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Integrating local ecological knowledge, ecological monitoring, and computer simulation to evaluate conservation outcomes

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Abstract

Successful conservation of long-lived species requires reliable understanding of long-term trends and historical baselines. We present a framework for evaluating abundance trends and conservation outcomes for long-lived marine species by integrating local ecological knowledge (LEK), ecological monitoring, and computer simulation, tested on a case-study of long-lived and heavily exploited green turtles (*Chelonia mydas*) in the Eastern Pacific. Models fit to LEK and monitoring data indicate that turtle abundance is increasing, but only after ~40 years of safeguarding the species' nesting and foraging habitats in Mexico. However, current abundance is at ~60% of baseline levels and historic population structure has not been reestablished, indicating the need for sustained, long-term conservation actions. We demonstrate the potential of linking LEK and ecological science to provide critical information for conservation, by establishing reference baselines and gauging population status with a long-term historical perspective, while promoting equitable and sustainable futures.

KEYWORDS

conservation, local ecological knowledge, long-term data, marine historical ecology, nonlinear modeling, sea turtles, transdisciplinary research

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[[]Correction added on 22/10/2022, after first online publication Equation 1 was corrected.]

1 | INTRODUCTION

Successful conservation of highly migratory, long-lived marine taxa requires efforts and policies implemented across large spatiotemporal scales, along with locally grounded data and practices (Mazaris et al., 2017; Vierros et al., 2020). Globally, many large marine taxa have shown patterns of slow changes over millennia, rapid depletion after the industrial revolution, and accelerated decline in the 20th and 21st centuries (Longo et al., 2015; Lotze & Worm, 2009). In these scenarios, understanding conservation status requires comparisons between current and preexploitation abundances. Achieving this is particularly challenging for species impacted by small-scale fisheries or subsistence hunting, for which technical or baseline abundance data are scarce or unavailable (e.g., Selgrath et al., 2018).

Long-term data generated from Local Ecological Knowledge (LEK) and historical sources is critical for evaluating conservation outcomes for long-lived and historically exploited marine megafauna such as sea turtles, slow-growing fishes, and marine mammals (e.g., Lotze & Worm, 2009; McClenachan et al., 2012; Sáenz-Arroyo et al., 2005). Integrative approaches can contribute to sound conservation and management by establishing local baselines and recovery targets, evaluating population status, integrating the cultural dimensions of humanenvironment interactions, and supporting equitable and inclusive practices (e.g., Lee et al., 2018; Poe et al., 2014). However, there is a need for innovative methodologies to integrate diverse knowledge systems and for guidelines to address practical challenges (e.g., Moon et al., 2019). We present a framework for evaluating abundance trends and conservation outcomes for long-lived marine species by integrating LEK, ecological monitoring, and computer simulation, demonstrated through the case study of green turtles (Chelonia mydas) in the Eastern Pacific.

Sea turtle species are highly susceptible to overexploitation given their complex life-history and prolonged maturation time. Worldwide, the long history of commercial exploitation of green turtle meat and eggs has depleted or extirpated several stocks (e.g., Chaloupka et al., 2008), with some populations collapsing as far back as the 18th century (e.g., McClenachan et al., 2012). Local, regional, and international conservation efforts, including nesting beach and habitat protection, bans or restrictions on direct use, and by-catch regulations, have reversed declines in several populations (e.g., Hawai'i, Atlantic, Indo-Pacific) (Broderick et al., 2006; Mazaris et al., 2017). However, this cosmopolitan species exhibits substantial inter-population variation, such that some stocks may increase as others decline or become locally extinct (Mazaris et al., 2017). As with many long-lived species (e.g., McDougall et al., 2017), green turtle conservation status evaluation is complicated by the lack of knowledge on fundamental parameters including maturation age, life stage duration, and population connectivity (Casale & Heppell, 2016; Seminoff & Shanker, 2008). Green turtles are highly migratory and occupy a broad range of habitats across different life stages, separated by hundreds or thousands of kilometers (see Seminoff et al., 2015). Recruitment age to foraging areas varies widely, with estimates between 1 and 7 years. Similarly, estimates of age at maturity range from 15 to 50 years globally, with ~30 years as a broadly accepted estimate (Avens & Snover, 2013).

Coastal foraging habitats are focal points for conservation strategies as they (i) host turtles of both sexes and a broad range of age classes, providing fundamental insights into population structure, dynamics, and trends and (ii) are where green turtles spend most of their lives during developmental and inter-breeding periods (Bjorndal et al., 2005; Seminoff & Shanker, 2008; Seminoff et al., 2003). However, globally, monitoring is heavily skewed towards nesting beaches, providing limited demographic data as only adult females and nesting output are quantified (Patrício et al., 2021; Seminoff & Shanker, 2008). Given that sea turtle populations consist primarily of juveniles, defining conservation and management policies based on the adult fraction of the population is unrealistic (Casale & Heppell, 2016). Thus, research on foraging habitats is crucial for informing conservation policy and practice.

We focus on the East Pacific green turtle (henceforth, green turtle), a distinct population segment (DPS) (Seminoff et al., 2015). Critical foraging habitats along the Baja California peninsula in northwestern Mexico provide a valuable case study given (i) their biological importance for the East Pacific DPS (Seminoff et al., 2015) and (ii) green turtles' cultural importance for the region's inhabitants as food staples and medicine since the earliest phases of human occupation in the terminal Pleistocene (~12,000 BP) (e.g., Early-Capistrán et al., 2018). Research in historical ecology has demonstrated that small human populations and geographic isolation kept captures sustainable until the mid-twentieth century (see Early-Capistrán et al., 2018, 2020a and references therein). From 1960 to 1980, intensive commercial fishing supplied green turtle meat to fast-growing cities along the U.S.-Mexico border, driving foraging populations to near extinction. This process coupled with intense egg collection at nesting beaches (Delgado-Trejo & Alvarado Díaz, 2012; Early-Capistrán et al., 2018) (Figure S1). Long-term conservation and research began in the late 1970s as green turtles diminished, and in the early 1980s the fishery collapsed (Early-Capistrán et al., 2020a; Seminoff et al., 2008) (Figure 1).



FIGURE 1 General chronology of green turtle fishing and conservation in Bahía de los Ángeles. Fishing efficiency increased along with demand between 1960 and 1980, leading to population collapse. Long-term conservation and research began in the late 1970s in response to diminishing populations. Fishing permits for green turtles were suspended by the Federal Government in 1983 as the fishery collapsed. Regulations and conservation measures across green turtle habitats increased from the late 1970s onward, reaching full legal protection with the total ban in 1990 (Early-Capistrán et al., 2020a; Márquez, 1996; Seminoff et al., 2008)

Green turtles are classified as endangered under Mexican legislation and by the IUCN, and all sea turtle exploitation in Mexico is banned since 1990 (DOF, 1990; IUCN, 2021). Decades of nesting beach and habitat protection across the species' range in Mexico supported population increases since the early 2000s (Seminoff et al., 2015). Unlike regions where large-scale human impacts occurred centuries ago (cf. McClenachan et al., 2012), the Baja California peninsula's unique geographic and historical conditions provide an important case study with an established historical baseline within living memory (see Early-Capistrán et al., 2018, 2020a).

We demonstrate a novel framework for linking ecological science, LEK, and computer simulation, promoting conservation processes by harnessing local and scientific capacities (Game et al., 2015). We integrated scientific monitoring data with historical catch rate reconstructions generated collaboratively with local fishers, resulting in (to our knowledge) the longest available standardized time-series (1952-2018) worldwide for a critical sea turtle foraging habitat. Our approach can be adapted and applied

to long-lived taxa to understand long-term change and inform management.

METHODS 2

Study site 2.1

Bahía de los Ángeles (BLA), Baja California, Mexico (28.951917°, -113.562433°) is a warm-temperate foraging area in the Gulf of California, which was one of the most important green turtle fishing grounds in the Eastern Pacific (Early-Capistrán et al., 2018) (Figure S1). This index site hosts significant in-water foraging aggregations and systematic monitoring, which began in 1995 and has continued as a collaboration between government, academic, and nongovernmental institutions (Figure 1; Early-Capistrán et al., 2020a). Establishing spatial and numerical links between foraging areas and nesting rookeries is challenging, due to (i) foraging areas' frequent incorporation of individuals from multiple genetic stocks;

(ii) limited animal-borne telemetry data for the East Pacific DPS; and (iii) limited data on foraging sites (Dutton et al., 2019; Seminoff et al., 2015). The index nesting beach for this population is Colola, Michoacán, Mexico (18.297392°, -103.410956°), ~1500 km southeast of BLA (Seminoff et al., 2003) (Figure S1). Colola is the only green turtle nesting site in the Northeast Pacific with long-term data (>30 years), and accounts for 56%–71% of green turtles in the Gulf of California (Delgado-Trejo, 2016; Koch, 2013).

To establish baseline abundance and analyze long-term change before scientific monitoring (1952–1982), we used a published data set of LEK-derived catch-per-unit-effort (CPUE) estimates (Early-Capistrán et al., 2020b). For theoretical framing, full methodological details, data sets, and code used for LEK-derived CPUE estimation, see Early-Capistrán and collaborators (2020a, 2020b) and Supporting Information 1 and 2.

To evaluate changes in abundance after the implementation of conservation measures (1995–2018), we used CPUE values from in-water monitoring. Data were provided by author Seminoff (2003; NOAA, Unpublished raw data), Comisión Nacional de Áreas Naturales Protegidas (CONANP) (unpublished raw data), and Grupo Tortuguero de Bahía de los Ángeles (unpublished raw data). For details on monitoring procedures and data, see Supporting Information 3.

During in-water monitoring, turtles were captured with set-nets of the same design as in commercial green turtle fishing (Seminoff et al., 2003). To enable direct comparison across time, CPUE values from monitoring and LEK were standardized to one 12-h in-water set for a single 100 m net (Seminoff et al., 2003). Mean annual CPUE values were analyzed to evaluate central tendencies (see Early-Capistrán, 2020a, 2020b] and Supporting Information 2–4; Figures S2 and S3 and Tables S1 and S2 for details).

2.2 | Analyses

2.2.1 | Nonlinear models and Multiple Imputation by Chained Equations (MICE)

We evaluated CPUE trends for two distinct processes: Commercial Fishing (1952–1983) and Conservation (1978–2018). We appended LEK values from 1978–1982 to the monitoring data set to interpolate values in the temporal gap between commercial fishing (1983) and in-water monitoring (1995). This is justified, as conservation efforts began in the late 1970s and increased over time (Figure 1) (Márquez, 1996; Seminoff et al., 2008) (Supporting Information 5).

We ran Multiple Imputation by Chained Equations (MICE) with the *mice* package in *R* 4.0.4 (van Buuren & Groothuis-Oudshoorn, 2011) to handle the high percentage

of missing data (i.e., blank observations or unavailable values) (Commercial Fishing = 48%, Conservation = 42%). This systematic method is robust for scenarios with up to 75% missingness (Takahashi, 2017) (Supporting Information 6; Figure S4). We assumed that values were missing at random (i.e., missingness was not systematically related to catch rates) (Thurstan et al., 2014).

Each missing value was replaced with a plausible value generated using Markov Chain Monte-Carlo simulations to sample subsets of observed values (van Buuren & Groothuis-Oudshoorn, 2011) (Supporting Information 6). We generated *m* complete data sets, equivalent to the percentage of missing values for each process, running 1500 iterations (Bodner, 2008) (Figures S5 and S6). Observed values were retained.

We fitted each of the *m* complete data sets separately to the model:

$$Y \sim a \cdot e^{(\beta x)}, \tag{1}$$

where *Y* is the response variable (CPUE), *x* is the independent variable (year), and α and β are fitted constants. We pooled results of the *m* fitted models using Rubin's Rules (Dong & Peng, 2013) to obtain parameter estimates with standard errors that (i) describe the uncertainty of imputed missing data and (ii) are unbiased and have valid statistical properties (van Buuren & Groothuis-Oudshoorn, 2011) (Figure S4) (Supporting Information 6.1–6.3; Table S3). Validity was ratified through residual analysis ($e_i \sim N(0, \sigma^2)$) (Nguyen et al., 2017) (Supporting Information 6.4). We developed an ad hoc method to (i) visualize a pooled trend line (broadly equivalent to regression line) and (ii) derive 95% confidence intervals using Rubin's Rules (Dong & Peng, 2013; Nguyen et al., 2017) (Supporting Information 6.5).

2.2.2 | Changes in population structure

We used curved carapace length (CCL) size distributions from monitoring data to analyze changes in population structure after the implementation of conservation measures. CCL values were converted to life stages based on mean nester size at Colola (82.0 cm CCL) (Seminoff et al., 2015); i.e., adults > 82.0. We used Mann–Whitney *U* tests ($\alpha = 0.05$) to compare size and life stage composition over time (Period 1: 1995–2005; Period 2: 2009–2018; Figure S7).

Given the high variability in size composition across time, we used LEK to describe general trends before scientific monitoring. LEK-based size composition is described using weight (kg), which fishers recollected accurately as the basis of payment for catches (see Early-Capistrán et al., 2020a).



FIGURE 2 Long-term trends in mean annual catch-per-unit-effort (CPUE) Annotations show key events in sea turtle conservation and management: (1) start of permanent sea turtle research efforts at Bahía de los Ángeles (1979); (2) start of nesting beach protection at Colola, Michoacán (1979); (3) suspension of green turtle fishing permits by the Federal Government (1983); (4) permanent ban on all sea turtle capture in Mexico (1990); (5) start of in-water monitoring at Bahía de los Ángeles (1990). Shaded area shows data derived from Local Ecological Knowledge (LEK). Values below *x*-axis represent missing data

3 | RESULTS

Our results suggest increasing green turtle abundance after ~40 years of conservation measures and ~30 years of full legal protection (Figures 2 and 3). Both processes, Commercial Fishing and Conservation, are described by a nonlinear model (Equation 1). Commercial Fishing shows high α and negative β ($\alpha = 24.271$, $\beta = -0.820$, p < 0.01; $R^2 = 0.845$), describing exponential decline. In contrast, Conservation shows low α and positive β ($\alpha = 0.002$, p < 0.01; $\beta = 0.136$, p = 0.746; $R^2 = 0.711$), describing prolonged latency followed by accelerated increase. Both models have robust residuals and good fits (Figure 3; Table 1).

The BLA population declined at a rate of 8.4% annually during commercial fishing, contrasting with 4.8% annual increase in response to conservation measures (Supporting Information 7; Table S4). Thus, declines occurred 75% faster than increases. Notably, there is a prolonged latency between the initial implementation of conservation measures (1979), initial signs of increase (~2000), and significant recovery after 2011 (Figure 2). The 33-year lapse between nesting beach protection and increases at foraging habitats roughly corresponds with one generation (~30 years) and one period of age-at-recruitment (~3–5 years) (Avens & Snover, 2013).

Despite the upward trend, maximum CPUE during scientific monitoring (11.2 turtles/12 h; 2018) represents ~60% of the maximum CPUE in the commercial fishery (18.5 turtles/12 h; 1959) (Figures 2 and 3). Furthermore, median CPUE is significantly lower in scientific monitoring (median = 0.66) than commercial fishing (median = 3.47) (Mann–Whitney U = 232, p < 0.05, 95% C. [0.81–7.75]) (Supporting Information 8; Table S5). Thus, green turtle abundance in BLA is comparable to the mid-1960s but remains below baseline levels.

3.1 | Life stage and size distribution

Patterns in life stage and size distribution suggest that population growth is driven by juvenile recruitment, and that historical population structure—with a slight juvenile bias and substantial numbers of large adults—has not been reached (Figures 4 and 5). Abundance increases after 2011 coincide with shifts toward a higher proportion of juvenile turtles. Period 2 (2009–2018; 72.22% juveniles) shows a strong juvenile bias compared with Period 1 (1995–2005; 55.71% juveniles). Median CCL was smaller in Period 2 (median = 75.5) than Period 1 (median = 80.8) (Mann–Whitney U = 71406, p < 0.001, 95% CI [1.99–5.20]) (Supporting Information 9; Tables S6 and S7).



Data type O Mean imputed values
Observed values
Source
LEK
Monitoring

FIGURE 3 Trends in catch-per-unit-effort (CPUE) for 1952–2018 using Multiple Imputation by Chained Equations (MICE). Data points show mean value for each year (mean imputed values are for illustrative purposes only). Pooled parameter estimates and R^2 values are shown for Commercial Fishing phase (1952–1983; blue box) and Conservation (1978–2018; green box). Solid trend line shows pooled predicted values across all *m* imputed models, and dashed lines show 95% confidence intervals for the pooled trend line (Supporting Information 6). Standard errors were pooled according to Rubin's Rules to account for within-model and between-model variance (Dong & Peng, 2013) (Supporting Information 6.5). Marginal rug plots show density distributions of imputed values for Commercial Fishing (blue rug plot, n = 630) and Conservation (green rug plot, n = 816) (see also Figures S5 and S6). Pooled 95% confidence intervals for parameter estimates and R^2 values are reported in Table 1.

			Pooled std.			
Parameter	Pooled estimate	Pooled 95% CI	error	p Value	Pooled df	Pooled R ²
Commercial Fishing (1952–1982; LEK data) Model: $y \sim \alpha \cdot e^{(\beta x)}$; df (complete data) = 29; m = 48; $e \sim N(0, \sigma^2)$ for mean residuals						
α	24.271	[19.669 to 28.873]	2.189	<0.01	17.800	0.845 [0.692 to 0.926]
β	-0.0820	[-0.101 to -0.0628]	0.00928	<0.01	24.060	
Conservation (1978–2018; LEK and Monitoring data [*]) Model: $y \sim \alpha \cdot e^{(\beta x)}$; df (complete data) = 38; $m = 42$; $e \sim N(0, \sigma^2)$ for mean residuals						
α	0.002	[-0.0122 to 0.0168]	0.00703	0.746	25.325	0.711 [0.364 to 0.890]
β	0.136	[0.0760 to 0.196]	0.0286	<0.01	17.376	

Note: Bold type indicates significant results at $\alpha = 0.05$. Parameter estimates, confidence intervals, standard error, and R^2 values were pooled using Rubin's Rules to account for uncertainty of the missing data and variance within and between the m imputed models (Dong & Peng, 2013) (Supporting Information 6). 95% confidence intervals for R^2 values are shown in brackets. Pooled degrees of freedom are included to account for the effects of missing data (Supporting Information 6.6) (van Buuren & Groothuis-Oudshoorn, 2011). See also Figure 3.

*LEK values from 1978 to 1982 were appended to the monitoring data set to allow for interpolation of values in the temporal gap between LEK and monitoring data sets.

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frequently.



* Size distribution is highly variable throughout the chronology. General trends during commercial fishing (1952-1982) obtained from LEK. Trends in "Conservation" stage were obtained from monitoring data. † Catch frequency describes approximate temporal intervals at which turtles of a given size were caught or encountered.

FIGURE 4 Trends in size distribution from Local Ecological Knowledge (LEK) and monitoring data. Adapted from Early-Capistrán et al. (2020a), table 4



FIGURE 5 Total captures per year in scientific monitoring for adult (Curved Carapace Length, CCL > 82.0 cm) and juvenile (CCL \leq 82.0 cm) green turtles. Size at maturity is based on mean size of nesting females at Colola (Figueroa et al. cited in Seminoff et al., 2015). Shaded area shows a time span with 30+ years of nesting beach protection in Colola (initiated in 1979) and 20+ years since the total ban on sea turtle capture in Mexico (initiated in 1990). Values below the *x*-axis represent missing data

4 | DISCUSSION

We demonstrate that integrating LEK, ecological monitoring, and computer simulation can gauge conservation outcomes for long-lived and heavily exploited species like sea turtles. Spatially and temporally widespread conservation measures (e.g., nesting and foraging habitat protection, by-catch regulation, protection from unsustainable use, etc.) are generating positive results for East Pacific green turtles (Mazaris et al., 2017). Population trends at BLA are encouraging but remain below baseline levels. Our results show that intensive, technologically efficient commercial fishing—even by a small fleet—can have severe impacts in short timeframes. In contrast, population recovery requires decades of sustained protection across habitats. This coincides with agent-based models, which suggest that time required for green turtle recovery is approximately twice that of human impact (Piacenza et al., 2017). This pattern of fast decline and slow population growth is consistent with other long-lived marine WILEY

taxa, including large sharks, sirenids, and cetaceans (cf. Chaloupka et al., 2008; McClenachan et al., 2012).

Our results correspond with consensus among senior fishers that green turtles are abundant but below numbers observed as young harpooners (Early-Capistrán et al., 2020a). Furthermore, historical trends in size class distribution suggest that large adults were extirpated during the commercial fishery (see Early-Capistrán et al., 2020a). The smaller mode size and absence of large adults (>150 kg) in ecological monitoring (Figure 4) suggest that historical population structure has not been reached. Considering green turtles' slow growth rates, decades of continued protection at foraging areas may be required to increase juvenile survivorship and prolonged adult growth in order to recover historical population structure (Seminoff et al., 2003). Our results are consistent with theoretical models that suggest ecological recovery may take at least four generations in populations where multiple life stages were impacted (Piacenza et al., 2017). Likewise, reduction in mean body sizes has been observed in recovering green turtle populations, as shifting recruitment dynamics drive changes in population structure (sensu Hays et al., 2022).

Synchronous over-exploitation across life stages and habitats from 1960-1980 drove steep population declines by simultaneously decreasing adult survivorship, hatchling production, and juvenile recruitment (sensu Seminoff & Shanker, 2008). Indeed, population trajectories at BLA largely coincide with trends at the Colola index nesting site, which was largely uninhabited until the 1950s. Like BLA's foraging population, the Colola rookery has grown substantially since ~2010: nesting rates increased 508% from 1982 (3383 nests/year) to 2015 (15,196 nests/year). Nevertheless, the degree of relative increase remains unclear due to the absence of preexploitation baseline data (Delgado-Trejo, 2016). The availability of synchronous time-series for nesting and foraging habitats will enable new insights into population dynamics (e.g., life stage duration, reproductive phenology, etc.) and for development of age-structure models for this population.

Our results suggest a robust causal relationship between abundance trends and key events in conservation and management policies (Figures 1 and 2). BLA's foraging population shows an encouraging trend related to decades of conservation measures enacted over broad spatiotemporal scales. Decades of fishing bans and nesting beach protection have generated a positive feedback loop of increased survivorship and recruitment across life stages and habitats. Demographic models suggest that impacts on adults and large sub-adults can generate dramatic population declines and, likewise, restoration of these life stages can have the greatest contribution to recovery (e.g., Crowder et al., 1994; Piacenza et al., 2017), highlighting the importance of foraging habitats as focal points of conservation research and practice.

Patterns of historical green turtle abundance, decline from overfishing, and growth following conservation efforts are documented in several populations (Broderick et al., 2006; Mazaris et al., 2017). LEK-based approaches will become increasingly relevant as sea turtle populations grow (e.g., Christianen et al., 2021), particularly as conservation conflicts can arise when management frameworks overlook or discount sea turtles' cultural and material importance (cf. Barrios-Garrido et al., 2018). Our results were only possible thanks to long-term, collaborative efforts with the BLA community, whose LEK was indispensable for establishing baseline levels and evaluating conservation outcomes. Importantly, LEK must be recognized for its inherent value and become integral to conservation policy and practice, with self-determination as the guiding principle of scientific collaboration (Mawyer & Jacka, 2018).

To succeed, future conservation and policy measures for long-lived and highly migratory species must integrate international and basin-wide approaches built upon locally grounded efforts (e.g., Vierros et al., 2020). Social dimensions to conservation are expanding as human impacts on marine environments increase. Thus, multiple forms of expertise—including local collaboration—are essential for creating diverse and inclusive approaches to conservation (e.g., Carman & González Carman, 2020). Our methods provide a tangible and adaptable system that fosters innovative and equitable approaches to marine conservation science and practice. LEK, held by people living with and from the sea, is indispensable for comprehending long-term change and building sustainable futures.

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SUPPORTING INFORMATION

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

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