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# Climate change, biological invasions, and the shifting distribution of Mediterranean fishes: A large-scale survey based on local ecological knowledge

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## Abstract

Climate change and biological invasions are rapidly reshuffling species distribution, restructuring the biological communities of many ecosystems worldwide. Tracking these transformations in the marine environment is crucial, but our understanding of climate change effects and invasive species dynamics is often hampered by the practical challenge of surveying large geographical areas. Here, we focus on the Mediterranean Sea, a hot spot for climate change and biological invasions to investigate recent spatiotemporal changes in fish abundances and distribution. To this end, we accessed the local ecological knowledge (LEK) of small-scale and recreational fishers, reconstructing the dynamics of fish perceived as "new" or increasing in different fishing areas. Over 500 fishers across 95 locations and nine different countries were interviewed, and semiquantitative information on yearly changes in species abundance was collected. Overall, 75 species were mentioned by the respondents, mostly warm-adapted species of both native and exotic origin. Respondents belonging to the same biogeographic sectors described coherent spatial and temporal patterns, and gradients along latitudinal and longitudinal axes were revealed. This information provides a more complete understanding of the shifting distribution of Mediterranean fishes and it also demonstrates that adequately structured LEK methodology might be applied successfully beyond the local scale, across national borders and jurisdictions. Acknowledging this potential through macroregional coordination could pave the way for future large-scale aggregations of individual observations, increasing our potential for integrated monitoring and conservation planning at the regional or even global level. This might help local communities to better understand, manage, and

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adapt to the ongoing biotic transformations driven by climate change and biological invaders.

**KEYWORDS**

biological invasions, climate change, fisheries, local ecological knowledge, Mediterranean, survey

## 1 | INTRODUCTION

The redistribution of Earth's species is among the most evident consequences of global warming (Parmesan & Yohe, 2003; Poloczanska et al., 2016) and a critical aspect for the health of both natural ecosystems and human populations worldwide (Pecl et al., 2017). These changes are usually greater for marine environments, because of their high environmental connectivity (Burrows et al., 2011) and because of the pivotal role of water temperatures, which strongly influence growth, survival, and reproduction in marine animals (Crozier & Hutchings, 2014; Reusch, 2014). In fact, even apparently modest changes in water temperature might trigger a rapid cascade of multiple pressures over marine organisms. Some species, unable to cope with these environmental alterations, or benefit from them, may change their abundances accordingly. However, mobile marine organisms also have another option: they can move to new areas where they were formerly absent (Cheung et al., 2009; Fogarty, Burrows, Pecl, Robinson, & Poloczanska, 2017). These two dynamics are not mutually exclusive, as they can be considered as different behavioral and demographic responses that might coexist in the same species or population.

Specifically, in the northern hemisphere, seawater warming has been associated with both the northward expansion of species and their increasing abundances (Fossheim et al., 2015; Perry, Low, Ellis, & Reynolds, 2005; Pörtner & Knust, 2007; Sabatés, Paloma, Lloret, & Raya, 2006). Yet, many studies provided evidence for the causal relationship between temperature, species distribution, and abundance (Cheung, Watson, & Pauly, 2013; Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013; Poloczanska et al., 2013) as well as their interplay with other global drivers, such as biological invasions, marine overexploitation, and pollution (Stergiou, 2002; Walther et al., 2009). These changes, which are taking place across many different taxa and through different regions of the globe, have significant implications for biodiversity, ecosystems, and society (McGeoch & Latombe, 2016) and are considered to be particularly apparent in the Mediterranean, a semi-enclosed sea, which is warming faster than any other marine region in the world (Schroeder, Chiggiato, Bryden, Borghini, & Ben Ismail, 2016; Vargas-Yáñez et al., 2008). In addition, maritime traffic, mariculture, aquarium trade and above all, entries through the Suez Canal (Edelist, Rilov, Golani, Carlton, & Spanier, 2013; Parravicini, Azzurro, Kulbicki, & Belmaker, 2015) contribute to the introduction of a large number of nonindigenous species

(hereafter referred as NIS) to this basin (Galil, Marchini, Occhipinti-Ambrogi, & Ojaveer, 2017; Golani et al., 2018; Zenetos et al., 2017), reshaping the structure of biological communities (Albouy et al., 2013, 2015, 2014; Katsanevakis et al., 2017) and impacting biodiversity and fishery resources (Edelist et al., 2013).

Despite the magnitude of these changes and their relevance for conservation and adaptation policy (Givan, Parravicini, Kulbicki, & Belmaker, 2017; Marras et al., 2015), observational studies are often fragmented in space (Elmendorf et al., 2015) and methodologically heterogeneous (Coll et al., 2010). This also applies to the northward expansions of warmwater species, a phenomenon that has been mostly described in the northwestern sectors of the Mediterranean basin, probably due to the uneven distribution of research efforts (Boero et al., 2008; Lejeusne, Chevaldonné, Pergent-Martini, Boudouresque, & Pérez, 2010; Marbà, Jordà, Agustí, Girard, & Duarte, 2015; Sabatés, Martín, & Raya, 2012). This fragmentation, together with the lack of coherent depictions of change, hampers the availability of reliable information to stakeholders and decision-makers (Grafton, 2010; Pauly & Zeller, 2016). Indeed, in light of profound impacts that have already affected both people and the ecosystems they depend on, many national and transnational authorities and agencies are engaged in efforts to build adaptive capacity, seeking reliable information to enable people to anticipate and appropriately respond to the ongoing change (Coulthard, 2012). This explains the growing need of integrated monitoring and assessment systems to capture the ongoing transformations of marine ecosystems (including the effects of a changing climate) and to bring them into the policy agendas (Creighton, Hobday, Lockwood, & Pecl, 2016). Certainly, our observational potential grew steadily during the last few years and increasing efforts are devoted to conceive global observation systems for up-to-date information on the state of biodiversity and the threats it faces (Tittensor et al., 2014). To achieve this, the use of standardized and cost-effective procedures is needed to underpin a large-scale observation strategy that can accommodate countries across a range of baseline knowledge levels and capabilities (Bélisle, Asselin, LeBlanc, & Gauthier, 2018; Latombe et al., 2017). These are key principles for collecting and integrating information from stakeholders across national boundaries. In this, fishers are a particularly interesting group of stakeholders, as they spend a considerable proportion of their lives in close contact with the marine environment and they become familiar with local species. Therefore, their personal experience gained through individuals' observations over

their lifetimes can provide precious complementary information about marine communities and be used to set effective monitoring practices. Yet, accessing this expert knowledge (hereafter referred as local ecological knowledge or LEK) is offering new opportunities to Mediterranean research (Azzurro, Bolognini et al., 2018; Azzurro, Moschella, & Maynou, 2011; Bastari, Beccacece, Ferretti, Micheli, & Cerrano, 2017; Coll et al., 2014; Damalas et al., 2015; Mavruk, Saygu, Bengil, Alan, & Azzurro, 2018), providing new opportunities to overcome practical and budgetary constraint, especially in poorly studied areas.

Here, we accessed the knowledge of Mediterranean fishers, to reconstruct changes in fish distribution and abundance, altogether with their related spatial and temporal dynamics. We did so by:

1. Compiling a dataset of species that were perceived as increasing or new by respondents (hereafter referred to as *increasing species*);
2. Using this multivariate information to explore the structure of perceived change across different subsectors of the Mediterranean Sea;
3. Testing for the effect of spatial gradients on the overall number of increasing species;
4. Exploring the spatiotemporal evolution of increasing species.

## 2 | MATERIALS AND METHODS

### 2.1 | Fishers' interviews

Drawing on the methodology conceived within a pilot experience (Azzurro et al., 2011) and according to the procedure described by Garrabou, Bensoussan, and Azzurro (2018), we used a semistructured questionnaire to reconstruct changes in distribution and abundance of Mediterranean fishes.

Knowledgeable small-scale fishers with more than 10 years of experience were identified and selected by each local research team and individual face-to-face interviews were realized according to a standard protocol. Respondents were asked to mention the species that increased in abundance or were perceived as "new" (i.e., never observed before) in their fishing areas. For each of these species, qualitative ranking of historical abundances was expressed along a yearly timeline and according to six categories (0 = ABSENT; 1 = RARE [once in a year]; 2 = OCCASIONAL [sometimes in a fishing period]; 3 = COMMON [regularly in a fishing period]; 4 = ABUNDANT [regularly in a fishing period and abundant]; 5 = DOMINANT [always in a fishing period and with great abundances]). To facilitate the process of reconstructing historical abundances, line drawings on a preprinted diagramming table were used by the interviewer. Colored pictures of fish and fish identification manuals were used as visual aids for accurate species identification, checking respondent's knowledge on specific taxonomic characters, whenever needed. The duration of a single interview ranged between 15 and 45 min. This protocol, which was initially tested

in Italy with a restricted number of fishers (Azzurro et al., 2011), was applied here across nine different countries and 95 locations (Figure 1) distributed into seven different Mediterranean subsectors (sensu Di Sciara, 2016): Algero-Provencal, Tyrrhenian, Adriatic, Strait of Sicily and Tunisian plateau, Ionian, North Aegean, and Levantin. This large spatial coverage was made possible through a collective and coordinated effort based on the engagement of an international team of researchers well connected with local fishery communities. The methodological transfer to the participating researchers was supported, from 2012 to 2016, by five training sessions carried out in Tunisia, Montenegro, Albania, Croatia, and Italy. Training included both theoretical lessons and joint field surveys made in collaboration with local fishers. Attendants were guided in performing standardized interviews and advised on how to reduce potential biases, such as the ones related to taxonomic identification and "memory recall" bias (Coughlin, 1990). Interviews were realized between 2009 and 2016 by local researchers in local languages (Albanian, Arabic, Croatian, Greek, Italian, Montenegrin, and Turkish). The LEK protocol is currently applied in other Mediterranean countries, such as Libya, Spain, and France and adopted by five Mediterranean marine protected areas generating new data, which were not included in the present study.

### 2.2 | Sample characteristics

A total of 513 Mediterranean fishers with more than 10 years of experience were selected and successfully interviewed. Their age ranged from 28 to 87 years (mean ± *SD*: 48 ± 11). Their cumulative working experience accounted for a total of 15,030 years of observations at sea. Overall, 59% of respondents were represented by professional fishers and 38% by recreational ones. Gillnets were the most common used gear among professionals (48%), followed by longlines (26%), traps (9%), purse (8%), and other gears (9%). Concerning recreational fishers, 64% of them were anglers and 34% were spearfishers (Figure 1). The entire dataset is available from Azzurro, Sbragaglia et al., (2018), as a .csv spreadsheet.

### 2.3 | Statistical approach

Based on available literature (Azzurro, 2008; Golani et al., 2018) and according to their origin and spatial trend, we classified fish species spontaneously mentioned by the respondents in three different groups: north expanding species of indigenous origin (NES); other indigenous species (OIS); non-indigenous species (NIS).

Based on the Bray–Curtis index, four different analyses of similarity were used to compare the groups of species mentioned by each respondent across the seven Mediterranean sectors: (a) we firstly used similarity percentages to see on which *increasing* species respondents agreed the most; (b) then, we adopted a nonmetric multidimensional scaling (nMDS) to represent the extent to which the increasing species cited from the different Mediterranean subsectors were similar; (c) we fit autosimilarity curves to see whether our interviews captured the entire amount
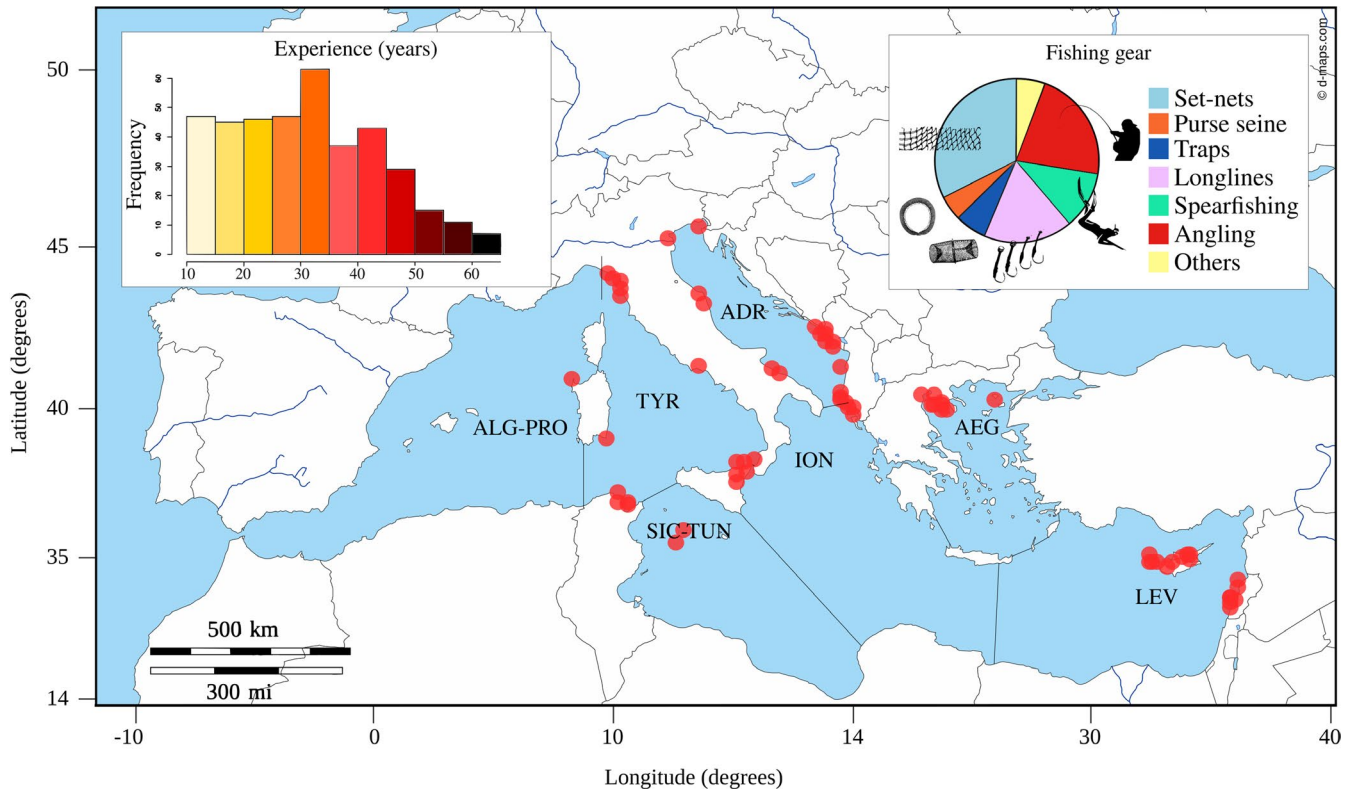
**FIGURE 1** Interview sites with reported distribution of the respondent's fishing experience(years) and employed fishing gears. ADR, Adriatic; AEG, North Aegean; ALP, Algero Provencal; ION, Ionian; LEV, Levantine; SIC-TUN, Strait of Sicily and Tunisa; TYR, Tyrrhenian

of increasing species in the different areas of the Mediterranean. Autosimilarity curves are adopted in community ecology to see if sample size is suitable to detect all the species within a community (Schneck & Melo, 2010). A curve is calculated by iteratively computing average resemblance values between randomly selected samples from a dataset. When resemblance attains an asymptote, sample size is deemed to represent a whole community. In this research, we regarded interviews as ecological samples. Therefore, autosimilarity curves told us whether our sampling in the various areas of the Mediterranean captured fisher's consensus about increasing species. We fit separate curves for NIS, NES, and OIS. Finally, to see the extent to which changes in fish communities were reflected in fisher's knowledge, (d) we modeled the effect of latitude and longitude over the total number of increasing species and over the number of increasing NES, NIS, and OIS, through generalized additive modeling (Guisan, Edwards, & Hastie, 2002; Hastie & Tibshirani, 1990; Wood, 2017a; Wood, Pya, & Säfken, 2016). To account for heterogeneity in sampling effort, we used the total number of interviews collected at each location as an offset. We chose a spline-based penalized likelihood estimator, with a fixed number of knots ($k = 6$), that was deemed large enough to avoid overfitting and Wald chi-square statistics was adopted to test for the significance of smooth terms (Wood, 2013).

Spatiotemporal changes in fish abundances were analyzed through breakpoint analyses of the historical time series of perceived abundances of the two most frequently cited NES and NIS

species. We determined the year at which each species-specific time series indicated a significant change in the perceived abundance (breakpoint) by using a binary segmentation method assuming a Poisson distribution of the data (Killick & Eckley, 2014). To quantify the intensity of this break, we also determined its jump, defined as the difference between the perceived abundance before and after the breakpoint. Since the breakpoint analysis was not sensitive in detecting the exact year of arrival of the "new" species, we also extracted from each species-specific time series the year of perceived arrival, which corresponded to the year at which the perceived abundance changed from 0 (absence) to any of the other scores (i.e., 1–5). Then, we explored the effect of latitude and longitude over the year of break, the jump, and the year of arrival, through another set of GAM with a gaussian distribution of the error. We implemented six models for each species using latitude and longitude as smoothing terms for the three variables (year of break, jump, and year of arrival). In all cases, the total number of interviews collected at each latitude and longitude was used as offset to account for different sampling efforts. Then, we used spline-based penalized likelihood estimators and a number of fixed knots ($n = 7$) and $F$ statistics was used to assess the significance of smooth terms (Wood, 2013).

Statistical analyses were run using the 3.4.3 version of R (https://www.R-project.org/). GAM modeling was carried out with the "mgcv" package (Wood, 2017b), breakpoint analysis with the package "changepoint" (Killick & Eckley, 2014), similarity percentages,

autosimilarity curves, and nMDS with the package "vegan" (Oksanen et al., 2013).

## 3 | RESULTS

Mediterranean fishers, with their varying cultural and political settings, were proved a fertile ground where to explore LEK on changes in fish diversity and abundance. In most of the cases, respondents were interested about the research questions, glad to share information with the researchers, and generally pleased to be regarded as experts. What most participants pointed out in their narratives was the rapid and dramatic ecological change, and the reconstruction provided here summarizes years of individual witnesses, which quantify our climate/invasive expectations. Fishers provided specific temporal reconstructions in the form of storylines. Here is a typical example:

> Interviewer: Do you know any species, which increased or appeared in your fishing area?
>
> Fisher: Oh, everything decreased, but we got some new guest in the last years and the cornetfish is one of them. I had never seen a cornetfish until early 2000s. I remember, it was 2013—the year when I had my second child—when I captured for the first time a cornetfish. Then, the species remained occasional for a few years and in the last 5 years it increased in abundance becoming very common. Now we capture cornetfish every day.

This kind of ecological memories are often linked to an emotional dimension (in this case a new species never seen before) and can be associated with personal histories (in this case the birth of the second child). This helped tracing back-specific temporal trends through the diagramming approach, transforming fisher's narratives in temporal series.

### 3.1 | Species perceived as increasing in abundance or new in respondent's fishing areas

Overall, 423 fishers (82%) told us that at least one species increased in abundance or appeared as new in their fishing area, for a total of 886 observations across 75 taxa. These included a number of 13 NIS (21% of citations), 20 NES (64% of citations), and other 42 OIS (15% of citations). A complete list of species is available in Figure S1.

The invasive *Lagocephalus sceleratus* and *Fistularia commersonii* were the most cited NIS (31% and 34% of total observations, respectively, see Figure S1), while *Pomatomus saltatrix* and *Sphyraena viridensis* were the most cited NES (30% and 15% of total observations, respectively, see Figure S1). Finally, *Sparus aurata*, *Synodus saurus*, and *Thunnus thynnus* were the most cited OIS (16%, 10%, and 9% of total observations, respectively, see Figure S1). Some

of the autosimilarity curves, based on the Bray–Curtis similarity index, reached an asymptote (Figure 2a), indicating that respondents strongly agreed on the increase of a specific group of species. This was observed for NES in all the subsectors of the Mediterranean but the Levantine, and for OIS, like *Sparus aurata*, in the Tyrrhenian and the Adriatic Sea (see Table S1). Respondents belonging to the same geographical subsectors generally provided coherent information about NIS, NES, and OIS, when interviews were collected from the same geographical sector (e.g., the Tyrrhenian Sea). On the contrary, significant differences can be highlighted for the group NIS, when distant areas are compared (e.g., Tyrrhenian vs. Levantine Sea; Figure 2b).

### 3.2 | Structure of perceived changes across areas

Nonmetric multidimensional scaling showed a good nonmetric ($R^2 = 0.95$) and linear ($R^2 = 0.735$) fit to the data in a two-dimensional form. The plot (Figure 2b) revealed a general similarity across areas, such as the Tyrrhenian, the Algero-Provencal, the Adriatic, and the Ionian Seas. Nevertheless, a variable level of separation can be highlighted between the Adriatic and the Levantine, between the North Aegean and the Strait of Sicily, and between the Tyrrhenian and the Levantine subsectors, indicating significant changes in the pool of increasing species across distant biogeographical sectors.

Similarity percentages expressed through the Bray–Curtis index (Table S1) showed the species which explained the most observed similarity between responses. For example, respondents from the Adriatic and Tyrrhenian areas provided similar depictions of change, because they agreed over the increase of *P. saltatrix* as the most important species accounting for the observed intragroup similarity (Table S1). Intragroup similarity, in other subsectors like the Tyrrhenian, the North Aegean, or the Strait of Sicily, was explained by a wider group of species (Table S1). A complete table of the various NIS, NES, and OIS cited as increasing in the various subsectors is available in Table S2.

### 3.3 | Spatial gradients in the overall number of increasing species

Latitude and longitude explained 33.5% of the deviance in the total number of species mentioned by the respondents ($R^2 = 0.54$; UMBRE = 0.267; see also Table S3). The number of cited NIS showed a significant and linear decrease along a northward gradient, with higher number of NIS at lower latitudes (Figure 3). On the contrary, no effect of longitude was highlighted ($p > 0.05$).

Concerning OIS, these species did not show any clear, nor significant ($p > 0.05$), latitudinal pattern. On the contrary, their number significantly decreased from lower to higher longitudes ($p < 0.001$). Finally, the number of NES increased between 33 and 40 degrees of latitude, and remained stable at higher latitudes (Figure 3, Table S3). A significant ($p < 0.001$) smooth effect of longitude with constant values up to 23 degrees, followed by a steep drop was also observed (Figure 3, Table S3).
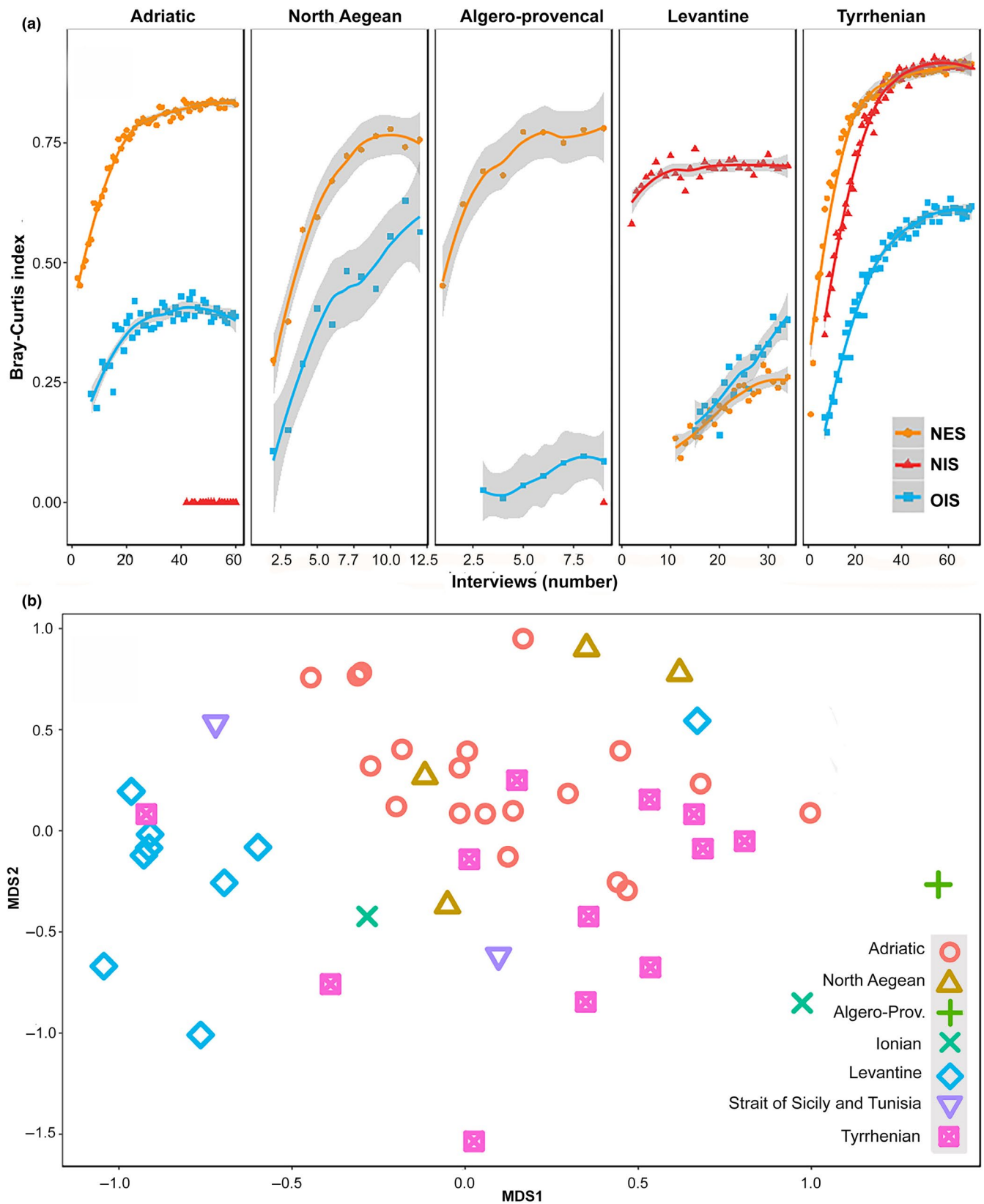
**FIGURE 2** (a) Autosimilarity curves for the five geographical subsectors; when a curve reached a plateau, respondents in that geographical sector agreed over the increase of that specific group of species. (b) Similarities in terms of cited increasing species are illustrated by the nonmetric multidimensional scaling ordination of centroids of the *n* = 95 interview locations based on the Bray–Curtis measure of dissimilarity. Abbreviations: NES, North Expanding Species of indigenous origin; NIS, Non Indigenous Species; OIS, Other Indigenous Species
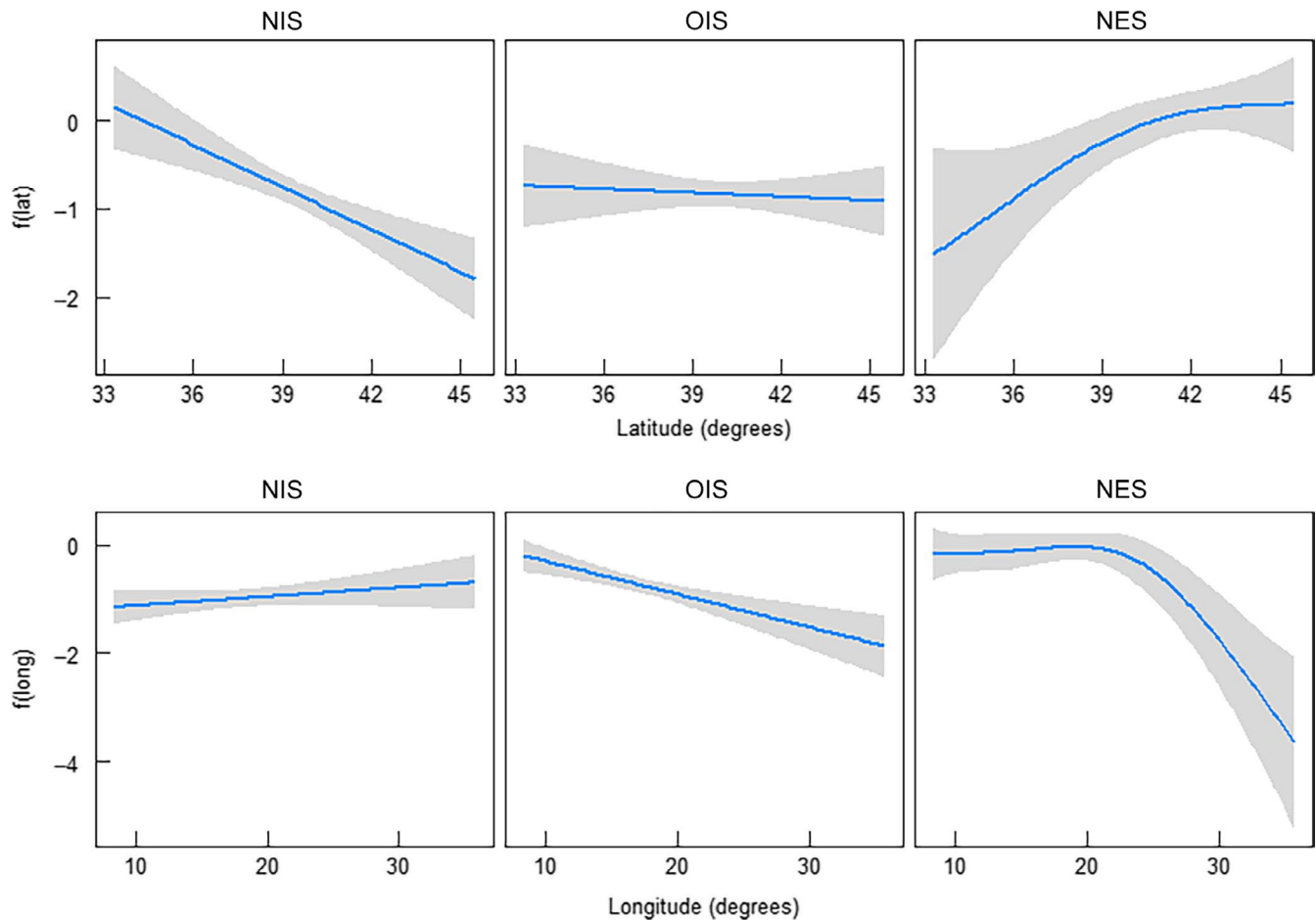
**FIGURE 3** Generalized additive model smoothing effects of latitude and longitude on the total number of increasing species. Gray-shaded area indicates standard errors above and below the estimates shown in solid blue lines.

## 3.4 | Temporal dynamics and their spatial variation

Breakpoint analysis indicated significant breaks for 561 time series (63%) across 45 taxa. Among them, NIS represented 27% of observations (10 taxa in total), while NES represented 66% of observations (18 taxa in total). Selecting the most cited NIS (i.e., *L. sceleratus* and *F. commersonii*) and the most cited NES (*P. saltatrix* and *S. viridensis*; Figure 4), we traced back their spatiotemporal dynamics. The number of significant breakpoints and observed first occurrences were 57 and 57 for *L. sceleratus*; 46 and 58 for *F. commersonii*; 134 and 123 for *P. saltatrix*; 48 and 49 for *S. viridensis*, respectively.

Concerning NIS, GAM indicated that at lower latitudes, the years of break and arrival started soon after 2000 for *F. commersonii* and positively increased toward 2010 at higher latitudes (Figure 5). The analysis of arrivals showed an even more consistent geographical pattern. The strength of the *F. commersonii* breaks indicated a sudden arrival at lower latitudes than higher ones (Figure 5). The smoothing effect of longitude on *F. commersonii* breaks and arrivals did not show specific trends; however, the strength of the breaks was higher at higher longitudes (Figure 6). On the contrary, the 57 breaks and arrivals of *L. sceleratus* were not modeled because they all occurred with a very strong jump (mean ± *SD*: 4.58 ± 0.75) between

2003 and 2010 in a limited spatial range confined to the southeastern area of the Mediterranean Sea (latitude: 33.3–35.0; longitude: 32.4–35.8).

Concerning NES, the smoothing effects of latitudes and longitudes on breaks and arrivals were weak or not significant for *P. saltatrix* (Figures 5 and 6, Table 1). No significant breaks and arrivals were present for latitudes lower than 38.1 and longitude higher than 23.3. On the contrary, GAM modeling indicated that in *S. viridensis*, there was a significant smooth effect of latitude and the years of break and arrival started around 1995 at 36 degrees of latitude and then positively increased toward 2005 at higher latitudes (Figure 5). Despite no clear pattern related to longitude, we did not detect significant breakpoints at longitudes higher than 26.0.

## 4 | DISCUSSION

In this research, we used for the first time LEK to reconstruct distributional changes in species across an entire geographical region, the Mediterranean Sea. Our approach responds to the idea of collecting a minimum set of *essential variables*, which can be used to ensure effective collaboration among countries and tangible information on a
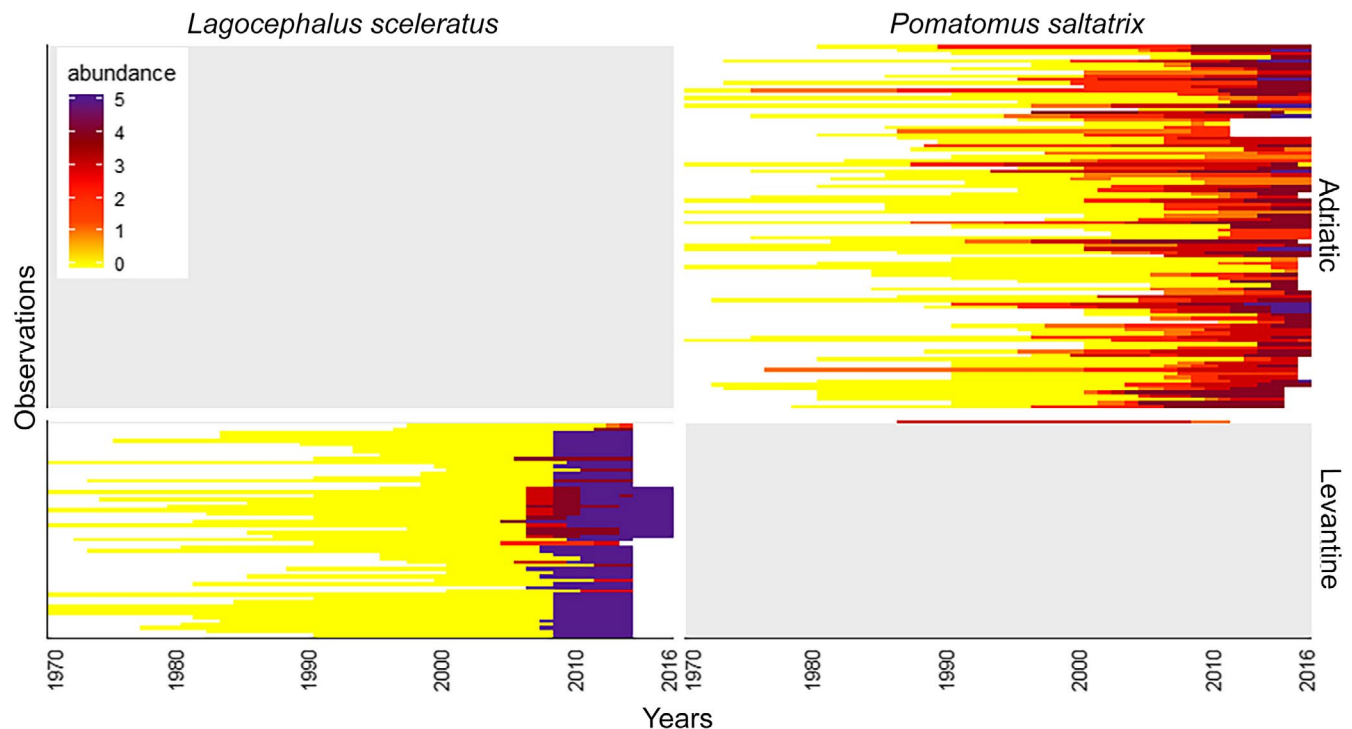
**FIGURE 4** Reconstruction of historical abundances according to fisher's knowledge: two representative examples of "increasing" species are given, *Lagocephalus sceleratus* and *Pomatomus saltatrix*, in two different geographical sectors (Adriatic and Levantine). A more complete set of species is available in Figure S2

specific ecological or societal phenomenon (Nativi et al., 2015). By gathering and combining the experience of Mediterranean fishers and everyday knowledge across different countries and varying social settings (Papaconstantinou & Farrugio, 2000), we traced back the geographical expansion of warm-adapted species of both native (NES) and exotic (NIS) origin, deepening our current understanding of the tropicalization of temperate marine ecosystems (e.g., Vergés et al., 2014).

Respondents, in almost all the subareas other than the Levantine, reported that an increase of NES and GAM modeling showed the effect of latitude and longitude on the total number of reported species, highlighting that the more evident manifestation of northward expansions in the northwestern sectors of the Mediterranean can be real and not only the result of a skewed concentration of research efforts in this area (Marbà et al., 2015). Northward spreads were extremely obvious for species such as the bluefish, *P. saltatrix*, which was reported to positively respond to seawater warming in both the northwestern Mediterranean (Sabatés et al., 2012) and in the Atlantic Ocean (Callihan, Takata, Woodland, & Secor, 2008). Similar to the bluefish, other native and exotic warm-adapted species might have taken the advantage of changing environmental conditions (Lasram & Mouillot, 2009) and latitudinal and longitudinal gradients reflect their spatial dynamics. While native fishes comprised a large number of species mentioned by a large number of fishers, nonindigenous taxa were entirely represented by *Lessepsian* fishes, entering the Mediterranean from the Red Sea through the Suez Canal. Lessepsians are typically very common in the eastern Mediterranean

sectors but may be rare or even absent in other geographical sectors, such as the eastern Adriatic, the North Aegean, and the most of the Northwestern Mediterranean Sea (Golani et al., 2018). Here, GAM highlighted a latitudinal and a longitudinal effect over the number of reported NIS, and the change in the NIS pool across longitude reflects the geographical structure of the Lessepsian bioinvasion, whose importance progressively increases when we move to the east and to the south of the basin (Golani et al., 2018). Fisher's observations also illustrated that the Lessepsian phenomenon, once confined to the eastern sectors of the Mediterranean, has rapidly progressed to the west, vanishing the boundaries of the so-called "Lessepsian Province" (Por, 1990). This was particularly clear for the Sicily strait, which was historically considered as an insurmountable barrier to the dispersal of Red Sea fishes and it is now colonized by species such as rabbitfishes (*Siganus luridus*) and cornetfish (*F. commersonii*).

While the picture provided by NES and NIS shows coherent responses over entire geographical subsectors, confirming the influence of large-scale drivers, the increase of the remaining species (OIS) can be mostly attributed to local causes, or to the finding of rare/uncommon species perceived as "new" by the respondents. This conclusion is supported by the large number of OIS, by the widespread disagreement on their increase, and by the lack of any clear latitudinal effect in GAM. Nevertheless, we acknowledge that some OIS, like *S. aurata*, were cited by many respondents from distant locations thus suggesting the existence of a real increase in this species over large geographical areas. The
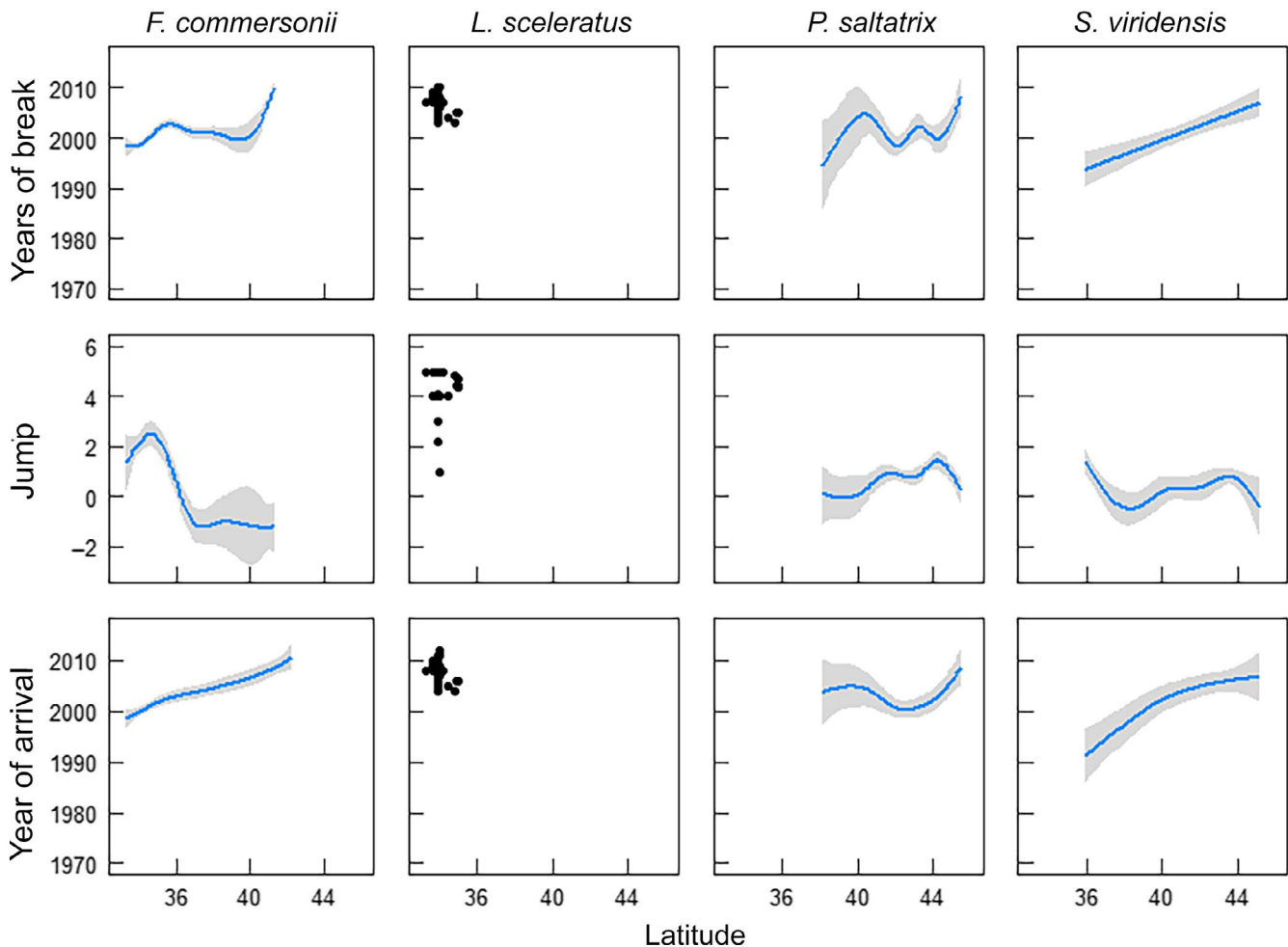
**FIGURE 5** Generalized additive model smoothing effects of latitude on the years of break, jump and year of arrival for the most common species perceived as in increase. Gray-shaded area indicates standard errors above and below the estimates shown in solid blue lines

increase of *S. aurata* all over the Mediterranean can be explained by its recent intensive and widespread mariculture and associated unintentional escapees (Dempster et al., 2018), which might act as inadvertent but continuous restocking of this species over large areas of the basin.

Spatial patterns are well illustrated by the nMDS (Figure 3) and the plotted distances of reported observations show that respondents from different subsectors of the Mediterranean might hold different experiences. For example, Levantine and Adriatic fishers did not overlap in terms of cited species, and this is primarily explained by the great differences held by these sectors in terms of community composition.

## 4.1 | Temporal dynamics and their spatial variation

The breakpoint analysis identified critical changes in both spatial and temporal dynamics of cited species. For example, the arrival of *F. commersonii* was extremely sudden at lower latitudes around the year 2000 and then positively increased toward 2010 with lower strength, matching the strength and rates of its invasion history, as reconstructed through published observations (Azzurro, Soto, Garofalo, & Maynou, 2013). The

expansion of *P. saltatrix* was mostly reported from the northwest of the Mediterranean Sea, while any significant breaks and/or arrivals were recorded in the southeast sectors of the Mediterranean, where the species historically occurs (Sabatés et al., 2012).

Overall, the first evidence on the northward expansion of warmwater species was provided in the 1990s (e.g., Bianchi, 2007; Bianchi et al., 2012; Francour, Boudouresque, Harmelin, Harmelin-Vivien, & Quignard, 1994), while a clear increase in sea temperature and important changes in the water circulation of the Mediterranean Sea are visible since the 1980s (Boero et al., 2008). The critical changes illustrated by our temporal reconstructions and breakpoints confirm and describe the increase of warmwater species at higher latitudes. For example, the dynamics of the bluespotted cornetfish *F. commersonii* agrees with the onset of its Mediterranean invasion (in 2000), and most interestingly, the strength of the breaks (jumps) was particularly great at higher latitudes, mirroring the rapid demographic explosion of this species in the easternmost sectors of the Mediterranean (Golani et al., 2018). A similar pattern of rapid population explosions was reconstructed for the silver-cheeked toadfish *L. sceleratus*, which showed very strong breaks in the easternmost sectors of the Mediterranean, since 2003, hence, immediately after its detection.
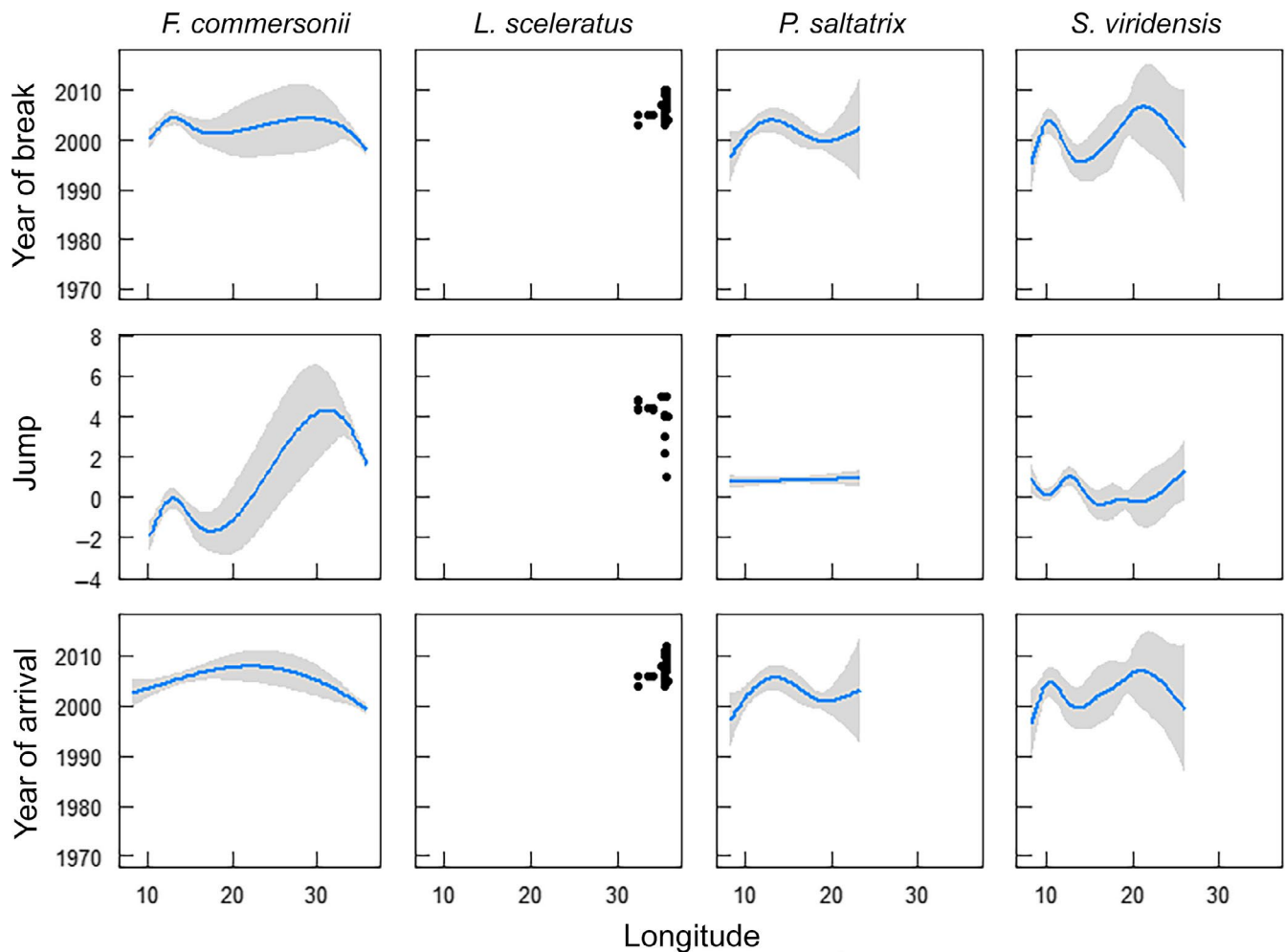
**FIGURE 6** Generalized additive model smoothing effects of longitude on the years of break, jump and year of arrival for the most common species perceived as in increase. Gray-shaded area indicates standard errors above and below the estimates shown in solid blue lines

## 4.2 | Strengths and weaknesses of a large-scale LEK survey

The non-structured approach of our interviews allowed each respondent to spontaneously mention "new" or increasing species in each fishing area, so each interview may be considered as an independent replicate in our design. The high degree of coherence among respondents from the same geographical subsector improved the confidence in the fact that trends reflect real patterns in the environment, with promising outcomes for large-scale investigations. Indeed, the logic of focusing on a regional change is analogous to that for global or climate changes itself. As highlighted by (Parmesan & Yohe, 2003), surveying for large-scale fingerprints does not require that any single species is driven by a large-scale determinant with 100% certitude. Rather, it seeks some defined level of confidence in the whole signal. Also, the extent of our geographical scale makes our findings relatively robust against cognitive biases, framing effects, and memory recall issues, that are likely to affect detailed and punctual records

in space and time, rather than overall, coarse, estimates (Vaske, 2008). This also apply to other potential sources of variability, such as the attitude of respondents, their different fishing gears (Azzurro et al., 2011), and the limited access to particular depths or areas (e.g., Beaudreau & Levin, 2014). Certainly, the influence of factors such as climate change and fisheries on the observed dynamics was not specifically tested in this study. In this regard, we might note that only a restricted subset of Mediterranean NIS was mentioned, representing only the most recent invasions. Other invaders were not cited by the respondents, because they were not perceived as new or increasing in their fishing areas. This is particularly evident in the Levantine sectors, where several invasive fishes settled in historical times, attaining commercial relevance and declining afterward under the pressure of intense fishing (M. Bariche, pers. comm.). These potential interactions with fishery and other potential drivers could be a subject for future cross-cultural investigations across the large spectrum of social, economical, and ecological conditions of the Mediterranean region.

**TABLE 1** Species-specific modelling results for the year of break and jump respect to latitude and longitude. Each model is represented together with the R squared adjusted values ($R^2$ Adj), the amount (%) of deviance explained (Dev), the generalized cross validation (GCV), the effective degrees of freedom (edf), the F statistics values ($F$) and the corresponding $p$ values for the smoothing term ($p$)

| Species | Model | $R^2$ Adj. | Dev. | GCV | edf | $F$ | $p$ |
|---|---|---|---|---|---|---|---|
| F. commersonii | Break ~ s(Lat) | 0.82 | 84.1 | 2.41 | 5.67 | 33.56 | <0.001 |
| | Jump ~ s(Lat) | 0.56 | 73.2 | 1.03 | 4.61 | 19.46 | <0.001 |
| | Arrival ~ s(Lat) | 0.65 | 65.0 | 6.66 | 3.05 | 25.93 | <0.001 |
| | Break ~ s(Long) | 0.47 | 53.3 | 6.88 | 4.69 | 8.11 | <0.001 |
| | Jump ~ s(Long) | 0.65 | 82.4 | 0.82 | 4.76 | 36.04 | <0.001 |
| | Arrival ~ s(Long) | 0.47 | 49.2 | 10.03 | 2.62 | 15.46 | <0.001 |
| P. saltatrix | Break ~ s(Lat) | 0.12 | 16.0 | 46.34 | 5.40 | 4.01 | <0.01 |
| | Jump ~ s(Lat) | −0.06 | 15.1 | 0.81 | 5.28 | 3.78 | <0.01 |
| | Arrival ~ s(Lat) | 0.10 | 13.3 | 51.82 | 3.47 | 3.86 | <0.01 |
| | Break ~ s(Long) | 0.07 | 8.1 | 48.18 | 3.13 | 2.28 | 0.056 |
| | Jump ~ s(Long) | −0.45 | 0.2 | 1.06 | 1.00 | 0.31 | 0.636 |
| | Arrival ~ s(Long) | 0.07 | 9.9 | 53.19 | 3.09 | 2.73 | <0.05 |
| S. viridensis | Break ~ s(Lat) | 0.32 | 33.6 | 37.45 | 1.00 | 23.25 | <0.001 |
| | Jump ~ s(Lat) | 0.41 | 41.9 | 0.57 | 4.77 | 5.18 | <0.001 |
| | Arrival ~ s(Lat) | 0.33 | 35.5 | 37.96 | 1.92 | 10.27 | <0.001 |
| | Break ~ s(Long) | 0.33 | 36.2 | 39.95 | 4.88 | 3.95 | <0.01 |
| | Jump ~ s(Long) | 0.28 | 34.8 | 0.71 | 5.35 | 3.80 | <0.01 |
| | Arrival ~ s(Long) | 0.17 | 22.8 | 49.74 | 4.72 | 2.07 | 0.100 |

## 4.3 | Concluding remarks

The whole Mediterranean is rapidly changing its biotic identity and accessing the knowledge of local fishers provided us with an improved understanding of the recent spatiotemporal dynamics of species "on the move," mainly represented here by warm-adapted fishes expanding across the basin. The resulting picture helps to fully appreciate the regional dimension of species redistributions, which will leave "winners" and "losers" in their wake (Pecl et al., 2017). Merging local efforts together, we build practical bridges to deal with these complex and large-scale transformations. To this regard, we must consider the inherent value of LEK on its own, and not only as sole ecological information. Indeed, individuals who inhabit sites of change might possess deeper readings of place and undisclosed capacities for interpretation (Mustonen, 2014) and adaptation (Berkes, Colding, & Folke, 2000). Therefore, the valorization of their knowledge is expected to reinforce our potential for adaptive ecosystem-based management, improving the operability of future actions in the real world (CIESM, 2018). The importance of this interplay, between ecological and social aspects, has been largely recognized by the scientific community (Allen, Fontaine, Pope, & Garmestani, 2011; Bennett et al., 2017; Berkes, 2004; McGeoch et al., 2016) and it is considered as a key ingredient to support robust and effective conservation policies in the Mediterranean region (Katsanevakis et al., 2017). In conclusion, advancing the use of LEK across large geographical scales allows bringing together the voices of people from different countries, ultimately preparing for a world of global ecological change. We believe that this beneficial partnership, which was here demonstrated to provide tangible results at the regional scale, could be extended to assessments at the global scale, if properly designed and organized.

## AUTHOR CONTRIBUTIONS

EA conceived and designed the LEK protocol, the experiments, and the local trainings and coordinated the collection of data with the help of PM, NM. MB, LB, JBS, EF, GB, AC, SC, JG, FG, FG, LG, RG, LL, CM, ETN, FP, AP, YSR, LS, JT, GV. JC, VS and EA analyzed the data; EA, JC, and VS wrote the paper, JC and EA designed the graphical abstract. All the authors contributed toward the discussion of the results.

## ETHICAL STATEMENT

Data collection was confidential, as interviewers did not record any sensitive personal information about respondents. At the beginning

of the interview, respondents were informed about the purposes of the study and gave informed consensus to use the provided information for scientific purposes.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.