RESEARCH PAPER
https://doi.org/10.1071/MF23108

MARINE & FRESHWATER RESEARCH

Congeneric and sympatric tropical mullets respond differently to environmental variability: insights into coexistence

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Handling Editor:
Bridie Allan

Received: 15 April 2023
Accepted: 18 April 2024
Published: 3 June 2024

Cite this: Rangely J *et al.* (2024) Congeneric and sympatric tropical mullets respond differently to environmental variability: insights into coexistence. *Marine and Freshwater Research* **75**, MF23108. doi:10.1071/MF23108

ABSTRACT

Context. Disentangling mechanisms influencing the seasonal and spatial distribution of fish is essential to understanding population dynamics. In the south-western Atlantic, the sympatric mullets *Mugil curema* and *M. rubrioculus* are closely related and use habitat similarly. However, which processes allow their coexistence is unknown. **Aims.** We tested the hypothesis that the two species exhibit temporally and spatially decoupled habitat-use patterns to allow sympatry due to different responses to environmental drivers. **Methods.** Bayesian zero-inflated count models were used to unravel spatial and temporal distribution patterns of those species in a south-western Atlantic lagoon. **Key results.** The two species display different distributions within the estuary, being spatially and temporally segregated, with *M. curema* mostly inhabiting the inner estuary and *M. rubrioculus* inhabiting coastal marine habitats. **Conclusions.** This decoupling in habitat use might be driven by distinct responses to environmental variability: *M. curema* is influenced by factors such as temperature and dissolved oxygen, whereas *M. rubrioculus* is influenced by variations in salinity. We suggest that the studied species evolved divergent responses to environmental variation to allow coexistence. **Implications.** This study suggests that environmental factors drive mullet abundance, and that zero-inflated count models incorporating those drivers are therefore useful in predicting their spatial and temporal distribution, as well as in standardising abundance trends for stock assessment efforts.

Keywords: ecology, estuary, fish, fisheries, habitat use, *Mugil*, salinity, temperature.

Introduction

Mechanisms underlying the spatial co-occurrence of species have always drawn the attention of ecologists (Winston 1995; Dufour *et al.* 2015). Because sympatric congeneric species tend to be ecologically similar, presenting similar habitat requirements and feeding on roughly the same available resources (Schoener 1974), insights into which mechanism allows their coexistence are considered to be of great importance to understand ecological differentiation and processes behind the structuration of biological communities (Ackerly *et al.* 2006), as well as to provide useful insights to management and conservation (Davidson-Watts *et al.* 2006; Di Bitetti *et al.* 2008; Jirapunpipat *et al.* 2009). Historically, many drivers of species coexistence such as differential habitat selection (Davidson-Watts *et al.* 2006), trait divergence (Ackerly *et al.* 2006; da Silva *et al.* 2019) and niche differentiation (da Silva and Fabré 2019) have been identified. However, the astonishing variability in strategies adopted by co-occurring species warrants a closer species-specific examination of its drivers, especially when it comes to closely related and commercially important species.

At a local scale, ecologically similar species are expected to exhibit morphological differences, as well as spatial or temporal segregation in microhabitat and resource use to reduce competition (Ackerly *et al.* 2006; Souto-Vieira *et al.* 2023). However, for a few congeneric species, these assumptions appear to be in contradiction. The family Mugilidae (mullets), for instance, contains a substantial number of co-occurring species, which are widespread in coastal marine and estuarine habitats in tropical and subtropical regions (Blaber 2000). Despite showing highly conservative morphological features

(Menezes *et al.* 2015) and similar ecological traits such as feeding habits (Garcia *et al.* 2018), habitat requirements have also been demonstrated to significantly overlap between species (Ibáñez *et al.* 2012). Although there is scant evidence of fine-scale habitat partitioning in mullets (Garcia *et al.* 2018), this is a likely mechanism that allows their coexistence since other ecological traits such as feeding habits and morphology are similar.

In the tropical Western Atlantic, mullets are represented by the abundant and commercially important genus *Mugil*, with eight species (Menezes *et al.* 2015). Out of these, *M. curema* and *M. rubrioculus* are closely related and the most morphologically similar species (Neves *et al.* 2020, 2021). *M. curema* and *M. rubrioculus* live in sympatry and have very similar life cycles (Ibáñez *et al.* 2012; Menezes *et al.* 2015; Avigliano *et al.* 2021). Although data for *M. rubrioculus* are highly scarce in the literature (da Silva *et al.* 2017*a*), *M. curema* was previously suggested to be in a state of overfishing or population decline (Mendonça and Bonfante 2011), highlighting the need of gathering relevant ecological information that may aid future management decisions and assessment efforts.

Classical ecological niche theory states that species with similar ecological requirements and life history need to partition resources to maintain coexistence, and habitat heterogeneity plays a crucial role in niche differentiation (Schoener 1974; Jenkins *et al.* 2019). Recent studies revealed that *M. curema* and *M. rubrioculus* display significant interspecific variation in some life-history traits such as length-at-age, maturity and allometry, possible evidence of niche differentiation reflected on ecological traits (Rangely *et al.* 2023). However, it is still not known how these species arrange themselves spatially and temporally relative to each other. The aim of this study was to identify spatial and temporal patterns in the distribution of the white mullet *M. curema* and redeye mullet *M. rubrioculus* in a tropical estuary of the south-western Atlantic. We addressed the following question: what is the role of environmental variability in shaping the distribution patterns of these fish at a local scale? We hypothesised that those morphologically similar, congeneric species may exhibit some degree of spatial and temporal segregation driven by different responses to environmental factors as a mechanism to allow coexistence.

Materials and methods

Study area and sampling

Sampling was executed in the Mundaú Lagoon, located in a tropical and semi-humid region of the south-western Atlantic coast. The area has two well-defined seasons characterised by rainfall patterns: a dry season from October to March and a rainy season from April to September. There, eight sampling sites were placed to cover the whole estuarine gradient: from the upper estuarine to the surf zone at the sea, with two sampling points in each region (upper, middle, lower estuary and sea) (Fig. 1). Each site was sampled monthly from November 2013 to October 2014 with a 1000-m-long and 3-m-wide seine net with a 35-mm mesh opening, a traditional local fishing gear usually utilised to capture mugilids. This net was deployed in the water by artisanal fishers using two small boats to enclose the sampling site for ~20 min, forming a semicircle with a set of baited hooks attached at the end of the net. All sampling procedures were executed systematically by the same fishing team to reduce potential effects of different fishing skills. In this way, we could assume absolute count data represent abundance since the effort was standardised. The two fishing sets from each region are more than 1 km distant from one another, which ensures independence between samples (e.g. de Barros *et al.* 2023). Two fishing sets per site per month were deployed, which totals 96 sets for the whole year. More replication would be necessary to obtain a more accurate picture of the spatial variability on mullet abundance, but we were limited by logistical constraints such as the need for the tides to be below a certain level. Although our sampling is limited regarding the spatial variability in mullet abundance, we argue the data are still sufficient to answer the main question posed in this study about how environmental factors influence mullet abundances because of sufficient temporal coverage. At each sampling point, the following physicochemical and environmental variables were recorded *in situ* from water samples: temperature (°C), turbidity (NTU), salinity, dissolved oxygen (mg L^{-1}), conductivity ($\mu\Omega$ cm^{-1}) and primary productivity (μg Chl-*a* L^{-1}). Abiotic variables were recorded with a YSI 6600 V2 Multiparameter Sonde. In addition, mean monthly rainfall (mm) for the corresponding region was retrieved from SEMARH (see https://semarh.al.gov.br/). Then, fish were identified in the laboratory by specialised taxonomic keys and processed. Sampling and transport were authorised by the Biodiversity Information and Authorisation System (SISBIO, license number 56293-1).

Data analysis

Because of the high proportion of zeros in the mullet count data, log-transformation was not effective in producing normally distributed data. Then, we compared fish counts with a non-parametric Mann–Whitney *U*-test. Effects of environmental variability on the abundance of *M. curema* and *M. rubrioculus* were modelled using Bayesian zero-inflated, random-effects models with Monte Carlo–Markov Chain (MCMC) algorithms. A zero-inflated model was considered the most appropriate after checking if a conventional generalised linear model (GLM) was underfitting zeros in the *R* package *performance* (ver. 0.11.0, see https://cran.r-project.org/package=performance; Lüdecke *et al.* 2021). The number of iterations was set to 500,000 with 10,000 burn-ins in the *R* package *r2jags* (ver. 0.03-08, see https://CRAN.R-project.org/package=R2jags), an implementation of the JAGS (Just Another Gibbs Sampler) for the *R* statistical software (R Foundation for

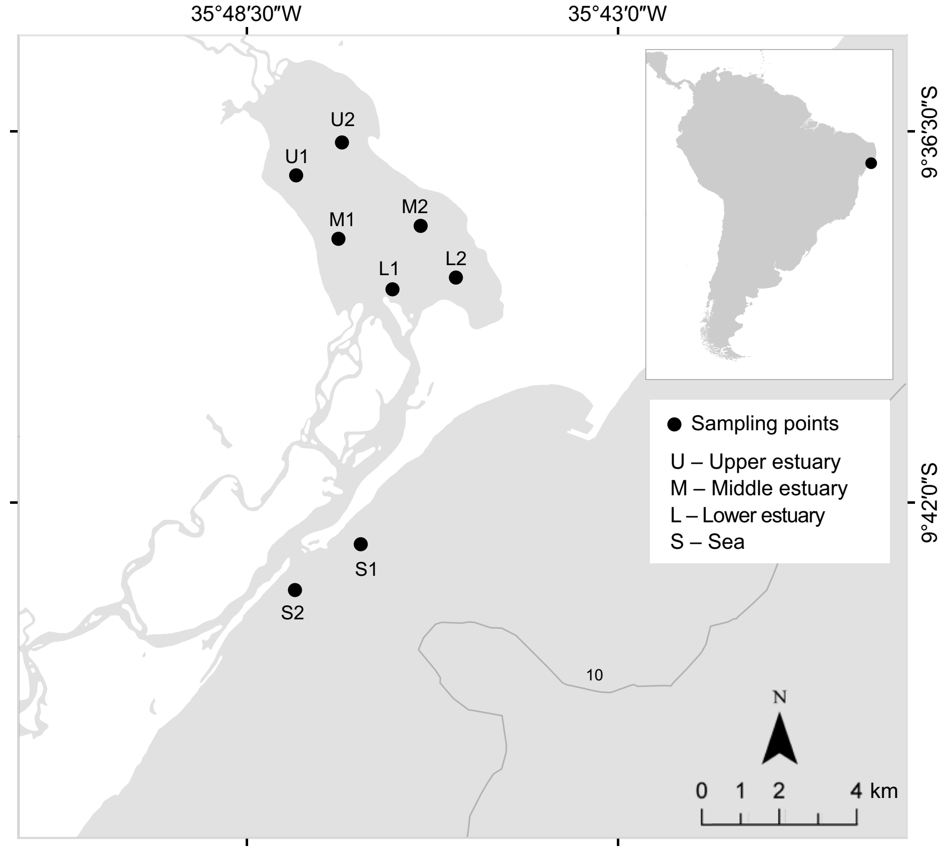

Fig. 1. Map showing the sampling points within the Mundaú Lagoon, north-western Atlantic.

Statistical Computing, Vienna, Austria, see https://www.r-project.org/). A complete description of the modelling framework is as follows: let $Y = \{y_i, i = 1, \ldots, N\}$ be a N-dimensional variable denoting the counts of *M. curema* and *M. rubrioculus* in the study area. We assume Y is generated by a mixture of two distinct processes as follows:

$$p(y_{[i]}|\theta,\lambda) = \begin{cases} \theta + (1-\theta)e^{-\lambda} & \text{for } y_i = 0 \\ (1-\theta)\left(\frac{\lambda^{y_{[i]}}}{y!}\right)e^{-\lambda} & \text{for } y_i > 0 \end{cases}$$

where θ is the overall probability of observing zeros in the data. We model θ as a function of covariates using the logit link:

$$\theta = \frac{e^{(\gamma_0 + \gamma_{[\kappa]}X)}}{1 + e^{(\gamma_0 + \gamma_{[\kappa]}X)}}$$

$$\gamma_0 \sim N(0, \sigma_{\gamma_0})$$

$$\sigma_{\gamma_0} \sim \text{half\_Cauchy}(0,1)$$

$$\gamma_{[\kappa]} \sim N\left(0, \sigma_{\gamma_{[\kappa]}}\right)$$

$$\sigma_{\gamma_{[\kappa]}} \sim \text{half\_Cauchy}(0,1)$$

where γ_0 is an intercept and γ_k is a K-dimensional vector of coefficients for each k-th covariate, whereas X represents a $K \times N$-dimensional matrix of covariates. Coefficients follow non-informative prior distributions centred at zero with half-Cauchy standard deviations. For data points that are not zero, Y is assumed to follow a Poisson distribution with rate parameter λ:

$$Y \sim \text{Poisson}(\lambda)$$

$$\lambda = e^{(\beta_0 + \beta_{[\kappa]}X)}$$

$$\beta_0 \sim N(0, \sigma_{\beta_0})$$

$$\sigma_{\beta_0} \sim \text{half\_Cauchy}(0,1)$$

$$\beta_{[\kappa]} \sim N\left(0, \sigma_{\beta_{[\kappa]}}\right)$$

$$\sigma_{\beta_{[\kappa]}} \sim \text{half\_Cauchy}(0,1)$$

where β_0 is an intercept and $\beta_{[k]}$ is a K-dimensional vector of coefficients for each k-th covariate, and X is the same $K \times$ N-dimensional covariate matrix as in above. The covariates included in the model are environmental data on salinity, temperature (°C), dissolved oxygen (mg L^{-1}), turbidity (NTU), chlorophyll concentration (μg L^{-1}) and rainfall (mm), as well as the abundance of the other mullet (number of individuals) and collection site (Fig. 1). The coefficient for collection site is random, whereas the other parameters are fixed for both count and presence-absence models. The resulting log-likelihood function for the Poisson zero-inflated model may be then written as follows:

$$\begin{aligned}\log L(\beta,\gamma) = {} & \textstyle\sum_{y_{[i]=0}} \log\left[e^{(X\gamma)} + \exp(-e^{(X\gamma)})\right] \\ & + \textstyle\sum_{y_{[i]>0}} \left[y_{[i]} X\beta - e^{(X\beta)} - \log\left(y_{[i]}!\right)\right] \\ & - \textstyle\sum_{i=1}^{N} \log\left[1 + e^{(X\gamma)}\right]\end{aligned}$$

Posterior predictive checks were conducted by sampling from the posterior predictive distributions for the models from both species and comparing these graphically to the observed data. We evaluated all possible model combinations, taking into consideration the list of explanatory variables considered in this study, and identified the set of most adequate models according to the smallest Bayesian Information Criterion (BIC) and Deviance Information Criterion (DIC). Explanatory variables were previously examined for collinearity using Spearman's rank correlation test at a threshold of $r > 0.7$ for highly correlated variables. If collinearity was detected, the models were executed separately with each variable to examine their respective BIC and DIC values. Then, the variable that generated a model with the lowest predictive error was selected for the general model, but the other was excluded. As a result, only water conductivity was excluded because of an expected high correlation with salinity ($r = 0.78$). For model diagnostics, MCMC convergence was checked with the potential scale reduction factor, which compares within and between-chain variances to test the null hypothesis of homogeneity of variances of posterior distribution among parallel chains (Brooks and Gelman 1998). The models were considered to converge when the upper limit of the convergence diagnostic was close to unity. Posterior predictive checks were executed by analysing model residual distribution after comparing predicted and simulated data (Gelman *et al.* 2000). Effects of explanatory variables were considered significant if 80% of the posterior distributions did not overlap zero, following standard procedures that require defined criteria for hypothesis tests within a Bayesian framework (Kruschke 2021).

Results

All measured environmental factors varied spatially and temporally within the study area. Temperature was at its highest (>30ºC) during the dry season and at its lowest during the wet season (<26ºC). The inner lagoon appeared to have hottest temperatures, whereas the sea was colder. Expectedly, salinity was highest at the sea and lowest at the upper and middle lagoon regions, and varied seasonally at all sampled regions with peaks during the dry season. Turbidity was spatially similar, but peaked inside the lagoon at the end of the wet season. Primary productivity was higher inside the lagoon, at which there were peaks during the wet season. Finally, dissolved oxygen was the lowest at the sea (Fig. 2).

A total of 1167 individuals were collected during the sampling period in 96 replicate net hauls, with 985 being *M. curema* and 182 *M. rubrioculus*. Evidently, the white mullet *M. curema* was far more abundant than the redeye mullet *M. rubrioculus* (Mann–Whitney *U*-test, $P < 0.0001$). Even though, the species appeared to exhibit substantial differences in their patterns of abundance within and outside the estuary, which also seems to vary seasonally (Fig. 3). Specifically, the white mullet is evenly distributed inside the estuary and less abundant at the sea during the dry season. In the rainy season, the white mullet is more abundant in the upper lagoon. The redeye mullet is much more abundant at the sea than inside the estuary in the rainy season, and it seems to enter estuarine regions with the advent of the dry season (Fig. 3).

According to the traceplots for the three MCMC chains and the potential scale reduction factor, Bayesian zero-inflated model outputs showed full convergence to the posterior for almost all model parameters after 500,000 iterations and 10,000 burn-ins. The regression coefficient for temperature was the only parameter that exhibited slight signs of non-convergence on the models for both species, possibly due to multiple local minima on the negative log-likelihood profile. Posterior predictive checks show that the model for *M. curema* can accurately predict the observed data, with a normal residual distribution. The model for *M. rubrioculus* was not as good on predicting all the variation and spread of the data, but still useful to describe its general trends (Fig. 4). In fact, after including all variables and random effects in the models, predictive error (DIC statistic) was reduced from more than 2000 to ~250–300 for both models. Posterior distributions and credible intervals of model parameters show that the examined species exhibit different responses to environmental variability. The abundance of the white mullet is positively influenced by temperature and primary productivity, and negatively by dissolved oxygen, turbidity and rainfall. Conversely, abundances of the redeye mullet are only positively influenced by salinity. Both species also seem to negatively respond to increased abundance of their congeneric (Fig. 5, Table 1).

Discussion

Current ecological theory states that sympatric, morphologically alike species with similar life-history traits such as *M. rubrioculis* and *M. curema* (Rangely *et al.* 2023) are

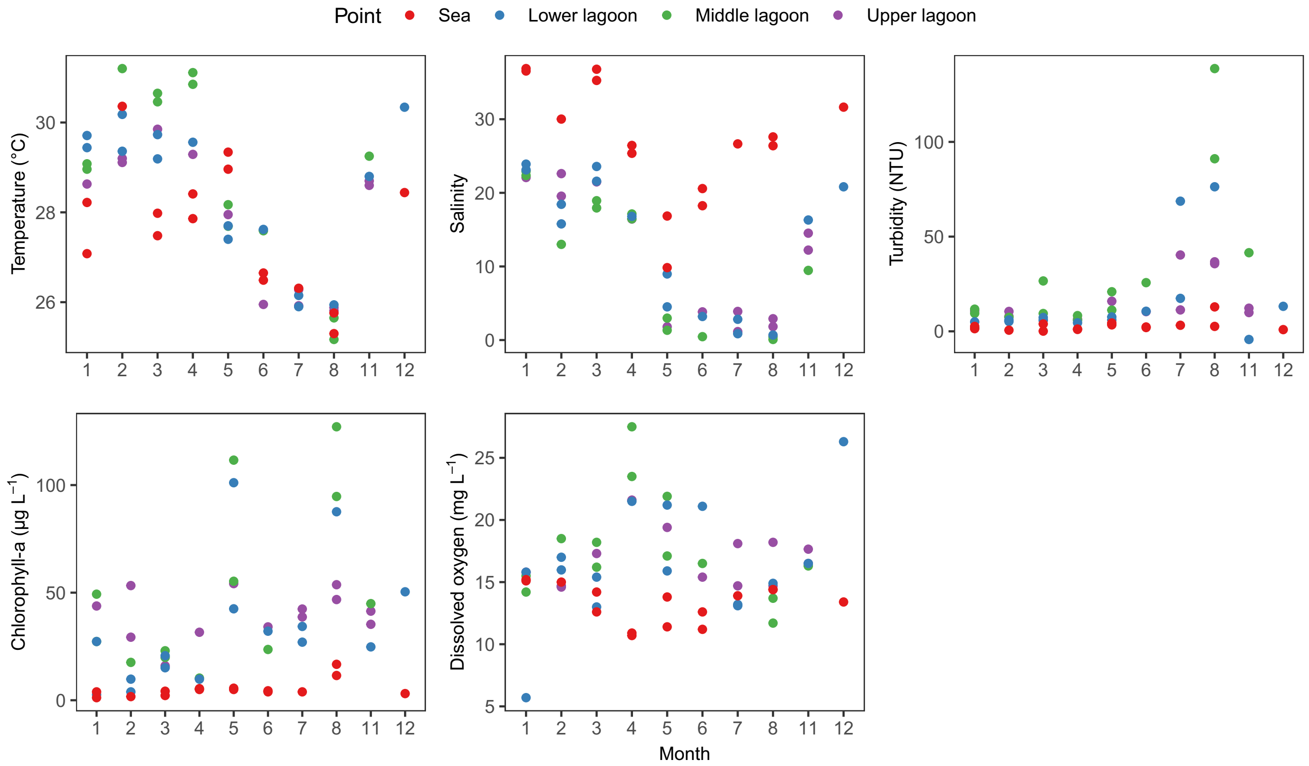

Fig. 2. Monthly variation in environmental parameters measured at different regions of the Mundaú Lagoon, north-western Atlantic.

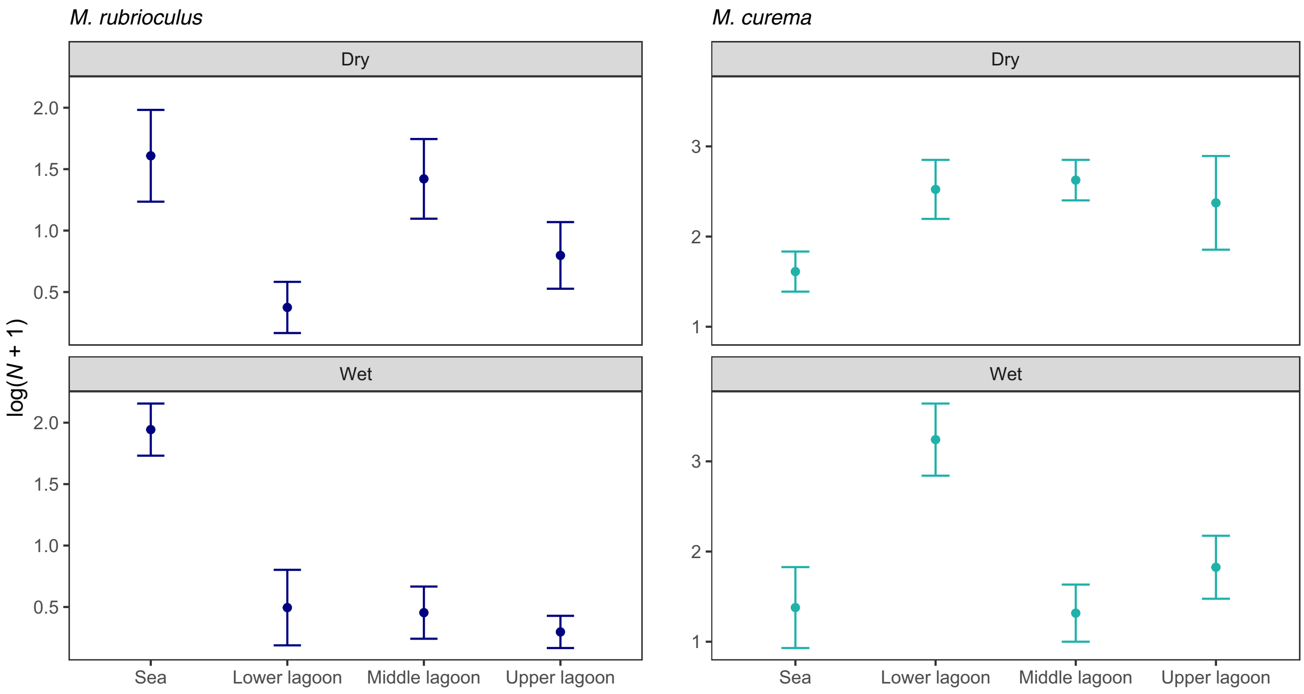

Fig. 3. Spatial and temporal variation in abundance (counts) of white and redeye mullets at the Mundaú Lagoon, north-western Atlantic. The vertical axis shows the log-transformed means and two standard errors of mullet counts.

expected to exhibit mechanisms to allow for coexistence and reduce overlap in resource use that often result in subtle trait divergences (Holt *et al.* 1994; Porreca *et al.* 2017). Our results suggest that the habitat-use patterns of the studied species are

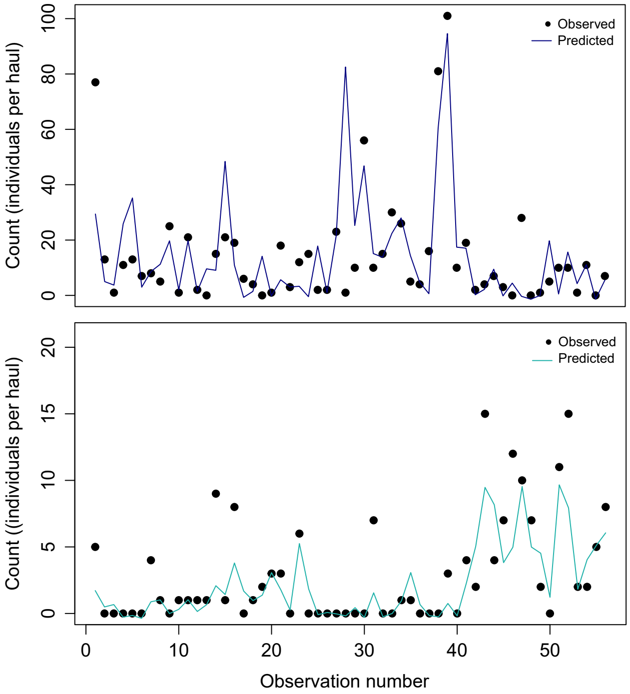

Fig. 4. Posterior predictive check for the Bayesian zero-inflated generalised linear models fit to count data of white (top) and redeye (bottom) mullet species sampled at the Mundaú Lagoon, north-western Atlantic. Individual data points represent observed quantities and coloured lines are median model fits.

spatially and temporally decoupled (Fig. 6) due to different responses to environmental variability. Specifically, *M. rubrioculus*, driven by salinity, occupies outer estuarine reaches and the sea, only penetrating inner estuarine areas during the dry season. *M. curema* is driven by temperature, dissolved oxygen, chlorophyll and turbidity, being able to occupy the inner estuary.

Evolutionary responses to coexistence leading to niche differentiation can vary considerably from mechanisms such as dietary mismatches and different life histories to distinct responses to varying environmental conditions (da Silva *et al.* 2017*b*; Ulrich and Tallman 2021; Rangely *et al.* 2023). The advent of different responses to abiotic factors in sympatric species has long been acknowledged as an evolutionary tool that makes each species have optimal competitive fitness in different environments, hence contributing to ecological partitioning (Lombarte *et al.* 2000). Therefore, one of the mechanisms that could have led to such decoupled life histories in tropical mullets is character displacement, acknowledged as a common process when sympatric species are found to differ in resource use (Goldberg and Lande 2006). Ecological character displacement can be explained as competition-induced differences in life-history traits through phenotypic plasticity, causing differential selection to take place (Slatkin 1980). This process is a key driver of species diversity, also often associated with sympatric speciation (Schluter and McPhail 1992; Tyerman *et al.* 2008). Despite being previously seen as relatively rare in nature because the presence of gene flow usually slows down trait divergence, sympatric speciation is now acknowledged as one of the main mechanisms leading to the formation of species with similar ecological requirements but with fine-scale divergences due to the presence of assortive mating among individuals with a particular trait (Barluenga *et al.* 2006; Jiggins 2006; Bird *et al.* 2012). Therefore, such process is thought to select individuals that perform better in certain environmental conditions (see Johannesson 2001 for a review on sympatric and parallel speciation and its mechanisms). In fact, phylogenetic studies on the genus *Mugil* found that *M. curema* and *M. rubrioculus* are the most closely related among tropical mullets, and their lineages have diverged more recently (Neves *et al.* 2020, 2021), which supports the occurrence of sympatric speciation.

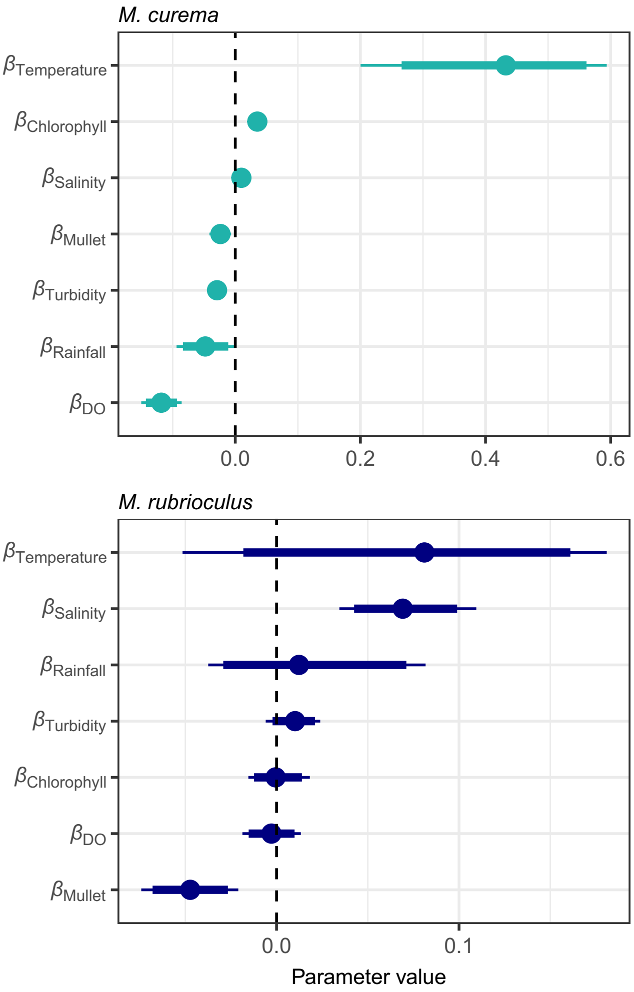

Fig. 5. Influence of environmental parameters on the abundance of white and redeye mullets within the Mundaú Lagoon, north-western Atlantic. Points represent Bayesian posterior medians from the zero-inflated models and lines represent the 80% credible intervals after 500,000 iterations. DO, dissolved oxygen.

Table 1. Summary of posterior distributions for the zero-inflated model parameters predicting the abundance of *M. curema* and *M. rubrioculus*.

	M. curema		***M. rubrioculus***	
Parameter	**Median estimate**	**80% credible interval**	**Median estimate**	**80% credible interval**
Probability of encounter	0.93	0.90 to 0.96	0.67	0.089 to 0.1
Temperature	**0.408**	**0.286 to 0.545**	0.115	−0.151 to 0.478
Salinity	0.002	−0.036 to 0.042	**0.072**	**0.044 to 0.104**
Turbidity	**−0.035**	**−0.044 to −0.026**	0.004	−0.029 to 0.018
Chlorophyll	**0.034**	**0.026 to 0.041**	−0.0014	−0.011 to 0.046
Mullet	**−0.024**	**−0.012 to −0.036**	**−0.047**	**−0.028 to −0.062**
Dissolved O_2	**−0.11**	**−0.149 to −0.072**	−0.042	−0.153 to 0.065
Rainfall	**−0.049**	**−0.077 to −0.01**	−0.001	−0.012 to 0.01

80% credible intervals were selected according to criteria for hypothesis testing within a Bayesian framework. Values highlighted in bold denote a 'significant' effect. 'Mullet' refers to the coefficient for the abundance of the congeneric species affecting the other.

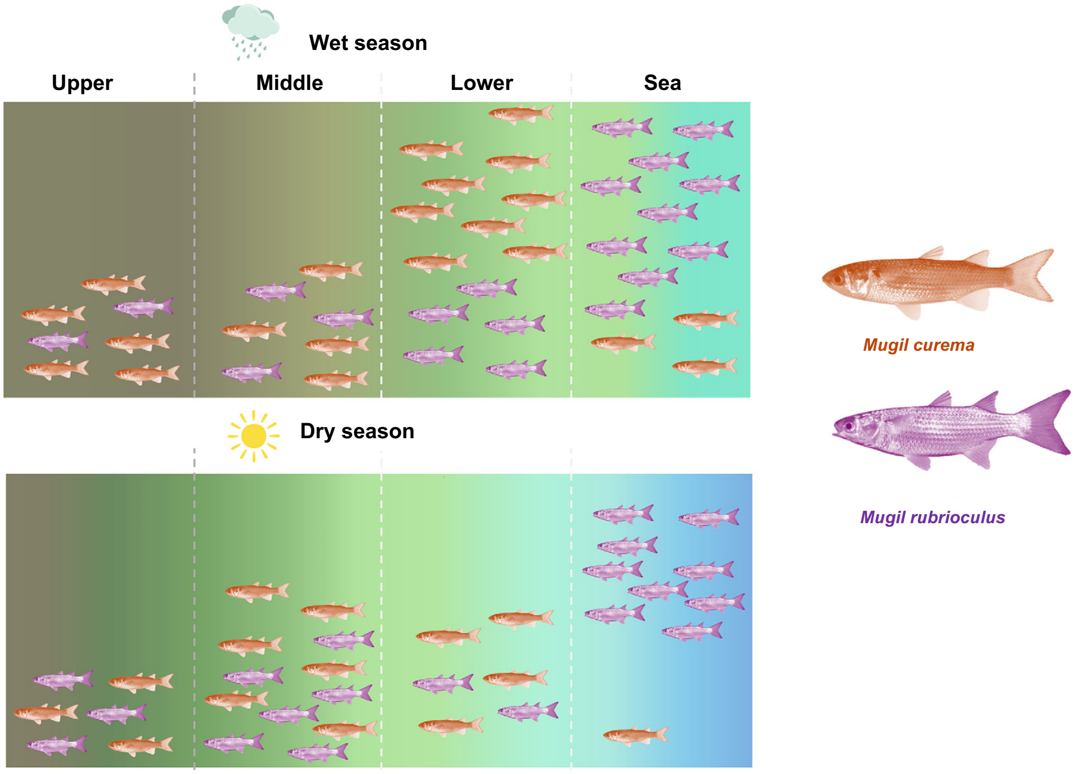

Fig. 6. Infographic illustrating the spatial-temporal movements of white and redeye mullet *M.curema* and *M. rubrioculus* in the Mundaú Lagoon, north-western Atlantic.

Complex interactions between biotic and abiotic variables come into place to explain variations in fish habitat use over time and space (da Silva *et al.* 2021, 2022). An important density-dependent effect on fish populations is interspecific competition, which can be particularly strong on sympatric, closely related species and influences processes such as growth and habitat use (Hasegawa 2016; Andersen *et al.* 2017). As a response, the niche overlap between populations of competing species tends to decrease to minimise competition (Lombarte *et al.* 2000; Johannesson 2001). The white mullet *M. curema*, ubiquitous inside the estuary, is a generalist predator able to adapt to various prey community structures (Garcia *et al.* 2018), which is usually favoured inside estuarine regions due to the commonly higher diversity and abundances of potential prey in its productive waters. Unfortunately, such information is not yet available for the redeye mullet. Even so, we speculate that this species may present less variable feeding habits and, consequently, a stricter ecological niche when compared to *M. curema* because of the less variable spatial distribution found in this study. Then, an apparent resource partitioning, apart from the evident spatial segregation, could be another mechanism allowing such species to coexist (when and where they do), which was previously observed in the study of Garcia *et al.* (2018) between *M. curema* and *M. liza* in a subtropical estuary.

The spatial and temporal decoupling showed by the studied species follows common dynamics of tropical coastal habitats. Estuaries are one of the most dynamic systems among coastal habitats, with marked variations in environmental conditions due to its connection with both terrestrial and oceanic systems (Ram *et al.* 2003; Macedo *et al.* 2023). Accordingly, biological communities are highly affected by such considerable environmental changes, including nekton (Childs *et al.* 2008; Jaureguizar *et al.* 2021). Unlike temperate regions, where temperature variations control most environmental changes and ecological cycles, nekton on tropical estuarine environments are usually driven by seasonal variations in rainfall (wet–dry seasons) (da Silva *et al.* 2018; Macedo *et al.* 2021; de Barros *et al.* 2022), which affect water mixing and nutrient dynamics on estuaries (Medeiros and Kjerfve 1993; Burford *et al.* 2012). The tropical rainy season drives allochthonous entrances from upstream that increase primary productivity, reduce salinity, dissolve oxygen and enhance water turbidity (Kress *et al.* 2002; Carrillo *et al.* 2009), whereas conditions in the dry season include the penetration of sea-like conditions inside the estuary (Azhikodan *et al.* 2021). Our results suggest *M. rubrioculus* might be more adapted to higher salinities (Fig. 5), being mostly restricted to occupy areas outside the estuary during the rainy season (Fig. 3). Conversely, the advent of the dry season allows this species to penetrate the estuary due to increased saltwater intrusion. *M. curema*, not restricted by salinity, was evenly distributed inside the estuary during the rainy season (Fig. 2), where dissolved oxygen is lower, but turbidity and primary productivity are higher. In the dry season, when *M. rubrioculus* can penetrate estuarine regions, *M. curema* showed higher abundances on the upper estuarine region, which could be attributed to effects of interspecific competition.

In marine ecology, it is common to conduct studies that consider single habitat types and disregard meaningful scales with potential influences on ecological patterns of key species with substantial mobility (Pittman and McAlpine 2003; Pittman *et al.* 2004). However, the need to consider broader spatial scales when evaluating the interplay between ecological patterns and processes has been increasingly recognised due to the popularisation of landscape theory (Turner 1989; Pittman *et al.* 2004). Examining broader spatial scales in a landscape perspective when assessing highly mobile species that use multiple habitats in distinct stages of their life cycle such as mullets is of particular importance due to the need to consider the role of habitat connectivity in shaping ecological patterns (Gillanders *et al.* 2003; Mumby *et al.* 2004; Sheaves 2006). Such approach is crucially important to management due to the need to encompass all relevant habitat patches to species of interest at any point of their life cycle on conservation strategies (Pittman *et al.* 2004; Meynecke *et al.* 2008). By showing that the different species studied here display contrasting patterns of habitat use among different elements of the seascape (e.g. different portions of the lagoon and surf zone at the sea) across seasons driven by different responses to environmental factors, we highlight that management decisions to conserve mullet stocks in the region such as habitat conservation strategies should consider all different habitats used throughout their life cycle.

Mullets are an important fishery resource in South America, but few mullet stocks are assessed in the region since those fisheries are artisanal and small scale. With some reports of overfishing (Mendonça and Bonfante 2011) and increasing fishing pressure due to population growth in the region (Blaber and Barletta 2016), assessment and management efforts will be vital to ensure the long-term sustainability of these resources. Fisheries stock assessments primarily rely on abundance indexes to infer trends in the population over time (Maunder and Punt 2004). However, raw abundance indexes often do not reflect the true abundance since variations in the index can also reflect numerous other factors such as sampling artifacts, variations in environmental conditions at the time of sampling, and fishing behaviour (Maunder *et al.* 2006). Therefore, data standardisation (i.e. 'removing' the influence of factors masking the 'true' abundance trajectories) is necessary for the index to be used as a reliable indicator of population trends (Hinton and Maunder 2004). In our study, we demonstrate that the abundances of *M. curema* and *M. rubrioculus* are affected by variations in environmental conditions, which should therefore be accounted for in future assessment efforts. We also highlight the usefulness of modelling frameworks that can handle overdispersed characteristics in the data such as zero inflation, being therefore highly useful for species with patchy distributions. In fact, zero-inflated models have been extensively used in catch per unit effort (CPUE) standardisation procedures, and produce reliable predictions when the correct explanatory variables are accounted for (Brodziak and Walsh 2013; Hiraoka *et al.* 2015; Alvarez-Berastegui *et al.* 2018).

Conclusions

The studied species showed significant spatial segregation in the Mundaú Lagoon estuary, which appears to be a result of divergent adaptation resulting in distinct responses to environmental conditions between species. As a result, the white mullet, which is more abundant, is substantially widespread inside the lagoon. Conversely, the redeye mullet exhibits a remarkably low abundance inside the estuary, whereas it is much more abundant at the sea. The inherent seasonality of tropical estuaries appears to rearrange the species distribution within the different estuarine regions due to different responses to environmental variability. Management decisions towards improving mullet conservation and stock productivity should incorporate the small-scale variability in spatial distribution assessed here into future species distribution models and assessment efforts. Further, the influence of predicted shifts in abiotic parameters due to climate change on the studied species could be explored.

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Data availability. The dataset used for analyses in this study can be made available upon reasonable request to the corresponding author.

Conflicts of interest. The authors declare that they have no conflicts of interest.

Declaration of funding. Data collection was partially funded by the State Funding Agency of Alagoas (FAPEAL) and the National Council for Scientific and Technological Development (CNPq). N. N. Fabré was funded by the Brazilian National Council for Scientific and Technological Development (CNPq, 304433/2022-5).

Acknowledgements. We thank all members of the Laboratory of Ecology, Fish and Fisheries at the Federal University of Alagoas. Special thanks to all fishers who helped with fish sampling and to Mônica Albuquerque for making the infographic art.

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