bound, $Q_{ij}^{max}$ (mol cell$^{-1}$):

$$V_{ij} = V_{ij}^{max} \left( \frac{[j]}{K_{ij} + [j]} \right) \left( \frac{Q_{ij}^{max} - Q_{ij}}{Q_{ij}^{max} - Q_{ij}^{min}} \right),$$

2. Model formulation

The model represents dynamics of population growth (i.e. reproduction), net nutrient uptake (i.e. assimilation), and nutrient recycling for bacterial populations ($A$, $B$) and their flagellated protozoan predators ($Z$). There are three potentially growth-limiting nutrients: organic carbon ($C$), inorganic nitrogen ($N$), and inorganic phosphorus ($P$). Supply dynamics and other boundary fluxes are assumed to follow the standard chemostat model, where a well-mixed habitat of constant volume is replenished by a nutrient medium with concentrations $C_{in}$, $N_{in}$, and $P_{in}$, that balances a constant outflow at a dilution rate $D$.

Bacterial dynamics are modeled with the “variable internal store” approach, where growth rate depends on intracellular nutrient content (Droop, 1974; Thingstad, 1987; Grover, 2003). Predator dynamics follow a similar approach (Grover, 2003). The only substantive change to these foundations is the addition of a second bacterial species to compete with the first. Model notation relies on two subscripts: $i$ to denote different populations ($i=A$, $B$, $Z$), and $j$ to denote nutrients ($j=C$, $N$, $P$).

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where $V_{ij}^\text{max}$ (mol cell$^{-1}$ d$^{-1}$) is the maximal uptake rate and $K_{ij}$ (mol$^{-1}$) the half-saturation constant for uptake, while the square brackets denote molar concentration of nutrient $j$.

Assuming that encounter rate determines predation by flagellates, the ingestion of prey occurs at a per capita rate (prey cells (predator cell)$^{-1}$ d$^{-1}$) of $aB$ for bacterial species B, and $a\phi A$ for bacterial species A. Here, $a$ is the “attack” or “clearance” rate (liters (predator cell)$^{-1}$ d$^{-1}$) of the predator for bacteria B, whose population density (cells l$^{-1}$) is B. Similarly, $A$ is the population density of bacterial species A, while $\phi$ is a dimensionless parameter measuring the preference of the predator for this prey species: $\phi < 1$ implies a lower preference for species A relative to species B, $\phi > 1$ a higher preference. From the combined ingestion of both prey species, predator cells acquire a flux of nutrient $j$ equal to $aBQ_{ij,B} + a\phi A Q_{ij,A}$ (mol (predator cell)$^{-1}$ d$^{-1}$). Assimilation of this flux is modulated by the current quota, vanishing when the upper bound $Q_{ij}^\text{max}$ is reached, and reaching a maximum of $e_{ij}$ (<1) when the lower bound $Q_{ij}^\text{min}$ is reached:

$$V_{ij,Z} = (ae_{ij,B}BQ_{ij,B} + a\phi e_{ij,A}AQ_{ij,A}) \left( \frac{Q_{ij,Z}^\text{max} - Q_{ij,Z}}{Q_{ij,Z}^\text{max} - Q_{ij,Z}^\text{min}} \right).$$

The assimilation of N and P is assumed to be complete (i.e. $e_{ij,N} = e_{ij,P} = 1$) under the limiting case of extreme deficiency of these nutrients (i.e. $Q_{ij,Z} \rightarrow Q_{ij,Z}^\text{min}$). To account for respiratory costs of foraging for prey, $e_{ij,C}$ is assumed to be less than one.

Rates of nutrient recycling, or respiration for C, $R_{ij}$ (mol cell$^{-1}$ d$^{-1}$) also differ between bacterial prey and flagellate predators. Bacteria are assumed to “immobilize” the inorganic nutrients N and P (Azam et al., 1983; Caron et al., 1988; Vadstein, 2000), by having negligible recycling, with $R_{NJ} = R_{PJ} = 0$, for $i = A, B$. Bacteria are assumed to respire C, converting it to inorganic carbon that vanishes from the accounting of the model. Bacterial respiration has a growth-related component proportional to the current growth rate and carbon quota, and a maintenance-related component proportional to the excess carbon quota above the minimum (Thingstad, 1987):

$$R_{i,j} = \rho_{i}^\mu Q_{i},i + \rho_{i}^m(Q_{C,i} - Q_{C,i}^\text{min}),$$

where the coefficients $\rho_{i}^\mu$ (dimensionless) and $\rho_{i}^m$ (d$^{-1}$) parameterize these components for bacterial species $i = A, B$. Flagellates ingest nutrients more rapidly than they are assimilated according to Eq. (3). For N and P, the balance of the nutrient not assimilated is assumed to be recycled to the dissolved inorganic form. As a simplifying assumption, the balance of C not assimilated is respired, although recycling of some ingested organic C from flagellates could occur. Rates of recycling or respiration follow expressions

$$R_{j,Z} = aBQ_{j,B} \left[ 1 - e_{j,B} \left( \frac{Q_{j,Z}^\text{max} - Q_{j,Z}}{Q_{j,Z}^\text{max} - Q_{j,Z}^\text{min}} \right) \right] + a\phi AQ_{j,A} \left[ 1 - e_{j,A} \left( \frac{Q_{j,Z}^\text{max} - Q_{j,Z}}{Q_{j,Z}^\text{max} - Q_{j,Z}^\text{min}} \right) \right].$$

(5)

The foregoing assumptions about biological rates are pulled together into a system of 15 ordinary differential equations. Three such equations govern population dynamics:

$$\frac{dA}{dt} = (\mu_A - D - m_A)A - a\phi AZ,$$

(6a)

$$\frac{dB}{dt} = (\mu_B - D - m_B)B - aBZ,$$

(6b)

$$\frac{dZ}{dt} = (\mu_Z - D - m_Z)Z.$$

(6c)

According to these equations, each population grows at a per capita rate $\mu_i$ (Eq. (1)), suffers dilution losses at a per capita rate $D$ and other density-independent mortality at a constant per capita rate $m_i$. For each of the three populations, three equations govern dynamics of nutrient quotas; these take the form

$$\frac{dQ_{ij}}{dt} = V_{ij} - \mu_i Q_{ij} - R_{ij}.$$

(6d)

According to these equations, nutrient quotas increase by assimilation, and decrease with utilization for growth at rates $\mu_i Q_{ij}$, and by recycling or respiration. Finally, three equations govern dynamics of dissolved nutrients; these take the form

$$\frac{d[j]}{dt} = D([j]_m - [j]) + m_A AQ_{j,A} + m_B BQ_{j,B} + m_Z ZQ_{j,Z} + Z R_{j,Z} - A V_{j,A} - B V_{j,B}.$$  

(6e)

The first term in Eq. (6e) is the chemostat supply term for nutrient $j$, the next three terms express an assumption that the nutrient content of cells lost to density-independent mortality is recycled. Otherwise, there is no recycling of nutrients from bacteria. The fifth term of Eq. (6e) represents recycling of nutrients in prey that are ingested but not assimilated, according to Eq. (5). This fifth term is omitted from the equation for dissolved organic C ($j = C$), because it is assumed that this flux is respired as inorganic C that disappears from the model’s accounting. The last two terms of Eq. (6e) represent bacterial assimilation of dissolved nutrients.

3. Parameterization and numerical simulation

The model posed here is sufficiently complex that numerical simulation is required for analysis, which was conducted using a well-tested Runge-Kutta algorithm with adaptive step-size control (Press et al., 1986).
Parameter assignments (Table 1) were carried over from similar studies (Thingstad, 1987; Grover, 2003), which in turn are based on many laboratory studies of planktonic bacteria and flagellates.

For bacterial population B, parameters from Grover (2003) were adopted, as were those parameters describing the flagellate population Z, apart from parameters specifically involved in its interaction with bacterial population A. These parameters portray bacterial population B as a relatively slow-growing species, with limited variations in C and N content, but a moderate capability to store P. The flagellate predator is modeled on laboratory studies of the genus *Paraphysomonas*, and its parameters dictate that it is prone to physiological N-limitation, and thus recycles P more effectively than N.

For bacterial population A, parameters were chosen to represent a competitive tradeoff that would produce stable coexistence of the two competing bacteria in the absence of the predator, for at least some nutrient supply conditions. Following classical principles of competition for two resources, two species coexist stably if each one is a superior competitor for one resource and an inferior competitor for the other, and if each consumes proportionally more of the resource for which it is the inferior competitor (León and Tumpson, 1975; Tilman, 1982; Grover, 1997). In the variable-internal-stores model of population growth based on Eqs. (1) and (2), several parameter differences confer differential competitive abilities, but differences in $Q^{\text{min}}$ always produce stabilizing differences in consumption. Thus, bacterial population A was assigned parameters

### Table 1

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Meaning</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$k_{\text{max}}$</td>
<td>Apparent maximal growth rates</td>
<td>6.0 d$^{-1}$</td>
</tr>
<tr>
<td>$P_{\text{Amax}}$, $P_{\text{Bmax}}$</td>
<td>Maximal C quotas</td>
<td>2.12 fmol cell$^{-1}$</td>
</tr>
<tr>
<td>$Q_{\text{Cmax}}$, $Q_{\text{Nmax}}$, $Q_{\text{Pmax}}$</td>
<td>Maximal N quotas</td>
<td>0.32 fmol cell$^{-1}$</td>
</tr>
<tr>
<td>$Q_{\text{Cmax},B}$, $Q_{\text{Nmax},B}$, $Q_{\text{Pmax},B}$</td>
<td>Maximal P quotas</td>
<td>0.06 fmol cell$^{-1}$</td>
</tr>
<tr>
<td>$Q_{\text{Amin},A}$, $Q_{\text{Bmin},B}$</td>
<td>Species A minimal C quota</td>
<td>0.8 fmol cell$^{-1}$</td>
</tr>
<tr>
<td>$Q_{\text{Bmin},A}$, $Q_{\text{Bmin},B}$</td>
<td>Species B minimal C quota</td>
<td>1.06 fmol cell$^{-1}$</td>
</tr>
<tr>
<td>$Q_{\text{Bmin},A}$, $Q_{\text{Bmin},B}$</td>
<td>Species A minimal N quota</td>
<td>0.12 fmol cell$^{-1}$</td>
</tr>
<tr>
<td>$Q_{\text{Amin},A}$, $Q_{\text{Bmin},B}$</td>
<td>Species B minimal N quota</td>
<td>0.16 fmol cell$^{-1}$</td>
</tr>
<tr>
<td>$Q_{\text{Amin},A}$, $Q_{\text{Bmin},B}$</td>
<td>Species A minimal P quota</td>
<td>0.03 fmol cell$^{-1}$</td>
</tr>
<tr>
<td>$Q_{\text{Bmin},A}$, $Q_{\text{Bmin},B}$</td>
<td>Species B minimal P quota</td>
<td>0.01 fmol cell$^{-1}$</td>
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<tr>
<td>$V_{\text{Cmax},A}$, $V_{\text{Cmax},B}$</td>
<td>Maximal uptake rates for C</td>
<td>52 fmol cell$^{-1}$ d$^{-1}$</td>
</tr>
<tr>
<td>$V_{\text{Pmax},A}$, $V_{\text{Pmax},B}$</td>
<td>Maximal uptake rates for N</td>
<td>7.7 fmol cell$^{-1}$ d$^{-1}$</td>
</tr>
<tr>
<td>$V_{\text{Pmax},A}$, $V_{\text{Pmax},B}$</td>
<td>Maximal uptake rates for P</td>
<td>1.25 fmol cell$^{-1}$ d$^{-1}$</td>
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<tr>
<td>$K_{\text{C,A},K_{\text{C,B}}}$</td>
<td>Half-saturation constant for C uptake</td>
<td>1 μmol l$^{-1}$</td>
</tr>
<tr>
<td>$K_{\text{N,A},K_{\text{N,B}}}$</td>
<td>Half-saturation constant for N uptake</td>
<td>0.1 μmol l$^{-1}$</td>
</tr>
<tr>
<td>$K_{\text{P,A},K_{\text{P,B}}}$</td>
<td>Half-saturation constant for P uptake</td>
<td>0.1 μmol l$^{-1}$</td>
</tr>
<tr>
<td>$\rho_{\text{A}}, \rho_{\text{B}}$</td>
<td>Growth-related respiration coefficient</td>
<td>1.0</td>
</tr>
<tr>
<td>$\rho_{\text{A},i}$, $\rho_{\text{B},i}$</td>
<td>Maintenance-related respiration coefficient</td>
<td>0.3 d$^{-1}$</td>
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<tr>
<td>$m_{\text{A}}, m_{\text{B}}$</td>
<td>Mortality</td>
<td>0.1 d$^{-1}$</td>
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</tbody>
</table>

### Flagellate parameters

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Meaning</th>
<th>Value</th>
</tr>
</thead>
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<tr>
<td>$k_{\text{max}}$</td>
<td>Apparent maximal growth rate</td>
<td>3.2 d$^{-1}$</td>
</tr>
<tr>
<td>$Q_{\text{Cmax},A}$</td>
<td>Maximal C quota</td>
<td>708 fmol cell$^{-1}$</td>
</tr>
<tr>
<td>$Q_{\text{Nmax},A}$</td>
<td>Maximal N quota</td>
<td>235 fmol cell$^{-1}$</td>
</tr>
<tr>
<td>$Q_{\text{Pmax},A}$</td>
<td>Maximal P quota</td>
<td>9.1 fmol cell$^{-1}$</td>
</tr>
<tr>
<td>$Q_{\text{Cmin},A}$</td>
<td>Minimal C quota</td>
<td>148 fmol cell$^{-1}$</td>
</tr>
<tr>
<td>$Q_{\text{Nmin},A}$</td>
<td>Minimal N quota</td>
<td>708 fmol cell$^{-1}$</td>
</tr>
<tr>
<td>$Q_{\text{Pmin},A}$</td>
<td>Minimal P quota</td>
<td>0.06 fmol cell$^{-1}$</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>Preference for bacteria A</td>
<td>0.8 (default)</td>
</tr>
<tr>
<td>$c_{\text{C,A}}$</td>
<td>Maximal assimilation efficiency of C from bacteria A</td>
<td>0.7</td>
</tr>
<tr>
<td>$c_{\text{C,B}}$</td>
<td>Maximal assimilation efficiency of C from bacteria B</td>
<td>0.65</td>
</tr>
<tr>
<td>$c_{\text{N,A}}, c_{\text{N,B}}$</td>
<td>Maximal assimilation efficiency of N</td>
<td>1.0</td>
</tr>
<tr>
<td>$c_{\text{P,A}}, c_{\text{P,B}}$</td>
<td>Maximal assimilation efficiency of P</td>
<td>1.0</td>
</tr>
<tr>
<td>$m_{\text{A}}$</td>
<td>Mortality</td>
<td>0.1 d$^{-1}$</td>
</tr>
</tbody>
</table>

### Environmental parameters

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Meaning</th>
<th>Value</th>
</tr>
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<tbody>
<tr>
<td>$D$</td>
<td>Dilution rate</td>
<td>1.5 d$^{-1}$</td>
</tr>
<tr>
<td>$C_{\text{A}}$</td>
<td>C supply</td>
<td>50 μmol l$^{-1}$ (default)</td>
</tr>
<tr>
<td>$N_{\text{A}}$</td>
<td>N supply</td>
<td>4–125 μmol l$^{-1}$</td>
</tr>
<tr>
<td>$P_{\text{A}}$</td>
<td>P supply</td>
<td>0.128–4 μmol l$^{-1}$</td>
</tr>
</tbody>
</table>
identical to population B, except that \( Q_{P,i}^{\min} \) was higher for species A, while \( Q_{C,J}^{\min} \) and \( Q_{N,J}^{\min} \) were lower. The relative differences in minimal quotas are consistent with the magnitude of observed interspecific differences in cell quotas for bacteria under nutrient limitation (Vrede et al., 2002). The minimal quotas for C and N were changed in parallel, because C:N ratios appear to be more strongly constrained in bacteria than ratios of C:P and N:P (Chrzanowski and Kyle, 1996; Vrede et al., 2002). According to the parameters used, bacterial species B is a superior competitor for P and an inferior competitor for C and N. Given a range of habitats with different nutrient supply conditions, the two species stably coexist for a range of intermediate C:P and N:P supply ratios, while low P supply favors species B, and low C or N supply favors species A.

The predator’s maximal assimilation efficiency for C from bacterial species A \( (e_{C,A}) \) is assumed to be higher than that for species B \( (e_{C,B}) \), owing to the likelihood that consuming the former would likely supply more of a limiting nutrient \( (N) \) for the predator, enabling more efficient assimilation. The predator’s preference for preying on species A was arbitrarily set at \( \phi = 0.8 \) by default, but was varied in some simulations.

In numerical explorations, the environmental parameter \( D \) was fixed at \( 1.5 \ d^{-1} \). Grover (2003) found that dynamics of the model with one prey population were qualitatively similar across a broad range of dilution rates, though higher dilution rates tended to stabilize predator–prey equilibria, and favored higher N and lower P recycling than lower dilution rates.

Numerical studies here focused on nutrient supplies and predator preference, as previous work on predation and competition in nutrient-based models suggests that these are likely to affect competitive outcomes (e.g. Holt et al., 1994; Grover and Holt, 1998; Grover, 2002). Simulations focused on the N:P supply ratio for two reasons. First, differential competitive ability for these nutrients, combined with differential recycling by the predator implies that the latter could alter competitive outcomes from those dictated by abiotic supply processes (Sterner, 1990). Second, much is known about total N and P concentrations in natural waters (analogous to the model supply concentrations \( N_{in} \) and \( P_{in} \)). In global data sets, total N typically ranges 5–65 \( \mu \)mol l\(^{-1} \), total P ranges 0.1–8.5 \( \mu \)mol l\(^{-1} \), and their molar ratio ranges 7–320 (Guildford and Hecky, 2000). To cover these ranges roughly, supply concentrations of N and P were constrained to the relationship

\[
N_{in}P_{in} = 16 \mu \text{mol}^2 \text{l}^{-2}.
\]

A range of \( N_{in} \) from 4 to 125 \( \mu \)mol l\(^{-1} \) and \( P_{in} \) from 0.128 to 4 \( \mu \)mol l\(^{-1} \) was considered, giving molar N:P supply ratios from 1 to 976. Thus, the N and P supply conditions chosen represent the range of likely natural supply conditions, although the strong negative relationship portrayed between N and P supplies is not evident in natural data (Guildford and Hecky, 2000).

Although the likely ranges of N and P supplies are constrained by data, this is less true for organic C supply. Therefore, one set of simulations combined the N:P supply gradient described above with a range of organic C supplies. Labile organic C concentrations and dynamics in natural waters are incompletely characterized. Primary productivity in well-lit marine waters ranges 0.1–100 \( \mu \)mol C l\(^{-1} \d^{-1} \) (Behrenfeld and Falkowski, 1997), with a similar range for inland waters (Wetzel, 1983). If 50% of this production makes its way to bacteria (Riemann and Sondergaard, 1986), supply concentrations \( (C_{in}) \) range 0.03–30 \( \mu \)mol l\(^{-1} \) at the assumed turnover rate of \( (D) \) of 1.5 \( d^{-1} \). However, shallow aquatic systems likely have additional organic C supplies from macrophyte photosynthesis and the terrestrial watershed. Thus a range of \( C_{in} \) up to 100 \( \mu \)mol l\(^{-1} \) was considered for simulations. For these simulations, predator preference \( (\phi) \) was set to 0.8.

Flagellates prey selectively on bacteria (Chrzanowski and Simko, 1990; Jürgens and DeMott, 1995; Jürgens and Matz, 2002), but available data suggest a wide range of quantitative preferences. Accordingly, a range of values for the preference parameter \( \phi \) from 0 to 2 was explored in simulations conducted over the N:P supply ratio gradient described above. At \( \phi = 0 \), the flagellate does not ingest bacteria A at all, while at \( \phi = 2 \) it exerts a strong preference for this prey. For these simulations, organic C supply \( (C_{in}) \) was set to 50 \( \mu \)mol l\(^{-1} \).

For the chosen ranges of parameters, simulations were conducted with the two separate predator–prey pairs, and the two competing prey, in addition to the full three-species system. To explore coexistence, all three-species simulations were first run with two initial conditions, corresponding to invasion of a small population of one prey species into a habitat in which the other prey species was resident with the predator. When these first two simulations suggested either predator extinction, or trajectories diverging to different attractors, simulations were run from several more initial conditions with widely ranging population densities (usually 5–10 initial conditions with densities differing by up to 5–6 orders of magnitude). All cases of multiple attractors involved two attractors (examples are presented in the results below) and these protocols appeared adequate to find them. However, it is always possible that simulations from a finite number of initial conditions will miss some attractors.

4. Results

4.1. Simulations examining organic C supply

For each prey species considered alone, a threshold C supply was required for predator persistence (Figs. 1a
and b), even though predator growth was always N-limited. Grover (2003) found that one nutrient can constrain the capacity of prey to “package” a second nutrient and make it available to predators. Flagellates went extinct for $C_{in}$ below about 30 $\mu$mol l$^{-1}$ when preying on species A alone, and for $C_{in}$ below about 28 $\mu$mol l$^{-1}$ when preying on species B alone. When preying on species A alone, flagellates also went extinct at a N:P supply ratio above about 72, when $P_{in}$ fell below about 0.47 $\mu$mol l$^{-1}$ and thus P supply failed to support a prey population large enough for predator persistence (Fig. 1a).

With predators preying on either bacterial species alone, sufficiently high supplies of all three nutrients produced limit cycle dynamics. With species A as prey, limit cycles occurred when organic C supply $C_{in}$ exceeded about 65 $\mu$mol l$^{-1}$, for N:P supply ratios from about 1.9 to 15, corresponding to $N_{in} > 5.5 \mu$mol l$^{-1}$ and $P_{in} > 1 \mu$mol l$^{-1}$ (Fig. 1a). With species B as prey, limit cycles occurred when organic C supply $C_{in}$ exceeded about 71 $\mu$mol l$^{-1}$, for N:P supply ratios from about 1.2 to 300, corresponding to $N_{in} > 4.4 \mu$mol l$^{-1}$ and $P_{in} > 0.23 \mu$mol l$^{-1}$ (Fig. 1b).

In the absence of the predator, the bacterial species coexisted for a range of N:P supply ratios, at all of the organic C supplies simulated (Fig. 1c). However, the position of this coexistence band shifted to lower N:P supply ratios as organic C supply increased. This is because, for the supplies considered here, bacteria are either C- or P-limited, but not N-limited, and thus competitive outcomes depend directly on the C:P supply ratio. The boundaries shown in Fig. 1c correspond to the C:P supply ratios at which species switch between C- and P-limitation. For C:P supply ratios >89, both species are P-limited, and the better competitor for P, species B, excludes the weaker competitor species A. For C:P supply ratios <69, both species are C-limited, and the better competitor for C, species A, excludes the weaker competitor species B. Within the coexistence band, species A is P-limited, and species B is C-limited, producing coexistence. For much higher C supply, or much lower N supply than those displayed here, coexistence and competitive exclusion would be directly related to the N:P supply ratio and involve switches between N- and P-limitation.

In the presence of the predator, the coexistence band for bacterial prey was shifted to higher N:P supply ratios, and became independent of organic C supply for high $C_{ip}$ (Fig. 1d). For $C_{ip}$ exceeding about 75 $\mu$mol l$^{-1}$, species B was excluded for N:P supply ratios <31, while species A was excluded for N:P supply ratios >48. The shift that the predator induced in the coexistence band resulted from two factors. First, the predator was N-limited and thus recycled little N and relatively more P, producing habitats that were effectively less P-limited than allowed by the abiotic nutrient supplies. Second, in the presence of the predator, coexistence under different nutrient supply conditions depended on the balance between resource competition and apparent competition, rather than on changes in the identity of limiting nutrients for the bacterial competitors. Throughout the coexistence band, and for adjacent parameter regions, bacterial species A was P-limited, while species B was C-limited, and they did not shift limitation status at the boundary of the coexistence band as they did in the absence of the predator. At the boundary where species B was excluded, lower N:P supply ratios entailed higher P supply, raising the size of the predator population.
supported by the P-limited species A. At the same time, the larger population of species A reduced the concentration of dissolved organic C. Faced with higher losses and a lower concentration of its limiting nutrient, the C-limited species B could no longer persist.

The boundary of the coexistence band where species A was excluded was more complex. For organic C supply below about 71 μmol l⁻¹, species B and the predator had a stable equilibrium when species A was absent. Under these circumstances, exclusion of species A at higher N:P supply ratios resulted from lower P supply, and a lower dissolved P concentration, that made the P-limited species A unable to persist.

For higher organic C supplies exceeding about 71 μmol l⁻¹, species B and the predator Z had a limit cycle, rather than a stable equilibrium, when species A was absent. P-limitation again rendered species A unable to persist at sufficiently high N:P supply ratios, but the position of this boundary was influenced by dynamical complications. In a wedge-shaped region of parameter space along this boundary, three-species limit cycles or multiple attractors occurred (Fig. 1d).

Examination of trajectories in this region of complex dynamics reveals that they are confined asymptotically to a cone-shaped manifold embedded in the three-dimensional phase (sub-)space of population densities (Figs. 2 and 3). The cone-shaped manifold connects a limit cycle on the BZ boundary of this space (A = 0) to an interior point equilibrium. Multiple attractors can lie on this manifold. For example, with \( C_{in} = 90 \mu mol l^{-1} \) and a N:P supply ratio of 44 (Fig. 2), there is a stable three-species limit cycle with relatively low values for the population density of species A. This limit cycle attracts initial conditions with a sufficiently low initial density of species A. For higher initial densities of species A, dynamics are attracted to a point equilibrium at the apex of the cone, in which all three species coexist with a relatively high density of species A. Dynamics resembling Fig. 2 were found for \( C_{in} \) above about 80 μmol l⁻¹, and a narrow range of N:P supply ratios just above those for which the three species equilibrium was the only attractor (e.g. N:P = 44 for Fig. 2).

For \( C_{in} = 90 \mu mol l^{-1} \) and higher N:P supply ratios (e.g. N:P = 46 for Fig. 3), there is a stable limit cycle for the predator Z and prey B, while prey species A goes extinct. This limit cycle attracts initial conditions with a sufficiently low initial density of species A. For higher initial densities of species A, dynamics are attracted to a point equilibrium in which all three species coexist with a relatively high density of species A. Dynamics resembling Fig. 3 were found in most of the parameter space supporting complex dynamics with \( C_{in} \) above about 80 μmol l⁻¹. Thus, exclusion of prey species A was often possible in this dynamically complex region. However, “neutral” coexistence (sensu Grover, 1997) of species A and B for long periods of time seems likely for parameters in this region, due to slow convergence to the limit cycle excluding species A.

For \( C_{in} \) between about 71 and 80 μmol l⁻¹, three-species limit cycles without other attractors were common in the wedge-shaped region of complex dynamics denoted in Fig. 1d. However, for these lower values of \( C_{in} \), such limit cycles arise only for a very narrow range of the N:P supply ratio. The approach to these stable cycles appeared confined to the cone-shaped manifold also observed for higher values of \( C_{in} \) (results not shown).

4.2. Simulations examining predator preference

A second set of simulations examined the role of the predator’s preference (\( \phi \)) for prey species A. For these simulations, N and P supplies were varied along the supply ratio gradient defined by Eq. (7), with C supply fixed at \( C_{in} = 50 \mu mol l^{-1} \), and \( \phi \) varied from 0 (no predation on species A) to 2 (strong preference for species A). The predator’s preference for species A does not affect its interaction with species B when species A is absent. For these nutrient supply conditions, the predator and prey species B always had a stable equilibrium, with P-limited prey growth at high N:P supply ratios, and C-limited prey growth at low N:P supply ratios, and N-limited predator growth for all N:P supply ratios. The predator’s preference also does not affect the outcome of competition between species A and B when the predator is absent. For the nutrient supply conditions used in this second set of simulations, the two prey species coexisted for N:P supply ratios between 31 and 51, with P-limitation eliminating A for higher N:P supply ratios, and C-limitation eliminating species B for lower N:P supply ratios.

Under the simple model of predator preference used here, a higher preference for species A implies higher predation on that species, regardless of whether species B is present. Thus with species B absent, a threshold preference was required for predator persistence, to ensure sufficient ingestion of prey for predators to grow in compensation for their losses (Fig. 4a). The threshold preference was lowest (\( \phi = 0.48 \)) for N:P supply ratios from 2.1 to 27, for which prey growth was C-limited. For lower N:P supply ratios, prey growth remained C limited, but prey assimilation of N was reduced, thus reducing food quality and raising the threshold preference for predator persistence. For higher N:P supply ratios, prey growth was P-limited, reducing food quantity raising the threshold for predator persistence. For sufficiently high predator preference, limit cycle dynamics occurred at low N:P supply ratios. High predator preference increased ingestion of species A, suppressing its density and inducing “prey escape” cycles (sensu Nisbet et al., 1991). However, sufficiently
high N:P supply ratios prevented such cycles, due to P-limitation of prey growth.

With all three species present, several outcomes were possible, depending on nutrient supplies and predator preference and (Fig. 4b). The fates of species A and B depended on changes in the impacts of resource and apparent competition. For sufficiently high N:P supply ratios or high predator preference for species A, this
species was excluded, and prey species B reached a stable equilibrium with the predator. For fixed values of $\phi$ in a range of about 0.5–1.2, outcomes differed depending on N:P supply ratios. The predator reached an equilibrium with both prey species for intermediate N:P supply ratios, producing a roughly “vertical” coexistence band. However, predator density had a local minimum within this coexistence band. For N:P supply ratios higher than this coexistence band, species A was excluded due to a combination of increased P-limitation and increased apparent competition as the equilibrium density of the predator increased. For N:P supply ratios lower than this coexistence band, species B was excluded due to a combination of increased C-limitation and increased apparent competition as the equilibrium density of the predator increased.

For a range of N:P supply ratios less than about 30, the coexistence band for species A and B with the predator became “horizontal” (Fig. 4b). Examining a fixed N:P supply ratio, and crossing this coexistence band with differing values of the preference coefficient $\phi$; at high $\phi$, species A was excluded because it suffered heavily from apparent competition, and reducing $\phi$ lessened the impact of apparent competition on species A. For $\phi$ less than about 1.6–1.7 (depending on the N:P supply ratio), the reduced impact of apparent competition on species A allowed P-limited species A to coexist with P-limited species B. As $\phi$ decreased below about 1.36, apparent competition shifted to impact species B more strongly, leading to its exclusion while A and Z persisted in a limit cycle. However, this boundary of the coexistence band was dynamically complex, with three-species limit cycles or multiple attractors co-occurring. As before, the multiple attractors usually included one coexistence state (equilibrium or limit cycle), and one exclusion state (a limit cycle with the predator and species A alone), with dynamics converging to attractors slowly, implying neutral coexistence over times of practical interest.

With species B absent, a threshold preference was required for the predator to coexist with species A, as noted above. With B present, the predator persisted despite preferences below this threshold, provided that nutrient supplies permitted species B to persist. Thus for $\phi$ less than about 0.5 and N:P supply ratios above about 31–40 (depending on $\phi$), species B and the predator persisted. For N:P supply ratios just above the limit allowing persistence of species B, species A also persisted, in the “vertical” coexistence band roughly in the lower middle of Fig. 4b. For $\phi$ less than about 0.5 and N:P supply ratios just below about 31–40 (depending on $\phi$), the predator was excluded, but both species A and B coexisted in its absence, while for N:P supply ratios below 31, species B was excluded and only species A persisted.

Fig. 3. Dynamics from two initial conditions for nutrient supplies that support complex dynamics in Fig. 1d ($C_\text{a} = 90 \mu\text{mol l}^{-1}$, N:P = 46.00). For both initial conditions, $Z(0) = 1.3 \times 10^7 \text{cells ml}^{-1}$ and $B(0) = 5 \times 10^6 \text{cells ml}^{-1}$. (a) Dynamics in the phase space of population densities from two initial values of $A(0) = 2 \times 10^6 \text{cells ml}^{-1}$ (dotted line) or $3 \times 10^6 \text{cells ml}^{-1}$ (solid line); initial points of the trajectories are marked by solid dots. (b) Dynamics of population densities from the initial value of $A(0) = 2 \times 10^6 \text{cells ml}^{-1}$. (c) Dynamics of population densities from the initial value of $A(0) = 3 \times 10^6 \text{cells ml}^{-1}$. 
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Fig. 4. Long-term outcomes of simulations examining predator preference for bacterial prey A over a range of N:P supply ratios: (a) flagellate predator Z and bacteria prey A only; (b) flagellate predator Z and bacterial prey A and B together.

5. Discussion

In the simulations presented here, competitive outcomes strongly depend on supplies of limiting nutrients, and the strength of the predator’s preference for attacking different prey, both in parameter regions characterized by stable equilibria, and in those characterized by greater dynamical complexity. For example, in the absence of predation, the bacterial competitors coexisted under nutrient supply conditions that intersected a region where each competitor exhibited periodic dynamics when alone with the predator (compare Figs. 1c, a, and b). When all three species interacted in this region (N:P supply ratio of ca. 10–20 (compare Figs. 1c, a, and b), the joint action of resource and apparent competition excluded one competitor (species B), leaving the other (species A) to persist in a limit cycle with the predator. For other parameter conditions, one competitor reached a stable equilibrium when alone with the predator, while the other cycled, and all three species coexisted at a stable equilibrium (e.g. preferences > 1 in Fig. 2). The potentially stabilizing impact of a competitor has been noted in previous analyses of similar models (Kooi and Kooijman, 2000).

The contemporary understanding of niche theory as elaborated by Leibold (1995) to include predation and resource competition appears adequate to understand most of the competitive outcomes seen here, despite the basis of most niche theory in models with stable equilibria. In a similar but simpler model of predation and competition, dynamical complexity arose only in relatively small regions of parameter space (Vayenas and Pavlou, 1999). As in the more complex model studied here, for broad regions of biologically reasonable parameter space differences among species in resource use and susceptibility to predation determined boundaries between different competitive outcomes, with dynamical complications emerging only near some of these boundaries.

Another contemporary theoretical thread, ecological stoichiometry, illuminates some of the results seen here. In particular, when nutrient supplies were varied with fixed predator preference (Fig. 1), the competitors coexisted without the predator for a band of intermediate N:P and C:P supply ratios. This band was shifted to higher N:P and C:P supply ratios, in accordance with stoichiometric principles (Sterner, 1990; Sterner and Elser, 2002). The flagellate predator modeled here strongly recycles P, weakly recycles N, and respires C. Thus it strengthens N and C limitation, while weakening P limitation relative to the abiotic supply conditions, producing the shifted coexistence band going from Fig. 1c (no predator) to Fig. 1d (predator).

Although heterotrophs are often treated as having fixed element stoichiometry (e.g. Sterner, 1990; Makino et al., 2003), there is at least moderate variability in the stoichiometry of bacteria (Vadstein and Olsen, 1989; Chrzanowski and Kyle, 1996; Goldman and Dennett, 2000; Vrede et al., 2002), protozoa (Goldman et al., 1985, 1987; Andersen et al., 1986; Nakano, 1994), zooplankton (DeMott et al., 1998; Villar-Argaiz et al., 2002), and many other organisms (Sterner and Elser, 2002; Cross et al., 2003). Such observations motivated formulation of the present model and its predecessor (Grover, 2003), in which variable nutrient content and stoichiometry of all populations are coupled to population growth, nutrient assimilation, and recycling. The implications of stoichiometric variability for many ecological processes are still poorly known. Based on the results presented here, it appears that one principle established largely from models lacking stoichiometric variability in predators will carry over to at least some situations of stoichiometric variability, namely that nutrient recycling alters the competitive arena (Sterner, 1990).

The weak influence of dynamics on competitive outcomes found here is perhaps surprising given well-known tendencies for oscillations to arise in predator–prey models (Volterra, 1926; May, 1972), and the clear potential for such oscillations to affect competitive outcomes (Vandermeer and Maruca, 1998; Abrams, 1999; Vayenas and Pavlou, 1999). Like other predator–prey models, the multinutrient model investigated here produces oscillations under enriched resource supply (Grover, 2003). Compared to many other predator–prey models, these oscillations have relatively low amplitude.
The two-fold variation in population density illustrated here (Figs. 2 and 3) is typical for this model, which produces high-amplitude cycles only when nutrient supply ratios approach the Redfield ratio (Grover, 2003). In contrast, many other predator–prey models easily produce very high-amplitude oscillations (May, 1972). Relatively tame oscillations result from the multiple constraints that several nutrients pose in the model considered here. It is common for prey to be limited by a different nutrient from predators, and in such circumstances enrichment with the predator’s limiting nutrient propagates poorly through prey constrained by a different nutrient. Observations of multiple nutrient limitation in natural bacterial communities (Felip et al., 1996; Elser et al., 1999; Chrzanowski and Grover, 2001) suggest that such multiple constraints might be common, and thus require theoretical attention.

Although the results presented here suggest a weak influence of complex dynamics on competitive outcomes, the robustness of this result is an open question. Here, competing prey were assumed to coexist stably in the absence of predation, given appropriate nutrient supply conditions. Although there is much evidence that different species of bacteria and other microorganisms compete for different nutrient resources (Grover, 1997), stable coexistence is not a universal outcome. Here, competing bacterial prey differed in the parameter \( g_{ij} \min \), leading to differential competitive ability and stable coexistence. However, differences in other bacterial parameters can produce competitive differences with bistability for intermediate nutrient supply ratios, in which competitive outcomes in the absence of predators depend on initial conditions. In such cases, the analog of Fig. 1c would display a bistable band rather than a coexistence band. It is reasonable to conjecture that dynamical complexities involving multiple attractors would then occur with predators present, and complicate the joint outcome of competition and predation.

It is also possible that dynamical complexities would arise if another of the present assumptions were relaxed—the simple encounter model for ingestion of prey. Flagellate predators may have saturating functional responses (Fenchel, 1986), a complication ignored here, but one that would likely enhance the tendency for predator–prey cycles, perhaps inducing more complex dynamics (Vayenas and Pavlou, 1999). It would also be interesting to explore alternative assumptions about flagellate preference. Flagellates generally prefer moderate-sized bacterial cells (Güde, 1989; Chrzanowski and Šimek, 1990; Jürgens and Matz, 2002), with very small cells and large cells or colonies less susceptible to predation. Nutrient contents, uptake rates, and growth rates covary with cell size, which could be an important factor in bacterial communities. As in the predecessor to the present model (Grover, 2003), realistic descriptions of predator ingestion and selectivity, and other important matters such as the complex chemistry of dissolved organic carbon, were sacrificed here to provide a clearer analysis of the role of stoichiometric variability in ecological interactions.

Stoichiometric approaches hold the potential to unify ecological theory across levels of organization, as they connect fundamental biochemical processes determining the element composition of biomass, to population dynamics and interactions, to biogeochemical processing of elements by ecological communities (Sterner and Elser, 2002). The element composition of many organisms is strongly related to a key aspect of life history—growth rate. Rapid growth entails higher demand for nutrient elements, especially through the need for P-rich ribosomes, a pattern evident in both intra- and interspecific comparisons (Elser et al., 1996, 2000, 2003). It is likely that other elements of life history also drive variation in organismal element composition, though these are currently less well documented (Sterner and Elser, 2002). In turn, variation in organismal nutrient content affects susceptibility to nutrient depletion and resource competition, and the food quality of a population for its natural enemies. The relative nutrient demands of natural enemies versus their victims then influences how the entire community processes nutrient elements (Sterner, 1990; Andersen, 1997; Grover, 2003), determining the extent of nutrient immobilization within a particular community versus mineralization to forms potentially transported from the community.

A fundamental principle of the emerging stoichiometric approach is the need to examine dynamics of several nutrient elements simultaneously. By doing so, the model presented here captures potentially important aspects of microbial interactions not represented by models with one, or even two nutrient resources. Limiting resources and selective predation strongly influence bacterial community composition in both laboratory experiments and natural systems (Jürgens and Matz, 2002). Given the central role that microbes play in nutrient dynamics in most ecosystems, these ecological interactions likely have biogeochemical consequences (e.g. Verhagen and Laanbroek, 1992). Theory that synthesizes predation, competition, and nutrient recycling for multiple nutrients will illuminate these consequences.

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