Mathematical Biology

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Periodic solutions in modelling lagoon ecological interactions

Abstract. In this paper we present and analyze a nutrient-oxygen-phytoplankton-zooplankton mathematical model simulating lagoon ecological interactions. We obtain sufficient conditions, based on principal eigenvalue criteria – for the existence of periodic solutions. A decoupled model which arises in the high nutrient regime is then considered in further detail for gathering some explicit conditions on parameters and averages of exogenous inputs needed for coexistence. An application to Italian coastal lagoons is finally obtained by parameter estimation and comparison with real data. A biological interpretation of the mathematical results is also presented.

1. Introduction

The management of Italian coastal lagoons is of considerable ecological and economic importance. In this paper we consider and investigate a mathematical model, based on the one presented in [17], that describes the interaction between the densities of phytoplankton, zooplankton, nutrients and oxygen in a prototypical lagoon. It is, in part, of the predator-prey type. Specifically, we consider the question of when positive periodic solutions exist, based upon the equation parameters. The model involves in particular the following features: mixed boundary conditions; no steady states due to (periodic) exogenous inputs; one equation linear in the corresponding variable. These are features that distinguish it from the models usually found in the literature. While these points do not present particular difficulties for the initial value problem, the situation appears to be more challenging for the question of the existence of positive periodic solutions. Our basic scheme for the latter is as follows: We employ topological arguments to show in turn the existence of a positive periodic solution for the oxygen–nutrient subsystem. Next, if

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the nutrient levels are sufficiently high, the existence of periodic positive solutions to the oxygen–nutrient–phytoplankton reduced model is obtained. Finally, if the level of the phytoplankton is sufficiently high, the existence of positive periodic solutions to the full oxygen–nutrients–phytoplankton–zooplankton system is shown. For this step, the actual equations structure of the model must be used. In essence we have a trophic cascade backwards. As might be expected, the suitable levels of the variables needed for the existence of positive solutions are formulated in terms of principal eigenvalues of related periodic-parabolic equations. In view of the high time/space variability of the exogenous inputs in the application we consider, it is however important for us to present eigenvalue bounds which are based on space/time integral averages of the coefficients rather than on max/min values as is done classically, (eg.[19]). We note that the possible presence of mixed boundary conditions causes some technical difficulty in the analysis: $C^{\alpha,\alpha/2}$ spaces must be employed, rather than the more convenient and commonly used C^1 spaces. We present in a preliminary lemma the needed eigenvalue results and sketch a brief proof. Since the equation for the zooplankton density is linear (in the zooplankton) in the final step we first perturb the problem and consequently obtain (one of) the necessary bounds. This process also bypasses the question of uniqueness of periodic solutions to a subsystem, as was done in the 2 equation case in [19], and which is not clear here. We point out that in our method of proof the parts of the boundary where a Dirichlet (resp. a Neumann) condition is satisfied must be the same for the phytoplankton and the zooplankton. The question of the full coexistence when this is not the case remains open, as does the question of uniqueness and the long time behaviour of the solutions.

It is a feature of the lagoons of interest to us that they may exist in a high nutrient regime (due to human activities). The system decouples in this situation, and we next focus on this case and further develop the results obtained earlier. In particular, we present some comparisons between numerical simulation results based on our model and actual physical measurements taken in the lagoon of Caprolace.

We comment that many types of phytoplankton, zooplankton and nutrients are actually present in the lagoons. Our constants and equations reflect the behaviour of "prototypical" entities. Furthermore, the lagoons of interest to us are very shallow ($\simeq 1$ meter), and we ignore in the model diurnal depth effects.

In conclusion we observe that lagoons and related ecological situations have been the subject of numerous biological researches. Associated and related mathematical models have also been examined. As already mentioned, the closest mathematical work appears to be the book by Hess, [19], and we have already mentioned several differences between the present work and [19]. An ordinary differential equation nutrient-prey-predator model is given in the work of Jang and Baglama, [20]. A mathematical model for phytoplankton is presented in Boushaba et al., [5], while Abdllaoui et al. present in [1] a study of dynamics of zooplankton-toxic phytoplankton systems. Spatial predator-prey interactions are considered by Palumbo and Valenti in [27] using a hyperbolic model. The other cited mathematical papers: [8], [11–13], [16], [18], [23], [33], [37] deal with related problems.

The ecology of shallow lakes is presented by Scheffer in his book, [30]. Cioffi et al. in [9] and [10] consider models and management strategies based on

simulations for the control of eutrophication processes in Italian lagoons. Ecological conditions and suggested actions are presented by Bucci et al. for another Italian lagoon, [6]. A one dimensional model and numerical simulations for oxygen dynamics in lagoon ecosystems are given by Lunardini and Di Cola in [24]. In [31], [32], Solidoro et al present modelling and simulation results for macroalgae evolution in the lagoon of Venice. Other results on related models, simulations, parameter estimations, can be found in [6], [14], [15], [25], [26], [28], [29]. We were unable, however, to find elsewhere the system discussed here under our conditions.

2. The model

Let v_1, v_2, v_3, v_4 denote the concentrations in the lagoon of phytoplankton, zooplankton, oxygen and nutrients respectively. The model we consider, based on the one used in [17] (and related to the ones considered in [20], [30] and elsewhere) is given by:

$$\frac{\partial v_1}{\partial t} - \varepsilon_1 \Delta v_1 - \mu_1 \vec{\nabla} \cdot (\vec{b} \, v_1) = k_{11} f(u_1, u_2, u_4) \frac{v_1 v_4}{k_X + v_4}$$
$$-k_{1,2} v_1^2 - k_{1,3} \frac{v_1 v_2}{k_p + v_1} \qquad (2.1')$$

$$\frac{\partial v_2}{\partial t} - \varepsilon_2 \Delta v_2 - \vec{\nabla} \cdot \left[\left(\mu_2 \vec{b} + \frac{\mu \vec{\nabla} v_1 r(v_1)}{1 + |\vec{\nabla} v_1|} \right) v_2 \right] = k_{2,1} \frac{v_1 v_2}{k_p + v_1} - k_{2,2} v_2$$
$$(2.2')$$

$$\frac{\partial v_3}{\partial t} - \varepsilon_3 \Delta v_3 - \mu_3 \vec{\nabla} \cdot (\vec{b} \, v_3) = k_{3,1} f(u_1, u_2, u_4) \frac{v_1 v_4}{k_X + v_4}$$
$$+k_{3,2}(O(u_2) - v_3) + k_{3,3} u_3$$
$$-k_{3,4} f_\alpha(v_3)[v_1 + v_2]$$
$$-[k_{3,5} v_1 + k_{3,6} v_2] v_3 - k_{3,6} v_3 \qquad (2.3')$$

where

$$f_\alpha(v_3) = \frac{v_3^2}{k_{AE} + v_3^2}.$$

$$\frac{\partial v_4}{\partial t} - \varepsilon_4 \Delta v_4 - \mu_4 \vec{\nabla} \cdot (\vec{b} \, v_4) = \left\{ k_{4,1} f_\alpha(v_3)[v_1 + v_2] \right.$$
$$+k_{4,2} \left(K_0 - \frac{v_3}{k_A + v_3} \right) \left. \right\} \left[K_1 - \frac{v_4}{k_B + v_4} \right]$$
$$-k_{4,3} f(u_1, u_2, u_4) \frac{v_1 v_4}{k_X + v_4}$$
$$+Q(x, t) - k_{4,5} v_4. \qquad (2.4')$$

Here ε_i represent the diffusivities, while $\vec{b} = \vec{b}(x, t)$ represents the water flow (unaffected by $(v_1, \ldots, v_4)$). Here the ε_i are assumed constants since we never

consider a situation of an anoxic crisis in this paper. The constants μ_i, μ represent mobilities, and $k_{i,j}, k_p, k_A, k_B, K_0, K_1$ denote positive constants. The functions $(u_1, \ldots, u_4)$, described in the following Table 1 represent periodic exogenous inputs of temperature, wind velocity and light, respectively.

The meaning of the terms on the right hand sides of (2.1') to (2.4') follows.

For equation (2.1') we have, in turn: the photosynthetic production of phytoplankton; its natural mortality; and the predation by the zooplankton. The function f represents the combined effect of photosynthetic active radiation and water temperature. The equation describing this effect is $f = k_1 u_1 u_4$ (see Table 1).

For equation (2.2') we have: the zooplankton growth due to the consumption of phytoplankton, followed by the natural mortality.

The functional form of eqs. (2.1')−(2.2') is a modified Rosenzweig-Mac Arthur model. It is based on a logistic predator-prey system with Holling II type response (see [39], pag. 72 for a reference) with linear mortality in the zooplankton equation ([30], pag. 152).

The extra term on the left hand side of equation (2.2') describes the possible movement of zooplankton in the direction of increasing phytoplankton, at a maximum rate determined by the mobility μ with $0 \leq r(v_1) \leq 1$, $r(v_1) = 0$ if v_1 is small enough to indicate that no drift of v_2 occurs in such a case.

For equation (2.3'), the terms represent: the oxygen production due to the photosynthetic action of the phytoplankton; the water-air oxygen exchange; the oxygenation of water due to the wind; the aerobic oxygen consumption occurring during organic matter degradation; the respiration oxygen consumption by phytoplankton and zooplankton. The effect of f_α is the consumption of oxygen by the bacterial activity, that re-mineralize the dead biomass (see the fourth term of eq. (2.3')).

The oxygen saturation value in water $O(u_2)$ is described by the equation $O(u_2) = 14.6 - 0.4u_2 + 0.008u_2^2$ (see [38]).

Finally, for equation (2.4'), the terms are: the production of inorganic nutrients due to aerobic degradation; sediment-water nutrient exchange. Both of these effects are limited by the water nutrient saturation threshold. The next term represents the photosynthetic consumption by the phytoplankton; and the last terms account for outside human interaction and natural nutrient washout. The function

Table 1. Driving environmental functions. See [17] for a reference on exogenous inputs definition.

function	biological meaning	units
$u_1(t) = 0.5 + 0.125 \sin\left(\frac{2\pi}{12}(t - 0.3)\right)$	photoperiod annual variation	$[t]$
$u_2(t) = 17.5 + 11 \sin\left(\frac{2\pi}{12}(t + 9)\right)$	water temperature	$[^\circ C]$
$u_3(t) = 1.8 + 0.8 \cos\left(\frac{2\pi}{12}(t + 4)\right)$	limiting v_1 growth factor	$[t]^{-1}$
$u_4(t) = 0.59 e^{0.0633 u_2(t)}$	limiting v_1 growth factor	$[t]^{-1}$

$Q(x, t)$ represents the nutrient source/sink due to human activities, specifically aquaculture, agriculture, run-off and waste water from the cities.

With system $(2.1' - 2.4')$ we associate the obvious natural boundary conditions on part of the boundary and, possibly, the most adverse conditions on another part. This is further discussed below.

3. Mathematical analysis

We consider the mathematical analysis of system $(2.1' - 2.4')$, and rewrite for convenience the equations in simpler form. Specifically, we collect similar terms; constants whose precise value is irrelevant to the mathematical analysis are chosen equal; some functions are described by their general properties rather than their explicit forms. These simplifications are done entirely for notation convenience in the mathematical analysis. System $(2.1' - 2.4')$ thus becomes:

$$\ell(\vec{v}) - \vec{\nabla} \cdot \left(F(x, t, v_1, \vec{\nabla} v_1) v_2\right) \vec{1}_2 = \vec{R} \tag{3.1}$$

$$\vec{1}_2 = (0, 1, 0, 0)$$
$$\ell(w) = w_t - \varepsilon \Delta w - \vec{\nabla} \cdot (\vec{b} w)$$
$$\vec{R} = (r_1, r_2, r_3, r_4) \quad \text{with :}$$
$$r_1 = [M(x, t)h_1(v_4) - f_1(v_1, v_2)]v_1$$
$$r_2 = f_2(v_1)v_2$$
$$r_3 = N(x, t)h_1(v_4)v_1 - g_1(v_1, v_2, v_3) + O(x, t) - v_3$$
$$r_4 = \{g_2(v_1, v_2, v_3) + [k_{4,1} - h_2(v_3)]\}[K - h_3(v_4)]$$
$$\quad - P(x, t)h_1(v_4)v_1 + Q(x, t) - v_4.$$

All coefficient functions in system (3.1) are assumed smooth, at least for nonnegative arguments. This is in particular true of the functions M, N, O, P, Q which represent periodic nonnegative exogenous inputs. From a biological point of view they account for the seasonality of exogenous inputs.

The simplified model (3.1) includes the original model $(2.1' - 2.4')$ as a special case. In fact the present system may be viewed as a generic competitive system for v_1 and v_2, due to the properties of f_1 and f_2 described below. r_3 is a generic representation of the main phenomena associated with the oxygen dynamics, such as photosynthesis, organic matter mineralization and exchanges with atmosphere. In the same way r_4 accounts for nutrients production by mineralization of biomass, the release of orthophosphate from/to the sediment. It describes also the saturation of nutrients in the water, consumption by photosynthesis, human interactions and washout.

Then the essential properties of the original system $(2.1' - 2.4')$ lead to the following conditions on the unknown function $\vec{v}$:

(i) Saturation. $h_i(\xi) = \xi/(k_i + |\xi|)$ for $i = 1, 2, 3$;

(ii) Competition. $f_2(\xi) = k_4 h_1(\xi) - k_5$
$f_1(\xi_1, \xi_2) \geq 0$, $f_1(0, 0) = 0$, $\frac{\partial f_1}{\partial \xi_1}(\xi_1, 0) > 0$, $\frac{\partial f_1}{\partial \xi_2}(\xi_1, \xi_2) > 0$,
$f_1(\xi_1, \xi_2) \to +\infty$ if $\xi_1 + \xi_2 \to +\infty$, $\xi_i \geq 0$ for $i = 1, 2$.
There exist constants $\gamma_0, \gamma_1, \gamma_2 > 0$ such that $f_1(\xi_1, \gamma_0 \xi_2)\xi_1 \geq f_2(\xi_1)\xi_2 + \gamma_1 \xi_1^2 + \gamma_2 \xi_2$ for any $\xi_1, \xi_2 \geq 0$.

(iii) Mineralization. $g_i(\xi_1, \xi_2, \xi_3) \geq 0$, $g_i(0, 0, \xi_3) = g_i(\xi_1, \xi_2, 0) = 0$, $\partial g_i / \partial \xi_3 \geq 0$ for $\xi_j \geq 0$, $= 0$ for $\xi_3 = 0$, with $i = 1, 2, j = 1, 2, 3$.

(iv) Zooplankton drift. For some constants $\delta, \delta_1 > 0$, $|\vec{F}(x, t, \xi, \vec{\eta})| \leq \delta$,
$\vec{F}(x, t, \xi, \vec{\eta}) = 0$ if $\xi \leq \delta_1$

(v) All $\varepsilon, k_i, k_{i,j}, K$ represent positive constants with K, $k_{4,1}$ less than 1.

We comment on the last condition in (ii). Observe that this condition is satisfied in the biological model and that the equation for v_2 is linear (in v_2). We thus may make the scale change $v_2 \to \gamma_0 v_2$ and take $\gamma_0 = 1$ in the sequel, without need to make other changes in the assumptions.

As stated earlier, we assume that $\partial\Omega = \partial\Omega_N \cup \partial\Omega_D$ with: $\partial\Omega_N \cap \partial\Omega_D = \emptyset$; $\partial\Omega_N, \partial\Omega_D$ smooth nonempty and $\partial\Omega_D$ closed. On $\partial\Omega_N$ we take the (natural) boundary condition: $\frac{\partial v_i}{\partial \vec{n}} + \mu \vec{b} \cdot \vec{n} v_i = 0$ with the obvious change if $i = 2$, $\frac{\partial v_2}{\partial \vec{n}} + (\mu \vec{b} + \vec{F}) \cdot \vec{n} v_2 = 0$, while we assume $v_i = 0$ on $\partial\Omega_D$, where $\vec{n} =$ unit outward normal, $x \in \Omega \subset R^3$ and $i = 1, \ldots, 4$. The above natural boundary conditions describe the fact that variables (e.g. biomass densities and chemicals) can't be introduced nor leave the lagoon through this part of the boundary, even though they are subject to currents and diffusion. The Dirichlet part of the boundary accounts for possible extremely hostile conditions to one or more densities due to, for example, chemical spills, etc. Other standard boundary conditions may be treated by routine modification of the methods we present. In particular if one of $\partial\Omega_N, \partial\Omega_D$ is empty, the procedures simplify, and we do not explicitly consider this case in the sequel unless otherwise specified.

For technical reasons, we also require that each point of $\partial\Omega_D \cap \overline{\partial\Omega_N}$ (if any) have a neighbourhood which is mappable – by a Lipschitz map – into a quarter sphere with the relevant part of $\partial\Omega_N$ mapped to a set in the $1/2$ plane: $x_2 = 0$, $x_3 > 0$ while the corresponding part of $\partial\Omega_D$ is taken to a set in the orthogonal $1/2$ plane: $x_3 = 0$, $x_2 > 0$. The precise details are given for example in [34] (see also [35], [36]). This assumption allows the application of $C^{\alpha,\alpha/2}$ interior estimates, [22], even to boundary points. We point out that while $\partial\Omega_D, \partial\Omega_N$ are taken to be the same for all v_i for convenience, it is important to the method that they actually be the same for v_1, v_2. Since these represent phytoplankton and zooplankton densities, this is a reasonable assumption. We also assume that for the smooth curve(s) $\mathcal{C}$ making up $\partial\Omega_D \cap \overline{\partial\Omega_N}$ there exists a constant C such that for any $h_0 > 0$ we can construct a tubular neighbourhood N_{h_0} of $\mathcal{C}$ with $|N_{h_0}| < Ch_0^2$ and function $\psi_{h_0} \in C^\infty$ with: $0 \leq \psi_{h_0} \leq 1$, $\psi_{h_0}(x) = 1$ if $x \in \Omega - N_{h_0}$, $\psi_{h_0}(x) = 0$ if dist$(x, \mathcal{C}) < h_0/2$, $|\nabla \psi_{h_0}| \leq C/h_0$. These conditions will be satisfied if the boundary of the lagoon is assumed sufficiently smooth.

All solutions will be understood to hold (at least) in the classical weak sense. Nonnegative nontrivial solutions will be called positive. Usually, this will actually be the case in $\Omega \times [0, T]$ by the strong maximum principle. Observe that by our assumptions the solutions will be classical except on $\partial \Omega_D \cap \overline{\partial \Omega_N}$.

Finally, α will always denote a generic positive constant less than one. Its specific value may change from proof to proof or within the same proof.

It will be useful to first present the following results. They are of significance here because the mixed boundary conditions lead us to use $C^{\alpha, \alpha/2}$ spaces rather than the more regular spaces commonly employed (see, e.g.: [19]). They also enable us to later avoid questions of uniqueness of solutions to subproblems as was done in ([19], p. 124) for a two species system, and give eigenvalue estimates based on coefficient mean values rather than extrema ([19]).

Lemma 3.1. *Consider the linear periodic-parabolic problem:*

$$\ell_1(w) \overset{\Delta}{=} w_t - \varepsilon \Delta w - \sum_{j=1}^{3} \frac{\partial}{\partial x_j}(\beta_j w) + hw = f$$

with: $w(x, 0) = w(x, T); \; w = 0 \text{ on } \partial \Omega_D; \; \frac{\partial w}{\partial n} + (\vec{\beta} \cdot \vec{n})w = 0 \text{ on } \partial \Omega_N$ *and:* $h, \vec{\beta} \in L^\infty(\Omega \times (0, T))$ *smooth,* $f \in L^2(\Omega \times (0, T)), \varepsilon > 0$ *constant with* $\vec{\beta} = (\beta_1, \beta_2, \beta_3)$. *Then:*

(a) *There exist positive constants K_0 and α such that if $h(x, t) > K_0$ then ℓ_1^{-1} maps $C^{\alpha, \alpha/2}(\overline{\Omega} \times [0, T])$ to itself and is completely continuous. If also $f \geq 0$, nontrivial, then $\ell_1^{-1}(f) > 0$ in $(\Omega \cup \partial \Omega_N) \times [0, T]$.*

(b) *The associated linear eigenvalue problem:*

$$\ell_1 w = \mu w$$

has a positive eigenvector w with associated real eigenvalue μ (called the principal eigenvalue). No other eigenvalue has an associated positive eigenvector and all other real eigenvalues exceed μ. The same results are true for the adjoint operator ℓ_1^*, formally given by

$$(\ell_1 u, v)_{L^2(\Omega \times (0, T))} = (u, \ell_1^* v)_{L^2(\Omega \times (0, T))}.$$

(c) *If $\mu > 0$ then for any $0 \leq f \in C^{\alpha, \alpha/2}$ there exists a unique $v \geq 0$ with $\ell_1 v = f$. Conversely, if for any such f there exists a unique $v \geq 0$ with $\ell_1 v = f$, then $\mu > 0$. If $h \geq 0$, then $\mu > 0$, unless $\partial \Omega_D = \emptyset$ and $h = 0$. In this case $\mu = 0$, $w \equiv 1$ is the associated eigenvector for ℓ_1^*.*

(d) *The eigenvalue μ depends monotonically and continuously (in $C^{\alpha, \alpha/2}$) on h. Furthermore:*

$$\mu \leq \inf_{\varphi \in H_0^1(\Omega \cup \partial \Omega_N)}$$

$$\times \left[\frac{\int_\Omega \varepsilon |\nabla \varphi|^2 + \sum_j (\tilde{\beta}_j)\varphi \frac{\partial \varphi}{\partial x_j} + \frac{1}{4\varepsilon} \sum_j (\tilde{\beta}_j^2)\varphi^2 + (\tilde{h})\varphi^2}{\int_\Omega \varphi^2} \right] \quad (3.5)$$

where: $\tilde{z} \overset{\Delta}{=} \frac{1}{T} \int_0^T z$, $H_0^1(\Omega \cup \Omega_N)$ denotes the closure in the Sobolev norm H^1 of functions of class $C^\infty(\overline{\Omega})$ with support in $\Omega \cup \Omega_N$. Consequently, $\mu < 0$ if h changes sign and h^- is large enough.

(e) Let $\varepsilon_1 > 0$ and $\frac{\partial g}{\partial u} \leq 0$. If u is any solution of $\ell_1 u = ug(x, t, u) + \varepsilon_1$ with $0 \leq u \in C^{\alpha, \alpha/2}$ then $u \geq v$ where $0 \leq v \in C^{\alpha, \alpha/2}$ is any solution of $\ell_1 v = vg(x, t, v)$. If $\frac{\partial g}{\partial u} \leq -k < 0$ and if there exist positive solutions v of $\ell_1 v = vg(x, t, v)$ then as $\varepsilon_1 \to 0$ a subsequence u_n converges in $C^{\alpha, \alpha/2}$ (and its (space) gradient pointwise) to one of the v.

(f) Let $0 \leq u \in C^{\alpha, \alpha/2}$ and $\ell_1 u \leq 0$. Then $u(x, t) \leq K\left[\int_0^T \int_\Omega u\right]$.

Proof. (a) Classical results, [22], immediately yield that there exists a solution u to the initial value problem if h is sufficiently large. The claim then follows from the Schauder Fixed Point Theorem applied to the Poincaré Map. That $u \in C^{\alpha, \alpha/2}$, for some $\alpha > 0$, also follows from [22], once we observe that interior estimates hold even at points on $\partial \Omega_D \cap \partial \overline{\Omega}_N$ by the assumptions on the mapping properties of domains of such points. The complete continuity is obtained by choosing a smaller value of α. If $f \geq 0$ then $u \geq 0$ by the weak maximum principle if h is big enough, [22], while if $u = 0$ at some point $(\overline{x}, \overline{t})$ with $\overline{x} \in \Omega$ or $\overline{x} \in \partial \Omega_N$ then $u \equiv 0$ by the strong maximum principle.

(b) Again, without loss of generality, suppose the conditions of (a) hold on h. Choose and fix $f \geq 0$, $f \in C_0^\infty(\Omega \times (0, T))$. Then $u = \ell_1^{-1}(f)$ is positive and thus $\ell_1^{-1}(f) > \eta f$ for some constant $\eta > 0$. We apply [20, p. 67] and conclude the existence of μ, w with $w > 0$. The same result holds for $(\ell_1^*)^{-1} : (\ell_1^*)^{-1} z = (1/\mu)z$ for some $z > 0$, by the very definition of ℓ_1^*. We conclude immediately that μ is the only eigenvalue with a positive eigenvector. If δ is any other eigenvalue of ℓ with eigenvector w_1 then $\delta > \mu$ follows by approximating w_1^- as in part (c) that follows.

(c) Suppose first that for any such f there exists $v \geq 0$ with $\ell_1 v = f$. Clearly $v \not\equiv 0$ and since $\ell_1^* z = \mu z$ with $z > 0$, then $0 < (z, \ell_1 v)_{L^2(\Omega \times (0,T))} = \mu(z, v)_{L^2(\Omega \times (0,T))}$ yields the result. Conversely, suppose $\mu > 0$, choose f and put

$$k_0 = \inf \{K_1 | \text{ if } k \geq K_1 \text{ there exists a unique } w \geq 0 \text{ such that } (\ell_1 + k)w = f\}.$$

If $k_0 < 0$, we are done. If $k_0 \geq 0$ choose $k' < k_0$ such that $\mu + k' > 0$ and $-k'$ is not in the spectrum of ℓ, i.e.: there exists a unique w such that $(\ell_1 + k')w = f$ but w changes sign. Approximate w^- by $w_n = \psi_{h_0}\left(\sqrt{w^2 + \frac{1}{n^2}} - w - \frac{1}{n}\right)/2$ where ψ_{h_0} is the function mentioned in the Introduction and observe that if $\ell_1^* z = \mu z$ with $z > 0$ then

$$(\mu + k')(z, w_n)_{L^2(\Omega \times (0,T))} \leq (z, (\ell_1 + k')w_n)_{L^2(\Omega \times (0,T))}$$

Letting $h_0 \to 0$ and then $n \to \infty$, we obtain by direct calculation,

$$(\mu + k')(z, w^-)_{L^2(\Omega \times (0,T))} \leq -\left(f\big|_{w^- > 0}, z\right)_{L^2(\Omega \times (0,T))}$$
$$\leq 0$$

and the needed contradiction.

Finally, that $h \geq 0$ implies $\mu \geq 0$ follows from the strong maximum principle applied to $(\ell_1^* - \mu)w = 0$. If $h \geq 0$ and $\mu = 0$ then w must be constant, which contradicts the assumption $\partial\Omega_D \neq \emptyset$. Observe that if $\partial\Omega_D = \emptyset$ and $h = 0$ then indeed $\mu = 0$.

(d) We modify some of the elliptic calculations of [3]. Direct calculations show that for $\ell_1^* w = \mu w$ with $w > 0$ and any $\varphi \in C_0^\infty(\Omega \cup \partial\Omega_N)$ we have

$$0 \leq \int_\Omega \int_0^T \left\{ \varepsilon w^2 \left| \nabla\left(\frac{\varphi}{w}\right) \right|^2 + \sum_j \beta_i \frac{\partial}{\partial x_j} \left(\frac{\varphi}{w}\right)(\varphi w) + \frac{1}{4} \frac{|\vec{\beta}|^2}{\varepsilon} \varphi^2 \right\}$$

$$= \int_\Omega \int_0^T \left\{ \varepsilon|\nabla\varphi|^2 + \sum \beta_j \varphi \frac{\partial\varphi}{\partial x_j} + \frac{1}{4} \frac{|\vec{\beta}|^2}{\varepsilon} \varphi^2 + h\varphi^2 \right\}$$

$$- \int_\Omega \int_0^T \frac{\varphi^2}{w} \left(-\varepsilon\Delta w + \sum \beta_j \frac{\partial w}{\partial x_j} + hw \right).$$

That is:

$$\mu T \int_\Omega \varphi^2 \leq \int_\Omega \left\{ \varepsilon T|\nabla\varphi|^2 + \sum_j \left(\int_0^T \beta_j \right)\varphi \frac{\partial\varphi}{\partial x_j} \right.$$

$$\left. + \frac{1}{4} \left(\int_0^T \frac{|\vec{\beta}|^2}{\varepsilon} \right)\varphi^2 + \left(\int_0^T h \right)\varphi^2 \right\}.$$

Passing to the limit gives the result for any $\varphi \in H_0^1(\Omega \cup \partial\Omega_N)$. Next to see that μ is monotone in h, let $\ell_1 u = \lambda u$, $(\ell_1 + \delta)v = \mu v$ with $\delta \geq 0$. Then $\ell_1 v \leq \mu v$, and without loss of generality assuming h is large, yields $\frac{1}{\mu} v \leq \ell_1^{-1}(v)$, whence $\frac{1}{\mu} \leq \frac{1}{\lambda}$ by [20, p. 67] and the result. The continuity is immediate from the limit process.

(e) Note that

$$\ell_1(u - v) = (u - v)[g(x, t, v)] + u[g(x, t, u) - g(x, t, v)] + \varepsilon_1.$$

If $v \equiv 0$, there is nothing to prove. If $v \geq 0$, nontrivial, then the eigenvalue δ of

$$\ell_1(\xi) - g(x, t, v)\xi - u\left[\int_0^1 \frac{\partial g}{\partial u}(x, t, \tau u + (1 - \tau)v)d\tau \right]\xi = \delta\xi$$

associated with a positive eigenvector ξ is positive due to the monotonicity of the eigenvalue as a function of the coefficient of linear term as shown in (d). The result then follows from part (c).

Next, let $\varepsilon_1 \to 0$ and observe that $\frac{\partial g}{\partial u} \leq -k < 0$ implies that the resulting sequence $\{u_n\}$ must be bounded and thus convergent in $C^{\alpha,\alpha/2}$, with its gradient converging pointwise. Since $u \geq v$, u cannot converge to zero and the claim is obtained.

(f) The integral estimate is one of the consequences of the classic sup norm estimates for nonnegative subsolutions, see e.g.: [22].

We now pass to the analysis of the solutions of system (3.1) and let T be the common period of the input functions M, N, O, P, Q. In practice, $T =$ one year and we recall that M, N, O, P, Q are nonnegative.   □

Theorem 3.2. *Assume there exists a constant $\mu_1 > 0$ such that*

$$\int_\Omega \int_0^T [\varepsilon|\vec{\nabla}\omega_2|^2 + (\vec{b} \cdot \vec{\nabla}\omega_2)\omega_2 + \omega_2^2] \geq \mu_1 \int_\Omega \int_0^T \omega_2^2$$

for all $\omega_2 \in L^2[0, T; H_0^1(\Omega \cup \partial\Omega_N)] \cap C[0, T; L^2(\Omega)]$, ω_2 of period T. Note that this will always be true if $\vec{b} = \vec{0}$.

(a) *Let v_3^* be the unique T-periodic solution of $\ell(v_3^*) + v_3^* = O(x, t)$. There exist T-periodic solutions of (3.1) of type $(0, 0, \overline{v}_3, \overline{v}_4)$ with $\overline{v}_3, \overline{v}_4$ positive if $[k_{4,1} - h_2(v_3^*)]K + Q \geq 0$. If $k_p + [k_{4,1} - h_2(v_3^*)] \geq 0$ such solution is unique.*

(b) *If for all $\overline{v}_4$ of (a) we have that the principal eigenvalue μ of*

$$\ell w - [M(x, t)h_1(\overline{v}_4)]w = \mu w$$

with the associated boundary conditions, is negative, then there exist T-periodic solutions of type $(\widehat{v}_1, 0, \widehat{v}_3, \widehat{v}_4)$, with $\widehat{v}_1, \widehat{v}_3, \widehat{v}_4$ positive.

(c) *If for all $\widehat{v}_1$ of (b) the principal eigenvalue of*

$$\ell w - \vec{\nabla} \cdot \left(\vec{F}(x, t, \widehat{v}_1, \vec{\nabla}\widehat{v}_1)w\right) - f_2(\widehat{v}_1)w = \mu w$$

with the associated boundary condition is negative while there also exists $\mu_2 > 0$ such that for all $0 \leq w_2$, as above in the Theorem statement, we further have

$$\int_\Omega \int_0^T \left\{\varepsilon|\vec{\nabla}w_2|^2 + \left([\vec{b} + \vec{F}_1] \cdot \vec{\nabla}w_2\right)w_2 + k_5\omega_2^2\right\} \geq \mu_2 \int_0^T \int_\Omega w_2^2$$

where k_5 is defined in (ii) *and $\vec{F}_1$ is any smooth vector field with $|\vec{F}_1| \leq \delta$ as given in* (iv), *then there exist T-periodic solutions of (3.1) of type (v_1, v_2, v_3, v_4) with $v_i > 0$, for $i = 1, \ldots, 4$.*

Proof. (a) We seek periodic solutions of type $(0, 0, \overline{v}_3, \overline{v}_4)$ and observe that system (1) reduces to

$$\ell(v_3) + v_3 = O(x, t)$$
$$\ell(v_4) + v_4 = [k_{4,1} - h_2(v_3)][K - h_3(v_4)] + Q.$$

By Lemma 3.1(c), there exists a unique solution v_3^* of the first equation. We substitute v_3^* for v_3 and v_4^+ for v_4 on the right hand side of the second equation and observe that the boundedness of Q, h_2, h_4 imply that Schauder's Fixed Point Theorem is applicable to a large $C^{\alpha,\alpha/2}$ ball. This shows the existence of a solution $\overline{v}_4$ to the resulting problem which must be nonnegative from the condition

$\left(k_{4,1} - h_2(v_3^*)\right)K + Q \geq 0$ by Lemma 3.1(c), and positive by the (strong) maximum principle. Finally the properties of h_3 and the usual difference argument show that if $k_3 + [k_{4,1} - h_2(v_3^*)] \geq 0$ then $\overline{v}_4$ is unique.

(b) In this case v_2 is chosen identically zero. For convenience, add v_1 to both sides of $\ell v_1 = r_1$. Consider the reduced problem:

$$\ell\left((v_1, 0, v_3, v_4)\right) \equiv \lambda(r_1, 0, r_3, r_4)$$

with $0 \leq \lambda \leq 1$ and v_1^+ in place of v_1 in r_1, v_4^+ in place of v_4 in r_3, r_4. We again observe that by classical results, [22], each v_i is bounded in $C^{\alpha,\alpha/2}$ for $i = 1, 3, 4$, and $\deg_{LS}\left((v_1, 0, v_3, v_4) - \ell^{-1}(r_1, 0, r_3, r_4), B_R, \overrightarrow{0}\right) = 1$ where $\deg_{LS}$ denotes the Leray-Schauder degree and B_R a cube (of large side R) in $C^{\alpha,\alpha/2}$. Note that this also shows that there are no solutions on $\|v_3\|_{C^{\alpha,\alpha/2}} = R$ or $\|v_4\|_{C^{\alpha,\alpha/2}} = R$ and R can be chosen independently of the specific v_1. Consider now the equation

$$\ell\left((v_1, 0, v_3, v_4)\right) = (r_1, 0, r_3, r_4) + (\lambda, 0, 0, 0)$$

for $\lambda \geq 0$ on the cylinder

$$S = \left\{(v_1, v_3, v_4) \big| \, \|v_1\|_{C^{\alpha,\alpha/2}} < \varepsilon_1, \, \|v_3\|_{C^{\alpha,\alpha/2}} < R, \, \|v_4\|_{C^{\alpha,\alpha/2}} < R\right\}.$$

We observe that there are no solutions on the part of ∂S where the $C^{\alpha,\alpha/2}$ norm of v_3 or v_4 equals R. On the other part of ∂S, where $\|v_1\|_{C^{\alpha,\alpha/2}} = \varepsilon_1$ we also cannot have solutions if ε_1 is small enough. For otherwise we choose a sequence of $\varepsilon_1 \to 0$ and corresponding sequence of solutions (v_1, v_3, v_4) and find that as $v_1 \to 0$ we must have $v_3 \to \overline{v}_3$, $v_4 \to \overline{v}_4$ with $\overline{v}_3, \overline{v}_4$ as in part (b). But recalling that

$$\ell(v_1) = [M(x, t)h_1(v_4) - f(v_1, 0)]v_1^+ + \lambda$$

and $f(0, 0) = 0$, by the continuity of the principal eigenvalue, we conclude that $\ell(w) - [M(x, t)h_1(v_4) - f(v_1, 0)]w$ has negative principal eigenvalue for ε_1 small, contradicting Lemma 3.1(c).

It follows by taking λ large that

$$\deg_{LS}\left((v_1, 0, v_3, v_4) - \ell^{-1}((r_1, 0, r_3, r_4)), S, 0\right) = 0$$

for if there were solutions in S then $\|v_1\|_{C^{\alpha,\alpha/2}} \leq \varepsilon$ and thus $\ell(v_1) \geq \lambda - C$ whence $\|v_1\|_{C^{\alpha,\alpha/2}}$ must be large. The desired existence of solutions of type $(\widehat{v}_1, 0, \widehat{v}_3, \widehat{v}_4)$ follows.

(c) We consider first a modified version of the situation considered in (b). Let $\varepsilon_1 > 0$ and consider any positive solutions to

$$\ell\left((v_1, 0, v_3, v_4)\right) = (\overrightarrow{r}_1, 0, \overrightarrow{r}_3, \overrightarrow{r}_4) + \varepsilon_1(1, 0, 0, 0).$$

If ε_1 is small enough, the process in (b) and the continuity of the degree show that there are some solutions with v_1 bounded in $C^{\alpha,\alpha/2}$. We observe that if ε_1 is small enough then the principal eigenvalue μ of the associated problem:

$$\ell(w) - \overrightarrow{\nabla} \cdot \left(\overrightarrow{F}(x, t, v_1, \overrightarrow{\nabla}v_1)w\right) - f_2(v_1)w = \mu w$$

must be negative, where (v_1, v_3, v_4) is any solution triple of the modified problem. Indeed, otherwise, let $\varepsilon_1 \to 0$ and assume we have solution triples (v_1, v_3, v_4) for which $\mu \geq 0$. We note that $v_1 \nrightarrow 0$ in $C^{\alpha, \alpha/2}$. Otherwise v_3, v_4 will converge to some nontrivial $\overline{v}_3, \overline{v}_4$ and thus the least eigenvalue μ_1 of

$$\ell(w) - [M(x, t)h_1(v_4)]w = \mu_1 w$$

will be negative for ε_1 small. This contradicts by Lemma 3.1(e) the fact that $0 < v_1$ satisfies

$$\ell(v_1) - [M(x, t)h_1(v_4) - f_1(v_1, 0)]v_1 = \varepsilon_1$$

with v_1 small and $f_1(0, 0) = 0$. It follows that as $\varepsilon_1 \to 0$, we can find a subsequence of (v_1, v_3, v_4) which converges in $C^{\alpha, \alpha/2}$ to a solution of type $(\widehat{v}_1, \widehat{v}_3, \widehat{v}_4)$, and $\overrightarrow{\nabla} v_1 \to \overrightarrow{\nabla} \widehat{v}_1$ pointwise. By continuity of the principal eigenvalue we must then have $\mu < 0$, contradicting the assumption.

We continue by considering the modified problem:

$$\ell(\overrightarrow{v}) = \overrightarrow{r} + \varepsilon_1(1, -v_2^2, 0, 0),$$

with $\varepsilon_1 > 0$, small. We repeat the process of the previous discussion as follows: given (w_1, w_2, w_3, w_4) we first find v_1, v_3, v_4 just as in (b). We insert the v_1 thus found on the left hand side of the equation for v_2 and thus set up a map $T(w_1, \ldots, w_4) = (v_1, \ldots, v_4)$. Again by the process in (b) we conclude that the Leray-Schauder degree is one in a large cube: $\|v_i\|_{C^{\alpha, \alpha/2}} < R(\varepsilon_1)$ for $i = 1, \ldots, 4$, and zero in the region $\|v_2\|_{C^{\alpha, \alpha/2}} < \varepsilon$, $\|v_i\|_{C^{\alpha, \alpha/2}} < R(\varepsilon_1)$ for $i = 1, 3, 4$ if $\varepsilon_1 > 0$ is small enough and the existence of positive solutions (v_1, v_2, v_3, v_4) to the modified problem follows. Now let $\varepsilon_1 \to 0$, and observe that we cannot have $v_1 \to 0$, for if this were the case, we would contradict the second equation for v_1 small enough. We also cannot have $v_2 \to 0$ or else we obtain a contradiction as (v_1, v_3, v_4) will converge to a solution $(\widehat{v}_1, \widehat{v}_3, \widehat{v}_4)$ of (b) contradicting the eigenvalue condition of (c) if v_2 is small enough. Thus $v_2 \nrightarrow 0$, and then in turn v_3, v_4 cannot converge to zero. Next, observe that v_1, v_3, v_4 are positive and thus bounded in $C^{\alpha, \alpha/2}$ by their respective equations using Lemma 3.1(f), but the bound on v_2 so far depends on ε_1. We claim that it is actually independent of ε_1. Indeed, rewriting the first two equations gives

$$\ell(v_1) = \varepsilon_1 + [M(x, t)h_1(v_4) - f_1(v_1, v_2)]v_1$$
$$\ell(v_2) - \overrightarrow{\nabla}\left(\overrightarrow{F} \cdot v_2\right) = [f_2(v_1) - \varepsilon_1 v_2]v_2$$

whence

$$\ell(v_1 + v_2) - \overrightarrow{\nabla}\left(\overrightarrow{F} \cdot v_2\right) \leq \varepsilon_1 + [M(x, t)h_1(v_4)]v_1 - \varepsilon_1 v_2^2 - k_5 v_2^2$$

from the last condition in (ii).

We thus have by choosing $v_1 + v_2$ as a test function (possible since $\partial\Omega_D$ is the same for all v_i)

$$\left(\tfrac{1}{2}\int_\Omega (v_1 + v_2)^2\right)_t + \int_\Omega \varepsilon|\nabla(v_1 + v_2)|^2 + \int_\Omega \vec{b}\cdot\nabla(v_1+v_2)(v_1+v_2)$$

$$+ \int_\Omega \vec{F}\nabla v_2(v_1+v_2) + \int k_5 v_2^2 \le K$$

for some K.

But $v_1, \nabla v_1$ are bounded in $L^2(Q_T)$. Thus by the second assumption of part (c) of the Theorem statement, $\int_0^T \int_\Omega v_2^2$ is bounded independently of ε_1. By the last estimate of the Lemma 3.1, $\|v_2\|_{L^\infty} \le C$ and we conclude that a subsequence of (v_1, v_2, v_3, v_4) converges in $C^{\alpha,\alpha/2}$, and that so does $\vec{F}(x, t, v_1, \vec{\nabla} v_1)$ in L^p for any p, by the properties of $\vec{F}$ and Lemma 3.1(e). The result follows, since the equation for v_2 (resp. v_1) shows $v_1 \not\to 0$ (resp. $v_2 \not\to 0$) as $\varepsilon_1 \to 0$.   □

4. The high nutrient regime

It is often the case that for many lagoons of interest to us, human input creates a situation where the nutrient level v_4 is high, i.e. $h_1(v_4) \simeq 1$ in equation (3.1). Alternatively, the exogenous term Q in r_4 of (3.1) is the dominant term, and thus v_4 can be taken to be a given function (independent of v_1, v_2, v_3). In this case the growth of the phytoplankton (and thus the zooplankton) is limited by the other effects (light, temperature), the system decouples and reduces to the two equations (2.1'), (2.2') (for v_1^*, v_2^*) (equivalent to suppose $k_X = 0$. We develop the above results in this special case.

We apply Lemma 3.1(d) and Theorem 3.2(b). For the existence of $v_1^* > 0$ (now unique) we require that there exist a function φ, $\varphi = 0$ on $\partial\Omega_D$, such that

$$\int_\Omega \left\{ \varepsilon|\nabla\varphi|^2 + \varphi(\vec{b})\cdot\vec{\nabla}\varphi + \frac{1}{4}\frac{|\widetilde{\vec{b}}|^2}{\varepsilon}\varphi^2 \right\} < \int_\Omega \widetilde{M}\varphi^2$$

while for the existence of a $v_2^* > 0$ we also ask that there exist ψ ($\psi = 0$ on $\partial\Omega_D$) such

$$\int_\Omega \left\{ \varepsilon|\nabla\psi|^2 + \psi[\vec{\widetilde{\beta}}\cdot\vec{\nabla}\psi] + \frac{1}{4}\frac{|\widetilde{\vec{\beta}}|^2}{\varepsilon}\psi^2 \right\} < \int_\Omega \widetilde{f_2(v_1^*)}\psi^2$$

where $\vec{\beta} = \vec{b} + \vec{F}(x, t, v_1^*, \vec{\nabla}v_1^*)$, while the second condition of Theorem 3.2(c) yields

$$\|\vec{b}\|_{L^\infty} + \delta < 2\sqrt{\varepsilon k_5}$$

as the other necessary condition by means of Hölder's Inequality. The simplest situation arises with pure Neumann boundary conditions, $\frac{\partial v_1}{\partial\vec{n}} = \frac{\partial v_2}{\partial\vec{n}} + \vec{F}\cdot\vec{n}\,v_2 = 0$

on $\partial\Omega$ and $\vec{b} = \vec{0}$ (no currents). The choices $\varphi = \psi \equiv 1$ are possible, and we obtain the sufficient conditions:

$$\int_\Omega \int_0^T M \, dt \, dx > 0; \quad \frac{\delta^2}{4\varepsilon} < min\left\{\frac{1}{|\Omega|T} \int_\Omega \int_0^T f_2(v_1^*), k_5\right\}. \quad (4.1)$$

It is possible to eliminate the dependence of the earlier result on v_1^* and obtain criteria based only on $M(x, t)$ and the coefficient functions.

Corollary 4.1. *Let* $f_1(\xi_1, \xi_2) = -k_2\xi_1 - \frac{k_3\xi_2}{k_p+\xi_1}$, $f_2(\xi) = \frac{k_4\xi}{k_p+\xi} - k_5$, *with* $k_2, k_3, k_4,$
$k_5, k_p > 0$, $\vec{b} = \vec{0}$. *If* $\frac{\partial v_1}{\partial \vec{n}} = \frac{\partial v_2}{\partial \vec{n}} + (\vec{F} \cdot \vec{n})v_2 = 0$ *on* $\partial\Omega$, $\delta < 2\sqrt{\varepsilon k_5}$ *and:*

$$k_4\left(\int_\Omega \int_0^T \sqrt{M}\right)^2 > \left[\int_\Omega \int_0^T \left\{\frac{1}{4\varepsilon}\delta^2 + k_5\right\}\right]$$
$$\times k_2\left[k_p|\Omega|T + \frac{(|\Omega|T)^{1/2}}{k_2}\left(\int_\Omega \int_0^T M^2\right)^{1/2}\right]$$

then there exists a positive periodic solution v_1^*, v_2^* *of the reduced (high nutrient) system.*

Proof. We have $M \geq 0$ nontrivial, and thus only need to check the conditions for the existence of v_2^*. Observe that since

$$\frac{\partial v_1^*}{\partial t} - \varepsilon \Delta v_1^* = [M - k_2 v_1^*]v_1^* \quad (4.2)$$

and $\frac{\partial v_1^*}{\partial u} = 0$ on $\partial\Omega$, then $\int_\Omega \int_0^T M v_1^* = k_2 \int_\Omega \int_0^T (v_1^*)^2$ whence

$$\int_\Omega \int_0^T (v_1^*)^2 \leq \frac{1}{k_2} \int_\Omega \int_0^T M^2$$

and

$$\int_\Omega \int_0^T v_1^* \leq \frac{1}{k_2}\left[\left(\int_\Omega \int_0^T M^2\right)|\Omega|T\right]^{1/2}.$$

Dividing (4.2) by $(k_p + v_1^*)v_1^*$ yields by periodicity and direct calculation:

$$\int_\Omega \int_0^T \left(\frac{M}{k_p + v_1^*}\right) \leq k_2 \int_\Omega \int_0^T \frac{v_1^*}{k_p + v_1^*}.$$

The second condition gives:

$$\frac{1}{4\varepsilon} \int_\Omega \int_0^T \delta^2 < \int_\Omega \int_0^T \left(\frac{k_4 v_1^*}{k_p + v_1^*}\right) - k_5|\Omega|T.$$

This condition will be satisfied if

$$\frac{1}{4\varepsilon} \int_\Omega \int_0^T \delta^2 + k_5|\Omega|T < \frac{k_4}{k_2} \int_\Omega \int_0^T \frac{M}{k_p + v_1^*}.$$

Now if $\alpha > 1$ then

$$\int_\Omega \int_0^T M^{1/\alpha} = \int_\Omega \int_0^T \frac{M^{1/\alpha}}{(k_p + v_1^*)^{1/\alpha}} (k_p + v_1^*)^{1/\alpha}$$

$$\leq \left(\int_\Omega \int_0^T \frac{M}{(k_p + v_1^*)} \right)^{1/\alpha} \left(\int_\Omega \int_0^T (k_p + v_1^*)^{\frac{1}{\alpha - 1}} \right)^{\frac{\alpha - 1}{\alpha}}.$$

The choice $\alpha = 2$ then gives

$$\left(\int_\Omega \int_0^T M^{1/2} \right)^2 \leq \left(\int_\Omega \int_0^T \frac{M}{k_p + v_1^*} \right) \left(\int_\Omega \int_0^T (k_p + v_1^*) \right)$$

$$\leq \left(\int_\Omega \int_0^T \frac{M}{k_p + v_1^*} \right) \left[k_p |\Omega| T + \frac{1}{k_2} (|\Omega| T)^{1/2} \left(\int_\Omega \int_0^T M^2 \right)^{1/2} \right]$$

and the result. We remark that if also $\vec{F} = \vec{0}$ and M, v_1^*, v_2^* are functions purely of time, then repeating the earlier procedure we get: $\int_0^T M = k_2 \int_0^T v_1^*$ and the condition becomes:

$$k_4 \left(\int_0^T \sqrt{M} \right)^2 > k_5 T k_2 \left[k_p T + \frac{1}{k_2} \int_0^T M \right]$$

which is modestly better. The previous Corollary compares the averages: $\left(\frac{1}{|\Omega| T} \int_\Omega \int_0^T \sqrt{M} \right)^2$ and $\left(\frac{1}{|\Omega| T} \int_\Omega \int_0^T M^2 \right)^{1/2}$. These reflect the variations (in space and time) of the nutrient level M. Observe that if M is a constant the two averages are the same. Implicit in the estimate is also present the restriction: $k_4 > k_5$. The next result shows that if $k_4 > k_5$ and the nutrient level is always high enough there still are positive periodic solutions, regardless of the variations of M.   □

Corollary 4.2. *If*

$$\frac{\delta^2}{4\varepsilon} + k_5 < \frac{k_4 M_{\sim}}{k_2 k_p + M_{\sim}}$$

where $M_{\sim} = \inf_{(x,t)} M(x, t)$, *then there exist positive periodic solutions* v_1, v_2. *If* $\delta = 0$, *this reduces to*

$$M_{\sim} > \frac{k_5 k_2 k_p}{k_4 - k_5} .$$

Proof. Since v_1^* is a positive periodic solution of

$$\frac{\partial v_1^*}{\partial t} - \varepsilon \Delta v_1^* = [M - k_2 v_1^*] v_1^*$$

then we immediately conclude by the maximum principle that $v_1^* \geq M_{\sim}/k_2$. For the existence of v_1, v_2 we require:

$$\frac{1}{4\varepsilon} \delta^2 |\Omega| T + k_5 |\Omega| T < \int_\Omega \int_0^T \frac{k_4 v_1^*}{k_p + v_1^*} .$$

Since $v_1^*/(k_p + v_1^*)$ is monotone (in v_1^*), this will hold if

$$\frac{\delta^2}{4\varepsilon} + k_5 < \frac{k_4 \underset{\sim}{M}}{k_2 k_p + \underset{\sim}{M}}$$

and the result follows.   □

In order to apply Corollary 4.1, it is useful to first observe the following comparison argument:

Corollary 4.3. *Let v_1 (resp. v_1') satisfy equation (4.2) with $M(x,t) \geq 0$ (resp. $R(x,t) \geq 0$) and pure Neumann boundary conditions $\frac{\partial v_1}{\partial \vec{n}} = 0$ (resp. $\frac{\partial v_1'}{\partial \vec{n}} = 0$). If $M \geq R$ then $v_1 \geq v_1'$.*

Proof. This follows immediately by applying Lemma 3.1 (c) to the difference $v_1 - v_1'$ and noting that v_1 satisfies a (linear) equation (in v_1) with principal eigenvalue zero.   □

As a consequence we note that if the exogenous input is sufficiently high in a subdomain Q_1 of $\Omega \times [0, T]$, then we have coexistence. The volume of Q_1 and the needed exogenous inputs are related to the coefficients. Specifically, we have:

Corollary 4.4. *Let the conditions on f_1, f_2, the constant coefficients and the boundary conditions be as in Corollary 4.1. Suppose: $\delta < 2\sqrt{\varepsilon k_5}$; there exists a subdomain Q_1 of $\Omega \times [0, T]$ and constant $a > 0$ such that in Q_1 there holds:*

$$M \geq a > \frac{\left[\frac{\delta^2}{4\varepsilon} + k_5\right] k_2 k_p}{k_4 \, Z^2 - \left[\frac{\delta^2}{4\varepsilon} + k_5\right] Z^{\frac{1}{2}}} \tag{4.3}$$

where $Z = \frac{|Q_1|}{(|\Omega|T)}$. Then the reduced nutrient system has a positive periodic solution.

Proof. Let $\Psi(x, t)$ be the characteristic function of Q_1 and put $N = a \Psi$. Let v_1' now denote the solution to equation (4.2) with N in place of M and observe that Corollary 4.3 implies $v_1^* \geq v_1$.
Inequality (4.3) implies, by the arguments of Corollary 4.1 (with N in place of M) and direct calculation, that:

$$\left(\frac{\delta^2}{4\varepsilon} + k_5\right)|\Omega|T < \frac{k_4}{k_2} \int_\Omega \int_0^T \frac{k_4 v_1'}{k_p + v_1'}.$$

But, since $\frac{k_4 \xi}{k_4 + \xi}$ is monotone in ξ and $v_1^* \geq v_1'$, then this also holds with v_1' replaced by v_1^*. The result then follows from inequalities (4.1).
We comment that if the nutrient levels are essentially unaffected by the biomass, then $M(x, t) = k_1 u_1 u_4 \frac{v_4}{k_p + v_4}$ and thus coexistence is possible even if v_4 is zero on parts of the cylinder $\Omega \times [0, T]$.   □

5. Application

To validate our model, we apply our previous considerations to the situation of the Caprolace lagoon, located 100 km south of Rome in the National Park of Circeo. It covers about 2.26 km^2 and is of 1.7 m average depth. It is characterized by spatially homogeneous conditions, no significant current flow and a modest degree of eutrophication although the nutrient loading is quite high.

The key parameter/functions (obtained in [2]) are given in Table 2.

The simulation results and actual measurements for phytoplankton and zooplankton densities are shown in Figures 1 and 2 respectively, which show the reasonably good agreement between theoretical prediction and actual readings taken in the lagoon.

The microalgae biomass (phytoplankton and zooplankton) seems to govern the main ecological process. We are thus in the high nutrient regime with pure Neumann boundary conditions described in Section 4 and with f_1, f_2 as taken in Corollary 4.1. Furthermore, in the depicted situation $M(x, t)$ in equation r_1 represents the total effect of u_1 and u_2 which are the annual variation of the photoperiod and the temperature respectively; in particular, $M(x, t) = k_1 u_1 u_4$.

It is interesting to note that with the given choice of parameters the sufficient conditions for coexistence given by Corollary 4.1 and 4.2 both fail. However, a routine numerical calculation shows that the basic condition (4.1), which now reduces to:

$$\int_0^T f_2(v_1^*) > 0,$$

with $v_1^* = v_1^*(t)$, is valid. Further simulation results and a detailed description of the simulation and parameter estimation procedures are given in [2].

6. Biological interpretation of the mathematical results

In this Section we point out some biological implications of the mathematical results presented in the paper. In particular, the following considerations hold:

par.	biological meaning	estimate	units
k_1	phytoplankton growth rate	0.4012	$[t]^{-1}$
k_2	phytoplankton natural mortality	0.0005	$[mg\ m^{-3}]^{-1}\ [t]^{-1}$
k_3	phytoplankton losses for grazing	0.24	$[t]^{-1}$
k_4	zooplankton growth rate	29	$[t]^{-1}$
k_5	zooplankton natural mortality	24.75	$[t]^{-1}$

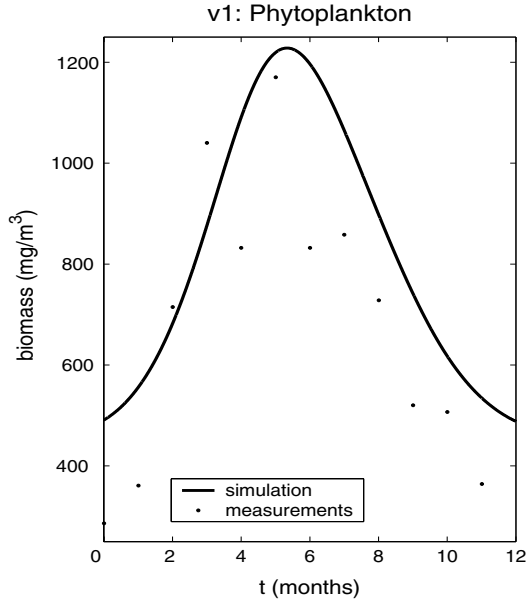**Table 2.** Estimated values of the model parameters.

Fig. 1. Simulation results and comparison with measurements of phytoplankton biomass
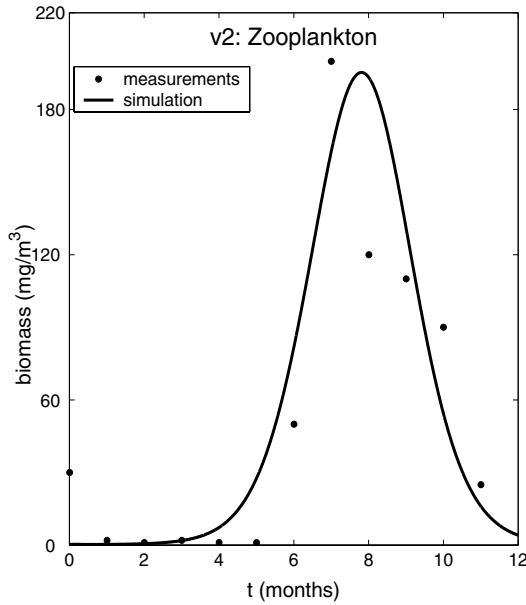

Fig. 2. Simulation results and comparison with measurements of zoplankton biomass

– The model analyzed accounts for slightly eutrophic lagoons, in the sense that while eutrophic, they are not yet subject to catastrophic events (like dystrophy or anoxic crises). In particular, the lagoon of Caprolace is taken as a prototypical ecosystem, where water quality and biodiversity are acceptable from an environmental point of view. Quantitative comparison of the model prediction with measured data gives a good agreement

– The estimated coefficients (see Section 5) correspond to a periodic solution that persists even if the coefficients are perturbed (due to principal eigenvalue continuity). The consequent robustness of the solution implies that extreme events can't easily arise, in keeping with the previous consideration.

– On the other hand, the fact that the coefficients don't satisfy the more restrictive conditions, expressed by Corollaries 4.1 and 4.2, for the existence of a periodic solution indicates that more complex dynamics can arise by the same model (for appropriate values of the parameters as well as of exogenous inputs).

– The main result of the paper giving the biological conditions that ensure the existence of a periodic solution in the real system are summarized as follows:
  a) Suppose that the biomass in the lagoon is 0. Then there is a positive solution of the oxygen-nutrients system driven by the exogenous terms.
  b) If the nutrients level in case (a) is sufficiently high (in terms of a principal eigenvalue), then there is a positive periodic solution of the phytoplankton-oxygen-nutrients system.
  c) If the phytoplankton biomass in case (b) is sufficiently high (again in term of a principal eigenvalue), then there is a positive periodic solution of the complete system.

– The levels of the nutrients required in (b) and of the phytoplankton required in (c) depend on the shape of the lagoon and on whether there are adverse conditions on boundary of the lagoon (i.e. $\partial \Omega_D \neq \emptyset$); as well as on the various coefficients by which the biological and chemical processes have been scaled. Heuristically, these levels must increase as $\partial \Omega_D$ becomes larger. The simplest case to describe is when there are: no adverse conditions on the boundary of the lagoon ($\partial \Omega_D = \emptyset$), high nutrient levels, as well as no water currents nor zooplankton drift. In this case, the positive exogenous photoperiod and temperature inputs suffice for the existence of a positive periodic phytoplankton density. On the other hand, even in this situation we require for the existence of a positive periodic zooplankton density that the integral average of the phytoplankton level over $\Omega \times [0, T]$ be sufficiently high - in the absence of zooplankton - so that the consequent zooplankton growth rate would dominate its mortality rate.

– Corollaries 4.3 and 4.4 provide an explicitly verifiable estimation of minimum values of the exogenous inputs (the parameter a in equation (4.3)), that depends on model parameters and on the volume of the chosen subdomain in the space/time cylinder for which the coexistence between species is always possible. It is equivalent to the fact that a lower bound (for example on nutrients and/or other exogenous inputs, generally speaking) exists for the activation of the main biological processes in the lagoon. If this level is met, possibly in different parts of the lagoon during the year, then coexistence is possible.

7. Discussion

In this paper we have introduced and analyzed a phytoplankton-zooplankton-oxy-gen-nutrient model for shallow lagoons. We have obtained conditions, based on suitable principal eigenvalues integral estimates, for the existence of coexistence states, i.e. of positive periodic solutions. Special consideration was given to the high nutrient regime. The results obtained were applied to the lagoon of Caprolace and the model validated by a comparison between simulated results and actual measurements in Section 5. More detailed biological considerations and implications were given in Section 6. Future work will focus on model modification to deal with the very high eutrophication, anoxic cases and abnormal proliferation of macroalgae, present in many other lagoons.

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