COMPARING TWO NEW ECOEPIDEMIC MODELS OF THE SALTON SEA

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Abstract.

We consider two models for the Salton Sea ecoepidemiology. In the first model, we assume Pelicans to feed on both sound and infected fish sub-populations with the same functional response: the sound prey contribute to the growth of the birds population, while the infected ones instead kill them. In the second model we refine the choice of the feeding functional response by taking it to be ratio-dependent instead of a simple Holling type II function. Our results indicate that a small probability for the occurrence of the origin and the interior coexistence equilibrium is possible for the second model, while the first one gives probability zero for these to occur. The second model therefore appears to be more realistic, since it allows the probable existence of an interior equilibrium.

1 Background

In the Salton Sea, botulism bacteria can grow and produce toxins very easily. Fish then get infected and rise to the water surface thus becoming an easy prey for fish eating birds, like the pelicans. In turn the latter get affected by feeding on diseased prey and die in large numbers as well. This situation has been considered in [5] and then modified in [4, 6, 10] to take into account different biological viewpoints. Most of the models classify the fish as susceptible or infected, and assume that either the birds feed just on infected fish, or the predation functional responses for the susceptible and the infected prey are different, but this may not always be realistic in the Salton sea context. Pelicans may in fact feed on both susceptible and infected fishes with the same functional responses.

The choice of which functional response type best fits the description of a particular situation is not easy, especially for theoretical studies. To shed some light on this question, here two new models are proposed for studying the eco-epidemiology of infections among fish and pelicans in the unique environment of the Salton sea, in which the prey hunting is respectively modeled as a simple Holling type II and a ratio-dependent functional response. We compare their predictions to better understand under which assumptions the model becomes more realistic.

To describe real world situations the Holling type II functional response is the most commonly used among the prey dependent functional responses [9], but, when predators have to share food or compete for it, a higher predator density leads to more frequent encounters between predators, causing a fall in predating efficiency due to the predators interference among each other. A more suitable predator-prey theory should then be based on the ratio-dependent theory, as field and laboratory experiments support it [1, 2, 3, 7]. Its meaning lies therefore in the fact that the per capita predator growth rate is a function of the ratio of prey to predator abundance.

2 The two new models

In the first model, we assume Pelicans to feed on both sound and infected fish sub-populations with the same functional response: the sound prey contribute to the growth of the birds population, while the infected ones instead kill them. Letting s and i denote sound and infected fish respectively, and p the Pelicans, we have

$$\frac{ds}{dt} = rs(1 - \frac{s+i}{K}) - \lambda is - \frac{\gamma_1 sp}{a+s+i} \quad \frac{di}{dt} = \lambda is - \frac{\gamma_2 ip}{a+s+i} - \mu i \quad \frac{dp}{dt} = -ep + \frac{\tilde{\gamma}_1 sp}{a+s+i} - \frac{\tilde{\gamma}_2 ip}{a+s+i} \quad (1)$$

The model (1) can be adimensionalized by the variable scalings $s = KS$, $i = KI$, $p = P$ and $\tau = rt$. In dimensionless form it reads

$$\frac{dS}{d\tau} = S(1 - S - I) - \tilde{\lambda} SI - \frac{\hat{r}_1 SP}{\tilde{a}+S+I} \equiv F_1(S,I,P) \cdot S, \quad \frac{dI}{d\tau} = \tilde{\lambda} SI - \frac{\hat{r}_2 IP}{\tilde{a}+S+I} - \tilde{\mu} I \equiv F_2(S,I,P) \cdot I, \quad (2)$$

$$\frac{dP}{d\tau} = -\tilde{e}P + \frac{\bar{r}_1 SP}{\tilde{a}+S+I} - \frac{\bar{r}_2 IP}{\tilde{a}+S+I} \equiv F_3(S,I,P) \cdot P,$$

where γ_1 and γ_2 are the search rates, $\tilde{\gamma}_1$ represents the conversion factor and $\tilde{\gamma}_2$ is the death rate of the predator population due to consumption of infected fish and with

$$\frac{e}{r} = \tilde{e}, \quad \frac{\tilde{\gamma}_1}{r} = \bar{r}_1, \quad \frac{\tilde{\gamma}_2}{r} = \bar{r}_2, \quad \frac{\lambda K}{r} = \tilde{\lambda}, \quad \frac{\gamma_2}{rK} = \hat{r}_2, \quad \frac{\mu}{r} = \tilde{\mu}, \quad \frac{\gamma_1}{rK} = \hat{r}_1, \quad \frac{a}{K} = \tilde{a}.$$

In the second model we refine the choice of the feeding functional response by taking it to be ratio-dependent instead of a simple Holling type II function. We thus have

$$\frac{ds}{dt} = rs\left(1 - \frac{s+i}{K}\right) - \lambda is - \frac{\gamma_1 sp}{ap+s+i} \quad \frac{di}{dt} = \lambda is - \frac{\gamma_2 ip}{ap+s+i} - \mu i \quad \frac{dp}{dt} = \frac{(\tilde{\gamma}_1 s - \tilde{\gamma}_2 i)p}{ap+s+i} - ep \quad (3)$$

with the same parameter interpretations as for (2).

Rescaling (3) again via $s = KS$, $i = KI$, and $ap = KP$, $\tau = rt$, defining the new parameters

$$\alpha = \frac{\lambda K}{r}, \ \beta_1 = \frac{\gamma_1}{ar}, \ \xi_1 = \frac{\gamma_2}{ar}, \ \beta_2 = \frac{\tilde{\gamma}_1}{r}, \ \xi_2 = \frac{\tilde{\gamma}_2}{ar}, \ \delta = \frac{e}{r}, \ \eta = \frac{\mu}{r},$$

we obtain

$$\frac{dS}{d\tau} = S(1 - S - I) - \alpha SI - \frac{\beta_1 SP}{P + S + I} \equiv G_1(S,I,P) \cdot S, \quad \frac{dI}{d\tau} = \alpha SI - \frac{\xi_1 IP}{P + S + I} - \eta I \equiv G_2(S,I,P) \cdot I, \quad (4)$$

$$\frac{dP}{d\tau} = -\delta P + \frac{\beta_2 SP}{P + S + I} - \frac{\xi_2 IP}{P + S + I} \equiv G_3(S,I,P) \cdot P.$$

The initial conditions are $S(0) = S_0 \geq 0$, $I(0) = I_0 \geq 0$ and $P(0) = P_0 \geq 0$.

3 Some analytical results

Standard analytical techniques ensure the boundedness of both systems' trajectories. Since solutions cannot escape to infinity, we can investigate the long term behavior of (2) and (4) by studying their equilibria.

3.1 Equilibria of the model (2)

The system (2) in addition to the origin $E_0 \equiv (0,0,0)$, has the following boundary equilibria:

$$E_1 \equiv (1,0,0), \quad E_2 \equiv \left(\frac{\tilde{\mu}}{\tilde{\lambda}}, \frac{\tilde{\lambda} - \tilde{\mu}}{\tilde{\lambda}(1 + \tilde{\lambda})}, 0\right), \quad E_3 \equiv \left(\frac{\tilde{a}\tilde{e}}{\bar{r}_1 - \tilde{e}}, 0, \frac{(\bar{r}_1 - \tilde{e} - \tilde{a}\tilde{e})\tilde{a}\bar{r}_1}{\hat{r}_1(\bar{r}_1 - \tilde{e})^2}\right)$$

and the interior equilibrium $E_* \equiv (S_*, I_*, P_*)$ with

$$S_* = \frac{\tilde{e}\tilde{a}(\hat{r}_2\tilde{\lambda} + \hat{r}_2) + (\tilde{e} + \bar{r}_2)(\hat{r}_2 + \tilde{\mu}\hat{r}_1)}{(\bar{r}_1 - \tilde{e})(\hat{r}_2\tilde{\lambda} + \hat{r}_2) + (\tilde{e} + \bar{r}_2)(\hat{r}_1\tilde{\lambda} + \hat{r}_2)}, \quad I_* = \frac{(\hat{r}_1\tilde{\mu} + \hat{r}_2) - S_*(\hat{r}_1\tilde{\lambda} + \hat{r}_2)}{(\hat{r}_2\tilde{\lambda} + \hat{r}_2)}, \quad (5)$$

$$P_* = \frac{(\tilde{\lambda}S_* - \tilde{\mu})}{(1 + \tilde{\lambda})\hat{r}_2^2}[\tilde{a}\hat{r}_2(1 + \tilde{\lambda}) + (\hat{r}_1\tilde{\mu} + \hat{r}_2) - S_*\tilde{\lambda}(\hat{r}_1 - \hat{r}_2)]. \quad (6)$$

Now, E_2 is feasible if $\tilde{\lambda} - \tilde{\mu} > 0$ i.e. for $\lambda K - \mu > 0$; E_3 is feasible if $\bar{r}_1 > \tilde{e}(1 + \tilde{a})$ i.e. for $\tilde{\gamma}_1 > e(1 + \frac{a}{K})$; E_* is feasible if $S_*, I_*, P_* > 0$ giving $A_* < S_* < B_*$ where

$$A_* = \frac{\tilde{\mu}}{\tilde{\lambda}}, \quad B_* = \max\left\{\frac{\tilde{a}\hat{r}_2(1 + \tilde{\lambda}) + (\hat{r}_1\tilde{\mu} + \hat{r}_2)}{\tilde{\lambda}(\hat{r}_1 - \hat{r}_2)}, \frac{\hat{r}_2 + \tilde{\mu}\hat{r}_1}{\hat{r}_2 + \tilde{\lambda}\hat{r}_1}\right\}.$$

3.2 Equilibria of the model (4)

The system (4) has the origin $D_0 \equiv E_0 \equiv (0,0,0)$ and the boundary equilibria $D_1 \equiv E_1 \equiv (1,0,0)$,

$$D_2 \equiv \left(\frac{\eta}{\alpha}, \frac{\alpha - \eta}{\alpha(1 + \alpha)}, 0\right), \quad D_3 \equiv \left(\frac{\beta_2 - \beta_1\beta_2 + \beta_1\delta}{\beta_2}, 0, \frac{\beta_2 - \beta_1\beta_2 + \beta_1\delta}{\beta_2}\frac{\beta_2 - \delta}{\delta}\right)$$

and the interior equilibrium is $D^*(S^*, I^*, P^*)$, with S^*, I^* and P^* denoting the positive solutions of the algebraic system $G(X) = \mathbf{0}$. This reduces to find a positive root S^* of the quadratic

$$AS^2 - BS + C = 0 \quad (7)$$

where $A > 0$, $B > 0$, $C > 0$, since

$$A = \alpha\beta_2(\xi_1 + \alpha\xi_1) + \xi_2\alpha(\alpha\beta_1 + \xi_1), \quad C = \eta\xi_2(\xi_1 + \eta\beta_1) + \xi_1(\delta + \xi_2)(\xi_1 + \eta\beta_1), \quad (8)$$

$$B = \eta\beta_2(\xi_1 + \alpha\xi_1) + \alpha\xi_2(\xi_1 + \eta\beta_1) + \xi_2\eta(\alpha\beta_1 + \xi_1) + \xi_1[(\beta_2 - \delta)(\xi_1 + \alpha\xi_1) + (\delta + \xi_2)(\alpha\beta_1 + \xi_1)].$$

and

$$I^* = \frac{(\xi_1 + \eta\beta_1) - S^*(\alpha\beta_1 + \xi_1)}{\xi_1 + \alpha\xi_1}, \tag{9}$$

$$P^* = \frac{[(\beta_2 - \delta)(\xi_1 + \alpha\xi_1) + (\delta + \xi_2)(\alpha\beta_1 + \xi_1)]S^* - (\delta + \xi_2)(\xi_1 + \eta\beta_1)}{\delta(\xi_1 + \alpha\xi_1)}. \tag{10}$$

Here D_2 is feasible for $\alpha > \eta$; D_3 is if both conditions $\beta_2 > \delta$ and $\beta_1 < 1$ are satisfied. The interior equilibrium point D^* is feasible if $L < S^* < M$ with

$$L = \frac{(\delta + \xi_2)(\xi_1 + \eta\beta_1)}{(\beta_2 - \delta)(\xi_1 + \alpha\xi_1) + (\delta + \xi_2)(\alpha\beta_1 + \xi_1)}, \quad M = \frac{\xi_1 + \eta\beta_1}{\alpha\beta_1 + \xi_1}.$$

3.3   Stability and Permanence

The following results whose proofs follow similar results in the literature, [4, 5, 6, 10] and references therein, characterize the systems' behavior near the equilibria.

Theorem 1. The steady state E_* of the model (2) is always unstable.

Theorem 2. If there are two interior equilibrium points of (4) then one is a saddle and the other one is a sink.

Theorem 3. If the predation rate on the infected prey is higher than or equal to that of the susceptible prey then no trajectory can reach the origin from the interior along a fixed direction. If the difference of the predation rates on sound and infected prey is bounded above, $\beta_1 - \xi_1 < \eta + 1$ then no trajectory can reach the origin from the interior following a spiral path.

Theorem 4. The conditions for the system (4) to be permanent are

$$(i) \ \alpha > \eta, \beta_2 > \delta; \quad (ii) \ \eta > \frac{\alpha(\xi_2 + \delta(1+\alpha))}{\xi_2 + \beta_2(1+\alpha)}; \quad (iii) \ \alpha > \frac{\beta_2\eta + \xi_1\beta_2 - \xi_1\delta}{\beta_2 + \beta_1\delta - \beta_1\beta_2}.$$

Proof. Consider the average Lyapunov function of the form $V(S,I,P) = S^{\alpha_1}I^{\alpha_2}P^{\alpha_3}$ with $\alpha_i > 0$ for $i = 1,2,3$. In the interior of the positive orthant $\mathbf{R}^3_{0,+}$, we have

$$\frac{\dot{V}}{V} \equiv \alpha_1\left[1 - S - I - \alpha I - \frac{\beta_1 P}{P+S+I}\right] + \alpha_2\left[\alpha S - \frac{\xi_1 P}{P+S+I} - \eta\right] + \alpha_3\left[\frac{\beta_2 S}{P+S+I} - \frac{\xi_2 I}{P+S+I} - \delta\right]. \tag{11}$$

As (4) is of Lotka-Voltera type, it suffices to show that the above function is positive for all equilibria $(S,I,P) \in \mathbf{R}^3_{0,+}$, for a suitable $\alpha_i > 0$, $i = 1,2,3$ and reduce to the following conditions corresponding to the boundary equilibrium (S), planar equilibria, (SI) and (SP), which hold in the assumptions of the theorem:

$$(S): \ \alpha_1 + \alpha_2(\alpha - \eta) + \alpha_3(\beta_2 - \delta) > 0; \quad (SI): \ \alpha_3\left(-\delta + \frac{\beta_2\eta(1+\alpha) + \xi_2\eta - \alpha\xi_2}{\alpha(1+\alpha)}\right) > 0; \tag{12}$$

$$(SP): \qquad \alpha_2\left(\alpha S_3 - \eta - \frac{\xi_1(\beta_2 - \delta)}{\beta_2}\right) > 0.$$

4   Comparison technique

We compare the two models (2) and (4) to find the probability for the existence and stability of the different equilibria of both systems in terms of all the parameter values using the **Latin hypercube sampling** (LHS) [8].

Table 1: The hypothetical values at which the parameters are kept fixed

Parameter	r	K	γ_1	γ_2	a	$\tilde{\gamma}_1$	$\tilde{\gamma}_2$	μ	e
Value	1	45	0.2	0.02	15	0.15	0.015	0.24	0.09

The algorithm used for finding the probability for the existence and stability of different equilibria consists of the following steps:

1. Choose the mean value and standard deviation of each parameter, the former being taken from Table 1 together with $\lambda = 0.011$, the latter being set to 0.01, so that all the parameters fall into the positive region.

2. With LHS technique draw 5000 random sets of all parameter values from the 10-dimensional parameter space, and put in the set 'S' the ones satisfying the basic assumption of the model, i.e, for which $\gamma_1 \geq \tilde{\gamma}_1$ and $\gamma_2 \geq \tilde{\gamma}_2$.

3. For each sample set make the quantities dimensionless and find the values of the equilibria; from the Jacobian determine their stability properties for both models. For each equilibrium store the number of sample sets for which the equilibrium point is feasible and stable.

4. Let S be the set of sample values for which a particular equilibrium point exists and $A \subset S$ the subset for which it is stable; let $n(S)$ and $n(A)$ respectively be the number of their elements. Then find the probability of an equilibrium to be stable by

$$P(A) = \frac{n(A)}{n(S)}. \tag{13}$$

5. Repeat steps (2) to (4) for 10 times to find the average of all the probabilities.

5   Conclusions

Comparing the steady state stability properties of the two proposed models, the system (4) possesses two positive equilibria, a saddle and a sink, whereas system (2) has just one, which is always a saddle and therefore unconditionally unstable. This is a radical difference, that may be used to validate them, by comparison with field data. it is also observed that under certain conditions all the populations in the (4) may become extinct. Hence the system (4) exbits the possibility for coexistence of the three species and as well as the possibility for total extinction.

Persistence of the three populations depends on two quantities, namely the incidence rate λ, since from (11) and (12) it follows $\lambda > \max(\frac{\mu}{K}, \frac{r\mu}{ek})$, and on the death rate d of the pelican population, since from (11) we have indeed $r - \frac{ar}{k\theta_1} < e < r$. Moreover, if $\lambda \to \max(\frac{\mu}{K}, \frac{r\mu}{ek})$ i.e. if we decrease the contact rate then the interior equilibrium point does not persist. In such case the system tends to the infection-free equilibrium (SP), since the system is unstable around the predator-free equilibrium point (SI). This gives then a usable criterion for possibly fighting the disease, by acting on the appropriate model parameters.

Before reporting the final results, a few remarks are in order. Using the above procedure, note that since the variational matrix is not defined at the origin, the probability for existence and stability of the D_0 for (4) cannot be evaluated. Moreover since (4) has two positive steady states, and we theoretically know already that whenever one state is stable the other one is unstable, in our numerical algorithm we have added the probabilities of both positive steady states denoting this single value by D^*. The results thus obtained are summarized in Table (2).

From Table 2 we observe that in (2) E_0 and the coexistence equilibrium E_* have zero probability of occurrence, while (4) allows a finite probability for the corresponding coexistence equilibrium D^*. The latter model therefore appears to be more realistic, since it allows the probable existence of an interior equilibrium. Note that in Table 2 the probabilities should not be added columnwise, as each number is the probability for the corresponding equilibrium to be stable, calculated according to (13).

Table 2: The result obtained for the systems (2) and (4) using the LHS tecnique.

Model	Equilibrium point	Probability of the equilibrium point to be stable
System (2)	E_0	0
	E_1	0.0062
	E_2	0.3107
	E_3	0.2671
	E_*	0
System (4)	D_1	0.001
	D_2	0.2344
	D_3	0.1620
	D^*	0.6815

6   References

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