

ANALYSIS OF A MATHEMATICAL MODEL FOR JELLYFISH BLOOMS AND THE CAMBRIC FISH INVASION

FLORIAN RUPP AND JÜRGEN SCHEURLE

Lehrstuhl für Höhere Mathematik und Analytische Mechanik
Technische Universität München, Fakultät für Mathematik
D-85747 Garching, Germany

ABSTRACT. Dramatic increases in jellyfish populations which lead to the collapse of formerly healthy ecosystems are repeatedly reported from many different sites, cf. [6, 8, 14]. Due to their devastating effects on fishery the understanding of the causes for such a blooming are of major ecological as well as economical importance. Assuming fish as the dominant predator species we model a combined two species system subject to constant environmental conditions. By totally analytic means we completely classify all biologically relevant equilibria in terms of existence and Lyapunov stability, and give a complete description of this system’s non-linear global dynamics supported by numerical simulations. This approach complements, from a systematic point of view, the studies given in the literature to better understand jellyfish blooms.

1. Introduction. When talking to experts in the field of maritime biology or just scanning the literature, e.g. the works [14] or [3], the emergence of jellyfish blooms seems to be far from being well understood. In terms of modeling, these jellyfish blooms manifest the catastrophic event of a more or less sudden change from a mixed fish/ jellyfish ecosystem into a jellyfish dominated regime. In their wonderful review article “the jellyfish joyride: causes, consequences and management responses to a more gelatinous future” [14] the authors describe heuristically the biological factors that may transfer a healthy ecosystem into one dominated by jellyfish – a situation known before the first fish species emerged during the Cambrian time and took over the oceans to eventually form today’s multi-faceted under water life. The authors of [14] argue, that “it is not unreasonable to suggest that jellyfish proliferations are held in check via a combination of competition for planktonic food and (perhaps) predation on ephyrae, small medusae or polyps by filter-feeding fish”, p. 317¹. Recently, e.g. in [3] a third trail of reasoning has been added by discussing and mathematically analyzing the effects of water quality. As fish depend on good visibility conditions for hunting, eutrophic oceans may favor jellyfish.

Thus, there are three reasonable causes for jellyfish blooms that are discussed currently: (1) the competition of jellyfish and fish for food, (2) the influence of water conditions on the predation success of jellyfish and fish, and (3) the predation

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¹ Ephyrae, medusae and polyps are certain early stages in the growth of jellyfish from egg to adulthood. Filter-feeding is a most common way of food intake for underwater creatures, loosely speaking they just open their mouth, suck in whatever does not escape fast enough and then filter out the undesired part of the intake.

of young jellyfish by (filter-feeding) fish. In the last decade, the aspect of preventing blooms became, beyond ecological reasons, essential for certain coastal regions (especially in Japan) due to heavily decreased amounts of fishing and fishing nets loaded with uneatable jellyfish during such blooms.

Despite, this economic relevance for understanding the causes of jellyfish blooms and managing them, to the best of our knowledge, so far only two studies addressing those issues have been carried out in the literature based on deterministic mathematical models: In [4] a 2-dimensional system is discussed which is derived under the assumption that cause (1) is the exclusive driving force for blooms, and [3] (as stated previously) assumes cause (2) exclusively influencing blooms. Note, causes (1) and (2) essentially deal with ecological issues as neither the predation behaviors nor water quality can be controlled by fishery regulations.

The present article closes a gap in this active field of research by studying the third of the above mentioned possible explanation mechanisms for jellyfish blooms with the aid of a deterministic 2-dimensional predator-prey model for the interaction of (filter-feeding) fish and (young) jellyfish. The discussion of cause (3) is interesting from two points of view: First, industrial fishery reduces the amount of fish worldwide and due to the thus reduced effects of the regulatory factor fish, the jellyfish population may grow extensively. The mixed fish/ jellyfish system addressed by cause (3) is tailored to allow external influence by fishery, as one can decide by purpose how many fish are taken out of this ecosystem. Concerning the life cycles of jellyfish, though, young jellyfish must live near reefs and more or less in rather shallow water in order to mature. In these ecosystems industrial fishery is restricted and the fish concentrations may be such that they keep the number of young jellyfish under control. Competition for planktonic food between adult jellyfish and fish takes place in open waters where industrial fishing can apply its complete arsenal without geological side conditions. Second, we can take the evolutionary point of view and ask if a species A can invade into an ecosystem dominated by species B , where A preys upon the young offspring of B ? Can a “stable” A - B -ecosystem form in such a situation? With this respect it seems not to be unreasonable to come up with the following hypothesis: As fish invaded the jellyfish ecosystem in Cambrian time it may not have been advantageous to compete with the dominant species for food, but instead find a niche and include predation upon the young offspring of the dominant species into their repertoire of survival mechanisms.

Low-dimensional differential equation models as discussed in [3, 4] and in the present article together with the complete understanding of phase and parameter space are quite unique for analyzing fish-jellyfish dynamics. Other studies on this subject focus either on phenomenological descriptions and heuristic plausibility arguments for certain observed scenarios, e.g. in [1, 6, 8, 14, 16], or apply statistical sampling methods to determine relevant correlations between observed species, e.g. in [2, 9, 10, 15, 13], or to determine the coefficients of Bertalanffy-type growth formulas for jellyfish populations at different locations and with respect to seasonal variations, e.g. in [5, 7, 11, 12].

For our model we assume a stationary plankton concentration as well as fish being the dominant predatory species feeding on (young) jellyfish. Here, the dynamics of this system (with 3-dimensional parameter space) is analyzed mathematically to the extent that all biologically relevant equilibria are classified in terms of existence and Lyapunov-stability. Moreover, a bifurcation landscape is established including numerically supported phase space illustrations for certain parameter regimes. In

particular, a bifurcation scenario is detected that allows for the mathematical description of jellyfish blooming, i.e. a sudden change of an asymptotically stable mixed species regime to a jellyfish dominated one.

Thus, we are able to show that within our model fish and jellyfish can form a system of stable coexistence as observed in nature and that jellyfish blooms are held back by predation. In particular this last insight is important for the sustainable management of maritime environments and indicates the relevance of avoiding over-harvesting the sea in order to reduce the more severe economic threat of an ecosystem collapsing into an pre-Cambrian jellyfish realm.

This article is structured as follows: In Sec. 2 we set-up our 2-dimensional analytic model for the fish-jellyfish ecosystem dynamics. Dating back to Lotka-Volterra there is a standard basic structure of the differential equations modeling predator-prey systems and leading to a “mass” exchange from the prey species to the predator species (besides additional birth-death influences that are proportional to the density of the corresponding species). While often used to describe the dynamics between animals, cf. [3], the Lotka-Volterra equations lack the description of limited resource intake. This saturation is taken into account by the seminal model proposed by Jacob-Monod that we apply here, cf. [4], too. Moreover, we make a second modification of traditional predator-prey models assuming variability due to changing environmental conditions from location to location in space. By including a specific carrying capacity of the ecosystem for fish their migration from and into the ecosystem is captured in an Malthusian-like way. Biology indicates, cf. [14], that the carrying capacity for jellyfish is much larger than that for fish and that jellyfish can survive in regimes where fish would die. Thus, we ignore such migration effects for jellyfish. Finally, a harvesting term for fish represents the effects of fishery. Next, we analyze the local and the global dynamics as already stated. Finally, Sec. 3 provides a short résumé.

2. The 2D model equations and their analysis. We start our analysis by assuming a constant plankton concentration and that the interactions between fish and jellyfish are such that fish prey upon jellyfish. For the fish population x we assume a Malthusian-like migration function $M(x)$ that allows fish to enter and leave the system, taking the ecological conditions of the habitat into account; namely $M(x) = r \left(1 - \frac{x}{K^*}\right) x$, where r is the migration speed factor indicating how fast migration into or out of the habitat takes place, and K^* to be the carrying capacity of the specific ecosystem. The negative quadratic term indicates that encounters of fish should be kept to a minimum in order to prevent strong competition for food. Moreover, we apply a Jacob-Monod like growth function $\beta_f := \frac{v^* y_2}{k^* + y_2} x$ that describes the increase of the fish population with respect to available jellyfish food resources in a well established way. Here, $v^* > 0$ is a combined uptake velocity and birth/ death coefficient, and $k^* > 0$ the saturation constant that assumes that a fish does only eat a certain amount of jellyfish. Finally, we assume a linear fishing function $H^* x$, with $H^* \leq 0$. This leads to the following ordinary differential equation

$$\dot{x} = r \left(1 - \frac{x}{K^*}\right) x + \frac{v^* y_2}{k^* + y_2} x + H^* x.$$

Note, H^* may be negative depending on how intense the effect of fishing is.

As we assume fish to prey upon young jellyfish which are part of plankton and not dangerous for fish due to a lack of stinging cells, it is natural to start with adult

y_1 and young y_2 jellyfish populations separately. Assuming linear relationships for the death of adult jellyfish ($-\delta y_1$), the maturity of young to adult jellyfish (αy_2) and the birth of young jellyfish ($\beta^* y_1$) we obtain

$$\dot{y}_1 = \alpha y_2 - \delta y_1, \quad \text{and} \quad \dot{y}_2 = \beta^* y_1 - \alpha y_2 - p_x \frac{v^* y_2}{k^* + y_2} x,$$

with a yield factor $p_x \in [0, \infty)$ for the fish population x that takes into account that not all jellyfish biomass is equivalently transferred to fish biomass.

To reduce the number of parameters involved, we define $K := (K^*)r^{-1}$ together with $\xi := xK^{-1}$, $c := H^* + r \in \mathbb{R}$, and $k := k^*(v^*)^{-1}$. As the adult jellyfish population is a direct consequence of the young jellyfish population we may as well just consider the later. We introduce a new net birth constant $\beta > 0$ to describe linear growth and use the scaled variable $y := y_2(v^*)^{-1}$ for the young jellyfish population. This leads to

$$\dot{\xi} = \left(c + \frac{y}{k+y} \right) \xi - \xi^2, \quad \text{and} \quad \dot{y} = \beta y - K p_x \frac{y}{k+y} \xi.$$

Finally, we define $\eta := yk^{-1}$ and $d := K p_x k^{-1} \beta^{-1} > 0$ which results in the 2-dimensional deterministic predator-prey model

$$\dot{\xi} = \left(c + \frac{\eta}{1+\eta} \right) \xi - \xi^2, \quad \text{and} \quad \dot{\eta} = \beta \left(\eta - d \frac{\eta \xi}{1+\eta} \right), \quad (1)$$

which depends on the three parameters $c \in \mathbb{R}$, and $\beta, d > 0$ only. Here, we can interpret c as a net birth rate for the fish population, β as a net birth and d as a net death/ predation rate for the jellyfish population.

For (1) the coordinate axes $\xi \equiv 0$ and $\eta \equiv 0$ are invariant such that every solution that starts in the positive quadrant $\mathfrak{P}_2 := \{(\xi, \eta) \in \mathbb{R}_0^+ \times \mathbb{R}_0^+\}$ stays therein for any time. I.e., non-biological negative values for the population sizes can not occur.

Moreover, the left hand sides of our autonomous first order ordinary differential equation system (1) are C^∞ -functions of ξ, η on \mathfrak{P}_2 and hence locally Lipschitz-continuous in ξ, η uniformly in $t \in \mathbb{R}$. In particular, $\dot{\xi} < \xi((c+1) - \xi) < 0$ if $\xi > c+1$, because $\eta(1+\eta)^{-1} \in [0, 1)$ for all $\eta \in \mathbb{R}_0^+$. This allows us to estimate $\xi(t) \leq \max\{c+1, \xi_0\} =: D$ for all $t \in \mathbb{R}$ and all initial states $\xi_0 \in \mathbb{R}_0^+$. Finally, the left hand side of (1) is linearly bounded, as

$$\begin{aligned} \left\| \begin{pmatrix} \dot{\xi} \\ \dot{\eta} \end{pmatrix} \right\|_2 &= \left\| \begin{pmatrix} \left(c + \frac{\eta}{1+\eta} \right) \xi - \xi^2 \\ \beta \left(\eta - d \frac{\eta \xi}{1+\eta} \right) \end{pmatrix} \right\|_2 \\ &\leq \left(c^2 \xi^2 + 2c \frac{\eta}{1+\eta} \xi^2 + (1 + d^2 \beta^2) \frac{\eta^2}{(1+\eta)^2} \xi^2 + \beta^2 \eta^2 + \xi^4 \right)^{1/2} \\ &\leq \sqrt{\tilde{C} \xi^2 + \beta^2 \eta^2 + D^4} \leq \max\{\tilde{C}^{1/2}, \beta\} \left\| \begin{pmatrix} \xi \\ \eta \end{pmatrix} \right\|_2 + D^2, \end{aligned}$$

due to $\eta(1+\eta)^{-1} < 1$ and $\xi^4 \leq D^4$. Here, $\tilde{C} := c^2 + 2c + 1 + d^2 \beta^2$.

Thus, for any time and all initial states in \mathfrak{P}_2 there is a unique global (in time) solution of (1). This allows an analysis by means of dynamical systems theory.

2.1. Equilibria and global weak Markov dynamics. Let us start our analysis by giving a complete classification of system's (1) equilibria in the positive quadrant. By standard arguments we almost immediately get:

Theorem 2.1. *For all choices of the parameters β, c, d the origin $(\xi, \eta) = (0, 0)$ is an equilibrium of the system (1). For $c > 0$ the point $(\xi, \eta) = (c, 0)$ is an additional*

equilibrium in \mathfrak{P}_2 and if the parameter values are such that $(c + 1)^2 - 4d^{-1} \geq 0$ together with

$$z_1 := \frac{1}{2} \left(c + 1 + \sqrt{(c + 1)^2 - 4d^{-1}} \right) > d^{-1}$$

and/ or

$$z_2 := \frac{1}{2} \left(c + 1 - \sqrt{(c + 1)^2 - 4d^{-1}} \right) > d^{-1}$$

hold, then points $(\xi, \eta) = (z_1, dz_1 - 1)$ and/ or $(\xi, \eta) = (z_2, dz_2 - 1)$ are equilibria in \mathfrak{P}_2 , too. These are all equilibria in \mathfrak{P}_2 .

A short calculation shows that z_2 is admissible if and only if

$$\begin{aligned} (c, d) \in \Gamma_2 := & \{ (c, d) \in (-1, 0] \times \mathbb{R}_0^+ : 4(1 + c)^{-2} \leq d \} \\ & \cup \{ (c, d) \in (0, 1) \times \mathbb{R}_0^+ : 4(1 + c)^{-2} \leq d \leq c^{-1} \}, \end{aligned}$$

and that z_1 is admissible if and only if

$$(c, d) \in \Gamma_1 \cup \Gamma_2, \quad \text{with } \Gamma_1 := \{ (c, d) \in \mathbb{R}^+ \times \mathbb{R}_0^+ : c^{-1} < d \}.$$

(Recall, for $c = d = 1$, we have $z_1 = z_2 = 1$ and consequently z_1, z_2 are not admissible.) Hence, except of the origin, system (1) can have at most three additional equilibria depending on the parameters c and d . Note, the existence of equilibria is independent of the jellyfish’s net birth factor β .

From a geometric point of view the curves $\eta = d\xi - 1$ ($\dot{\eta} = 0$) and $\xi = c + \eta(1 + \eta)^{-1}$ ($\dot{\xi} = 0$) divide the phase space into connected regions due to Jordan’s theorem, where the sign of $\dot{\xi}$ and $\dot{\eta}$ does not change, as sketched in Fig. 1. The equilibria $(z_1, dz_1 - 1)$ and $(z_2, dz_2 - 1)$ are located at the intersection points of the curves $\eta = d\xi - 1$ and $\xi = c + \eta(1 + \eta)^{-1}$. We refer to these partitions as weak Markov partitions. From Fig. 1 it already becomes apparent that for small fish populations steadily increasing jellyfish concentrations may occur which can be interpreted as a blooming of this species.

2.2. Non-linear stability of the equilibria and local dynamics. For system (1) the right hand side’s Jacobian matrix $J(\xi^*, \eta^*)$ evaluated at an equilibrium point (ξ^*, η^*) reads as

$$J(\xi^*, \eta^*) = \begin{pmatrix} c + \frac{\eta^*}{1 + \eta^*} - 2\xi^* & \frac{\xi^*}{(1 + \eta^*)^2} \\ -\beta d \frac{\eta^*}{1 + \eta^*} & \beta - d\beta \frac{\xi^*}{(1 + \eta^*)^2} \end{pmatrix}.$$

This lays the foundation for determining the stability of system’s (1) equilibria and immediately leads to the following Proposition.

Proposition 1. *The matrix of linearization evaluated at the origin reads as $J(0, 0) = \text{diag}(c, \beta)$. Its eigenvalues are thus given by $\lambda_1 = c$ with the normalized eigenvector $\mathbf{e}_1 = (1, 0)^T$ and $\lambda_2 = \beta$ with the normalized eigenvector $\mathbf{e}_2 = (0, 1)^T$.*

If $c > 0$, the matrix of linearization around the point $(c, 0)$ and its characteristic polynomial $\chi_J(\lambda)$ read as

$$J(c, 0) = \begin{pmatrix} -c & c \\ 0 & \beta - cd\beta \end{pmatrix} \Rightarrow \chi_J(\lambda) = (\lambda + c)(\lambda - \beta(1 - cd)).$$

Thus its eigenvalues are given by $\lambda_1 = -c < 0$ with the normalized eigenvector $\mathbf{e}_1 = (1, 0)^T$ and $\lambda_2 = \beta(1 - cd)$ with an eigenvector $\mathbf{v} = (c, c + \beta(1 - cd))^T$.

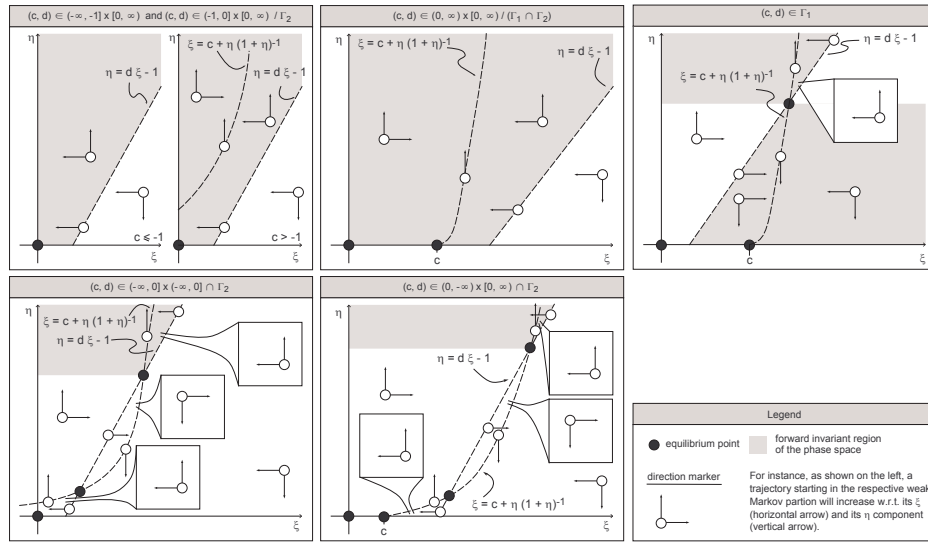


FIGURE 1. Orientation with respect to increasing time of the solution components of (1) within different parameter regimes. Obvious parts of forward invariant regions are highlighted in gray color. For instance, as shown on the left, for a trajectory starting in the respective regime of phase space, both the ξ - (horizontal arrow) as well as the η -component (vertical arrow) will increase.

In particular, at $c = 0$ the origin and the equilibrium at $(c, 0)$ give rise to a saddle-node bifurcation.

Due to the principle of linearized stability the properties of the linearization can be carried over to the non-linear system. Consequently, there, the origin is a saddle point for $c < 0$ and a Lyapunov-unstable node for $c > 0$ with a 2-dimensional unstable manifold. For $c = 0$, zero is an eigenvalue of $J(0, 0)$ the algebraic and geometric multiplicity of which coincide. Hence, for $c = 0$, the origin is a saddle point and has a Lyapunov-stable manifold tangential to \mathbf{e}_1 . Analogously, in the non-linear setting, the equilibrium point at $(c, 0)$, $c > 0$, is asymptotically Lyapunov-stable for $d \geq c^{-1}$ and a saddle point for $0 \leq d < c^{-1}$.

Note, that the jellyfish-independent net birth rate $c > 0$ makes sense from a biological point of view because young jellyfish are just part of the food supply for fish. (For $c < 0$ a pure fish equilibrium state does not exist in \mathfrak{P}_2 .)

Next we discuss the linearized stability of the equilibria at the points $(z_1, dz_1 - 1)$ and $(z_2, dz_2 - 1)$. Provided that they exist, the matrix of linearization around $(z_i, dz_i - 1)$, $i = 1, 2$, reads as

$$J(z_i, dz_i - 1) = \begin{pmatrix} j_i & \frac{1}{d^2 z_i} \\ -\beta d \frac{dz_i - 1}{z_i} & \beta \frac{dz_i - 1}{dz_i} \end{pmatrix} \quad \text{with} \quad j_i := c + 1 - 2z_i - (dz_i)^{-1},$$

and its characteristic polynomial $\chi_i(\lambda)$ is given by $\chi_i(\lambda) = \lambda^2 + \kappa_{1,i}\lambda + \kappa_{0,i}$, where

$$\begin{aligned} \kappa_{1,i} &:= -\text{tr}(J(z_i, dz_i - 1)) = -(dz_i)^{-1} (j_i dz_i + \beta (dz_i - 1)) \\ \kappa_{0,i} &:= \det(J(z_i, dz_i - 1)) = \beta (dz_i)^{-2} (dz_i - 1) (j_i dz_i + 1). \end{aligned}$$

Application of Descartes’s sign rule to the sequence 1, $\kappa_{1,2}$, $\kappa_{0,1}$ shows

Proposition 2. *Let (c, d) be such that there exists an equilibrium at $(z_1, dz_1 - 1)$. Then, $(z_1, dz_1 - 1)$ is a (hyperbolic) saddle point.*

Finally to the equilibrium at $(z_2, dz_2 - 1)$. As we will see this is the only equilibrium the stability of which depends on the (net birth) parameter β . In order to state the spectral properties for this equilibrium, we need some information about the range of $j_2 dz_2$.

Lemma 2.2. *Let $(c, d) \in \Gamma_2$ be such that there exists an equilibrium at $(z_2, dz_2 - 1)$. Then, $j_2 dz_2 \in (-1, 0)$.*

Proof. It follows that $j_2 dz_2 = dz_2 \sqrt{(c + 1)^2 - 4d^{-1}} - 1 \in (-1, 1)$ because of

$$\begin{aligned} j_2 dz_2 &= \frac{1}{2}d \left((c + 1) - \sqrt{(c + 1)^2 - 4d^{-1}} \right) \sqrt{(c + 1)^2 - 4d^{-1}} - 1 \\ &= \frac{1}{2}d(c + 1)\sqrt{(c + 1)^2 - 4d^{-1}} - \frac{1}{2}d(c + 1)^2 + 2 - 1 = 1 - d(c + 1)z_2. \end{aligned}$$

Moreover, if $(c, d) \in \Gamma_2 \cap \{c \in [0, 1]\}$, then $j_2 dz_2 = 1 - d(c + 1)z_2 < 1 - dz_2 < 0$ as $dz_2 > 1$. Next, let us assume, without further restrictions on $(c, d) \in \Gamma_2$ that there are values of c, d such that

$$\begin{aligned} j_2 dz_2 &= 1 - d(c + 1)z_2 \stackrel{!}{=} 0 \\ \Leftrightarrow -\sqrt{(c + 1)^2 - 4d^{-1}} &= 2(d(c + 1))^{-1} - (c + 1) = (2 - d(c + 1)^2)(d(c + 1))^{-1} \\ \Leftrightarrow (c + 1)^2 - 4d^{-1} &= (4 - 4d(c + 1)^2 + d^2(c + 1)^4)(d(c + 1))^{-2} \Leftrightarrow 0 = 4. \end{aligned}$$

Thus, we have a contradiction, i.e., $j_2 dz_2$ is either always < 0 or > 0 for all $(c, d) \in \Gamma_2$. We already showed $j_2 dz_2 < 0$ for $(c, d) \in \Gamma_2 \cap \{c \in [0, 1]\}$. Hence, $j_2 dz_2 \in (-1, 0)$ for all $(c, d) \in \Gamma_2$. \square

This allows a concise proof of the spectral properties of the equilibrium point at $(z_2, dz_2 - 1)$ and of the existence of an Andronov-Hopf bifurcation that takes place at the critical value $\beta = -j_2 dz_2 (dz_2 - 1)^{-1}$.

Proposition 3. *Let $(c, d) \in \Gamma_2$ be such that there exists an equilibrium at $(z_2, dz_2 - 1)$ and let*

$$\beta_- := \frac{2 + j_2 dz_2 - 2\sqrt{1 + j_2 dz_2}}{dz_2 - 1} > 0 \quad \text{and} \quad \beta_+ := \frac{2 + j_2 dz_2 + 2\sqrt{1 + j_2 dz_2}}{dz_2 - 1} > 0.$$

Then, the equilibrium at $(z_2, dz_2 - 1)$ is hyperbolic and asymptotically Lyapunov-stable for all values of $0 < \beta < -j_2 dz_2 (dz_2 - 1)^{-1} =: \beta^$. In particular, it is a Lyapunov-stable node if $\beta \in (0, \beta_-)$, it is asymptotically stable node if $\beta = \beta_-$ and it is a Lyapunov-stable focus if $\beta \in (\beta_-, \beta^*)$. The equilibrium at $(z_2, dz_2 - 1)$ is hyperbolic and unstable in the sense of Lyapunov for all values of $\beta > \beta^*$. In particular, in this case it is a Lyapunov-unstable focus if $\beta \in (\beta^*, \beta_+)$, it is a unstable node if $\beta = \beta_+$ and it is a Lyapunov-unstable node if $\beta \in (\beta_+, \infty)$. The equilibrium at $(z_2, dz_2 - 1)$ is non-hyperbolic for $\beta = \beta^*$, there the matrix of linearization around $(z_2, dz_2 - 1)$ has a pair of purely imaginary eigenvalues.*

Proof. Due to Lemma 2.2 we have $j_2 dz_2 \in (-1, 0)$ and thus that $\kappa_{0,2} > 0$. Hence, depending on the discriminant $\Delta_2 = (dz_2)^{-2} \left((j_2 dz_2 - \beta(dz_2 - 1))^2 - 4\beta(dz_2 - 1) \right)$ of the quadratic polynomial $\chi_2(\lambda) = \lambda^2 + \kappa_{1,2}\lambda + \kappa_{0,2}$ we get for $J(z_2, dz_2 - 1)$ the existence of (i) a pair of complex conjugate eigenvalues with negative real part ($\kappa_{1,2} > 0$ and $\Delta_2 < 0$), (ii) a pair of purely imaginary eigenvalues ($\kappa_{1,2} = 0$

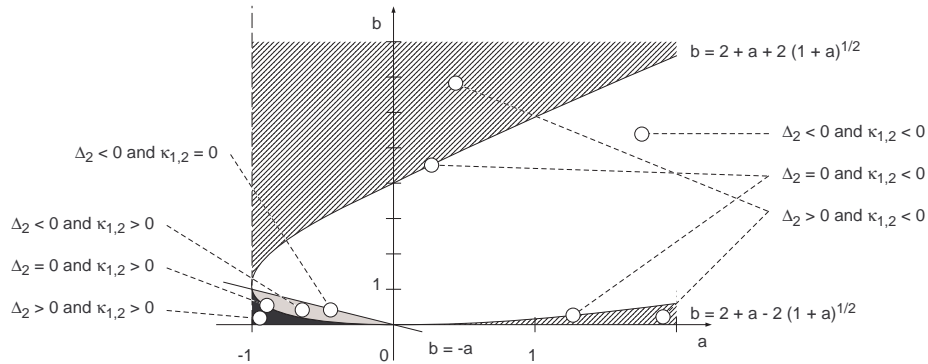


FIGURE 2. Dependence of the signs of $\kappa_{1,2}$ and Δ_2 on the relation between $a \in (-1, 2)$ and $b > 0$.

and $\Delta_2 < 0$), (iii) a pair of complex conjugate eigenvalues with positive real part ($\kappa_{1,2} < 0$ and $\Delta_2 < 0$), or, in each case counted by multiplicity, (iv) two negative real eigenvalues ($\kappa_{1,2} > 0$ and $\Delta_2 \geq 0$) or (v) two positive real eigenvalues ($\kappa_{1,2} < 0$ and $\Delta_2 \geq 0$). The case of one positive and one non-positive root of $\chi_2(\lambda)$ is excluded due to Descartes’s sign rule.

For $(c, d) \in \Gamma_2$ the parameter β still is to our disposal in order to determine the sign of $\kappa_{1,2}$ and Δ_2 . We define, $a := j_2 dz_2 \in (-1, 0)$ and $b := \beta(dz_2 - 1) > 0$, such that $\text{sign}(-(a + b)) = \text{sign}(\kappa_{1,2})$ and $\text{sign}((a - b)^2 - 4b) = \text{sign}(\Delta_2)$. In particular, $\kappa_{1,2} < 0$ if and only if $b > -a$ and $\Delta_2 = 0$ if and only if $0 = (a - b)^2 - 4b$, i.e. $b_{1/2} = 2 + a \pm 2\sqrt{1 + a}$, which completely determines the spectral properties of the linearization around $(z_2, dz_2 - 1)$, see Fig. 2. In particular, non-linear stability follows as asserted for the hyperbolic cases.

Following [17], pp. 270, in order to finally verify the existence of an Andronov-Hopf bifurcation at $\beta = \beta^*$ it remains to show $\frac{d}{d\beta} \text{Re}(\lambda_{1/2}(\beta))|_{\beta=\beta^*} \neq 0$, where $\lambda_{1/2}(\beta)$ are the roots of $\chi_2(\lambda(\beta))$. We have

$$\begin{aligned} \frac{d}{d\beta} \text{Re}(\lambda_{1/2}(\beta)) \Big|_{\beta=\beta^*} &= -\frac{1}{2} \frac{d}{d\beta} \kappa_{1,2}(\beta) \Big|_{\beta=\beta^*} \\ &= (dz_2)^{-1}(dz_2 - 1) > 0. \end{aligned}$$

which shows the required transversality condition. □

Note, from an evolutionary point of view we can interpret those parameter values that lead to the asymptotically stable mixed species equilibrium at $(z_2, dz_2 - 1)$ as corresponding to suitable environmental conditions that favor the invasion of the fish species into a jellyfish dominated ecosystem like in Cambrian time with the emergence of a robust coexistence of these two species.

Due to lack of space, here, we omit here to discuss non-linear stability for the non hyperbolic case, i.e., if $\kappa_{1,2} = 0$ (recall $\kappa_{0,2} > 0$).

Finally, Fig. 3 summarizes our findings and displays, supported by numerical simulations for the position of heteroclinic orbits, a sketch of the phase space dynamics for various parameter regimes. Moreover for $c \geq 0$, our numerical simulations indicate that the Andronov-Hopf bifurcation is sub-critical and that (for $\beta > \beta^*$) initial conditions very close to the mixed species equilibrium are driven away from this

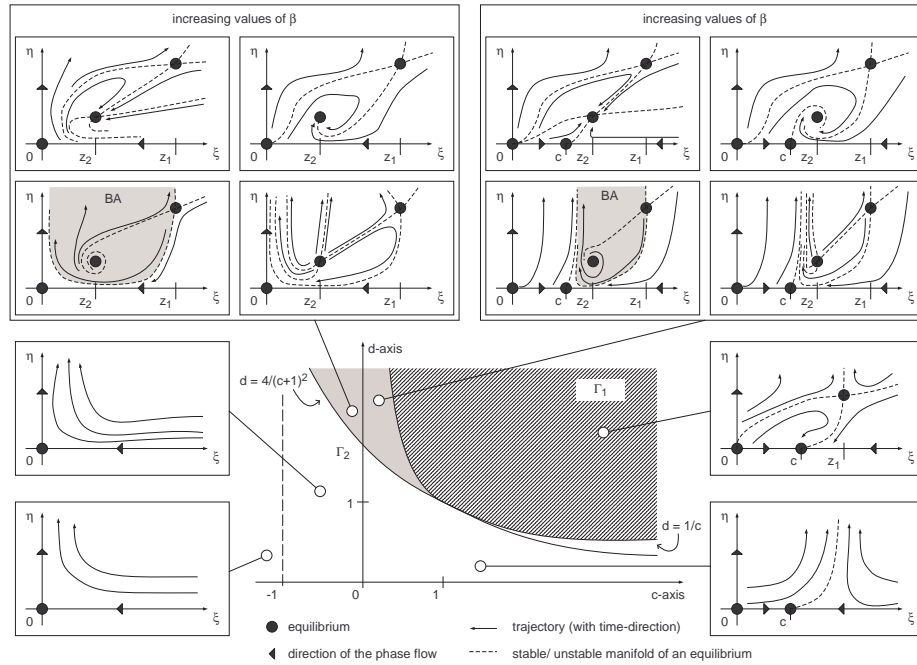


FIGURE 3. Sketch of the regions Γ_1 (light gray) and Γ_2 (shaded) in the c - d -parameter space together with illustrations of the location of the equilibria corresponding to special choices of c and d as well as of the global dynamics for representative parameter values.

equilibrium in such a way that the η -component eventually increases dramatically. This blooming area (BA) is shown as a shaded region in Fig. 3. For $c < 0$ the mixed species equilibrium undergoes a Andronov-Hopf bifurcation as well, and a blooming area eventually forms, too.

3. Résumé & outlook. Our discussion is based on a mathematical two-species population model that assumes predation by (filter-feeding) fish to be the main driving force. From a mathematical perspective the rich dynamics of this model is discussed by means of dynamical systems theory. A complete classification of this system's equilibria with respect to the 3-dimensional parameter space allows the detection of a diversified bifurcation landscape. Hereby, an asymptotically stable mixed species equilibrium is of great importance from a biological point of view as perturbations of this situation die out very fast allowing a clear observation of the coexistence. Supported by numerical simulations, we show that this model is capable to explain jellyfish blooms in terms of a sub-critical Andronov-Hopf bifurcation from this mixed species equilibrium (see Proposition 3).

Certainly, further empirical studies are required to specify relevant parameter regimes governing real fish-jellyfish ecosystems, as well as comparisons with the other causes for jellyfish blooms given in the literature and cited in the introduction, i.e., [4] and [3], to decide upon the validity of either of them or certain combinations as a local or general explanation for jellyfish blooms.

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Received August 2012; revised May 2013.

E-mail address: rupp@ma.tum.de

E-mail address: scheurle@ma.tum.de