The effects of mixotrophy on the stability and dynamics of a simple planktonic food web model

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Abstract

Recognition of the microbial loop as an important part of aquatic ecosystems disrupted the notion of simple linear food chains. However, current research suggests that even the microbial loop paradigm is a gross simplification of microbial interactions due to the presence of mixotrophs—organisms that both photosynthesize and graze. We present a simple food web model with four trophic species, three of them arranged in a food chain (nutrients–autotrophs–herbivores) and the fourth as a mixotroph with links to both the nutrients and the autotrophs. This model is used to study the general implications of inclusion of the mixotrophic link in microbial food webs and the specific predictions for a parameterization that describes open ocean mixed layer plankton dynamics. The analysis indicates that the system parameters reside in a region of the parameter space where the dynamics converge to a stable equilibrium rather than displaying periodic or chaotic solutions. However, convergence requires weeks to months, suggesting that the system would never reach equilibrium in the ocean due to alteration of the physical forcing regime. Most importantly, the mixotrophic grazing link seems to stabilize the system in this region of the parameter space, particularly when nutrient recycling feedback loops are included.

1. Introduction

Since revision of the classic aquatic food web to include the concept of the microbial loop (Pomeroy, 1974; Azam et al., 1983), the importance of microbial interactions in aquatic food webs has become paradigmatic (Sherr and Sherr, 1991; Holen and Boraas, 1995). However, as data on microbial food webs has accumulated, it has become clear that these systems are far more complex than the loop structure originally proposed (Fig. 1). One complicating factor that is receiving increasing attention is the influence of mixotrophs—organisms that defy traditional trophic level classification by both photosynthesizing and grazing.

Mixotrophy has some apparent advantages compared to pure autotrophy or pure heterotrophy and appears to be an important adaptation to life in planktonic habitats (Laybourn-Parry, 1992). Field studies have demonstrated that mixotrophy can increase access to growth-limiting nutrients (Veen, 1991; Caron et al., 1993; Nygaard and Tobiesen, 1993; Jones, 1994; Bockstahler and Coats, 1993b; Arenovski et al., 1995; Holen and Boraas, 1995; Li et al., 1999, 2000), carbon (Veen, 1991; Bockstahler and Coats, 1993b; Jones, 1994) or other growth factors (Bockstahler and Coats 1993b; Caron et al., 1993; Jones, 1994). Mixotrophic algae are able to sustain growth when they are mixed out of the euphotic

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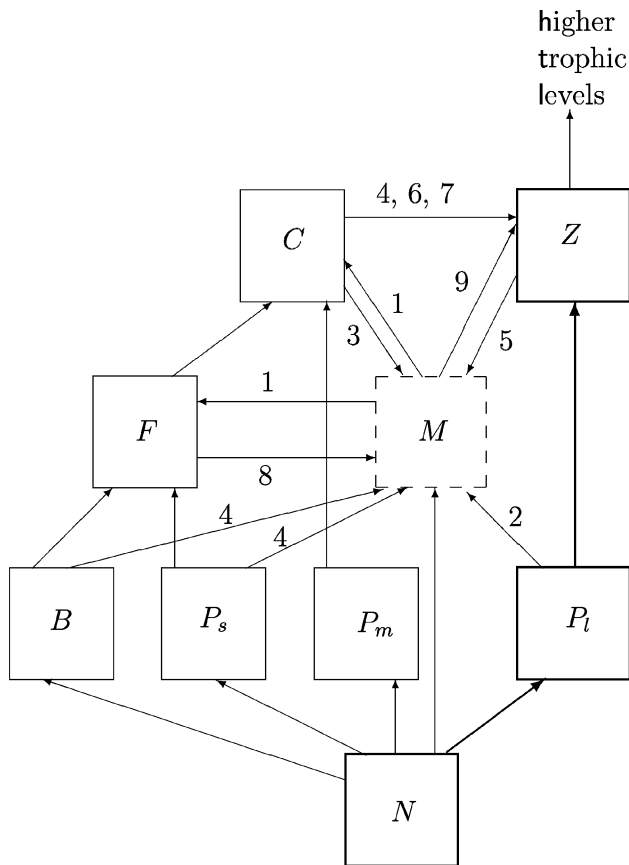E-mail address: jost@cict.fr (C. Jost).

Fig. 1. A schematic representation of the relationships between the classical food chain (thick lines, Steele, 1974), the microbial loop (fine lines, Fenchel, 1988), and mixotrophic interactions in marine planktonic food chains. N, nutrient; P_l, large phytoplankton; P_m, medium phytoplankton; P_s, small phytoplankton; F, flagellates; C, ciliates; B, Bacteria; M, mixotrophs and Z, mesozooplankton. Numbers refer to example references documenting linkages. 1, Arenovski et al. (1995); 2, Sherr and Sherr (1994); 3, Bockstahler and Coats (1993a, b); 4, Sanders and Porter (1988); 5, Kleppel (1993); 6, Stoecker and Capuzzo (1990); 7, Fessenden and Cowles (1994); 8, Neuer and Cowles (1994); 9, Jeong (1994).

zone by switching to phagotrophy (Bird and Kalff, 1989; Bockstahler and Coats, 1993b). During periods of low nutrient concentrations, phagotrophic behavior may enable mixotrophic algae to survive in competition with purely phototrophic organisms (Arenovski et al., 1995). Conversely, mixotrophy in primarily heterotrophic organisms may be a competitive advantage over pure heterotrophic forms, since photosynthesis could enable the survival of periods of reduced particulate food (Bockstahler and Coats, 1993b) despite the lower predation rates of the mixotrophs (Schnepf and Elbrachter, 1992; Holen and Boraas, 1995; Rothhaupt, 1996a).

While mixotrophy is a very common nutritional mode in aquatic systems (see review in Riemann et al., 1995), empirical studies of the influence of mixotrophic organisms upon aquatic food webs are difficult,

particularly in marine systems where field logistics often limit the scope and duration of experiments. As such, models of mixotrophic food webs may be a useful tool for investigating the potential impact of mixotrophs on these systems (Thingstad et al., 1996; Baretta-Bekker et al., 1998; Stickney et al., 2000). While the most studied mixotrophic eukaryotes in planktonic marine microbial food webs are plastid-retaining ciliates (Blackbourn et al., 1973; Jonsson, 1987; Stoecker et al., 1987; Stoecker and Michaels, 1991), their feeding ecology is complex (Stoecker and Silver, 1990; Stoecker, 1991). The simplest mixotrophic strategy appears to be that of photosynthetic dinoflagellates. As such this study focuses on development and analysis of a general model that includes mixotrophic behavior and we will study it in particular for photosynthetic marine dinoflagellates. Moreover, there is a current interest in this group because their importance as grazers may have been grossly underappreciated (Bockstahler and Coats, 1993a, b; Li et al., 1996; Stoecker et al., 1996).

Many photosynthetic dinoflagellates thought to be important as grazers, such as *Gyrodinium* sp., *Gymnodinium* sp., and *Ceratium* sp., are large ($>40\ \mu$m). As such we will assume that our model mixotroph has a diameter of at least 40 μm. This size is similar to that of ciliates known to be important grazers (Verity and Langdon, 1984); the second grazer in our model will, therefore, be a ciliate (hereafter, referred to as herbivore) with a spherical diameter of 40 μm. The prey for these grazers will be a photosynthetic flagellate (10 μm, hereafter, referred to as autotroph) with whom the mixotroph will also compete for dissolved nutrients. Since mixotroph and herbivore are of similar size there is no grazing link between the two organisms, they are pure competitors.

Two biological considerations can guide the choice of parameters for the model. First, because body size is an important factor determining many ecological rates (Peters, 1983), the scaling relationship between the autotroph and mixotroph suggests that the maximum nutrient uptake rate and the half-saturation constant of the autotroph should be greater than and less than those of the mixotroph, respectively; these relationships are commonly seen in the ocean where smaller cells tend to have higher maximum nutrient uptake rates (Harris, 1986) and smaller half-saturation constants for nutrient uptake (Valiela, 1995) than do large cells. Second, the inherent trade-off between phagotrophy and autotrophy should make mixotrophs inferior competitors relative to phagotrophic and phototrophic specialists. As stated above, this pattern is seen in aquatic systems, with predation rates of mixotrophs being lower than those of pure phagotrophs (Schnepf and Elbrachter, 1992; Holen and Boraas, 1995; Rothhaupt, 1996a; Raven, 1997). These relationships between the autotrophs, mixotrophs and herbivores will be used as assumptions in the model.

In this study, we will first present the development of the model and derive general conditions for the existence of a non-trivial equilibrium. This information, together with the parameters estimated to represent mixotrophic dinoflagellates, will then be taken to explore analytically and numerically (Monte Carlo simulations) the influence of the mixotrophic link on existence and stability of an equilibrium, both for general parameter values and for the estimated parameters. This will be done with and without the recycling of nutrients, thus testing for combined effects of mixotrophy and recycling.

2. The mathematical model

We study a chemostat-like model with four state variables: dissolved nutrient (N), nutrient in autotrophs (P), nutrient in herbivores (Z) and nutrient in mixotrophs (M) (see Fig. 2). N represents a pool of limiting nutrient and is modeled as a conservation equation that has a stable state in the absence of biotic uptake and release ($\frac{dN}{dt} = I_n - l_n N$). We assume the amount of nutrients in autotroph, mixotroph or herbivore biomass to be a fixed mean fraction γ of their total biomass. Thus, modeling the biomass or only the nutrient in the biomass is a difference in scaling only and we will follow the latter approach. A general model for autotrophic organisms (autotrophs or mixotrophs) with density $u(t)$ is therefore

$$\frac{du}{dt} = r(N)u - (l_u + r_u)u,$$

where l_u is a loss of nutrients stored in organism biomass due to washout or emigration of autotrophs and r_u is either loss due to direct recycling to the nutrient pool N or indirect recycling through a detrital compartment. We do not include the detrital compartment as a state variable to keep the model simple. This is equivalent to instantaneous detrital regeneration and is a common assumption in plankton models (Franks and Walstad, 1997; Edwards et al., 2000). Note that any non-
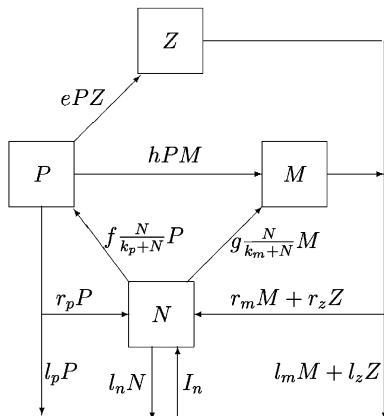
assimilated ingested nutrient is accounted for in the parameters l_u and r_u, thus no assimilation efficiency has to be added to the model. Nutrient uptake $r(N)$ is assumed to be controlled solely by the external level of available nutrients and modeled as a Monod type function (e.g., DiToro, 1980; Auer et al., 1986). The predation on autotrophs by mixotrophs and herbivores is modeled as a Lotka–Volterra interaction. Non-linear functional responses are more realistic for both heterotrophic and mixotrophic organisms (Rothhaupt, 1996b), but the Lotka–Volterra form may serve as a reasonable approximation and was chosen to keep the model as simple as possible. We do not include a grazing link between mixotrophs and herbivores because of their similar size. All these considerations lead to the model

$$\frac{dN}{dt} = I_n - l_n N - f \frac{N}{k_p + N} P - g \frac{N}{k_m + N} M$$
$$+ r_p P + r_m M + r_z Z, \tag{1}$$

$$\frac{dP}{dt} = f \frac{N}{k_p + N} P - hPM - ePZ - l_p P - r_p P, \tag{2}$$

$$\frac{dM}{dt} = g \frac{N}{k_m + N} M + hPM - l_m M - r_m M, \tag{3}$$

$$\frac{dZ}{dt} = ePZ - l_z Z - r_z Z. \tag{4}$$

A list of the state variables, parameters and their units is given in Table 1. Note that, apart from the non-linear nutrient uptake function and the recycling of nutrients, our system represents a subsystem of the one explored analytically by Thingstad et al. (1996) and most of their results apply also to our system. However, they had a different target organism in mind (bacterivorous mixotrophs) and we will focus in our study on the influence of mixotrophic behavior and recycling on the existence and stability of an equilibrium.

The model must fulfill several assumptions in order to describe the behavior of our target mixotroph:

1. The autotrophs should be the better competitors for nutrient than the mixotrophs, thus

$$\frac{(l_p + r_p)k_p}{f - (l_p + r_p)} < \frac{(l_m + r_m)k_m}{g - (l_m + r_m)} \tag{5}$$

(see, e.g., DeAngelis, 1992 or Holt and Polis, 1997). As described in the previous section, the maximum nutrient uptake rate of the mixotroph is less than that of the autotroph and the half-saturation constant of the autotroph is smaller than that of the mixotroph,

$$g < f \quad \text{and} \quad k_p < k_m. \tag{6}$$

2. The herbivore is a better grazer on autotrophs than the mixotroph,

$$h < e. \tag{7}$$

Fig. 2. Flow diagram of the mathematical model.

Table 1
Summary of model parameters

	Biological interpretation	Unit	Estimated range	EAV	CV
N	Dissolved nutrient	mmol N/m^3			
P	Nutrients in autotrophs	mmol N/m^3			
Z	Nutrients in herbivores	mmol N/m^3			
M	Nutrients in mixotrophs	mmol N/m^3			
I_n	Nutrient inflow to the system	mmol N/(m^3 d)	0.027–0.037	0.032	25%
l_n	Loss rate of nutrients	d^{-1}	0.0008–0.003	0.003	?
l_p	Loss rate of autotrophs	d^{-1}	0–0.003	0	—
l_z	Loss rate of herbivores	d^{-1}	0.2–0.387	0.2	30%
l_m	Loss rate of mixotrophs	d^{-1}	0.2–0.387	0.2	30%
r_p	Recycling rate of autotrophs	d^{-1}	0–0.003	0	—
r_z	Recycling rate of herbivores	d^{-1}	0.2–0.75	0.3	50%
r_m	Recycling rate of mixotrophs	d^{-1}	0.2–0.75	0.2	50%
f	Maximum nutrient uptake rate of autotrophs	d^{-1}	0.6–0.8	0.7	15%
k_p	Half-saturation constant of autotrophs	mmol N/m^3	0.2–0.6	0.5	25%
g	Maximum nutrient uptake rate of mixotrophs	d^{-1}	0.41–0.5	0.5	20%
k_m	Half-saturation constant of mixotrophs	mmol N/m^3	0.2–0.6	0.6	20%
h	Maximum ingestion rate of mixotrophs	m^3/(mmol N d)	0.88–1.32	1.0	25%
e	Maximum ingestion rate of herbivores	m^3/(mmol N d)	2–3	2.7	20%

The model parameters, their biological interpretation, units, estimated average (EAV) and the quality of the estimates, given as the coefficient of variation (CV) with the estimated average taken as the expectation value.

3. In order for the mixotroph or the autotroph to grow autotrophically without the presence of the other and with nutrients available in high concentration, we derive the conditions

$$l_m + r_m < g, \tag{8}$$

$$l_p + r_p < f. \tag{9}$$

2.1. The equilibrium and some of its properties

This system has a unique non-trivial equilibrium $(N^\star, P^\star, M^\star, Z^\star)$ (see Appendix A). It is positive if the parameters fulfill the following conditions:

$$0 < \frac{A}{eh} < \frac{g}{h} \quad \text{and} \quad G < f < H \text{ if } hl_z < el_m \tag{10}$$

$$\text{or} \quad G > f > H \text{ if } hl_z > el_m \tag{11}$$

with

$$A = e(l_m + r_m) - h(l_z + r_z),$$
$$B = eg - (e(l_m + r_m) - h(l_z + r_z)) = eg - A,$$
$$H = \frac{(Ak_m + Bk_p)(e(egI_n - A(k_ml_n + I_n)) + B(r_pl_z - r_zl_p))}{ABk_ml_z},$$
$$G = \frac{(Ak_m + Bk_p)(el_m - hl_z)(l_p + r_p)}{eAk_ml_m} + \frac{hl_z}{el_m}H. \tag{12}$$

Washout from mixotrophs and from heterotrophs being approximately the same, $l_m \approx l_z$, together with the assumption $h < e$ (Eq. (7)), indicates that the condition $hl_z < el_m$ (Eq. (10)) is the biologically plausible one in our system.

Since $\frac{A}{eg} \left(= \frac{(l_m+r_m)}{h} - \frac{(l_z+r_z)}{e} \right)$ is restricted to the interval $(0, \frac{g}{h})$ it is evident that there must be a balance between the loss-to-gain ratios from the mixotroph and herbivore compartments. High herbivore predation e and mixotrophic nutrient uptake g increase the region over which this balance occurs; a larger e also enlarges the interval for f (in Eqs. (10) or (11)). In relation to the conditions imposed on our model we may remark that condition (8) ensures that $\frac{A}{eg} < \frac{g}{h}$, while condition (7) with the assumption of approximately equal outwash and recycling rates of mixotrophs and herbivores ensures $0 < A$, making the first inequality in Eq. (10) biologically plausible.

If the condition $l_p = r_p = 0$ (no washout or recycling from the autotrophs) is imposed on Eq. (12), then we get $G = \frac{hl_z}{el_m} H$. In such conditions, Eqs. (10) and (11) can be reformulated as

$$\frac{hl_z}{el_m} H \overset{(>)}{<} f \overset{(>)}{<} H.$$

The necessary conditions for the existence of an equilibrium, $\frac{hl_z}{el_m} H < H$ with condition (10) and $\frac{hl_z}{el_m} H > H$ with condition (11), are then granted. If $l_p > 0$ and $r_p > 0$ then the existence interval of f becomes smaller: recycling and washout from autotrophs make existence of this system less likely (in Eq. (12), condition (10) constrains the first term of G to be positive. Further assuming that the term $(r_pl_z - r_zl_p)$ in H is, as the difference of two similar parameters, very close to zero, the difference $H - G$ becomes thus smaller than with $l_p = r_p = 0$). However, l_p and r_p are small compared to grazing (Table 1) and they cause considerable complication in the analysis of the subsystems (see below).
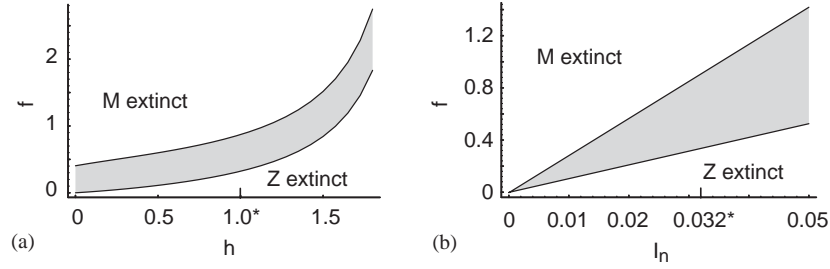
Fig. 3. Regions of the parameter space where the equilibrium exists; (a) f, h-space, (b) f, I_n-space. Parameters above the two lines result in a negative mixotroph equilibrium abundance, while below the two lines the same is true for the herbivore equilibrium biomass. An $\star$ marks the estimated parameter values.

Therefore, we will assume that $l_p = r_p = 0$. Note that in this case condition (5) is automatically fulfilled whenever condition (8) holds. Ecologically, this is equivalent to the reasonable assumption that all autotroph loss is due to grazing (Sharp, 1977; Ward and Bronk, 2001).

For the parameters in Table 1, the existence of an equilibrium as a function of f and either the mixotrophic grazing link h or enrichment of the system I_n was explored numerically. The size of the parameter region with positive equilibria is independent of mixotrophic grazing activity h (the difference $H - G$ may in general increase or decrease, but in the plotted neighborhood of the estimated parameters it only increases by factor 2), but with an increasing mixotrophic grazing rate h the autotrophic growth rate f must also increase to avoid the herbivore going extinct (Fig. 3a). This implies that the mixotrophic grazing link has a weak influence on the existence of an equilibrium in a realistic region of parameter space. In contrast the nutrient input I_n strongly influences the size of this parameter region (Fig. 3b): as when I_n increases, the parameter region also increases. I_n may be interpreted as an enrichment indicator; the effect of changing I_n is similar to that of changing the carrying capacity in models where the dynamics of the lowest trophic level follow a logistic growth equation. As such, enrichment enlarges the region in parameter space where equilibria may exist.

It can also be shown that while the system without recycling may exist, the system with full recycling and washout from the nutrient pool only (no washout of autotrophs, mixotrophs, and herbivores) has no equilibrium.

2.2. Subsystems, their equilibria and their stability

We study the subsystems $N - P - Z$ and $N - P - M$ for two reasons: first, the subsystems can give a better understanding of the functional roles of the herbivore and the mixotroph in the whole system. Second, in the case of instability of the whole system, the invasion criteria of these subsystems (see Appendix B) will indicate if there is unstable coexistence of all four trophic species or if one of them might go extinct. For

this analysis, let $r_p = l_p = 0$ (as justified in the previous section).

The system without mixotrophs: Consider system (1)–(4) without mixotrophs

$$\frac{dN}{dt} = I_n - l_n N - f \frac{N}{k_p + N} P + r_z Z, \qquad (13)$$

$$\frac{dP}{dt} = f \frac{N}{k_p + N} P - ePZ, \qquad (14)$$

$$\frac{dZ}{dt} = ePZ - l_z Z - r_z Z. \qquad (15)$$

This is a simple 3-level food chain with a unique positive (stable or unstable) equilibrium. If we consider the subsystem without recycling ($r_z = 0$), we get a globally stable food chain (see Appendix A). This food chain would remain stable if we allow for washout from autotrophs ($l_p \neq 0$). We see in this example that recycling ($r_z \neq 0$) can lead to unstable equilibria.

The system without herbivores: Consider system (1)–(4) without herbivores

$$\frac{dN}{dt} = I_n - l_n N - f \frac{N}{k_p + N} P - g \frac{N}{k_m + N} M + r_m M, \quad (16)$$

$$\frac{dP}{dt} = f \frac{N}{k_p + N} P - hPM, \qquad (17)$$

$$\frac{dM}{dt} = g \frac{N}{k_m + N} M + hPM - l_m M - r_m M. \qquad (18)$$

This system has a unique equilibrium (stable or unstable) that is positive if the autotrophic activity of the mixotrophs is small compared to losses by washout or recycling

$$r_m + l_m > g \frac{N_{3,Z}^{\star}}{k_m + N_{3,Z}^{\star}} \qquad (19)$$

(see Appendix A, Eq. (A.2)). More interesting is that the mixotrophic grazing allows coexistence of all 3 species. To see this, consider the above system without the mixotrophic interaction hPM and where we allow again washout and recycling from autotrophs (otherwise the autotrophs follow a positive or negative exponential

growth, since $N^\star$ may be determined from the mixotrophic equation alone).

$$\frac{dN}{dt} = I_n - l_n N - f\frac{N}{k_p + N}P - g\frac{N}{k_m + N}M$$
$$+ \; r_p P + r_m M,$$

$$\frac{dP}{dt} = f\frac{N}{k_p + N}P - l_p P - r_p P,$$

$$\frac{dM}{dt} = g\frac{N}{k_m + N}M - l_m M - r_m M.$$

The autotroph and the mixotroph equation each determine a value for the nutrients at equilibrium. This contradiction is most likely to be resolved by competitive exclusion of either P or M, i.e., the more efficient consumer (the one that can exploit nutrients to a lower level, here P because of condition (5)) will survive.

3. Parameterizing the model and simulation setup

We use the model developed above to study: (1) the effect of mixotrophic behavior on the existence of equilibria and on their stability, and (2) the link between this relation and recycling of nutrients. The question about existence can be studied analytically, but the analytical expressions for the stability analysis of the 4-level system become unwieldy. Therefore, we use a Monte-Carlo approach to study existence and stability by creating large numbers of random parameter sets that create positive equilibrium values of all state variables, both with and without the mixotrophic link or recycling, and that fulfill the minimal conditions (6)–(9). The effects of the mixotrophic grazing link and of recycling are then examined by comparing the stability of systems with and without the mixotrophic link and of systems with and without recycling for each random parameter set. The random parameters are chosen in two ways: (a) first estimating expectation and standard deviation of all parameters to represent an open ocean planktonic system with mixotrophic dinoflagellates (see Appendix C for details on the estimation and Table 1 for the values), which are then used to create lognormally distributed random parameter sets around these estimates (Limpert et al., 2001), and (b) with a uniform distribution from the interval (0,3) (note that this interval includes the estimated ranges of all the parameters). The lognormal random parameters are created by taking the estimated value as the mean with a constant coefficient of variation (CV = standard deviation divided by the mean) as a measure of how exact this mean value has been calculated (a high CV indicates a high uncertainty of the value). Compared to normally distributed random variables the lognormal distribution has the advantage of only producing positive values. This approach also constrains the Monte Carlo para-

meter sets to a distribution reminiscent of the often quoted "rule of thumb" that parameter values are $\frac{1}{2}$ to 2 times their average parameter values (e.g., Fasham et al., 1990). The lognormally distributed random parameter sets will also be referred to as ecologically relevant parameter sets or the 'real system' since they are near the values estimated from the literature. By using these two types of random parameter sets, we will gain some insight as to whether the estimated parameters are in a region of the parameter space that has special properties when compared to parameters that were chosen by chance alone.

Stability was determined by applying the Routh–Hurwitz criteria (see, e.g., Edelstein-Keshet, 1988) to the analytical form of the community matrix (the Jacobian at the equilibrium), thus eliminating numerical errors that can occur when calculating the eigenvalues directly from the parameterized (numerical) community matrix.

4. Simulations and results

In the first part of this section we will discuss the general dynamics of the mathematical system while in the second part the specific questions regarding mixotrophy and recycling will be addressed in detail. As justified previously we will set $r_p = 0$ and $l_p = 0$ for all simulations of this section.

4.1. General dynamic behavior of the system

With the estimated parameters (see Table 1) the model shows a stable equilibrium with $(N^\star, P^\star, M^\star, Z^\star) = (0.45, 0.19, 0.048, 0.11)$ (see Fig. 4 for a simulation). The subsystem $N - P - M$ also exists (stable) with $(N^\star_{3,Z}, P^\star_{3,Z}, M^\star_{3,Z}) = (0.15, 0.30, 0.16)$ as well as the subsystem $N - P - Z$ with $(N^\star_{3,M}, P^\star_{3,M}, Z^\star_{3,M}) = (0.68, 0.19, 0.15)$ (units are always mmol N/m^3).

After pulse perturbations of the full system by a five-fold increase or decrease of the state variables from the equilibrium values (all possible combinations of increased and decreased state variable initial conditions were tested by simulation) the system always returned with damped oscillations to the equilibrium. In contrast, with ten-fold increases or decreases, extinction of one population (Z) was occasionally observed. Moreover, in some simulations a long lasting depletion of the herbivore population to very low levels was observed (e.g., with starting points being five times the equilibrium values). This behavior was caused by the herbivores having only one food source and thereby overgrazing the autotrophs. The herbivores remained scarce until the autotroph population recovered; this recovery was delayed by the grazing activity of mixotrophs on autotrophs. These low levels of

herbivores (that may be forced arbitrarily close to 0) also show that our system is not persistent (sensu Yodzis, 1989). However, mutual invasibility (see below and Appendix B) is possible in our system, i.e., if either autotroph, mixotroph or herbivore go extinct locally in the ocean then the system will settle to a new equilibrium where invasion by the lost trophic species is possible. Therefore, our local model in the dynamic mixing environment of the open ocean will allow for long-term coexistence of all levels.

The dynamic behaviors of the system with the random parameter sets are summarized in Table 2. We see that most parameter sets that fulfill the minimal conditions (6)–(9) show a stable equilibrium (99.9% for the lognormally distributed parameter sets, 92% for the uniformly distributed parameter sets). The remaining parameter sets with an unstable equilibrium show extinction of the herbivore and subsequent stabilization of the 3-species subsystem $N - P - M$ (determined by numerical simulation) for all of the lognormally distributed parameter sets and for all except 3 of the uniformly distributed parameter sets (1 with recycling, 2 without recycling). These 3 parameter sets result in unstable coexistence of all four state variables. Calculation of their Lyapunov exponents (with the algorithm described in Wolf et al., 1985) showed that the dynamics

are simple non-chaotic oscillations. It should be pointed out that extinction of the herbivore or coexistence was always equivalent to violation or fulfilling of the invasion criterion (B.1) (see Appendix B). This criterion is much less costly to calculate than to simulate system (1)–(4) numerically. We can conclude that the system with biologically relevant parameters (lognormally distributed) is more likely to show a stable equilibrium and any population fluctuations would arise from exogeneous stochastic forcing.

Invasion of the subsystems $N - P - Z$ or $N - P - M$ by the mixotroph or the herbivore species respectively have been mentioned several times. This is interesting to explore because extinction is possible in our local model, but the invasibility criterion (see Appendix B) tells us whether recolonization is possible given the relative competitive and consumptive abilities of the autotrophs, herbivores and mixotrophs. A necessary condition for a successful invasion is that the per capita rate of change of the invading population must be positive for low densities of this population. Testing these conditions with the estimated parameters in Table 1 we get positive values in both cases that are of the same magnitude (although the herbivore has a per capita rate of change that is 6 times larger than that of the mixotroph). Therefore, invasion of both populations can be considered to be equally likely. It can also be shown that if the autotroph goes extinct then the system $N - M$ (the herbivore will of course also go extinct without its prey) has a unique stable equilibrium. With the estimated parameters the autotroph can invade this system. We have therefore full mutual invasibility in our real system.
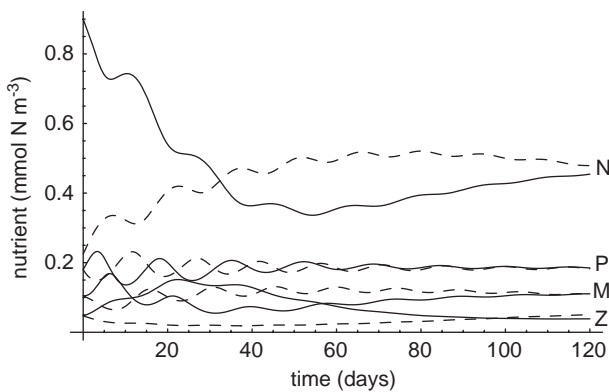

Fig. 4. Return of system (1)–(4) to its equilibrium after perturbing the nutrients by a two-fold increase (straight lines) or decrease (dashed line).

4.2. Existence and stability of the whole system in relation to mixotrophic behavior and recycling

In this section we will explore by analytical arguments and by Monte-Carlo simulations the relation between existence (and stability) of the non-trivial equilibrium and the presence or absence of either the mixotrophic link or recycling.

Table 2
Monte Carlo simulations 1

	Lognormal distribution		Uniform distribution	
Number of parameter sets:	200,000		1,000,000	
	Recycling	No recycling	Recycling	No recycling
Fulfill min. conditions	45367	50128	529	692
All systems stable	45292	50128	436	690
Two subsystems stable	75 (75)	0	90 (89)	2 (0)
N–P–Z–M and N–P–Z stable	0	0	3 (3)	0

Absolute numbers of random parameter sets that produced various stability behaviors (see text). The numbers in parentheses indicate how many of the unstable systems showed extinction of the herbivore or the mixotroph (with subsequent stabilization of the subsystem).

4.2.1. Mixotrophy and existence of equilibrium

For zero mixotrophy grazing, $h = 0$, (8) ensures that the condition $0 < A < eg$ (equivalent to $0 < \frac{A}{eh} < \frac{g}{h}$) will always be fulfilled. A is a linear function in h and will decrease with increasing h, but the interval $(0, eg)$ remains unchanged; therefore, an increasing h must be compensated by an increasing herbivore grazing rate e to maintain A in the interval $(0, eg)$. The difference $H - G$ will always be positive as mentioned above, but it may either increase or decrease with increasing h. Fig. 5(a) illustrates this relationship: while with the estimated parameters $H - G$ increases with increasing h, a slightly different value for r_z results in the inverse relationship. Similar results were obtained when testing the relationship between the strength of the mixotrophic grazing and the intervals for the other grazing parameters e and g for which the non-trivial equilibrium exists (other parameters fixed at their estimated value). With increasing h, the existence interval for g becomes smaller while the one for e increases. There is, therefore, no unique connection between the strength of the mixotrophic grazing link and the interval of values of f, g and e for which an equilibrium exists.

To corroborate these findings we tested the full 4-level system for existence with randomly generated parameter sets with either $h \neq 0$ or $h = 0$. We calculated the proportions of all the random parameter sets where (1) the system with and without mixotrophic link existed, (2) only one of these systems existed and (3) neither of them existed. This setup allows us to determine whether the mixotrophic grazing link enlarges the parameter region of existence. However, we cannot test if this link reduces the region because the two systems being compared have a different number of parameters; with randomly chosen parameters a system with fewer parameters is always equally or more likely to exist. The results are summarized in Fig. 6. In most cases the system without the mixotrophic grazing interaction is more likely to exist. However, the single case in which the mixotrophic link produces an increased range of existence of a (stable or unstable) equilibrium is the most ecologically realistic case: the lognormal distribution with recycling.

4.2.2. Recycling and existence of equilibrium

For simplification let $r := r_m = r_z$. The interval $(0, eg)$ is not affected by this parameter, and A is a linear function of r, so recycling does not influence the likelihood that the first inequality in condition (10) will be fulfilled. Since $H - G = (1 - \frac{hl_z}{el_m})H$ (see Appendix A) we can study the influence of recycling on the size of $H - G$ by studying $\frac{\partial H}{\partial r}$ only. Because of condition (7) we have $\frac{\partial A}{\partial r} > 0$. $\frac{\partial H}{\partial A}$ is in general either positive or negative, but for the estimated parameters and a recycling rate $r \in (0, 0.3)$, it is negative (note that B has been replaced by $eg - A$ for this and the following computation). Since $\frac{\partial H}{\partial r} = \frac{\partial H}{\partial A} \frac{\partial A}{\partial r}$ we can conclude that recycling will reduce the region in parameter space for which an equilibrium exists. This is illustrated in Fig. 5b: the positive slope of $\frac{\partial H}{\partial r_m}$ (the dashed curve where r_z is fixed) is annuled by the negative slope of $\frac{\partial H}{\partial r_z}$ (the dashed curve where r_m is fixed) again because of condition (7). A numerical existence analysis for the parameters g and e in relation to r reveals a slight increase of the existence interval for g with increasing r. In contrast, e has only a lower bound for $r < 0.32$. For larger r no equilibrium exists.
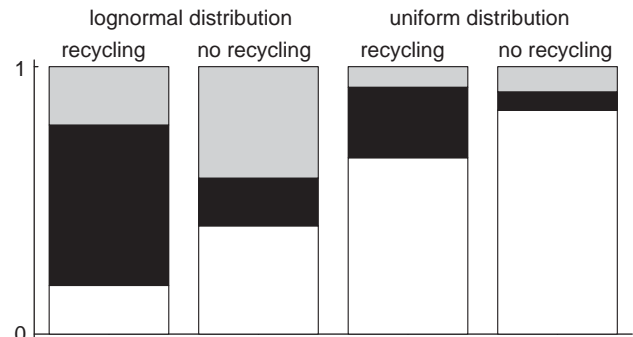

Fig. 6. The relationship between mixotrophic behavior and existence of a positive equilibrium, based on 1,000,000 random parameter sets for each type of distribution. We retained only parameter sets that fulfilled conditions (6)–(9) and where the equilibria with or without mixotrophic link were positive. The bars represent the proportions between existence of both systems (gray), only system with mixotrophic link existing (black) and only system without mixotrophic link existing (white).
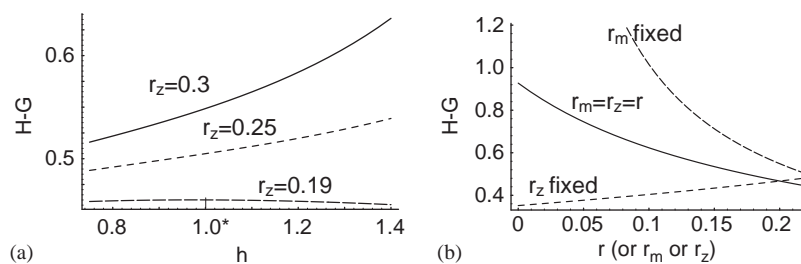

Fig. 5. Sensitivity of the region in parameter space where an equilibrium exists to the mixotrophic interaction (a) and recycling (b). The difference $H - G$ is plotted in (a) against h with different values of r_z. In (b) the straight line is the difference $H - G$ if both recycling coefficients are the same size (r), the dashed lines are the difference if either r_z or r_m is fixed to the estimated value and the other parameter is varied.

4.2.3. Mixotrophy and stability

Plotting the real part of the dominant eigenvalue λ of the community matrix with the estimated parameters (see Fig. 7a) we see that in the neighborhood of the estimated value of h increasing mixotrophic activity is stabilizing, but further away the equilibrium may become either more or less stable. To test the general impact of mixotrophy on stability we used all of the random parameter sets where the equilibrium for the full system, both with and without the mixotrophic grazing link ($h \neq 0$ or $h = 0$), existed and was stable. For these parameter sets we then calculated the logarithm of the ratio of the dominant eigenvalue with mixotrophic link divided by the dominant eigenvalue without mixotrophic link ($\log(\frac{\text{Re}(\lambda_{h \neq 0})}{\text{Re}(\lambda_{h=0})})$, calculated numerically). Therefore, a positive value indicates that the system with mixotrophic grazing link is more stable. Fig. 8 shows the distributions of these values for lognormal

and uniform random parameter sets, both with and without recycling. These distributions confirm the trend described in the paragraph about existence, i.e., the real system is in a region of the parameter space where the mixotrophic link has a stabilizing effect. In contrast, using the biologically less realistic uniform distributions, mixotrophy seems to have a slightly destabilizing effect. Again, the latter observation might be a result of comparing the stability of two systems with a different number of parameters.

4.2.4. Recycling and stability

The stability of the equilibrium using the estimated parameter set (Table 1) was examined in relation to recycling (r_z and r_m) by plotting the dominant eigenvalue at the equilibrium (Fig. 7b). Increasing the recycling rate (i.e., both r_z and r_m at the same rate) destabilizes the equilibrium. This result corroborates the findings in
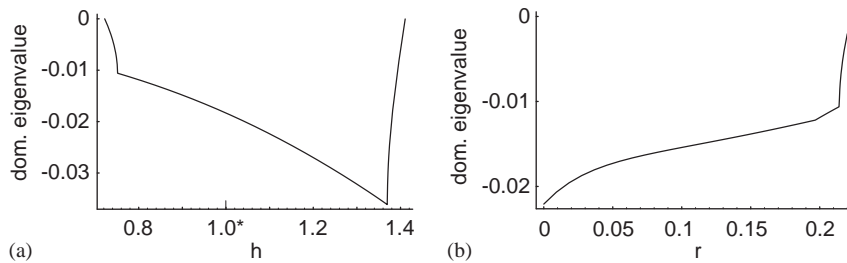

Fig. 7. The real part of the dominant eigenvalue of the community matrix plotted against the mixotrophic activity h (a) or against the recycling rate r (b) if we set $r := r_m = r_z$ (both curves are plotted over the range of the argument where an equilibrium exists).
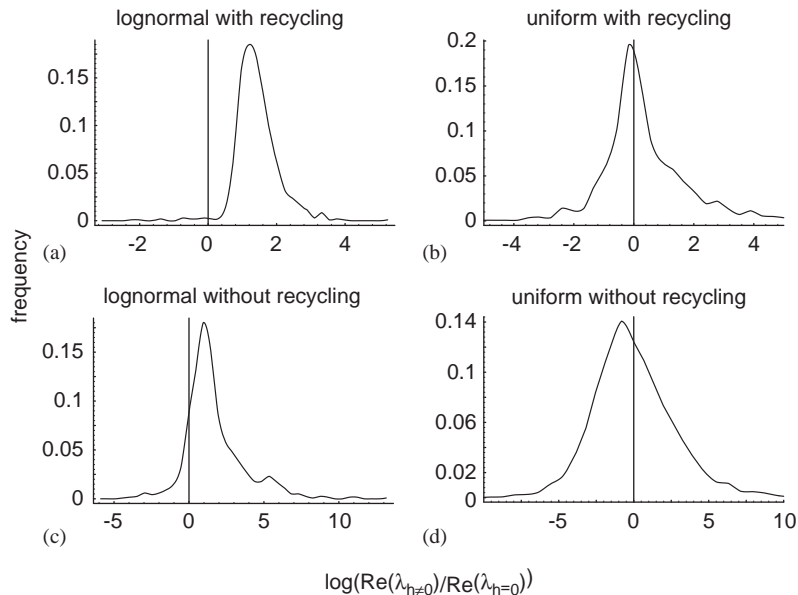

Fig. 8. Stability of randomly parameterized systems with and without the mixotrophic link. The figures show the empirical distributions of $\log(\frac{\text{Re}(\lambda_{h \neq 0})}{\text{Re}(\lambda_{h=0})})$ (λ is the dominant eigenvalue, a peak for positive x means that the system with the mixotrophic link is more likely to be stable). Graphs (a) and (c) show the distributions with or without recycling for the lognormal random parameter sets, while graphs (b) and (d) show these distributions for the uniform random parameter sets.

Table 2 where most unstable equilibria occurred with recycling.

5. Discussion

With ecologically realistic parameters our model shows stable coexistence of autotrophs, mixotrophs and herbivores at biologically reasonable concentrations. This is consistent with the findings of Stickney et al. (2000) and reinforces their suggestion that mixotrophy is a viable resource niche under summertime quasi-steady-state conditions.

The model has in general a stable equilibrium (whenever it exists) or, in rare cases, oscillating coexistence (maybe even chaotic behavior). This unstable coexistence can be predator-mediated, as recently observed in model systems by Abrams (1999), or due to the mixotrophic grazing link (Holt and Polis, 1997). However, the simulations in the neighborhood of the estimated parameters converged within weeks to a stable equilibrium (Fig. 4). Therefore, assuming that our model and parameters are ecologically realistic, then an absence of observed equilibrium states in the ocean cannot be attributed to chaotic dynamics; alteration of the environmental forcing producing stochasticity in the parameters would instead be responsible for fluctuating population densities that appear to be chaotic (Hastings, 1995). Studying the time evolution of the model when such disturbances are included may give further insight into the system. The absence of chaotic dynamics is consistent with the general trend that either a productive environment or very high turnover rates are necessary prerequisites for chaotic dynamics (McCann and Yodzis, 1994); our model parameters describe a system with a moderate turnover rate and low standing crop. However, phase-locking with environmental fluctuations could occur, driving the system to truly chaotic dynamics.

Pulse perturbations of our model can lead to herbivore extinction. However, because the mutual invasibility criterion is assured (see Appendix B), extinction of a species in the system does not imply permanent exclusion of the locally extinct species. If we consider the model to be a local dynamical description, the mutual invasibility criterion together with the possibility of migrations from neighboring areas or mixing in the ocean's surface layer permit recolonization and make a strong "plausibility argument" (Yodzis, 1989) for coexistence of all trophic species.

There is no unidirectional trend in the influence of the mixotrophic grazing parameter h nor the recycling rates r_m and r_z on the size of the parameter space where an equilibrium exists. However, the system as parameterized for the ocean appears to lie in a parameter region where increasing h increases the existence interval while increasing recycling decreases this interval. Moreover, mixotrophy has a stabilizing effect on equilibrium points in this area of parameter space. This stabilizing effect appears to overcome the general destabilizing effect that is caused by tight recycling (e.g., DeAngelis, 1992). This effect may be similar to the stabilizing effect caused by prey switching in model systems (e.g., Murdoch and Oaten, 1975; Tansky, 1978).

The relationship between the mixotroph and autotroph in our model system is more similar to that of intraguild predation (IGP) than of simple prey switching. The hallmark of IGP is that the intraguild predator reduces the pressure of competition for a resource by preying upon its competitor (Polis et al., 1989; Holt and Polis, 1997). This is the same relationship that the mixotroph and autotroph exhibit in the studied model: they compete for nutrients and the mixotroph grazes on the autotroph, thereby reducing competitive effects of the autotroph. The mixotrophic link thus permits the two competitors to coexist on a unique resource, which is also one of the features of IGP. The principal difference between existing models on IGP and mixotrophy lies in the "growth" function of the lowest trophic level, $f(P)P$ for living organisms compared to $I_n - r_n N$ for nutrients. None of the results mentioned in Polis et al. (1989) or Holt and Polis (1997) seems to be sensitive to this difference. Furthermore, McCann and Hastings (1997) observed that the omnivorous link in a classical IGP model stabilizes the system (experimentally confirmed by Holyoak and Sachdev, 1998), similar to the stabilizing effect of our mixotrophic link. This reinforces the idea that IGP theory also applies to the mixotrophic nutritional link and that it is instructive to think of mixotrophy in the ocean in this context.

As mentioned by Polis and Strong (1996), mixotrophy is one factor undermining the concept of discrete trophic levels. As such, planktonic interactions in aquatic food webs are more complex than can be described by simple food chains. Studying simple model systems that include mixotrophy or other forms of IGP may increase our understanding of how these interactions may influence the dynamics of planktonic food webs. However, static analysis must be applied with care to systems in fluctuating environments such as the ocean. For example, nutrient recycling is destabilizing under static, equilibrium conditions (DeAngelis, 1992) but it can be beneficial in maintaining systems under more realistically fluctuating conditions (Stone and Berman, 1993). As such, the analysis presented in this paper is only a starting point for understanding the influence of mixotrophy on planktonic food webs. Simulations with fluctuating/periodic parameters may give further insights into the adequacy and the predictive power of our model to describe plankton dynamics.

6. Conclusion

Our simple planktonic food web has shown that mixotrophy of an organism can mediate coexistence with other competitors (equivalent to intraguild predation), and that the planktonic system as parameterized for the ocean resides in a region of the parameter space where this mixotrophic link enhances stability, overcoming the destabilizing effect of rapid nutrient recycling. In this region, mixotrophy also enhances existence of a non-trivial equilibrium. Thus, mixotrophy may be an important stabilizing link in ocean planktonic ecosystems.

Appendix A. The equilibrium of the 4-level system and its subsystems

Setting Eq. (4) equal to 0 gives us the equilibrium of the autotrophs,

$$P^\star = \frac{l_z + r_z}{e}.$$

Using this result and setting Eq. (3) equal to 0 gives us the equilibrium for the dissolved nutrient,

$$N^\star = \frac{k_m(e(l_m + r_m) - h(l_z + r_z))}{eg - (e(l_m + r_m) - h(l_z + r_z))} =: \frac{k_m A}{B}.$$

Now setting Eqs. (1) and (2) equal to 0 gives the equilibria for the nutrient contained in the mixotrophs and the nutrient contained in the autotrophs,

$$M^\star = \frac{C(e(egI_n - A(k_m l_n + I_n)) + B(r_p l_z - r_z l_p)) - fABl_z k_m}{BC(el_m - hl_z)},$$

$$Z^\star = \frac{Afk_m - C(l_p + r_p)}{eC} - \frac{h}{e} M^\star,$$

with $C = Ak_m + Bk_p$. Now we may derive the conditions for which this equilibrium is positive. For $el_m > hl_z$ we get:

$$N^\star > 0 \Leftrightarrow A, B > 0 \Leftrightarrow \frac{g}{h} > \frac{A}{eh} > 0,$$

$$M^\star > 0 \Leftrightarrow f < \frac{C(e(egI_n - A(l_n k_m + I_n)) + B(r_p l_z - r_z l_p))}{ABk_m l_z},$$

$$Z^\star > 0 \Leftrightarrow$$

$$\frac{C(B(el_m - hl_z)(l_p + r_p) + h(e(egI_n - A(l_n k_m + I_n)) + B(r_p l_z - r_z l_p)))}{eABk_m l_m} < f. \tag{A.1}$$

For $el_m < hl_z$ the latter two inequalities change the direction. If there is no washout or recycling from the autotrophs ($l_p = r_p = 0$) a necessary condition for Eq. (A.1) to hold is

$$I_n > \frac{Al_n k_m}{eg - A} = l_n N^\star.$$

This is biologically meaningful since the nutrient inflow must be bigger than the nutrient outflow from one compartment.

A.1. The subsystem without mixotrophs

Let $r_p = l_p = 0$. Eq. (15) immediately yields

$$P_{3,M}^\star = \frac{l_z + r_z}{e} > 0.$$

Substituting this solution into Eqs. (13) and (14) allows to solve them for the remaining two equilibria:

$$N_{3,M}^\star = \frac{D + \sqrt{4e^2 I_n k_p l_n + D^2}}{2el_n} > 0,$$

$$Z_{3,M}^\star = \frac{f}{e} - \frac{2fk_p l_n}{D + \sqrt{e^2(I_n + k_p l_n)^2 - l_z f(2D + fl_z)}}$$

with $D = eI_n - ek_p l_n - fl_z$. $Z_{3,M}^\star$ may be positive.

The community matrix (the Jacobian at the equilibrium points) at this equilibrium has the form

$$\begin{bmatrix} -l_n - fP_{3,M}^\star \dfrac{k_p}{(k_p+N_{3,M}^\star)^2} & -f\dfrac{N_{3,M}^\star}{k_p+N_{3,M}^\star} & r_z \\[2ex] fP_{3,M}^\star \dfrac{k_p}{(k_p+N_{3,M}^\star)^2} & 0 & -eP_{3,M}^\star \\[2ex] 0 & eZ_{3,M}^\star & 0 \end{bmatrix}$$

$$=: \begin{bmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix}$$

and thus has the sign structure

$$\begin{bmatrix} - & - & + \\ + & 0 & - \\ 0 & + & 0 \end{bmatrix}.$$

Applying either a Routh–Hurwitz test or the color test by Jeffries (1974) (both tests may be found in Edelstein-Keshet (1988)) shows that this subsystem can have a stable or unstable non-trivial equilibrium ($b_1 = -a_{11} > 0$, $b_3 = a_{32}a_{11}a_{23} - a_{32}a_{13}a_{21}$ and $b_1 b_2 - b_3 = a_{11}a_{12}a_{21} - a_{13}a_{21}a_{32}$ may be positive or negative). If we set $r_z = 0$ then we get the sign structure

$$\begin{bmatrix} - & - & 0 \\ + & 0 & - \\ 0 & + & 0 \end{bmatrix}.$$

In this system the Routh–Hurwitz conditions are always fulfilled, therefore without recycling the food chain $N - P - Z$ has a stable non-trivial equilibrium whenever it exists.

A.2. The subsystem without herbivores

This system has at most one positive equilibrium

$$N_{3,Z}^\star = \frac{E + \sqrt{4h^2 I_n k_p l_n + E^2}}{2hl_n},$$

$$M_{3,Z}^\star = \frac{fN_{3,Z}^\star}{h(k_p + N_{3,Z}^\star)},$$

$$P_{3,Z}^\star = \frac{k_m l_m + k_m r_m + N_{3,Z}^\star(l_m + r_m - g)}{h(k_m + N_{3,Z}^\star)} \tag{A.2}$$

with $E = hI_n - fl_m - hk_p l_n$. $N_{3,Z}^\star$ and $M_{3,Z}^\star$ are always positive, while $P_{3,Z}^\star$ is positive whenever the numerator of Eq. (A.2) is positive, which is equivalent to Eq. (19). Biologically this means that $P_{3,Z}^\star$ is positive whenever the mixotrophs do not gain more nutrients by photosynthesis than they lose through washout and recycling.

The community matrix at this equilibrium has the form

$$\begin{bmatrix} -l_n - fP_{3,Z}^\star \dfrac{k_p}{(k_p + N_{3,Z}^\star)^2} - gM_{3,Z}^\star \dfrac{k_m}{(k_m + N_{3,Z}^\star)^2} & -f\dfrac{N_{3,Z}^\star}{k_p + N_{3,Z}^\star} & -g\dfrac{N_{3,Z}^\star}{k_m + N_{3,Z}^\star} + r_m \\[3ex] fP_{3,Z}^\star \dfrac{k_p}{(k_p + N_{3,Z}^\star)^2} & 0 & -hP_{3,Z}^\star \\[3ex] gM_{3,Z}^\star \dfrac{k_m}{(k_m + N_{3,Z}^\star)^2} & hM_{3,Z}^\star & 0 \end{bmatrix}$$

and thus has the sign structure

$$\begin{bmatrix} - & - & ? \\ + & 0 & - \\ + & + & 0 \end{bmatrix}.$$

Applying Routh–Hurwitz shows that this equilibrium may be unstable.

Appendix B. Criteria for invasion

A necessary condition for a population to invade an existing system is that the invader can grow at low densities. Since its growth rate depends on the abundances of the other populations it is usually assumed that these populations are at equilibrium before the invasion. For our system this means that for herbivore or mixotroph invasions, respectively, the following conditions must hold:

$$\frac{1}{Z}\frac{dZ}{dt} = eP_{3,.}^\star - l_z - r_z > 0, \tag{B.1}$$

$$\frac{1}{M}\frac{dM}{dt} = g\frac{N_{3,.}^\star}{k_m + N_{3,.}^\star} + hP_{3,.}^\star - l_m - r_m > 0, \tag{B.2}$$

where $N_{3,.}^\star$ and $P_{3,.}^\star$ are the (positive) equilibria of the relevant 3-population subsystem before the invasion (see Appendix A).

Appendix C. Parameter estimation from the literature

The 4-level model contains 14 parameters, many of which are not spatially and temporally constant in the ocean. To circumvent this problem, we adopted the general conditions seen during the North Atlantic Bloom Experiment (NABE, see Ducklow and Harris, 1993) as a framework to guide our estimates of parameters. Collection of much of the NABE data occurred during the end of the spring phytoplankton bloom and during the development of the summer microbially dominated planktonic food web. Where possible, we have derived our parameters from NABE or from areas with similar oceanographic conditions; however, it should be noted that because of the number of parameter estimates needed for the model that it was necessary to take some parameters from systems dissimilar to the NABE conditions. As such, a few parameter ranges were altered ad hoc to obtain positive model equilibria. The parameter value ranges and standard values estimated are summarized in Table 1.

The nutrient input rate to the system, I_n, which we take to be the nitrate flux into the mixed layer, was estimated from Fasham et al. (1990) (hereafter referred to as FDM) by two different methods. First, the annual nitrate flux from FDM's Fig. 17 was converted to an average daily flux, assuming a typical NABE mixed layer depth of 30 m (Marra and Ho, 1993). Second, the second term in FDM's Eq. (19) was used to calculate the nitrate input by using the FDM standard run across thermocline mixing rate and assuming that (1) the mixed layer depth was 30 m (Marra and Ho, 1993) and constant and (2) the nitrate concentrations above and below the mixed layer were 2 and 9 μM, respectively, as seen during NABE (Garside and Garside, 1993). These two estimates bracket the range for I_n given in Table 1. These two methods were also used to estimate the range for l_n.

For the biological components of the system, several assumptions were made to constrain the estimation of parameters. First, the autotrophs, mixotrophs and herbivores were assumed to have equivalent spherical diameters of 10, 40, and 40 μm, respectively. Volume specific carbon contents were assumed to be constant but were estimated separately for each component (Sieracki et al., 1993; Putt and Stoecker, 1989; Verity and Langdon, 1984 and references contained therein). The relationship between carbon and chlorophyll was assumed to be invariant and a ratio of 40 was used (Morales et al., 1991). The Redfield ratio was used to convert between carbon and nitrogen for all components.

The input rates of regenerated nutrient to the system (i.e., ammonium input) was estimated separately for the autotrophs, mixotrophs and herbivores, assuming that there was no non-biological loss from the system (i.e., no

downward diffusion out of the mixed layer) and that regeneration was instantaneous. The data on cell-specific nitrogen regeneration rates for the mixotrophs and herbivores were estimated from estuarine and freshwater organisms (Gast and Horstmann, 1983; Verity, 1985) because data for the open ocean were not available; these values were converted to appropriate units using the conversion factors as discussed above. Because these estimates were not based on the species present during NABE, we chose an interval within the estimated range consistent with the assumed sizes and characteristics of our model constituents.

The loss rates of herbivores and mixotrophs from the model were assumed to be equivalent to grazing on these constituents by higher trophic levels. Non-grazing losses were considered to be negligible to simplify the model. The grazing rates of microzooplankton and mesozoo-plankton on phytoplankton were measured during NABE (Lenz et al., 1993). These grazing rates were assumed to also represent the potential range of grazing rates of higher trophic levels (e.g., copepods) upon the mixotrophs and herbivores.

The nutrient uptake parameters for the autotroph and mixotroph were estimated as follows. The maximum nutrient uptake rates for the autotroph and mixotroph were calculated from the allometric equations of Moloney and Field (1989). These calculations assumed the previously listed cell sizes and conversion factors for volume specific carbon content. The range of values calculated for the autotroph compared favorably with those of Lieberman et al. (1994) while those of the mixotroph were similar to those of coastal dinoflagellates (Neuer and Cowles, 1995). However, because it was not possible to estimate all of the necessary parameters from NABE and because preliminary simulations showed that using an autotroph maximum nutrient uptake rate in the range calculated from Moloney and Field (1989) destabilized the model (resulting in extinction of the herbivores), the maximum values adopted (Table 1) were somewhat lower than those calculated from Moloney and Field (1989). The range of half-saturation constants from the literature spanned 0.2–0.6 mmol N m^{-3} (Fasham et al., 1990; Marra and Ho, 1993). A slightly higher half-saturation constant was used for the mixotroph compared to that of the autotroph as justified above.

The Lotka–Volterra grazing parameters for the mixotroph and herbivore were estimated by assuming that the parameter is equivalent to the initial slope of the saturating functional response curve for grazing. The ingestion rate of the herbivore was calculated from the grazing data in Fig. 3 of Verity (1985) with cell sizes taken from Verity and Langdon (1984); the ingestion rate was converted to appropriate units using the factors described above. The organisms in Verity (1985) were larger and smaller than our assumed herbivore size in

the model; therefore, these ingestion rates were assumed to represent the range of possible ingestion rates. The average mixotroph ingestion rate was calculated from that of the herbivore average ingestion rate assuming that the ratio of the mixotroph to ciliate grazing rate was 0.44; this ratio was derived by averaging available grazing rates for similar sized ciliates (taken to be the herbivore) and gymnodinoids (taken to be the mixotroph) from Neuer and Cowles (1995). This method was used rather than the equation of Moloney and Field (1989) because that equation was derived from a data set comprised mostly of grazing rates from much larger animals.

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