



A Mathematical Bioeconomic Model for Competing Marine Species Under Harvesting Pressure [†]

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Abstract

This study develops a mathematical bioeconomic framework to analyze competition between two marine species under harvesting pressure. The central hypothesis is that asymmetric interspecific competition fundamentally shapes population stability and optimal harvesting strategies. Ecological dynamics are described using coupled logistic growth equations with competition terms. System stability is analyzed via Jacobian eigenvalue evaluation, revealing that the coexistence equilibrium is locally asymptotically stable when each species' intrinsic growth rate exceeds the competitive pressure from the other species. Harvesting strategies are optimized using Karush–Kuhn–Tucker (KKT) conditions under biomass non-negativity constraints. Numerical simulations, including time series, phase-plane trajectories, and sensitivity analysis, reveal trade-offs between profitability and sustainability. Competition coefficients exhibit the highest sensitivity, making them critical for management. The framework provides a flexible tool for competing fisheries systems.

Keywords: bioeconomic model; Lotka–Volterra competition; KKT optimization; sustainable harvesting; competition hypothesis

1. Introduction

Marine ecosystems face increasing pressure from harvesting activities, requiring sophisticated management approaches that balance economic profitability with ecological sustainability [1,2]. Mathematical bioeconomic models provide powerful tools for analyzing these trade-offs and designing optimal harvesting strategies [3,4]. When two species share similar habitats and food resources, interspecific competition for limited resources becomes a fundamental ecological process that shapes population dynamics and ecosystem stability. According to Gause's competitive exclusion principle [5], complete competitors cannot coexist indefinitely. However, asymmetric competition where one species has a competitive advantage can allow stable coexistence under specific conditions [6,7].

This study builds upon our previous bioeconomic modeling work [8–10]. Unlike the full journal article that applies the model to specific Moroccan coastal waters, this proceedings paper presents the theoretical framework with hypothetical species, focusing on mathematical foundations, hypothesis testing, and numerical analysis. The central hypotheses tested are: stable coexistence requires each species' growth rate to exceed competitive



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pressure from the other species; asymmetric competition produces different stability thresholds; profit-maximizing harvesting must incorporate biomass non-negativity constraints; and competition coefficients are the most sensitive parameters affecting system stability.

The remainder of this paper is organized as follows. Section 2 presents the biological competition model, including equilibrium analysis and stability conditions. Section 3 describes the numerical simulations, including time series, phase-plane trajectories, and sensitivity analysis that confirm the stability results. Section 4 extends the framework to incorporate harvesting and economic optimization using Karush–Kuhn–Tucker (KKT) conditions. Section 5 discusses the limitations and concludes with future research directions.

2. Biological Competition Model

The biological model describes the population dynamics of two competing marine species with biomasses denoted by R (Species 1) and P (Species 2). The dynamics are governed by the classical Lotka–Volterra competition system with logistic growth [5–7]. The rate of change of each population depends on its intrinsic growth rate, environmental carrying capacity, and the negative effects of interspecific competition. The equations are:

$$\frac{dR}{dt} = r_R R \left(1 - \frac{R}{K_R}\right) - h_{RP} R P \quad (1)$$

$$\frac{dP}{dt} = r_P P \left(1 - \frac{P}{K_P}\right) - h_{PR} P R \quad (2)$$

In these equations, r_R and r_P represent the intrinsic growth rates measured in year^{−1}, indicating how rapidly each population would grow in the absence of resource limitations. The carrying capacities K_R and K_P , measured in tons, represent the maximum population sizes that the environment can sustain. The competition coefficients h_{RP} and h_{PR} , measured in tons^{−1} year^{−1}, quantify the negative effect of one species on the other through resource competition. The terms $-h_{RP} R P$ and $-h_{PR} P R$ reflect that when both species are present, each experiences a reduction in growth rate proportional to the abundance of the competitor. This formulation assumes competition is symmetric in form but potentially asymmetric in strength, as the coefficients may differ.

The system exhibits four equilibrium points, which are states where both populations stop changing. The first equilibrium, $S_1(0, 0)$, represents extinction of both species. The second, $S_2(K_R, 0)$, represents Species 1 at its carrying capacity while Species 2 is extinct. The third, $S_3(0, K_P)$, represents the opposite situation where Species 2 dominates. The fourth, $S_4(R^*, P^*)$, represents coexistence where both species persist simultaneously. The coexistence equilibrium coordinates are derived by setting the time derivatives to zero and solving the resulting algebraic system:

$$R^* = \frac{K_R r_P (K_P h_{RP} - r_R)}{K_P K_R h_{PR} h_{RP} - r_P r_R}, \quad P^* = \frac{K_P r_R (K_R h_{PR} - r_P)}{K_P K_R h_{PR} h_{RP} - r_P r_R} \quad (3)$$

For these biomasses to be biologically meaningful, both must be strictly positive. This gives the feasibility conditions $r_R > h_{RP} K_P$ and $r_P > h_{PR} K_R$, meaning each species' intrinsic growth rate must exceed the competitive pressure exerted by the other species. When these conditions hold, the coexistence equilibrium exists.

The stability of each equilibrium is determined by evaluating the Jacobian matrix, which contains the partial derivatives of the system, and computing its eigenvalues. The Jacobian matrix is:

$$J(R, P) = \begin{bmatrix} r_R \left(1 - \frac{2R}{K_R}\right) - h_{RP} P & -h_{RP} R \\ -h_{PR} P & r_P \left(1 - \frac{2P}{K_P}\right) - h_{PR} R \end{bmatrix} \quad (4)$$

At the extinction equilibrium $S_1(0,0)$, the Jacobian becomes diagonal with eigenvalues equal to the intrinsic growth rates $\lambda_1 = r_R > 0$ and $\lambda_2 = r_P > 0$. Since both eigenvalues are positive, any small perturbation away from zero will grow exponentially. Therefore, S_1 is an unstable node, meaning the system naturally moves away from extinction. This is ecologically intuitive: if both species are present even in tiny numbers, they will begin to grow.

At the single-species equilibrium $S_2(K_R,0)$, the Jacobian has eigenvalues $\lambda_1 = -r_R < 0$ and $\lambda_2 = r_P - h_{PR}K_R$. From the feasibility condition, $\lambda_2 > 0$, so the eigenvalues have opposite signs. This makes S_2 an unstable saddle point: stable in one direction (along the Species 1 axis) but unstable in the other direction (allowing Species 2 to invade). Similarly, at $S_3(0,K_P)$, the eigenvalues are $\lambda_1 = r_R - h_{RP}K_P > 0$ and $\lambda_2 = -r_P < 0$, also producing a saddle point. Ecologically, these results indicate that while one species can dominate in the absence of the other, the excluded species can always reinvade if conditions allow.

At the coexistence equilibrium $S_4(R^*,P^*)$, the Jacobian simplifies using the equilibrium conditions to:

$$J_4 = \begin{bmatrix} -\frac{r_R R^*}{K_R} & -h_{RP} R^* \\ -h_{PR} P^* & -\frac{r_P P^*}{K_P} \end{bmatrix} \quad (5)$$

The trace (sum of diagonal elements) is negative because all terms are negative. The determinant is positive because $r_R r_P > h_{RP} h_{PR} K_R K_P$ from the feasibility conditions. When the trace is negative and the determinant is positive, both eigenvalues have negative real parts, confirming that the coexistence equilibrium is locally asymptotically stable. This means that if the system is slightly perturbed away from equilibrium, it will naturally return to the coexistence state over time. Table 1 lists the baseline ecological parameters used for numerical illustration. These are theoretical reference values chosen to demonstrate model behavior.

Table 1. Baseline ecological parameters (theoretical reference values for Species R and P).

Parameter	Value
r_R	0.7 year ⁻¹
r_P	0.5 year ⁻¹
K_R	1500 tons
K_P	1200 tons
h_{RP}	0.00042 tons ⁻¹ year ⁻¹
h_{PR}	0.00027 tons ⁻¹ year ⁻¹

3. Numerical Simulations and Stability Confirmation

Numerical simulations confirm the analytical stability results. Figure 1 shows the dynamics near the extinction equilibrium. When starting from very low initial biomasses of 0.02 and 0.01 tons, both populations exhibit exponential growth without oscillation because competition and density dependence are negligible at such low densities. The phase-plane trajectory diverges outward from the origin, confirming that S_1 acts as a source. From a management perspective, this instability suggests that even severely depleted stocks have the potential to recover if harvesting ceases and environmental conditions remain favorable. However, precautionary policies must still safeguard minimum viable populations to prevent stochastic extinction events.

Figure 2 illustrates dynamics near the single-species equilibrium where Species 1 dominates. Starting with Species 1 near carrying capacity (1450 tons) and Species 2 at a very low level (0.01 tons), Species 2 gradually increases and invades the system. Species 1 remains near carrying capacity, while Species 2 grows slowly but steadily. The phase-plane

trajectory moves away from the equilibrium point along the unstable direction. This saddle-point behavior means that eradicating one species to favor the other is an unsustainable management strategy; the model predicts a natural tendency toward recolonization of the excluded competitor.

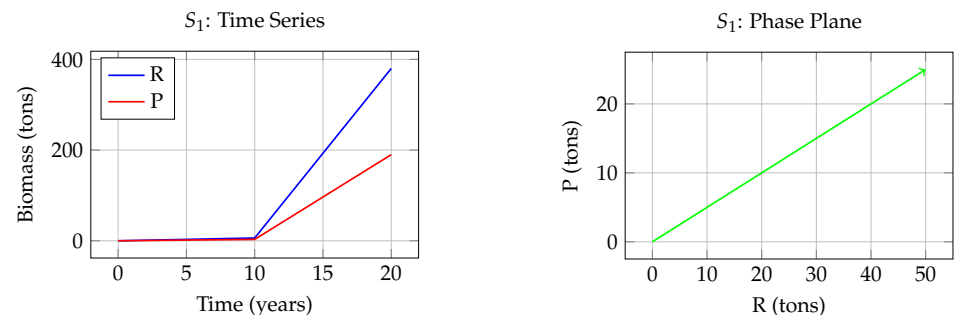


Figure 1. Population dynamics near the extinction equilibrium $S_1(0,0)$. The time series shows exponential growth from near-zero conditions. The phase-plane trajectory diverges from the origin, confirming instability (unstable node).

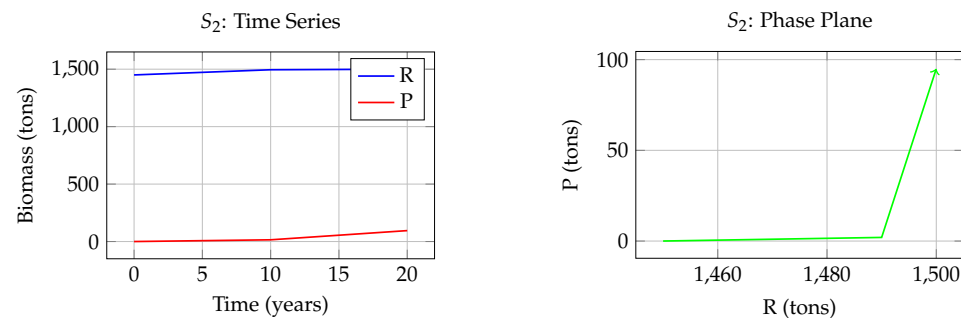


Figure 2. Population dynamics near the Species R-only equilibrium $S_2(1500,0)$. Species P invades the system, moving away from the equilibrium. The mixed-sign eigenvalues confirm this as an unstable saddle point.

Figure 3 shows the symmetric case where Species 2 initially dominates. Starting with Species 2 near carrying capacity (1150 tons) and Species 1 at a low level (0.02 tons), Species 1 invades and grows. The phase-plane trajectory again diverges from the equilibrium, confirming saddle-point behavior. The invasion eigenvalue for Species 1 at this state is larger than that of Species 2 at the previous state, indicating that Species 1 has a competitive advantage under baseline parameters.

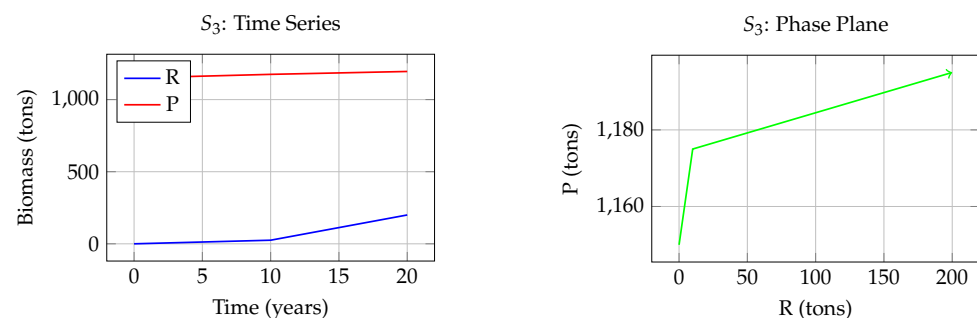


Figure 3. Population dynamics near the Species P-only equilibrium $S_3(0,1200)$. Species R invades the system, moving away from the equilibrium. This confirms another unstable saddle point.

Figure 4 presents the most important scenario: the coexistence equilibrium. Starting at 70% of the steady-state levels (705 tons for Species R and 383 tons for Species P), both

populations increase monotonically with a slight damped oscillation before converging smoothly to the stable equilibrium. The phase-plane trajectory spirals gently toward the attractor. The eigenvalues at this point are both negative ($\lambda_1 = -0.627$ and $\lambda_2 = -0.071$), confirming local asymptotic stability. The slow eigenvalue implies a characteristic recovery time of approximately 14 years, while the fast eigenvalue dictates an adjustment phase of about 1.6 years. Sustainable management must target this stable attractor, keeping in mind that recovery from severe shocks may progress slowly due to the dominant slow eigenmode.

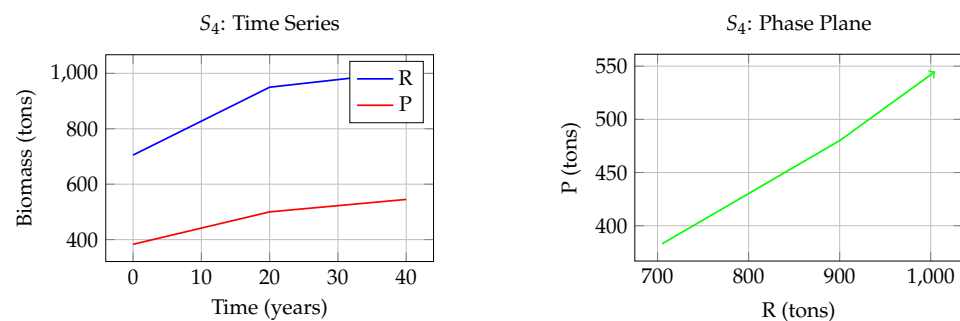


Figure 4. Population dynamics near the coexistence equilibrium $S_4(1008, 547)$. Both populations converge to the steady state, and the phase-plane trajectory spirals into the attractor. Negative eigenvalues confirm local asymptotic stability.

Sensitivity analysis reveals how the coexistence equilibrium responds to parameter variations. Figure 5 shows that increasing the intrinsic growth rate of either species benefits its own population but harms the competitor. The competition coefficients exhibit the highest elasticities: a 50% increase in h_{PR} reduces the equilibrium biomass of Species P by over 90%, driving it toward the extinction threshold. This high sensitivity means that even minor shifts in competitive intensity can rapidly destabilize coexistence. Managers must therefore use a precautionary approach, maintaining ecological parameters within safe operating spaces.

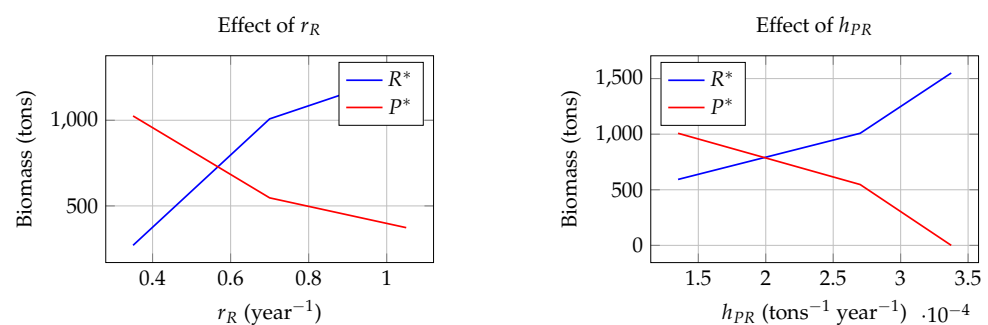


Figure 5. Sensitivity analysis showing the effect of intrinsic growth rate r_R (left) and competition coefficient h_{PR} (right) on equilibrium biomasses. Competition coefficients exhibit the highest elasticities, confirming their critical role in system stability.

4. Bioeconomic Model and KKT Optimization

When harvesting is included, the population dynamics incorporate additional mortality terms proportional to fishing effort and catchability [8,9]. The modified equations become:

$$\frac{dR}{dt} = r_R R \left(1 - \frac{R}{K_R} \right) - h_{RP} R P - q_1 E_1 R \quad (6)$$

$$\frac{dP}{dt} = r_P P \left(1 - \frac{P}{K_P} \right) - h_{PR} P R - q_2 E_2 P \quad (7)$$

Here, q_1 and q_2 are catchability coefficients representing the efficiency of the fishing gear, and E_1 and E_2 are fishing efforts measured in standardized units. At equilibrium, solving these equations yields biomasses as affine functions of fishing efforts: $R = a_{11}E_1 + a_{12}E_2 + R^*$ and $P = a_{21}E_1 + a_{22}E_2 + P^*$. The coefficients are defined in the Appendix A.

The profit function for a single fishing enterprise combines revenue from both species minus operating costs:

$$\pi(E_1, E_2) = p_1 q_1 E_1 R + p_2 q_2 E_2 P - c_1 E_1 - c_2 E_2 \quad (8)$$

where p_1, p_2 are prices per ton and c_1, c_2 are costs per unit effort. The optimization problem maximizes profit subject to biological feasibility constraints, specifically requiring that biomasses remain non-negative: $R \geq 0$ and $P \geq 0$. Additionally, fishing efforts cannot be negative. This problem is solved using the Karush–Kuhn–Tucker (KKT) conditions, which generalize Lagrange multipliers to handle inequality constraints. The KKT conditions are:

1. Stationarity: $\nabla \pi(E^*) + A^\top \lambda - \mu = 0$.
2. Primal feasibility: $AE^* \leq b$, $E^* \geq 0$.
3. Dual feasibility: $\lambda \geq 0$, $\mu \geq 0$.
4. Complementary slackness: $\lambda_i (AE^* - b)_i = 0$, $\mu_j E_j^* = 0$.

The multipliers λ (associated with biomass constraints) and μ (associated with non-negativity of fishing efforts) represent the shadow prices of these constraints. In economic terms, λ measures the marginal increase in profit that would result from relaxing the biomass non-negativity constraint by one unit. For the interior solutions presented in Table 2, the biomass constraints are not active, meaning $\lambda = 0$. However, at boundary solutions where harvesting would drive a species to extinction, λ becomes strictly positive, indicating the shadow cost of maintaining that species above extinction. Similarly, $\mu_j > 0$ when the optimal effort $E_j^* = 0$, representing the marginal profitability threshold that must be exceeded to justify positive fishing effort. The analysis reveals that for the premium price scenario, the constraint on Species P biomass becomes nearly binding, suggesting that profit-maximizing strategies naturally approach the sustainability limit.

Table 2 presents optimal harvesting strategies under different price scenarios. The interior solution (harvesting both species) yields the highest profits, with values increasing from 714 at low prices to nearly 60,000 at premium export levels. However, this strategy exerts strong pressure on Species 2 (P), whose biomass declines substantially as prices rise. Species P-only harvesting provides stable and ecologically safer outcomes with moderate profits, making it suitable for contexts with limited monitoring capacity. The sensitivity analysis confirms two critical policy levers: improving catchability through technological investments simultaneously increases profits while reducing required fishing effort, whereas cost-control measures directly enhance profitability.

Table 2. Optimal harvesting strategies under varying price scenarios for Species R (price p_1) and Species P (price p_2).

p_1	p_2	E_1^*	E_2^*	π^*
10	15	0.70	0.35	714
20	30	0.70	0.36	1395
50	75	0.69	0.36	6938
100	150	0.69	0.36	13,952

5. Discussion and Conclusions

This study confirms that stable coexistence requires each species' growth rate to exceed competitive pressure ($r_R > h_{RP}K_P$, $r_P > h_{PR}K_R$), with asymmetric competition creating different stability thresholds. The KKT framework identifies profit-maximizing harvesting under biomass constraints, while sensitivity analysis shows that competition coefficients have the highest elasticities (up to -4.10), making them critical for management. Limitations include spatial homogeneity, time-invariant parameters, and theoretical values. Despite these, the framework provides a flexible foundation for competing fisheries worldwide, directly supporting SDG 14 (Life Below Water) and SDG 12 (Responsible Consumption and Production).

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Appendix A. Coefficients for Equilibrium Biomasses

The coefficients for the affine equilibrium expressions are:

$$a_{11} = -\frac{K_R q_1 r_P}{\Delta}, \quad a_{12} = \frac{K_R h_{RP} K_P q_2}{\Delta}, \quad a_{21} = \frac{K_P h_{PR} K_R q_1}{\Delta}, \quad a_{22} = -\frac{K_P q_2 r_R}{\Delta} \quad (A1)$$

where $\Delta = r_R r_P - h_{PR} h_{RP} K_P K_R$.

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