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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