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Combinations of biological attributes predict temporal dynamics of fish species in response to environmental changes

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ABSTRACT

Assessing species vulnerability to environmental changes is a major challenge for conservation. Combinations of biological attributes have already been successfully used for this purpose, allowing large-scale prediction of inter-specific differences in demographic parameters (e.g. abundance) or endangered status. However, studies investigating whether biological attributes could be used to predict the temporal demographic responses of species in a changing environment are still scarce. In this work, we tackled this issue by taking advantage of a multi-decadal survey of concomitant changes in fish communities and environmental conditions within the Terminos lagoon (Mexico). Based on this rare dataset, we first characterized changes in abiotic parameters that occurred in this ecosystem since the 80s. Then, we adapted a multivariate index accounting for changes in both species abundance and occurrence to assess concomitant demographic changes for the 25 dominant fish species in the lagoon, classifying them into five various types of trajectories ("Increasing", "Decreasing", "Constant", "Hump-shape" and "U-shape"). Finally, we assessed the accuracy in prediction of these temporal responses for all possible combinations of 15 biological attributes including taxonomy, ecological and life-history traits.

Our results showed that fish specific demographic changes over the last 30 years could be accurately predicted (72% accuracy) using a combination of five biological attributes (spawning season, order, maximum salinity, width of salinity range, oocyte size) among which three could be related to the increase in average salinity occurred in the lagoon over this period. Appropriate sets of complementary biological attributes could similarly allow prediction of inter-specific differences in demographic changes in other areas, thereby offering an additional pragmatic tool for ecosystem managers to identify vulnerable species at the local scale.

1. Introduction

Human activities have strongly and sometimes irreversibly impacted all ecosystems on Earth, either directly or through global change (Vitousek, 1997). These disturbances induce deep modifications of ecological communities and a loss of the biodiversity upon which ecosystem goods and services depend. Because the magnitude and the frequency of human-mediated disturbances are likely to intensify over the coming decades (Millennium Ecosystem Assessment, 2005), there is an urgent need to understand their effects on communities, in order to improve our ability to predict potential impacts of environmental modifications.

Changes in biodiversity can be complex because species of the same community can exhibit markedly different responses to disturbances (Hughes, 2000). Contrary to expectations from the neutral theory, species demographic response to disturbances (e.g. changes in occurrence, abundance or biomass) is not a random process (Kadmon and Benjamini, 2006). Disturbances tend to affect some species more than others, as a probable result of differences in their biology and physiology (Mouillot et al., 2013b). Disentangling the intrinsic drivers of the species decline are therefore some of the major challenges in predicting community responses to disturbance, and thus closely linked to conservation objectives.

Among the multiple causes of interspecific variation in species responses to environmental disturbances (e.g. historical abundance or geographical range), species biological attributes (i.e. phylogeny, ecology and physiology) probably play a central role (Purvis et al., 2000). Ecological and life-history traits (ELHT) in

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particular have often been shown to drive species sensitivity to disturbance and thus seemed be good indicators of the endangered status (McKinney, 1997; Olden et al., 2006). This influence of ELHT on species vulnerability is now well documented for mammals (Purvis et al., 2000; Cardillo and Bromham, 2001, 2003; Dulvy et al., 2003; Cardillo et al., 2005; Davidson et al., 2009), birds (Bennett and Owens, 1997; Norris and Harper, 2004; Jiguet et al., 2007; Kruger and Radford, 2008), insects (Williams et al., 2010) and fishes (Olden et al., 2007; Field et al., 2009), where one of the most striking examples is perhaps the relationship between asymptotic body size of fish and sensitivity to fishing effort, with large-bodied species being depleted first (Olden et al., 2008). The link between ELHT of species and their responses to disturbance has resulted in an increasing number of authors investigating the use of biological attributes, alone or combined, for evaluating species vulnerability to environmental changes (Davies et al., 2000; Cardillo et al., 2008; Dalgleish et al., 2010; Angert et al., 2011). This has confirmed the value of multiple combinations of biological attributes to predict species occurrence and relative abundance within communities or habitats (Newbold et al., 2013), or their endangered status (Murray et al., 2011; Cardillo et al., 2008; Anderson et al., 2011; Allen et al., 2012). However, studies investigating the links between combinations of biological attributes and inter-specific variations in temporal demographic response to perturbations are still sparse (Olden et al., 2006; Pocock, 2010).

In the present work, we build on the data gathered through three decades of extensive and standardized annual sampling of fish communities and abiotic parameters in a vast tropical ecosystem (the Terminos lagoon, Mexico) to investigate whether some combinations of biological attributes can be indicators of temporal changes in species demography caused by environmental disturbances. After testing for abiotic environmental modifications in the lagoon over the last thirty years, we developed a methodology to characterize temporal responses of fish species (i.e. “demographic trajectories”) and tested how accurately these responses can be predicted by combinations of biological attributes (mixing ELHT and taxonomy). This information is particularly relevant for fish species, since few evaluations of their sensitivity to environmental changes have been based on multiple combinations of traits (e.g. Olden et al., 2006; Villéger et al., 2010). Assessing and disentangling the drivers of community responses to perturbations in tropical estuarine environments is also particularly relevant because these fragile ecosystems provide many critical goods and services for human populations (Costanza et al., 1997; Rochette et al., 2010;Layman et al., 2011). The multiple disturbances linked to human activities in the littoral zone have already strongly impacted their biological communities (Lotze et al., 2006; Halpern et al., 2008). Therefore, in the absence of appropriate conservation measures, the predicted > 60% increase in human populations living within 100 km of the coastline by 2050 (Lefebvre, 2011; Vitousek, 1997) might result in irreversible alterations of their biodiversity and functions.

2. Material and methods

2.1. Study area

The Terminos Lagoon (90°00′–90°20′W18°25′–19°00′N) is the largest estuarine system along the coast of Mexico and the third largest lagoon in the world. Located in the southwest part of the Gulf of Mexico (Fig. 1), it communicates with the sea through only two outlets, located at both ends of Carmen island (30 km long and 2.5 km wide): the Puerto Real outlet to the east and the Carmen outlet to the west. Depths in the lagoon are low (2.5 ± 1.0 m) and water temperatures are high throughout the year (mean = 27.8 °C), with a minimum of 20 °C, but maximum values can rise above 32 °C (Villéger, 2008; Ramos-Miranda et al., 2005a). Freshwater inputs to the lagoon originate mainly from three rivers located on its southern coastline (Rio Palizada in the west and Rio Chumpan and Rio Candelaria in the east). Due to the general east-west direction of water circulation in the lagoon, brackish waters are mainly found in its southwest parts while marine salinities prevail in the northwest of the ecosystem (Carvalho et al., 2009; Villéger et al., 2010). Tropical climate in the area is characterized by three distinct seasons: the classical dry (D) and wet (W) seasons, from February to May and from June to September, respectively, and the “nortes” (N) season from October to January (Yáñez-Arancibia and Day, 1982) characterized by a decrease of the temperatures and by strong winter storms coming from the North. As a result, water salinity also varies throughout the year in the lagoon, with maximum observed in the dry season and minimum during the rainy season.

Around 120 fish species have been reported in Terminos. Among them, 10% are permanent residents in the lagoon, 45% use it as a nursery area and the remaining 55% as a feeding or spawning area (Carvalho et al., 2009). This ecosystem therefore represents an important “hotspot” of fish biodiversity that it is urgent to preserve. However, since the early eighties, the lagoon has suffered from diverse anthropogenic pressures, including fishing by artisanal shrimp trawlers, off-shore oil exploitation, increasing human populations along its shoreline and associated pollution (Ramos-Miranda et al., 2005a,b). This has resulted in marked shifts in its abiotic and biotic parameters (Ramos-Miranda et al., 2005a,b; Sosa-López et al., 2005; Villéger et al., 2010), the consequences of which might already be irreversible. Nonetheless this also provided us with a unique opportunity to study fish communities’ responses to multiple environmental perturbations and investigate the causes for inter-specific variations in temporal demographic trajectories.

2.2. Data collection

The data in the present work originate from three identical sampling programs conducted in the lagoon for 12 consecutive months in 1980–1981, 1997–1998 and 2010–2011 (Villéger et al., 2010). For all three campaigns, sampling was conducted monthly at the same 17 stations (Fig. 1), selected before the first sampling campaign to best reflect the environmental diversity within the whole lagoon area (Yáñez-Arancibia and Day, 1982). Sampling at each month and station, involved measurement of depth (in m), bottom and surface salinities and temperatures (in °C), along with water pH and clarity (in m, from Secchi disk readings). Fish communities were also consistently sampled with a 5 m long shrimp trawl with 2.5 m mouth opening diameter and 19 mm mesh size. In each case, the trawl was towed for 12 min at a speed of 2.5 knot (i.e. 4.6 km/h), resulting in a sampled volume of water of 4500 m^3. All fish collected were identified in the laboratory, and specimens for each species were counted, measured (in mm) and weighed (in g) to obtain corresponding occurrence, abundance and biomass data per station and sampling date. Each of the annual sampling campaigns for the three decades studied therefore allowed the collection of 204 separate estimates for all parameters (abiotic and biotic) within the lagoon, with high-resolution sampling ensuring appropriate coverage of the spatial and temporal variability of the ecosystem.

2.3. Delineation of temporal shifts in lagoon abiotic parameters

Temporal abiotic changes over the three decades studied were evaluated separately for each parameter. In each case, this involved comparing the values recorded for the three sampling campaigns (1980, 1997 and 2011) by one-way analyses of variance, or Kruskal–Wallis tests when data were not normally

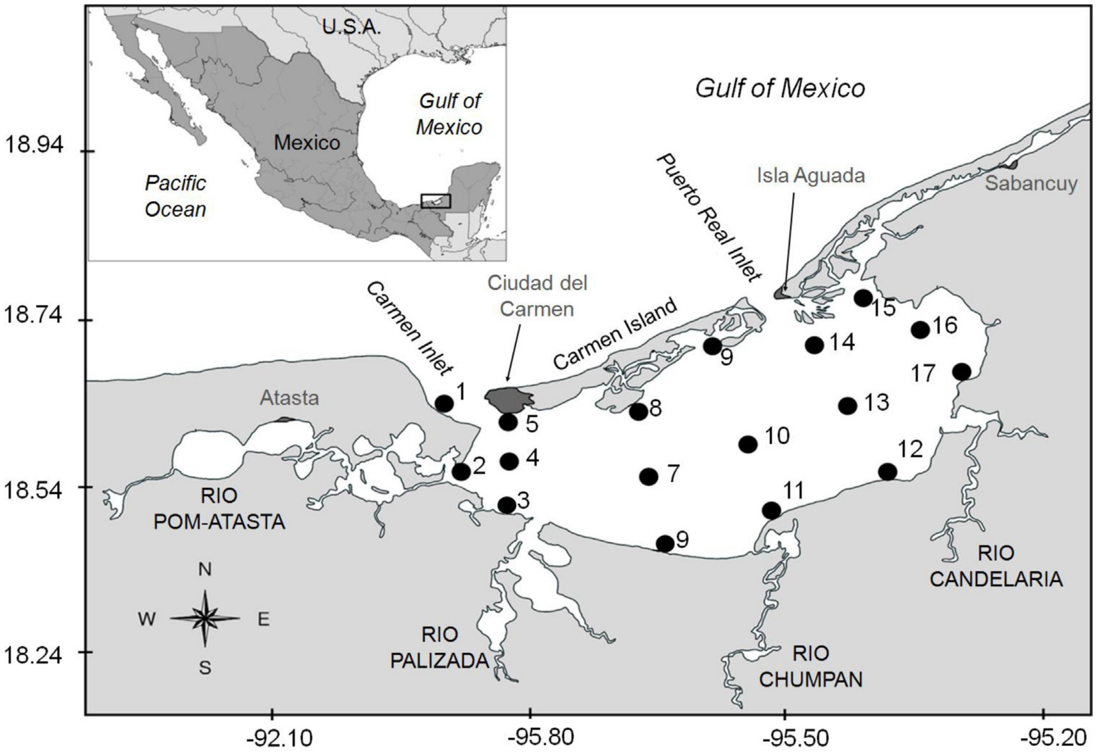

Fig. 1. Map of the study area (Southern Gulf of Mexico). The 17 sampling sites within Terminos lagoon are indicated by black spots and the main cities are in dark gray.

distributed or had heterogeneous variances. When significant differences were observed, additional pairwise comparisons between sampling periods were performed by Tukey's test for normal data, or Mann–Whitney tests with Bonferroni correction for non-parametric data.

2.4. Assessing temporal changes in fish communities

Dynamic responses over the period studied were evaluated separately for 25 fish species, all present in at least 10% of the hauls for each sampling campaign (1980, 1997 and 2011). We developed an approach derived from the "indicator value method" of Dufresne and Legendre (1997) that combined information about species abundance and frequency of occurrence across space to describe their demographic status for each decade (i.e. each annual sampling campaign). The index we used (IndVal index) combines in one single value, two complementary demographic descriptors: specificity (S), based on species relative abundance in a period, and fidelity (F), based on species frequency of occurrence within the ecosystem. Originally, this index was developed to compare populations among sites and link species to communities based on habitat conditions (Cáceres and Legendre, 2009). In the present study however, we modified it to compare periods instead of sites (Mouillot et al., 2002), resulting in the following formula for each species i and period p:

$$\mathrm{IndVal}_{ip} = 100 \times S_{ip} \times F_{ip}$$

with specificity (S_{ip}) defined by:

$$S_{ip} = \frac{N_{\mathrm{individual}_{ip}}}{N_{\mathrm{individual}_i}}$$

where $N_{\mathrm{individual}_{ip}}$ is the mean abundance per unit effort for a species i on all the samples from the p period, and $N_{\mathrm{individual}_i}$ is the total abundance per unit effort of species i over the three periods (Dufresne and Legendre, 1997; Mouillot et al., 2002).

And with fidelity defined by:

$$F_{ip} = \frac{N_{\mathrm{site}_{ip}}}{N_{\mathrm{site}_p}}$$

where N_{site_p} is the total number of sites sampled during period p and $N_{\mathrm{site}_{ip}}$ is the number of sites sampled during period p where the species i is present (Dufresne and Legendre, 1997; Mouillot et al., 2002).

Thus in our case, the IndVal index was used to produce robust estimates of temporal modifications, decade by decade, of population size and spatial distribution in the lagoon for each of the 25 species studied. Differences among periods for each species were determined using permutation tests. Temporal changes of IndVal allowed assigning species into five possible demographic trajectories: (1) the "constant" trajectory, corresponding to an absence of significant change in IndVal value over the study period; (2) the "increasing" and (3) "decreasing" trajectories, when final IndVal value (for 2011) was significantly higher or lower, respectively, than the initial one (for 1980); and (4) the "hump-shape" and (5) "u-shape" trajectories, when intermediate IndVal value (for 1997) was significantly higher or lower, respectively, than those for 1980 and 2011.

2.5. Disentangling the links between biological attributes and species trajectories

To test whether biological attributes could be considered as indicators of species trajectories, we assessed how inter-specific differences in temporal demographic trajectories over the study period could be predicted from species biological attributes. Fifteen taxonomic, ecological and life-history traits (Appendix A) were then compiled for all 25 species, from the reference literature (Chavance et al., 1984; Yànez-Arancibia and Lara-Dominguez, 1988; Ayala-Pérez, 2006; Ayala-Pérez et al., 2008; Waggy et al., 2006) and scientific databases (e.g. fishbase.org). These included two taxonomic attributes (the order and the family), three ecological traits describing the salinity niche of the species within Terminos lagoon (the minimum and maximum salinities at which the species was observed in the lagoon and the corresponding width of the salinity range i.e. the difference between the maximum salinity and the minimum salinity) and ten life-history traits commonly used to describe fish reproduction, diet and growth. For reproduction, six traits were considered: size at first sexual maturity (total length in mm at which 50% of females are mature), spawning behavior (pelagic, demersal or nesting), spawning season and duration (months), absolute fecundity and oocyte diameter (in mm). Diet was described by average trophic level of species. For growth, we considered the allometric coefficient of the length-weight relationship and the mean total length of adults. Maximum longevity was also included in the dataset.

Flexible discriminant analyses (FDAs) were used to test whether species trajectories could be explained according to their biological attributes. This method predicts membership of statistical units (here fish species) to predefined classes (here type of trajectory) by building discriminant axes that are combinations of predictor variables (here biological attributes) in order to maximize the between-class dispersion and minimize within-class dispersion by projection (Hastie et al., 1994; Desbois, 2003).

For this purpose, quantitative ELHT were standardized to give equal weight to all biological attributes. Then, FDAs were performed on all possible combinations of 1 to 15 traits in order to (i) investigate the influence of the number of biological attributes considered and (ii) find the best combination(s) for discrimination of fish demographic trajectories. In each case, the global accuracy in species assignment to demographic trajectories was evaluated using a cross-validation method. More precisely, the total dataset was split into two parts: a training dataset used to build the model and a test dataset which evaluated assignment accuracy. Here, as the number of species was low, we used the "leave one out cross validation method", which removes one species and tests the robustness of the model. Model accuracy was calculated from a confusion matrix as the mean percentage of correct assignments (Kohavi and Provost, 1998). Finally, a classification tree method (Random Forest, Breiman, 2001) was applied to the dataset leading to the best trajectories discrimination to identify the respective contributions of the biological attributes comprised within the "optimal combination" to overall discrimination success.

All analyses were performed using R software (R Development Core Team, 2013).

3. Results

3.1. Environmental constraints: Description of abiotic shifts

Abiotic parameters showed very different temporal evolutions over the three decades studied (Fig. 2). Both surface and bottom salinities increased significantly, from 22.8 ± 0.6 (mean ± SE) to 26.8 ± 0.5 and from 24.6 ± 0.5 to 27.9 ± 0.5, respectively, between 1980 and 2011. The water pH increased from 7.7 ± 0.1 in 1980 to 8.9 ± 0.4 in 1997, then decreased back to 7.94 ± 0.47 in 2011. Meanwhile, depth and water clarity both significantly decreased between 1980 and 1997, from 2.84 ± 0.81 to 2.03 ± 1.10 m for depth and from 0.92 ± 0.42 to 0.79 ± 0.48 for clarity, then increased back to 2.81 ± 0.99 m and 0.96 ± 0.54, respectively. No significant modification of surface or bottom mean temperature was detected. Moreover, the occurrence of extreme phenomena increased in the lagoon: for example salinities greater than 38 were 15 to 20 times more frequent in 1997 and 2011 than in 1980.

3.2. Species responses to environmental constraints

The 25 species in this study represented together >80% (in both abundance and biomass) of annual fish catches in the lagoon irrespective of the sampling period. Species experienced marked modifications of their abundance and occurrence over the three decades studied (see Appendices B and C for detailed values). Species responses to environmental modifications in the lagoon were highly diversified, with all five possible demographic trajectories identified for at least two species (Fig. 3). The "constant" and "hump-shape" trajectories were the most commonly observed within the fish community, for nine and eight species, respectively, while "decreasing" and "u-shape" trajectories concerned three species each, and with only two species exhibiting "increasing" trajectories.

3.3. Association of biological attributes with species sensitivity

Accuracy in species assignment to demographic trajectories was highly dependent not only on the size, but also on the composition of the combination of biological attributes used to build the FDA (Fig. 4). Maximum accuracy with combinations only using taxonomic attributes was limited to 40%, while 60% was achieved with combinations including only ELHT. The highest accuracy (72% correct assignment) was obtained combining ELHT and taxonomy and was reached using only five biological attributes out of the 15 investigated (Fig. 4). Accuracy decreased for bigger combinations, indicating that many of the biological attributes investigated bring more noise than signal in the prediction of species demographic response.

Three different combinations of biological attributes allowed reaching the maximum prediction accuracy. As mentioned above, each of these combinations included five biological attributes, one taxonomic attribute (the order) and four ELHT (the oocyte size, the spawning season, plus any two out of the three descriptors of salinity niche investigated). As inter-correlation was the lowest (0.03) between maximum salinity and salinity range width, the combination of biological attributes allowing best prediction of fish demographic trajectories was finally considered to be:

Spawning season–oocyte size–order–maximum salinity–salinity range width

Misclassification with this combination, when present, mostly concerned the two species with "increasing" trajectories. Percentage of correct reassignment was otherwise of 100% for the species with "u-shape" and "decreasing" trajectories, and 87% and 55%, respectively, for the species with "hump-shape" and "constant" trajectories. The decision tree showed that spawning season was the most important biological attribute for discriminating demographic responses in fish (Fig. 5), separating species with "hump-shape" or "u-shape" trajectories (which spawn in the wet season) from all others (which spawn in the dry season). Among "wet season" spawners, oocyte size (below or above 0.85 mm) was the second most distinctive biological attribute, allowing final discrimination between fish with "hump-shape" versus "u-shape" trajectories. For "dry season" spawners, Order was the second most distinctive biological attribute, followed by maximum salinity, as only Clupeiforms or Perciforms unable to tolerate salinities above 38 exhibited a "decreasing" trajectory. All the other "dry season" spawners investigated exhibited "constant" trajectories.

4. Discussion

Our results demonstrate that even the complex and diverse demographic responses of the fish species can be accurately predicted when combining appropriate biological attributes. This

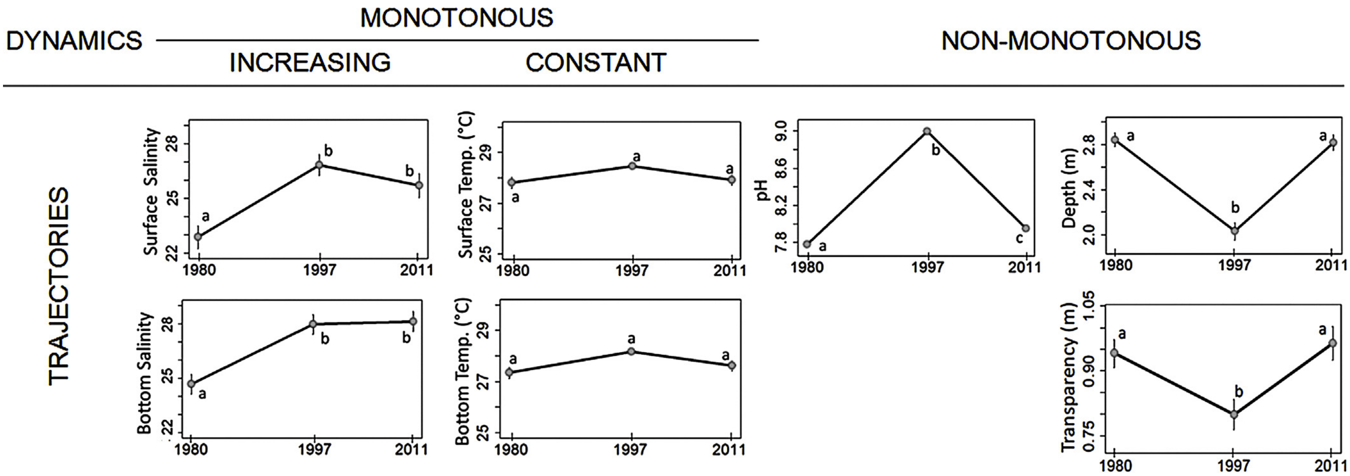

Fig. 2. Environmental changes (mean ± SE) across the three studied periods (1980, 1997 and 2011). Different letters depict significant differences among periods ($p < 0.05$) using ANOVA and Tukey's tests for normal data and Kruskal–Wallis and Mann–Whitney tests with Bonferroni correction for non-normal data.

validates the used of biological attributes, especially ELHT, as indicators of species vulnerability to local perturbations and stresses their potential value for predicting future temporal changes in the composition of local fish communities.

4.1. Benefit of a multivariate index for monitoring temporal dynamic of species

In this study, reliable description of biotic shifts was reached by transposing the indicator species index of Dufresne and Legendre (1997), initially developed to characterize spatial patterns in species composition. This transposition allows assessing species temporal demographic changes by taking in account two complementary parameters: species abundance and frequency of occurrence within the ecosystem. Associated with permutation tests to validate the statistical significance of the observed changes over time (Mouillot et al., 2002), the use of this index therefore allows more accurate assessment of changes in species dominance (i.e. discrimination between "loser" and "winner" species) over time than when considering changes in abundance or biomass only. For instance, Villéger et al. (2010) reported the species *Archosargus rhomboidalis* to be a "loser" species in terms of abundance between 1980 and 1997, while its temporal trajectory with our method was reported as "constant". Investigation of our dataset showed that this difference was due to the fact that, during this period, while the relative abundance of the species decreased in Terminos (Appendix B), its frequency of occurrence within the lagoon increased (Appendix C). Taking into account both findings gives a more objective view of variation in species dynamics (Mouillot et al., 2002). This can prove especially valuable when comparing the response of species with different life strategies (e.g. endemism versus dispersion).

4.2. Inter-specific differences in demographical trajectories in a context of environmental shifts

The multivariate index confirmed that composition shifts in fish communities result from complex biological processes causing inter-specific differences in demographic responses to the same perturbation, be it multiple or not. Indeed, among the dominant species in the fish communities of Terminos, all five possible types of demographic responses investigated were observed, confirming the high diversity in species sensitivity already shown for this taxon (Olden et al., 2006, 2007; Chessman, 2013). Surprisingly few species exhibited "decreasing" or "increasing" responses in our case, but, since we only considered the most abundant species in the lagoon, we might have underestimated the decline of the rarest, and therefore most vulnerable species in the lagoon (Mouillot et al., 2013a). The fact that many (36%) of the 25 species studied did not experience any significant change in their demographic status across time might also reflect the high tolerance of estuarine species to abiotic modifications (Blaber, 1997). However, complex temporal responses (with reversing trends since 1997) were the most commonly observed in the species investigated (44%). Our results confirmed the conclusions from previous studies on fish community changes in the lagoon, for instance the marked increases of both *Eugerres plumieri* and *Stellifer lanceolatus* between 1980 and 1997 (Ramos-Miranda et al., 2005a). However, based on the comparison of abundance shifts between these two dates only, both species were falsely diagnosed as "winner" in the face of environmental changes in the lagoon. The reversal of this trend after 1997 illustrates the need to consider greater periods of time with a monitoring at regular intervals to accurately describe species responses to perturbations within communities.

Modifications of fish communities may result from both direct and indirect effects of environmental modifications (Vitousek, 1994). In Terminos, our results confirmed significant changes in abiotic conditions, as already suggested by previous studies in the area (Ramos-Miranda et al., 2005b; Villéger et al., 2010). They show that over the last 30 years, salinity in the lagoon has increased considerably, both on average and through the increase of extreme salinity events. Meanwhile complex evolution patterns, with opposite trends before and after 1997, were observed for pH, depth and clarity. In addition to these modifications, habitats within the lagoon were affected by a marked increase of pollution, at least in pesticides (Carvalho et al., 2009), paraffin (Botello and Mandelli, 1978) and heavy metals (Vélez and Botello, 1992; Vanegas et al., 1997). These environmental changes may result from the global increase of anthropogenic influence in the region, through the installation of off-shore oil platforms, the deforestation of the drainage basin for agriculture and the urbanization of Carmen Island, but also from modifications in local marine currents and precipitation regimes (Ramos-Miranda et al., 2005b). All these environmental modifications may directly lead to the demographic response of species over time. However, they may also indirectly affect the final response of the fish community. For example, the increase of turbidity in the lagoon over the last decades, its eutrophication caused by poor wastewater management and the intensification of shrimp trawling in the area has resulted in a

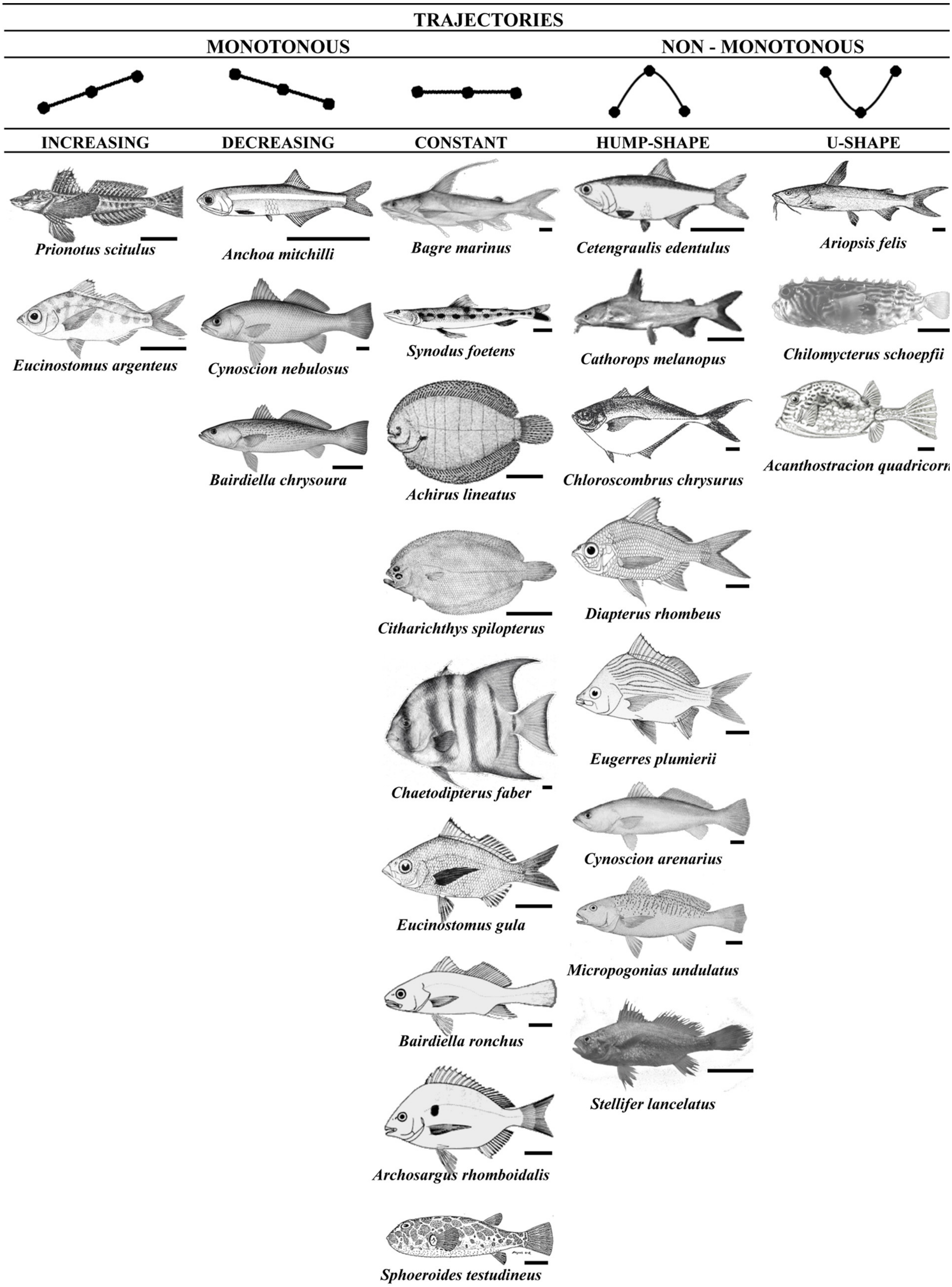

Fig. 3. Species responses to environmental changes during the three periods (1980, 1997 and 2011). Type of trajectory was discriminated using the IndVal index (see text for details). Scale bar for each species = 5 cm. Pictures are from FAO, Fishbase and the Smithsonian Marine Station.

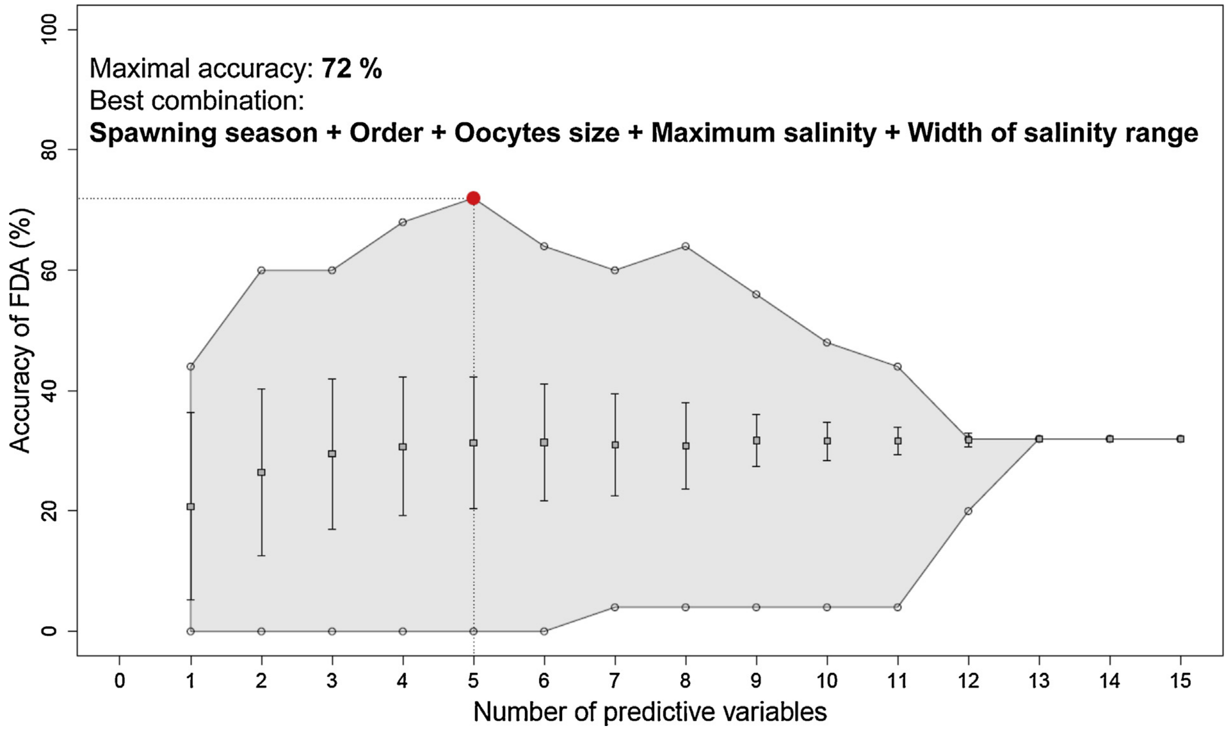

Fig. 4. Classification accuracy (%) of species trajectories according to taxonomic and ecological and life-history traits (ELHT) obtained with flexible discriminant analysis (FDA). For each number of variables, mean (±SD) accuracy among all combinations of traits is shown with black bars and minimal/maximal accuracies delimit the gray area.

drastic reduction of seagrass habitats (Short and Wyllie-Echeverria, 1996), which are key habitats for breeding or for food acquisition for species such as *A. rhomboidalis* and *Sphoeroides testudineus* (McEachran and Fechhelm, 2006).

Such complexity in the processes underlying both the impacts of perturbations and the relative responses of species explains why predictive models based on species biological attributes can be so valuable for assessing the fate of biodiversity within such complex systems, with the rationale that taxonomy, ecological and life-history traits will determine, at least partly, species sensitivity to multiple environmental pressures.

4.3. Biological attributes as indicators of species temporal trajectories in a changing environment

Our results validated that fish species responses are not random (otherwise mid-term species dynamics would not be so accurately predicted by biological attributes). Previous studies had already shown that variables such as abundance/occurrence or endangered status could be predicted by biological attributes (Cardillo and Bromham, 2001; Cardillo et al., 2008; Murray et al., 2011; Newbold et al., 2013; González-Suárez et al., 2013). Our results go one step further by showing that some biological attributes can be

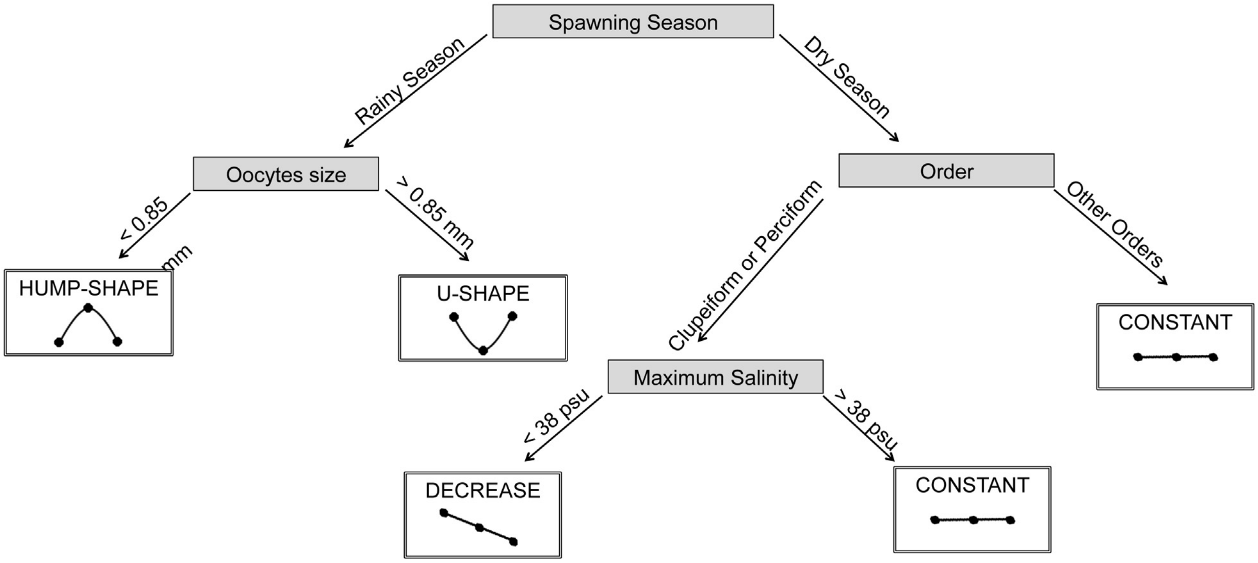

Fig. 5. Decision tree obtained with the classification tree accounting for the best model selected with the FDA: trajectory = maximum salinity + width of salinity range + oocyte size + spawning season + order.
Salinity parameters (Maximum salinity and Width of salinity range) referred to the values where species occurred in the Terminos Lagoon. The decision tree was not able to take into account the "Increasing" trajectory due to the low number of species in this class.

indicators of temporal changes in species abundance and occurrence. To our knowledge, only few studies (Jennings et al., 1998; Olden et al., 2006; Chessman, 2013) have attempted to infer temporal demographic modifications (i.e. based on abundance and/or occurrence differences between two sampling periods) from biological attributes. These studies adopted two different approaches: Chessman (2013) and Jennings et al. (1998) investigated the effects of each trait on species responses (i.e. using traits without combining them) contrary to Olden et al. (2006) who combined a set of traits to predict the species trajectories (i.e. multi-traits approach).

In environments where disturbances are complex and often multiple, a multi-traits approach is apparently essential. Indeed, maximum correct reassignment with a single trait in our case (44%) was far lower than that with combinations of five (72%) or even just four (68%) biological attributes. Studies attempting to predict global species status from multiple combinations of traits in birds or mammals found much higher percentages of correct reassignments, up to 82–92% (Davidson et al., 2009, 2012; Newbold et al., 2013). This is not particularly surprising since their approaches differed drastically from ours, not only in terms of biological models (birds or mammals versus fish) or geographic scales (global versus local) but also in the statistical methods employed. It is also likely that the differences in prediction accuracy observed result from the fact that we tried to predict more complex data (temporal trajectories versus static status). As far as we know, only one study so far (Olden et al., 2006) investigated the value of multi-traits approaches for predicting the dynamic response of fish to environmental perturbations. However this study was based on multiple regressions, which do not provide an estimate of correct reassignment and thus no accuracy percentage.

The highest classification accuracy (72%) was obtained using only 5 biological attributes among the 15 investigated, confirming that some traits sometimes bring more noise than signal to the discrimination (Tournois et al., 2013). The best combination included both taxonomic attributes and ELHT, indicating that these bring complementary information and must be combined to better model species sensitivity to disturbances with the underlying hypothesis that some critical traits not taken into account are conserved through lineages (Cadotte et al., 2009). However, considering only species taxonomy provided a 1.8 times lower accuracy in demographic trajectories prediction (40%). Indeed, most species from the same family did not share the same temporal trajectory. For example, among Ariidae, *Bagre marinus* exhibited a “constant” trajectory, *Cathorops melanopus* a “hump-shape” trajectory and *Ariopsis felis* a “u-shape” trajectory. Among Sciaenidae, the temporal trajectory was “decreasing” for *Bairdiella chrysoura*, “constant” for *Bairdiella ronchus* and “hump-shape” for *Cynoscion arenarius*. This suggests the predominance of ELHT over taxonomy for explaining species sensitivity to perturbations.

The best combinations of traits in our case all involved only ELHT linked to salinity niche, taxonomy, spawning season and oocyte size. Contrary to what could be expected from previous studies (e.g. Cardillo and Bromham, 2001; Dulvy et al., 2003; Olden et al., 2006, 2008; Davidson et al., 2009), neither fish size, age at maturity nor trophic level were good indicators of species trajectories in Terminos. This might be due to differences in spatial scales between these studies and ours. Indeed, at large scales, the strong differences in disturbances experienced by the various ecosystems may even out the effects of environmental modifications, resulting in a higher predictive power of the biological attributes common to all ecosystems (e.g. maximum size or age at maturity). At local scales however, like within the Terminos lagoon, all disturbances experienced by the ecosystems can potentially drive species response over time. In this case, the most discriminant traits are apparently those most related, directly or indirectly, to local environmental modifications. For example, among the species spawning during the dry season, only the clupeiforms and perciforms that did not occur at salinities above 38 were identified as potential “loser” species. This is quite logical since the increase in salinity within the lagoon (4 units on average since 1980) constitutes a double threat for these species. The first threat concerns adults, which cannot physiologically tolerate high salinities (Nissling and Westin, 1997). However, because salinity is already high in the lagoon during the dry season, extreme salinity events during this period may also negatively and irremediably affect egg survival (Winger and Lasier, 1994). This example stresses the importance of improving our physiological knowledge of species to understand, and thus predict their response to disturbance (Hartley et al., 2010). Explaining why the other traits like order and oocyte size are included in the five most discriminant biological attributes is less straightforward. Two hypotheses may be advanced: (i) we are missing some important mechanisms of environmental disturbances affecting species response (e.g. impact of pollutant on individual fitness); (ii) these biological attributes are involved in the best combinations due to their indirect effect on species response. Unraveling the exact role of each trait in species response would thus require deeper biological and physiological investigations on these species.

5. Conclusions

Our study validates the feasibility of accurately predicting temporal trajectories of fish species in a context of changing environment directly from combinations of appropriate biological attributes. This paves the ways to more complex models to predict future demographic changes in fish communities. The list of discriminant traits might be different in environments undergoing other environmental changes. Therefore, the next step would be to investigate whether the set of traits obtained here in the Terminos lagoon matches that from other systems. It would also be interesting to test the value of biological attributes for predicting temporal trajectories of other biological models with completely different life histories. Indeed, generalization of temporal predictive approaches would provide a valuable additional tool for conservation managers.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2014.07.038.

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