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Thermal affinity as the dominant factor changing Mediterranean fish abundances

Or Givan[1] | Dor Edelist[2] | Oren Sonin[3] | Jonathan Belmaker[1,4]

[1]George S. Wise Faculty of Life Sciences, School of Zoology, Tel Aviv University, Tel Aviv, Israel

[2]Israel Oceanographic and Limnological Research, Tel-Shikmona, Haifa, Israel

[3]Department of Fisheries and Aquaculture, Ministry of Agriculture and Rural Development, Beit-Dagan, Israel

[4]The Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv, Israel

Correspondence
Or Givan, George S. Wise Faculty of Life Sciences, School of Zoology, Tel Aviv University, Tel Aviv, Israel.
Email: orgivan@post.tau.ac.il

Abstract

Recent decades have seen profound changes in species abundance and community composition. In the marine environment, the major anthropogenic drivers of change comprise exploitation, invasion by nonindigenous species, and climate change. However, the magnitude of these stressors has been widely debated and we lack empirical estimates of their relative importance. In this study, we focused on Eastern Mediterranean, a region exposed to an invasion of species of Red Sea origin, extreme climate change, and high fishing pressure. We estimated changes in fish abundance using two fish trawl surveys spanning a 20-year period, and correlated these changes with estimated sensitivity of species to the different stressors. We estimated sensitivity to invasion using the trait similarity between indigenous and nonindigenous species; sensitivity to fishing using a published composite index based on the species' life-history; and sensitivity to climate change using species climatic affinity based on occurrence data. Using both a meta-analytical method and random forest analysis, we found that for shallow-water species the most important driver of population size changes is sensitivity to climate change. Species with an affinity to warm climates increased in relative abundance and species with an affinity to cold climates decreased suggesting a strong response to warming local sea temperatures over recent decades. This decrease in the abundance of cold-water-associated species at the trailing "warm" end of their distribution has been rarely documented. Despite the immense biomass of nonindigenous species and the presumed high fishing pressure, these two latter factors seem to have only a minor role in explaining abundance changes. The decline in abundance of indigenous species of cold-water origin indicates a future major restructuring of fish communities in the Mediterranean in response to the ongoing warming, with unknown impacts on ecosystem function.

KEYWORDS
biotic interactions, climate change, community ecology, ecological traits, fish, fishery, invasion, Mediterranean

1 | INTRODUCTION

Recent decades have seen profound changes in species abundance and community composition (Dirzo et al., 2014; Dornelas et al., 2014; Mccauley et al., 2015). Many of these changes have been attributed to anthropogenic drivers (Dirzo et al., 2014; Lyons et al., 2016; Mccauley et al., 2015). In the marine environment, the major drivers include direct exploitation, invasion by nonindigenous species, and climate change.

Fishing is considered a major determinant of changes in fish abundance (Jackson et al., 2001). For example, since the nineteenth century the industrialization of UK bottom trawl fishing has led to a large decline in fish abundance (Thurstan, Brockington, & Roberts, 2010). Current trends in exploited stocks appear to differentiate between regions showing stabilization of fish biomass at low levels and regions with a continuing decline (Worm & Branch, 2012). Worldwide, marine invasions are accelerating (Grosholz, 2005; Ricciardi & Macisaac, 2000; Rilov & Galil, 2009), with less than 16% of marine ecoregions currently having no reported marine invasions (Molnar, Gamboa, Revenga, & Spalding, 2008). Such invasions can impact indigenous species abundance, as seen in the widespread lionfish invasion throughout the Caribbean (Albins & Hixon, 2008; Green, Akins, Maljkovic, & Cote, 2012). Nevertheless, direct evidence of invasion-induced change in abundance in open marine systems is relatively scarce (Edelist, Rilov, Golani, Carlton, & Spanier, 2013a; Golani, 2010). Finally, climate change strongly affects marine species abundance and distribution (Poloczanska et al., 2013). For example, at high latitudes climate warming is inducing a northward range expansion (Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013; Fossheim et al., 2015; García Molinos et al., 2015) and spatial biotic homogenization (Magurran, Dornelas, Moyes, Gotelli, & Mcgill, 2015). However, a negative effect of climate change on species abundances at their warm "trailing-end" has been less documented (Kerr et al., 2015; Rilov, 2016; Sinervo et al., 2010).

The above drivers of change (fishing, species invasions, and climate change) may interact. For example, in marine environments, climate change can lead to improved conditions for warm-water invaders (Albouy et al., 2013; Lasram et al., 2010; Raitsos et al., 2010; Walther et al., 2009) or the formation of nonanalog environments where invasions are common (García Molinos et al., 2015). In addition, fishing may reduce the size of populations, making them more sensitive to additional stressors such as climate change (Cheung, Watson, & Pauly, 2013a). However, although widely speculated, empirical evidence of such interactions has been limited (Côté, Darling, & Brown, 2016).

The relative importance of these stressors has been extensively debated (Clavero & Garcia-Berthou, 2005; Crain, Halpern, Beck, & Kappel, 2009; Didham, Tylianakis, Hutchison, Ewers, & Gemmell, 2005; Young & Larson, 2011). Nevertheless, very few studies have empirically estimated their relative importance. For example, Last et al. (2011) compared climate change and fishing pressure effects on fishes in the Tasmanian Sea and found that whereas fishing has historically been the dominant driver of abundance change, warming has been the major driver in recent years (Last et al., 2011). To our knowledge, no study has as yet empirically estimated the relative importance of competition with nonindigenous species, fishing pressure, and climate change within a single system.

The Mediterranean Sea is a semi enclosed sea highly impacted by humans (Lejeusne, Chevaldonne, Pergent-Martini, Boudouresque, & Perez, 2010). Fishing pressure in this region is substantial and has resulted in the decline of many stocks (Vasilakopoulos, Maravelias, & Tserpes, 2014). In addition, the opening of the Suez Canal (1869) has led to a continuous invasion of species from the Red Sea, making the Eastern Mediterranean a hotspot for marine invasion (Coll et al., 2010; Elleouet, Albouy, Lasram, Mouillot, & Leprieur, 2014; Lasram et al., 2008; Parravicini, Azzurro, Kulbicki, & Belmaker, 2015). For fishes, the biomass of invasive species may exceed that of indigenous species (Edelist et al., 2013a; Rilov & Galil, 2009). Finally, the Mediterranean is warming at a rate that substantially exceeds the global average (Belkin, 2009; Nykjaer, 2009). Satellite observations indicate that over the last decades the temperature in the upper layer of the Mediterranean Sea has been increasing at an average rate of $0.03 \pm 0.008°C \ yr^{-1}$ for the western basin and $0.05 \pm 0.009°C \ yr^{-1}$ for the eastern basin (Nykjaer, 2009). Moreover, many indigenous species are adapted to cold temperatures, leading to concerns about their long-term population sustainability (Albouy et al., 2013; Lasram et al., 2010). Seeking a better understanding of the relative impact of these drivers, Claudet and Fraschetti (2010) conducted a meta-analysis across various Mediterranean habitats in order to identify the relative magnitude of these threats. However, their small sample sizes precluded robust conclusions, drawing attention to the critical lack of empirical knowledge.

In this study, we used two fish trawl surveys spanning a 20-year period to estimate the magnitude and relative importance of anthropogenic stressors for changes in fish relative abundance. We focus on the Eastern Mediterranean, a region where all three major anthropogenic disturbances (competition with nonindigenous species, fishing pressure, and climate change) are known to be substantial. Thus, the results will be pertinent for forecasting changes in regions that have hitherto not been exposed to these levels of threat.

2 | MATERIALS AND METHODS

We first sought to quantify a species-based estimate of intrinsic sensitivity to the three main drivers of change: fishing, competition from invasive species, and climate change. We then compared which of these drivers best explains the patterns of abundance change over time, across all species.

2.1 | Species data

Our data set was based on fish surveys on board commercial trawlers in the Israeli Mediterranean waters over two periods: (i) April 1990 to December 1994 (267 hauls) and (ii) October 2008 to March 2011 (183 hauls). The trawls covered the same fishing fields and depth range, 15–300 m, on the continental shelf and upper slope (see Appendix S1 for a map of the study region). In both study periods, 15–22 m overall length stern trawlers dragged 40 mm diamond mesh nets. The catch sampling protocol constituted selecting a representative subsample from each haul using a standard-sized box comprising an average of 260 ($\pm$10 SE) individuals. This sampling protocol is useful for estimating the relative abundance but not total abundance of species in the catch. All fishes in the samples were taxonomically identified to species level. Over both periods, 167 fish

species were sampled out of which 133 were indigenous to the Mediterranean and 34 were nonindigenous species (Edelist, Sonin, Golani, Rilov, & Spanier, 2011; Edelist et al., 2013a).

To estimate the change in abundance between periods, we defined the proportional change A_i^P in species i relative abundance between $t = 0$ (first survey) and $t = 1$ (second survey) as:

$$A_i^P = \frac{A_i^{t=1}}{A_i^{t=0}} \tag{1}$$

where $A_i^{t=0}$ and $A_i^{t=1}$ are the relative abundances of species i at time $t = 0$ and $t = 1$, respectively.

We divided the samples into three depth strata: Shallow (15–37 m), Medium (38–82 m), and Deep (>83 m). We expected the effect of all three drivers to be strongest at the shallow depth, as it is presumably the most susceptible to all such disturbances.

2.2 | Sensitivity to fishing

In the study region, fishing is mostly done by nonselective trawling. Targeted fishing, may it be commercial or artisanal, is rare (Edelist et al., 2013b). Furthermore, the Israeli portion of the Mediterranean Sea is small (coastal length is 187 km) and homogenous (see Appendix S1) thus presenting a single habitat that can be covered within a single commercial fishing day. Therefore, fishers in the region are unselective, which reduces the potential biases associated with fishery-dependent catch data. This means that relative fishing effort on each species is assumed to be comparable across time. Under such conditions, the impact of fishing will mostly depend on the intrinsic sensitivity of fishes to this fishing. For example, large and slow-growing species will suffer heavier declines compared to small and fast-growing species. Therefore, our first hypothesis was that, over time, species sensitive to fishing would show a decline in their relative abundance in response to fishing pressure, while the relative abundance of less sensitive species would increase or remain the same. Thus, we expected a negative relationship between sensitivity to fishing and the change in species relative abundance. We used a composite index of *intrinsic* sensitivity to fishing (Cheung, Pitcher, & Pauly, 2005), which integrates life-history and ecological characteristics, such as maximum body length, age at first maturity, von Bertalanffy growth parameter K, natural mortality rate, maximum age, geographic range, annual fecundity, and strength of aggregation behavior. Intrinsic sensitivity to fishing scores were collected directly from fishbase (Froese & Pauly, 2015).

We additionally quantified the fishing effort applied on the species using an index based on the overlap between the observed fishing activities and the species' observed depth distribution (Appendix S9). Thus, fish species for which fishing effort overlaps substantially with their depth distribution will suffer more heavily than species for which fishing rarely occurs at the depth they inhabit. For this we quantified, for each species, the overlap between the trawled depths and the observed depth distribution of each species standardized according to the number of hauls at each depth. Depth distributions were first smoothed using a nonparametric

kernel density function, with the smoothing bandwidth selected according to Sheather and Jones (1991). We used data from all trawl samples to calculate the total fished depth distribution, which is typical of the fishing effort of the entire Israeli trawl fleet (Edelist et al., 2011). We then calculated the relative area of the observed species density which overlaps with the depth distribution of trawl depths. For this index, high overlap means the species experiences high fishing pressure and low overlap means the species experiences low fishing pressure. However, we found that our index of overlap was comparable to the index of intrinsic sensitivity to fishing (Appendix S9) and thus we show only the latter in the main text.

2.3 | Sensitivity to nonindigenous species

Our second hypothesis was that competition from nonindigenous species would cause a decline in species abundances. To assess the change in competitive pressure exerted on indigenous species, we estimated changes in the abundance of nonindigenous species, weighted by their niche dissimilarity to the focal species. We assume that high niche dissimilarity is associated with low competitive pressure and low niche dissimilarity with high competitive pressure (Elleouet et al., 2014; Mouillot, Mason, & Wilson, 2007). To estimate the fishes' niches, we examined their ecological traits. We used six ecologically important traits: diet, home range, activity, schooling level, water column position, and body size. These traits are commonly used to describe the ecological role of fish species in the community (Albouy et al., 2015; Givan, Parravicini, Kulbicki, & Belmaker, 2017; Mouillot et al., 2014). The trait categorization follows Givan et al. (2017) and a complete description of the traits examined can be found in Appendix S2. All traits were given equal weights in the analysis; however, the results were robust to variation in the weighting scheme (Appendix S6). Trait data were compiled from Golani, Öztürk, and Başusta (2007) and Froese and Pauly (2015), augmented with expert opinion. The traits represent species-level attributes that do not accommodate intraspecific variation in trait values. Given the scale of our study, we could not account for intraspecific variability of traits among life stages and treated the species caught as adults only.

Using the extended Gower dissimilarity index (Podani, 1999), we constructed a trait dissimilarity matrix for the entire species pool. Following Mouillot et al. (2007), we estimated the total potential competitive pressure C_i that the indigenous species i is experiencing by calculating a competitive pressure index based on the abundance of all nonindigenous species, weighted by their trait dissimilarity as:

$$C_i = \sum_{i \neq j}^{s} \frac{KA_j}{R_{ij}^d} \tag{2}$$

where S is the community species richness, A_j is nonindigenous species j relative abundance, and R_{ij} is trait dissimilarity between species i and j. K and d are constants that control the effects of other species abundances and dissimilarities, respectively, on the focal species abundance. These constants were fitted to the examined community

for each time period and depth group separately. However, the values of the fitted parameters were extremely similar between any of these categories ($K \in [-0.0066, -0.0055]$, $D \in [0.18, 0.19]$).

The proportional change in nonindigenous potential competitive pressure C_i^P, on species i between the periods $t = 0$ and $t = 1$ is therefore:

$$C_i^P = \frac{C_i^{t=1}}{C_i^{t=0}} \tag{3}$$

We were also interested in understanding what drives changes in the abundance of nonindigenous species. In this case, possible "biotic resistance" (the ability of indigenous species to reduce the establishment success of nonindigenous species; Elton, 1958) can be estimated as the competition indigenous species exert on nonindigenous species. This can be done by transforming the above calculation to estimate the competitive pressure indigenous species exert upon nonindigenous species in the community. Thus, we were able to also examine a complementary hypothesis; that an increase in indigenous species competitive pressure on nonindigenous species would result in a decline of that nonindigenous species' relative abundance.

2.4 | Thermal affinity

Our third hypothesis was that the observed warming ocean temperature might result in a decline in the relative abundance of species that are adapted to cooler climates and an increase in species that are adapted to warmer ones. To estimate thermal affinity, we overlapped species occurrence and environmental layers. Species occurrences were taken from the Global Biodiversity Information Facility (GBIF, http://www.gbif.org/). We refrained from using data from within the Mediterranean because all species observed in the Eastern Mediterranean occur within an extreme temperature regime and hence they must either cope with the local thermal conditions or represent sink populations. These possibilities cannot be differentiated and thus we prefer to estimate thermal affinity for each species from its Atlantic distribution only where there is great variation in observed thermal maxima. Nevertheless, the results were extremely similar when using also the Mediterranean distribution of the species (Appendix S8).

Duplicated values and occurrences that fell outside the known distributional range were removed from the collected data. In total, the data contained 24,867 occurrences of 167 species (Appendix S2). Species distributions were estimated from occurrence data using convex hulls. Environmental layers were extracted from Bio-ORACLE (Tyberghein et al., 2012) and included mean, minimal, and maximal monthly Sea-Surface Temperature (*SST*). We then used the average, minimal, and maximal value of these layers, respectively, across each species range as predictors. In all analyses, we found *Mean SST* to be both the strongest predictor (Table S.5.1 in Appendix S5) and the one that provides the best statistical properties (in terms of the distribution of residual variations) and hence this was used in all subsequent analyses. If climate warming affects species relative abundance, we would expect to find a positive relation between the proportional change in species relative abundance and thermal affinity, as species adapted to cold temperatures decline in abundance.

2.5 | Statistics

The log ratio of the relative abundance of each species A_i^P between the first and second time periods was used as the response variable.

$$\ln A_i^P = \ln\left(\frac{A_i^{t=1}}{A_i^{t=0}}\right) \tag{4}$$

We conducted two separate analyses for indigenous and nonindigenous species. Within each group, we used two methods to examine the relative influence of the three classes of predictors (fishing sensitivity, competitive pressure, and thermal affinity) on the relative abundances of species:

1. *Meta-analysis* We applied a meta-analytical technique to account for the difference in sample size and hence confidence in abundance change estimates, among species. The relative abundance log ratio was treated as the effect size, and competition, fishing sensitivity and thermal affinity indices were continuous predictors. We applied this analysis to each depth group separately. The following models were compared using AIC (Akaike, 1987): each of the three main drivers alone, all possible pairwise combinations of the three main drivers both as an additive and interactive effect, and a complete model with all three main drivers.

We weighted each species inversely to its sampling variance; thus the weight ω_i for each species i was calculated as $\omega_i = \frac{1}{\sigma_i^2}$. To calculate the variance σ_i^2 of the log ratio estimate, we used Hedges, Gurevitch, and Curtis (1999) formulation:

$$\sigma_i^2 = Var\left(\ln A_i^P\right) = \frac{(S_i^{t=0})^2}{N_i^{t=0}(A_i^{t=0})^2} + \frac{(S_i^{t=1})^2}{N_i^{t=1}(A_i^{t=1})^2} \tag{5}$$

where S_i is the standard deviation of species i and N is the sample size. The meta-regression was conducted using the "metafor" package (Viechtbauer, 2010) in R.

2. *Random forest* In order to gain deeper insights into the relative importance of predictors, taking into account possible complex interactive and nonlinear patterns, we conducted a random forest analysis (see, "randomForest" package by Liaw and Wiener (2002)). Random forest is based on the aggregation of a large number (1,000 in our case) of un-pruned decision trees based on bootstrap samples from the original data. Each decision tree is constructed by repeatedly splitting the data into two mutually exclusive groups as homogeneous as possible defined by a single randomly chosen explanatory variable. The three predictors were randomly sampled as candidates at each split to assess their importance. We grew 1,000 trees to ensure that every input row

would be predicted at least a few times. As we could not apply weights for this analysis, we excluded species whose total abundance over the two time periods was below τ individuals. For the final analyses, we chose τ = 5 as it produced the model with the highest R^2 (=7.5%). However, the major results were robust to the threshold choice (Appendix S7). All of the study analyses were conducted in R (R Core Team, 2016).

3 | RESULTS

3.1 | Abundance trends between survey periods

Changes in relative abundance between the periods 1990–1994 and 2008–2011 differ between shallow water (15–37 m) indigenous and nonindigenous species, with declining trends for indigenous species and increasing trends for nonindigenous species. The overall proportion of indigenous individuals sampled decreased between the surveys from 66.2% to 25.6% (Mean log ratio = −0.35 (±0.19 SE), Median = −0.21; Figure 1a), while that of nonindigenous species increased (Mean log ratio = 1.39 (±0.49 SE), Median = 0.62; Figure 1b). This difference was found to be significant (Wilcoxon rank sum test; W = 889.5, p < .004). In deeper waters, the patterns were less dramatic. Among the medium depth group (38–82 m), the proportion of indigenous individuals dropped from 78.5% to 48.8% of the total catch, with nonindigenous species showing higher increases in abundance than the indigenous species (Wilcoxon rank sum test; W = 581.5, p < .001); while in deep waters (>83 m) indigenous species relative abundance showed a minor drop from 93.1% to 80.2% of the total catch, with a significant difference in abundance change patterns between indigenous and nonindigenous species (Wilcoxon rank sum test; W = 541, p < .002). For additional patterns, see Appendix S3.

3.2 | Stressors sensitivity and niche overlap

In shallow waters, indigenous species were found to be more sensitive to fishing (mean sensitivity score = 42.82 (±1.69 SE), Figure 2a) than nonindigenous species (mean sensitivity score = 27.03 (±2.86 SE)). The mean proportional change in the potential competitive

pressure exerted on indigenous species by nonindigenous species increased between the study periods (mean ratio = 2.35 (±0.03 SE), Figure 2b), whereas the potential pressure exerted on nonindigenous species decreased (mean ratio = 0.43 (±0.006 SE)). Moreover, for a dissimilarity radius (Gower dissimilarity of 0.1), the mean number of neighboring species for indigenous species (27.38 (±1.47 SE) species) was higher than that of nonindigenous species (22.22 (±1.81 SE) species), suggesting that nonindigenous species inhabit relatively vacant niches in the Mediterranean. Unsurprisingly, the Mean SST of species occurrence of indigenous species was lower (species Mean SST = 21.89 (±0.42 SE) °C) than that of nonindigenous species (species Mean SST = 27.51 (±0.11 SE) °C), suggesting low overlap in their thermal affinities (Figure 2c). The above trends were consistent across all three depth groups (Appendix S4).

3.3 | Meta-regression

The model selection (Table 1) revealed that the best supported meta-regression model for indigenous species abundance changes in the shallow depth strata (Figure 3) contained Mean SST (estimated slope = 0.18, p = .01) as the sole predictor explaining R^2 = 18.8% of the variance in the data. This indicates that indigenous species with an affinity to high temperatures occupied an increasingly larger proportion of the community compared to indigenous species with an affinity to low temperatures. Two other models displayed similar AIC scores: [Mean SST + Fishing] (ΔAIC = 1.92, R^2 = 17.42%, Table 1) and Mean SST + Competition (ΔAIC = 1.94, R^2 = 17.1%, Table 1). However, neither Fishing (p = .79) nor Competition (p = .81) was found to be significant predictors in these models. All alternative models (including interactive ones) gained lower support (ΔAIC > 2, Table 1). Analysis of the medium and deep depth groups showed that all models had extremely low explanatory power (R^2 < 3% for medium depth groups, R^2 < 0.01% for deep depth groups) and were nonsignificant (Table S.5.2 and S.5.3 in Appendix S5). Similar analyses for nonindigenous species, for all depth groups, did not detect a model that was clearly superior to the others, and even the best supported models were not significant (moderators' omnibus test p > .15 for each examined model, results not shown).

FIGURE 1 (a) Relative abundance ratio for indigenous and nonindigenous species between the periods 1990–1994 and 2008–2011. (b) Density distribution of log abundance ratios for indigenous (blue) and nonindigenous species (red) at the shallow depth (for medium and deep depth groups see Appendix S3). Nonindigenous and indigenous species display different trends in relative abundance between 1990–1994 and 2008–2011 (Wilcoxon rank sum test; W = 889.5, p < .004)
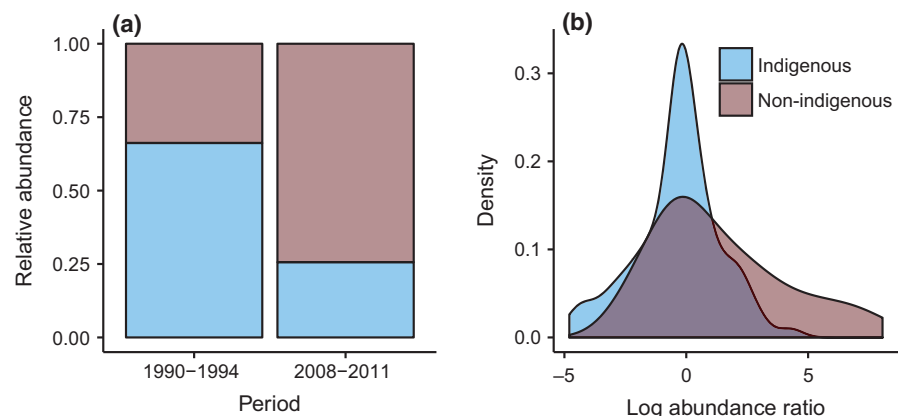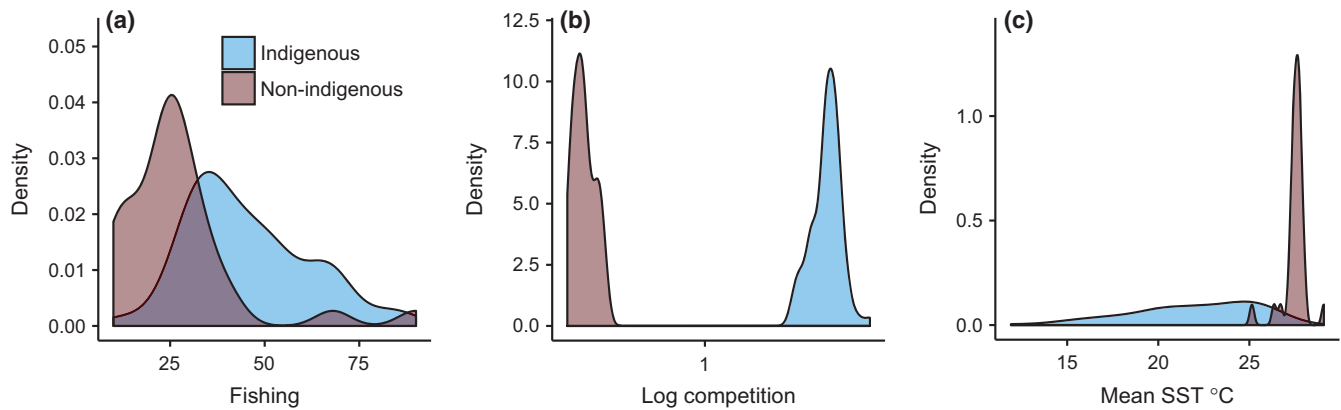
FIGURE 2 Indigenous (blue) and nonindigenous (red) community density plots of stress indicators for shallow waters: (a) Sensitivity to fishing. Indigenous species are more sensitive to fishing than nonindigenous ones. (b) Competitive pressure change between the periods 1990–1994 and 2008–2011. (c) *Mean SST* of species occurrence. Indigenous species are associated with a colder temperature range than nonindigenous ones

TABLE 1 Comparison of the meta-regression models for the shallow depths

Fixed effect	AIC	ΔAIC	R^2%	*p*
Mean SST	276.04	0	18.82	.011
Mean SST + Fishing	277.96	1.92	17.42	.039
Mean SST + Competition	277.98	1.94	17.10	.040
Mean SST × Competition	279.26	3.22	17.65	.065
Mean SST × Fishing	279.41	3.37	17.14	.071
Mean SST + Competition + Fishing	279.91	3.87	15.66	.092
Mean SST × Competition + Fishing	281.24	5.20	16.00	.129
Mean SST × Fishing + Competition	281.32	5.28	15.58	.134
Mean SST + Fishing × Competition	281.95	5.91	13.83	.176
Fishing	282.21	6.17	0.00	.654
Competition	282.26	6.22	0.00	.663
Fishing + Competition	284.11	8.07	0.00	.816
Mean SST × Competition × Fishing	284.36	8.32	18.49	.179
Fishing × Competition	286.19	10.15	0.00	.938

Species relative abundance log ratio between the time periods 1990–1994 and 2008–2011 was used as the effect size. We then compared different combinations of moderators, comprising *Mean SST* of species occurrences, sensitivity to fishing, and competitive pressure from indigenous species. Models were compared using Akaike's information criterion (AIC), where ΔAIC represents the difference from the minimal AIC score.

3.4 | Random forest

For indigenous species at shallow depths, *Mean SST* was the most important predictor of relative abundance changes (13.5% increase in the model's mean squared error (MSE); full model R^2 = 7.5%, Figure 4a). We found 20.5°C to be the threshold, with indigenous species occurring at lower temperatures had decreased their relative abundance. In contrast, *Fishing* and *Competition* were associated with only 7.1% and 5.6% MSE increase, respectively). Similar to the meta-regression analysis, models for the medium and deep depth groups, as well as for nonindigenous species (all depth
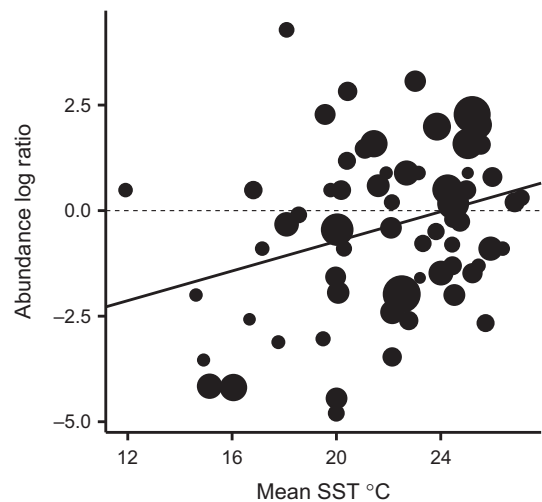

FIGURE 3 The change in relative abundance between the periods 1990–1994 and 2008–2011 across *Mean SST* of species occurrences. Results are for shallow depth (see Appendix S5 for medium and deep depths). Each dot represents a different species and dot size indicates its weight in the meta-regression (inversely related to *SD*). Meta-regression results show a significant positive trend between *Mean SST* and log abundance ratio

groups), yielded poorly fitted random forest analyses (R^2 < 0% for each model).

4 | DISCUSSION

In this study, we quantified the relative sensitivity to three main human-induced disturbances—fishing pressure, nonindigenous species, and climate change—of fish species in the eastern part of the Mediterranean sea, a system in which all three drivers are postulated to exert strong pressure. We found that the most important driver of relative population size is the *Mean SST* within an indigenous species' range (Table 1; Figure 4a), which is used here as an estimate of

FIGURE 4 Random forest analysis results for the indigenous species at the shallow depth. (a) Variable importance, as measured by the increase in the model's mean squared error (MSE) when the examined variable is excluded. (b) The marginal effect of *Mean SST* on species relative abundance. Indigenous species relative abundance tended to decrease for species with *Mean SST* lower than 20.5°C
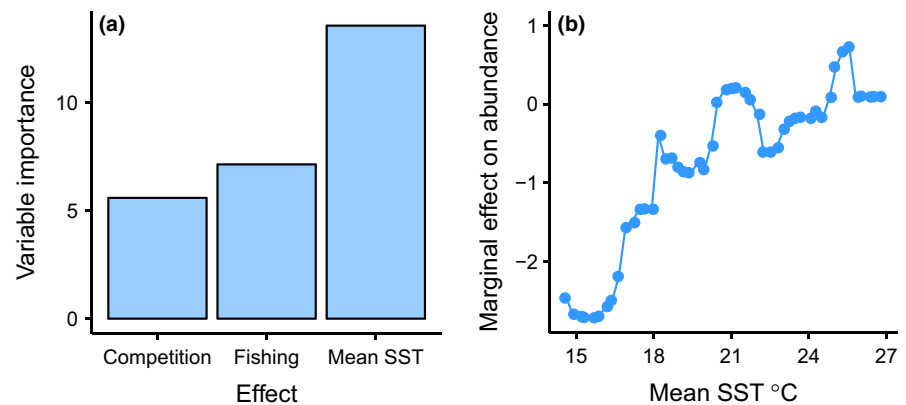
species sensitivity to climate warming. Species with an affinity to warm climates increased in relative abundance and, more pronouncedly species with an affinity to cold climates decreased (Figures 3 and 4b). This suggests a strong response of fish abundance to the increase in Mediterranean temperature over recent decades (Belkin, 2009), with fishing and biological invasion playing smaller roles.

Shrinking geographical distribution of indigenous Mediterranean species has been previously estimated using correlative species distribution models (SDMs; Lasram et al., 2010; Albouy et al., 2013). These models suggest that, with warming waters, species might become trapped within the northernmost, coldest parts of the different basins and unable to disperse further northwards to mitigate temperature changes. However, direct evidence for a climate-mediated decline in local abundance has thus far been lacking. This is important, as most correlative models are used to estimate species presence or absence only and are not designed to estimate changes in abundance. While a recent study has found abundance declines in intertidal invertebrates (Rilov, 2016), our study is one of the first to show direct abundance declines of cold water fish species in the warming Mediterranean (Azzurro, Moschella, & Maynou, 2011).

Here, we present evidence for relative abundance declines at the trailing edge of the range for cold-water-associated fishes. Several studies have found increases in the abundance of warm-water species at the leading, cold-limited, edge of their distribution, in conjunction with warming waters (Fossheim et al., 2015; Last et al., 2011; Pinsky et al., 2013; Sunday, Bates, & Dulvy, 2012). These warm-water species show an expansion of their geographical range with the potential to cause a rapid homogenization of communities (Magurran et al., 2015). However, climate-mediated shifts in species distribution at the trailing warm edge of their distribution are much rarer. For example, Dulvy et al. (2008) found that species are shifting to colder, deeper waters in the North Sea. The physiological mechanisms causing these declines in abundance are still not clear. It is possible that warming waters, which are associated with more frequent heat waves, pose severe physiological stress to cold-adapted species (Marbà, Jordà, Agustí, Girard, & Duarte, 2015). It is also possible that warming waters induce oxygen limitation that may compromise ecological function (Cheung et al., 2013b; Portner & Knust,

2007; Van Rijn, Buba, Kiflawi, & Belmaker, 2017). Whatever the physiological mechanism is, it is clear that increased water warming is likely to cause major shifts in community composition.

Sensitivity to fishing was found to be second in importance to thermal affinity (Figure 4a), with a relatively small effect on indigenous species relative abundance changes (Table 1). However, other studies have found a strong effect of fishing on Mediterranean fish (Vasilakopoulos et al., 2014). These findings may not be mutually exclusive if fishing impacts are high but relatively stable. Hence, while many species may be over depleted, fishing may be causing little additional change in abundance (Worm et al., 2009). This scenario fits well with evidence of a static catch per unit effort in the local trawl fisheries in recent decades (Van Rijn et al., 2014) but no increase in total fishing effort. Alternatively, nonselective fishing by trawling (Thurstan et al., 2010) may cause a strong decline in abundance that will be similar across species, hence displaying little change in species relative abundance (which was our response variable). Finally, it may be that the index of intrinsic sensitivity to fishing, by not accounting for fishing impact, does not capture the actual ranking of fishing pressure experienced by species. However, this will mostly be a problem when fishing efforts targets specific species, possibly switching gear and fishing methods through time. Fishing in the Eastern Mediterranean region is characterized by nonselective multispecies fishing with few species specifically targeted by the trawling fleet (Edelist et al., 2013b). In this case, intrinsic sensitivity to fishing is likely to be a reliable proxy for fishing impact.

Competition with nonindigenous species was found to be the least important predictor (Table 1; Figure 4a). This is intriguing, as the number of nonindigenous species in the region and their relative abundance are immense, leading to the often mentioned "tropicalization" of the Eastern Mediterranean (Bianchi, 2007). Moreover, an effect of nonindigenous species on indigenous species has been repeatedly postulated (Edelist et al., 2013a; Rilov & Galil, 2009). Nevertheless, as pointed out by Golani (2010), direct evidence for the overall decline of local indigenous populations by competitive displacement is lacking. Moreover, recent studies suggest that nonindigenous species are mostly established in ecological niches that are relatively unoccupied by indigenous species (Azzurro et al., 2014; Givan et al., 2017). Thus, successful nonindigenous species

may be using resources not exploited by indigenous species, potentially reducing their impact. While our study suggests that most nonindigenous species may be ecologically benign, specific species may still have overarching detrimental ecological effects. For example, rabbitfishes (*Siganus rivulatus* and *Siganus luridus*) have already outcompeted native Eastern Mediterranean herbivorous fishes such as *Sarpa salpa* and *Sparisoma cretense* (Sala, Kizilkaya, Yildirim, & Ballesteros, 2011). Although we found little evidence of negative effects of direct competition, nonindigenous species may still strongly impact communities through trophic associations (such as predation) or more diffused indirect competition. One possible example of this is the recently introduced lionfish (Kletou, Hall-Spencer, & Kleitou, 2016), which is considered extremely harmful to Caribbean fishes (Albins & Hixon, 2013) but whose impact on the Mediterranean is still undetermined.

We found that the most substantial changes in indigenous species abundance occurred at shallow depths. Shallow depths are predicted to be highly impacted by all three of the examined anthropogenic disturbances. First, these depths are more invaded than deeper ones by nonindigenous species (see, Appendix S3 and Goren, Galil, Diamant, Stern, & Levitt-Barmats, 2016), presumably due to the shallow depth of the main invasion vector—the Suez Canal (Rilov & Galil, 2009). Second, most fishing effort is concentrated in the shallow depths. The Israeli trawling fleet operates almost exclusively on the continental shelf between 15 and 150 m depth, with a growing trend in recent years to shallower trawls (Edelist et al., 2011). Finally, climate warming, especially as estimated from sea-surface temperature, is expected to be less pronounced in deeper waters. Hence, it is not surprising that deepwater species show little change in relative abundance over the studied period.

Our analysis found no significant interactions between any of the three predictors (Table 1), in spite of speculations that these interactions may be strong (Brook, Sodhi, & Bradshaw, 2008). Our findings are thus in line with recent studies that found little support for a synergistic effect of multiple stressors in field studies (Côté et al., 2016). Nevertheless, we cannot rule out that our analyses may have had low statistical power that might have prevented us from detecting such interactive patterns.

While variation in abundance change among indigenous species was well explained by thermal affinity, we could not explain changes in nonindigenous species abundance by any of our predictors. Previous studies have related the success of Mediterranean nonindigenous species to pelagic propagules (Lasram et al., 2008), pelagic life style (Samaha, Zu Dohna, & Bariche, 2016), shallow depths (Arndt & Schembri, 2015), species forming schools, and species with large home ranges (Belmaker, Parravicini, and Kulbicki (2013). We suggest that nonindigenous species success in the Mediterranean (Figure 1) can be also explained by their low sensitivity to all of the examined disturbances. Indeed, all nonindigenous species in this region are associated with warm waters (Figure 2c; Raitsos et al., 2010), are less sensitive to fishing than indigenous species (Figure 2a) and are also uniformly under lower competitive

pressure (Figure 2b; Azzurro et al., 2014; Givan et al., 2017). Thus, many nonindigenous species may be successful, with the relative change in their abundance being governed by a combination of their traits, stochastic processes (Belmaker, Brokovich, China, Golani, & Kiflawi, 2009), and hard to predict time lags (Azzurro, Maynou, Belmaker, Golani, & Crooks, 2016).

Understanding the relative importance of different anthropogenic stressors for changes in abundance is crucial for predicting future community responses to these changes (Halpern et al., 2008). However, comprehensive comparisons among multiple stressors within a single ecological community are sparse (Claudet & Fraschetti, 2010). By using comparable abundance data from two sampling periods spanning the last two decades, we were able to assess the relative importance of sensitivity to fishing, competition with nonindigenous species, and thermal affinity on Mediterranean fish. We found thermal affinity to be the most important stressor driving changes in the Mediterranean fish abundance. This suggests that future sea warming will continue to impose extreme changes on indigenous communities, with unknown impacts on community function.

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