



A nonlinear multispecies fisheries model for Namibian coastal waters: Implications for food security and marine ecosystem resilience

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Abstract

Background: The Benguela Current Large Marine Ecosystem supports major fisheries that are essential to Namibia's food security and economy. The dynamics of Cape hake, horse mackerel, and sardine are strongly influenced by ecological interactions and harvesting, highlighting the need for mathematically rigorous multispecies fisheries models.

Aims: This study aims to develop an analytically tractable nonlinear multispecies fisheries model that describes the ecological interactions among Cape hake, horse mackerel, and sardine under harvesting pressure, while providing a rigorous mathematical framework for evaluating ecosystem stability and sustainable fisheries management.

Method: The proposed model integrates logistic growth, predator-prey interactions, interspecific competition, and species-specific harvesting mortality. Qualitative analysis is performed using nonlinear dynamical systems theory to establish existence and uniqueness, positivity, boundedness, equilibrium conditions, and local and global stability. Local stability is analyzed using linearization and the Routh-Hurwitz criterion, whereas global stability is established through a Volterra-type Lyapunov function and LaSalle's Invariance Principle. In addition, a harvesting-rate estimation framework based on fisheries catch, effort, and biomass data is formulated to facilitate future model calibration.

Result: The mathematical analysis establishes the well-posedness of the proposed model and derives analytical conditions for biologically feasible coexistence and system stability. Numerical simulations validate the theoretical results by demonstrating convergence toward a stable coexistence equilibrium under biologically realistic parameter values. The simulations further show that increasing harvesting intensity reduces equilibrium biomass and ecosystem resilience, while excessive exploitation of sardine populations indirectly destabilizes higher trophic levels by reducing prey availability for predator species.

Conclusion: The proposed model provides a mathematically rigorous framework for analyzing multispecies fisheries dynamics and offers quantitative insights into the ecological consequences of harvesting. The results support ecosystem-based fisheries management by providing a scientific basis for evaluating sustainable harvesting strategies, establishing science-based catch quotas, identifying precautionary harvesting thresholds, and informing evidence-based policies to strengthen the long-term resilience and sustainability of Namibia's marine fisheries.

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INTRODUCTION

The Benguela Current Large Marine Ecosystem (BCLME) is one of the world's most productive eastern boundary upwelling systems and supports fisheries that are fundamental to the economies of Namibia, Angola, and South Africa ([Belhabib et al., 2015](#); [Plagányi et al., 2006](#); [Shannon et al., 2006](#)). Among the commercially exploited species, Cape hake (*Merluccius capensis* and *M. paradoxus*), horse mackerel (*Trachurus capensis*), and sardine (*Sardinops sagax*) occupy key ecological positions within the Benguela food web and collectively account for a substantial proportion of Namibia's marine fish production ([Engelhard et al., 2024](#); [Heymans et al., 2009](#); [Kirchner & Leiman, 2014](#)). Sardine functions as a principal forage species linking lower and higher trophic levels, horse mackerel occupies an intermediate trophic position and competes for similar food resources, whereas Cape hake is a major demersal predator whose abundance depends partly on the availability of pelagic prey. Consequently, perturbations in one population may propagate throughout the ecosystem, altering trophic structure, ecosystem stability, and fisheries productivity. These ecological interdependencies, together with harvesting pressure, environmental variability, and climate change, make these three species an appropriate system for investigating multispecies fisheries dynamics and ecosystem resilience ([Nhiwatiwa et al., 2026](#); [Sumaila & Vasconcellos, 2000](#)).

Beyond their ecological and economic importance, sustainable fisheries are increasingly recognised as strategic resources that contribute to national resilience, food security, environmental security, and maritime governance. Declining fish stocks may reduce protein availability, threaten coastal livelihoods, decrease export revenue, and increase the vulnerability of marine ecosystems to illegal, unreported, and unregulated (IUU) fishing and environmental disturbances. Mathematical models capable of predicting stock responses under different harvesting scenarios therefore provide valuable decision-support tools for fisheries management, strategic resource planning, and evidence-based policy development aimed at balancing resource exploitation with ecosystem conservation ([Christensen & Pauly, 1992](#); [Heymans et al., 2004](#); [Jahedi et al., 2023](#); [Lotka, 1925](#); [Roux et al., 2013](#); [Wilhelm et al., 2008](#)).

Mathematical modelling has long provided the theoretical foundation for fisheries science. The classical logistic growth equation introduced by Verhulst describes density-dependent population growth through

$$\frac{dX}{dt} = rX \left(1 - \frac{X}{K}\right) \quad (1)$$

where $X(t)$ denotes fish biomass, r is the intrinsic growth rate, and K is the environmental carrying capacity ([Charlebois & Balázs, 2019](#); [Murray, 2002](#); [Verhulst, 1838](#)). Incorporating harvesting into the logistic framework yields the classical Schaefer model,

$$\frac{dX}{dt} = rX \left(1 - \frac{X}{K}\right) - qEX \quad (2)$$

with harvesting function

$$Y(t) = qE(t)X(t) \quad (1)$$

where q denotes the catchability coefficient and $E(t)$ represents fishing effort. These models provide the mathematical basis for estimating Maximum Sustainable Yield (MSY), harvesting effort, and equilibrium biomass, and continue to underpin many fisheries management strategies ([Clark, 1990](#); [Ilahi & Widiana, 2019](#); [Schaefer, 1991](#)).

Although the logistic and Schaefer models provide elegant mathematical descriptions of single-species population dynamics, they assume that each fish stock evolves independently of other species. This assumption is inappropriate for the Benguela ecosystem, where Cape hake, horse mackerel, and sardine are linked through predator-prey interactions, trophic dependence, and competition for shared resources. For example, reductions in sardine biomass may decrease food availability for Cape hake, while competition between sardine and horse mackerel may alter the

productivity of both populations. Consequently, harvesting one species may indirectly influence the abundance and stability of the others through ecological feedback mechanisms that cannot be represented by the classical Schaefer framework. Capturing these nonlinear trophic interactions therefore requires a multispecies dynamical model capable of describing the coupled evolution of interacting fish populations ([Martin et al., 2024](#); [Soetaert & Herman, 2009](#); [Watermeyer et al., 2016](#)).

Recent research has therefore shifted towards nonlinear multispecies dynamical systems formulated as coupled ordinary differential equations that explicitly incorporate predator--prey interactions, competition, harvesting, and environmental variability. These models permit rigorous mathematical investigation of equilibrium existence, positivity, boundedness, persistence, Lyapunov stability, bifurcation behaviour, and resilience under harvesting and environmental perturbations ([Howell et al., 2021](#); [Karp et al., 2023](#)). Advances in nonlinear dynamical systems theory, together with ecosystem-based fisheries modelling, have substantially improved understanding of marine ecosystem dynamics and harvesting strategies ([Couve et al., 2024](#); [Xu et al., 2024](#)). Within the Benguela Current Large Marine Ecosystem, ecosystem studies have further demonstrated that the dynamics of Cape hake, horse mackerel, and sardine are strongly influenced by trophic interactions, climate variability, and fishing pressure, highlighting the importance of integrated multispecies modelling for sustainable fisheries management ([Howell et al., 2021](#); [Xu et al., 2024](#)).

Although considerable progress has been achieved in ecosystem modelling, most existing multispecies fisheries models rely predominantly on numerical ecosystem simulation platforms, such as Ecopath with Ecosim, or stock assessment frameworks that provide biomass projections under different harvesting scenarios. While these approaches have substantially improved understanding of ecosystem functioning, they generally provide limited analytical insight into the nonlinear mechanisms governing multispecies coexistence, persistence, equilibrium structure, stability transitions, and harvesting thresholds. In particular, mathematically tractable nonlinear differential equation models describing the coupled dynamics of Cape hake, horse mackerel, and sardine remain scarce, and rigorous analyses of well-posedness, invariant regions, asymptotic stability, and long-term ecosystem persistence are largely unavailable. This theoretical limitation restricts the derivation of explicit analytical conditions that can guide precautionary harvesting policies and evaluate marine ecosystem resilience.

Motivated by these challenges, this study develops a nonlinear multispecies dynamical model describing the coupled population dynamics of Cape hake, horse mackerel, and sardine under species-specific harvesting pressure. In contrast to existing multispecies fisheries models that rely primarily on ecosystem simulation or numerical stock assessment, the proposed framework is analytically tractable and permits rigorous mathematical investigation of the underlying nonlinear dynamics. The principal novelty of the study lies in integrating logistic self-regulation, predator--prey interactions, interspecific competition, and harvesting mortality within a unified system of nonlinear ordinary differential equations while establishing explicit analytical conditions for well-posedness, positivity, boundedness, persistence, coexistence, and local and global stability. The resulting framework not only advances the mathematical theory of multispecies fisheries models but also provides quantitative decision-support tools for evaluating sustainable harvesting policies, strengthening marine ecosystem resilience, improving food security, and supporting ecosystem-based fisheries management in Namibian coastal waters.

METHOD

Let

$$X(t) = \begin{pmatrix} H(t) \\ M(t) \\ S(t) \end{pmatrix} \in \mathbb{R}_+^3,$$

where $H(t)$, $M(t)$, and $S(t)$ denote the biomasses of Cape hake, horse mackerel, and sardine populations, respectively, at time t . The model is constructed to describe the joint effects of density-dependent growth, ecological interactions, and harvesting mortality on the long-term dynamics of these three commercially and ecologically important fish species in Namibian coastal waters.

Model Assumptions

The nonlinear dynamical system is formulated under the following mathematical assumptions.

- (A1) The state variables $H(t), M(t), S(t) \in \mathbb{R}_+$, represent the biomasses of Cape hake, horse mackerel, and sardine, respectively. Hence, the state vector $X(t) = (H(t), M(t), S(t))^T$ evolves in the biologically feasible region $\Omega = \mathbb{R}_+^3$.
- (A2) In the absence of harvesting and interspecific interactions, each species evolves independently according to the logistic equation $\frac{dX_i}{dt} = r_i X_i \left(1 - \frac{X_i}{K_i}\right)$, $i \in \{H, M, S\}$, where $r_i > 0$, $K_i > 0$.
- (A3) Ecological interactions are represented by continuously differentiable bilinear terms satisfying $\mathcal{B}(X, X) \in C^1(\Omega)$, with positive interaction coefficients $\alpha_1, \alpha_2, \beta_1, \beta_2 > 0$. The coefficients α_1 and α_2 describe trophic gains to Cape hake arising from prey availability, whereas β_1 and β_2 quantify competitive effects between horse mackerel and sardine.
- (A4) Harvesting follows the classical Schaefer proportional harvesting law, $H_i(X_i) = q_i E_i X_i$, where $q_i > 0$, $E_i \geq 0$, for each species $i \in \{H, M, S\}$.
- (A5) All model parameters are assumed to be constant throughout the analysis; that is, $r_i, K_i, q_i, E_i, \alpha_j, \beta_j$ are time-independent positive constants. Consequently, environmental variability and seasonal forcing are neglected.
- (A6) Recruitment, natural mortality, and intra-specific competition are incorporated implicitly within the logistic growth term, while all interspecific effects are represented explicitly through the interaction operator $\mathcal{B}(X, X)$.
- (A7) The vector field defining the nonlinear system is assumed to satisfy $F(X) \in C^1(\Omega)$, which guarantees local existence and uniqueness of solutions by the Picard–Lindelöf theorem.
- (A8) Initial conditions satisfy $X(0) = X_0 \in \Omega$, so that all population trajectories remain biologically meaningful throughout the analysis.

Origin and Mathematical Interpretation of Parameters

Let the parameter vector be defined by $\Theta = (r_H, r_M, r_S, K_H, K_M, K_S, q_H, q_M, q_S, E_H, E_M, E_S, \alpha_1, \alpha_2, \beta_1, \beta_2) \in \mathbb{R}_+^{16}$, where all parameters are assumed to be positive constants.

The intrinsic growth parameters $r_i > 0$, $i \in \{H, M, S\}$ represent the per-capita biomass growth rates of Cape hake, horse mackerel, and sardine, respectively. They appear in the logistic growth term $r_i X_i \left(1 - \frac{X_i}{K_i}\right)$, and determine the local exponential growth rate when population density is sufficiently small, namely $\lim_{X_i \rightarrow 0} \frac{1}{X_i} \frac{dX_i}{dt} = r_i$.

The carrying capacities $K_i > 0$, $i \in \{H, M, S\}$, represent the environmental equilibrium biomass in the absence of harvesting and interspecific interactions. Mathematically, $\lim_{t \rightarrow \infty} X_i(t) = K_i$, for the isolated logistic equation $\frac{dX_i}{dt} = r_i X_i \left(1 - \frac{X_i}{K_i}\right)$.

The harvesting parameters consist of the catchability coefficients $q_i > 0$, and fishing efforts $E_i > 0$, whose product defines the instantaneous harvesting mortality $h_i = q_i E_i$.

Consequently, the harvesting term satisfies $H_i(X_i) = q_i E_i X_i = h_i X_i$, which corresponds to the classical Schaefer proportional harvesting assumption.

The ecological interaction coefficients $\alpha_1, \alpha_2, \beta_1, \beta_2 > 0$, parameterise the bilinear interaction operator $\mathcal{B}(X, X)$ where $\alpha_1 HS$ and $\alpha_2 HM$ represent trophic gains to Cape hake arising from prey availability, while $-\alpha_1 HS$ and $-\alpha_2 HM$ describe the corresponding biomass losses experienced by sardine and horse mackerel due to predation. Similarly, $-\beta_1 MS$ and $-\beta_2 SM$ represent interspecific competition between horse mackerel and sardine, with the coefficients β_1 and β_2 quantifying the intensity of competitive interactions.

In practical applications, the parameter vector Θ may be estimated using fisheries stock-assessment models, biomass time-series observations, catch-per-unit-effort (CPUE) data, scientific

trawl surveys, trophic interaction studies, or inverse parameter estimation techniques. Mathematically, parameter estimation may be formulated as the constrained optimisation problem $\hat{\Theta} = \arg \min_{\Theta \in \mathbb{R}_+^{16}} \sum_{k=1}^N \|X_{\text{obs}}(t_k) - X_{\text{model}}(t_k; \Theta)\|^2$ where X_{obs} denotes observed biomass data and X_{model} denotes the solution of the proposed nonlinear dynamical system.

Biological Rationale for the Interactions

The interaction structure reflects known ecological relationships in the Benguela Current ecosystem. Cape hake occupies a relatively high trophic position and feeds on smaller pelagic and demersal organisms. Therefore, an increase in sardine or horse mackerel biomass may enhance food availability for Cape hake, producing positive terms $\alpha_1 HS$ and $\alpha_2 HM$ in the hake equation.

Horse mackerel and sardine occupy overlapping ecological niches and may compete for planktonic food resources, particularly during periods of limited productivity. This motivates the negative competitive terms $-\beta_1 MS$ in the horse mackerel equation and $-\beta_2 SM$ in the sardine equation. Sardine also experiences predation pressure from Cape hake, represented by the term $-\alpha_1 HS$, while horse mackerel experiences negative trophic pressure from Cape hake through $-\alpha_2 HM$.

Thus, the signs of the interaction terms are biologically motivated as $\alpha_1 HS > 0$ and $\alpha_2 HM > 0$ represent trophic benefits to Cape hake, while $-\alpha_1 HS$, $-\alpha_2 HM$, $-\beta_1 MS$, and $-\beta_2 SM$ represent losses due to predation or competition.

Dimensional Model

The intrinsic growth of each species follows logistic dynamics:

$$G(X, X) = \begin{pmatrix} r_H H \left(1 - \frac{H}{K_H}\right) \\ r_M M \left(1 - \frac{M}{K_M}\right) \\ r_S S \left(1 - \frac{S}{K_S}\right) \end{pmatrix}$$

Ecological interactions are represented by the bilinear operator

$$\mathcal{B}(X, X) = \begin{pmatrix} \alpha_1 HS + \alpha_2 HM \\ -\beta_1 MS - \alpha_2 HM \\ -\beta_2 SM - \alpha_1 HS \end{pmatrix}$$

Under the Schaefer harvesting assumption, harvesting mortality is $Q(X) = QX$, where

$$Q = \begin{pmatrix} q_H E_H & 0 & 0 \\ 0 & q_M E_M & 0 \\ 0 & 0 & q_S E_S \end{pmatrix}$$

Consequently, the multispecies system is given by

$$\frac{dX}{dt} = (R - Q)X - D(X)X + \mathcal{B}(X, X), \quad (4)$$

$$\text{where } R = \begin{pmatrix} r_H & 0 & 0 \\ 0 & r_M & 0 \\ 0 & 0 & r_S \end{pmatrix} \text{ and } D(X) = \begin{pmatrix} \frac{r_H}{K_H} H & 0 & 0 \\ 0 & \frac{r_M}{K_M} M & 0 \\ 0 & 0 & \frac{r_S}{K_S} S \end{pmatrix}.$$

Writing Equation (4) component wise gives

$$\frac{dH}{dt} = H \left[r_H \left(1 - \frac{H}{K_H} \right) + \alpha_1 S + \alpha_2 M - q_H E_H \right] \quad (5)$$

$$\frac{dM}{dt} = M \left[r_M \left(1 - \frac{M}{K_M} \right) - \beta_1 S - \alpha_2 H - q_M E_M \right] \quad (6)$$

$$\frac{dS}{dt} = S \left[r_S \left(1 - \frac{S}{K_S} \right) - \beta_2 M - \alpha_1 H - q_S E_S \right] \quad (7)$$

Non-Dimensional Model

To reduce parameter complexity, introduce $x = \frac{H}{K_H}$, $y = \frac{M}{K_M}$, $z = \frac{S}{K_S}$, and $\tau = r_H t$. The resulting non-dimensional system becomes

$$\frac{dx}{d\tau} = x[1 - x + a_{1z} + a_2 y - h_H], \quad (8)$$

$$\frac{dy}{d\tau} = y[\rho_M(1 - y) - b_1 z - a_3 x - h_M] \quad (9)$$

$$\frac{dz}{d\tau} = z[\rho_S(1 - z) - b_2 y - a_4 x - h_S] \quad (10)$$

The dimensionless parameters are defined as

$$\rho_M = \frac{r_M}{r_H}, \quad \rho_S = \frac{r_S}{r_H}, \quad h_H = \frac{q_H E_H}{r_H}, \quad h_M = \frac{q_M E_M}{r_H}, \quad h_S = \frac{q_S E_S}{r_H}$$

and

$$a_1 = \frac{\alpha_1 K_S}{r_H}, \quad a_2 = \frac{\alpha_2 K_M}{r_H}, \quad a_3 = \frac{\alpha_2 K_H}{r_H}, \quad a_4 = \frac{\alpha_1 K_H}{r_H}, \quad b_1 = \frac{\beta_1 K_S}{r_H}, \quad b_2 = \frac{\beta_2 K_M}{r_H}$$

Define

$$u = \begin{pmatrix} x \\ y \\ z \end{pmatrix}, \quad c = \begin{pmatrix} 1 - h_H \\ \rho_M - h_M \\ \rho_S - h_S \end{pmatrix},$$

and

$$A = \begin{pmatrix} -1 & a_2 & a_1 \\ -a_3 & -\rho_M & -b_1 \\ -a_4 & -b_2 & -\rho_S \end{pmatrix}.$$

Then the dimensionless system is written compactly as

$$\frac{du}{d\tau} = \text{diag}(u)(c + Au).$$

The coexistence equilibrium u^* satisfies

$$c + Au^* = 0.$$

Provided $\det(A) \neq 0$, the coexistence equilibrium is

$$u^* = -A^{-1}c.$$

A biologically meaningful coexistence equilibrium exists whenever

$$-A^{-1}c \in \mathbb{R}_+^3.$$

Equation (5) – Equation (7) provides the mathematical foundation for the subsequent analysis of positivity, boundedness, invariant regions, equilibrium structure, local and global stability, and numerical simulations. It also provides a quantitative basis for evaluating sustainable harvesting strategies, marine ecosystem resilience, food security, and ecosystem-based fisheries management in Namibian coastal waters.

RESULTS AND DISCUSSION

Existence and Uniqueness of Solutions

Consider the fishery system

$$\frac{dX}{dt} = \mathcal{F}(X), \quad X(0) = X_0, \quad (11)$$

where

$$X(t) = \begin{pmatrix} H(t) \\ M(t) \\ S(t) \end{pmatrix} \in \mathbb{R}_+^3 \quad \text{and} \quad \mathcal{F}(X) = (R - Q)X - D(X)X + \mathcal{B}(X, X).$$

Theorem 1.

For every initial condition $X_0 \in \mathbb{R}_+^3$, there exists a unique maximal solution $X(t) \in C^1([0, T_{\max}), \mathbb{R}_+^3)$ of Equation (11). Furthermore, the solution depends continuously on the initial data.

Proof.

The vector field $\mathcal{F} = (f_1, f_2, f_3)^T$ is composed of quadratic polynomial functions,

$$\begin{aligned} f_1(H, M, S) &= H \left[r_H \left(1 - \frac{H}{K_H} \right) + \alpha_1 S + \alpha_2 M - q_H E_H \right], \\ f_2(H, M, S) &= M \left[r_M \left(1 - \frac{M}{K_M} \right) - \beta_1 S - \alpha_2 H - q_M E_M \right], \\ f_3(H, M, S) &= S \left[r_S \left(1 - \frac{S}{K_S} \right) - \beta_2 M - \alpha_1 H - q_S E_S \right]. \end{aligned}$$

Hence, $\mathcal{F} \in C^1(\mathbb{R}^3, \mathbb{R}^3)$, and therefore $\mathcal{F}$ is locally Lipschitz continuous on every bounded subset of $\mathbb{R}^3$. By the Picard–Lindelöf theorem, the initial-value problem Equation (11) admits a unique local solution $X(t) \in C^1([0, T], \mathbb{R}^3)$ for some $T > 0$. Moreover, standard continuation theory implies that the solution can be extended uniquely to a maximal interval $[0, T_{\max})$, and continuous dependence on initial conditions follows directly from Grönwall's inequality. Therefore, Equation (11) is locally well posed.

Corollary 1.

The nonlinear fishery model generates a unique local semiflow $\Phi_t: \mathbb{R}_+^3 \rightarrow \mathbb{R}_+^3$, defined by $\Phi_t(X_0) = X(t; X_0)$.

Positivity of Solutions

The biological relevance of the model requires that all population biomasses remain non-negative for all future time.

Theorem 2.

Let $(H(0), M(0), S(0)) \in \mathbb{R}_+^3$ with $H(0) > 0$, $M(0) > 0$, and $S(0) > 0$. Consequently, the positive cone $\mathbb{R}_+^3 = \{(H, M, S) \in \mathbb{R}^3: H \geq 0, M \geq 0, S \geq 0\}$ is positively invariant.

Proof.

The system can be written in the factorized form

$$\frac{dH}{dt} = H\Phi_1(H, M, S), \quad \frac{dM}{dt} = M\Phi_2(H, M, S), \quad \frac{dS}{dt} = S\Phi_3(H, M, S),$$

where

$$\begin{aligned}\Phi_1(H, M, S) &= r_H \left(1 - \frac{H}{K_H}\right) + \alpha_1 S + \alpha_2 M - q_H E_H, \\ \Phi_2(H, M, S) &= r_M \left(1 - \frac{M}{K_M}\right) - \beta_1 - \alpha_2 H - q_M E_M, \\ \Phi_3(H, M, S) &= r_S \left(1 - \frac{S}{K_S}\right) - \beta_2 M - \alpha_1 H - q_S E_S.\end{aligned}$$

Integrating each equation yields

$$\begin{aligned}H(t) &= H(0) \exp\left(\int_0^t \Phi_1(H(s), M(s), S(s)) ds\right), \\ M(t) &= M(0) \exp\left(\int_0^t \Phi_2(H(s), M(s), S(s)) ds\right), \\ S(t) &= S(0) \exp\left(\int_0^t \Phi_3(H(s), M(s), S(s)) ds\right).\end{aligned}$$

Since $H(0) > 0, M(0) > 0, S(0) > 0$, and the exponential function is strictly positive, it follows that $H(t) > 0, M(t) > 0, S(t) > 0, \forall t > 0$. Therefore, trajectories originating in $\mathbb{R}_+^3$ remain in $\mathbb{R}_+^3$, proving the positive invariance of the non-negative cone.

Corollary 2.

The biologically feasible region $\mathbb{R}_+^3$ is invariant under the semiflow generated by the fishery model.

Invariant Region

To establish a biologically feasible region, define the total biomass $N(t) = H(t) + M(t) + S(t)$. Adding Equation (5) – Equation (7) yields,

$$\begin{aligned}\frac{dN}{dt} &= r_H H \left(1 - \frac{H}{K_H}\right) + r_M M \left(1 - \frac{M}{K_M}\right) + r_S S \left(1 - \frac{S}{K_S}\right) - \beta_1 MS - \beta_2 SM - q_H E_H H \\ &\quad - q_M E_M M - q_S E_S S.\end{aligned} \quad (12)$$

The predator–prey transfer terms cancel identically, and the harvesting and competition terms are non-positive. Therefore,

$$\frac{dN}{dt} \leq r_H H + r_M M + r_S S - \frac{r_H}{K_H} H^2 - \frac{r_M}{K_M M^2} - \frac{r_S}{K_S} S^2. \quad (13)$$

Let $r_{\max} = \max\{r_H, r_M, r_S\}$ and $\eta = \min\left\{\frac{r_H}{K_H}, \frac{r_M}{K_M}, \frac{r_S}{K_S}\right\}$. Then $r_H H + r_M M + r_S S \leq r_{\max} N$, and $\frac{r_H}{K_H} H^2 + \frac{r_M}{K_M M^2} + \frac{r_S}{K_S} S^2 \geq \eta(H^2 + M^2 + S^2)$. Using $H^2 + M^2 + S^2 \geq \frac{1}{3}(H + M + S)^2 = \frac{N^2}{3}$, gives

$$\frac{dN}{dt} \leq r_{\max} N - \frac{\eta}{3} N^2. \quad (14)$$

Hence $\frac{dN}{dt} \leq r_{\max} N \left(1 - \frac{N}{K^*}\right)$, where $K^* = \frac{3r_{\max}}{\eta}$.

By the scalar comparison theorem for differential inequalities, $0 \leq N(t) \leq \max\{N(0), K^*\}$, $t \geq 0$. Consequently, if $N(0) \leq K^*$, the set $\Omega = \{(H, M, S) \in \mathbb{R}_+^3 : H + M + S \leq K^*\}$ is positively invariant.

Theorem 3.

The region $\Omega = \{(H, M, S) \in \mathbb{R}_+^3 : H + M + S \leq K^*\}$ is a positively invariant and biologically feasible region for system (5)–(7).

Boundedness of Solutions

The boundedness of solutions follows immediately from the positively invariant region established in the previous section.

Theorem 4.

Every solution of Equation (5) – Equation (7) with initial condition $(H(0), M(0), S(0)) \in \mathbb{R}_+^3$ is uniformly bounded on $[0, \infty)$.

Proof.

From Theorem above of invariant region, the total biomass $N(t) = H(t) + M(t) + S(t)$ satisfies,

$$\frac{dN}{dt} \leq r_{\max}N - \frac{\eta}{3}N^2. \quad (15)$$

where $r_{\max} = \max\{r_H, r_M, r_S\}$ and $\eta = \min\left\{\frac{r_H}{K_H}, \frac{r_M}{K_M}, \frac{r_S}{K_S}\right\}$. The scalar comparison theorem for differential inequalities,

$$0 \leq N(t) \leq K^*, \quad t \geq 0,$$

where $K^* = \frac{3r_{\max}}{\eta}$.

Since $H(t), M(t), S(t) \geq 0$, it follows that $H(t) \leq N(t)$, $M(t) \leq N(t)$, and $S(t) \leq N(t)$. Therefore, $0 \leq H(t), M(t), S(t) \leq K^*$ with $t \geq 0$. Hence all solutions remain uniformly bounded in the positively invariant region $\Omega = \{(H, M, S) \in \mathbb{R}_+^3 : H + M + S \leq K^*\}$.

Corollary 3.

The fishery system is dissipative and possesses the compact absorbing set $\Omega = \{(H, M, S) \in \mathbb{R}_+^3 : H + M + S \leq K^*\}$.

Equilibrium Analysis

Equilibrium points of the system are obtained by setting $\frac{dH}{dt} = \frac{dM}{dt} = \frac{dS}{dt} = 0$. Consequently,

$$H \left[r_H \left(1 - \frac{H}{K_H} \right) + \alpha_1 S + \alpha_2 M - q_H E_H \right] = 0 \quad (16)$$

$$M \left[r_M \left(1 - \frac{M}{K_M} \right) - \beta_1 S - \alpha_2 H - q_M E_M \right] = 0 \quad (17)$$

$$H \left[r_H \left(1 - \frac{S}{K_S} \right) - \beta_2 M - \alpha_1 H - q_S E_S \right] = 0 \quad (18)$$

- The model admits four biologically relevant classes of equilibria,
1. **Extinction Equilibrium**
The trivial equilibrium is $E_0 = (0, 0, 0)$, which corresponds to the extinction of all fish populations.
 2. **Boundary Equilibria**
The single-species equilibria are $E_H = \left(K_H \left(1 - \frac{q_H E_H}{r_H} \right), 0, 0 \right)$, $E_M = \left(0, K_M \left(1 - \frac{q_M E_M}{r_M} \right), 0 \right)$, and $E_S = \left(0, 0, K_S \left(1 - \frac{q_S E_S}{r_S} \right) \right)$. These equilibria exist whenever $q_H E_H < r_H$, $q_M E_M < r_M$, and $q_S E_S < r_S$.

3. Coexistence Equilibrium

The interior equilibrium $E^* = (H^*, M^*, S^*)$ is obtained by solving

$$r_H \left(1 - \frac{H^*}{K_H}\right) + \alpha_1 S^* + \alpha_2 M^* - q_H E_H = 0 \quad (19)$$

$$r_M \left(1 - \frac{M^*}{K_M}\right) - \beta_1 S^* - \alpha_2 H^* - q_M E_M = 0 \quad (20)$$

$$r_S \left(1 - \frac{S^*}{K_S}\right) - \beta_2 M^* - \alpha_1 H^* - q_S E_S = 0 \quad (21)$$

Equivalently, $A \begin{pmatrix} H^* \\ M^* \\ S^* \end{pmatrix} = b$ where $A = \begin{pmatrix} \frac{r_H}{K_H} & -\alpha_2 & -\alpha_1 \\ \alpha_2 & \frac{r_M}{K_M} & \beta_1 \\ \alpha_1 & \beta_2 & \frac{r_S}{K_S} \end{pmatrix}$ and $b = \begin{pmatrix} r_H - q_H E_H \\ r_M - q_M E_M \\ r_S - q_S E_S \end{pmatrix}$. Provided

$\det(A) \neq 0$ the coexistence equilibrium is uniquely given by $E^* = A^{-1}b$. A biologically feasible coexistence state exists whenever $H^* > 0$, $M^* > 0$, and $S^* > 0$. Therefore, the existence of a positive equilibrium is reduced to verifying that $A^{-1}b \in \mathbb{R}_+^3$.

This equilibrium represents the long-term coexistence of Cape hake, horse mackerel, and sardine populations under ecological interactions and harvesting pressure.

Local Stability Analysis

To investigate the local behaviour of solutions near an equilibrium point, we linearize the nonlinear system around the coexistence equilibrium $E^* = (H^*, M^*, S^*)$. The Jacobian matrix of the system is given by

$$J(H, M, S) = \begin{pmatrix} J_{11} & \alpha_2 H & \alpha_1 H \\ -\alpha_2 M & J_{22} & -\beta_1 M \\ -\alpha_1 S & -\beta_2 S & J_{33} \end{pmatrix}$$

where

$$\begin{aligned} J_{11} &= r_H - \frac{2r_H}{K_H} H + \alpha_1 S + \alpha_2 M - q_H E_H \\ J_{22} &= r_M - \frac{2r_M}{K_M} M - \beta_1 S - \alpha_2 H - q_M E_M \\ J_{33} &= r_S - \frac{2r_S}{K_S} S - \beta_2 M - \alpha_1 H - q_S E_S \end{aligned}$$

Evaluating the Jacobian at E^* yields $J^* = J(H^*, M^*, S^*)$. The local dynamics are determined by the eigenvalues of J^* , which satisfy the characteristic equation

$$\det(\lambda I - J^*) = \lambda^3 + a_1 \lambda^2 + a_2 \lambda + a_3 = 0 \quad (22)$$

where

$$a_1 = -\text{tr}(J^*) \quad (23)$$

$$a_2 = \sum \text{principal minors of order two} \quad (24)$$

$$a_3 = -\det(J^*) \quad (25)$$

Theorem 5.

The coexistence equilibrium E^* is locally asymptotically stable if

$$a_1 > 0, \quad a_2 > 0, \quad a_3 > 0, \quad a_1 a_2 > a_3. \quad (26)$$

Proof.

The characteristic polynomial of Equation (22) is cubic. By the Routh–Hurwitz criterion, all roots of Equation (22) have negative real parts if and only if the conditions in Equation (26) hold. Consequently, all sufficiently small perturbations around E^* decay exponentially with time, implying that E^* is locally asymptotically stable.

Global Stability Analysis

We establish sufficient conditions for the global asymptotic stability of the coexistence equilibrium $E^* = (H^*, M^*, S^*)$. Consider the Volterra-type Lyapunov function

$$V(H, M, S) = \sum_{i=1}^3 \left(X_i - X_i^* - X_i^* \ln \frac{X_i}{X_i^*} \right) \quad (27)$$

where $X_1 = H$, $X_2 = M$, and $X_3 = S$.

Explicitly, $V = \left(H - H^* - H^* \ln \left(\frac{H}{H^*} \right) \right) + \left(M - M^* - M^* \ln \left(\frac{M}{M^*} \right) \right) + \left(S - S^* - S^* \ln \left(\frac{S}{S^*} \right) \right)$. Since $x - 1 - \ln x \geq 0$ for $x > 0$, it follows that $V(H, M, S) \geq 0$, with equality if and only if $(H, M, S) = (H^*, M^*, S^*)$.

Differentiating Equation (27) along solutions of the system gives

$$\dot{V} = \sum_{i=1}^3 \left(1 - \frac{X_i^*}{X_i} \right) \frac{dX_i}{dt} \quad (28)$$

Substituting the governing equations and using the equilibrium relations yields

$$\dot{V} = -\frac{r_H}{K_H} (H - H^*)^2 - \frac{r_M}{K_M} (M - M^*)^2 - \frac{r_S}{K_S} (S - S^*)^2 + C \quad (29)$$

where C contains the interaction terms. If the interaction matrix

$$A = \begin{pmatrix} -\frac{r_H}{K_H} & \alpha_2 & \alpha_1 \\ -\alpha_2 & -\frac{r_M}{K_M} & -\beta_1 \\ -\alpha_1 & -\beta_2 & K_S \end{pmatrix}$$

satisfies

$$A + A^T < 0, \quad (30)$$

then $C \leq 0$ and consequently

$$\dot{V} \leq 0 \quad (31)$$

Moreover, $\dot{V} = 0$ if and only if $H = H^*$, $M = M^*$, and $S = S^*$.

Theorem 6.

Suppose the coexistence equilibrium E^* exists and condition $A + A^T < 0$ hold. Then S^* is globally asymptotically stable in the positively invariant region $\Omega = \{(H, M, S) \in \mathbb{R}_+^3 : H + M + S \leq K^*\}$

Proof.

From Equation (27), V is positive definite and radially unbounded in Ω . By Equation (31), $\dot{V} \leq 0$, and the largest invariant subset of $\{(H, M, S) \in \Omega : \dot{V} = 0\}$ consists solely of the equilibrium E^* . Therefore, LaSalle's Invariance Principle implies that every solution in Ω satisfies

$$(H(t), M(t), S(t)) \rightarrow (H^*, M^*, S^*), \quad t \rightarrow \infty$$

Hence E^* is globally asymptotically stable.

Harvesting Rate Estimation

The harvesting component of the model is based on the classical catch equation

$$Y(t) = qE(t)X(t), \quad (32)$$

where $Y(t)$ denote catch, $X(t)$ is stock biomass, $E(t)$ represents fishing effort, and q is the catchability coefficient.

For Cape hake, horse mackerel, and sardine, the species-specific catch equations are

$$Y_H(t) = q_H E_H(t) H(t), \quad (33)$$

$$Y_M(t) = q_M E_M(t) M(t), \quad (34)$$

$$Y_S(t) = q_S E_S(t) S(t). \quad (35)$$

Hence, the corresponding catchability coefficients are estimated by

$$q_H = \frac{Y_H(t)}{E_H(t)H(t)}, \quad (36)$$

$$q_M = \frac{Y_M(t)}{E_M(t)M(t)}, \quad (37)$$

$$q_S = \frac{Y_S(t)}{E_S(t)S(t)}. \quad (38)$$

If observations are available over n years, the average catchability estimates are

$$\hat{q}_H = \frac{1}{n} \sum_{k=1}^n \frac{Y_{H,k}}{E_{H,k}H_k}, \quad (39)$$

$$\hat{q}_M = \frac{1}{n} \sum_{k=1}^n \frac{Y_{M,k}}{E_{M,k}M_k}, \quad (40)$$

$$\hat{q}_S = \frac{1}{n} \sum_{k=1}^n \frac{Y_{S,k}}{E_{S,k}S_k}. \quad (41)$$

The harvesting mortality rates are therefore

$$F_H = q_H E_H, \quad F_M = q_M E_M, \quad F_S = q_S E_S. \quad (42)$$

Consequently, the harvesting terms appearing in the dynamical system may be written as $F_H H$, $F_M M$, and $F_S S$.

For a compact representation, define $Y = \begin{pmatrix} Y_H \\ Y_M \\ Y_S \end{pmatrix}$ and $q = \begin{pmatrix} q_H \\ q_M \\ q_S \end{pmatrix}$, then

$$Y = Zq, \tag{43}$$

where $Z = \text{diag}(E_H H, E_M M, E_S S)$.

Given observed catch, effort, and biomass data, the catchability vector may be estimated using ordinary least squares,

$$\hat{q} = (Z^T Z)^{-1} Z^T Y. \tag{44}$$

Equation (43) – Equation (44) provide a direct link between the theoretical harvesting terms in the model and measurable fisheries quantities, enabling calibration of the multispecies system using observed Namibian fisheries data.

Numerical Simulations

Numerical simulations were performed to illustrate the qualitative dynamics of the proposed Cape hake–horse mackerel–sardine model. The simulations investigate species coexistence, ecosystem stability, and the effects of harvesting pressure on long-term population persistence. The Equation (5) – Equation (7) was solved numerically using biologically plausible parameter values shown in Table 1.

Table 1. Baseline parameter values used in the numerical simulations.

Parameter	Value	Descriptive
r_H	0.45	Cape hake growth rate
r_M	0.65	Horse mackerel growth rate
r_S	0.90	Sardine growth rate
K_H	6.0×10^5	Hake carrying capacity
K_M	1.2×10^6	Horse mackerel carrying capacity
K_S	9.0×10^5	Sardine carrying capacity
α_1	1.0×10^{-7}	Hake–sardine interaction
α_2	6.0×10^{-8}	Hake–mackerel interaction
β_1	4.0×10^{-8}	Competition coefficient
β_2	5.0×10^{-8}	Competition coefficient
q_H	2.0×10^{-4}	Hake catchability
q_M	1.5×10^{-4}	Mackerel catchability
q_S	1.0×10^{-4}	Sardine catchability
E_H	0.40	Hake fishing effort
E_M	0.35	Mackerel fishing effort
E_S	0.30	Sardine fishing effort

The initial biomasses were chosen as $H(0) = 2.5 \times 10^5$, $M(0) = 5.0 \times 10^5$ and $S(0) = 4.0 \times 10^5$. The simulations examine coexistence dynamics, long-term boundedness, harvesting sensitivity, equilibrium responses to fishing effort, and ecosystem stability under varying harvesting regimes.

1. Population Dynamics

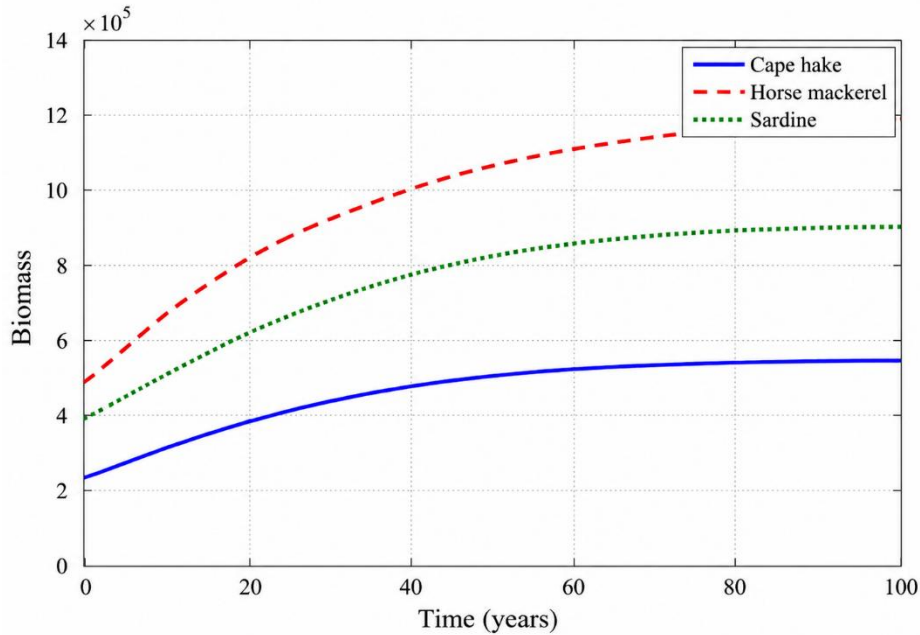


Figure 1. Time evolution Cape hake, horse mackerel and sardine biomasses. All species converge toward a positive coexistence state.

Figure 1 demonstrates convergence of all three populations toward a stable coexistence equilibrium, supporting the analytical stability results.

2. Total Biomass Dynamics

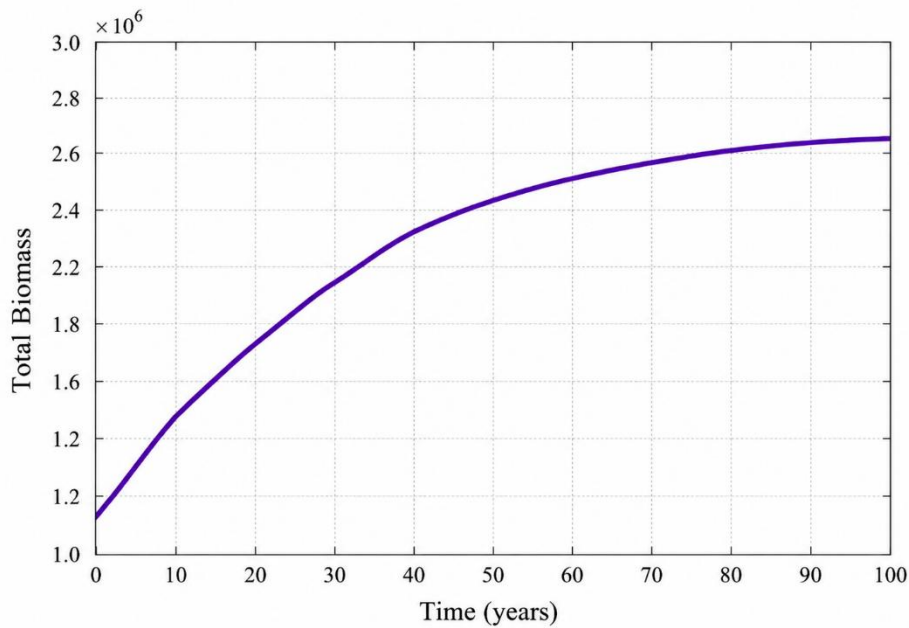


Figure 2. Total ecosystem biomass $N(t) = H(t) + M(t) + S(t)$.

Figure 2 confirms that the total biomass remains bounded and approaches a finite carrying level, consistent with the invariant-region analysis.

3. Harvesting Stability Landscape

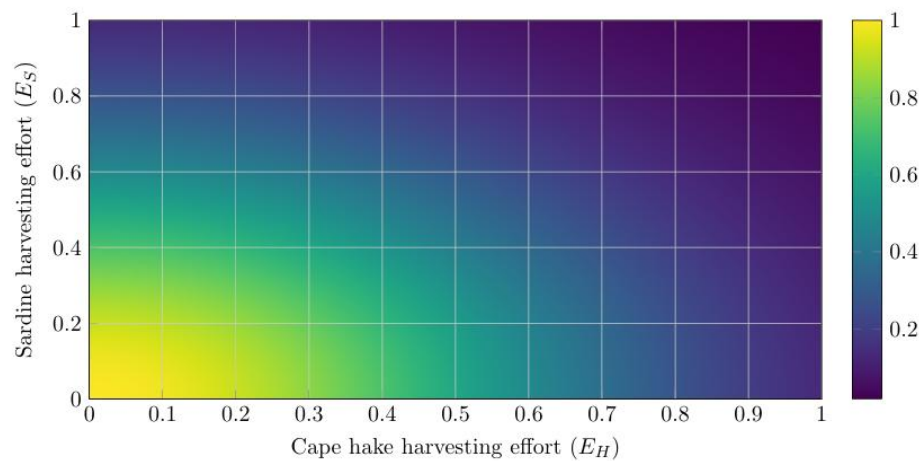


Figure 3. Illustrative stability landscape under varying harvesting efforts.

Figure 3 illustrates how ecosystem stability changes as harvesting pressure varies across species. Regions of low stability correspond to increased vulnerability of the coexistence equilibrium.

4. Harvesting Sensitivity

Figure 4 shows that increasing sardine harvesting effort substantially reduces sardine biomass while indirectly affecting Cape hake and horse mackerel through ecological interactions. The sharp decline observed at high harvesting intensities suggests the existence of a critical harvesting threshold beyond which stock collapse may occur.

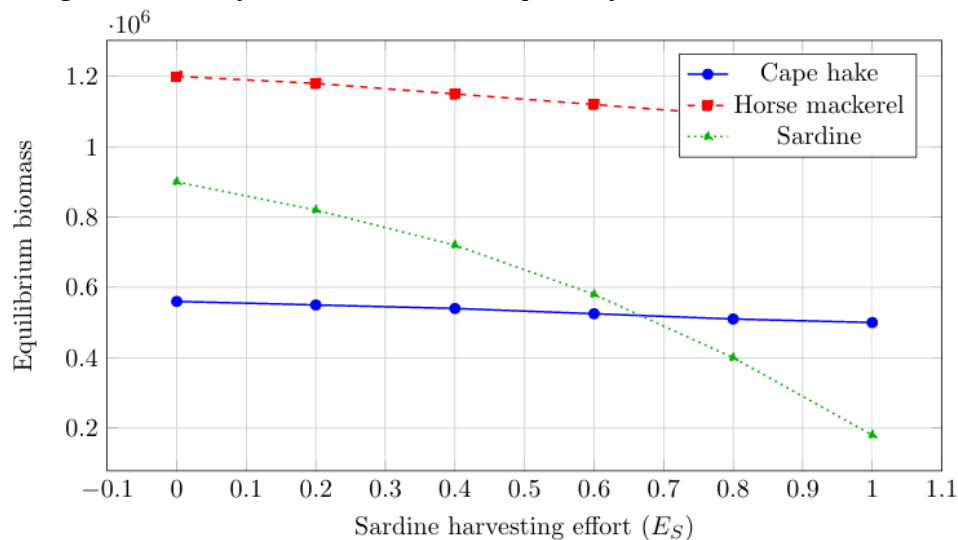


Figure 4. Equilibrium biomass response to increasing sardine harvesting effort.

5. Discussion of Numerical Results

The numerical simulations corroborate the analytical findings established in the previous discussions. In particular:

- All trajectories remain positive and bounded,
- The coexistence equilibrium acts as an attractor for biologically feasible initial conditions,
- Increasing effort in harvesting reduces equilibrium biomass,
- Excessive exploitation of sardine destabilizes ecosystem structure because of its role as a forage species,

- e. Sustainable fisheries management require balanced harvesting across interacting species.

Overall, the simulations support the theoretical results on positivity, boundedness, coexistence, and stability, while highlighting the ecological risks associated with excessive harvesting pressure.

Discussion and Policy Implications

The proposed nonlinear multispecies model extends the classical logistic and Schaefer fisheries models by integrating predator–prey interactions, interspecific competition, and species-specific harvesting within a unified nonlinear dynamical systems framework. The positivity, boundedness, and stability analyses establish the mathematical well-posedness of the model and guarantee biologically feasible solutions. These findings are consistent with recent multispecies fisheries studies but extend previous ecosystem simulation approaches by providing explicit analytical conditions for coexistence, persistence, and asymptotic stability ([Couve et al., 2024](#); [Howell et al., 2021](#); [Karp et al., 2023](#); [Xu et al., 2024](#)).

The coexistence equilibrium represents a stable ecological state in which Cape hake, horse mackerel, and sardine persist simultaneously under biologically realistic harvesting levels. This prediction agrees with empirical observations and ecosystem modelling studies in the Benguela Current Large Marine Ecosystem, which identify balanced trophic interactions and controlled exploitation as essential for long-term ecosystem stability ([Belhabib et al., 2015](#); [Heymans et al., 2009](#); [Roux et al., 2013](#); [Shannon et al., 2006](#)). In particular, the analytical and numerical results demonstrate that sardine, as the principal forage species, plays a critical role in maintaining trophic connectivity. Excessive harvesting of sardine reduces prey availability for higher predators such as Cape hake, thereby weakening ecosystem resilience and increasing the risk of trophic instability. Similar ecological responses have been reported in previous studies of the Benguela ecosystem ([Howell et al., 2021](#); [Roux et al., 2013](#); [Xu et al., 2024](#)).

The numerical simulations further identify critical harvesting thresholds beyond which equilibrium biomass declines rapidly, and the coexistence equilibrium loses stability. These thresholds were identified by progressively increasing harvesting mortality and monitoring changes in equilibrium biomass and long-term population trajectories. The results demonstrate that relatively small increases in harvesting effort beyond sustainable levels may trigger substantial biomass declines and increase the likelihood of stock collapse. This finding reinforces the need for ecosystem-based harvesting strategies that explicitly account for multispecies interactions rather than relying solely on independent single-species assessments.

From a management perspective, the proposed model provides a quantitative decision-support framework for determining sustainable harvesting policies, precautionary effort limits, and ecosystem-based catch quotas. By identifying harvesting levels that maintain long-term species coexistence and ecosystem stability, the model can help sustain fish biomass and reduce the risk of stock depletion. This has important implications for food security, as stable fish populations contribute to a reliable supply of marine protein and support the livelihoods of fishing communities. Consequently, the model contributes to fisheries governance by promoting ecosystem resilience, sustainable resource utilization, and evidence-based maritime management. In regions where marine fisheries constitute a major source of dietary protein, maintaining ecological stability through sustainable harvesting is closely linked to long-term food security and resilience against fluctuations in fish availability ([Eyo et al., 2026](#); [Fu et al., 2022](#); [Saba et al., 2024](#); [Wang et al., 2025](#)). However, the present formulation assumes constant environmental conditions and does not explicitly incorporate climate variability, stochasticity, spatial structure, migration, age classes, or seasonal recruitment. Future work should therefore extend the model to include stochastic environmental forcing, reaction–diffusion processes, age-structured dynamics, and optimal harvesting control to improve predictive capability under changing environmental conditions. Overall, the proposed framework strengthens the mathematical basis of ecosystem-based fisheries management while providing practical guidance for the sustainable utilisation of Namibia’s marine fishery resources.

CONCLUSION

A nonlinear multispecies dynamical model describing the interactions among Cape hake, horse mackerel, and sardine populations was developed and analyzed. The model incorporates logistic population growth, ecological interactions, and species-specific harvesting mortality within a unified mathematical framework. Theoretical analysis established the existence and uniqueness of solutions, positivity of trajectories, boundedness of populations, and the existence of a positively invariant region. Equilibrium analysis identified extinction, boundary, and coexistence equilibria, while local stability conditions were obtained using the Routh-Hurwitz criterion. A Lyapunov-based approach provided sufficient conditions for global asymptotic stability of the coexistence equilibrium. A harvesting-rate estimation framework was formulated to facilitate calibration of the model using fisheries data. Numerical simulations illustrated species coexistence, harvesting sensitivity, and ecosystem stability under varying exploitation levels. The analysis of analytical stability, supported by the numerical simulations, reveals that excessive harvesting of sardine stocks may adversely affect the persistence of Cape hake and horse mackerel through ecological feedback mechanisms by reducing prey availability and weakening trophic connectivity within the Benguela ecosystem.

The study demonstrates that sustainable management of Namibian fisheries requires recognition of ecological interdependence among species. Balanced harvesting strategies, adaptive management policies, and continuous biomass monitoring are therefore essential for maintaining the long-term productivity and resilience of the Benguela marine ecosystem. Future work may extend the model by incorporating environmental variability, climate-driven ecosystem changes, stochastic effects, spatial heterogeneity, age structure, and optimal control strategies. Such extensions would further strengthen the application of mathematical modelling to ecosystem-based fisheries management and marine conservation.

AUTHOR CONTRIBUTIONS

P.N.N.: Conceptualization, methodology, formal analysis, investigation, software, data curation, visualization, writing – original draft preparation, and numerical simulations. D.I.I.: Conceptualization, methodology, validation, formal analysis, supervision, writing – review and editing, and project administration. A.S.E.: Conceptualization, validation, supervision, writing – review and editing, and project administration.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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