
Long-term data show alarming decline of majority of fish species in a Lower Mekong basin fishery

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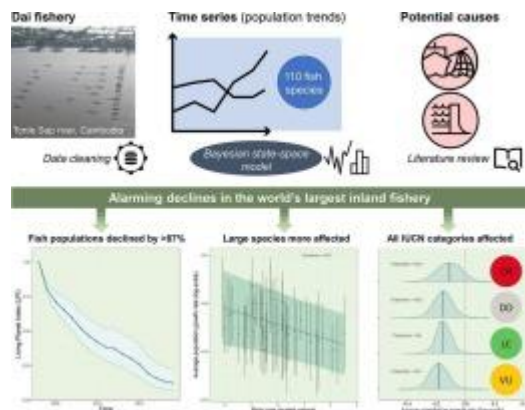
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Abstract :

Overexploitation, habitat fragmentation, and flow alteration are major threats to freshwater biodiversity that can lead to fisheries collapse and species extinction. These threats are particularly alarming in poorly monitored ecosystems where resource use supports the livelihoods of numerous people. The Tonle Sap Lake in Cambodia is such an ecosystem, supporting one of the world's largest freshwater fisheries. Tonle Sap Lake fishes are the focus of indiscriminate harvest affecting species stocks, community composition and food-web structure. Changes in the magnitude and timing of the seasonal flood pulse have also been linked to declines in fish stocks. Yet, changes in fish abundance and species-specific temporal trends remain poorly documented. Analyzing 17 years' time series of fish catch data for 110 species, we show that fish populations have declined by 87.7 %, owing to a statistically significant decline for >74 % species, particularly the largest ones. Despite large variations in species-specific trends - going from locally extinct to >1000 % increase - declines were found across most migratory behaviors, trophic positions or IUCN threat categories, though uncertainty regarding the magnitude of effect precluded us drawing conclusions in some cases. These results, reminiscent of alarming declines in fish stocks in many marine fisheries, provide unequivocal evidence that Tonle Sap fish stocks are increasingly depleted. The consequences of this depletion on ecosystem function are unknown but will undoubtedly affect the livelihoods of millions of people, stressing the need to set-up management strategies aimed to protect both the fishery and its associated diversity. Flow alteration, habitat degradation / fragmentation - especially deforestation of seasonally inundated areas and overharvest - have been reported as major drivers in population dynamics

and community structure, highlighting the need for management efforts aimed at preserving the natural flood pulse, protecting flooded forest habitats, and reducing overfishing.

Graphical abstract



Highlights

► We quantified global and species-wise temporal changes in the biomass of 110 species. ► Overall, fish populations have declined by 87.7 % between 2003 and 2019. ► Declines concerned >70 % species regardless of migratory behavior or IUCN status. ► Management actions are urgently needed to ensure future ecosystem sustainability.

Keywords : Tonle Sap Lake, indiscriminate fishery, living planet index, state-space model, IUCN status, migration.

1 Introduction

Tropical freshwater systems support fisheries that provide food security and incomes for hundreds of millions of people worldwide, often in some of the world's poorest countries (Allan et al., 2005). To date, the majority of research has been conducted in temperate systems (Costello et al., 2012; Heilpern et al., 2022; Pauly et al., 2002) implying that we still know little about the status of biodiversity in tropical systems and therefore about the sustainability of tropical freshwater fisheries, which differ in important ways from temperate fisheries (Welcomme et al., 2010). Tropical fisheries are often composed of extremely diverse species assemblages relative to temperate fisheries, and are also characterized by a diverse array of fishing practices (e.g., large-scale commercial to artisanal and subsistence). This broad set of fishing tactics produces indiscriminate fisheries, in contrast to target fisheries, such that all sizes and species are harvested (Brooks et al., 2008). This indiscriminate approach likely has severe, but relatively unconsidered, implications for the sustainability and maintenance of food production in these highly diverse ecosystems (McCann et al., 2016).

The Mekong River, home to approximately 1000 species of fish, supports the largest inland fishery in the world, producing over two million tons of fish each year (Baran and Myschowoda, 2009; Vu et al., 2022). In Cambodia alone, hundreds of thousands of fish are harvested each year, particularly within the Tonle Sap Lake, providing food and livelihoods for millions of people (Pin et al., 2020). Per capita rates of fish consumption are among the highest in the world and fish provide the majority of protein for the people in the region (Baran et al., 2007). This biodiversity-rich ecosystem is however facing strong pressures including overharvest, habitat fragmentation, and hydrologic alteration; particularly changes related to the Mekong River's seasonal flood pulse.

In Cambodia, indiscriminate fishing has led to declines in the abundance of large-bodied and migratory fish species (Ngor et al., 2018b), though species-specific declines (i.e. population trends of individual species) have not been well studied nor are they well understood. Beyond fishing practice, habitat fragmentation, including the loss of free-flowing status of the Mekong River in China, Lao PDR, and on major tributaries of river in Thailand and Cambodia, is believed to negatively impact fish stocks, particularly migratory fish populations (Arias et al., 2019).

Hydropower-related flow alteration, including higher dry season water levels, lower wet season water levels, and altered flood duration within the Tonle Sap Lake (i.e. the flood pulse; Junk et al., 1989), has also been shown to influence fish production (Lamberts, 2006; Lamberts and Koponen, 2008) and diversity (Chea et al., 2020; Heng et al., 2018, 2017; Ngor et al., 2018a, 2018c; Tudesque et al., 2019). These studies notably showed that higher dry season water levels have negative impacts on fish habitats and spawning areas, including flooded forests along the Cambodian Mekong and the Tonle Sap Lake (Arias et al., 2013, 2012; Kummur and Sarkkula, 2008). Further, lower water levels during the wet season were correlated with lower fish harvests within the Tonle Sap Lake ecosystem as reported from the arrow traps and the Dai fisheries (Ngor et al., 2018b). Reduced flood pulse has also been shown to disrupt spawning cues and fish reproduction (Chea et al., 2020; Hogan, 2011) while hydropeaking alteration in the Sekong, Sesan and Srepok rivers (so-called 3S river basin) has been associated with decreased fish diversity and biomass (Montaña et al., 2020).

Taken together, these threats may have significant, widespread impacts on fish populations and could represent an existential threat to Mekong River fisheries. Previous studies have predicted future Mekong freshwater megafauna (i.e. mammals, fish, reptiles and amphibians that can reach 30 kg or more) declines owing to connectivity loss (He et al., 2021). Likewise, research from

other river basins has shown dramatic decline of fisheries and biodiversity facing similar threats (Liu et al., 2019; Turvey et al., 2010). While these studies provide important knowledge regarding the dynamic and the putative fate of biodiversity in tropical fisheries, we still have a poor understanding of fish biodiversity trends (at population, species or community levels) within the world's largest inland fishery. To date, only one study investigated fish population trends within the Tonle Sap Lake (Ngor et al., 2018b). It highlighted strong declines in the catch of large-bodied migratory fish, while some small-bodied species increased, resulting in an overall stable fish harvest. Consistent with the predicted effects of indiscriminate fishing theory (McCann et al., 2016), these previous observations may be a warning signal of future negative impacts and emphasize the urgent need for continued monitoring of fish catch to estimate ongoing population trends. Indeed, a robust assessment of population trends is paramount to provide a useful perspective on the direction and future condition of biodiversity (Leung et al., 2020; Puurtinen et al., 2022). For instance, population trends, whether increasing, stable, or declining, are important factors in assessing extinction risk, and time series data, where available, is a key input into Red List assessments (Butchart et al., 2006). This knowledge is also of paramount importance for biodiversity conservation practitioners who need robust assessments of extinction risk (at global, regional, national and local scales) to prioritize the use of limited resources (Fox et al., 2019; Maes et al., 2015). Overall, a robust characterization of population – and more generally of biodiversity – trends is particularly important given that fisheries collapse would have widespread and disastrous implications for food supply and livelihoods in the lower Mekong River Basin.

In this study, we expanded on the work of Ngor et al. (2018a) by using a robust hierarchical state-space approach and analyzing the most recent data available to provide an updated assessment of

trends for each of the 110 fish species using relative change measures. We further evaluated overall changes for the whole community of fish using the Living Planet Index (LPI). Finally, we explored how trends varied depending on fish size, IUCN threat categories, trophic position and migratory status. Our results provide compelling evidence that fish stocks have declined dramatically for most species, particularly the largest ones, regardless of their IUCN status.

2 Material and Methods

2.1 Study site

2.1.1 Tonle Sap River

The Tonle Sap River is characterized by a unique reversal of its flow across the year (Arias et al., 2013; Heng et al., 2017). The river connects the Mekong River to the Tonle Sap (floodplain) Lake, the largest lake in Southeast Asia, which is situated about 130 km northwest of the junction with the Mekong River (Fig. 1). The reversal of the Tonle Sap River flow (inflow) occurs each year during the wet season (late June to September) when the rising water levels of the Mekong River inundate the Tonle Sap Lake and its surrounding floodplains. When the Mekong's water level recedes - usually after the peak flow in early October - the Tonle Sap River resumes its normal flow (outflow) from the Tonle Sap Lake to the Mekong River.

During the period of inflow, a significant quantity of both larval and adult fish is transported through the Tonle Sap River within the Tonle Sap Lake and its surrounding floodplains (Chhuoy et al., 2022; Cowx et al., 2015). These fishes are composed mainly of migratory species that spawn upstream in the Mekong River system and that subsequently use the downstream floodplains of Tonle Sap system as a feeding and rearing ground; a key component of their life

cycles (A.S. Halls et al., 2013). During the outflow period, these migratory fish species migrate back to the Mekong River through the Tonle Sap River to escape the harsh environmental conditions (shallow, anoxic conditions) characteristic of the Tonle Sap floodplain during the dry season (Cowx et al., 2015; Ngor et al., 2018c). The Tonle Sap River is therefore a strategic location acting as a natural fish pass for many Mekong migratory fishes to complete their life cycles. More than 100 species of the Mekong fishes have been recorded to use the Tonle Sap River during the inflow period while some 140 species of fish use this river during the outflow period to migrate back to the Mekong River (Halls et al., 2013; Ngor et al., 2018a). The phenomenon of seasonal flood pulse drives fisheries productivity in the Lower Mekong Basin which hosts one of the world's largest inland fisheries on Earth (Cooperman et al., 2012).

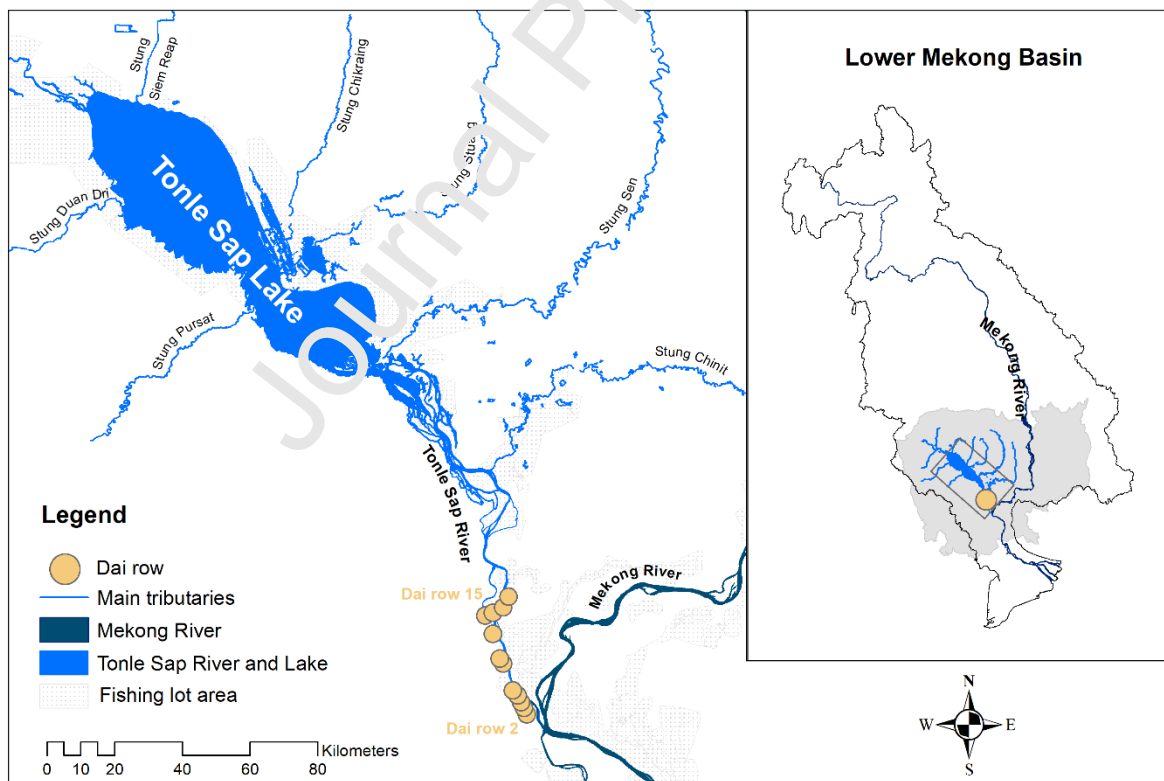


Fig 1. Map of the Tonle Sap lake and its main tributaries within the Lower Mekong Basin. The position of Dai units along the Tonle Sap River where the data have been collected are highlighted as yellow points.

2.1.2 The Dai Fishery

The Dai Fishery is a century-old, commercial-scale fishery, and the largest fishery in the Lower Mekong Basin (Halls et al., 2013). It consists of a stationary bag net, facing the downstream flow, to filter the fishes that migrate between the Tonle Sap floodplain and the Mekong River. The fishery operates in the lower reach of the Tonle Sap River, some four to thirty-five km north of Phnom Penh (Halls et al., 2013; Ngor, 2000; Ngor et al., 2018b). The fishery, as defined by the law on Cambodian fisheries, takes place only during the dry season (from October through March) when water is flowing from the Tonle Sap Lake to the Mekong River. In any given year, this fishing season may start late or end early depending on the magnitude of the flood pulse. Details about the specifications of the Dai fishing gears, season of fishing, position of Dai units and its fishing operation in river as well as the fish species composition reported at Dai Fishery are described in (Deap et al., 2003; Halls et al., 2013; Ngor et al., 2018b).

2.2 Data

2.2.1 Dai Fishery data

Catch data collected at the Dai Fishery has routinely been assessed since the 1994-1995 fishing season by the Mekong River Commission in collaboration with the Fisheries Administration.

However, a more consistent sampling method has been applied for the catch assessment of the

fishery since the 2000-2001 fishing season (Grenouillet et al., 2021). Specifically, the Mekong River Commission initiated a stratified sampling method defined by administrative location (Kandal Province and Phnom Penh Municipality), yield (high and low yield Dai) and lunar phase (peak and low period) to assess the monthly and seasonal catch by species of the fishery. For more information regarding the general concepts and formula used for catch assessments at the Dai Fishery, see (Halls et al., 2013; Ngor et al., 2018b; Stamatopoulos, 2002).

In this study we used biomass data from the 2002/2003 to 2018/2019 fishing seasons. Data for the seasons 2000/2001 and 2001/2002 were discarded owing to concerns regarding the reliability of data for some species where catches were not reported before 2003. Overall, our analysis is based on 110 species with time series length equal to 96 (6 months x 16 years). Missing values were added for the months for which biomass was not reported (these missing values are then estimated in the model; see below).

2.2.2 *Fish trait data*

Overall, our trait data consist of four variables: one continuous variable (body size) and three categorical variables: IUCN threat categories, migration guild and trophic position. Body size ranged from 6 to 300 cm (mean=51.6, sd=54.9). This variable was standardized to z-score (mean=0, sd=1) before model fitting to improve convergence. IUCN categories comprised four modalities: CR (critically endangered; 5 species), DD (data deficient, 13 species), LC (least concerned, 83 species) and VU (vulnerable, 9 species). Migration behavior comprised four modalities: long (long distance migrators, 70 species), short (short distance migrators, 21 species), resident (resident species within the Tonle Sap Lake, 11 species) and estuarine (species spending part of its life cycle in marine estuaries or at sea, 7 species). Trophic position was

represented by three modalities: carnivores (51 species), herbivores (14 species) and omnivores (45 species). Data on body size and trophic position were extracted from FishBase (Froese and Pauly, 2021) whereas information on migration behavior was extracted from Ngor et al., (2018d).

2.3 Statistical analyses

2.3.1 Bayesian model

To analyze the fish biomass time series, we used a hierarchical Bayesian population state-space model accounting for sampling error (de Valpine and Hastings 2002). While such models are traditionally used on log-population count data they are also suited to model other types of continuous variables (e.g. biomass; Millar and Meyer 2000, Marandel et al. 2016). All species were analyzed with the same model, thus making it possible to estimate both species-specific population growth rates and the relationship between population growth rates and species traits at the same time. Specifically, biomass of species s at year t for month m ($X_{s,t,m}$) was assumed to follow a normal distribution with mean $\mu_{s,t,m}$ and species-specific process error variance σ_s^{proc} :

$$X_{s,t,m} \sim \text{Normal}(\mu_{s,t,m}, \sigma_s^{proc})$$

On the log scale, $\mu_{s,t,m}$ was assumed to follow an exponential growth and was therefore modeled using the following state process equation:

$$\mu_{s,t,m} = X_{s,t-1,m} + \alpha_s + \varepsilon_m$$

where $X_{s,t-1,m}$ is the log biomass at time t-1 for month m, α_s is the estimated population growth rate of species s and ε_m is a random effect accounting for the effect of months. Species

population growth rates were assumed to be linearly related to body size (Size), IUCN category (Iucn), migration status (Mig) and trophic position (Troph) following:

$$\alpha_s = \mu_\alpha + \beta_1 \times Size_s + \beta_2 \times Iucn_s + \beta_3 \times Mig_s + \beta_4 \times Troph_s + \varepsilon_s$$

where μ_α is the average population growth rate across all species in the absence of effect of species traits, β_{1-4} are coefficients representing the effect of each species traits and ε_s is a Gaussian error term assumed to follow a normal distribution with mean 0 and standard deviation σ_α representing departure from the mean. We linked the logarithm of the observed biomass to the logarithm of the true (unobserved latent variable) log-biomass ($Y_{s,t,m}$) using the following observation equation:

$$Y_{s,t,m} \sim Normal(X_{s,t,m}, \sigma_s^{obs})$$

where σ_s^{obs} represents the species-specific observation error variance.

2.3.2 Parameter estimation

Posterior samples of model parameters were obtained by Monte Carlo Markov chain (MCMC) sampling with JAGS (Plummer 2003) run through the R environment (R Core Team 2019) using the package R2jags (Su and Yajima 2013). The model was run with three chains with a burn-in of 1,000 iterations and an additional 10,000 iterations with a thinning interval of 10 iterations. For each chain, initial values were randomly selected in different regions of the parameter space. For fixed intercepts (μ_α) and slope coefficients (β_{1-4}) we used normal prior distributions with mean zero and precision of 0.1 (equivalent to a standard deviation of 3.1). Note that since parameters β_2 , β_3 and β_4 are associated to categorical variables, these parameters are actually vectors of coefficients representing the effect of each modality on species population growth rates. To

ensure model identifiability, the first modality was set to zero (Kruschke 2014). For standard deviations (σ_s^{proc} , σ_s^{obs} and σ_α), we used half-Cauchy distributions (Gelman et al. 1996).

Missing values were considered as parameters within the model.

Effect sizes of species traits were estimated using the median of their posterior distributions while significant departures from zero (indicating an effect) were estimated using 95% Highest Posterior Density (HPD) intervals (function `boa.hpd` in the R package `boa`; Smith 2007).

2.3.3 *Convergence assessment and model fit*

Convergence was assessed for all parameters using the Gelman and Rubin convergence diagnostic with a threshold fixed to 1.1 (Gelman and Rubin 1992). As a posterior predictive check, we use the sum of squared standardized Pearson residuals (Gelman et al. 2013). This metric was calculated for both the observed data and a replicated dataset derived from model estimates. From the obtained values, we quantified the proportion of MCMC samples in which the distance of observed data to the model is greater than the distance of replicated data to the model. This quantification defines the so-called Bayesian p-value where values close to 0.5 indicate a good model fit, whereas values close to 0 or 1 indicate a lack of fit. The Bayesian p-value of our model equaled 0.55 indicating a good fit to the data.

2.3.4 *Measuring biodiversity and species-specific trends*

To measure the temporal trend of the whole community of fish (i.e. the 110 species), we used the Living Planet Index (LPI) which has been widely used in recent years to measure global population changes of various taxonomic groups (see e.g. Pacoureau et al. 2021 for sharks and

rays). The LPI can be calculated for a given region or taxonomic group by averaging LPI over the relevant spatial (e.g. sites within a region) or taxonomic (e.g. species within families) units. Here, the LPI at time t (where t is a sampling season stretching from October to March) was calculated as:

$$LPI_t = LPI_{t-1} \times 10^{\bar{d}_t}$$

where $LPI_{t=1}$ is equal to 1 and where \bar{d}_t is the mean of the logarithm of the predicted growth rate in a given year t across species. It was calculated as:

$$\bar{d}_t = \frac{1}{Nsp} \sum_{i=1}^{Nsp} \log_{10} \left(\frac{I_t}{I_{t-1}} \right)$$

where Nsp is the number of species and I_t denotes the posterior distribution of the estimated biomass in year t averaged over the sampling season (i.e. from October to March). Note that the LPI does not measure changes in abundance or biomass and that if the LPI is erroneously interpreted as such, the measure is biased downwards because geometric averaging treats proportional increases and decreases as equal, when the impacts on abundance (or biomass) actually differ (Puurtilinen et al., 2022). Still, the LPI provides comparable estimations of population trends.

To evaluate temporal changes in the biomass estimated for each of the 110 species, we calculated, for each year and species, the relative change in the biomass estimated in year t relative to the one estimated for the first year of the time series as:

$$R_{s,t} = \frac{Y_{s,t}}{Y_{s,1}}$$

where $R_{s,t}$ is the posterior distribution of the estimated relative change in biomass for species s and year t (i.e. averaged through October to March). Similar to the LPI, the index R equals one for the first year whereas values below and above one indicate decline and increase, respectively. To provide a direct assessment of the extent to which the biomass estimated for the different species has changed over the course of the study period, we only report the relative change estimated for the last year of the time series.

While the LPI is useful to highlight global trends in biodiversity, the use of the geometric mean can provide a biased overview of the evolution of biomass in the study system. For instance, if the majority of species is declining but the resulting loss in biomass is compensated by a few increasing species, this compensation would not be captured by the LPI (Puurtilinen et al., 2022). Thus, in addition to the LPI, we also estimated the relative change in the total biomass over time using the same formula as the one used to estimate species-wise relative changes. Total biomass was calculated by summing the biomass estimated for each species, month and year (and sample from the posterior distribution) and then by averaging over month for each year.

For estimated relative changes (both species-specific and total), uncertainties in posterior distribution estimates are reported using 95% HPD intervals.

3 Results

Over the course of the study period, 10 species were no longer present in the 2018-2019 season. Among them, six were also not present in the previous season (*Balantiocheilos melanopterus*, *Channa lucius*, *Clarias batrachus*, *Hemibagrus filamentus*, *Pangasianodon gigas* and *Trichopodus microlepis*). The observed relative change in total biomass strongly varied over the

sampling seasons with a maximum of +99.2% in 2011-2012 and a minimum of -86.5% in 2016-2017. The observed relative change was negative for the last five sampling seasons and equaled -34.7% in the last season.

Overall, we estimated that fish populations have declined by 87.7% according to the LPI (95% HPD interval, [77.9%, 93.2%]) between 2003 and 2019 (Fig. 2A). Among the 110 species considered, 82 (74.5%) showed significant population declines (average relative change: -90.3%; 95% HPD interval: [-72.2%; -98.0%]) while only one (*Polynemus melanochir*) showed a significant increase (relative change: +1281%; 95% HPD interval: [196%; 3755%]) (Fig. 2C). The remaining 27 species (24.5%) showed too large uncertainties to draw any firm conclusion, though the average tendency was clearly toward an increase (average relative change: +241%; 95% HPD interval: [-75.3%; 891%]). The resulting balance is a large decline in the estimated total biomass (average relative change: -75.2%; 95% HPD interval: [-53.9%; -89.5%]; Fig. 2B).

overlapping zero) for negative and positive trends, respectively, whereas grey colors highlight species where estimated changes are too uncertain to draw meaningful conclusions.

Large-bodied species showed larger declines (i.e. more negative population growth rates; $\beta_1 = -0.04$; 95% HPD interval = $[-0.07, -0.01]$) than small-bodied species (99.7% posterior probability for this pattern; Fig. 3A). Declines were also larger for species that were originally abundant (e.g. *Helicophagus leptorhynchus*, *Channa micropeltes*) whereas species that were originally absent (e.g. *Polynemus melanochir*, *Rasbora borapetensis*) or rare (e.g. *Polynemus aquilonaris*, *Trichopodus trichopterus*) rather showed a tendency for an exponential increase (Fig. 3B).

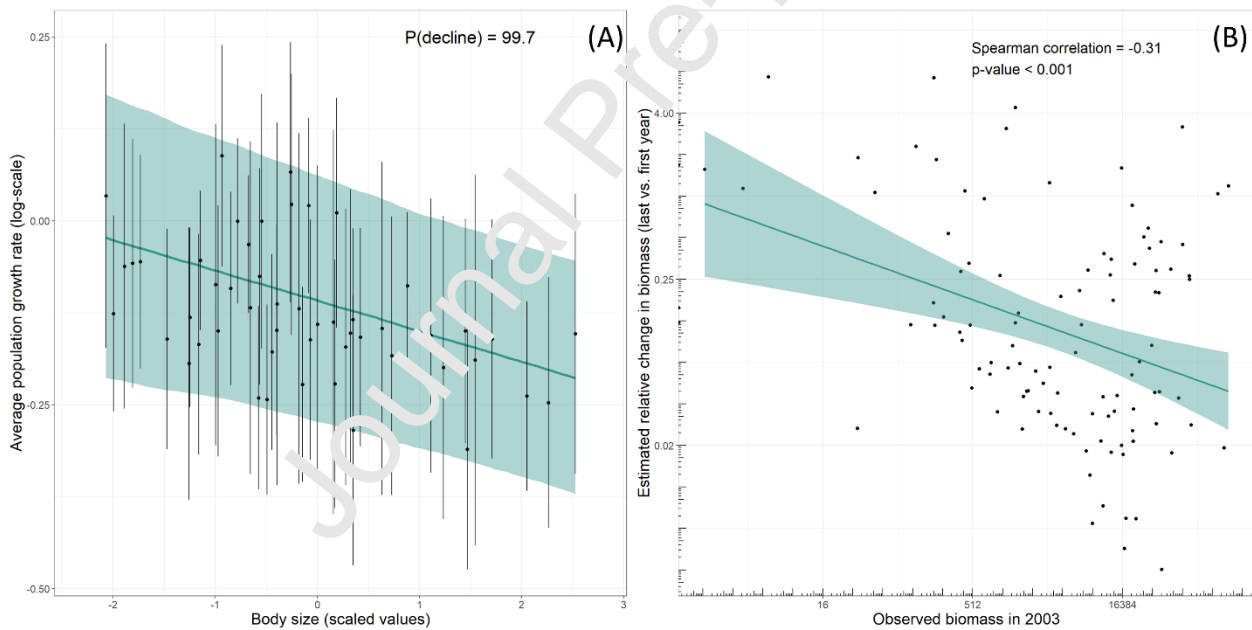


Fig 3. Influence of species body size and original biomass on species trends. (A) Estimated relationship (parameter β_1 in the Bayesian model) between body size (scaled) and the estimated species-wise growth rate (parameter α_s in the Bayesian model) where the green line denotes the median of the posterior distribution and the shaded area the corresponding 95% Highest Posterior Density (HPD) interval. Black points and associated vertical black lines represent the

median and 95% HPD interval of species-wise growth rates. $P(\text{decline})$ is the proportion of Monte Carlo Markov chain (MCMC) samples with a negative value and can be interpreted as the probability that the relationship is actually negative. (B) Relationship between the estimated relative change in biomass (ratio between the biomass estimated for the last and first years) and the observed biomass in the first year of the time series. The line and the shaded area are results from a linear regression but are only shown for illustrative purposes (the relationship was tested with a Spearman rank correlation).

Regarding the effect of other species traits (trophic position, migratory behavior and IUCN threat categories), although effects were uncertain in some cases (wide 95% HPD intervals), strong posterior probabilities for declines were observed in most cases (Fig. 4). For instance, for the migratory behavior, resident ($\beta_{2, \text{resident}} = -0.11$; 95% HPD interval = [-0.26, 0.06]) and short-distance migrators ($\beta_{2, \text{short}} = -0.13$; 95% HPD interval = [-0.29, 0.03]) showed 90.3% and 94.4% probabilities for declines, respectively, whereas estuarine ($\beta_{2, \text{estuarine}} = -0.02$; 95% HPD interval = [-0.22, 0.15]) and long-distance migrators ($\beta_{2, \text{long}} = -0.08$; 95% HPD interval = [-0.22, 0.07]) showed lower probabilities (53.9% and 85.4%, respectively) for declines indicating a larger uncertainty for this pattern (Fig. 4A). Regarding trophic status, larger declines (and stronger associated posterior probabilities) were detected for herbivores ($\beta_{4, \text{herbivorous}} = -0.11$; 95% HPD interval = [-0.29, 0.05]; probability for decline = 90%) and carnivores ($\beta_{4, \text{carnivorous}} = -0.10$; 95% HPD interval = [-0.26, 0.06]; probability for decline = 90%) relative to omnivores ($\beta_{4, \text{omnivorous}} = -0.08$; 95% HPD interval = [-0.25, 0.07]; probability for decline = 84.4%) species (Fig. 4B). Except for species classified as “critically endangered” where estimates were too uncertain ($\beta_{3, \text{CR}} = -0.10$; 95% HPD interval = [-0.26, 0.07]; probability for decline = 90.3%), we found strong

probabilities for declines for the remaining three IUCN threat categories (all posterior probabilities for decline > 98%) (Fig. 4C).

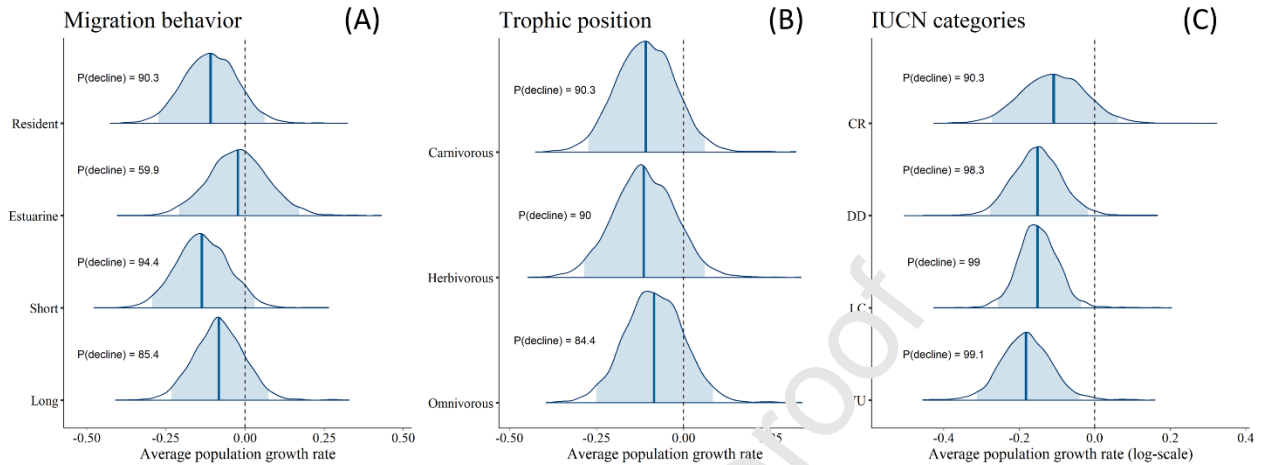


Fig 4. Outputs from the Bayesian model showing the posterior distribution and the posterior probabilities for decline (proportion of Monte Carlo Markov Chain (MCMC) samples with negative growth rates) for (A) migratory behavior, (B) trophic position and (C) IUCN categories.

4 Discussion

Catch data from the largest commercial fishery in the Mekong River Basin indicate populations have declined drastically between 2003 and 2019. Of 110 species, populations of 90 species (8 of which with uncertain estimates) declined by an average of 90% while populations of 20 species (19 of which with uncertain estimates) increased by an average of 366%. These results mirror downward trends shown in other studies, which highlight declines in freshwater fish globally (Cooke et al., 2012), migratory fish (Deinet et al., 2020), and large-bodied fish (He et al., 2019). Moreover, our analysis was based on a comprehensive, continuously updated, publicly available data set that provides quantitative support for predictions that have been made about decreasing

Mekong catch due to main channel and tributary dams (ICEM, 2010), flow alteration and drought (Ringler and Cai, 2007), and overfishing (Chan et al., 2020). While the decline of large-bodied species has been documented by anecdotal accounts and local ecological knowledge surveys (Campbell et al., 2020; Gray et al., 2017), this study is the first to document widespread decline across species assemblages, trophic groups, and life history strategies, and suggests that threats to Mekong fish species extend beyond a small group of what is currently considered the most vulnerable species. Up until now, quantitative analysis indicating broad decline in the population status of most Mekong species has not been available, underscoring the importance of long-term species-specific catch data to detecting trends (White, 2019). These patterns have been difficult to separate out from larger trends, in part because of concomitant increases in the biomass of a smaller number of more resilient species, such as *Polyemus melanochir* in the multi-species fishery.

The pervasive nature of the declines has implications for livelihoods, species conservation, and threat analysis (Hallmann et al., 2021; Ogutu et al., 2009). From a livelihoods perspective, the decline of both overall catch and harvest of the majority of individual species means less food and economic benefit for people and also indicates that the fishery is increasingly supported by a smaller and smaller number of species, potentially influencing overall system stability and adaptive capacity. For example, the number of Dai units in operation in Tonle Sap River has decreased over the study period, dropping from 66 units in the 2014/15 fishing season to 53 units in the 2018/19 fishing season and even to only 44 units in 2021/22 (data from field recording; Peng Bun Ngor personal communication). The percentage of the catch made up of the most common species has increased, and these species have been increasingly targeted by new and more effective fishing gears, which could eventually lead to fisheries collapse, even of fisheries

based on the most resilient species (Heilpern et al., 2022). In the context of species conservation, extinction risk assessments are often based on trends in abundance. The species-specific trends reported here, if found throughout the species' range, would likely qualify many species for listing on the IUCN Red List of Threatened Species (Fox et al., 2019; Vié et al., 2008). For example, populations of species *Channa micropeltes*, *Channa lucius*, and *Trichopodus microlepis* have declined by 99%, 94.3% and 99.5% respectively, virtually disappearing from the fishery over the past 15 years. While these are floodplain resident species (and seem to be relatively common in the Tonle Sap Lake itself), more information is needed from other regions where these fish occur, and initial analysis underscores pervasive declines that transcend taxonomic group or life-history strategy. Likewise, the ubiquitous nature of decline suggests that threats from habitat fragmentation and loss, flow modification, species overexploitation, and climate change transcend the study site and the Tonle Sap River fishery. Indeed, mounting evidence suggests that widespread and rapid deforestation of flooded forest (Lohani et al., 2020), water infrastructure projects within the Tonle Sap Basin (Baran et al., 2007; Winemiller et al., 2016), Mekong tributaries (Ziv et al., 2012), and the Mekong main channel, and overharvest and illegal fishing in both rearing and spawning areas (Sok and Yu, 2021), as well as extreme recent drought events, likely all contribute to fish decline (Arias et al., 2019). More specifically, flow alteration associated with the boom in construction of hydropower dams in the Mekong basin, has been shown to strongly alter the flood-pulse functioning and the duration of the dry season of the Tonle Sap Lake (Kummu and Sarkkula, 2008) with reported effects on fish communities (Chea et al., 2016b; Heng et al., 2017), food-web structure (Chea et al., 2016a; Pool et al., 2017), ecosystem functioning (Holtgrieve et al., 2013), fish abundance (Ngor et al., 2018b), individual fish size (Kc et al., 2017) and fisheries' productivity (Lamberts and Koponen, 2008). Similar trends and patterns have been reported in other highly biodiverse river basins (i.e. Congo,

Amazon) resulting in calls for a more careful strategic planning of dam construction to find a balance between energy needs and the protection of key natural resources (Winemiller et al., 2016).

The results of this study strongly suggest that indiscriminate fishing, coupled with other threats, has led to a dramatic, long-term decline in biomass of most species. Current fishing practices, as well as river basin development more generally, are unsustainable and likely to impact the livelihoods of millions of people (Soukhaphon et al., 2021). Nonetheless, more data is needed, both from other locations within the river basin and from other fisheries, to determine whether the Tonle Sap River Dai fishery is indicative of taxa-level extinction risk. For example, a study of striped catfish *Pangasianodon hypophthalmus* found heavy fishing pressure and decreasing abundance in the Tonle Sap Lake, the Cambodian Mekong River, and the Chao Phraya River in Thailand, resulting in assessment of the species as endangered by IUCN (Campbell et al., 2022; Vidthayanon and Hogan, 2013). Other studies have shown significantly different patterns of abundance and population trends depending on fishing gear and location (Kelson et al., 2021). Moreover, while the Tonle Sap River fishery is the largest commercial harvest in the region, it is only one of dozens of fisheries in the Tonle Sap River, targeting fish of multiple migration guilds, and so a closer analysis of other fisheries would help determine if observed trends hold constant across gear types (Loury et al., 2021). Despite this uncertainty, this analysis clearly showed declines of almost all species regardless of their migratory behavior, trophic position or IUCN status stressing the need to set-up management strategies targeting all fish species. For example, ecosystem based fisheries management, use of indicator species, or prioritization of biodiversity concerns as well as harvest, can help determine overall sustainability of the fishery (Newman et al., 2018; Pikitch et al., 2004). Management strategies, facilitated through partnerships with all

stakeholders and designed to broadly benefit fisheries and biodiversity include environmental flows, improving water quality, protecting essential habitats, regulating resource extraction (e.g. fisheries, timber extraction, sand mining), and safeguarding ecological connectivity (Tickner et al., 2020; Twardek et al., 2022, 2021). Cooke et al. (2022) also recently suggested aggregating data streams for fisheries management while Maasri et al. (2022) highlighted the needs for prioritization of research to benefit fisheries and freshwater biodiversity conservation (Cooke et al., 2022; Maasri et al., 2022). While these steps will be challenging to implement, ongoing efforts to curb overfishing, integrate real-time data streams into research management, and prioritize research that leads to conservation and policy outcomes will benefit both the Mekong's rich aquatic biodiversity and the millions of people in the region.

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Formal analysis: M. Chevalier

Funding acquisition: Z. Hogan

Investigation: G. Grenouillet, M. Chevalier, Z. Hogan

Methodology: M. Chevalier

Project administration: Z. Hogan

Supervision: Z. Hogan, G. Grenouillet

Visualization: M. Chevalier

Writing – original draft: Z. Hogan, M. Chevalier

Writing – review & editing: All authors

Declaration of interests

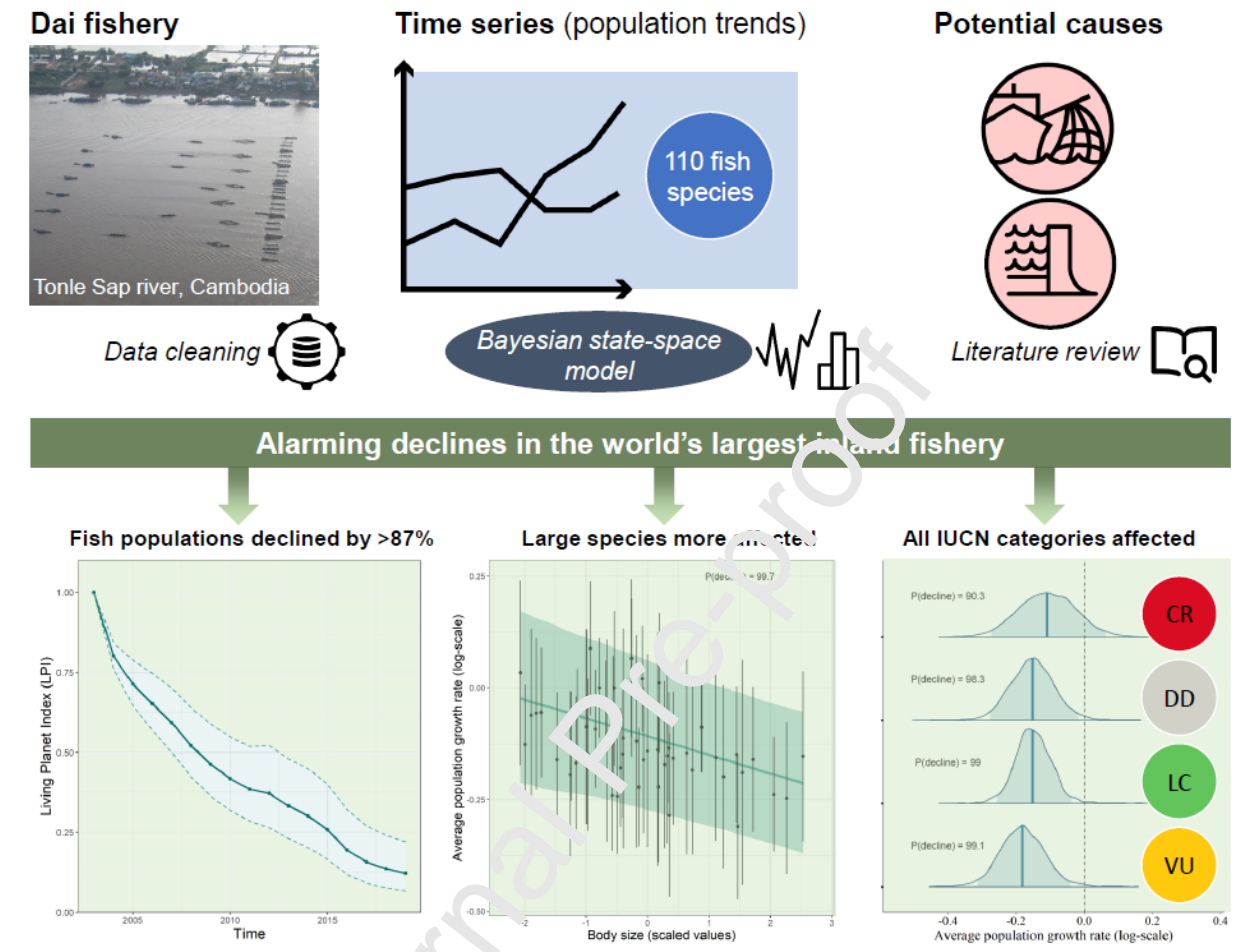
The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Zeb Hogan reports financial support was provided by USAID. Gael Grenouillet reports financial support was provided by French National Research Agency.

Journal Pre-proof

Graphical abstract



Highlights

- We quantified global and species-wise temporal changes in the biomass of 110 species
- Overall, fish populations have declined by 87.7% between 2003 and 2019
- Declines concerned >70% species regardless of migratory behavior or IUCN status
- Management actions are urgently needed to ensure future ecosystem sustainability

Dai fishery

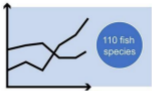


Tonle Sap river, Cambodia

Data cleaning



Time series (population trends)



Bayesian state-space model



Potential causes

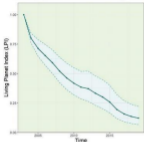


Literature review

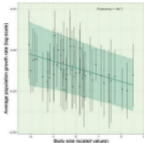


Alarming declines in the world's largest inland fishery

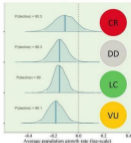
Fish populations declined by >87%



Large species more affected



All IUCN categories affected



Graphics Abstract

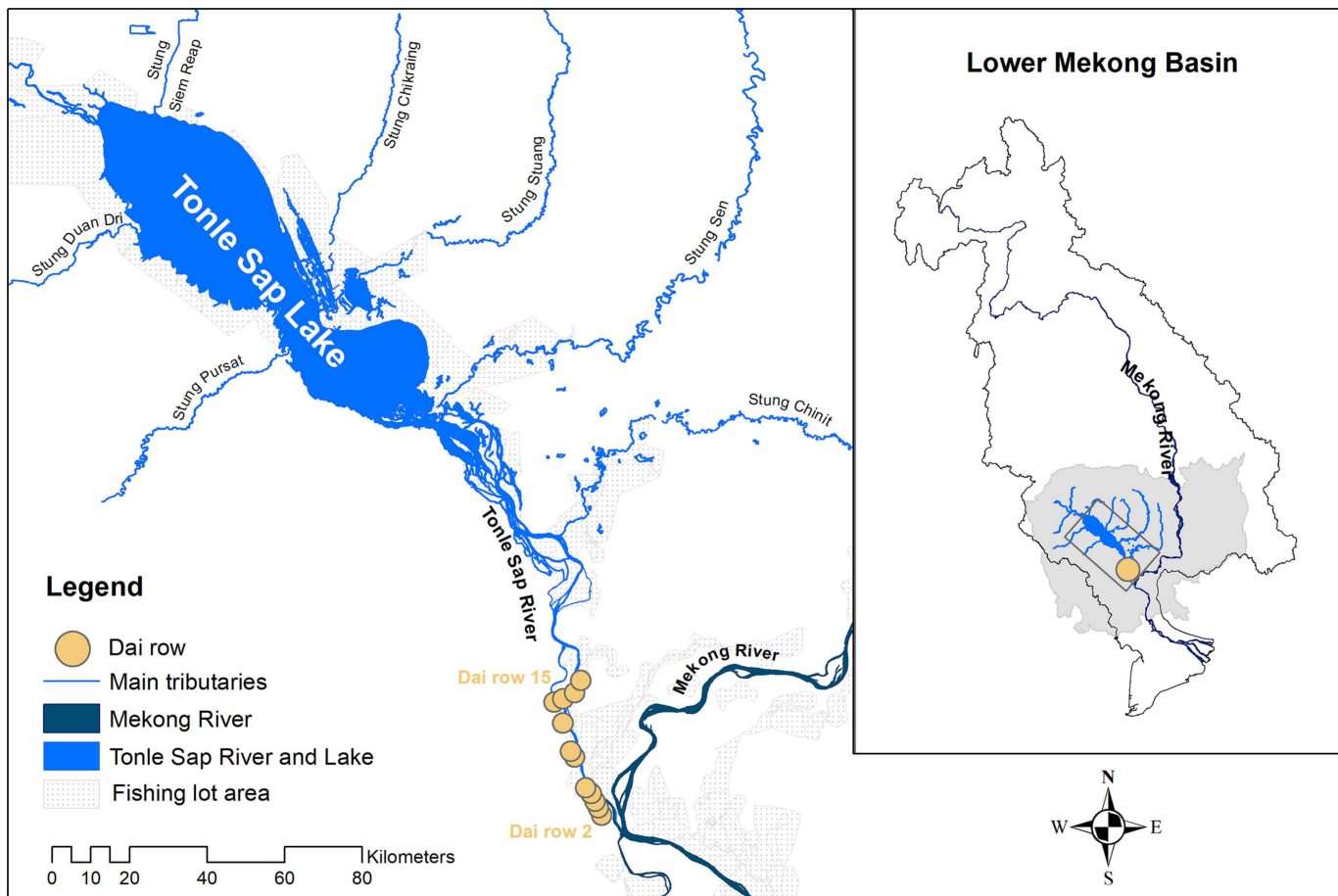


Figure 1

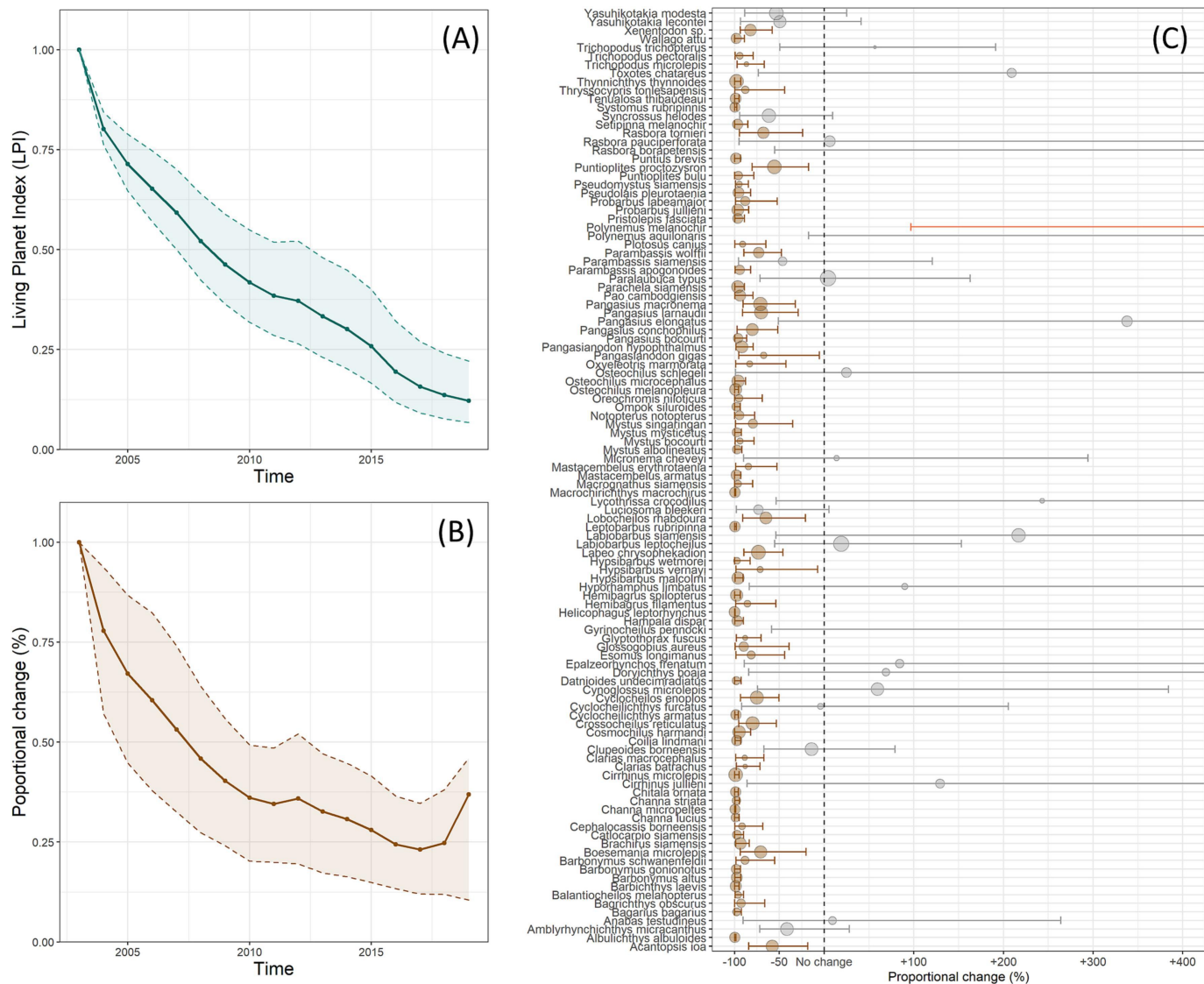


Figure 2

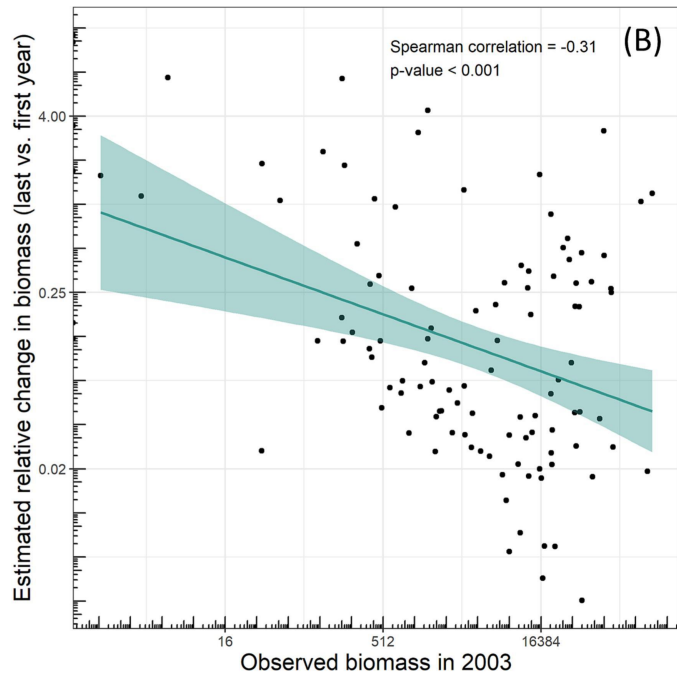
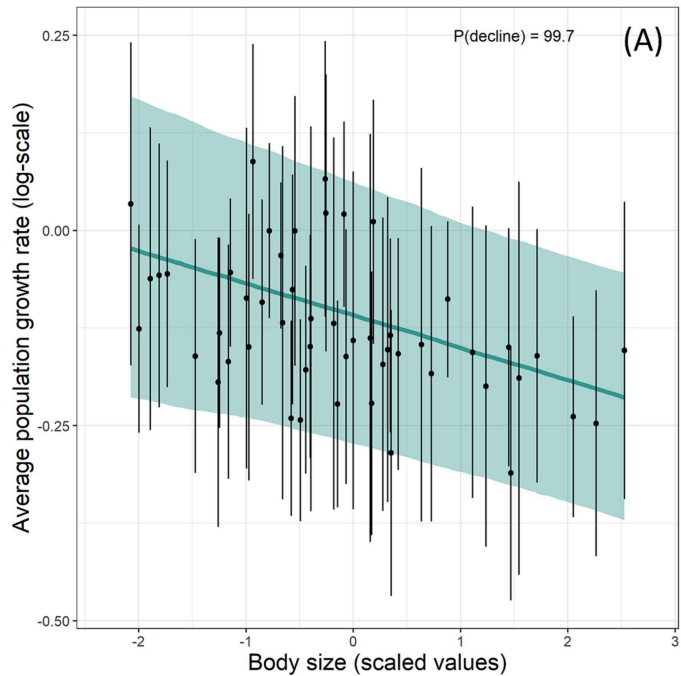


Figure 3

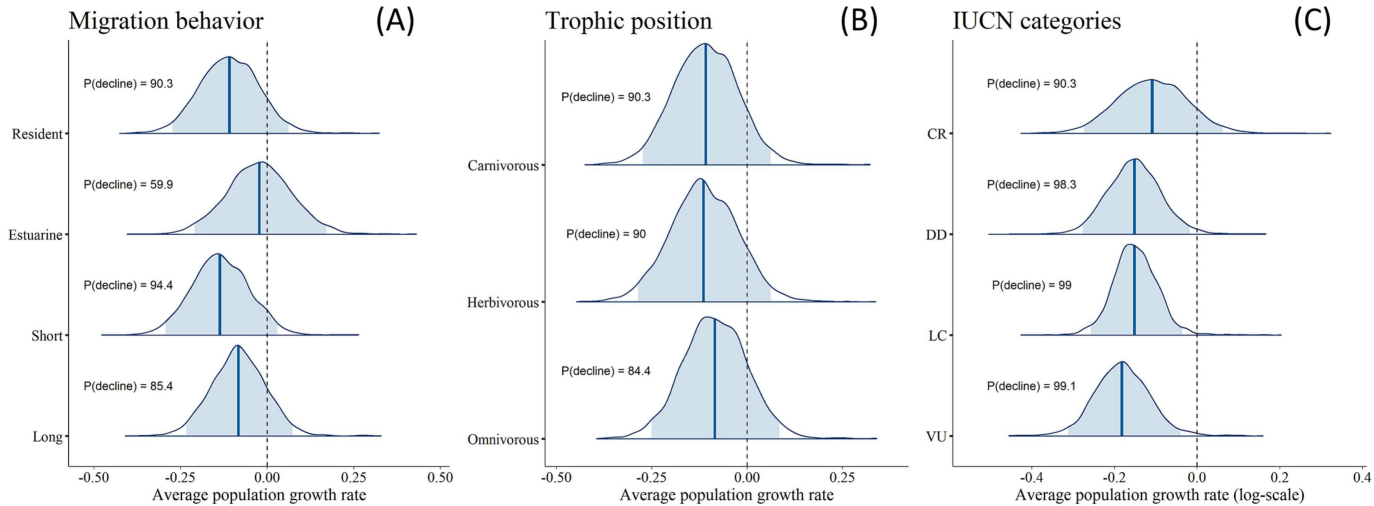


Figure 4