Virtual Population Analysis of the critically endangered Scalloped Hammerhead (Sphyrna lewini) in the Eastern Tropical Pacific.

Running page head: Hammerhead Virtual Population Analysis

Miguel de Jesús Gómez García*[1], Alex Hearn[2,3], Mario Espinoza[2,4,5], Easton R. White[1]

[1] Department of Biological Sciences, University of New Hampshire, Durham, New Hampshire 03824, USA

[2] MigraMar, Bodega Bay, CA 94923, USA.

[3] Universidad San Francisco de Quito USFQ/Galápagos Science Center, Quito 170901, Ecuador

[4] Centro de Investigación en Ciencias del Mar y Limnología, Universidad de Costa Rica, San Pedro, San José 11501-2060, Costa Rica.

[5] Escuela de Biología, Universidad de Costa Rica, San Pedro, San José 11501-2060, Costa Rica.

*Correspondence author: mideigoga@gmail.com

ABSTRACT

The scalloped hammerhead (*Sphyrna lewini*) is one of the most critically endangered shark species in the Eastern Tropical Pacific (ETP). Despite its wide distribution and relatively high fecundity, overfishing and bycatch have led to sustained population declines across the region. We developed a spatially implicit, stage-structured, two-sex virtual population model for the ETP population of *S. lewini* using a Bayesian framework. Our model outputs were aligned with observed population trends using underwater visual census data collected at the Galápagos Archipelago, Ecuador, and Cocos Island, Costa Rica, from 1993 to 2024. Missing life-history parameters for the scalloped hammerheads population were estimated using model outputs. We conducted elasticity analyses to identify key life stages driving population growth and evaluated ten management scenarios aimed at species recovery. Our results provide the first stage-specific estimates of demographic parameters for both sexes in the ETP, including natural and fishing mortality. Adult and sub-adult stages were the main contributors to variation in population growth for both sexes. Growth to reproductive stages and in-stage survival were the most critical life history parameters for females and males, respectively. Under current conditions, the probability of scalloped hammerhead population recovery is < 1%. Most scenarios allowing continued fishing yielded recovery probabilities below 50%. A 75% reduction in adult mortality produced the most favorable outcome, with a 63% probability of positive population growth. Our results provide researchers and decision makers with a baseline for increasing the accuracy of demographic studies and improving management of scalloped hammerhead populations across the ETP.

Key words. VPM. Scalloped Hammerhead. Eastern Tropical Pacific. Lefkovitch matrix. Matrix Model. Fisheries Management.

INTRODUCTION

Sharks play a vital role in marine ecosystems, contributing both to energy transfer and the resilience of ecosystems to disturbances (Carrier et al., 2012; Shipley et al., 2023). Yet, over a third of shark populations are in threatened with extinction (Dulvy et al., 2021), with perhaps an even larger number facing declines due to fishing-related mortality(Carr et al., 2013; Davis & Harasti, 2020; González-Andrés et al., 2020). Sharks experience such high fishing pressure due to commercial demand for their fins and meat (Ferretti et al., 2020), susceptibility to local and international fisheries during seasonal migrations (Coiraton et al., 2020; Grant et al., 2020), and as bycatch of other commercially important fisheries (Oliver et al., 2015). Additionally, factors such as global warming, (Cerutti-Pereyra et al., 2024) habitat loss (Braun et al., 2023; Kanno et al., 2023), and competitive exclusion (Condamine et al., 2019; Dhellemmes et al., 2021; Espinoza et al., 2024) can accelerate population declines. Further, sharks present unique challenges for sustainable management and conservation due to their slow growth, late maturation, and low fecundity (Bonanomi et al., 2017).

Virtual population models (VPMs) are valuable tools for analyzing population dynamics, and incorporating life history parameters, such as growth rate, age at maturity, fecundity, and natural mortality, to project future population dynamics (Quinn, 2003). Although population matrix analyses and demographic models have traditionally been used for studying shark species (Simpfendorfer, 2005), recent advances like Bayesian estimators in VPMs enable researchers to parameterize populations with varying levels of data availability and uncertainty (Pons et al., 2020; Tsai et al., 2019). For instance, VPMs have proven effective in parameterizing highly exploited, data-limited shark populations in the West Atlantic Ocean (Tsai et al., 2019) and improving our understanding of shark demographic processes through incorporating uncertainties in model parametrization (Cortés, 2002; Liu, Huang, et al., 2021).

The data used for parametrizing elasmobranch population models is often limited and fisheries-dependent, forcing researchers to work around uncertainty and model assumptions (Mejía-Falla et al., 2019). For example, Heupel and Simpfendorfer (2002) attempted to parametrize juvenile survival and fishing mortality in blacktip sharks using indirect methods and acoustic telemetry. They found the highest estimated mortality occurred during the first weeks after leaving nursery grounds but noted that their methods were only applicable to small sample sizes and restricted distribution areas. Another example of the importance and challenges of parametrization in shark populations is the work of Liu et al., (2021), who assessed modeling methods based on several life history traits. They found model effectiveness varies with species longevity, maturity, and preferred habitat, and noted that variation in life history traits across weight classes leads to biased model outputs if not considered. Furthermore, Huynh et al., (2023) found distinct levels of vulnerability in hammerhead sharks (*Sphyrna spp.*) according to sex and age class, along with a disproportionate impact of fishing activities on male hammerheads. The authors argue that although sexual dimorphism is a widely acknowledged phenomenon in marine species, few studies consider sexual differences in life history traits. Demographic models that incorporate uncertainty across age classes can provide insights into species vulnerabilities throughout development and fill knowledge gaps for managing vulnerable elasmobranch species (Huynh & Tsai, 2023; Simpfendorfer, 2005).

The scalloped hammerhead shark (*Sphyrna lewini*) is widely distributed across ocean basins, particularly in tropical waters (Elizondo-Sancho et al., 2022; Rigby et al., 2019). Despite their relatively high fecundity, heavy fishing and bycatch have caused severe population declines, driving the species to be listed as Critically Endangered according to the IUCN Red List (Rigby et al., 2019). In the Eastern Tropical Pacific (ETP), scalloped hammerheads are faced with constant fishing pressure through bycatch and targeted fisheries in both coastal and pelagic waters (Elizondo-Sancho et al., 2022; Harned et al., 2022). Regional scalloped hammerhead population assessments have independently reported noticeable declines and high juvenile mortality in areas like Mexico (Rodriguez-Arana et al., 2022), Colombia (Bessudo et al., 2011), and Ecuador (White et al., 2026), with at least one historically abundant sub-population being depleted by overfishing in the Gulf of California (Pérez-Jiménez, 2014). Genetic studies aimed at understanding the complex population dynamics of scalloped hammerheads in the ETP have revealed evidence of philopatry (Elizondo-Sancho et al., 2022; Harned et al., 2022), closed populations (Alfonso-González et al., 2025), and population resilience even after local extirpation events (Nance et al., 2011; Pérez-Jiménez, 2014). Other research efforts on scalloped hammerheads have focused on understanding their movements through remote sensing (Corgos & Rosende-Pereiro, 2022; Ketchum et al., 2014) and environmental preferences (Rodriguez-Burgos et al., 2022). Despite the growing interest in evaluating hammerhead populations in the ETP, only two studies have determined life history parameters for the species, using fisheries-dependent data constrained to small spatial scales (Anislado-Tolentino et al., 2008; Estupiñán-Montaño, Carrera-Fernández, et al., 2021). The limited amount of baseline information about landings, capture size, and age distribution restricts the scope of population modeling and management for scalloped hammerheads in the ETP.

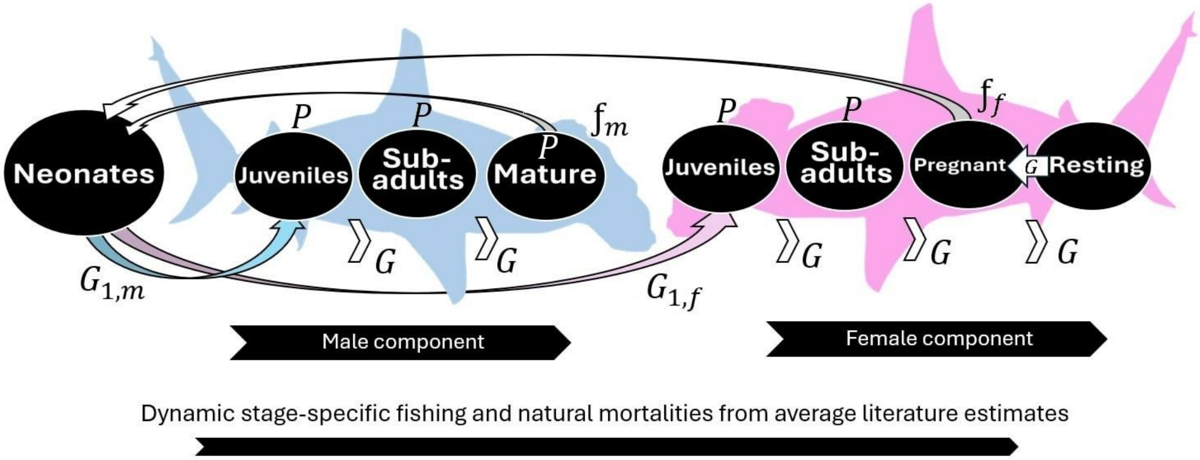
In this study, we developed a virtual population model incorporating Bayesian priors to improve our understanding of the scalloped hammerhead shark populations across the ETP. Our goal was to create a relatively simple, spatially implicit VPM that accounts for uncertainty in life history parameters. Our specific objectives were to: (1) construct and parametrize a VPM for scalloped hammerheads in the ETP; (2) determine the effects of each life stage and sex on population growth; and (3) evaluate management scenarios that could lead to population recovery in the ETP. Given the connectivity, philopatric and demographic processes, and the relatively low genetic diversity within scalloped hammerhead subpopulations in the ETP (Elizondo-Sancho et al., 2022), we believe that a spatially implicit virtual population model is an important first step. It will help develop better conservation and management measures for this critically endangered species.

MATERIALS AND METHODS

For our first objective, we developed a flexible, Leslie matrix model following the stage-based approach first proposed by Caswell (1989) and adapted for long-living shark species by Brewster-Geisz and Miller (2000). We incorporated the life-history formulations and sex-based methodologies suggested by Huyn and Tsai (2023). We represented our virtual shark population dynamics mathematically with an 8 x 8 transition matrix A, expressing changes in our virtual population with the equation:

$$\vec{N}_{t+1} = \mathrm{A} * \vec{N}_t \qquad (1)$$

Where $\vec{N}$ is a vector of individuals in each life stage at time step t, and A is the two-sex, stage-based matrix for scalloped hammerheads (Fig. 1). We classified both male and female neonates as N_0. We divided males into three stages: N_1 (juveniles), N_2 (subadults), and N_3 (adults), and females into four stages: N_4 (juveniles), N_5 (subadults), N_6 (pregnant females), and N_7 (resting females). Our model includes a "resting" stage for females to reflect the biannual reproductive cycle of the species, where only pregnant females contribute new neonates, and then enter the resting phase for a year. The resulting life-history projection matrix A_t captures stage transitions and reproductive contributions across the life cycle, parameterized according to stage-specific demographic traits (Fig. 1).



$$\begin{bmatrix} N0_{t+1} \\ N1_{t+1} \\ N2_{t+1} \\ N3_{t+1} \\ N4_{t+1} \\ N5_{t+1} \\ N6_{t+1} \\ N7_{t+1} \end{bmatrix} = \left[\begin{array}{cccc|cccc} 0 & 0 & 0 & f_m & 0 & 0 & 0 & G_{8,f} * f_f \\ G_{1,m} & P_{2,m} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & G_{2,m} & P_{3,m} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & G_{3,m} & P_{4,m} & 0 & 0 & 0 & 0 \\ G_{1,f} & 0 & 0 & 0 & P_{5,f} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & G_{5,f} & P_{6,f} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & G_{6,f} & 0 & G_{8,f} \\ 0 & 0 & 0 & 0 & 0 & 0 & G_{7,f} & 0 \end{array}\right] * \begin{bmatrix} N0_t \\ N1_t \\ N2_t \\ N3_t \\ N4_t \\ N5_t \\ N6_t \\ N7_t \end{bmatrix}$$

Figure 1. Life history matrix model conceptualization. The top panel shows a diagram of scalloped hammerhead life history incorporating a male (left, blue) and female (right, pink) component. Each stage is represented by a circle, with arrows signaling transitions and contributions from stage to stage. The bottom panel shows the matrix design of the population model. Stage-structured population for subsequent years is calculated by multiplying the current population (Nt) by the population matrix. Matrix columns show the transitions of individuals from one stage to the next, and matrix rows represent the origin of individuals at each stage. Survival is represented by P, growth by G, and fecundity by f. Subindices f and m show the male and female components.

Transition probabilities are represented as *Pi*, the probability of surviving but not growing into the next stage (same stage transition), and *Gi*, the probability of surviving and growing to the next stage, according to the equations:

$$\begin{aligned} P_i &= \sigma_i(1-\gamma_i) \\ G_i &= \sigma_i\gamma_i \end{aligned} \tag{2}$$

Where *σi* and *γi* are the probabilities of surviving at stage *i* and growing to the next stage *i*, respectively. These parameters were calculated for each sex *s* as:

$$\begin{cases} \sigma_{i,s} = e^{-(M_{i,s}+F_{i,s})} \\ \gamma_{i,s} = \dfrac{(\sigma_{i,s})^{T_{i,s}} - (\sigma_{i,s})^{T_{i,s}-1}}{(\sigma_{i,s})^{T_{i,s}} - 1} \end{cases} \tag{3}$$

Where the components of *σ* correspond to total mortality *Z*, the sum of natural mortality *M,* and fishing mortality *F*, following standard practices in shark fisheries modeling (Simpfendorfer et al., 2005). *T* represents the in-stage durations for each stage *i*, estimated as the number of years scalloped hammerheads spend at each life stage according to the literature (Supplementary Table 1).

We incorporated the effect of each sex through a fertility coefficient (f_i, shown in Figure 2), defined as the product of stage-specific fecundity and the corresponding survival rate (σ_i). We applied the modified harmonic mean birth function developed for scalloped hammerhead sharks by Huyn and Tsai (2023):

$$f_{i,s}(n) = \begin{cases} \dfrac{kn_s}{n_f+n_m} = s = (m), \\ \dfrac{kn_s}{n_f+n_m} = s = (f) \end{cases} \tag{4}$$

Where *k* denotes litter size for *i* life stages and *s* sexes, and n_m and n_f are the relative densities of male and female sharks capable of reproducing, respectively. The birth sex ratio was set as 0.5.

We incorporated uncertainty into our model outputs through Markov Chain Montecarlo Simulations (MCMC). We allowed unknown parameter priors (θ) to vary stochastically with informed distributions based on the literature as:

$$\theta \sim N(\mu, \sigma^2) \tag{5}$$

We calculated the finite population growth rate λ by solving the equation $|A - \lambda I| = 0$, where A is the life-history matrix, and I is the identity matrix. The intrinsic rate of population increase "*r*" can be derived from λ $r = ln(\lambda)$. In simple terms, λ reflects the combined effect of transition and survival probabilities across all life stages. When λ is close to 1, the population is stable, with values below 1 indicating decline, and values above 1 suggesting growth. By iteratively multiplying an output matrix A by N_{it} as in equation 4, we can explore how the stochastic variation of life history parameters affects λ and r.

We obtained the general population and biological data for scalloped hammerheads from the literature (Supplementary Table 1). We estimated natural mortality using multiple equations, including the von Bertalanffy growth model and previously applied formulas for scalloped hammerheads (Huynh & Tsai, 2023). We used the mean natural mortality from all the different estimates in simulations and further analysis. For parameters with multiple reported values (age at maturity, growth rate, litter size, L infinity, L zero, and maximum age), we used the average of all reported values as their estimated value. We used expert knowledge, when possible, to assign prior parameters for mortality. When no information was available, we used a biologically meaningful diffuse prior (Table 1).

We compared our model output with population trends observed in scalloped hammerhead populations in the ETP. We used data from underwater visual censuses collected at the Galapagos Archipelago, Ecuador, and Cocos Island, Costa Rica from 1993 to 2024 (refer to Bravo-Ormaza et al. (2023) and Gomez-Garcia et al (2025) for details about data collection). We averaged the yearly relative shark abundance between both sites to estimate the species' population trends in the ETP. Throughout the study period, we then calculated the percentage population change of each year from the initial population by:

$$\Delta\chi_t = \frac{\chi_t - \bar{\chi}}{\bar{\chi}} \tag{6}$$

Where $\bar{\chi}$ represents the initial population size. We used the yearly population change values to build a simple linear model ($\Delta\chi_t$~ year) of relative abundance, extracting the slope of population change for scalloped hammerheads in the ETP. Finally, we calculated the slope of population change from each iteration of our virtual population model and kept only those that were not statistically different from the actual calculated population trend ($\alpha=0.05$) for posterior analysis. We then parametrized the scalloped hammerhead population by extracting the mean value of each life history parameter from the VPMs that agreed with observed population trends.

Table 1. Prior values used for the VPM of scalloped hammerheads in the ETP. Adult natural mortality was calculated and averaged from several formulas incorporating values from literature sources, as shown in Supplementary Table 1. Notations Fn and Mn are the components of survival (σ) in equation 3.

Parameter	Stage	Notation	Sex	Prior	Source	Note
Fishing Mortality (P-Fi)	Neonates	F1	Combined	Uniform. 0.1 - 0.15	NA	Fishing mortality of neonates is expected to be low in relation to natural mortality.
	Juveniles	F5	Females	Uniform. 0.1 - 0.4	NA	Diffuse prior for fishing mortality
		F2	Males	Uniform. 0.1 - 0.4	NA	Diffuse prior for fishing mortality
	Subadults	F6	Females	Uniform. 0.1 - 0.4	NA	Diffuse prior for fishing mortality
		F3	Males	Uniform. 0.1 - 0.4	NA	Diffuse prior for fishing mortality
	Adults	F7	Females	Uniform. 0.1 - 0.4	NA	Diffuse prior for fishing mortality
		F4	Males	Uniform. 0.1 - 0.4	NA	Diffuse prior for fishing mortality
	Resting	F8	Females	Uniform. 0.1 - 0.4	NA	Diffuse prior for fishing mortality
Natural Mortality (P-Mi)	Neonates	M1	Combined	Uniform. 0.4 - 0.8	NA	Neonate total mortality estimates range from 50-90%. Prior between 40-80% allows total mortality to be influenced by fishing

	Juveniles	M5	Females	2*Normal (0.19 + 0.05)	Literature	Calculated as twice the adult natural mortality
		M2	Males	2*Normal (0.19 + 0.05)	Literature	Calculated as twice the adult natural mortality
	Subadults	M6	Females	Normal (0.19 + 0.05)	Literature	Same as adult natural mortality
		M3	Males	Normal (0.19 + 0.05)	Literature	Same as adult natural mortality
	Adults	M7	Females	Normal (0.19 + 0.05)	Literature	Calculated from literature
		M4	Males	Normal (0.19 + 0.05)	Literature	Calculated from literature
	Resting	M8	Females	Normal (0.19 + 0.05)	Literature	Calculated from literature
Fecundity (f)	Adults	f	Combined	Uniform. 16 - 41	Literature	Sample from the entire possible range of litter sizes

For our second objective, we used the virtual population outputs closely resembling population trends in the ETP to evaluate life-stage elasticities. Additionally, by extracting the eigenvectors from our resulting matrix, we can evaluate matrix “elasticities”, a ratio of the relationship between individual matrix entries a_{ij} and population growth parameters. Elasticities were calculated as:

$$e_{ij} = \frac{a_{ij}}{\lambda}\frac{\partial\lambda}{\partial a_{ij}} \tag{7}$$

We then determined the contribution of each life stage per sex to population growth by summing the corresponding matrix values. In particular, we determined the importance of life-history parameters to population growth by summing the elasticity values of entries related to growth, reproduction, and survival. We built density plots to visually evaluate the contribution of each stage and matrix entry to elasticity.

For our third objective, we repeated our analysis under different fisheries management and mortality scenarios to evaluate the contribution of different life stages to population growth. Since juvenile and neonate mortality due to small scale fisheries has been reported as a cause for concern in the ETP, we also included scenarios with increased juvenile and neonate mortality. Scenarios are as follows: doubling and tripling our calculated neonate and juvenile fishing mortalities, 90% reduction in neonate fishing mortality, 75% reduction in neonate and juvenile fishing, 25% reduction in fishing across all stages, 50% reduction in fishing across all stages, 75% reduction in adult fishing mortality, 75% reduction in adult fishing mortality along tripling increase in fishing mortality (extreme elasticity scenario) and an idealistic scenario with no fishing mortality. We compared the posterior population growth of each scenario with the conditions currently observed in the ETP.

We performed sensitivity analysis by building matrix models using fixed mean values of natural mortality and fecundity from literature (Supplementary Table 1) and setting separate fixed values for fishing mortality under 6 scenarios: no fishing mortality, low (15%), medium (25%) and high (40%) fishing mortality, juveniles protected, and adults protected.

We built our matrix models using custom functions in R programming (R Core Team, 2016). We conducted MCMC simulations using the r2jags package (Su & Yajima, 2015) and performed sensitivity analyses using the popbio package (Stubben & Milligan, 2007). Annotated code can be reviewed and branched from our GitHub repository at https://github.com/Miguelbirostris/S.lewini_ETP_VPM.

RESULTS

Posterior growth rates of our virtual populations ranged from 0.70 to 1.15 (mean ± SD = 0.90 ± 0.06), with only 6% having increasing population trends (lambda >1). The population trend of scalloped hammerhead sharks based on field observations showed a decreasing slope of relative yearly abundance of -0.13. For our stochastically generated virtual populations, 10% (n= 1651) showed a lambda value within the 5% percentile of lambda 1 (lambda critical). In addition, 36% of our simulations had the same slope of yearly population change with each other, but only 4% (n= 783) followed a similar population trend to what has been observed in the past 30 years (Figure 2). Lambda values of ETP virtual populations with the same population growth slope as data from field observations ranged from 0.703 to 0.99 (mean ± SD = 0.853 ± 0.058). Table 2 shows our estimated parameters for the ETP scalloped hammerhead virtual population.

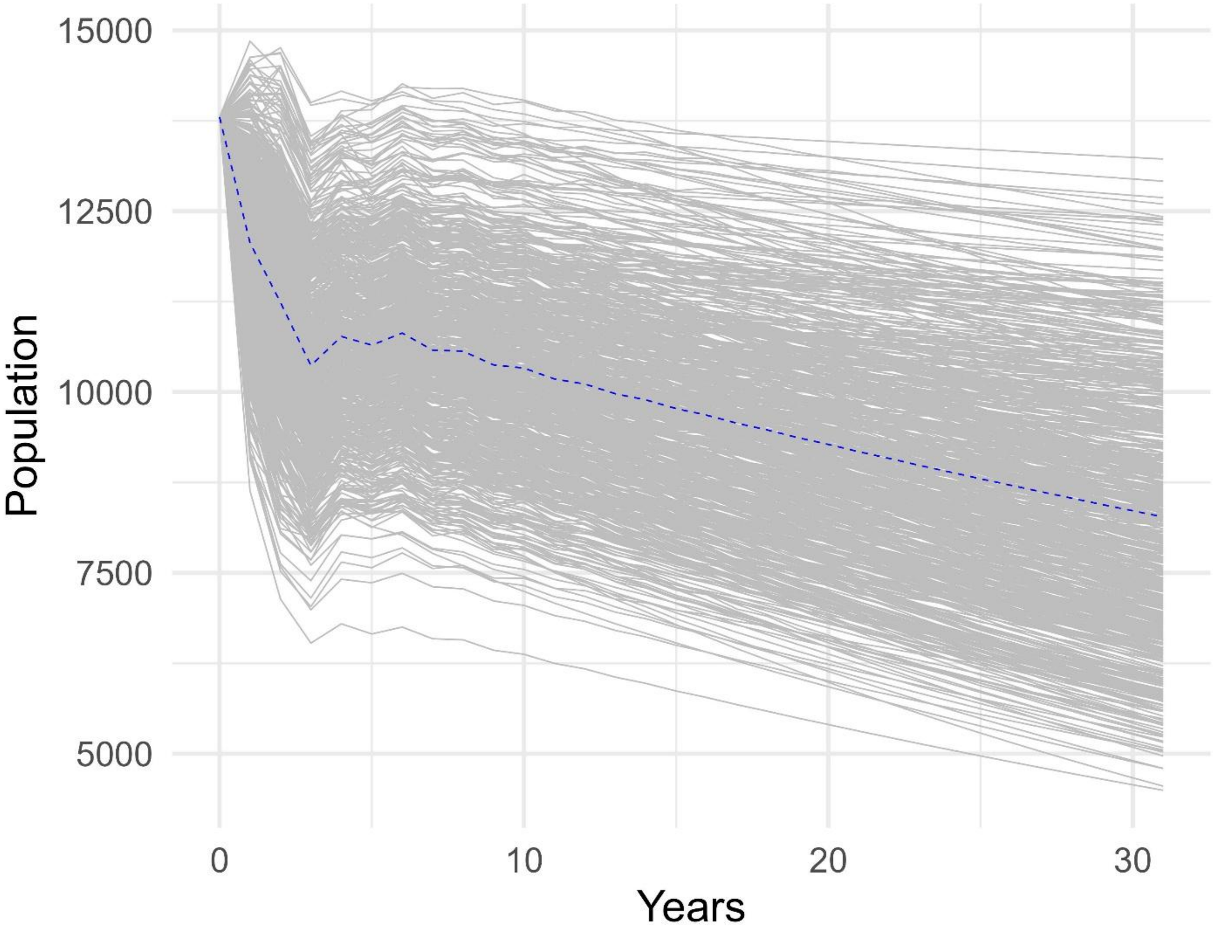


Figure 2. Scalloped hammerhead virtual populations that follow population changes observed in the ETP for the past 30 years. We only show virtual populations with a similar trend to the ETP, and which were not driven to extinction in 30 years.

Table 2. Estimated population parameters for scalloped hammerheads in the ETP derived from our VPMs.

Parameter	Stage	Sex	Mean	SD	Minimum	Maximum

Fishing Mortality	Neonates	Combined	0.126	0.014	0.100	0.150
	Juveniles	Females	0.258	0.087	0.100	0.400
		Males	0.257	0.086	0.100	0.400
	Subadults	Females	0.267	0.084	0.100	0.400
		Males	0.269	0.084	0.100	0.400
	Adults	Females	0.259	0.086	0.100	0.400
		Males	0.265	0.084	0.100	0.400
	Resting	Females	0.257	0.086	0.100	0.400
Natural Mortality	Neonates	Combined	0.674	0.100	0.400	0.800
	Juveniles	Females	0.379	0.035	0.253	0.508
		Males	0.378	0.035	0.268	0.525
	Subadults	Females	0.194	0.051	0.005	0.366
		Males	0.195	0.050	0.029	0.380
	Adults	Females	0.193	0.050	0.019	0.409
		Males	0.194	0.049	0.027	0.396
	Resting	Females	0.191	0.050	0.015	0.367
Total Mortality	Neonates	Combined	0.800	0.101	0.505	0.948
	Juveniles	Females	0.637	0.094	0.408	0.899
		Males	0.636	0.093	0.380	0.885
	Subadults	Females	0.461	0.096	0.143	0.734
		Males	0.464	0.097	0.173	0.737
	Adults	Females	0.453	0.100	0.170	0.803
		Males	0.459	0.096	0.152	0.792
	Resting	Females	0.447	0.099	0.146	0.724
Fecundity	Adults	Combined	26.284	7.008	16.002	40.993
Lambda	Population	Combined	0.853	0.058	0.703	1.000

Our elasticity analysis showed that under current fishing conditions, subadults and adults are the highest contributors to scalloped hammerhead population growth rates (Figure 3a). Females displayed higher elasticities in general, but stage-elasticity proportions were similar for both sexes (Figure 3b). Regarding elasticities by life-history parameter, survival and growth showed higher elasticities than reproductive output (Figure 4a). Growth to a different stage showed higher elasticities for females, while survival in the current stage was higher for males (Figure 4b).

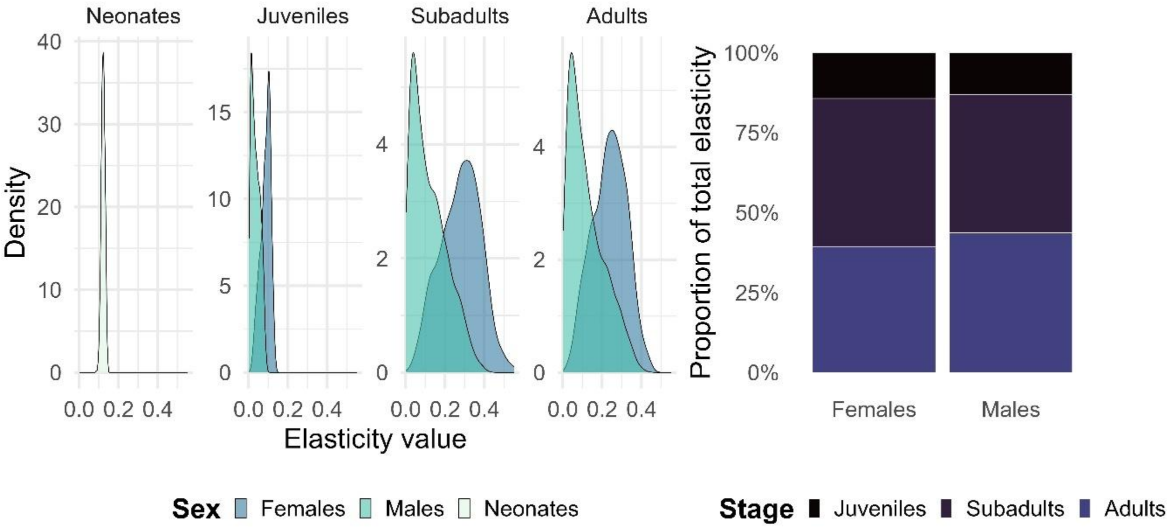


Figure 3. Elasticity analysis per stage estimated for the ETP scalloped hammerhead virtual population. Densities of estimated elasticities per life stage are shown in the left panel (a). Proportional elasticity by stage for each sex is shown in the right panel (b).

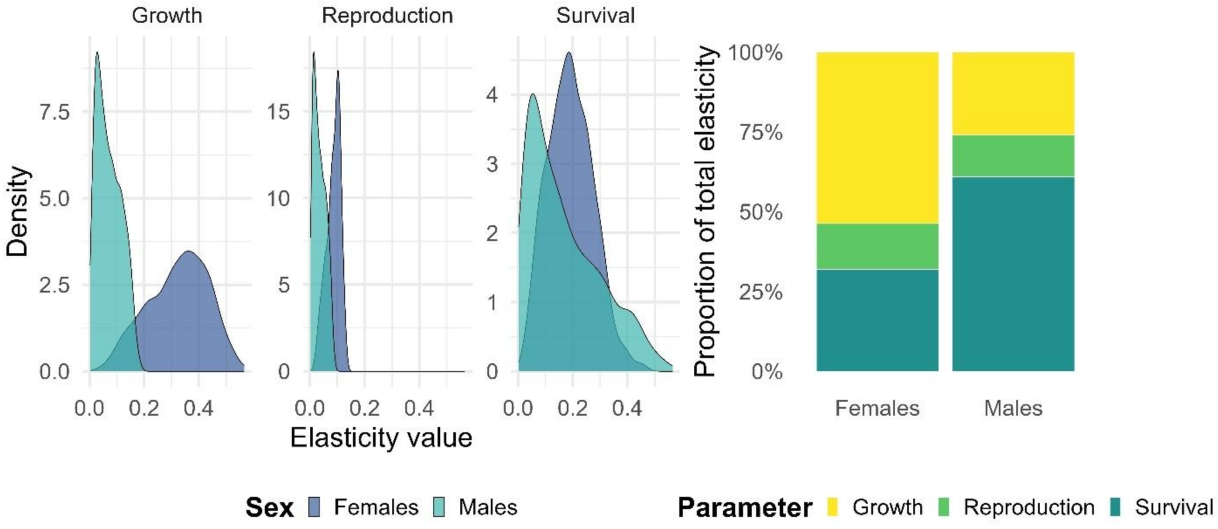


Figure 4. Elasticity analysis per life history parameter estimated for the ETP scalloped hammerhead virtual population. Densities of estimated elasticities are shown in the left panel (a). Proportional elasticity by life history parameter for each sex is shown in the right panel (b).

Our estimates of the ETP's population growth rate under different management scenarios showed that, under current conditions, the probability of population recovery was less than 1% (Figure 5). Most scenarios suggest the probability of increasing population growth rates is below 50%, even when protecting juveniles and neonates (Supplementary Table 2). Adult protection was the next best scenario, with a 63% probability of increasing the population growth rate (1.02 ± 0.05) followed by fishing mortality scenario with a 99% probability of increasing the population growth rate (1.16 ± 0.06). Simulations with fixed parameter values, which disregard observed trends in the ETP, showed that population recovery occurs only under a complete reduction of fishing mortality, yielding a population growth rate of λ = 1.07. The next best scenarios still projected population decline, with λ = 0.95 under adult protection and λ = 0.93 under juvenile protection (Supplementary Figure 1).

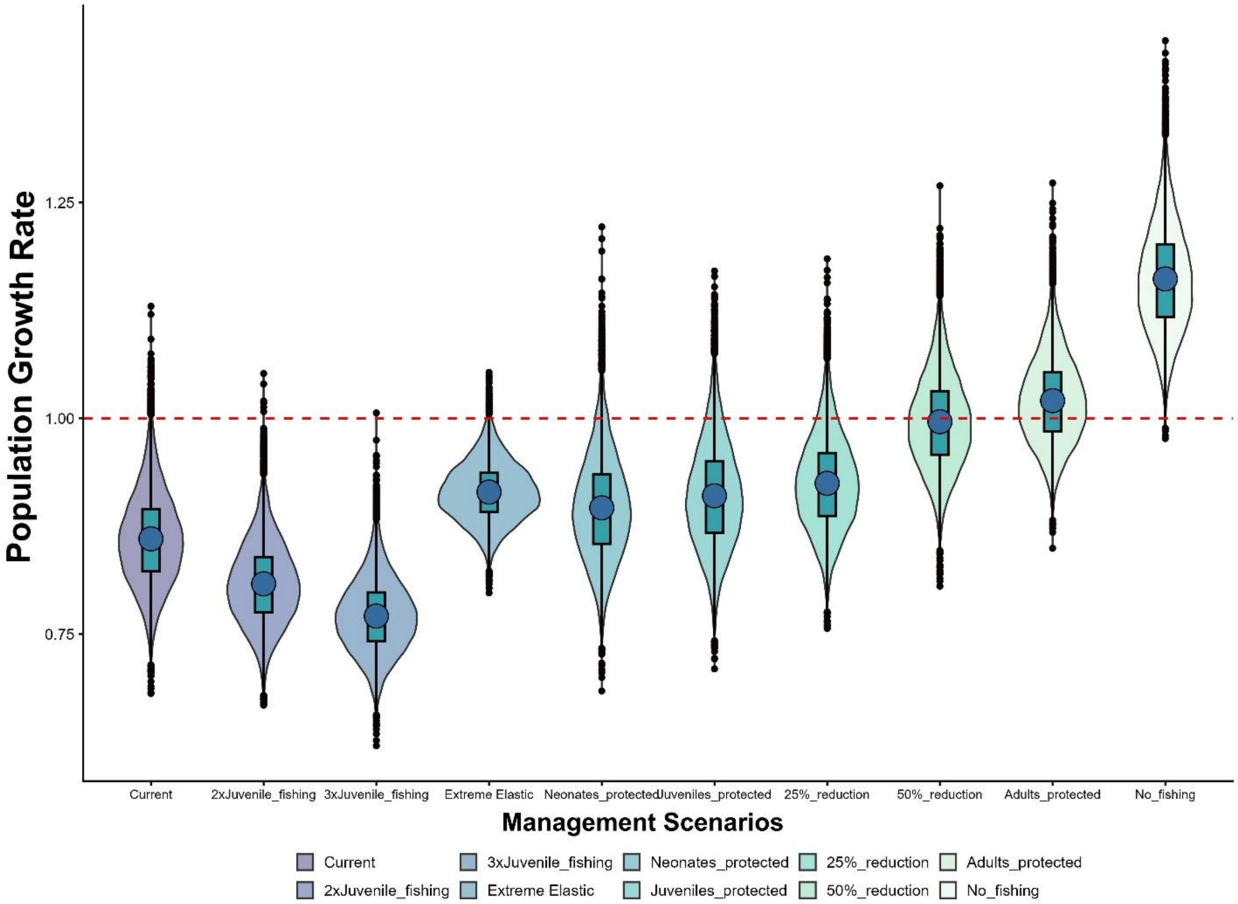


Figure 5. Population growth rate distribution under different management scenarios. Y axis shows the population growth rate; x axis shows the different management scenarios. All scenarios use the life history parameters estimated for the ETP scalloped hammerhead population as a baseline ("Current" Model).

DISCUSSION

Population trend

Unregulated fishing pressure remains a major factor affecting shark populations in the ETP (Barreto et al., 2016; Jorgensen et al., 2022). Only 6% of our simulations under current fishing conditions showed a chance of population recovery for scalloped hammerheads and 36% showed a slow decline, with the remaining 58% showing faster declines than current estimations for the species. Recent studies (Vaudo et al., 2026; White et al., 2026) suggest that reducing fishing mortality is a more effective conservation measure than increasing the size of MPAs for larger and more migratory species, which often move beyond protected areas and between jurisdictions. Effective management becomes even more challenging in the ETP due to additional confounding factors such as habitat degradation due to climate change (Cerutti-Pereyra et al., 2024), and the impact of unregulated small scale and artisanal fisheries over neonate and juvenile populations. For the ETP, where spatial protection alone may not be enough to recover populations, management plans that directly limit fishing mortality may be a better alternative for sustainable management. For example, Ecuador protected all hammerheads in its EEZ in 2020, bycatch from both industrial and artisanal fleets continues, with many longline vessels operating around the Galápagos Marine Reserve flagged as local vessels (White et al., 2026). The challenges in managing multi-jurisdictional elasmobranch fisheries in the ETP is exacerbated by the nature of Latin American fisheries, where bycatch of non-target species is widespread and difficult to regulate (López-Angarita et al., 2021; Oliver et al., 2015).

Advances in population projection techniques have improved our ability to incorporate unknowns and knowledge gaps when analyzing poorly understood marine populations (Cortés, 2002; Geng et al., 2021; Tsai et al., 2019). Simulation-based quantitative stock evaluations remain among the most reliable approaches for assessing overfished populations, particularly when fishery-independent data are scarce or unreliable (Hilborn, 2012). The population growth rate ($\lambda = 0.85$) we calculated from matching field observations of scalloped hammerheads in the ETP with our VPM was lower than both our estimates using only literature estimates of unknown parameters ($\lambda = 0.9$) and the Atlantic population estimate ($\lambda = 1.18$) reported by Huynh and Tsai (2023) 0.98 in this study. Similarly, population parameters such as age of maturity and longevity appear to be lower in the ETP (Table S1). According to a review of demographic studies on sharks, population growth rate is negatively correlated with warmer temperatures (Mejía et al., 2025). This may be due to decades of unregulated fishing, which may have pushed the species toward earlier maturity and faster growth rates. Consequently, overfished tropical populations have a harder time reaching maturity due to both physiological and anthropogenic factors, which may contribute to the differences we observe between the ETP and the Atlantic population growth rates.

Our results suggest that neonate and juvenile survival contribute less to population growth than adult survival regardless of litter size variation. Neonate and juvenile protection did increase the probability of population growth, but to a much lesser degree than reductions in adult fishing or fishing mortality across all stages. Recent evidence that pupping may occur around protected oceanic islands (Chiriboga-Paredes et al., 2022) further suggests that early-life mortality could be lower than previously assumed, at least for oceanic breeding grounds. Nonetheless, the impact of fishing mortality on nursery grounds along the coast may have a bigger impact on population dynamics since juveniles constitute a higher proportion of local fishery catches (Corgos & Rosende-Pereiro, 2022; Nance et al., 2011). Estimates of juvenile survival are typically derived from fisheries-dependent data (Benson et al., 2018), are limited to narrow spatial and seasonal scales (Kanno et al., 2023), and may be biased toward certain size classes (Jensen et al., 2012). Despite the lower contribution of juveniles to population recovery when compared to mature life stages, our scenarios incorporating extreme increases in fishing mortality suggest they can undermine population recovery caused by adult protection. Therefore, current efforts to reduce neonate and juvenile mortality, such as seasonal fishing bans and regulation of fishing gear should continue, given the importance of juvenile recruitment to long-term population stability (Mollet & Cailliet, 2002).

Research on the subadult and adult life stages of scalloped hammerheads largely focus on population genetics (Elizondo-Sancho et al., 2022; Harned et al., 2022) and trophic ecology (Estupiñán-Montaño, Galván-Magaña, et al., 2021). However, our results suggest that adult survival to maturity and offspring production may be contributing more to scalloped hammerhead population growth in the ETP than juvenile survival. Unfortunately, adult scalloped hammerheads remain frequent targets of illegal fishing due to the high value of their fins in Asian markets (Dulvy et al., 2008, 2024), and large aggregations occur in areas with longline and purse-seine fisheries (Cambra et al., 2021). Despite widespread juvenile bycatch, the only documented regional collapse occurred in Mexican waters in the 1990s after a poorly managed increase of targeted adult fisheries (Pérez-Jiménez, 2014). Unfortunately, management efforts in the ETP are still hindered by a lack of enforcement in MPAs and varying degrees of legal and unregulated fishing (Rastoin-Laplane et al., 2023). Our findings suggest that management strategies protecting mature individuals and migratory corridors may aid in population recovery.

According to our elasticity analysis, females contributed more to overall population recovery than males, although both sexes life stages are similarly important for population growth when ignoring the other sex contributions. Differences in elasticity between sexes may reflect constant male reproductive output and physiological differences, including earlier maturity and faster growth in males, as well as sex-dependent variations in dispersal and ontogenetic movement (Alejo-Plata et al., 2007; Estupiñán-Montaño, Carrera-Fernández, et al., 2021). Previous studies show the importance of incorporating sexual dimorphism in population models, and how management plans that fail to address sex-specific dynamics may hinder stage-specific recovery (Gerber et al., 2025; Huynh & Tsai, 2023). For instance, in the ETP, female hammerheads show higher year-round residency around oceanic islands and migrate periodically to coastal pupping grounds in response to oceanographic cues, whereas males move more frequently between oceanic sites (Bessudo et al., 2011). Consequently, our results support the development of sex-specific management prioritizing the protection of females during pupping migrations and reducing male exposure during inter-island movements. Adaptive management and substantial reductions in adult fishing mortality may be more effective than a uniform reduction in fishing mortality across all stages, a challenging goal to evaluate and enforce.

Data caveats

The biggest caveat in our results is the limited amount of available test data for our models. Our estimated population parameters assume that our fisheries-independent scalloped hammerhead counts accurately represent population trends throughout the ETP. Recent genetic analyses revealed that scalloped hammerheads comprise six subpopulations across the ETP, with higher connectivity and diversity in central and southern regions driven by male-mediated dispersal and female philopatry (Elizondo-Sancho et al., 2022). If our data do represent the populations of the central-southern genetic subpopulation, then our estimates could be accurate for at least the subpopulation spanning from Costa Rica to Peru. Nevertheless, despite the overall high dispersal potential and genetic diversity of scalloped hammerheads, the northern ETP populations show persistent declines in genetic diversity. This matches the observed declines in populations and fishery landings, supporting our estimated population declines (Alfonso-González et al., 2025). Hence, while our results may be valid as a general baseline for the ETP, a natural next step is to delve into how population parameters vary within each known subpopulation. Incorporating variation across the ETP sub populations would require the continued development of more certain, region-specific estimations of stage-specific mortality and fecundity rates and the age at maturity. Having separate demographic models for each *S. lewini* subpopulation would enable a deeper understanding of the population dynamics of the species and potentially lead to a more spatially explicit macro-ecological model.

We provide the first stage-specific estimates of crucial life-history parameters for scalloped hammerheads in the ETP. No fisheries-independent estimates exist for the species in the ETP at the time of writing this paper, and large data gaps remain in crucial parameters such as longevity, site-specific growth rate, and fecundity. We accounted for these gaps when determining life-history parameters by producing several different outcomes incorporating priors in mortality and fecundity. Fecundity, for example, is a crucial parameter for population growth that varies due to stochastic processes year by year (Cortés, 2002). Years when fecundities are particularly high or low can substantially alter the population growth rate. Nevertheless, our approach considers these possible if unlikely events, since some of our virtual simulations projected both population growth and decline despite the variation in fecundity values (Supplementary Figure 2). Similarly, we tested uncertainty around fishing mortality, the most challenging parameter to accurately determine, and show results as the entire range of possible population growth estimations given the best knowledge available. Nevertheless, we recognize that a possible bias exists in our results from indirect formulaic estimates of parameters such as natural and fishing mortality. As such, even though our population parameter distributions may reflect potential population outcomes under different scenarios for the ETP, accurate experimental estimates for each of the uncertain parameters we show in Table 2 would lead to more confident results. Thus, we encourage continued research of baseline biological parameters for this species at local and regional scales.

We acknowledge we did not address the effect of density dependence on population growth. Smirkey and Musick (1995) suggested three mechanisms of compensation in sharks: decreases in natural mortality of younger sharks with the reduction of large predators; increases in fecundity when food is abundant; and an increase in growth and earlier maturity caused by the decrease in natural mortality. Density dependence is a poorly understood process in shark populations that can greatly impact population growth and resilience (Brewster-Geisz & Miller, 2000; Tsai et al., 2019). However, the role of density-dependence compensatory mechanisms in ETP scalloped hammerhead populations and how they interact with the ontogenetic migrations and different sources of mortality remain unknown. Additionally, recent studies suggest inter-specific interactions between scalloped hammerheads and potential competitors such as tiger sharks (*Galeocerdo cuvier*) may have an impact on population growth (Espinoza et al., 2024; Gómez-García et al., 2026). Additionally, climate change introduces a layer of complexity that is not addressed by our model thought potentially compressing the vertical and horizontal distribution of pelagic species in the ETP. Warming sea surface temperatures, declining dissolved oxygen, and shifts in the oxygen minimum zone may collectively restrict suitable habitat (Espinoza et al., 2024). This compression has two important implications: First, species abundance may be underestimated in conventional surveys around oceanic islands, particularly those relying on shallow methods such as diving or camera deployments. Second, reduced habitat volume may increase mortality risk by concentrating individuals into narrower depth ranges, potentially enhancing both natural and fishing mortality. Climate change, density dependence, and species-interactions are likely to play a role in population changes of scalloped hammerheads in the ETP, but these specific ecological drivers are out of the scope of our study. We hope our constrained estimations of uncertain life history parameters could at least pave the way forward for better population management that allows us to develop more ecologically focused models in the future.

Management recommendations and future work

Fish populations across the ETP are declining due to a combination of overfishing, limited enforcement within protected areas, and changing oceanographic conditions (McKinley et al., 2025). According to population models, fishing mortality frequently exceeds 10% across life stages, even under optimistic management scenarios for threatened species (Tsai et al., 2019), and collapses have occurred in comparatively well-managed fisheries with mortality targets near 20% (Hilborn, 2012). Our results serve as a starting point for developing hypotheses for the decline and potential recovery of scalloped hammerheads. However, the spatially implicit nature of our model limits our conclusions to broad, region-wide patterns in the ETP. Future work could prioritize the development of spatially explicit demographic models that incorporate genetic subpopulations and regional connectivity. Linking demographic processes to population structure across jurisdictions could enable case-specific regulations tailored to distinct management units within the ETP.

Our models cannot fully capture the mechanisms driving declines in scalloped hammerheads in the ETP, but our results suggest that current levels of fishing mortality are one of the potential causes for population decline. Previous population models for scalloped hammerheads suggest that reducing fishing mortality to near natural levels could allow populations to recover, whereas scenarios incorporating fishing consistently predict decline (Huynh & Tsai, 2023). Protection of single life stages, such as juveniles or adults, may have a beneficial effect on population recovery. However, developing fishing techniques or regulations that selectively avoid one life stage while effectively protecting others remains a major challenge (Brewster-Geisz & Miller, 2000). Our results suggest that protecting individual life stages or sexes is unlikely to ensure long-term recovery, and broader, multi-stage management strategies may be required to stop ongoing population declines.

CONCLUSION

Finally, it is worth noting that we were unable to find reliable estimates in the ETP of crucial baseline parameters like fishing mortality from either government or scientific sources. We need to continue evaluating gaps in basic population parameters such as fishing mortality in the region, especially for critically endangered species like scalloped hammerheads. The current lack of population assessments and fisheries evaluations not only hinders our scientific understanding of endangered population but also challenges the development of meaningful management plans. Importantly, scalloped hammerheads are not the only poorly evaluated, endangered shark species in the ETP. Climate change is another consideration that future adaptative management plans must take into consideration. Dynamic spatial and seasonal closures developed with the effects of temperature anomalies in mind would improve our chances of recovering populations of highly mobile species with narrow thermal limits (Cerutti-Pereyra et al., 2024). Comparative, multispecies approaches remain a necessity for designing management strategies given the importance of inter-specific processes in oceanic elasmobranch communities (Espinoza et al., 2024; Gómez-García et al., 2026). We need additional studies that address the impacts of different fishing techniques on a species-by-species basis, especially given the differences in post-release mortality and high levels of bycatch driven by multi-specific fisheries (Oliver et al., 2015). Finally, management plans and research strategies that balance ecological recovery with socio-economic realities, along with constantly improving monitoring and modeling programs may be a cost effective and ecologically meaningful solution for managing endangered elasmobranch communities in the ETP.

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