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Hidden demographic impacts of fishing and environmental drivers of fecundity in a sea turtle population

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Abstract

Fisheries bycatch is a critical threat to sea turtle populations worldwide, particularly because turtles are vulnerable to multiple gear types. The Canary Current is an intensely fished region, yet there has been no demographic assessment integrating bycatch and population management information of the globally significant Cabo Verde loggerhead turtle (*Caretta caretta*) population. Using Boa Vista island (Eastern Cabo Verde) subpopulation data from capture–recapture and nest monitoring (2013–2019), we evaluated population viability and estimated regional bycatch rates (2016–2020) in longline, trawl, purse-seine, and artisanal fisheries. We further evaluated current nesting trends in the context of bycatch estimates, existing hatchery conservation measures, and environmental (net primary productivity) variability in turtle foraging grounds. We projected that current bycatch mortality rates would lead to the near extinction of the Boa Vista subpopulation. Bycatch reduction in longline fisheries and all fisheries combined would increase finite population growth rate by 1.76% and 1.95%, respectively. Hatchery conservation increased hatchling production and reduced extinction risk, but alone it could not achieve population growth. Short-term increases in nest counts (2013–2021), putatively driven by temporary increases in net primary productivity, may be masking ongoing long-term population declines. When fecundity was linked to net primary productivity, our hindcast models simultaneously predicted these opposing long-term and short-term trends. Consequently, our results showed conservation management must diversify from land-based management. The masking effect we found has broad-reaching implications for monitoring sea turtle populations worldwide, demonstrating the importance of directly estimating adult survival and that nest counts might inadequately reflect underlying population trends.

KEYWORDS
artisanal fisheries, bycatch, Cabo Verde, Canary Current, industrial fisheries, longline, management, trawler

Impactos demográficos ocultos de la pesca y determinantes ambientales de la fecundidad en una población de tortugas marinas

Resumen: La captura accidental de las pesquerías es una amenaza importante para la población mundial de tortugas marinas pues estos reptiles son vulnerables a muchos tipos de artes de pesca. Aunque la Corriente de Canarias es una zona de pesca intensa, no se han realizado análisis demográficos que integren información de la captura accidental y

el manejo poblacional de la tortuga caguama de Cabo Verde (*Caretta caretta*), una población de importancia mundial. Usamos datos de captura-recaptura y monitoreo de nidos (2013-2019) de la subpoblación de la isla Boa Vista (Cabo Verde occidental) para evaluar la viabilidad poblacional y además estimamos el volumen de captura accidental a nivel regional (2016-2020) de las pesquerías de palangre, arrastre, red de cerco y artesanal. También analizamos las tendencias de la anidación en el contexto de las estimas actuales de captura accidental, del posible impacto del traslado de las puestas a viveros y de la variabilidad ambiental (productividad primaria neta) en la zona donde se alimentan las tortugas. Proyectamos que, de persistir, la tasa actual de mortalidad por captura accidental llevaría a la subpoblación de Boa Vista al borde de la extinción. La reducción de la captura accidental en la flota de palangre incrementaría la tasa finita de crecimiento poblacional en un 1.76% y la reducción en todas las flotas un 1.95%. El traslado de las puestas a viveros incrementó la producción de crías y redujo el riesgo de extinción, pero no logra el crecimiento poblacional por sí solo. Los incrementos a corto plazo en el conteo de nidos (2013-2021), causados posiblemente por los incrementos temporales en la productividad primaria neta, pueden estar ocultando un declive poblacional. Cuando relacionamos la fecundidad con la productividad primaria neta, nuestros modelos retrospectivos pronosticaron correctamente ambas tendencias, a corto y largo plazo. Como consecuencia, nuestros resultados mostraron que la gestión de la conservación debe diversificarse más allá de las medidas aplicadas durante la fase terrestre. Los efectos ocultos que descubrimos tienen implicaciones generales para el monitoreo de las poblaciones de tortugas marinas en otras partes del mundo, lo que demuestra la importancia de la estimación directa de la supervivencia de adultos y que el conteo de nidos podría no refleja correctamente las tendencias poblacionales subyacentes.

PALABRAS CLAVE
arrastre, Cabo Verde, captura accidental, Corriente de Canarias, gestión, palangre, pesquerías artesanales, pesquerías industriales

渔业对海龟的潜在种群影响及海龟种群繁殖力的环境驱动因素

【摘要】渔业兼捕是对全世界海龟种群面临的重要威胁，尤其是海龟容易受到多种渔具的影响。加那利洋流区是一个渔业密集的地区，但目前仍没有研究整合具有全球重要性的佛得角蠵龟 (*Caretta caretta*) 的种群管理信息与渔业兼捕信息，以对其进行种群参数估计。本研究利用佛得角东部Boa Vista岛蠵龟亚种群的标记重捕数据和巢穴监测数据 (2013-2019年)，估计了蠵龟的种群生存力及延绳钓、拖网、围网和手工渔业的区域兼捕率 (2016-2020年)。我们基于兼捕率估计值、现有孵化场保护措施和海龟觅食地的环境 (净初级生产力) 变化，进一步评估了当前的海龟筑巢趋势。我们预测，目前的兼捕死亡率将导致Boa Vista岛亚种群濒临灭绝。减少延绳钓兼捕与所有渔业兼捕将使有限种群增长率分别增加1.76%和1.95%。保护海龟孵化场可以增加幼体孵化数量并降低灭绝风险，但仅依赖这项措施并不能实现种群增长。可能由净初级生产力的短期增加所驱动的巢穴数量的短期增长 (2013-2021年) 或掩盖了正在发生的种群长期下降。当将繁殖力与净初级生产力挂钩时，我们的后报模型同时预测了这些相反的长期和短期趋势。因此，我们的结果表明，保护管理必须在土地管理的基础上多样化。我们发现的掩盖效应对监测全球海龟种群具有广泛的意义，强调了直接估计成体存活率的重要性，以及巢穴计数可能不足以反映潜在的种群趋势。【翻译:胡怡思;审校:聂永刚】

关键词: 手工渔业, 兼捕, 佛得角, 加那利洋流, 商业渔业, 延绳钓, 管理, 拖网渔船

INTRODUCTION

Bycatch, the incidental capture of nontarget species (Davies et al., 2009), is a global problem with consequences ranging from direct population declines to subsequent trophic downgrading and a reduction in marine ecosystem health and functionality (Britten et al., 2014; Casini et al., 2009; Lewison et al., 2014). Bycatch is expected to have a disproportionate impact on long-lived species with delayed sexual maturity, such as those composing the marine megafauna community (Žydelis et al., 2009). However, demonstrating the demographic impact of bycatch is often problematic because of the absence

of accurate estimates of total bycatch mortality and the difficulty parameterizing demographic models. Detecting bycatch impacts is further complicated when demographic parameters are strongly driven by temporal environmental variability (Neeman et al., 2015) or when adult population size is assessed from proxies such as nesting activity (Moore et al., 2013).

Among marine megafauna, sea turtle species are air breathers and good divers, which generates interactions and vulnerabilities with multiple fishing gear types—in addition to land-based mortality during reproductive phases. Their decades-long life spans and delayed sexual maturation (Dalleau et al., 2014; Mayne et al., 2020) are typical megafauna life-history traits that result in high demographic sensitivity to bycatch. Unusually among megafauna, sea turtles also have relatively high fecundity (albeit with low juvenile survival), which can increase the sensitivity and responsiveness of populations to environmental variation and perturbations (Smallegange et al., 2020). With these life-history traits, bycatch mortality may have high-impact demographic consequences that may be mitigated or exacerbated by environmental variation, and populations can exhibit variable responses to conservation measures.

The Canary Current Large Marine Ecosystem (CCLME) is a highly productive region that supports a high diversity of marine megafauna (McIvor et al., 2022) due to the nutrient-rich upwelling along the coast of northwest Africa (Benazzouz et al., 2014; Gómez-Letona et al., 2017). As in other eastern boundary upwelling ecosystems, primary productivity in the CCLME fluctuates greatly over time (Gómez-Letona et al., 2017), and interannual fluctuations drive the population dynamics of species at intermediate trophic positions (Sambe et al., 2016; Sánchez-Garrido et al., 2019). The region is also intensively fished (Failler, 2020; Sambe et al., 2016), which inevitably results in the bycatch of marine megafauna, including sea turtles (Coelho et al., 2015; Lewison et al., 2014; Wallace et al., 2010, 2013; Zeeberg et al., 2006), but nothing is known about the demographic relevance of this regional bycatch.

The loggerhead turtle (*Caretta caretta*) is one of the most abundant sea turtle species in the CCLME, and the Cabo Verde archipelago supports the only regular nesting beaches in the region (Marco et al., 2012; Wallace et al., 2013). The Cabo Verde population is classified as endangered (IUCN; Casale & Marco, 2015) and is subject to very high levels of adult mortality (Martins, Cardona, et al., 2022). However, little has been done to mitigate bycatch, and conservation efforts since 2000 have focused on translocating clutches to hatcheries to improve hatching success (Martins et al., 2021), although the demographic value of this management effort remains unclear. Recently, the nest counts in Cabo Verde have increased dramatically (Laloë et al., 2020; Martins, Cardona, et al., 2022; Patino-Martinez et al., 2022), but the underlying reasons are unknown.

We used population matrix modeling to assess the demographic relevance of current fisheries bycatch mortality for the Cabo Verde (Boa Vista island) population. To achieve this, we combined Boa Vista subpopulation data (2013–2019; representing 60% of Cabo Verde nesting activity; A.M., unpublished data), detailed bycatch information from onboard observers (2016–2021), and regional fishing effort from Global Fishing

Watch (GFW) (www.globalfishingwatch.org) and International Commission for the Conservation of Atlantic Tunas (ICCAT) (www.iccat.int) databases. Finally, we explored the possibility that recent increases in nest counts might result from increased hatchling production or short-term environmentally driven fecundity.

METHODS

Bycatch data and estimation

Satellite telemetry, niche modeling, and genetic markers revealed that adult, Cabo Verde origin loggerhead turtles forage primarily in the CCLME between latitude 5°N and 20°N (Hawkes et al., 2006; Pikesley et al., 2015; Scales et al., 2015; Varo-Cruz et al., 2013) and that juveniles also occur in the northeastern Atlantic Ocean and the western Mediterranean Sea (Clusa et al., 2014; Karaa et al., 2016; Monzón-Argüello et al., 2009, 2010; Stewart et al., 2019; Varo-Cruz et al., 2016). Accordingly, we estimated loggerhead turtle bycatch and mortality in 2 areas of the northeastern Atlantic Ocean and the western Mediterranean (subareas A [5–25°N, 35°W], B [25–45°N, 5–35°W], and C [5°W–16°E] [Appendix S1]). In these subareas, we assumed that loggerheads originating from Cabo Verde constituted 100%, 25%, and 3.2% of the stock compositions, respectively, and that the remaining percentage originated from North American and (eastern) Mediterranean loggerhead populations (Clusa et al., 2014; Karaa et al., 2016; Monzón-Argüello et al., 2009; Stewart et al., 2019). We calculated the loggerhead turtle bycatch mortality in each subarea for each respective fishing fleet and subsequently calculated the number of Cabo Verde origin loggerhead turtles according to the reported stock compositions.

For the longline fleet in the northeastern Atlantic, we used a database collected from 2017 to 2020 by observers onboard Spanish vessels (*n* = 933 sets; 5% Spanish fishing effort) to calculate the number of loggerhead turtles captured per 1000 hooks, total hooks deployed annually, and total loggerhead bycatch for the Spanish longline fleet in the Atlantic study areas. We later extrapolated the results to the whole international fleet according to fishing effort distribution data collected by ICCAT. A mortality rate of 0.408 was used to adjust bycatch figures into mortality (Appendix S1). For the western Mediterranean, we directly used previously estimated adjusted annual mortality (approach 2 in Báez et al. [2019]) and extrapolated to the whole fleet with the same ICCAT fishing effort data.

For the trawl fleet in the northeastern Atlantic Ocean, we obtained onboard observer data from Spanish, Mauritanian, Chinese, Turkish, Senegalese, Guinean, Korean, and Gambian vessels (*n* = 5637 sets) operating on the African continental shelf and slope. We calculated the number of turtles bycaught per fishing hour in the slope and the shelf of each subarea and total bycatch according to international fishing effort in each subarea and depth stratum based on total fishing time reported in GFW database 2019–2020. The adjusted total mortality rate was 0.40 (Appendix S1).

To estimate purse seine fisheries mortality in subareas A and B, we obtained onboard observer data from Spanish, Mauritanian, Senegalese, and Gambian vessels ($n = 1029$ sets). Only 3 loggerhead turtles died during 2 operations of the same vessel. Furthermore, no postrelease mortality has been reported in the literature after bycatch in purse seines. We therefore considered that these results could not be extrapolated to the whole fleet to assess total mortality, and we do not report on purse-seine bycatch further.

For artisanal fisheries, we directly used recent estimates of artisanal loggerhead bycatch in Cabo Verde (Martins, Tiwari, et al., 2022). These estimates were derived from comprehensive interviews with fishers in Cabo Verdean ports and represent diverse fishing gear types deployed locally. We assumed these estimates describe total mortality. No information is available for artisanal fisheries operating in other areas.

Population matrix modeling

Population capture–recapture (encounter) data were collected over 6 nesting seasons (2013–2018) from João Barrosa beach, Boa Vista (16.014°N, 22.735°W) (Martins, Cardona, et al., 2022) and provide the basis for population matrix modeling. Where possible, demographic parameter estimates were derived directly from this data set or from previous Boa Vista subpopulation studies, although hatchling, juvenile, and immature stage survival parameters are from estimates in the literature. Estimated fecundity parameters that were later varied in model scenarios included within-season total clutch frequency (TCF) (4.761 clutches•female^{-1}•year^{-1} [95% confidence interval, CI 4.333–5.136]) and interseason remigration interval (RI) (mean [SD] = 3.06 years [1.12]). Complete details of all parameters, uncertainty, and sources are provided in Appendices S2 and S3.

We created a stage-based deterministic matrix model (Crowder et al., 1994), modified specifically to describe the Boa Vista subpopulation (Figures 1 & 2). Hatchling (≤16.7 cm, survival [φ] = 0.744), small juvenile (16.8–42.9 cm, φ = 0.744), and immature (43–72.9 cm, φ = 0.830) stages were defined. We also defined 3 reproductively mature adult-stage sizes: small (73–79.9 cm, φ = 0.870), medium (80–88.9 cm, φ = 0.870), and large (≥89 cm, φ = 0.880) (Martins, Cardona, et al., 2022). The 73-cm size cutoff for adults represents the 97.5th quantile of the breeding adult size distribution, and the 43-cm cutoff represents the smallest bycaught individuals, likely indicating different juvenile–immature buoyancy and swimming capabilities (Revelles et al., 2007). All sizes are curved carapace lengths.

From humeral growth rings, we estimated individuals reached reproductive maturity at ~28.75 years old and 73 cm, and once mature, adults had a slower constant adult growth rate of 0.34 cm•year^{-1} (L.C., unpublished data; Eder et al., 2012; Martins, Cardona, et al., 2022). Necessarily turtles grow incrementally, yet highly variable growth rates in immature developmental environments result in turtles of different sizes at maturation (Dalleau et al., 2014). Consequently, we modeled direct transitions from immature individuals to small- (S), medium- (M), or large (L)-sized adults at observed proportions

(P) in the breeding population (Figure 1) ($P_M = 0.57$, $P_L = 0.06$, $P_S = 1 - P_M - P_L$). Given the maximum life span estimate we used (62.8 years [59.1–66.5, 5.9% error interval] [Mayne et al., 2020]), slow adult growth permits further adult size transitions (Figure 1). Consequently, young- and old-aged medium- and large-sized adults comprised separate model stages, with respective remaining life spans and transitions. Model stage durations (D) were thus as follows: hatchlings, 1 year; small juvenile, 9 years; immature, 18.75 years; small adult, 20.6 years; young medium adult, 26.5 years; old medium adult, 13.5 years; young large adult, 34.1 years; old large adult, 7.6 years. Transition rates between life stages were calculated by estimating a within-stage distribution of individuals and their probability of transitioning (originally equation A1 in Crowder et al. [1994]) and by using stage-specific survival, stage durations, and population growth rate in an iterative procedure (details in Appendix S2).

Finally, there is consensus that adult loggerheads from the Cabo Verde population exhibit several alternative foraging strategies, but evidence for size-related habitat occupancy remains equivocal (Cameron et al., 2019; Cardona et al., 2017; Eder et al., 2012; Hawkes et al., 2006; Varo-Cruz et al., 2013). Hence, we proportionally differentiated dichotomous oceanic and neritic foraging strategies according to neritic settlement rate for all adult sizes ($k = 0.223$ [Cameron et al., 2019]). Without evidence of differential bycatch risk in oceanic habitat, we modeled a single oceanic subtype. Model metrics were calculated with popbio R package (Stubben & Milligan, 2007).

Deterministic model parameters were varied in stochastic models to account for parameter uncertainty and demographic stochasticity. Stochastic parameter distributions were defined precisely when possible (e.g., with mean and standard deviation for a normal distribution). Where necessary, parameters with differing uncertainty units had such distribution-defining values approximated to allow stochastic variation (e.g., with 95% CIs ≈ 2 SD) (Appendix S2) to better reflect natural processes. Stochastic annual values for survival rates for all stages, hatching success, and clutch size were drawn from truncated normal distributions, truncated either by bounds, 95% CIs, or possible values (0–1). The TCF was drawn from a uniform distribution to avoid a relatively invariable narrow distribution. The RI was randomly drawn from the observed empirical distribution (fishmethods::remp [Nelson, 2022]) and had separate values drawn for small, medium, and large adult size classes. Parameter uncertainty around population size and maximum life span (and therefore stage durations) was incorporated at the simulation level, and values were drawn from truncated normal distributions. Stochastic models were projected for 5000 simulations of 100 annual cycles, and the stochastic population growth rate (λ_s) was calculated (Appendix S2).

Model scenarios

We considered the current scenario as the stochastic model with our point estimates for all parameters. To assess the impact of bycatch by longline, trawler, and artisanal fisheries, we took an approach that first used the deterministic model at stable-stage
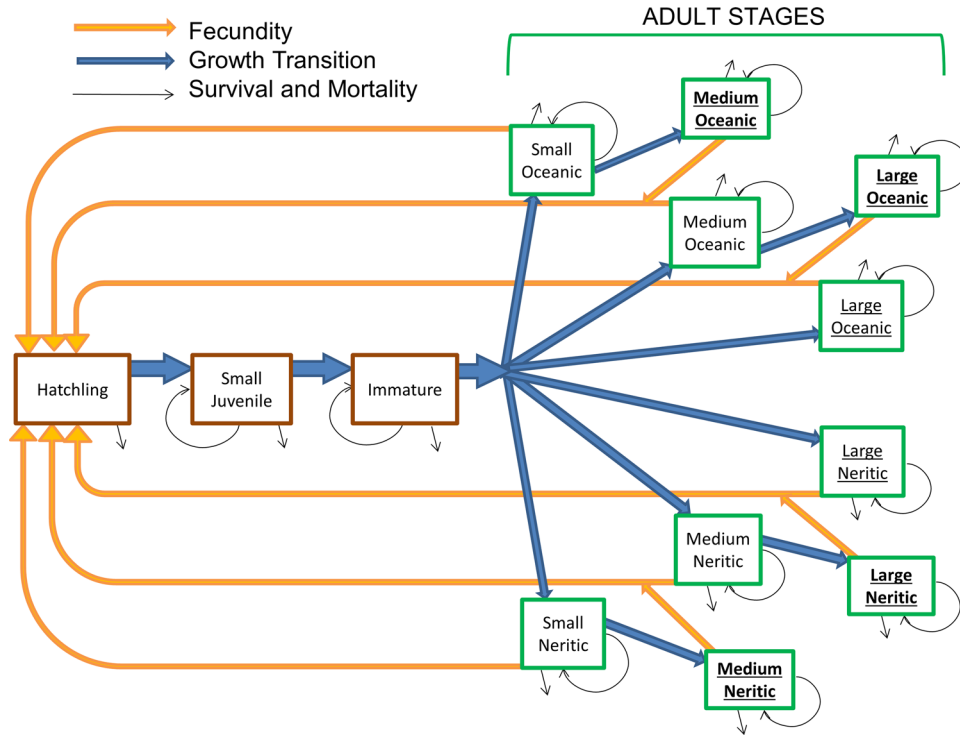
FIGURE 1 Schematic diagram of matrix model of Boa Vista loggerhead population. Each turtle enters 4 or 5 life stages along transition arrows; adult growth allows further adult transitions. Immature individuals may recruit as small-, medium-, or large-sized individuals in neritic or oceanic habitat. Adult classes have size-specific fecundity rates. Duplicate medium and large classes differentiate young animals from old (bold) animals of the same size that have growth-transitioned as adults. Terminal stages are underlined.

	H	J	I	OS	OMY	OMO	OLY	OLO	NS	NMY	NMO	NLY	NLO
H	0	0	0	$f_c\phi_c(1-\gamma_c)+f_c^{t+1}\phi_c\gamma_c$	$f_c\phi_c(1-\gamma_c)+f_c^{t+1}\phi_c\gamma_c$	$f_c\phi_c$	$f_c\phi_c$	$f_c\phi_c$	$f_c\phi_c(1-\gamma_c)+f_c^{t+1}\phi_c\gamma_c$	$f_c\phi_c(1-\gamma_c)+f_c^{t+1}\phi_c\gamma_c$	$f_c\phi_c$	$f_c\phi_c$	$f_c\phi_c$
J	$\phi_c\gamma_c$	$\phi_c(1-\gamma_c)$	0	0	0	0	0	0	0	0	0	0	0
I	0	$\phi_c\gamma_c$	0	0	0	0	0	0	0	0	0	0	0
OS	0	0	$\phi_c\gamma_c P_S(1-k)$	$\phi_c(1-\gamma_c)$	0	0	0	0	0	0	0	0	0
OMY	0	0	$\phi_c\gamma_c P_M(1-k)$	0	$\phi_c(1-\gamma_c)$	0	0	0	0	0	0	0	0
OMO	0	0	0	$\phi_c\gamma_c$	0	$\phi_c-(\phi_c\gamma_c)$	0	0	0	0	0	0	0
OLY	0	0	$\phi_c\gamma_c P_L(1-k)$	0	0	0	$\phi_c-(\phi_c\gamma_c)$	0	0	0	0	0	0
OLO	0	0	0	0	$\phi_c\gamma_c$	0	0	$\phi_c-(\phi_c\gamma_c)$	0	0	0	0	0
NS	0	0	$\phi_c\gamma_c P_S k$	0	0	0	0	0	$\phi_c(1-\gamma_c)$	0	0	0	0
NMY	0	0	$\phi_c\gamma_c P_M k$	0	0	0	0	0	0	$\phi_c(1-\gamma_c)$	0	0	0
NMO	0	0	0	0	0	0	0	0	$\phi_c\gamma_c$	0	$\phi_c-(\phi_c\gamma_c)$	0	0
NLY	0	0	$\phi_c\gamma_c P_L k$	0	0	0	0	0	0	0	0	$\phi_c-(\phi_c\gamma_c)$	0
NLO	0	0	0	0	0	0	0	0	0	$\phi_c\gamma_c$	0	0	$\phi_c-(\phi_c\gamma_c)$

FIGURE 2 Deterministic model matrix for Boa Vista loggerhead population (model stages: H, hatchling; J, small juvenile; I, immature; O/N, oceanic or neritic; S, small; M, medium; L, large; Y, young; O, old; parameters: φ, survival rate; γ, stage transition rate; f, fecundity; k, neritic settlement rate; P_S, P_M, and P_L, settlement [recruitment] rates into mature adult size classes; subscripted c, stage-specific according to size and habitat). With a postbreeding census, fecundity depends on prior survival and transition for nonterminal adult stages. For terminal stages $\varphi_c - (\varphi_c\gamma_c)$ is added to reduce the survival rate by the transition rate of individuals reaching maximum stage duration (i.e., maximum lifespan), which cannot survive indefinitely.

TABLE 1 Annual bycatch mortality (ABM) of Boa Vista female loggerhead turtles and their lost reproductive potential (RP) stratified by fishery, foraging habitat, and size class, with values corresponding to the expected bycatch mortality at stage-specific Boa Vista current survival rates used in matrix population models.

Size class	Metric	Longline[a,b]		Trawler[a,b]		Artisanal[b]		Combined[b]		Total ABM (95% CI)[b,c]
		O	N	O	N	O	N	O	N	
Immature (45–73 cm CCL)	ABM	2480	51	1	9	0	0	2481	60	2541 (2386–2735)
Small adult (73–80 cm CCL)	ABM	327	5	0	6	25	8	353	19	372 (344–412)
Medium adult (80–89 cm CCL)	ABM	95	1	0	5	39	12	135	18	153 (143–179)
Large adult (>89 cm CCL)	ABM	96	2	2	30	4	2	102	34	136 (110–176)
										Total RP
Immature (45–73 cm CCL)	RP[d]	117.1	2.4	0.0	0.4	0.0	0.0	117.1	2.8	119.9
Small adult (73–80 cm CCL)	RP	240.1	3.7	0.0	4.4	18.4	5.9	258.5	14.0	272.4
Medium adult (80–89 cm CCL)	RP	73.2	0.8	0.0	3.8	30.1	9.2	103.3	13.9	117.1
Large adult (>89 cm CCL)	RP	84.3	1.7	1.8	26.2	3.5	1.7	89.6	29.7	119.3
Total	RP	514.8	8.6	1.8	34.9	51.9	16.9	568.5	60.4	628.9

Abbreviations: CCL, curved carapace length; N, neritic; O, oceanic.

[a]Overall estimates pertain to all Cabo Verde loggerheads; values were multiplied by the Boa Vista proportion of the Cabo Verde population (0.6).

[b]Values are female only and derive from overall mortality estimates for each fishery multiplied by primary sex ratio (0.675).

[c]Totals show oceanic and neritic combined, and bootstrapped 95% confidence intervals (CIs). Integers were rounded up.

[d]Reproductive potential is sum of reproductive values (RVs) for all individuals killed per corresponding table category, scaled to the highest RV stage. Medium and large adults are weighted for young and old stages according to deterministic stable-stage distribution.

distribution to reintroduce stratified annual mortality numbers for each fishery to the population (Table 1) (i.e., calculated the population size change had there been no bycatch) and then reverse-calculated the stage-specific survival rates given the starting population size (details in Appendix S4). However, using this approach with additive sources of mortality meant that uncertainty around bycatch estimates and other demographic parameters accumulated and produced unfeasible survival estimates in a total bycatch removal scenario. Consequently, we used alternative initial parameter values within the confidence limits of point estimates to estimate the demographic relevance of each fishery in a deterministic model. For stochastic comparison with the current scenario, we projected an optimal scenario in which adult (all sizes) and immature survival rates were improved to 0.9 and 0.87, respectively, and egg survival (hatching success) was improved to 0.30.

To assess the impact of Boa Vista hatchery conservation, based on detailed hatching success data from the João Barrosa beach hatchery (2013–2018) (Table 1 in Martins, Tiwari, et al. [2022]), we calculated the annual number of hatchlings reaching the sea produced by hatchery intervention (i.e., surplus to wild production that would not have survived). We created a hatchery intervention scenario by boosting hatchling numbers entering the current model each year, by this annual hatchery production rate, drawn from a normal distribution (mean [SD] = 32,543 additional hatchlings [10,800]).

To assess net primary productivity (NPP) as a putative driver of nesting activity, we created an NPP-linked scenario in which fecundity parameters covaried with NPP (TCF positively and RI negatively). Additionally, maturation would be accelerated and duration of the immature stage would decrease as NPP increased. We extracted daily NPP data

(2001–2021) (GLOBAL_MULTIYEAR_BGC_001_029, EU Copernicus Marine Environment Monitoring Service), spatially defined by a 90% minimum convex polygon around adult loggerhead tracks ($n = 25$ individuals, 1999–2006) acquired using Argos platform transmitters (Hawkes et al., 2006; Pikesley et al., 2015; Scales et al., 2015). A rolling 24-month mean NPP ($mg \cdot C \cdot m^{-3} \cdot day^{-1}$) was used, which closely correlated with annual nest numbers with a ~3-year lag time (Appendix S5). To covary these parameters in stochastic models, we drew random annual NPP values from the observed empirical distribution (fishmethods::remp), defined the percentile of that value, and then drew values for TCF and RI at their corresponding distribution percentiles. For maturation, a 25% absolute increase from the mean NPP value was calibrated to a 25% reduction in immature stage duration (18.75 to 14.06 years), whereas stage duration remained unchanged at NPP values drawn less than the mean NPP. Stage transition rates were iteratively updated annually. Finally, we used this NPP-linked scenario model to hindcast a predicted population size and annual number of nests by using real observed NPP values in the model. Predicted nest numbers were solved by rearranging the fecundity equation (Appendix S2).

RESULTS

Bycatch

For both longline and trawlers, mortality of Cabo Verde turtles was orders of magnitude greater in the southern subarea A (Table 2), not just due to assumed genetic origin, but also due to higher capture rates. We estimated longliners in subarea A alone

TABLE 2 Estimates of annual captures and mortality estimate of loggerhead bycatch by fishery and subarea.

Fishery	Subarea	Annual captures	Annual mortality	Scope[a]
Longline	A	18,324	7478	CV
	B	31	13	CV
	C[b]	243	86	CV
Trawler	A	321	129	CV
	B	12	5	CV
	C[c]	–	–	–
Artisanal	A[d]	128	128	BV

[a]Population level at which the estimate is applicable (CV, entire Cape Verde population; BV, Boa Vista subpopulation only). In models, Boa Vista was assumed to represent 60% of the CV population.
[b]Mortality estimated directly from Báez et al. (2019).
[c]No estimate made on trawler activity in Mediterranean.
[d]Mortality estimated directly from Martins, Tiwari, et al. (2022).

captured 18,324 individuals annually (bootstrap 95% CI 17,194–19,777). Capture events were primarily of single individuals with several sets notably capturing multiple individuals (for sets with capture, mean = 1.4, range = 1–18). Trawlers in subarea A captured an estimated 321 individuals annually (bootstrap 95% CI 140–672).

The total annual mortality of Cabo Verde loggerheads from longline fisheries was 7574 individuals (bootstrap 95% CI 7084–8148), and the majority were immature (∼83%, <73 cm). For trawlers, this figure was only 133 individuals (bootstrap 95% CI 58–278). The majority were adults (∼70%, >73 cm), and half were large adults (>89 cm). Artisanal fisheries annual mortality in Boa Vista was 128 adults captured during the breeding season (Martins, Tiwari, et al., 2022).

Population modeling

The current-scenario deterministic model had a finite population growth rate of $\lambda = 0.964$, approximately a 3.6% annual decline (deterministic model properties in Appendix S5). At stable-stage distribution, the adult female population constituted only 1% of all individuals; 22% were hatchlings, 66% were small juveniles, and 11% were immatures. However, adult stage reproductive values were high (range = 146.9–281.8) compared with immatures (13.3). An elasticity (proportional sensitivity) analysis indicated that population growth rate was most strongly influenced by immature survival (0.27), followed by medium-sized oceanic adult survival (0.18), whereas fecundity had relatively low importance (0.04, summed fecundity row elasticity).

In stochastic modeling, lambda values across 5000 simulations were normally distributed for each scenario (Appendix S5). The current scenario stochastic population growth rate was $\lambda_s = 0.966$ (95% CI 0.960–0.974) (Figure 3a). The female population approached extinction after 100 years; remaining individuals numbered only in the hundreds (mean = 223 [95% CI 109–338]). Comparatively, hatchery intervention reduced

extinction risk by maintaining a population around 1703 (1277–2307) individuals, but was unable to obtain population growth with $\lambda_s = 0.990$ (0.984–0.996) (Figure 3b). When the fecundity parameters were NPP linked, projected population decline was slower ($\lambda_s = 0.987$ [0.974–0.999]) (Figure 3c). Hindcasting this dynamic environmental component better predicted observed increases in Boa Vista nest numbers compared with the current scenario hindcast model (Figure 4a,b), despite a simultaneously declining female population (Figure 4c). Lastly, the optimal scenario with improved egg, immature, and adult survival parameters was capable of population growth in many simulations, but largely the population remained stable ($\lambda_s = 1.000$ [0.993–1.007]) (Figure 3d).

In bycatch removal scenarios with altered initial demographic parameters, deterministic models showed that bycatch removal from all fisheries relatively improved population growth rates (Table 3). Removal of longline bycatch, however, clearly made the greatest contribution to this improvement with a 1.76% increase in population growth, out of a total 1.95% increase with cumulative removal of all fisheries bycatch. Reduced bycatch mortality in longline fisheries had 5.35 and 11.67 times more impact than trawler and artisanal fisheries, respectively, on the population growth rate of Boa Vista loggerheads.

DISCUSSION

The current impact of fisheries in the CCLME could drive the Boa Vista loggerhead population to near extinction within a century if left unchanged. Hatchery interventions, despite having positive conservation benefits, could not compensate for this demographic impact. We estimated that Cabo Verde loggerheads are captured in the tens of thousands and killed in the thousands every year in the combined subareas (Table 2). We assert that with a 1.95% reduction to population growth rate, primarily driven by drifting longliners, fisheries bycatch is occurring at a demographically relevant scale and the population is likely in decline. Indeed, the true mortality is almost certainly higher than our estimate, given that illegal, unreported, and unregulated fishing exists in the region (Davies et al., 2009) and that Cabo Verde loggerheads likely experience fisheries mortality where they occur in low numbers outside the study area (Stewart et al., 2019). Although artisanal fisheries and trawler bycatch caused fewer turtle deaths, their impacts remain considerable due to the high reproductive potential and per turtle population impact of valuable reproductively mature individuals (Table 1). Nevertheless, the sheer number of primarily immature and small adult individuals caught in longline fisheries is having the greatest demographic impact, which stresses the importance of this mortality source (this study; Coelho et al., 2015). The population would respond most strongly to improved immature survival (Appendix S5), making drifting longline bycatch mitigation a clear target for population management and future research.

Despite our Boa Vista loggerhead population model clearly showing a population decline, recent increasing trends of nest counts in Boa Vista (Martins, Cardona, et al., 2022) and other
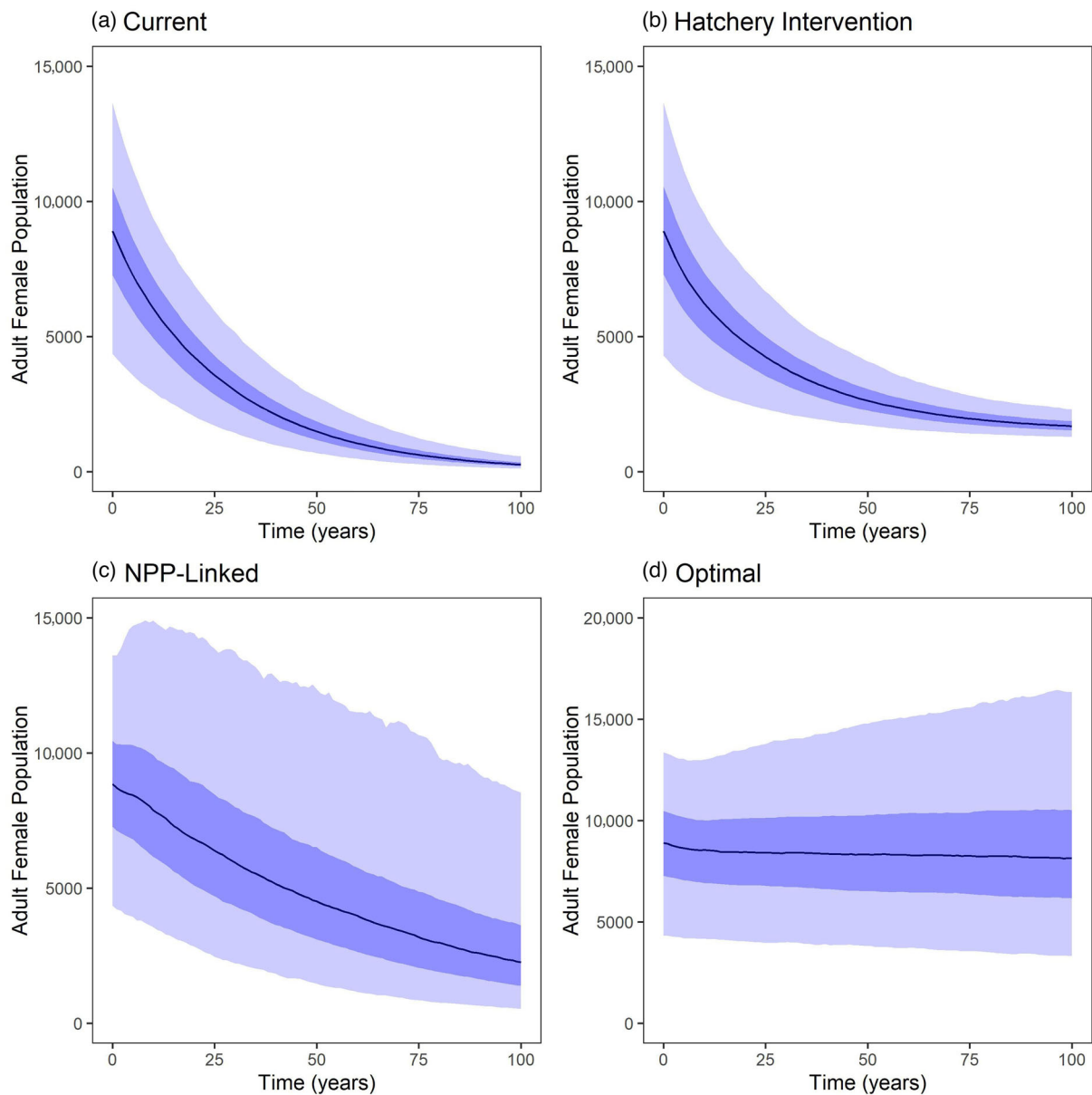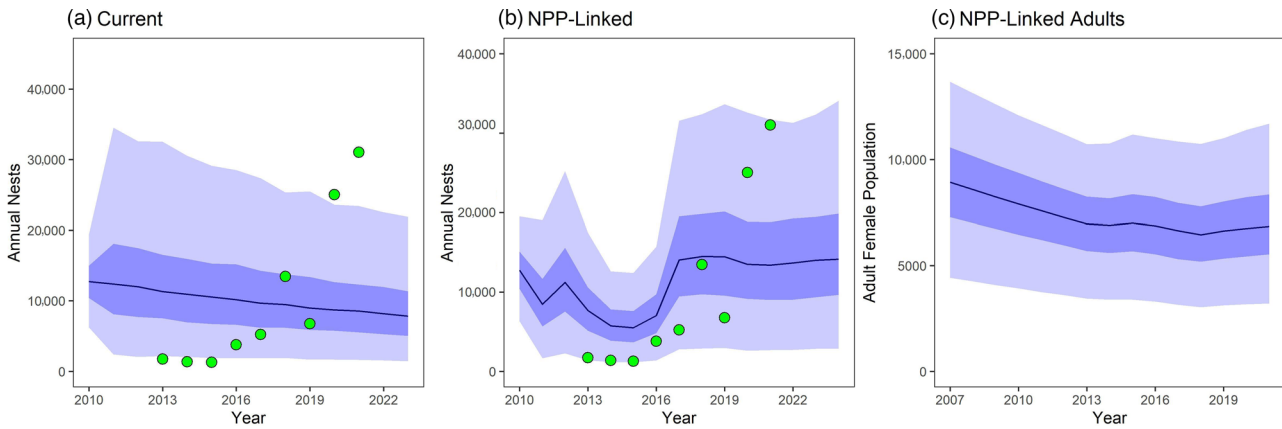
FIGURE 3 Projected adult female populations of Boa Vista loggerhead turtles under alternative model scenarios: (a) current (point estimates and uncertainty for all demographic parameters), (b) hatchery intervention (additional annual boost to hatchling production), (c) net primary productivity (NPP)-linked (remigration interval, total clutch frequency, and immature stage duration explicitly covarying annually with NPP), and (d) optimal (increased egg, immature, and adult survival) (black lines, median from stochastic projections; dark blue, 50% confidence interval [CI]; light blue, 95% CI from 5000 simulations over 100 years).

islands (Laloë et al., 2020; Patino-Martinez et al., 2022) challenge this result and suggest a dramatic increase in nesting activity, possibly due to an apparently increasing adult female population. Our results indicate that translocating clutches to hatcheries might help mitigate the impacts of bycatch in a limited demographic capacity, but it cannot explain the recent manifold increase in nest counts. The annual rate of hatchery intervention in Boa Vista we considered (~32,000 additional hatchlings) came from the management of 750–1000 nests (Martins et al., 2021), but the population was unable to grow even with this annual boost. We estimated that ~220,000 hatchlings produced through management of 5150–6850 nests would be required to maintain a Boa Vista female breeding population

of ~10,000 individuals. In 2021, ~2200 nests were translocated (A.M., unpublished data), but efforts would need to be tripled to achieve stability at this level, which is possibly unfeasible. Hatcheries have many conservation benefits, such as education, raising public awareness, and socioeconomic support, which may also have helped reduce hunting of nesting females in recent years. Complementary conservation efforts are required to target immature or adult survival through bycatch reduction as a more effective way to improve population trajectories (Appendix S5).

In our models, environmentally linked fecundity parameters explained increasing nesting trends in the context of high bycatch estimates better than our current scenario model

FIGURE 4 Annual numbers of loggerhead turtle nests in Boa Vista projected under the (a) current and (b) net primary productivity (NPP)-linked hindcast model scenarios and (c) adult female population under the NPP-linked hindcast model scenario (green dots, observed Boa Vista nest counts 2013–2021; black lines, median in stochastic projections; dark blue, 50% confidence interval [CI]; light blue 95% CI from 5000 simulations from 2007–2021). Nesting lags NPP by 3 years.

TABLE 3 The relative contribution of fisheries to population growth and loggerhead survival rates (φ) in bycatch removal scenarios with alternative initial model parameters.

	Alternative initial parameters[a]			Bycatch removal scenarios			
Model stage[b]	N_0	Total bycatch	With bycatch survival rates	Removed longline bycatch survival rates	Removed trawler bycatch survival rates	Removed artisanal bycatch survival rates	Removed all bycatch survival rates
Hatchling	289,117	0	0.744	0.744	0.744	0.744	0.744
Small juvenile	908,189	0	0.744	0.743	0.743	0.743	0.743
Immature	166,000	2385	0.830	0.842	0.829	0.829	0.842
Oceanic small adult	3193	325	0.820	0.902	0.820	0.825	0.907
Oceanic medium adult	6521	132	0.850	0.862	0.850	0.856	0.868
Oceanic large adult	856	96	0.850	0.942	0.851	0.856	0.948
Neritic small adult	917	13	0.820	0.826	0.821	0.825	0.832
Neritic medium adult	1872	15	0.850	0.850	0.850	0.856	0.857
Neritic large adult	247	18	0.850	0.854	0.901	0.856	0.910
Model outcome[c]							
Lambda (λ)			0.956	0.973	0.959	0.958	0.975
% change in λ			–	1.76	0.33	0.15	1.95
Fishery relative importance			–	×11.67	×2.18	×1	

[a]Alternative initial parameters (higher starting population size [N_0] at stable-stage distribution; lower bycatch estimates; lower survival rates) were used to estimate bycatch removal scenario survival rates with bycatch removed from each fishery.
[b]Young and old model stages of medium and large adults are aggregated.
[c]With derived scenario survival rates, deterministic models indicated changes in population growth rate and allowed inferences.

(Figure 4). Nest counts for most sea turtle populations worldwide show major interannual variability, and species foraging at lower trophic positions could be more tightly coupled to environmental variation (Hays et al., 2022). Loggerhead turtles nesting in Cabo Verde are primarily oceanic foragers foraging at a low trophic position (Cameron et al., 2019; Cardona et al., 2017; Eder et al., 2012; Hawkes et al., 2006) and probably experience major changes in food availability coupled to variable upwelling rates (Benazzouz et al., 2014). We provide some evidence that changes in NPP could explain the recent increase in nest counts, although further research would be required to explicitly determine which potentially correlated environmental conditions drive specific sea turtle fecundity or recruitment vital rates (Ascani et al., 2016; Neeman et al., 2015; Patel et al., 2015) and to establish influential time frames and lags. The NPP linkage in our models also improved λ_s, suggesting that pulses of remigration and increased fecundity when conditions are favorable are part of natural breeding dynamics that vitally contribute

to population maintenance (Boyce et al., 2006). We recommend that this be explicitly considered in future population models—possibly for all sea turtles with similar life histories and sensitivities to environmental variation (Smallegange et al., 2020).

The NPP-linked scenario also demonstrated that the adult female population is likely in long-term decline, despite short-term increasing nesting trends. In fact, individual simulations from this model scenario (Appendix S5) suggest that nest numbers could increase to 100,000 per year with annual variability in the short term while the adult population is still in long-term decline. Estimating female population size from variable nest numbers alone is therefore problematic and has the potential to be misleading in the short term because it has very little power to detect long-term trends (Hays et al., 2022). A deeper understanding of the environmental dynamics driving nesting variability (e.g., Neeman et al., 2015) might allow calibration of observed nest numbers with environmental data to infer adult population sizes. Alternatively, intensive capture–recapture studies would be more appropriate for estimating and monitoring population sizes.

Heterogeneity in bycatch may also be linked to environmental variability, potentially intensifying bycatch both spatially and temporally. Given that Cabo Verde loggerheads associate with nutrient upwellings and thermal fronts at multiple scales (Cameron et al., 2019; Scales et al., 2015), the timing and location of longline sets could make the difference between the observed single captures and mass-mortality events of 18 turtles in a single set. Characterizing spatiotemporal foraging patterns and turtle-fishery interactions may identify opportunities to modify fishing practices and make substantial demographic gains.

Model limitations

For many model parameters, only uncertainty estimates around parameter value estimates were available. Although using uncertainty to assess annual stochastic variation may be more informative than using fixed parameter values, this approach conflates measurement and process errors.

Directly estimating survival rates for hatchling, small juvenile, and immature life stages; the maximum life span; and postrelease mortality rate was not possible for Boa Vista subpopulation, so we used estimates from other populations (Báez et al., 2019; Mayne et al., 2020; Warden et al., 2015). Given that our population model was most sensitive to immature survival and that longline bycatch severely affected the immature stage, having a borrowed parameter value is not ideal. The need to use alternative initial model parameters in reduced bycatch scenarios could result from even lower true immature survival than the borrowed parameter value, which is plausible given the longline bycatch rates of immature individuals. If so, the population could be declining faster than our projections and longline bycatch is having even more of an effect.

For the Boa Vista loggerhead population to persist, a hypothetical scenario with reduced anthropogenic mortality and a (stochastic) population growth rate >1 must exist. We did not find such a scenario among deterministic reduced bycatch scenarios or the stochastic optimal scenario with improved egg, immature, and adult survival rates. Our conservative bycatch and demographic parameter estimates might offer one explanation for this (e.g., here RI = 3 years, previously estimated RI = 2.4 years [Varo-Cruz et al., 2007]). However, hindcast models suggest the current scenario requires some environmental linkage to fully capture population dynamics. When combining optimal scenario parameter values with NPP-fecundity covariation, a more theoretically optimistic $\lambda_s = 1.017$ (95% CI 1.008–1.028) is obtained.

Finally, Boa Vista is the best studied loggerhead subpopulation in Cabo Verde, but information is comparatively scarce for other key subpopulations on Maio and Sal islands. These populations could be larger than previously thought, genetically distinct, without neritic foragers, and more susceptible to climate change (Cameron et al., 2019; Laloë et al., 2020; Patino-Martinez et al., 2022; Stiebens et al., 2013; Tanner et al., 2019). Although we expect Maio and Sal populations to experience similar bycatch risk, these populations warrant independent assessments of how current bycatch estimates affect their population dynamics, ideally with 2-sex models given anticipated future female-biased sex ratios.

Addressing bycatch

To directly tackle projected Boa Vista loggerhead subpopulation decline, fisheries bycatch—critically longline bycatch—must be reduced, which would almost certainly benefit all Cabo Verdean nesting subpopulations. This will require multinational cooperation to regulate fishing practices and cannot be achieved through land-based conservation measures alone. Land-based conservation is necessary to reduce hunting and improve hatching success, but for population-scale management the focus must be extended to bycatch reduction. Using circle hooks baited with mackerel in drifting longlines (Coelho et al., 2015), dynamic ocean management tools (Hazen et al., 2018), or seasonal restrictions to artisanal fisheries around nesting beaches (Martins, Tiwari, et al., 2022) could all be employable mitigation measures. Finally, to meaningfully assess bycatch mitigation management outcomes, long-term investment into demographic studies of the population will be required because monitoring nest numbers alone could yield false conclusions, a finding potentially relevant to many sea turtle populations.

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REFERENCES

Ascani, F., Van Houtan, K. S., Di Lorenzo, E., Polovina, J. J., & Jones, T. T. (2016). Juvenile recruitment in loggerhead sea turtles linked to decadal changes in ocean circulation. *Global Change Biology*, 22, 3529–3538.

Báez, J. C., García-Barcelona, S., Camiñas, J. A., & Macías, D. (2019). Fishery strategy affects the loggerhead sea turtle mortality trend due to the longline bycatch. *Fisheries Research*, 212, 21–28.

Benazzouz, A., Mordane, S., Orbi, A., Chagdali, M., Hilmi, K., Atillah, A., Lluís Pelegrí, J., & Hervé, D. (2014). An improved coastal upwelling index from sea surface temperature using satellite-based approach – The case of the Canary Current upwelling system. *Continental Shelf Research*, 81, 38–54.

Boyce, M., Haridas, C., & Lee, C., The NCEAS Stochastic Demography Working Group. (2006). Demography in an increasingly variable world. *Trends in Ecology and Evolution*, 21, 141–148.

Britten, G. L., Dowd, M., Minto, C., Ferretti, F., Boero, F., & Lotze, H. K. (2014). Predator decline leads to decreased stability in a coastal fish community. *Ecology Letters*, 17, 1518–1525.

Cameron, S. J. K., Baltazar-Soares, M., Stiebens, V. A., Reischig, T., Correia, S. M., Harrod, C., & Eizaguirre, C. (2019). Diversity of feeding strategies in loggerhead sea turtles from the Cape Verde archipelago. *Marine Biology*, 166, 130.

Cardona, L., Martins, S., Uterga, R., & Marco, A. (2017). Individual specialization and behavioral plasticity in a long-lived marine predator. *Journal of Experimental Marine Biology and Ecology*, 497, 127–133.

Casale, P., & Marco, A. (2015). *Caretta caretta (North East Atlantic subpopulation)*. The IUCN Red List of Threatened Species. https://doi.org/10.2305/IUCN.UK.2015-4.RLTS.T83776383A83776554.en

Casini, M., Hjelm, J., Molinero, J.-C., Lövgren, J., Cardinale, M., Bartolino, V., Belgrano, A., & Kornilovs, G. (2009). Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 197–202.

Clusa, M., Carreras, C., Pascual, M., Gaughran, S. J., Piovano, S., Giacoma, C., Fernández, G., Levy, Y., Tomás, J., Raga, J. A., Maffucci, F., Hochscheid, S., Aguilar, A., & Cardona, L. (2014). Fine-scale distribution of juvenile Atlantic and Mediterranean loggerhead turtles (*Caretta caretta*) in the Mediterranean Sea. *Marine Biology*, 161, 509–519.

Coelho, R., Santos, M. N., Fernandez-Carvalho, J., & Amorim, S. (2015). Effects of hook and bait in a tropical northeast Atlantic pelagic longline fishery: Part I—Incidental sea turtle bycatch. *Fisheries Research*, 164, 302–311.

Crowder, L. B., Crouse, D. T., Heppell, S. S., & Martin, T. H. (1994). Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. *Ecological Applications*, 4, 437–445.

Dalleau, M., Benhamou, S., Sudre, J., Ciccione, S., & Bourjea, J. (2014). The spatial ecology of juvenile loggerhead turtles (*Caretta caretta*) in the Indian Ocean sheds light on the "lost years" mystery. *Marine Biology*, 161, 1835–1849.

Davies, R. W. D., Cripps, S. J., Nickson, A., & Porter, G. (2009). Defining and estimating global marine fisheries bycatch. *Marine Policy*, 33, 661–672.

Eder, E., Ceballos, A., Martins, S., Pérez-García, H., Marín, I., Marco, A., & Cardona, L. (2012). Foraging dichotomy in loggerhead sea turtles *Caretta caretta* off northwestern Africa. *Marine Ecology Progress Series*, 470, 113–122.

Failler, P. (2020). Fisheries of the Canary Current Large Marine Ecosystem: From capture to trade with a consideration of migratory fisheries. *Environmental Development*, 36, 100573.

Gómez-Letona, M., Ramos, A. G., Coca, J., & Arístegui, J. (2017). Trends in primary production in the canary current upwelling system—A regional perspective comparing remote sensing models. *Frontiers in Marine Science*, 4, 370.

Hawkes, L. A., Broderick, A. C., Coyne, M. S., Godfrey, M. H., Lopez-Jurado, L.-F., Lopez-Suarez, P., Merino, S. E., Varo-Cruz, N., & Godley, B. J. (2006). Phenotypically linked dichotomy in sea turtle foraging requires multiple conservation approaches. *Current Biology*, 16, 990–995.

Hays, G. C., Mazaris, A. D., & Schofield, G. (2022). Inter-annual variability in breeding census data across species and regions. *Marine Biology*, 169, 54.

Hazen, E. L., Scales, K. L., Maxwell, S. M., Briscoe, D. K., Welch, H., Bograd, S. J., Bailey, H., Benson, S. R., Eguchi, T., Dewar, H., Kohin, S., Costa, D. P., Crowder, L. B., & Lewison, R. L. (2018). A dynamic ocean management tool to reduce bycatch and support sustainable fisheries. *Science Advances*, 4, eaar3001.

Karaa, S., Maffucci, F., Jribi, I., Bologna, M. A., Borra, M., Biffali, E., Bradai, M. N., & Hochscheid, S. (2016). Connectivity and stock composition of loggerhead turtles foraging on the North African continental shelf (Central Mediterranean): Implications for conservation and management. *Marine Ecology*, 37, 1103–1115.

Laloë, J.-O., Cozens, J., Renom, B., Taxonera, A., & Hays, G. C. (2020). Conservation importance of previously undescribed abundance trends: Increase in loggerhead turtle numbers nesting on an Atlantic island. *Oryx*, 54, 315–322.

Lewison, R. L., Crowder, L. B., Wallace, B. P., Moore, J. E., Cox, T., Zydelis, R., McDonald, S., DiMatteo, A., Dunn, D. C., Kot, C. Y., Bjorkland, R., Kelez, S., Soykan, C., Stewart, K. R., Sims, M., Boustany, A., Read, A. J., Halpin, P., Nichols, W. J., & Safina, C. (2014). Global patterns of marine mammal, seabird, and sea turtle bycatch reveal taxa-specific and cumulative megafauna hotspots. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 5271–5276.

Marco, A., Abella, E., Liria-Loza, A., Martins, S., López, O., Jiménez-Bordón, S., Medina, M., Oujo, C., Gaona, P., Godley, B. J., & López-Jurado, L. F. (2012). Abundance and exploitation of loggerhead turtles nesting in Boa Vista island, Cape Verde: The only substantial rookery in the eastern Atlantic. *Animal Conservation*, 15, 351–360.

Martins, S., Cardona, L., Abella, E., Silva, E., de Santos Loureiro, N., Roast, M., & Marco, A. (2022). Effect of body size on the long-term reproductive output of East Atlantic loggerhead turtles (*Caretta caretta*). *Endangered Species Research*, 48, 175–189.

Martins, S., Ferreira-Veiga, N., Rodrigues, Z., Querido, A., de Santos Loureiro, N., Freire, K., Abella, E., Oujo, C., & Marco, A. (2021). Hatchery efficiency as a conservation tool in threatened sea turtle rookeries with high embryonic mortality. *Ocean and Coastal Management*, 212, 105807.

Martins, S., Tiwari, M., Rocha, F., Rodrigues, E., Monteiro, R., Araújo, S., Abella, E., de Santos Loureiro, N., Clarke, L. J., & Marco, A. (2022). Evaluating loggerhead sea turtle (*Caretta caretta*) bycatch in the small-scale fisheries of Cabo Verde. *Reviews in Fish Biology and Fisheries*, 32(3), 1001–1015.

Mayne, B., Tucker, A. D., Berry, O., & Jarman, S. (2020). Lifespan estimation in marine turtles using genomic promoter CpG density. *PLoS ONE*, 15, e0236888.

McIvor, A. J., Williams, C. T., Alves, F., Dinis, A., Pais, M. P., & Canning-Clode, J. (2022). The status of marine megafauna research in Macaronesia: A systematic review. *Frontiers in Marine Science*, 9, 819581.

Monzón-Argüello, C., Rico, C., Carreras, C., Calabuig, P., Marco, A., & López-Jurado, L. F. (2009). Variation in spatial distribution of juvenile loggerhead turtles in the eastern Atlantic and western Mediterranean Sea. *Journal of Experimental Marine Biology and Ecology*, 373, 79–86.

Monzón-Argüello, C., Rico, C., Naro-Maciel, E., Varo-Cruz, N., López, P., Marco, A., & López-Jurado, L. F. (2010). Population structure and conservation implications for the loggerhead sea turtle of the Cape Verde Islands. *Conservation Genetics*, 11, 1871–1884.

Moore, J. E., Curtis, K. A., Lewison, R. L., Dillingham, P. W., Cope, J. M., Fordham, S. V., Heppell, S. S., Pardo, S. A., Simpfendorfer, C. A., Tuck, G. N., & Zhou, S. (2013). Evaluating sustainability of fisheries bycatch mortality for marine megafauna: A review of conservation reference points for data-limited populations. *Environmental Conservation*, 40, 329–344.

Neeman, N., Spotila, J. R., & O'Connor, M. P. (2015). A simple, physiologically based model of sea turtle remigration intervals and nesting population dynamics: Effects of temperature. *Journal of Theoretical Biology*, 380, 516–523.

Nelson, G. A. (2022). *fishmethods: Fishery science methods and models*. R package version 1.11-3.

Patel, S., Panagopoulou, A., Morreale, S., Kilham, S., Karakassis, I., Riggall, T., Margaritoulis, D., & Spotila, J. (2015). Differences in size and reproductive output of loggerhead turtles *Caretta caretta* nesting in the eastern Mediterranean Sea are linked to foraging site. *Marine Ecology Progress Series*, 535, 231–241.

Patino-Martinez, J., Dos Passos, L., Afonso, I. O., Teixidor, A., Tiwari, M., Székely, T., & Moreno, R. (2022). Globally important refuge for the loggerhead sea turtle: Maio Island, Cabo Verde. *Oryx*, 56, 54–62.

Pikesley, S. K., Broderick, A. C., Cejudo, D., Coyne, M. S., Godfrey, M. H., Godley, B. J., Lopez, P., López-Jurado, L. F., Elsy Merino, S., Varo-Cruz, N.,

Witt, M. J., & Hawkes, L. A. (2015). Modelling the niche for a marine vertebrate: A case study incorporating behavioural plasticity, proximate threats and climate change. *Ecography*, *38*, 803–812.

Revelles, M., Carreras, C., Cardona, L., Marco, A., Bentivegna, F., Castillo, J. J., de Martino, G., Mons, J. L., Smith, M. B., Rico, C., Pascual, M., & Aguilar, A. (2007). Evidence for an asymmetrical size exchange of loggerhead sea turtles between the Mediterranean and the Atlantic through the Straits of Gibraltar. *Journal of Experimental Marine Biology and Ecology*, *349*, 261–271.

Roast, M. J., Martins, S., Fernández-Peralta, L., Báez, J. C., Diame, A., March, D., Ouled-Cheikh, J., Marco, A., González-Solís, J., & Cardona, L. (2023). *Data from: Hidden demographic impacts of fishing and environmental drivers of fecundity in a sea turtle population*. Dryad. https://doi.org/10.5061/dryad.69p8cz95d

Sambe, B., Tandstad, M., Caramelo, A. M., & Brown, B. E. (2016). Variations in productivity of the Canary Current Large Marine Ecosystem and their effects on small pelagic fish stocks. *Environmental Development*, *17*, 105–117.

Sánchez-Garrido, J. C., Werner, F. E., Fiechter, J., Rose, K. A., Curchitser, E. N., Ramos, A., García Lafuente, J., Arístegui, J., Hernández-León, S., & Rodríguez Santana, A. (2019). Decadal-scale variability of sardine and anchovy simulated with an end-to-end coupled model of the Canary Current ecosystem. *Progress in Oceanography*, *171*, 212–230.

Scales, K., Miller, P., Varo-Cruz, N., Hodgson, D., Hawkes, L., & Godley, B. (2015). Oceanic loggerhead turtles *Caretta caretta* associate with thermal fronts: Evidence from the Canary Current Large Marine Ecosystem. *Marine Ecology Progress Series*, *519*, 195–207.

Smallegange, I. M., Flotats Avilés, M., & Eustache, K. (2020). Unusually paced life history strategies of marine megafauna drive atypical sensitivities to environmental variability. *Frontiers in Marine Science*, *7*, 597492.

Stewart, K. R., LaCasella, E. L., Jensen, M. P., Epperly, S. P., Haas, H. L., Stokes, L. W., & Dutton, P. H. (2019). Using mixed stock analysis to assess source populations for at-sea bycaught juvenile and adult loggerhead turtles (*Caretta caretta*) in the north-west Atlantic. *Fish and Fisheries*, *20*, 239–254.

Stiebens, V. A., Merino, S. E., Roder, C., Chain, F. J. J., Lee, P. L. M., & Eizaguirre, C. (2013). Living on the edge: How philopatry maintains adaptive potential. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20130305.

Stubben, C., & Milligan, B. (2007). Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software*, *22*(11), 1–23.

Tanner, C., Marco, A., Martins, S., Abella-Perez, E., & Hawkes, L. (2019). Highly feminised sex-ratio estimations for the world's third-largest nesting aggregation of loggerhead sea turtles. *Marine Ecology Progress Series*, *621*, 209–219.

Varo-Cruz, N., Bermejo, J. A., Calabuig, P., Cejudo, D., Godley, B. J., López-Jurado, L. F., Pikesley, S. K., Witt, M. J., & Hawkes, L. A. (2016). New findings about the spatial and temporal use of the Eastern Atlantic Ocean by large juvenile loggerhead turtles. *Diversity and Distributions*, *22*, 481–492.

Varo-Cruz, N., Cejudo, D., & López-Jurado, L. F. (2007). Reproductive biology of the loggerhead turtle (*Caretta caretta* L. 1758) on the island of Boavista (Cape Verde, West Africa). In L. F. López-Jurado & A. Liria (Eds.), *Marine turtles: Recovery of extinct populations* (pp. 127–144). Instituto Canario de Ciencias Marinas.

Varo-Cruz, N., Hawkes, L. A., Cejudo, D., López, P., Coyne, M. S., Godley, B. J., & López-Jurado, L. F. (2013). Satellite tracking derived insights into migration and foraging strategies of male loggerhead turtles in the eastern Atlantic. *Journal of Experimental Marine Biology and Ecology*, *443*, 134–140.

Wallace, B. P., Kot, C. Y., DiMatteo, A. D., Lee, T., Crowder, L. B., & Lewison, R. L. (2013). Impacts of fisheries bycatch on marine turtle populations worldwide: Toward conservation and research priorities. *Ecosphere*, *4*, art40.

Wallace, B. P., Lewison, R. L., McDonald, S. L., McDonald, R. K., Kot, C. Y., Kelez, S., Bjorkland, R. K., Finkbeiner, E. M., Helmbrecht, S., & Crowder, L. B. (2010). Global patterns of marine turtle bycatch. *Conservation Letters*, *3*, 131–142.

Warden, M. L., Haas, H. L., Rose, K. A., & Richards, P. M. (2015). A spatially explicit population model of simulated fisheries impact on loggerhead sea turtles (*Caretta caretta*) in the Northwest Atlantic Ocean. *Ecological Modelling*, *299*, 23–39.

Zeeberg, J., Corten, A., & de Graaf, E. (2006). Bycatch and release of pelagic megafauna in industrial trawler fisheries off Northwest Africa. *Fisheries Research*, *78*, 186–195.

Žydelis, R., Wallace, B. P., Gilman, E. L., & Werner, T. B. (2009). Conservation of marine megafauna through minimization of fisheries bycatch. *Conservation Biology*, *23*, 608–616.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.