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Climate effects on fish diversity in the subtropical bays of Texas

Michaela Pawluk[a,*], Masami Fujiwara[b], Fernando Martinez-Andrade[c]

[a] Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX, 77843-2258, USA
[b] Department of Ecology and Conservation Biology, Texas A&M University, College Station, TX, 77843-2258, USA
[c] Coastal Fisheries Division, Texas Parks and Wildlife Department, 6300 Ocean Dr., NRC Bldg. Suite 2500, Corpus Christi, TX, 78412, USA

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ABSTRACT

Climate change affects temperatures, sea level, and salinities, all of which can affect fish distributions. In order to assess the impact of climate change on the marine fish communities of Texas, fish diversity response to climate variables was modeled. Leveraging 33 years of gillnet survey data from eight major bays along the coast of Texas, asymptotic Shannon diversity was estimated for each bay, season, and year using rarefaction analysis. This allowed for the estimation of spatial, temporal, and seasonal trends in fish diversity. In order to assess the impact of climate-related variables on the fish communities of Texas, we associated the Shannon diversity index with environmental variables using a repeated measures model approach. We found significant increasing trends in fish diversity across all eight bays in fall and six of eight bays in spring. Among the variables identified as significant, temperature, salinity, and sea level stood out as most important for driving the increase in fish diversity. Our results suggest that observed increases may be attributable to changing habitat availability resulting from sea-level rise and increasing winter temperatures. Mangrove expansion and warmer winters are likely allowing for range expansion by tropical species, driving the observed increase in fish diversity.

1. Introduction

Biodiversity is recognized as an important community metric for conservation and management due to positive associations with functional diversity and redundancy, and thus with ecosystem stability, resilience, and functioning (Hooper et al., 2005; Stachowicz et al., 2007; Tilman and Downing, 1994; Tilman et al., 1997). Additionally, biodiversity has been shown to be associated with productivity (Danovaro et al., 2008; Hooper et al., 2005; Micheli et al., 2014). Therefore, the maintenance of biodiversity should be one of the top priorities for both conservation and fishery management purposes.

Despite the importance of maintaining marine fish diversity, it is currently changing at an unprecedented rate globally (Hutchings et al., 2010; Worm et al., 2006). Global marine biomass is predicted to decrease substantially over the next century in response to a changing climate especially at higher trophic levels (Jones et al., 2014; Lotze et al., 2019); this will likely negatively impact marine biodiversity (Bryndum-Buchholz et al., 2019). On the other hand, in some temperate coastal ecosystems, the changing climate has led to an expansion of southern associated species leading to increased fish diversity (Beare et al., 2004; Collie et al., 2008; Hiddink and Ter Hofstede, 2008; Murawski, 1993). In general, the response of marine ecosystems to changing climate is highly variable among regions. Consequently, our ability to predict regional changes in biodiversity from climate change is still limited.

While many threats to biodiversity come directly from human interaction through habitat degradation (e.g., increased nutrient input from agriculture, pollution by pesticides and microplastics, and loss of marshland due to development), fragmentation, and over-harvesting (Wood et al., 2000), the indirect anthropogenic effect of climate change is a particularly serious concern because of its large-scale effects on multiple environmental variables that affect marine ecosystems. Coastal ecosystems, in particular, will experience increasing temperatures, sea-level rise, ocean acidification, and increased intensity of storms and extreme weather events (He and Silliman, 2019). As the effects of climate change are thought to be reaching their tipping points, studies of climate impacts on coastal ecosystems are urgently needed. A variety of studies have sought to address this issue; however, relatively few have focused on fish species diversity (Comte and Olden, 2017; Hare et al., 2016; Nicolas et al., 2011; Poloczanska et al., 2016). In particular, it is crucial to identify significant trends in fish diversity and quantify important drivers of fish community dynamics in order to properly

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* Corresponding author. Texas A&M University, College Station, TX, 77843-2258, USA.
E-mail address: pawlukm@aggienetwork.com (M. Pawluk).

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manage and conserve these valuable and highly vulnerable marine ecosystems.

Environmental data from the bays of Texas suggests that abiotic conditions in the bays are shifting, with temperatures increasing, sea level rising, and salinity changing (Fujiwara et al., 2019). Additionally, studies in the Gulf of Mexico, including the Texas coast, have shown expansion of mangrove habitat, suggesting a shift in fish habitat availability (Armitage et al., 2015; Comeaux et al., 2012; Guo et al., 2017). These changes are likely to affect the distribution of fish species within the bays, and thus may affect the diversity and composition of the fish assemblages. Although a recent study focusing on juvenile fish in the bays of Texas found evidence for increasing fish diversity (Fujiwara et al., 2019), it is unclear whether the observed increase simply represents increased dispersal of juveniles to the bays without the subsequent establishment of adults.

Within the Gulf of Mexico, Texas is a major contributor to marine fisheries, with approximately 29 percent of the total fisheries value in the Gulf coming from Texas landings (NOAA Fisheries). The coastal bays of Texas also serve as important nursery habitat for many juvenile fish and invertebrate species (Rozas et al., 2007; Zimmerman and Minello, 1984), highlighting not only the economic importance but the ecological importance of this ecosystem as well. Understanding how climate change will affect marine fish biodiversity within Texas is thus of high importance.

Here, we investigate the change in biodiversity of adult fishes along the subtropical coast of Texas in order to address three main questions: 1) Has climate change affected the adult fish assemblages along the Texas coast? 2) What environmental variables are responsible for driving trends in adult fish diversity? 3) Do seasonal differences exist in the fish community response to the changing climate? We answer these questions using the intensive monitoring data along the Texas coast collected by the Texas Parks and Wildlife Department (TPWD) over a 33-year study period. In order to identify temporal, spatial, and seasonal trends in adult fish diversity, and relate those trends to changing climatic conditions, we estimated the Shannon index for fish in eight major bays along the Texas coast, for spring and fall, in all years. The long-term intensive monitoring data along the Texas coast has provided a rare opportunity to study the change in fish biodiversity in the subtropics, which have been studied far less when compared with temperate and tropical systems.

2. Methods

2.1. Data collection

The species data used for this study were collected by the Coastal Fisheries Division of the TPWD from 1986 to 2018. Data consist of samples collected from Sabine Lake, Galveston Bay, Matagorda Bay, San Antonio Bay, Aransas Bay, Corpus Christi Bay, Upper Laguna Madre, and Lower Laguna Madre (Fig. 1). Sampling was conducted twice each year during a spring sampling season (April–June) and a fall sampling season (September–November). A total of 45 gillnet samples were collected for each bay in all sampling seasons. The gillnets used in sampling consisted of four equal length (45.7 m) panels of differing mesh sizes (76 mm, 102 mm, 127 mm, and 152 mm). Each sampling area was divided into a 1-min latitude by a 1-min longitude sample grid, with each grid square divided into 144 gridlets of 5-s latitude by 5-s longitude. Sampling was conducted following a stratified cluster sampling protocol, whereby grid locations were randomly selected without replacement from the predefined sample grid within each bay, and locations within each grid randomly selected for net placement. Nets were set perpendicular to the shoreline, with the smallest mesh size nearest to the shore, and allowed to soak from sunset to sunrise for an average of 13.5 h (Martinez-Andrade, 2015).

For each sample, all organisms were identified to the lowest taxonomic level possible (often species) and counted. The total catch for each species in each sample was recorded. Total catch data were converted to presence-absence (incidence) data for the sample-based rarefaction method (see Rarefaction Analysis). In addition to the species composition data, concurrent environmental data were recorded for each sample, as well as latitude and longitude of the sample location. Environmental data collected by TPWD included temperature ($^{\mathrm{o}}$C), salinity, dissolved oxygen (ppm), and turbidity (Nephelometric Turbidity Units).

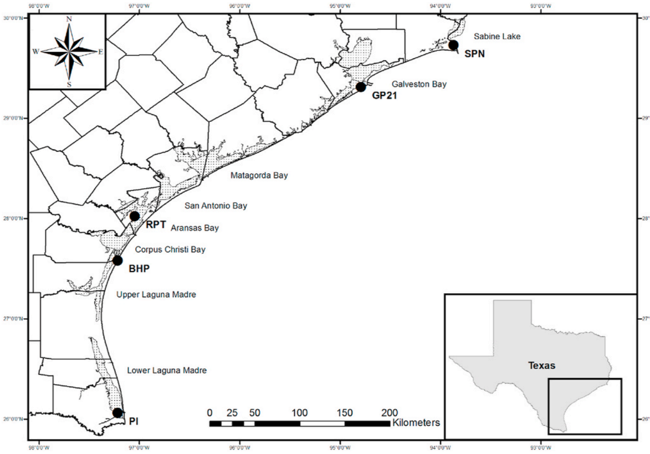

Fig. 1. Locations of the NOAA water level stations for the data used in this study. SPN= Sabine Pass North, station #8770570; GP21 = Galveston Pier 21, station #8771450; RPT = Rockport, station #8774770; BHP=Bob Hall Pier, station #8775870; PI=Port Isabel, station #8779770.

In addition to the environmental data, sea level was included as a potential predictor of species diversity in this study. The monthly mean sea level was obtained from the NOAA Center for Operational Oceanographic Products and Services (CO-OPS, 2018). The stations used for this study were selected based on data availability from 1986 to 2018 (Fig. 1). Sea level data was assigned to each bay based on the closest available station. For all environmental variables, seasonal averages over the sampling periods were calculated for each bay and then standardized using a z-score. Additionally, the data were reduced to only include fish species; invertebrates and genus or family level data were excluded from analyses. Species for which fewer than 3 individuals were observed over the entire study period were considered to be too rare for inclusion and thus were excluded from further analyses. The removal of these species had very little effect on the outcome due to the diversity metric used in this study, Shannon diversity, which takes into account the frequency of each species observed. Additionally, some concern may exist for uncertainty in the data inherent in long-term monitoring studies (Carstensen and Lindegarth, 2016); however, the sampling was done consistently based on the detailed sampling protocols as described by Martinez-Andrade (2015) and was overseen by a quality control committee. Additionally, the TPWD gillnet monitoring program has been recognized for its high quality (Gruss et al., 2018). All analyses conducted in this study were done using the R language and environment for statistical computing (R Core Team, 2018).

2.2. Rarefaction analysis

When comparing species diversity indices across multiple sites, it is necessary to account for the sampling effort at each site in order to make a comparison. This is due to the fact that as sampling effort increases, the number of species observed will also increase (Colwell and Coddington, 1994; Fisher et al., 1943; Sanders, 1968; Simberloff, 1972). Although in this study sampling effort was standardized across bays, rarefaction analyses provide the additional benefit of being able to extrapolate the diversity of a given site to its asymptotic value, thereby estimating the "true" diversity of the system (i.e. the diversity you would calculate given infinite sampling effort). In order to assess the fish species diversity in each bay for each season and year, estimates for the Asymptotic Shannon Diversity Index were calculated following the methods for sample-based rarefaction described by Chao et al. (2014), whereby a species accumulation curve is estimated using resampling methods and then extrapolated out to an asymptote. In order to calculate the asymptotic Shannon diversity, an unbiased estimator for Shannon diversity ($\widehat{D}(\infty)$), which is given as the exponential of Shannon entropy ($\widehat{H}(\infty)$) (Chao et al., 2014); is calculated using equation (1):

$$\widehat{H}(\infty)=\sum_{k=1}^{n-1}\frac{1}{k}\sum_{1\le X_i\le n-k}\frac{X_i}{n}\frac{\binom{n-X_i}{k}}{\binom{n-1}{k}}+\frac{f_1}{n}(1-A)^{-n+1}\left\{-\log(A)-\sum_{r=1}^{n-1}\frac{1}{r}(1-A)^r\right\} \tag{1}$$

where $A = 2f_2/[(n-1)f_1 + 2f_2$, n is the sample size, X_i is the frequency of the ith species, and f_k is the number of species with observed frequency k (Chao et al., 2014). The asymptotic Shannon diversity is thus ${}^1\widehat{D}(\infty) = \exp[\widehat{H}(\infty)]$. Asymptotic diversity estimates were calculated using the "iNEXT" package in the R statistical computing environment (Hsieh et al., 2018). Once these estimates were calculated, along with an associated standard error for each estimate, they were used as the response variable for modeling the effects of environmental drivers on fish species diversity. Additionally, analysis of variance (ANOVA) was conducted on the diversity estimates in order to determine whether fish diversity was significantly different among bays and seasons.

2.3. Trend analysis

A trend analysis was conducted in order to test the significance of observed trends in asymptotic Shannon diversity. Our response variable was an estimate and not an observed value; therefore, a parametric bootstrap method was used to test the significance of the trend (Efron and Tibshirani, 1986). For each diversity estimate (i.e. for each bay, season, and year combination), 999 additional estimates were randomly generated following a normal distribution with a mean equal to the value of the estimate, and the standard deviation equal to the standard error for the given estimate. This resulted in one thousand time-series for each season (x2) in each bay (x8). For each time-series, a simple linear regression was fit to the bootstrapped data with the diversity estimates as the response variable and year as the explanatory variable. For each linear model, the slope and p-value of the slope were recorded. The number of slopes out of one thousand that were positive and significantly different from 0 at the 5% significance level were recorded for each bay in each season. If a bay had more than 950 significant positive slopes for a given season, it was considered to have a significant increasing trend over time. Spring and fall assemblages were modeled separately in order to account for differences in fish occupying the bays in different seasons.

2.4. Repeated measures analysis

In order to test for the effects of environmental variables on fish species diversity, repeated measures analysis was used (Laird and Ware, 1982). Repeated measures models are appropriate when multiple measurements have been taken from the same subject (in this case, each bay is a subject) through time, and multiple subjects are being modeled concurrently. It is advantageous in that it accommodates a variety of covariance structures in the response variable, an important consideration for repeated measures data where independence and homogeneity assumptions are violated. Standard least squares methods cannot be employed in this case due to the fact that observations taken from a given bay will be more similar to one another than observations from other bays, and observations taken more closely together in time will be more similar than those taken farther apart (Laird et al., 1987; Laird and Ware, 1982). Repeated measures analysis using mixed-effects models allows for the specification of both fixed and random effects, as well as a covariance structure, thereby accounting for between-individual variation, as well as within-individual autocorrelation. In our study, by specifying bay as a random factor, and environmental variables as fixed factors, we were able to model environmental driving variables with a constant effect (slope) across bays, while allowing for random intercepts for each bay, thereby accounting for differences in the diversity of each bay at the start of the study period.

For the repeated measures analysis, the assemblages were again modeled by season, with a separate model estimated for spring and fall. For each model, all environmental variables were included in the initial model, as well as, lagged variables (lag 1 – last year's observation for the given variable, and lag 2 – observation from 2 years ago for the given variable) for temperature, salinity, and sea level (i.e. in the spring model, lag 1 of temperature would be last spring's temperature). Lags were included in order to account for the delayed response of the diversity metric to changing environmental conditions. A delayed response may be particularly likely in this system due to the fact that environmental variables will operate most strongly on larval and juvenile fishes, which require time to grow before they are large enough to be captured in a gillnet.

Environmental variables were modeled as fixed effects, while the grouping factor, bay, was modeled as the random effect to allow for independent intercepts for each bay. Each model was fit using maximum likelihood, and the fixed effects were reduced based on the associated p-values for the parameter estimates (backward selection process). The maximum likelihood method is appropriate for comparing models with differing fixed effects, while the restricted maximum likelihood method is preferred for comparing candidate covariance structures and making final inferences on the significance and effect size of explanatory variables (Commenges and Jacqmin-Gadda, 2016). Odds ratio tests were used after each removal of a variable in order to confirm the significance of a variable. If the p-value of the odds ratio test was not significant, the removal of that variable did not significantly reduce the explanatory power, and thus it was permanently removed from the model. This process was conducted until all remaining variables had significant explanatory power.

Next, candidate covariance structures were tested in order to determine the covariance structure that best fits the data. Models were fit using the restricted maximum likelihood method with either no covariance structure specified or an auto-regressive process of order 1. Because the models were not nested (i.e. same fixed effects, only covariance structure differed), the Akaike Information Criterion (AIC) was used to select the best covariance structure. In the event that previously significant variables became non-significant after accounting for correlation structure (i.e. the p-value associated with the parameter estimate was no longer below 0.05), the model with specified covariance was fit using the maximum likelihood method and variables with non-significant p-values were removed. Odds ratio tests were then used to test the significance of the parameter removals (as previously described). Once the final model had been selected (i.e. all non-significant variables removed) and correlation structure accounted for, the final model was fit using the restricted maximum likelihood method, and the results from this model were used for inference on parameter significance and effect sizes.

3. Results

3.1. Rarefaction and trend analysis

The results of the rarefaction analysis showed clear spatial differences in fish diversity (ANOVA p-val < 0.001). In spring, Galveston Bay, Matagorda Bay, Corpus Christi Bay, and San Antonio Bay, had consistently higher diversity compared to the other bays. In fall, the assemblages were less closely grouped; however, Matagorda, Corpus Christi, and San Antonio bays were consistently higher in diversity. Galveston Bay was slightly lower in diversity than Matagorda, Corpus Christi, and San Antonio bays, but still higher than the remaining bays (Figs. 4 and S1). Seasonal differences were also evident (ANOVA p-val <0.001), with fish diversity being consistently higher in fall assemblages compared to spring (Fig. 4).

The trend analysis was conducted to determine the significance of temporal trends in fish diversity. The results showed that, for spring assemblages, six out of eight bays had significant increasing temporal trends – Sabine Lake and Lower Laguna Madre were not significant (Fig. 2, Table 1). For fall assemblages, all eight bays showed significant increasing temporal trends (Fig. 3, Table 1). The distributions of slopes from the trend analysis revealed clear differences in the rate of increase between bays for both spring and fall assemblages, with Sabine Lake, Upper Laguna Madre, and Lower Laguna Madre showing slower rates of increase than the other bays in spring, and Sabine Lake and Lower Laguna Madre showing the slowest increase in fall (Figs. 5 and S2).

3.2. Repeated measures analysis – spring model

The results from the repeated measures analysis using backward selection showed that spring fish assemblage diversity was best modeled by temperature, salinity, lag-1 salinity (salinity from 1 year ago), mean sea level, and lag-2 sea level (mean sea level from 2 springs ago). The final model for spring was:

$$\hat{y}_{ij} \sim \boldsymbol{\beta}_{0i} + \boldsymbol{\beta}_1 \boldsymbol{T}_{ij} + \boldsymbol{\beta}_2 \boldsymbol{S}_{ij} + \boldsymbol{\beta}_3 \boldsymbol{S}_{ij-1} + \boldsymbol{\beta}_4 \boldsymbol{L}_{ij} + \boldsymbol{\beta}_5 \boldsymbol{L}_{ij-2} \qquad (2)$$

where $\hat{y}_{ij}$ is the predicted asymptotic Shannon diversity in the spring for

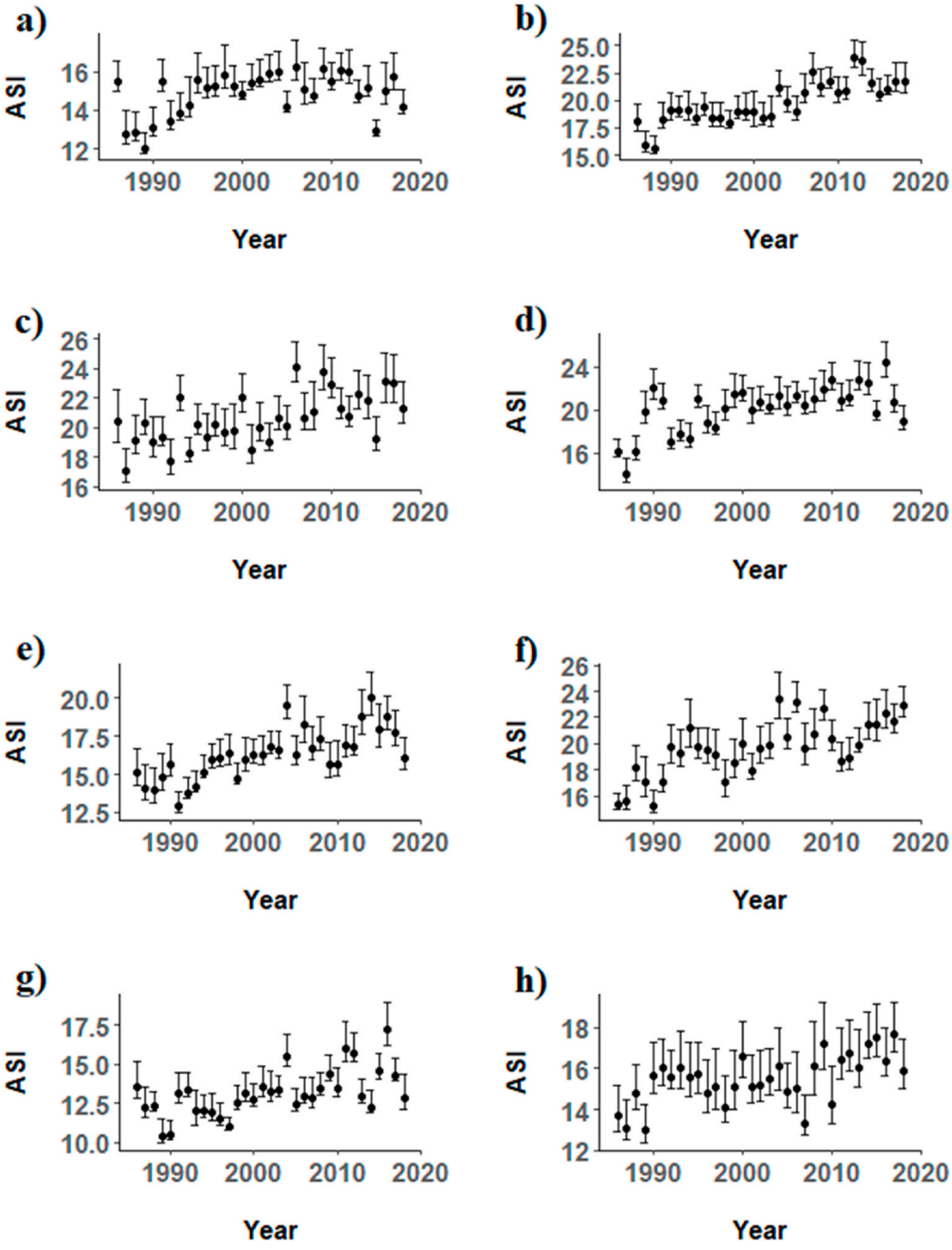

Fig. 2. Spring Assemblage Rarefaction analysis results. Asymptotic Shannon Diversity estimates for spring fish assemblages in the bays of Texas from 1986 to 2018. Error bars show the 95% confidence interval for the diversity estimate. Panel a) Sabine Lake, b) Galveston Bay, c) Matagorda Bay, d) San Antonio Bay, e) Aransas Bay, f) Corpus Christi Bay, g) Upper Laguna Madre, and h) Lower Laguna Madre.

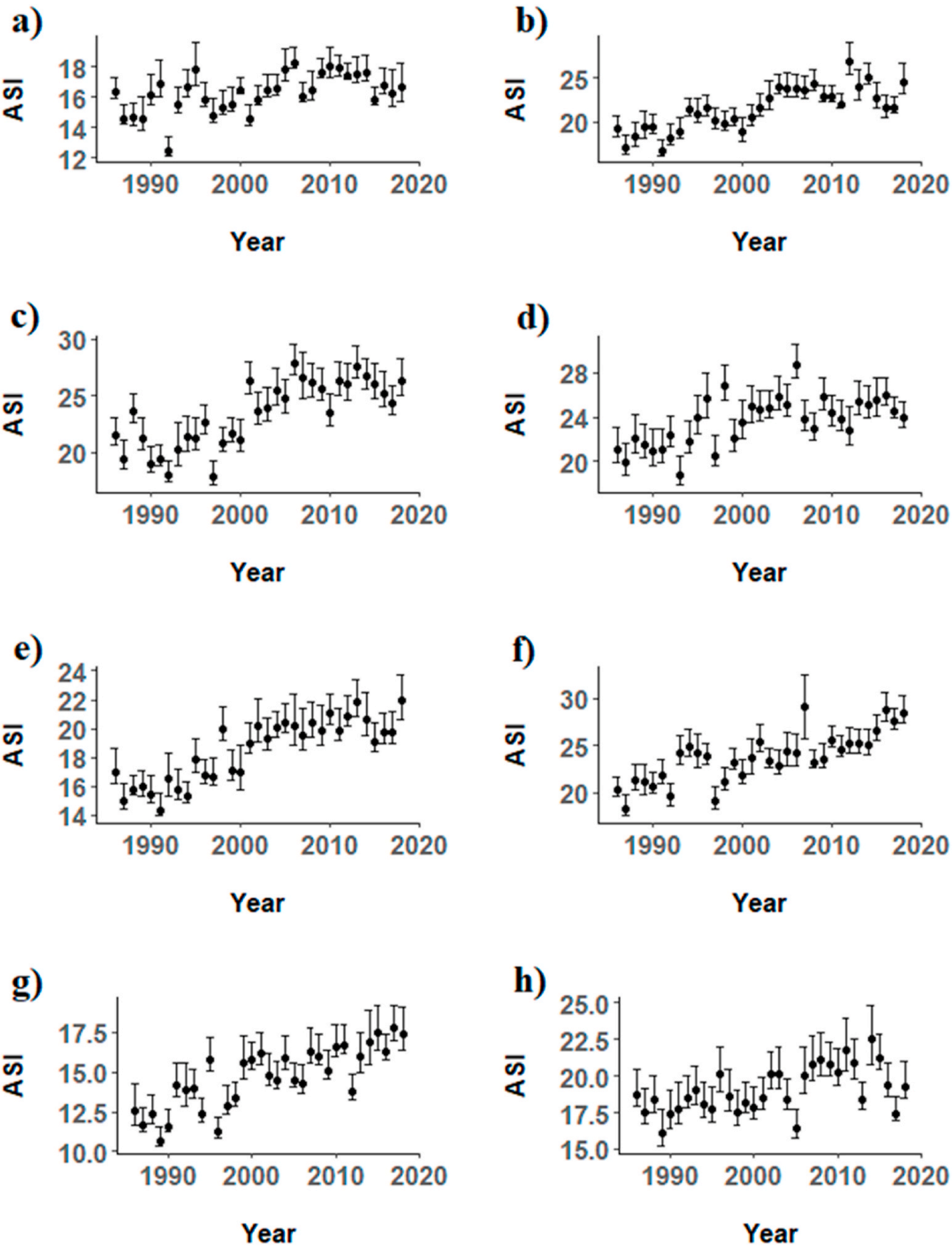

Fig. 3. Fall Assemblage Rarefaction analysis results. Asymptotic Shannon Diversity estimates for fall fish assemblages in the bays of Texas from 1986 to 2018. Error bars show the 95% confidence interval for the diversity estimate. Panel a) Sabine Lake, b) Galveston Bay, c) Matagorda Bay, d) San Antonio Bay, e) Aransas Bay, f) Corpus Christi Bay, g) Upper Laguna Madre, and h) Lower Laguna Madre.

bay *i* and year *j*, β_{0i} is the bay-specific intercept, β_1 is the effect of temperature, T_{ij} is the observed mean spring temperature in bay *i* and year *j*, β_2 is the effect of salinity, S_{ij} is the observed mean spring salinity in bay *i* and year *j*, β_3 is the effect of the previous year's salinity, S_{ij-1} is the observed mean spring salinity in bay *i* and year *j-1*, β_4 is the effect of sea level, L_{ij} is the observed mean sea level in bay *i* and year *j*, β_5 is the effect of sea level from two years prior, and L_{ij-2} is the observed mean spring sea level in bay *i* and year *j-2*. The effect sizes and associated p-values for $\beta_1 - \beta_5$ are presented in Table 2. The lag-2 sea level had the largest effect size, followed by sea level, temperature, lag-1 salinity, and salinity. This highlights the importance of a delayed response to changes in sea level. The individual estimates for β_{0i} are presented in Table 3, and larger intercept values correspond to bays with higher diversity. It should be noted that the intercept value listed in Table 2 is simply the mean of the random factor intercepts (β_{0i}).

The final model also included a first-order autoregressive covariance structure with autoregressive parameter (φ) = 0.332. This covariance structure accounted for temporal autocorrelation in the data within a given bay. It is important to note that the covariance structure is associated with the covariance matrix of the response, and is thus not a parameter in equation (2), and was not used in calculating $\widehat{y}_{ij}$. The covariance structure is taken into account when fitting the model, and thus affects the parameter estimates and p-values of the parameter estimates, but is not explicitly included in equation (2). Plotting the observed Shannon diversity estimates versus the fitted values (Fig. 6a) shows that the model has a good fit to the data.

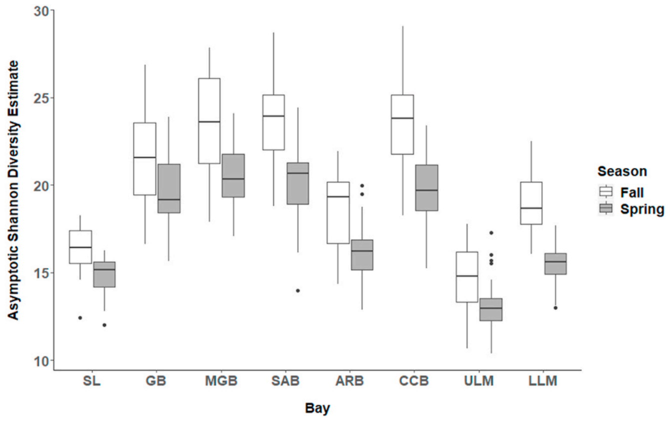

Fig. 4. Distributions of the asymptotic Shannon diversity estimates over the 33-year study period, by season. Fall diversity distributions are shown in white, and spring distributions in grey. Black dots represent outliers following the standard definition of Q1 and Q3 ±1.5IQR.

Table 1
Trend analysis results. Columns show the number of linear regression models out of 1000 that had a significant positive slope ($\alpha = 0.05$). A bay is considered to be significantly increasing if more than 950 trials resulted in a significant positive slope. Asterisks show bays with a significant increasing trend.

Major Area	Spring	Fall
Sabine Lake	596	980*
Galveston Bay	1000*	1000*
Matagorda Bay	998*	1000*
San Antonio Bay	1000*	1000*
Aransas Bay	1000*	1000*
Corpus Christi Bay	1000*	1000*
Upper Laguna Madre	999*	1000*
Lower Laguna Madre	937	984*

3.3. Repeated measures analysis – fall model

The results from the repeated measures analysis for the fall assemblages showed that fish diversity was best modeled by temperature, sea level, lag-1 sea level, dissolved oxygen, and lag-1 salinity. The final model for fall was thus:

$$\hat{y}_{ij} \sim \beta_{0i} + \beta_6 T_{ij} + \beta_7 L_{ij} + \beta_8 L_{ij-1} + \beta_9 D_{ij} + \beta_{10} S_{ij-1} \qquad (3)$$

Table 2
Repeated Measures Model Results. Parameter estimates and associated p-values for the fixed effects of the repeated measures model for spring (a) and fall (b) fish assemblage diversity. All variables were standardized by z-score prior to analysis to control for effect size. The intercept listed here is the mean of the random factor intercepts estimated for each bay. Bay-specific intercepts are provided in Table 3.

Parameter	Estimate	Standard Error	Degrees of Freedom	t-value	p-value
a. Spring Model					
Mean of the random factor β_{0i}	17.597	1.053	232	16.708	<0.001
Temperature (β_1)	0.253	0.091	232	2.789	0.006
Salinity (β_2)	0.191	0.092	232	2.077	0.039
Lag-1 Salinity (β_3)	−0.196	0.085	232	−2.303	0.022
Sea Level (β_4)	0.435	0.111	232	3.920	<0.001
Lag-2 Sea Level (β_5)	0.533	0.107	232	4.980	<0.001
b. Fall Model					
Mean of the random factor β_{0i}	20.144	1.264	229	15.938	<0.001
Temperature (β_6)	0.307	0.112	229	2.741	0.007
Sea Level (β_7)	0.458	0.151	229	3.038	0.003
Lag-1 Sea Level (β_8)	0.680	0.152	229	4.463	<0.001
Dissolved Oxygen (β_9)	−0.296	0.120	229	−2.472	0.014
Lag-1 Salinity (β_{10})	0.278	0.113	229	2.459	0.015

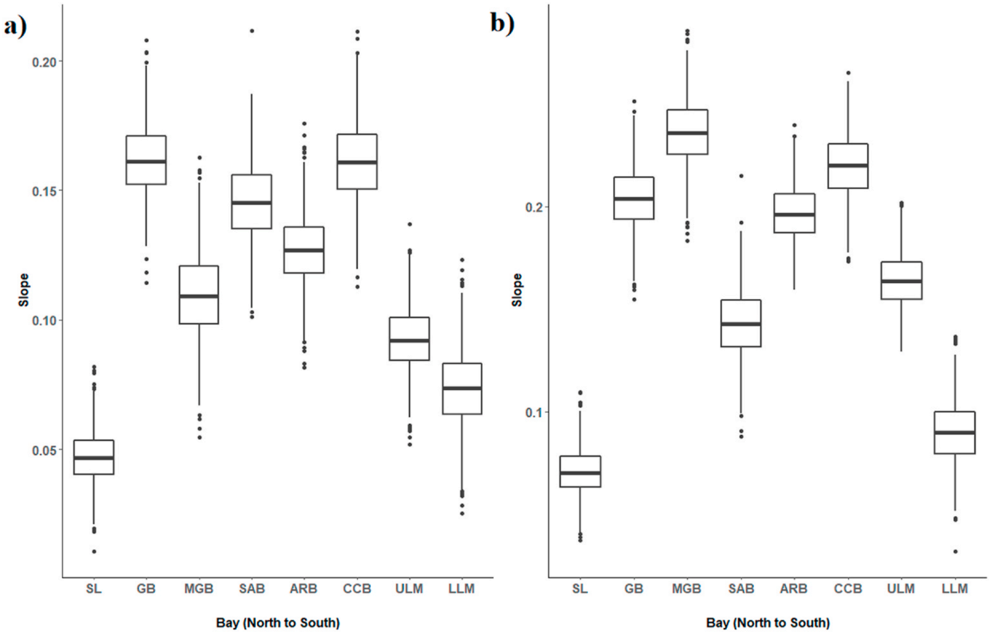

Fig. 5. Regression slope distributions from the bootstrapped data. Spring (a) and Fall (b) slopes from the linear models fit to the bootstrapped data by bay. Boxplots for each bay are arranged from North to South. SL= Sabine Lake, GB = Galveston Bay, MGB = Matagorda Bay, SAB=San Antonio Bay, ARB = Aransas Bay, CCB=Corpus Christi Bay, ULM=Upper Laguna Madre, and LLM = Lower Laguna Madre.

Table 3
Bay-specific Model Intercepts. Parameter estimates for the intercepts for each bay. As previously noted, models were constructed assuming a constant effect of environmental variables across bays (i.e. same slope for environmental effects, regardless of bay).

Major Area	Spring Model Intercept	Fall Model Intercept
Sabine Lake	14.868	16.294
Galveston Bay	19.890	21.547
Matagorda Bay	20.634	23.390
San Antonio Bay	20.415	23.719
Aransas Bay	16.378	18.439
Corpus Christi Bay	19.866	23.875
Upper Laguna Madre	13.130	14.862
Lower Laguna Madre	15.592	19.026

where $\widehat{y}_{ij}$ is the asymptotic Shannon diversity in the fall for bay i and year j, β_{0i} is the bay-specific intercept, β_6 is the effect of temperature, T_{ij} is the observed mean fall temperature in bay i and year j, β_7 is the effect of sea level, L_{ij} is the observed mean fall sea level in bay i and year j, β_8 is the effect of the previous year's sea level, L_{ij-1} is the observed mean fall sea level in bay i and year $j\text{-}1$, β_9 is the effect of dissolved oxygen, D_{ij} is the observed mean dissolved oxygen in bay i and year j, β_{10} is the effect of salinity from the previous year, and S_{ij-1} is the observed mean fall salinity in bay i and year $j\text{-}1$. The effect sizes and associated p-values for $\beta_6 - \beta_{10}$ are presented in Table 2. As with the spring model, current and past sea level had the largest effect size. The individual intercept values (β_{0i}) for the fall model are presented in Table 3. As with the spring model, the final model included a first-order autoregressive covariance structure. The autoregressive parameter for the fall model was $(\varphi) = 0.430$, which was a slightly larger magnitude compared to spring, and may be indicative of stronger temporal autocorrelation in fall assemblages when compared to spring. Fig. 6b shows the observed versus predicted plot for the fall model, and as with spring, the model fit appears strong.

4. Discussion

Our results show that species diversity has increased significantly through time in the bays of Texas (Figs. 2 and 3, Table 1). In addition to clear temporal trends, spatial and seasonal differences in fish diversity were evident (Fig. 4). Trend analysis showed significant increases in diversity in both spring and fall assemblages, with fall assemblages increasing at a faster rate than spring (Fig. 5). The higher underlying diversity in fall assemblages and a faster rate of increase may be the result of different mechanisms operating on fish entering and leaving the bays. Fall salinity is consistently higher than spring salinity (*t*-test of paired differences, p-val <0.001) suggesting that a minimum salinity threshold may be needed before tropical species will enter the bays, while retention within the bays may be mediated by winter water temperatures, with cold water forcing movement of tropical species out of the bays prior to spring sampling. Because there is a higher diversity of fish in the tropics compared to subtropics (Hillebrand, 2004), it is predicted that fish diversity and production will shift poleward as species adjust their distributions to changing climate (Barange et al., 2014; Cheung et al., 2010), our results are consistent with this prediction, showing increasing fish diversity through time.

While many studies have shown species diversity to have a positive relationship with ecosystem functioning (Chapin III et al., 2000; Hooper et al., 2005; Naeem et al., 1994; Schlapfer and Schmid, 1999; Tilman, 1999; Tilman and Downing, 1994), this is not always the case, and in fact, an increase in species diversity can potentially lead to a decrease in functional diversity (Mayfield et al., 2010). These shifts in distribution, and thus in community structure, are also interesting in the Gulf of Mexico where species are limited in their ability to continue shifting northward due to the presence of the coastline. The inability of subtropical species in the Gulf of Mexico to continue their shift northward may lead to novel interactions and unexpected functional consequences, highlighting the importance of not only determining how fish diversity is changing but also the implications of that change. This remains to be explored in the future research.

In order to better understand and predict future changes to fish assemblages in the face of climate change, it was necessary to identify the environmental variables which may be responsible for driving the observed increase in diversity. Repeated measures models identified several environmental covariates that are likely responsible for the observed increase. In particular, temperature, salinity, and sea level

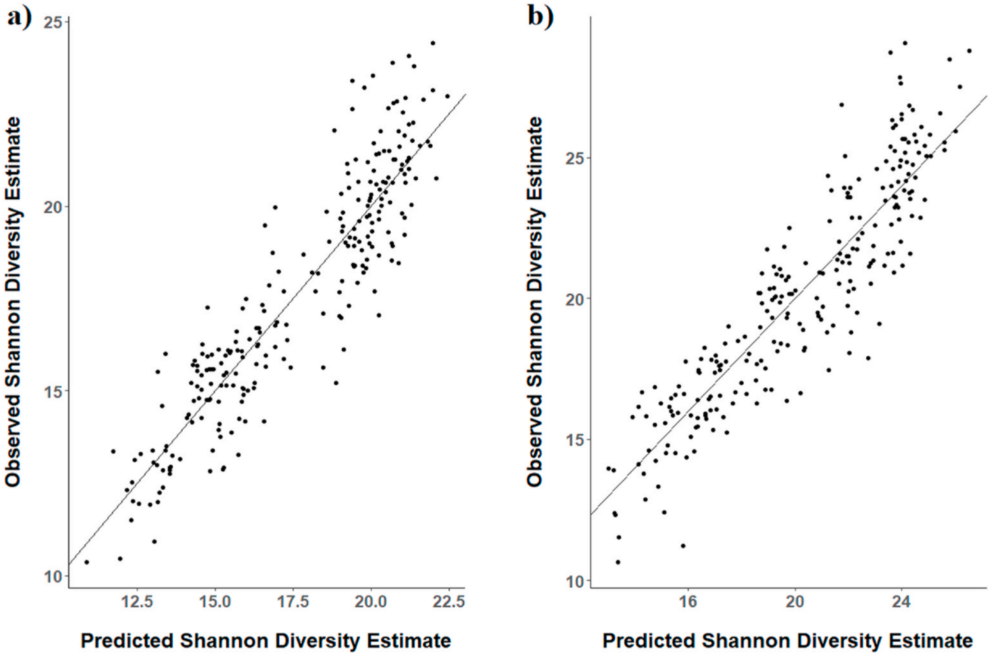

Fig. 6. Observed versus predicted plots for repeated measures models. Panel a) shows the observed versus predicted values for the spring assemblage model. Panel b) shows the observed versus predicted values for the fall assemblage model.

were identified as important covariates in both the spring and fall models, either as current or lagged variables. The importance of lagged variables in the repeated measures models highlights the delayed response of the adult fish assemblage to changing environmental factors. Due to the highly selective nature of gillnets (Hamley et al., 1975), fish caught in this study were predominantly larger, consisting mainly of adult fish. It is thought that environmental filters tend to act most strongly on larval and juvenile fish (e.g. Fuiman and Werner, 2009); therefore, changes in the fish assemblage due to changing environmental variables may not be observed in gillnet samples until the fish have grown large enough to be available to the sampling gear, which may take a year or more.

Salinity showed a significant positive relationship with diversity for the spring assemblage, while lagged salinity showed a significant negative relationship in spring and a positive relationship in fall. Salinity may be responsible for seasonal and spatial differences in diversity, as it was consistently lower in spring than fall, suggesting more tropical species may be unable to enter the bays under brackish conditions. Salinity has been shown to affect the growth rate of many species, whether freshwater, marine, or estuarine (Boeuf and Payan, 2001). Ontogenetic shifts in species distribution have been shown to correlate with the development of salinity tolerance in many species (Varsamos et al., 2005). Additionally, some studies have shown distributional changes of fish within an estuary in response to salinity gradients (Barletta et al., 2005; Martino and Able, 2003). Increasing salinity in the bays of Texas may be allowing for distributional changes in fish species, with increasing abundance of more marine species and potentially a decrease in abundance of fresh- and brackish-water associated species.

Temperature showed a significant positive relationship with diversity for both the spring and fall assemblages. Temperature has been shown to affect fish growth, survival, and distribution (Fuiman and Werner, 2009), and many studies have shown distributional shifts of temperate species in response to the warming climate (Collie et al., 2008; Murawski, 1993; Perry et al., 2005; Wernberg et al., 2016). In the bays of Texas, temperatures are rising, thereby allowing for potential colonization by tropical species, which had previously been excluded from this system. Relaxation of an important environmental filter (temperature) combined with changing vegetation cover in the bays of Texas are likely working synergistically to drive the observed increase in fish diversity.

Sea level was also identified as a significant variable explaining fish diversity. One possible explanation could be related to changing vegetation type and cover in response to rising sea level. In both salt marshes and mangrove forests, stabilizing biophysical feedbacks allow for the expansion of these habitat types in response to sea-level rise (Kirwan and Megonigal, 2013). In Texas, mangrove species appear to be competitively dominant over native salt marsh species, when not limited by cold winter air temperatures (Armitage et al., 2015; Kirwan and Megonigal, 2013). Evidence from previous studies suggests that mangrove cover has been increasing through time in the bays of Texas (Armitage et al., 2015; Bianchi et al., 2013), likely in response to both increasing winter minimum temperatures and rising sea level. Mangroves function as important nursery habitat for juvenile fish (Beck et al., 2001; Lee, 2008; Lee et al., 2014; Nagelkerken et al., 2008), provide refuge from predators (Guo et al., 2017; Nanjo et al., 2014), and may serve as a valuable feeding ground for larger fish (Lugendo et al., 2007). Thus, we hypothesize that in addition to changing abiotic filters (i.e. temperature and salinity), the changing biotic environment may have contributed to increasing fish diversity, via increased mangrove cover, for which sea level may be a reasonable proxy variable. However, further research to associate the change in sea level and vegetation coverage or other environmental factors is needed to draw a definitive conclusion.

Additionally, dissolved oxygen was found to have a significant negative relationship with diversity in fall. While dissolved oxygen was identified as being a significant predictor of fall assemblage diversity, this may be an artefact of the relationship between temperature, salinity, and dissolved oxygen. The mean dissolved oxygen in fall ranged between 6 and 12 ppm for 99% of observations, meaning the dissolved oxygen was not likely dropping out of normal ranges, though there was a consistent decreasing trend through time. The combined effect of increasing temperature and salinity is likely leading to a decreasing trend in dissolved oxygen, and thus, a significant negative correlation with our increasing diversity estimates.

The results found in this study are consistent with findings from a previous study conducted by Fujiwara et al. (2019) in the bays of Texas. In their study, Fujiwara et al. (2019) analyzed data collected using bag seines, which target juvenile fish. Diversity trend analyses and occupancy analyses were conducted, and the results showed that for small fish and invertebrates occurring nearshore, abundance and diversity increased through time. The majority of species modeled showed increasing occupancy probability through time, with fewer species showing decreasing trends. Species showing increasing trends were predominantly tropical, and tended to be associated with submerged vegetation, suggesting a change in the aquatic habitat may be contributing to the change in prevalence. Additionally, their occupancy analyses found that salinity was the most important driver of differences among bays, while temperature and sea level were important in explaining temporal trends in a variety of species, which was consistent with the important abiotic drivers identified in the current study. These results are consistent with our hypothesis that relaxed abiotic filters (temperature and salinity), combined with increased mangrove cover due to rising sea level may be contributing to increasing fish diversity in the bays of Texas. These analyses together provide a better picture of the fish community dynamics in the bays of Texas, showing that the observed increases at the larval or juvenile stage are persisting, and new species are surviving and recruiting to the adult assemblages.

5. Conclusion

Our results demonstrate that adult fish diversity is increasing through time in the Gulf of Mexico, with distinct spatial and seasonal differences in the underlying diversity of the bays, and the rate of increase in diversity. The results of our modeling analysis suggest that the observed increase is likely the result of tropical species expanding their geographic ranges into the bays. While temperature is often assumed to be the most important driving variable in fish distribution shifts in response to climate change, our study identified rising sea level as an important contributing variable. These results may suggest that in subtropical systems where temperature is less limiting, habitat availability may be important in driving distribution shifts.

The goal of our study was to identify the effects of climate change on the subtropical fish communities of Texas, and our results have clearly answered the questions we had identified; however, it has also identified new questions. While increasing biodiversity is generally considered beneficial to the ecosystem, the fact that invasion of species is leading to the observed increase in this system suggests that there may be unintended functional consequences to this increase. In order to assess the impact of this increase on the functioning of this system, further studies will seek to investigate changes to the functional diversity and structure of this system and the potential effects of climate change on the assembly mechanisms of this system.

Author declaration

Michaela Pawluk: Conceptualization, Methodology, Software, Formal analysis, Writing – Original Draft, Writing – Review and Editing, Visualization. Masami Fujiwara: Conceptualization, Writing – Review and Editing, Supervision, Project administration, Funding acquisition. Fernando Martinez-Andrade: Conceptualization, Investigation, Data Curation, Writing – Review and Editing.

Declaration of competing interest

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2020.107121.

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