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Imputation of Fisheries Reference Points for Endangered Data-Poor Fishes, With Application to Rhino Rays

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ABSTRACT

For data-limited fish species, sustainable management frequently relies on biological metrics that are derived from life-history trait data, as opposed to high-resolution time series of catch and abundance. These biological metrics are used to assess a species' recovery potential at low population densities, as well as their extinction risk. However, for really data poor species, the life-history traits required to derive these metrics are also often only partially known. Addressing this gap is essential for informing regulatory and conservation actions for vulnerable species and stocks lacking assessments. We developed a generalisable, phylogenetically informed framework for imputing missing life-history traits across different taxa and applied it to 57 species within the order *Rhinopristiformes* (rhino rays), an evolutionarily distinct and highly threatened group with notably sparse life-history data. We then used the imputed traits to derive four key management and conservation metrics: steepness of the Beverton–Holt stock–recruitment relationship, spawning potential ratio at maximum sustainable yield, maximum intrinsic population growth rate and generation length. We found strong correlations between mean life-history traits and three management metrics. While uncertainty in management metrics remained high due to intraspecific variability, measurement error and limited data, using reconstructed traits reduced uncertainty compared to using surrogate trait data from other populations or congeneric species. We provide imputed trait values and corresponding management and conservation metrics alongside uncertainty bounds that should be recognised in any subsequent conservation assessments and management strategy evaluations. The proposed framework enables the generation of first-order, evidence-based management and conservation metrics for data-limited taxa, thereby supporting more informed decision-making for species without comprehensive species-level assessments.

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A substantial proportion of exploited and threatened fish species lack the long-term biological and fisheries data required to support conventional stock assessments methodologies. These methods, such as surplus production models, statistical catch-at-age models, stock–recruitment models, delay-difference models and virtual population analysis models, depend on high-resolution time series of catch, effort, abundance and demographic structure. In the absence of such data, alternative approaches that use life-history trait data to estimate single-species management metrics have been proposed as more feasible pathways for guiding precautionary management (Mangel et al. 2010, 2013). These composite metrics include management reference points that describe recovery potential at low population density (e.g., maximum intrinsic population growth rate $r_{\max}$), as well as biological parameters that define temporal thresholds for population decline (e.g., generation length). Key life-history traits used to estimate these management metrics include age at maturity, natural mortality (often inferred from longevity) and reproductive output (e.g., fecundity and recruitment potential). However, for many species, these traits are estimated with considerable uncertainty, or are entirely absent from the literature (Guy et al. 2021; Kindsvater et al. 2018). This data deficiency cannot be solved with even the most ambitious data collection strategy, and thus poses a major constraint on efforts to regulate fisheries sustainably and quantify extinction risk under frameworks such as the International Union for Conservation of Nature (IUCN) Red List, or Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). In this context, identifying biologically plausible and empirically grounded values for life-history parameters represents a critical challenge for scientific advisory bodies and resource management agencies tasked with supporting the conservation of data-poor species (D'Alberto et al. 2019; Pardo, Kindsvater, Cuevas-Zimbrón, et al. 2016).

Predictive approaches that combine hierarchical modelling, available life-history data and prior distributions based on established life-history theory, offer a new avenue for reconstructing a species' or population's life-history strategy, and addressing taxonomic, spatial and temporal gaps in trait data (Horswill et al. 2019, 2021; Thorson et al. 2017). These methods consider multiple life-history traits, populations and species simultaneously in a Bayesian framework, and reconstruct missing values based on the established life-history trade-offs (i.e., covariation) connecting different traits. Life-history trade-offs are widely recognised across animal and plant taxa (Bakewell et al. 2020; Healy et al. 2019; Jeschke and Kokko 2009; Salguero-Gómez et al. 2016), and reflect the physiological connections between fitness-related traits, such as body growth, reproduction and survival (Bennett and Owens 2002; Gravel et al. 2024; Lande 1982; Stearns 1992; Wong et al. 2021). For instance, some species exhibit slow growth, late maturation, low fecundity and high rates of survival, whereas others show the opposite pattern (Bennett and Owens 2002; Lande 1982; Stearns 1992). Predictive Bayesian hierarchical approaches using life-history theory to reconstruct missing values have previously facilitated the estimation of life-history traits that are poorly monitored and challenging to measure empirically (Horswill et al. 2019, 2021). The measures of uncertainty associated with reconstructed parameters have also been incorporated into projections of population size to provide a range of plausible outcomes that reflect, and maximise information from, available population-specific data (Horswill et al. 2021).

Despite progress in reconstructing life-history trait values, there have been surprisingly few studies using these values to resolve composite management metrics across broad spatial or taxonomic scales (but see Thorson 2020). Furthermore, previous research suggests that theoretical estimates of management metrics show little correlation with life-history traits (Thorson 2020). Understanding correlations between management metrics and major axes of life-history variation helps predict how different species respond to exploitation, especially data-limited species. However, these relationships are inherently complex (Goodwin et al. 2006; Myers et al. 2002; Shertzer and Conn 2012; Thorson 2020) and, as yet, have not been examined using life-history derivations.

Chondrichthyan fishes (Class Chondrichthyes), encompassing sharks, rays and chimaeras, are among the most data-deficient vertebrate taxa in global fisheries (Walls and Dulvy 2020). These species typically have a long lifespan, slow growth rate and low fecundity, leading to low productivity and relatively high vulnerability to fishing. For many species, there is also a lack of both high-resolution time-series data, as well as species-specific life-history data. The absence of these fundamental data impedes the development of both quantitative stock assessments and management metrics, respectively. The Order *Rhinopristiformes* (hereafter referred to as rhino rays) exemplifies these critical knowledge gaps. This order encompasses seven phylogenetically distinct families, many of which are classified as highly threatened under the IUCN Red List criteria (Dulvy et al. 2021). On average, each species within this order represents over 10 million years (MY) more evolutionary time than the other chondrichthyan species (Stein et al. 2018). The loss of these taxa would therefore represent a disproportionate erosion of evolutionary heritage.

Most rhino ray species inhabit shallow, dynamic coastal ecosystems, such as estuaries, mangrove forests and nearshore soft-sediment environments. These habitats are often logistically difficult to access and survey. Monitoring is further complicated by weak fisheries regulation and low reporting accuracy (Jabado 2019; Sherman et al. 2023). Targeted and incidental captures in multispecies fisheries constitute major threats to rhino rays across their range (Harrison and Dulvy 2014; Robillard and Séret 2006). Larger-bodied families, specifically sawfishes (*Pristidae*), wedgefishes (*Rhinidae*) and giant guitarfishes (*Glaucostegidae*), have been particularly affected due to their disproportionate market value in the international shark fin trade (McClenachan et al. 2016). This economic demand has contributed to widespread population declines, with many species now extirpated or severely reduced in parts of their historical range (Dulvy et al. 2016; Jabado 2018; Seidu et al. 2022). Despite recent progress in estimating $r_{\max}$ for the nine best-studied rhino ray species (D'Alberto et al. 2019), most taxa within the order remain poorly understood (e.g., Dulvy and Simpfendorfer 2022). The combination of data scarcity and weak regulatory oversight has resulted in minimal formal management of rhino rays (Sherman et al. 2023), posing a significant risk to the long-term viability of wild populations (Dulvy et al. 2021; Jabado 2019).

To support the conservation and management of rhino rays, the recent IUCN Red List Reassessment for Chondrichthyes inferred species-specific estimates of generation length by heuristically 'borrowing' congeneric life-history information using expert assessments of taxonomic affinity and relative body size (Dulvy et al. 2021; Kyne et al. 2020). Integrating surrogate and observed life-history trait data can overlook the life-history trade-offs that physiologically link a species' demographic traits (Stearns 1992), leading to potential biases and inaccuracies (Devenish-Nelson et al. 2013; Hernández-Camacho et al. 2015; Johnson et al. 2010). It also means that conservation assessments, such as the IUCN Red List, and trade regulations, such as CITES, are restricted to using simpler management metrics that can be estimated with limited life-history trait data, such as $r_{\max}$ and generation length. Predictive approaches using life-history theory to reconstruct missing trait data (Horswill et al. 2019, 2021) offer a promising new avenue for resolving more complex management metrics that are based on many life-history traits, such as spawning potential ratio at maximum sustainable yield. Such approaches would expand the body of information than can be applied to the conservation and management of data-poor fishes, such as rhino rays.

In this study, we extend our Bayesian hierarchical approach (Horswill et al. 2019, 2021) to reconstruct an 11-trait vector of life-history parameters for 57 species of rhino ray. We then use these reconstructed life-history strategies to demographically derive four species-specific management metrics that are commonly used to regulate fisheries and assess extinction risk in fishes (Kindsvater et al. 2016). The selected metrics are three management reference points (steepness of the Beverton–Holt stock recruitment relationship, spawning potential ratio at maximum sustainable yield and $r_{\max}$) and one biological parameter frequently used in conservation assessments to infer extinction risk and define temporal thresholds for population decline (generation length). We provide a new framework for deriving steepness of the Beverton–Holt stock recruitment relationship and spawning potential ratio at maximum sustainable yield from life-history data. We also examine whether using the reconstructed life-history trait values to estimate management metrics, as opposed to trait data from other populations of the same or congeneric species, reduces associated uncertainty in the derived metrics. We then assess correlations between management metrics and major axes of life-history variation, as well as relationships among the different metrics themselves. Finally, to understand the transferability of the proposed framework to species where phylogeny is poorly resolved, we assess the importance of accounting for taxonomic proximity during life-history trait imputation.

1 | Methods

1.1 | Life-History Traits for the Rhino Rays

We collated data for an 11-trait life-history strategy across 57 species of rhino ray (Figure 1). This included species within the following genera (in alphabetical order): *Acroteriobatus*, *Anoxypristis*, *Aptychotrema*, *Glaucostegus*, *Pristis*, *Pseudobatos*, *Rhina*, *Rhinobatos*, *Rhynchobatus*, *Trygonorrhina*, *Zanobatus*, *Zapteryx*. We excluded species *Trygonorrhina melaleuca* and *Rhinobatos formosensis* because they are considered synonyms of *Trygonorrhina dumerilii* and *Rhinobatos schlegelii*, respectively (Fricke et al. 2024). Of the 11 traits, 10 were selected to support the calculation of the four focal management metrics (Cortés 2016; Mangel et al. 2010, 2013; Pardo, Kindsvater, Cuevas-Zimbrón, et al. 2016). These 10 traits were: length at 50% maturity (L_{mat}, cm), length at birth (L_{birth}, cm), maximum age ($A_{\max}$, years), age at 50% maturity (A_{mat}, years), reproductive frequency per year (V; also known as the inter-brood interval), litter size (F), the somatic growth coefficient (k) and asymptotic body length (L_{∞}) estimated from von Bertalanffy's growth function, and finally, the intercept (c) and slope (b) parameters describing the length (L) to weight (W) exponential relationship with age (a; i.e., $W(a) = cL(a)^{b}$). For the eleventh trait, we included maximum length ($L_{\boldsymbol{max}}$, cm) because life-history theory predicts that this variable is strongly correlated with many of the other life-history traits, and the ease of measuring body length means that an estimate of this trait is available for all species (Figure 1). Varying amounts of information on the remaining traits were available for each species (Figures 1 and 2; Appendix S2, Table A2). Few studies provided information on more than one or two life-history traits, and therefore, examination of trade-offs between life-history traits at the individual-study level was not possible.

1.2 | Model of Life-History Traits

To reconstruct a full 11-trait life-history strategy for the 57 species of rhino ray in our study, we used an established Bayesian hierarchical approach (Horswill et al. 2019, 2021). The hierarchical model consisted of a demographic component with shared terms to describe covariation among life-history traits across species, and an observation component to account for species-level process variation and important sources of uncertainty (Horswill et al. 2019, 2021). In the demographic component, we imputed mean values for the ith life-history trait in the jth species ($\widehat{T}_{i,j}$) using linear predictor functions (Equation 1). We scaled the observed trait data between 0 and 1 using generous minimum and maximum trait-specific bounds on the observed scale. To define the minimum and maximum bounds for each trait, we buffer the observed minimum and maximum values by two standard deviations estimated from the observed trait-specific data. We also truncated the lower bound at zero or at a specified biological threshold to prevent implausible values (Appendix S2, Table A3). We then transformed these data to the logit scale to constrain the imputation of outliers within biologically plausible ranges for each trait. Finally, to promote convergence during model fitting we standardised each trait to a mean of 0 and a standard deviation of 1 (Congdon 2003). For species with published trait-specific values, original data points were highly correlated with the back-transformed median posterior reconstructed values, indicating that the data transformations did not generate shrinkage towards the imputed correlations connecting different traits (Appendix S2, Figure A4).

To account for possible phylogenetic nonindependence between species (Figure 1), we included a grouped random

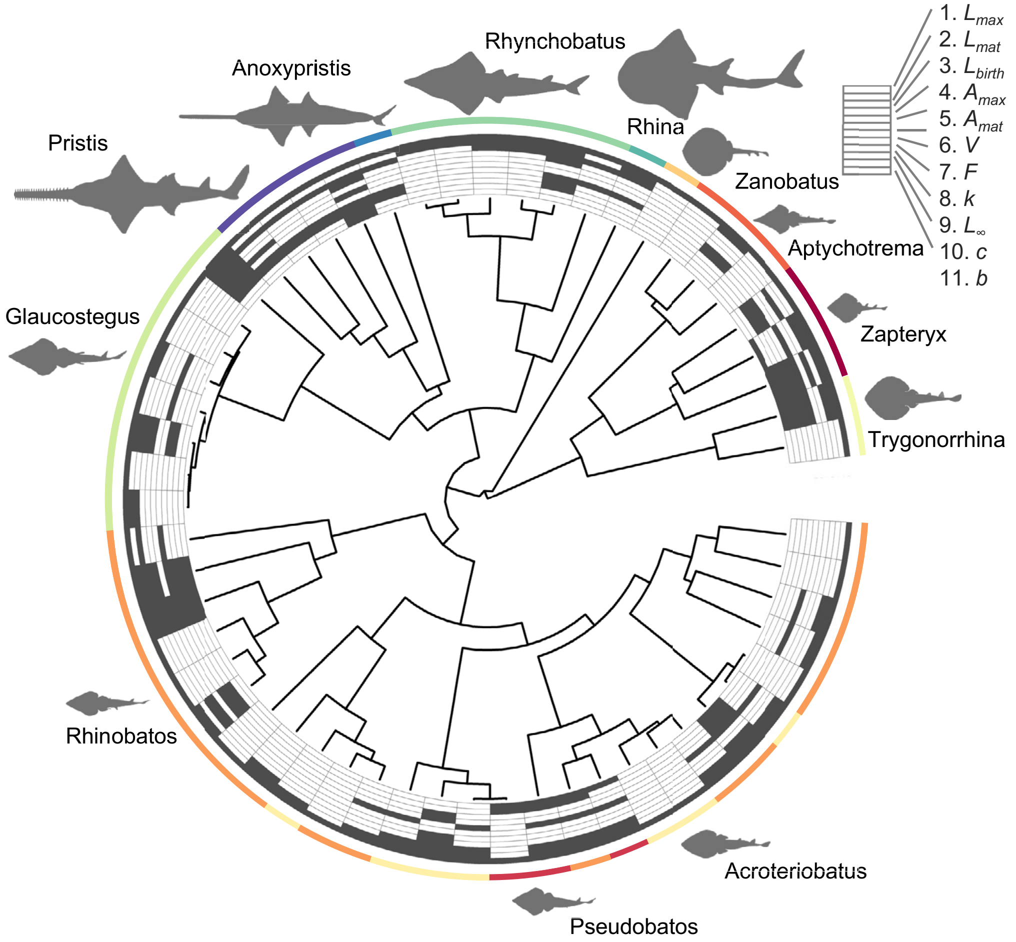

FIGURE 1 | Phylogeny of rhino rays (order Rhinopristiformes, tree trimmed from Stein et al. 2018). Stacks show the availability of empirical data for each species ($n = 57$) across an 11-trait life-history strategy (key denotes corresponding trait where the top is the outer most cell). Shaded cells indicate that life-history data are available in the original dataset for that species. Coloured external ring identifies genus and matches the colour legend in Figure 2. Size of the genus body silhouette comparatively reflects maximum length. Traits are: Maximum length ($L_{\max}$, cm), length at birth (L_{birth}, cm), length at 50% maturity (L_{mat}, cm), maximum age ($A_{\max}$, years), age at 50% maturity (A_{mat}, years), reproductive frequency per year (V), litter size (F), the somatic growth coefficient (k) and asymptotic length (L_{∞}) from von Bertalanffy's growth function, and finally the intercept (c) and slope (b) parameters describing the species-level length (L) to weight (W) exponential relationship with age (a) (i.e., $W(a) = cL(a)^b$). Appendix S2, Table A2 shows number of studies for each species per trait.

effect (γ) in the trait functions that was specific to each trait (i, Equation 1). This term predicted a grouped (m) mean value for each trait, where species were categorically coded and grouped according to their phylogenetic branch lengths from the tips. This involved slicing the tree at 100 MY and grouping the descendant species (Appendix S2, Figure A2, phylogenetic tree selected from Stein et al. 2018). We chose to group species based on phylogenetic distances to allow phylogenetic information to inform the reconstruction of missing values simultaneously with covariance among life-history traits. We also tested the sensitivity of our results to the phylogenetic distance used to define taxonomic groups (see The Importance of Accounting for Taxonomic Proximity When Imputing Life-History Traits and Management Metrics and Appendix S2). In addition, we included a second trait-specific random effect (δ, Equation 1) to quantify life-history trade-offs between traits at the species level (j).

$$\hat{T}_{i,j} = \gamma_{i,m} + \delta_{i,j} \tag{1}$$

We modelled the two random-effect terms (γ and δ) using multivariate normal (MVN) distributions. Here, the multivariate normal distribution for the grouped random-effect term (γ) predicts the mean trait (i) values for each phylogenetic group (m) as a function of a trait-specific mean value (μ_{γ}) and a variance–covariance matrix ($\sum_{\gamma}$) that describes trait correlations across the different groupings of taxonomic proximity (Equation 2). Similarly, the multivariate normal distribution for the species term (δ) predicts the mean trait values for each species as a function of a phylogenetically grouped mean value (μ_{δ}) and a variance–covariance matrix ($\sum_{\delta}$) that describes trait correlations within different groupings of taxonomic proximity. Here, we assume the same variance–covariance structure between traits across groupings. We assigned the trait-specific mean values (μ) of both multivariate normal distributions using normal prior distributions centred on zero (Equation 2). For the grouped term (γ), being centred on zero reflects the expectation that transformed trait values have a group mean value close to zero. For the species term (δ), being centred on zero allows this function to operate as a classic random effect,

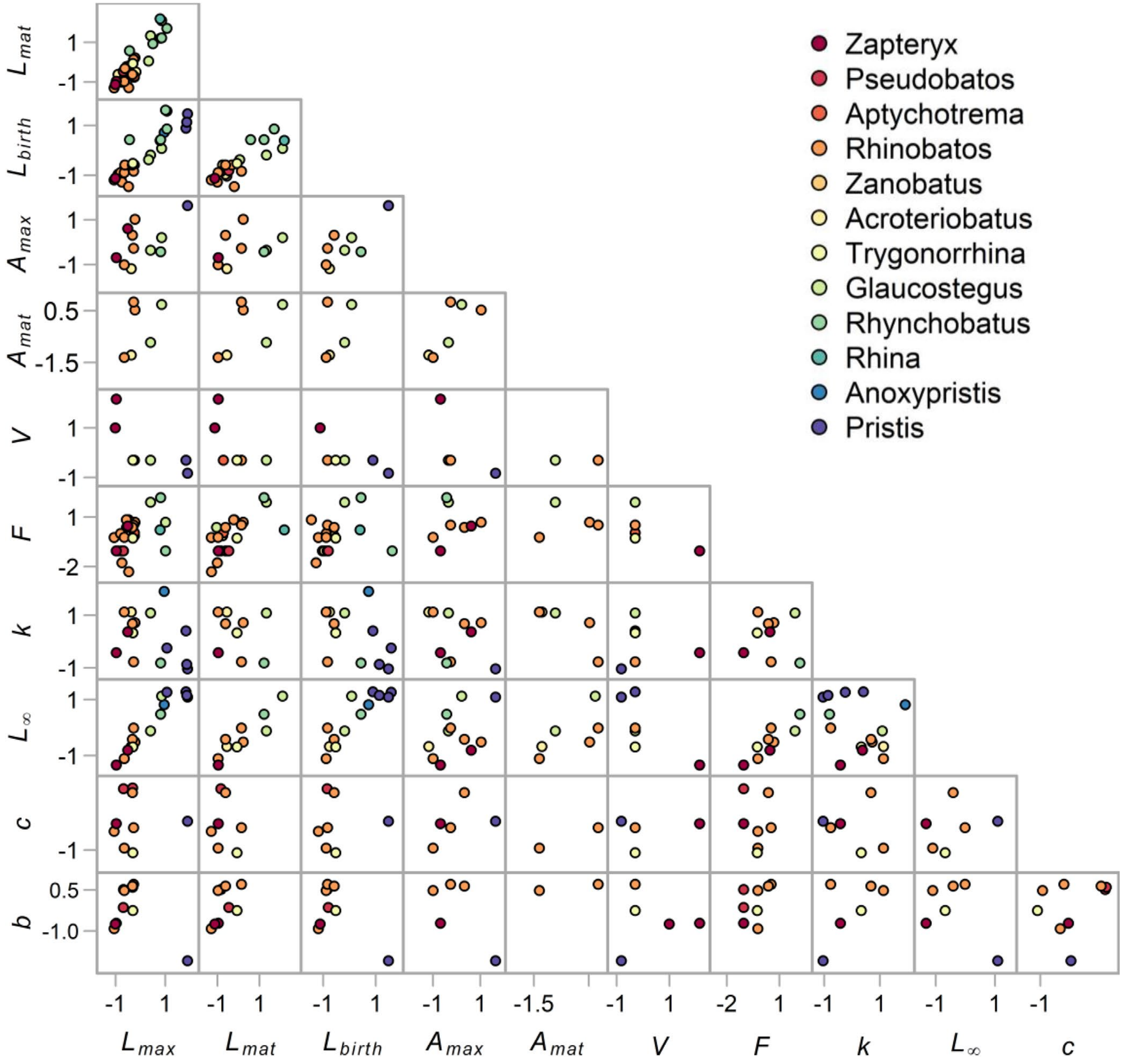

FIGURE 2 | Strength of trade-offs between the original data trait available for an 11-trait life-history strategy of 57 species of rhino ray (order Rhinopristiformes). Traits shown on the logit scale. Species are coloured by genus with the colour ramp corresponding to the observed gradient in the observed data for body size ($L_{\max}$), from small (red) to large (blue). This figure reflects analysis based on phylogenetic Tree 1 (slice length = 100 MY, Appendix S2, Figure A2). Trait notation detailed in Figure 1.

that is, estimating species-level residuals from the group mean for each trait ($\gamma_{i,m}$). Following previous work imputing trade-offs at different taxonomic levels (Horswill et al. 2019), we set the standard deviation of these prior distributions to 0.26 (i.e., a precision of 15) and 0.14 (i.e., a precision of 50) for the grouped and species-level terms, respectively. Assigning a standard deviation less than 1 prevents imputation of the grouped terms from being overly flexible:

$$\begin{aligned}\gamma_{i,m} &\sim \mathrm{MVN}\left(\mu_\gamma, \sum_\gamma\right), \mu_\gamma \sim N(0, 15)\\ \delta_{i,j} &\sim \mathrm{MVN}\left(\mu_\delta, \sum_\delta\right), \mu_\delta \sim N(0, 50)\end{aligned} \tag{2}$$

The variance–covariance matrices ($\sum_\gamma$ and $\sum_\delta$: Equation 2) of the multivariate normal distributions were assigned scaled inverse Wishart prior distributions (Gelman and Hill 2006). This approach allows the life-history trade-offs (i.e., correlations) among the full set of life-history traits to emerge during model fitting. We report the estimated pairwise correlations between life-history traits using Spearman correlation coefficients, calculated from the median posterior values of each trait. To keep the inverse Wishart prior distributions uninformed and allow the strength and direction of trade-offs to be determined during model fitting, we used an identity matrix (I) for the scale matrix (Ω) and set the degrees of freedom to one more than the dimensions of the variance–covariance matrix ($n = 11$ traits). This achieves a uniform prior distribution on the individual correlation parameters, that is, an equally likely probability between −1 and 1 (Gelman and Hill 2006). We also incorporated a scaling parameter (ξ), assigned from a uniform distribution bound between 0 and 5, to overcome any constraints on the variance parameters of the variance–covariance matrices associated with using an inverse Wishart model (Gelman and Hill 2006). For example, for the group level multivariate normal distribution, the Wishart prior distribution was:

$$\begin{gathered}\Omega_\gamma = I_n \\ Q_\gamma \sim \text{InvWishart}\left(\Omega_\gamma, n+1\right) \\ \sum_\gamma = \text{Diag}\left(\xi_\gamma\right) Q_\gamma \text{Diag}\left(\xi_\gamma\right) \\ \xi_\gamma \sim U(0, 5)\end{gathered} \tag{3}$$

We used the observation component of the hierarchical model (Equation 4) to account for trait-specific uncertainty associated with measurement error and species-level process variability in the data (e.g., spatial and temporal variation). We assumed a normal (N) error structure around the imputed trait values ($\hat{T}_i$) for each species (j, Equation 1) and assigned the precision of these distributions (τ) from trait-specific prior distributions centred on 50 (Equation 4). This assumes a high precision on the observed values to minimise shrinkage during model fitting towards the imputed correlations connecting different traits. The observation component thus not only supports the imputation of missing values but also allows posterior distributions for observed data points to be obtained. Finally, to incorporate trait-specific uncertainty generated by spatial and temporal variation, as well as observation error, we included the observed trait data (T) at the study level (p) for each trait (i) and species (j):

$$\begin{gathered}T_{p,i,j} \sim N\left(\hat{T}_{i,j}, \tau_i\right) \\ \tau_i \sim N(50, 0.1)\end{gathered} \tag{4}$$

We implemented the above hierarchical model in JAGS (v. 4.3.0) via the 'jagsUI' library (v 1.4.9) for program R (v. 4.4.2, R Core Team 2024). Models were fitted by running three Monte Carlo Markov chains (MCMC) for 1×10^5 iterations and retaining every 10th step to increase the effective MCMC sample size for the same amount of computer memory. The first 5000 MCMC draws were removed as burn-in and each chain was initialised at different points in the parameter space. Convergence of the chains was confirmed using the Brooks–Gelman–Rubin diagnostic tool (all values $\hat{r} \leq 1.01$) and the effective sample size for each parameter (minimum effective sample size = 1410).

1.3 | Calculating Management Metrics: Steepness, Spawning Potential Ratio, Maximum Intrinsic Population Growth Rate and Generation Length

We back-transformed the imputed life-history trait data from the hierarchical model (Equations 1–4) and used these values on the observed scale to estimate four species-specific management metrics: steepness of the Beverton–Holt stock recruitment relationship (h, steepness from hereon), spawning potential ratio at maximum sustainable yield (SPR_{MSY}, spawning potential ratio from hereon), maximum intrinsic population growth rate ($r_{\max}$) and generation length (GL). In the following sections we explain how each management metric can be resolved from the life-history trait values imputed by our hierarchical model; however, for simplicity in our notation, we drop the species index (j). As rhino rays are viviparous, we define steepness as the recruitment (year class) produced by reproductive females when biomass is 20% of unfished levels, relative to recruitment produced by reproductive females when the population is unfished (Mace and Doonan 1988). Similarly, spawning potential ratio (SPR_{MSY}) is defined as the reproductive biomass per recruit from a population fished to the biomass that produces maximum sustainable yield, relative to the reproductive biomass per recruit when a population is unfished (Mangel et al. 2013). Based on these definitions, steepness and spawning potential ratio both reflect the productivity of a stock at low density. We define $r_{\max}$ as the maximum population growth rate of a severely depleted stock in an unlimited environment, that is, in the absence of density-dependent regulation (Cortés 2016; Pardo, Kindsvater, Reynolds, and Dulvy 2016). Finally, we define generation length (GL) based on its use within the IUCN Red List assessment process for Chondrichthyes, that is, as a time-scaler that accounts for differences between species' life histories (here, age of maturity and maximum age; Dulvy et al. 2021; Pardo, Kindsvater, Cuevas-Zimbrón, et al. 2016). We estimated all management metrics using program R (v. 4.4.2, R Core Team 2024). To account for uncertainty in the life-history trait parameters used to estimate the four management metrics, we randomly selected 500 thinned MCMC draws (minimum effective sample size available for traits = 4299) from the complete joint posterior distribution of the hierarchical model reconstructing life-history traits. This approach also maintains covariance between different combinations of traits in the estimated management metrics (e.g., Horswill et al. 2021).

1.4 | Estimating Steepness and Spawning Potential Ratio From Life-History Traits

The Beverton–Holt stock recruitment relationship can be formulated so that the two key parameters are maximum productivity per unit spawning biomass (i.e., *per capita* productivity) and a measure of the strength of density dependence (Mangel 2021). However, Mangel et al. (2010, 2013) showed that when formulated in this manner management reference points, steepness (h) and spawning potential ratio (SPR_{MSY}), can be estimated independently of the second density dependence parameter and approximated as a function of: (1) the number of offspring per unit reproductive biomass (defined below as α—because we are considering viviparous species we exchange the term 'number of eggs' with 'number of pups'), and (2) the spawning biomass in the steady-state population (defined below as $\overline{W}_f$). These key parameters (α and $\overline{W}_f$) can be derived considering the age-structured dynamics of a focal population using seven of the life-history parameters imputed by our hierarchical model.

When the population reaches a stable age distribution, the number of individuals of age a is independent of time. From here on, we consider only the female population and assume a 1:1 sex ratio. We denote the number of females in each age class as $\overline{N}(a)$, where an overbar is used to separate this variable from the notation used to define a stochastic normal distribution (e.g., Equation 4). Total population size ($\overline{N}$) is then estimated as:

$$\overline{N} = \sum_{a=0}^{A\max} \overline{N}(a) \tag{5}$$

If $\overline{N}(0)$ is the number of recruits when the population is in a stable age distribution and $S(a)$ is cumulative survival from recruit to age a, then $\overline{N}(a) = S(a)\overline{N}(0)$. We also make the common assumption in fisheries that survival to age a follows an exponential distribution with rate of natural mortality (M), so that $S(a) = e^{-Ma}$.

Next, we follow Kenchington (2014) to determine the rate of natural mortality from maximum age ($A_{\max}$):

$$M = \frac{4.3}{A_{\max}} \tag{6}$$

This estimator of natural mortality is considered suitable for Chondrichthyes (Kenchington 2014), although different estimators are available (Zhou et al. 2022). Following the assumption that Equation 6 describes natural mortality, the number of individuals of age a in a stable age distribution is estimated as:

$$\overline{N}(a) = \overline{N}(0)e^{-Ma} \tag{7}$$

Using this formulation, total population size in the steady state is the sum over all ages: $\overline{N} = \sum_{a=0}^{A\max} \overline{N}(a) = \overline{N}(0) \sum_{a=0}^{A\max} e^{-Ma}$. Here, the steady-state number of recruits is moved outside of the summation because it is independent of age.

Next, to determine pup production of the steady-state population, we let $p_m(a)$ denote the fraction of individuals of age a who are reproductively mature; for simplicity, we assumed that $p_m(a)$ is 0 for ages below the age of maturity (A_{mat}) and 1 for ages equal to or above the age of maturity. We let $W(a)$ denote the weight of individuals of age a and estimate this based on the species-specific allometric relationship between length (L) and weight (W) at age a (i.e., $W(a) = cL(a)^b$), assuming an asymptotic relationship between length and age (i.e., $L(a+1) = L_\infty\left(1 - e^{-k}\right) + L(a)e^{-k}$, von Bertalanffy 1938) and that length at birth (L_{birth}) reflects length in the first age class (i.e., $L(1)$).

If α is the number of pups per unit spawning biomass that survive to recruitment, then total pup production in the steady state is:

$$\overline{E} = \alpha \sum_{a=0}^{A\max} \overline{N}(a) p_m(a) W(a) \tag{8}$$

We again replace $\overline{N}(a)$ by $\overline{N}(0)e^{-Ma}$ and move the number of recruits outside of the summation to write:

$$\overline{E} = \alpha\overline{N}(0) \sum_{a=0}^{A\max} e^{-Ma} p_m(a) W(a) \tag{9}$$

The number of pups produced per individual is therefore:

$$\frac{\overline{E}}{\overline{N}} = \frac{\alpha\overline{N}(0) \sum_{a=0}^{A\max} e^{-Ma} p_m(a) W(a)}{\overline{N}(0) \sum_{a=0}^{A\max} e^{-Ma}} = \alpha \frac{\sum_{a=0}^{A\max} e^{-Ma} p_m(a) W(a)}{\sum_{a=0}^{A\max} e^{-Ma}} \tag{10}$$

One of the outputs of our hierarchical model is the annual number of pups produced by a mature female. This quantity is the product of the following three parameters: the average litter size for a species (F), reproductive frequency per year (V) and 0.5 (to account for the fact we are considering female births only). For viviparous rhino rays, survival of pups in their first year of life is very high relative to spawning teleost fishes; while some mortality is expected, it is likely to be comparable to the rate of natural mortality estimated in Equation 6 (e.g., Kindsvater et al. 2018). Therefore, we can assume that:

$$0.5FV = \frac{\overline{E}}{\overline{N}} = \alpha \frac{\sum_{a=0}^{A\max} e^{-Ma} p_m(a) W(a)}{\sum_{a=0}^{A\max} e^{-Ma}} \tag{11}$$

From this, we estimate the annual number of offspring per unit reproductive biomass as:

$$\alpha = \frac{0.5FV}{\left(\frac{\sum_{a=0}^{A\max} e^{-Ma} p_m(a) W(a)}{\sum_{a=0}^{A\max} e^{-Ma}}\right)} \tag{12}$$

Next, we follow Mangel et al. (2010, 2013), Mangel (2021) and Myers et al. (1999) to let $\overline{W}_f$ denote the mass of reproductive females in a steady-state population:

$$\overline{W}_f = \sum_{a=A_{\mathrm{mat}}}^{A\max} e^{-Ma} W(a) \tag{13}$$

so that steepness is:

$$h = \frac{\alpha\overline{W}_f}{4 + \alpha\overline{W}_f} \tag{14}$$

In the Appendix S1, we provide a new derivation of Equation 14 from a starting point based on total egg (or pup) production rather than spawning biomass and illuminate the assumptions about reproductive biology that allow steepness to be determined by spawning biomass, as in Equation 14. For reporting purposes, we truncated all values of steepness at a lower bound of 0.2 for reasons explained in He et al. (2006). Finally, we used the estimated species-specific values of steepness (h) to derive species-specific spawning potential ratios ($\mathrm{SPR}_{\mathrm{MSY}}$) following Mangel et al. (2013) as follows:

$$\mathrm{SPR}_{\mathrm{MSY}} = \sqrt{\frac{1-h}{4h}} \tag{15}$$

1.5 | Estimating Maximum Intrinsic Population Growth Rate ($r_{\max}$) From Life-History Traits

We estimated species-specific values of $r_{\max}$ using a simplified version of the Euler–Lotka equation that accounts for juvenile mortality (Cortés 2016; Pardo, Kindsvater, Cuevas-Zimbrón, et al. 2016; Pardo, Kindsvater, Reynolds, and Dulvy 2016):

$$l_{\mathrm{Amat}} b = \left(e^{r_{\max}}\right)^{A_{\mathrm{mat}}} - e^{-M}\left(e^{r_{\max}}\right)^{A_{\mathrm{mat}}-1} \tag{16}$$

Here, l_{Amat} is survival to maturity and is calculated as $l_{\mathrm{Amat}} = e^{-M\mathrm{Amat}}$, b is the annual reproductive output of females (i.e., $0.5FV$), A_{mat} is age at maturity in years, and M is natural mortality estimated following Equation 6. We then solved Equation 16 numerically for $r_{\max}$ using the nlmimb function in the core Program R stats package (v. 4.4.2, R Core Team 2024).

1.6 | Estimating Generation Length (GL) From Life-History Traits

To estimate species-specific values of generation length (GL), we followed the approach used in the IUCN Red List reassessment for Chondrichthyes (Dulvy et al. 2021):

$$\mathrm{GL} = A_{\mathrm{mat}} + z\left(A_{\max} - A_{\mathrm{mat}}\right) \tag{17}$$

Here, A_{mat} and $A_{\max}$ are age at maturity and maximum age, respectively, and the constant z depends on the total mortality rate of adults, which is typically around 0.3 for mammals (Pacifici et al. 2013). In agreement with previous work on Chondrichthyes (Dulvy et al. 2021), we assumed a more conservative value of $z = 0.5$ to account for the likelihood that measured age structures are likely to be truncated by overexploitation (Barnett et al. 2017) and due to concerns of systematic underestimation of chondrichthyan ages (Harry 2018).

1.7 | Comparing Management Metrics Used in Assessments, and Estimated Using Observed Life-History Traits, With Those Derived From Reconstructed Life-History Traits

To examine the influence of using reconstructed life-history data to estimate the four management metrics (i.e., steepness, $\mathrm{SPR}_{\mathrm{MSY}}$, $r_{\max}$ and GL), we compared metrics calculated using four different methods. First, we collated estimates of species-specific generation length used in the recent IUCN red listing process for rhino rays (Dulvy et al. 2021). Data were available for 42 of our study species, and were either empirically estimated from species-specific ageing studies ($n = 12$), or taken from congeneric species and scaled relative to body size ($n = 30$, Kyne et al. 2020). Second, we randomly sampled the empirical dataset to combine available species-specific life-history trait data. Third, we randomly selected species-specific reconstructed life-history parameters from the posterior distribution of the hierarchical model excluding the imputed covariance between life-history traits. To remove covariance between traits, we randomly selected life-history parameters from independent trait-specific uniform distributions that were bound by the minimum and maximum back-transformed posterior values for each trait imputed by the hierarchical model. This method offers a particularly conservative approach because it provides equal weighting in the marginal aspects of the posterior distribution during trait selection. Finally, we retained the imputed covariance between life-history traits by randomly selecting reconstructed life-history parameters from the complete joint posterior distribution of the hierarchical model. For all methodologies, we assumed that drawing life-history parameters from the full range of published (i.e., observed) or reconstructed values accounts for uncertainty associated with temporal and spatial variation in traits, and represents scenarios under a range of density-dependent regulation. We estimated all four management metrics across each method using program R (v. 4.4.2, R Core Team 2024).

1.8 | Relationships Between Life-History Traits and Management Metrics, and the Importance of Maintaining Covariation Between Life-History Traits for Detecting These Relationships

Although theoretical predictions indicate that steepness and asymptotic size should be positively correlated (Andersen and Beyer 2015; Mangel et al. 2013), relationships between management metrics and life-history traits have proved challenging to demonstrate in practice (Myers et al. 2002; Shertzer and Conn 2012; Thorson 2020). We examined whether it was possible to detect a linear relationship between each management metric and the imputed species-specific trait values for asymptotic body length (L_{∞}) and natural mortality (M) by calculating the Spearman correlation coefficient between mean values. To understand the components influencing these relationships, we also examined whether their detection relied on maintaining the imputed covariance between life-history traits. Analysis was conducted using program R (v. 4.4.2, R Core Team 2024).

1.9 | Relationships Between Management Metrics

Given the number of species-specific life-history parameters required to estimate each management metric (Equations 5–17), it can be argued that $r_{\max}$ and generation length are considerably easier to resolve than steepness and spawning potential ratio. These simpler metrics are also already used in conservation assessments, such as the IUCN Red Listing process and CITES. To examine whether $r_{\max}$ and generation length can provide information on steepness and spawning potential ratio within these existing assessment frameworks, we estimated the Spearman correlation coefficient between metrics based on the mean derived values.

1.10 | The Importance of Accounting for Taxonomic Proximity When Imputing Life-History Traits and Management Metrics

To examine whether model fit or outputs (i.e., the derived management metrics) were considerably altered by the method used to group taxonomically similar species, we tested five additional structures for describing taxonomic proximity. Specifically, as well as the baseline 100 MY slice, we considered 125 and 150 MY slices (Appendix S2, Figure A2). We also grouped species together in a single taxonomic random-effect term (γ, Equation 1); removed this taxonomic proximity term from the model; and finally, replaced the phylogenetic slice with genus groupings (i.e., $n_m = 12$). We included two options for removing the taxonomic random-effect term (i.e., grouping species in a single random-effect term and removing this term from the model) to control for any change in parameter constraint generated by term removal. Finally, to examine the influence of the phylogenetic tree used to determine taxonomic distance, we reran the analysis using four additional randomly selected trees from Stein et al. (2018) (Appendix S2: Figure A1.1).

2 | Results

2.1 | Model of Life-History Traits

We obtained published values for 65% of life-history traits across an 11-trait life-history strategy and 57 species of rhino ray. This equates to 410 out of 627 traits having available data (Figure 2). We identified pairwise correlations between the traits that have comparatively more data (Figure 2). The reconstructed dataset (Figure 3) was also characterised by strong pairwise correlations between most trait combinations ($\rho \leq -0.35$ or $\rho \geq 0.35$), with the exception of the somatic growth coefficient (k) from von Bertalanffy's growth function and the intercept (c) and slope (b) parameters describing the species-specific length to weight relationship with age (Figure 3). These three parameters were positively correlated with each other. In addition, the intercept demonstrated a positive correlation with maximum age and age at 50% maturity, and the slope parameter demonstrated a negative correlation with length at birth (Figure 3, Appendix S2, Table A4).

There was a large degree of overlap in life-history traits within and across genera reflecting the similar range of life-history strategies among these closely related species (Figure 3). As might be expected, the 95% credible intervals of reconstructed traits increased when data were missing (e.g., see maximum age, age at 50% maturity and reproductive frequency, Appendix S2, Figure A3, Tables A5.1 and A5.2). This pattern was also observed in the subsequent calculation of natural mortality (Appendix S2, Table A6). Finally, for species with published trait-specific values, original data points were highly correlated with the median posterior reconstructed values (Appendix S2, Figure A4).

2.2 | Comparing Management Metrics Used in Assessments, and Estimated Using Observed Life-History Traits, With Those Derived From Reconstructed Life-History Traits

The values of generation length used in the IUCN red listing process for rhino rays that were estimated from ageing studies exhibited a strong positive correlation with our derived values of generation length based on the reconstructed life-history traits (Figure 4A). By contrast, we identified a much weaker correlation between our derived values and the values of generation length used in the IUCN red listing process that were scaled estimates from congeneric species (Figure 4B).

The empirical dataset of observed rhino ray life-history traits (Figure 1,2) supported the data-driven demographic estimation of species-specific steepness and spawning potential ratio for one species, $r_{\max}$ for two species, and generation length for six species (Appendix S2, Table A2, Figure 5). The calculated management metrics based on these data produced large estimates of uncertainty (Figure 5), with the exception of generation length for *Acroteriobatus annulatus* where only one estimate of maximum age ($A_{\max}$) and age at 50% maturity (A_{mat}) was available, preventing an estimate of uncertainty from being calculated (Figure 5D). Using the reconstructed life-history parameters to estimate the four management metrics altered the mean values and decreased the level of uncertainty associated with all metrics (Figure 5). Maintaining covariance between the reconstructed life-history traits did not markedly alter the calculated mean values, although levels of uncertainty generally decreased.

Management metrics derived using the imputed dataset of rhino ray life-history traits generated large estimates of uncertainty with many species having comparable bounds (Figures 6 and 7; Appendix S2, Table A7, Figure A3). This uncertainty reflects temporal and spatial variation in observed life-history traits, as well as measurement error and data availability. Based on the derived mean values, steepness ranged from 0.48 to 0.84 (low: *Rhinobatos irvinei*, and high: *Zapteryx exasperate*), spawning potential ratio ranged from 0.18 to 0.24 (low: *Pristis pectinata, Pristis pristis, Rhinobatos horkelii, Zapteryx exasperate*, and high: *Rhinobatos percellens*), $r_{\max}$ ranged from 0.01 to 0.59 (low: *Rhinobatos productus*, and high: *Glaucostegus obtusus*), and generation length ranged from 5.14 to 21.25 (low: *Acroteriobatus annulatus*, and high: *Pristis pristis*; Appendix S2, Table A7).

2.3 | Relationships Between Life-History Traits and Management Metrics, and the Importance of Maintaining Covariation Between Life-History Traits for Detecting These Relationships

Based on the mean posterior values, we found that rhino ray asymptotic body length and natural mortality were strongly correlated with steepness, spawning potential ratio and generation length (Figure 6A–H,M–P). By contrast, the correlations between mean asymptotic body length, natural mortality and maximum intrinsic population growth rate ($r_{\max}$) were weaker (Figure 6I–L). We also identified that mean steepness, generation length and $r_{\max}$ were greatest in larger-bodied, longer-lived species, whereas mean spawning potential ratio was greatest in smaller-bodied, shorter-lived species (Figure 6). Maintaining covariance between the reconstructed life-history traits when calculating management metrics did not qualitatively alter the identified correlations connecting mean asymptotic body length and natural mortality with management metrics (Figure 6). Derived values of steepness, spawning potential ratio, $r_{\max}$ and generation length are provided at the species and genus level in Appendix S2, Tables A7 and A8 (Figure 6).

2.4 | Relationships Between Management Metrics

We identified strong positive correlations between steepness, $r_{\max}$ (Figure 7A, Spearman correlation coefficient $\rho = 0.44$) and generation length (Figure 7B, $\rho = 0.64$). We also identified strong negative correlations between spawning potential ratio, $r_{\max}$ (Figure 7C, $\rho = -0.51$) and generation length (Figure 7D, $\rho = -0.71$). We infer this occurs because maximum sustainable

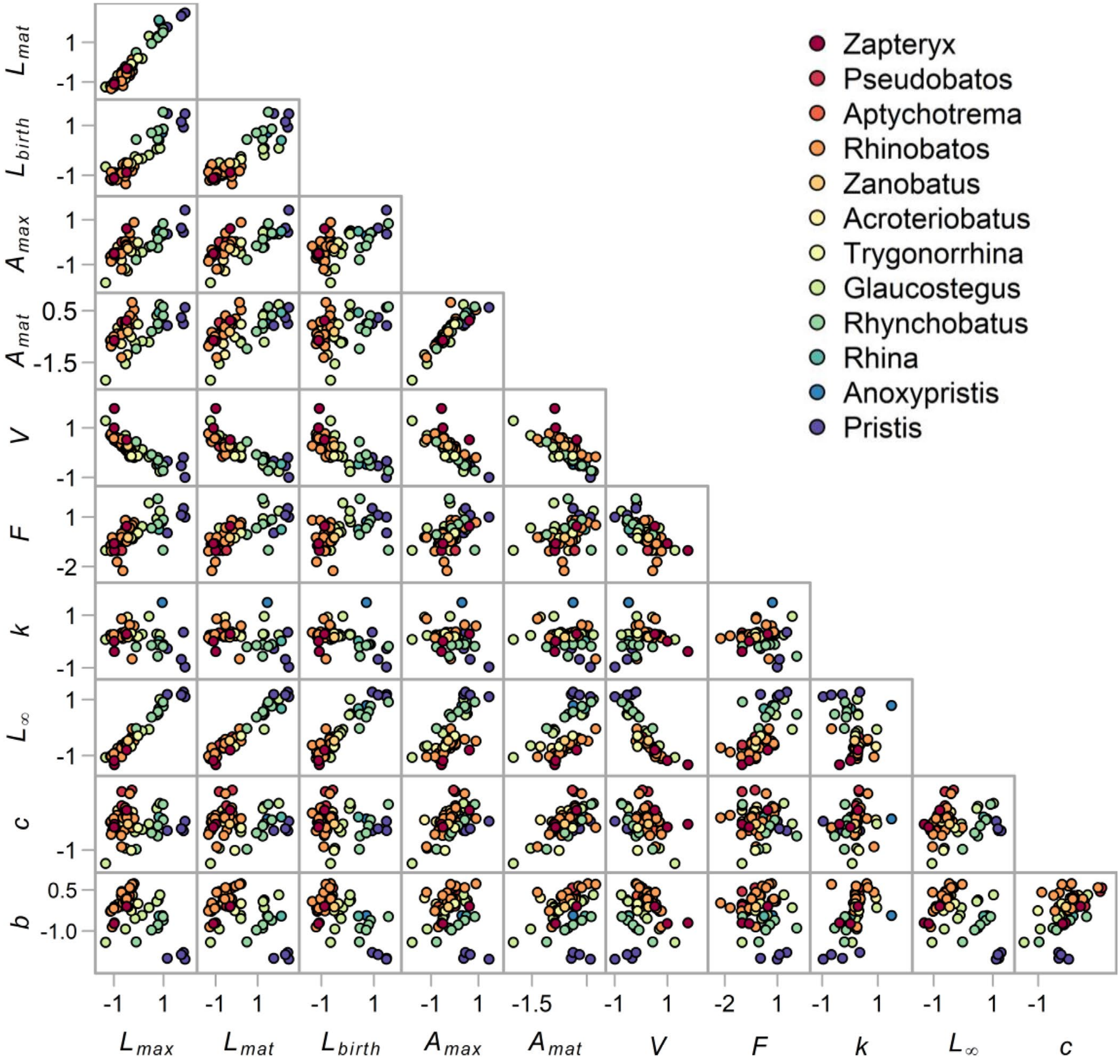

FIGURE 3 | Strength of trade-offs between the reconstructed (posterior median) values for an 11-trait life-history strategy of 57 species of rhino ray (order Rhinopristiformes). Traits shown on the logit scale. Species are coloured by genus with the colour ramp corresponding to the observed gradient in the observed data for body size (L_{max}), from small (red) to large (blue). This figure reflects analysis based on phylogenetic Tree 1 (slice length = 100 MY, Appendix S2, Figure A2). Trait notation detailed in Figure 1.

yield will be at a lower biomass for species with higher r_{max} and generation lengths, compared to species with lower r_{max} and generation lengths, such that the difference in spawning biomass per recruit with and without fishing will be greater (Figure 7).

2.5 | The Importance of Accounting for Taxonomic Proximity When Imputing Life-History Traits and Management Metrics

Changing the structure used to taxonomically group species did not appear to qualitatively alter the fit of the hierarchical model reconstructing life-history traits or influence the derived species-specific management metrics (Figure 8, Appendix S2: Table A1.2, Figure A1.5). These results were also replicated across four additional randomly selected phylogenetic trees (Appendix S2: Table A1.1, Figures A1.2–A1.4).

3 | Discussion

In this study, we describe a framework for imputing species-specific life-history parameters for data-limited fishes and detail

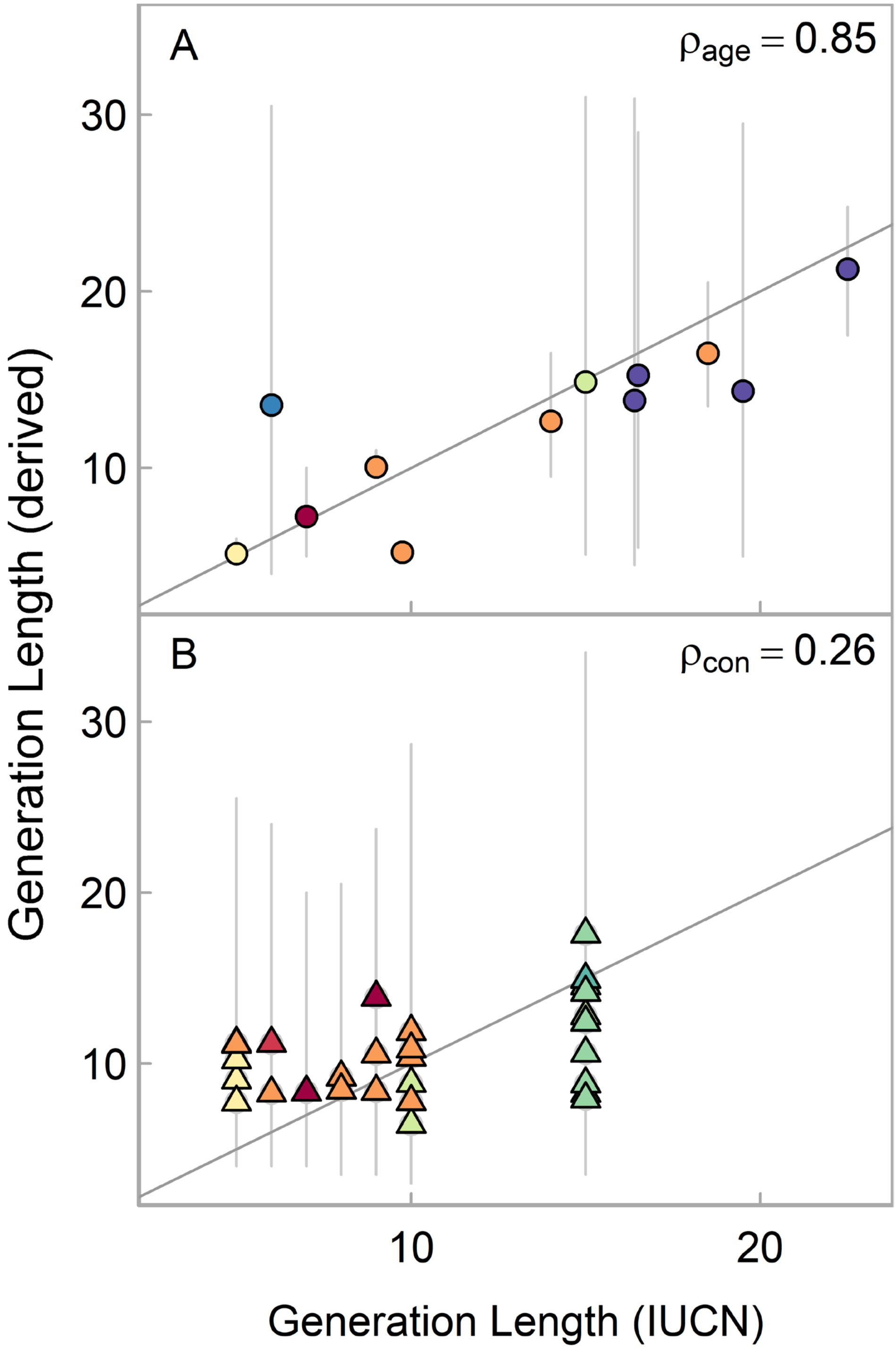

FIGURE 4 | (A) Values of generation length estimated from ageing studies and used in the IUCN red listing process for rhino rays (circles) exhibited a strong positive correlation with our derived values of generation length based on reconstructed life-history traits (Spearman correlation coefficient, ρ_{age}). (B) We identified much weaker correlation with the scaled congeneric values of generation length (triangles; ρ_{surr}). Species are coloured by genus following the legend shown in Figure 2. Uncertainty in the derived values reflects the 500 randomly selected thinned MCMC draws of the life-history trait data used for calculation; mean values with 95% credible intervals. For reference, the 1:1 relationship is also shown as a grey diagonal line.

how these values can be used to demographically resolve four key management metrics commonly used to regulate fisheries and assess extinction risk (Kindsvater et al. 2016). The key metrics included in this study are steepness of the Beverton–Holt stock–recruit relationship, spawning potential ratio at maximum sustainable yield, maximum intrinsic population growth rate (r_{max}) and generation length. We apply our framework to a highly threatened group of species, rhino rays, that includes some of the most data-poor, evolutionarily distinct and highly threatened taxonomic families on the planet. Our study represents one of the first to demographically resolve species-specific values of steepness, spawning potential ratio, r_{max} and generation length

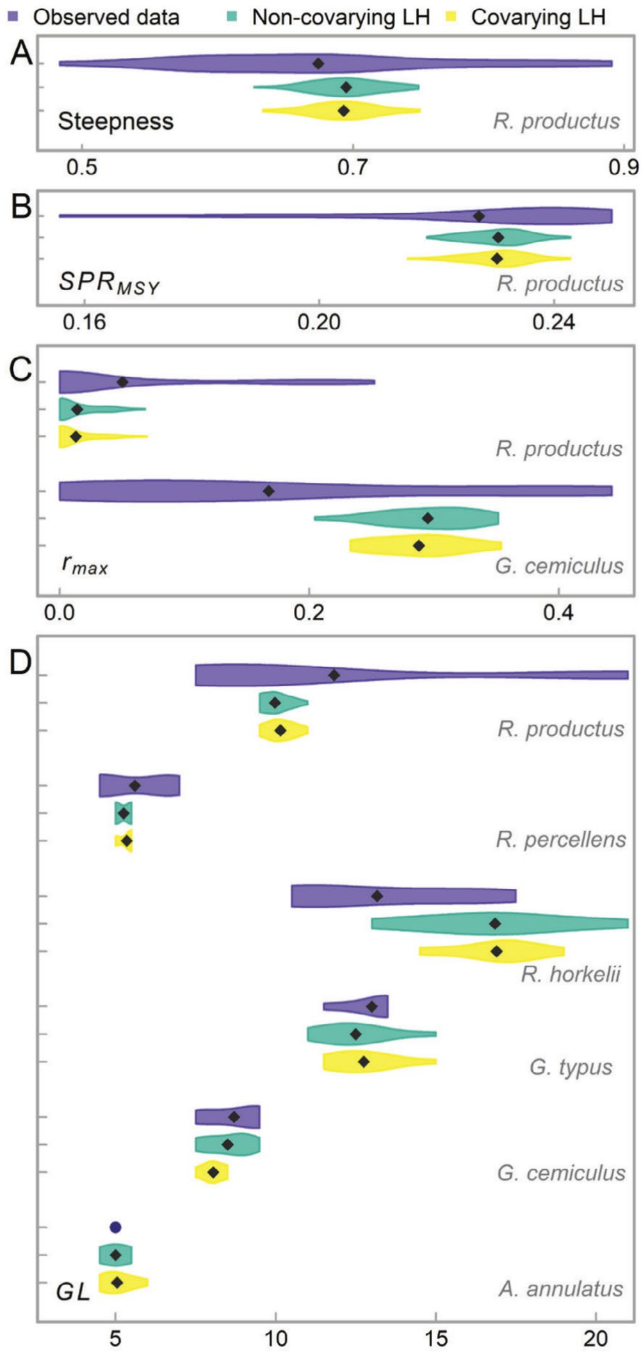

FIGURE 5 | Metrics of population dynamics (A—steepness, B—spawning potential ratio at maximum sustainable yield SPR_{MSY}, C—maximum per capita growth rate of a population r_{max}, D—generation length GL) were estimated with greater uncertainty using the observed life-history trait data (purple), compared to the reconstructed parameters without (green) and with (yellow) covariance retained. This analysis only included species with published values of the life-history traits required to calculate each management metric. Mean values are shown as black points.

across a large group of data-poor fishes. This was possible, in part, due to the relatively narrow range of annual fecundity values among viviparous species. Using reconstructed life-history trait values to calculate management metrics provides a first approximation of these values for extremely data-limited species. We also show that using reconstructed life-history trait values can markedly decrease associated uncertainty in the derived management metrics compared to using empirical trait data from other populations of the same, or congeneric, species (Figures 4 and 5). Despite this improvement, uncertainty in the derived management metrics was still large across species. Based on mean values, we found strong correlations between life-history traits (asymptotic body length and natural morality) and three management metrics (Figure 6), as well as between the data-intensive management metrics (i.e., steepness and spawning potential ratio) and those that can be resolved with relatively fewer life-history traits and are already used in the conservation assessment of Chondrichthyes including rhino rays (i.e., r_{max} and generation length, Figure 7). Finally, we show that the derived management metrics are relatively insensitive to the phylogenetic structure used to group species when reconstructing missing life-history traits (Figure 8, Appendix S2).

The derived management metrics are provided with large estimates of uncertainty across species. This uncertainty reflects intraspecific variability and measurement error in the observed data, as well as model uncertainty associated with limited empirical data across species. Uncertainty in the derived management metrics should be incorporated into any subsequent conservation assessments and management strategy evaluations. Based on the mean values, rhino ray values of steepness were generally higher than reported for other commercially important fish families (Sebastidae, Salmonidae, Scombridae and Lutjanidae, Thorson 2020). This challenges assumptions that long lived, large-bodied species have lower steepness values (Shertzer and Conn 2012). However, the estimated range of mean spawning potential ratios was still clustered in the high teens and low twenties indicating poor spawning potential and high risk of recruitment overfishing (Goodyear 2014). Taken together, these results present a rather optimistic conclusion, whereby an enforced catch moratoria on rhino ray families could support population recovery.

Despite using seven life-history traits to derive steepness and spawning potential ratio, using the mean values we identified strong correlations between these management metrics and major axes of life-history variation (asymptotic body length and mortality). Specifically, we find that mean steepness is generally greater for larger-bodied, longer-lived rhino rays. This result likely reflects the greater litter sizes and lengths at birth of the larger-bodied species relative to the shorter-lived rhino rays in this group, such that a greater number of recruits can be produced each year. Coupled with their longer lifespans, this will allow a higher standing population biomass under natural conditions. This finding agrees with previous research based on a limited number of species reporting that larger rhino ray species from Rhinidae and Glaucostegidae have comparatively higher r_{max} values compared to smaller species from the same families (D'Alberto et al. 2019). That we found strong relationships between mean steepness and major axes of fish life-history variation (i.e., asymptotic body length and mortality) also contrasts with previous studies examining this relationship at higher taxonomic levels and reporting considerably weaker associations (Shertzer and Conn 2012; Thorson 2020). We show that accounting for covariance between life-history traits at the species level does not influence the detection of this relationship (Figure 6). However, we identify large variation in steepness within a

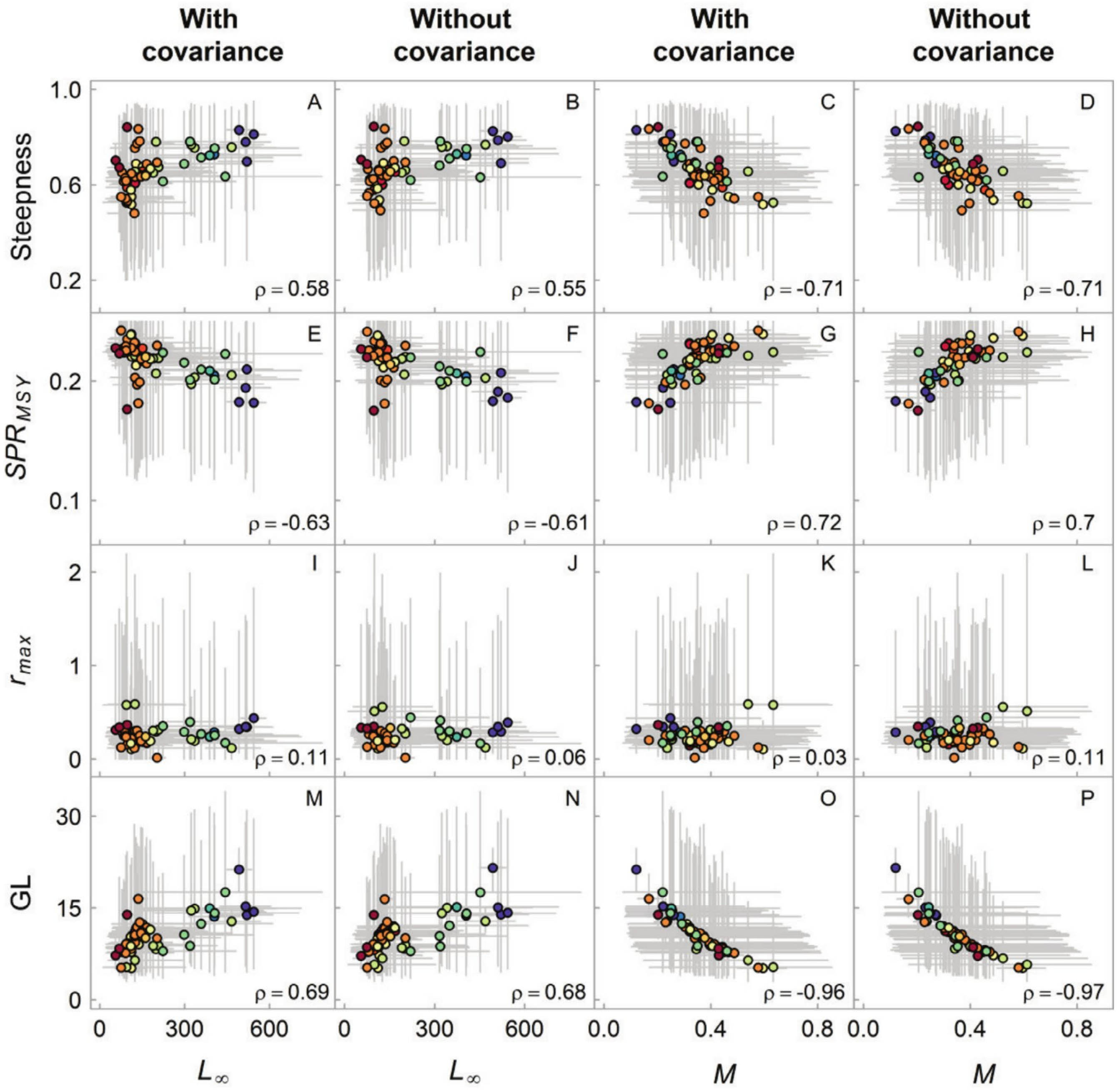

FIGURE 6 | In rhino rays (order Rhinopristiformes), asymptotic body length (L_∞) and natural mortality (M) demonstrate strong correlations with steepness (A–D; lower bound truncated at 0.2 for reasons explained in He et al. 2006) and spawning potential ratio ($\mathrm{SPR}_{\mathrm{MSY}}$; panels E–H). Correlations between life-history traits and intrinsic population growth rate ($r_{\max}$) were weaker (panels I, J), whereas correlations with generation length (GL) were also strong (panels M–P). These results were unaltered by omitting covariance between life-history traits. Uncertainty reflects the 500 randomly selected thinned MCMC draws of the life-history trait data used to calculate the management metrics; mean values with 95% credible intervals. Spearman correlation coefficients (ρ) detailed in each panel. This figure reflects analysis based on phylogenetic Tree 1 (slice length = 100 MY, Appendix S2, Figure A2). Species are coloured by genus following the legend shown in Figure 2. Trait notation detailed in Figure 1.

genus, as well as overlap between genera, and hypothesise that this likely complicates the relationship between steepness and life-history traits when examined using higher taxonomic groupings.

Strong, positive correlations between steepness and asymptotic size are predicted from size-structured community theory (Andersen and Beyer 2015). A correlation between steepness and life-history traits is also implicitly predicted in the derivation of steepness using an age-dependent model (Mangel et al. 2013). However, the estimation of stock–recruitment parameters, such as steepness, is historically based on time series of spawning biomass and subsequent recruitment (Myers 2001; Myers et al. 2002). Therefore, the derivation of this measure has been largely limited to species and populations subject to long-term monitoring. The framework detailed in our study allows species-specific values of steepness and potential spawning ratio to be demographically resolved in data-poor situations.

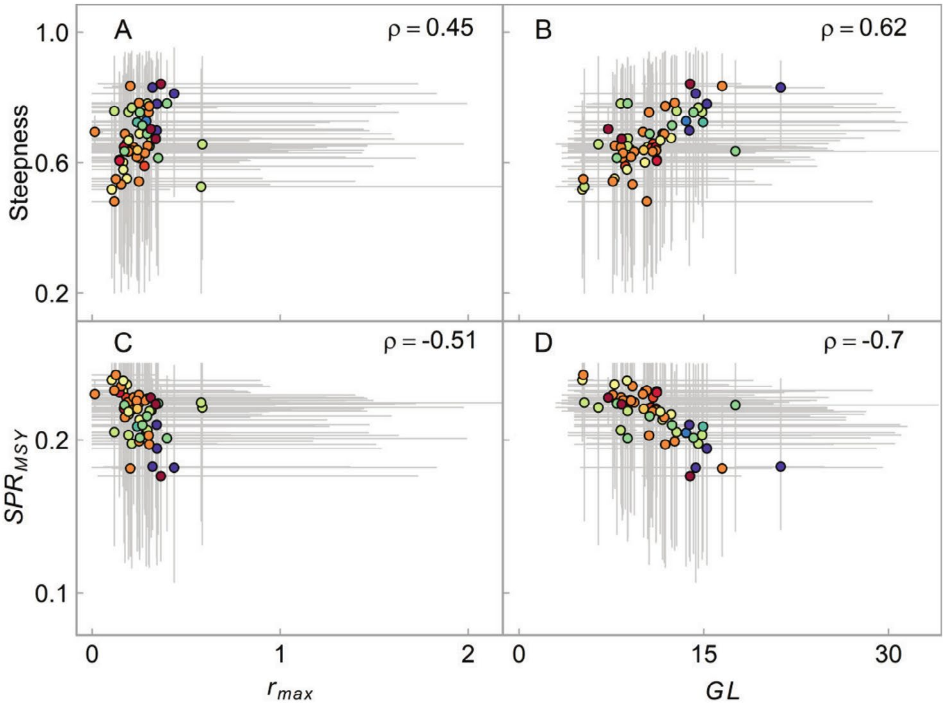

FIGURE 7 | In rhino rays (order Rhinopristiformes), derived estimates of (A, B) steepness (lower bound truncated at 0.2 for reasons explained in He et al. 2006) and (C, D) spawning potential ratio (SPR_{MSY}) demonstrate strong correlations with intrinsic population growth rate (r_{max}) and generation length (GL). Uncertainty reflects the 500 randomly selected thinned MCMC draws of the life-history trait data used to calculate the management metrics; mean values with 95% credible intervals. Spearman correlation coefficients (ρ) detailed in each panel. This figure reflects analysis based on phylogenetic Tree 1 (slice length = 100 MY, Appendix S2, Figure A2). Species are coloured by genus following the legend shown in Figure 2.

This enables first-order estimates of key management metrics for species where, to date, it has not been possible to assess the status of a fish stock and determine whether management action is needed.

Steepness and spawning potential ratio were obtained using imputed life-history parameters, where maximum observed age was used to calculate natural mortality based on the empirical estimator proposed by Kenchington (2014) (Equation 6). This estimator is considered suitable for elasmobranchs and other taxa exhibiting life histories that diverge from the teleost archetype. However, its application requires that the maximum observed age reflect pre-exploitation conditions. Given that rhino rays are subject to both targeted and incidental capture in multispecies fisheries throughout their range, the observed maximum ages used in this analysis likely reflect truncated age structures due to historical and ongoing exploitation. As a result, estimates of natural mortality derived using this method may be downwardly biased, potentially leading to underestimation of population recovery potential. Future analyses would benefit from evaluating the sensitivity of derived management metrics to alternative natural mortality estimators (e.g., Zhou et al. 2022), as well as from comparative assessments using independent methods to estimate management reference points from life-history traits (e.g., Zhou et al. 2020). Furthermore, steepness is not a fixed species-specific trait but can vary over space and time in response to environmental conditions and population dynamics (Thorson et al. 2019). However, for most *Rhinopristiformes*, data limitations preclude temporal reconstruction of life-history traits or intraspecific variation in management metrics. This constraint reflects a broader challenge common to many chondrichthyan taxa, in contrast to more data-rich groups where such analyses are feasible (e.g., Horswill et al. 2019, 2021). Nonetheless, the hierarchical modelling framework used in this study incorporates reported intraspecific variability and measurement error in life-history traits via the observation component. This design allows uncertainty associated with such variation, as well as data availability, to be propagated through to the estimated management metrics. As empirical trait data become increasingly available, re-application of our analysis will improve precision and refine inference.

The reported values of steepness, spawning potential ratio, r_{max} and generation length, with their associated measures of uncertainty (Appendix S2, Table A7), can be used to provide first-order information on species where assessments are currently limited or incomplete. For example, the IUCN Red Listing process and CITES use r_{max} and generation length to define temporal thresholds for population decline and determine extinction risk. We show that our method for deriving values of generation length is potentially more reliable for data-limited species, compared to using scaled estimates from congeneric species (Figure 4). In addition, we show that a species' r_{max} and generation length empirically relates to its steepness and spawning potential ratio. This has been shown theoretically (Mangel et al. 2010), however by demonstrating the relationship at the species level, we show that easily resolved management metrics (i.e., r_{max} and generation length) can provide information on a species ability to respond to direct and indirect fishing pressure. This finding is useful for the current assessment frameworks already using r_{max} and generation length, although the analytical framework described in our paper also facilitates the straightforward calculation of

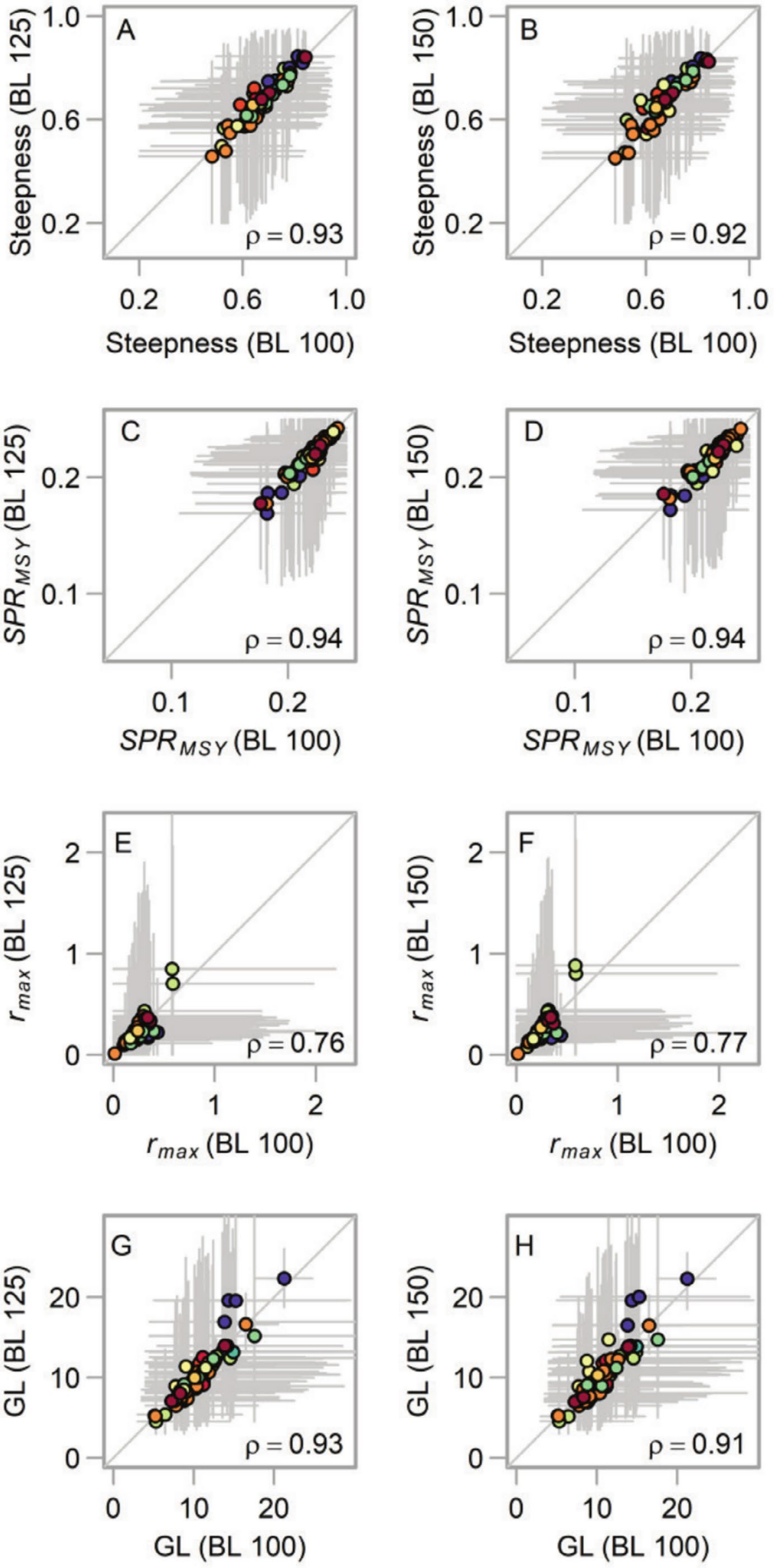

FIGURE 8 | Legend on next page.

FIGURE 8 | Estimated values of (A, B) steepness, (C, D) spawning potential ratio (SPR_{MSY}), (E, F) intrinsic population growth rate (r_{max}) and (G, H) generation length (GL) were not qualitatively altered by changing the phylogenetic branch length (BL) used to group taxonomically similar species. Species are coloured by genus following the legend shown in Figure 2. Uncertainty reflects the 500 randomly selected thinned MCMC draws of the life-history trait data used to calculate the management metrics; mean values with 95% credible intervals. For reference, the 1:1 relationship is also shown as a grey diagonal line. This figure reflects analysis based on phylogenetic Tree 1 (slice length = 100 MY, Appendix S2, Figure A2). We also provide replicate figures for the other phylogenetic trees considered in the Appendix S2, Figures A1.2–A1.4.

additional reference points (i.e., steepness of the Beverton–Holt stock recruitment relationship and spawning potential ratio at maximum sustainable yield), that could considerably enhance the depth of information available for species management.

We tested several methods to account for phylogenetic nonindependence between species when imputing life-history traits. This included no structuring (i.e., all species are considered independent), taxonomically grouping species using genus and phylogenetically grouping species using three different measures of phylogenetic distance. We did not identify a qualitative difference between these approaches based on model fit or the imputed management metrics (Appendix S2). This likely reflects the closely related nature of the species considered in our study (Uyeda et al. 2018). However, it indicates that our framework may also be transferable to other closely related groups of data-poor species where taxonomy is poorly resolved. It also suggests that our results are unlikely to change as the phylogeny of rhino rays is refined. Future work may also consider using the continuous phylogenetic distance between pairwise combinations of species to provide a prior for the multivariate normal distributions determining life-history trade-offs in the hierarchical model (Equation 2). This development will require some consideration of how to connect the dimensions of a species-by-species matrix describing phylogenetic distance to the dimensions of a trait-by-trait matrix linking life-history parameters.

In this study, we describe a modelling framework for imputing life-history traits and deriving management metrics for taxonomic groups of fishes where data limitation prevents stock assessment and the estimation of management and conservation metrics. We show that using reconstructed life-history trait values to derive management metrics can markedly decrease uncertainty compared to using empirical trait data from other populations of the same, or congeneric, species. Based on mean values and applying this framework to *Rhinopristiformes*, we identified strong correlations between major axes of life-history variation and three key management metrics: steepness of the Beverton–Holt stock–recruitment relationship, spawning potential ratio at maximum sustainable yield and generation length. These relationships remained robust when accounting for covariance among life-history traits and phylogenetic nonindependence among species, indicating that the framework may be applicable to other closely related groups where taxonomy is poorly resolved. In addition to point estimates, we provide associated uncertainty intervals with all trait estimates and management metrics that reflect temporal and spatial variation, measurement error and data availability. These uncertainty estimates should be explicitly incorporated into conservation assessments and management strategy evaluations to support precautionary, evidence-based decision-making. Collectively, our findings offer a practical and generalisable approach for maximising information from fragmented datasets to derive first-order estimates of key life-history and management parameters for severely data-limited fish families.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The rhino ray (Rhinopristiformes) dataset was compiled from Mull et al. (2022), accessible from https://www.sharkipedia.org/.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.