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Title: The shifting distribution of Mediterranean fishes: a spatio-temporal assessment based on Local Ecological Knowledge

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Abstract

A major problem worldwide is the rapid change in species abundance and distribution, which is rapidly restructuring the biological communities of many ecosystems under changing climates. Tracking these transformations in the marine environment is crucial but our understanding is often hampered by the absence of historical data and by the practical challenge of survey large geographical areas. Here we focus on the Mediterranean Sea, a region which is warming faster than the rest of the global ocean, tracing back the spatio-temporal dynamic of species, which are emerging the most in terms of increasing abundances and expanding distributions. To this aim, 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 area. Over 500 fishers across 95 locations and 9 different countries were interviewed and semi-quantitative information on yearly changes in species abundance was collected. Overall, 75 species were mentioned by the respondents, being the most frequent citations related to warm-adapted species of both, native and exotic origin. Respondents belonging to the same biogeographic sectors described coherent spatio-temporal dynamics, and gradients along latitudinal and longitudinal axes were revealed. This information provides a more complete understanding of recent bio-geographical changes in the Mediterranean Sea 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 macro-regional coordination, could pave the ground for future large-scale aggregations of individual observations, increasing our potential for integrated monitoring and conservation planning at the regional or even global level.

Keywords:

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Collaborative research, small scale fishery, recreational fishery, climate change, biological invasions, interviews

Introduction

The redistribution of Earth's species is among the most evident consequences of global warming (Parmesan & Yohe, 2003; Poloczanska, Burrows, Brown, García Molinos, Halpern *et al.*, 2016) and a critical aspect for the health of both, natural ecosystems and human populations worldwide (Pecl, Araújo, Bell, Blanchard, Bonebrake *et al.*, 2017). These changes are usually greater for marine environments, because of their high environmental connectivity (Burrows, Schoeman, Buckley, Moore, Poloczanska *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 facts, 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 benefiting 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, Lam, Sarmiento, Kearney, Watson *et al.*, 2009; Fogarty, Burrows, Pecl, Robinson & Poloczanska, 2017). These two dynamics are not mutually exclusive, as they can be considered as different behavioural and demographic responses that might co-exist in the same species or population.

Specifically, in the northern hemisphere, sea water warming has been associated to both the northward expansion of species and their increasing abundances (Fossheim, Primicerio, Johannesen, Ingvaldsen, Aschan *et al.*, 2015; Perry, Low, Ellis & Reynolds, 2005; Pörtner & Knust, 2007; Sabatés, Paloma, Lloret & Raya, 2006). Yet, many studies provided evidence for the causal

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relationship between temperature, species distribution and abundance (Cheung, Watson & Pauly, 2013; Pinsky, Worm, Fogarty, Sarmiento & Levin, 2013; Poloczanska, Brown, Sydeman, Kiessling, Schoeman *et al.*, 2013), as well as their interplay with other global drivers, such as biological invasions, marine overexploitation and pollution (Stergiou, 2002; Walther, Roques, Hulme, Sykes, Pyšek *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 (Vargas-Yáñez, García, Salat, García-Martínez, Pascual *et al.*, 2008; Schroeder, Chiggiato, Bryden, Borghini, & Ben Ismail, 2016). 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 introduce a large number of non-indigenous species (hereafter referred as NIS) to this basin (Galil, Marchini, Occhipinti-Ambrogi & Ojaveer, 2017; Golani, Orsi-Relini, Massuti, Quignard, Dulčić *et al.*, 2018; Zenetos, Çinar, Crocetta, Golani, Rosso *et al.*, 2017), re-shaping the structure of biological communities (Albouy, Guilhaumon, Leprieur, Lasram, Somot *et al.*, 2013; Albouy, Leprieur, Le Loc'h, Mouquet, Meynard *et al.*, 2015; Albouy, Velez, Coll, Colloca, Le Loc'h *et al.*, 2014; Katsanevakis, Mackelworth, Coll, Fraschetti, Mačić *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, Cucco, Antognarelli, Azzurro, Milazzo *et al.*, 2015), observational studies are often fragmented in space (Elmendorf, Henry, Hollister, Fosaa, Gould *et al.*, 2015) and methodologically heterogeneous (Coll, Piroddi, Steenbeek, Kaschner, Ben Rais Lasram *et al.*, 2010). This also applies to the northward expansions of warm-water species, a

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phenomenon that has been mostly described in the North-Western sectors of the Mediterranean basin, probably due to the uneven distribution of research efforts (Boero, Féral, Azzurro, Cardin, Riedel *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, Walpole, Hill, Boyce, Britten *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 (Latombe, Pyšek, Jeschke, Blackburn, Bacher *et al.*, 2017; Bélisle, Asselin, LeBlanc, Gauthier, 2018). 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 can provide precious complementary information about marine communities

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and be used to set effective monitoring practices. Yet, accessing this knowledge (hereafter referred as Local Ecological Knowledge or LEK), is offering new opportunities to Mediterranean research (Azzurro, Bolognini, Dragičević, Drakulović, Dulčić *et al.*, 2018; Azzurro, Moschella & Maynou, 2011; Damalas, Maravelias, Osio, Maynou, Sbrana, & Sartor, 2015; Bastari, Beccacece, Ferretti, Micheli & Cerrano, 2017; Coll, Carreras, Ciércoles, Cornax, Gorelli *et al.*, 2014; 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 spatio-temporal evolution of increasing species.

Methods

Fishers' interviews

Drawing on the methodology conceived within a pilot experience (Azzurro, Moschella & Maynou, 2011) and according to the procedure described by an online video tutorial (*in prep*), we used a semi-structured questionnaire (**Annex** 1a,b), to reconstruct changes in distribution and abundance of Mediterranean fishes.

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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 pre-printed diagramming table was used by the interviewer (**Annex** 1**)**. Coloured 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 minutes. This protocol, which was initially tested in Italy with a restricted number of fishers (Azzurro, Moschella & Maynou, 2011) , was applied here across 9 different countries and 95 locations (Fig. 1) distributed into 7 different Mediterranean subsectors (sensu di Sciara, 2016): Algero-Provencal, Tyrrhenian, Adriatic, Strait of Sicily and Tunisian plateau, Ionian, 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

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taxonomical identification and 'memory recall' bias (Coughlin, 1990). Interviews were realized between 2009 and 2016 by local researcher 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.

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 15030 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 (Fig. 1).

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: i) we firstly used similarity percentages to see on which *increasing* species respondents agreed the most

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ii) 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; iii) we fit autosimilarity curves to see whether our interviews captured the entire amount 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 data set. 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, iv) we modelled the effect of latitude, longitude over the total number of increasing species and over the number of increasing NES, NIS and OIS, through Generalized Additive Modelling (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 estimators, 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).

Spatio-temporal changes in fish abundances were analysed trough 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

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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 modelling 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, Blanchet, Kindt, Legendre, Minchin *et al.*, 2013).

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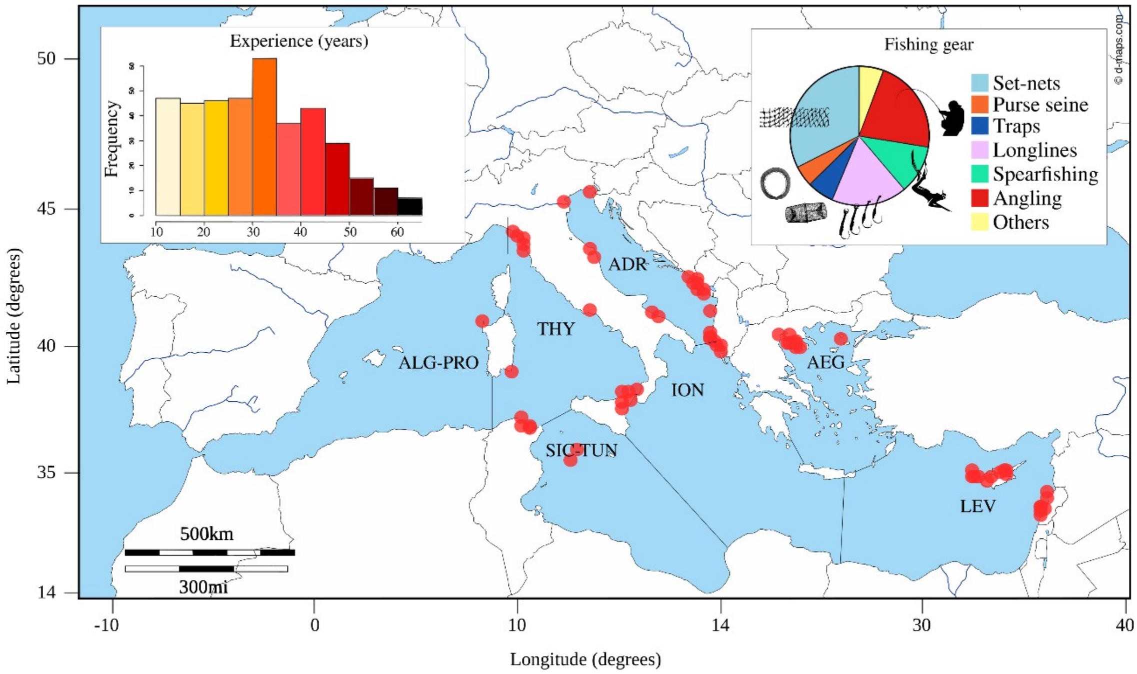

Figure 1 – Map of the Mediterranean region where the red dots indicate the sampling sites where interviews were conducted. On the top-left of the map the distribution of the fishing experience (years) of the interviewed is reported. On the top-right the different fishing gears used by the interviewed are reported.

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 the 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.

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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 (Annex 2). 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 Fig. S1), whilst *Pomatomus saltatrix* and *Sphyraena viridensis* were the most cited NES (30% and 15% of total observations, respectively, see Fig. S1). Finally, *Sparus aurata*, *Synodus saurus* and *Thunnus thynnus* were the most cited OIS (16%, 10% and 9% of total observations, respectively, see Fig. S1).

Some of the autosimilarity curves, based on the Bray-Curtis similarity index, reached an asymptote (Fig. 2a), indicating that respondents strongly agreed on the increase of a specific group of species. This was observed for NES in all the sub-sectors of the Mediterranean but the Levantine, and for OIS, like *Sparus aurata*, in the Thyrrenian 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 Thyrrenian sea). On the contrary, significant differences can be highlighted for the group NIS, when distant areas are compared (e.g. Thyrrenian *vs* Levantine Sea) (Fig. 2b).

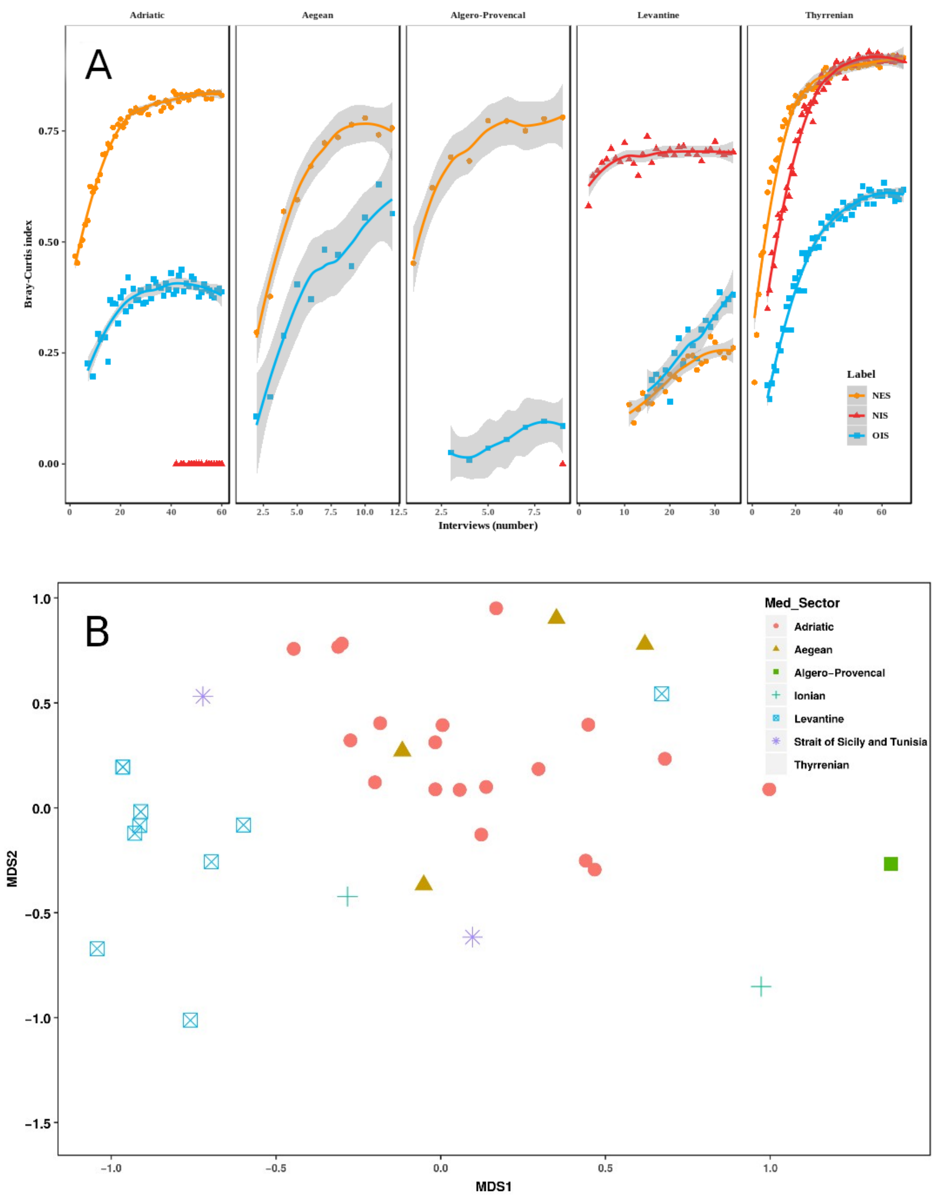

Figure 2. a) Upper panel: autosimilarity curves, for NIS/NES/OIS in the 5 geographical subsectors; when a curve reached a plateau, respondents in that geographical sector agreed over the increase of that specific group of species. b) Lower panel: Non-metric Multi Dimensional Scaling, indicating the degree of overlapping between the various geographical sectors in term of cited increasing species.

Structure of perceived changes across areas

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Non-metric Multi Dimensional Scaling (nMDS) showed a good nonmetric (R^2 = 0.95) and linear (R^2 = 0.735) fit to the data in a two-dimensions form. The plot (Fig. 2b) revealed a general similarity across areas, such as the Thyrrenian, 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 Aegean and the Strait of Sicily and between the Thyrrenian and the Levantine subsectors, indicating significant changes in the pool of increasing species across distant bio-geographical sectors.

Similarity percentages, expressed through the Bray-Curtis index (Table S1) showed the species which explained the most the observed similarity between responses. For example, respondents from the Adriatic, Levantine or Algero-Provencal areas provided similar depictions of change, because they agreed over the increase of *P. saltatrix* or *L. sceleratus* that accounted to about one third of observed intragroup similarity, respectively (Table S1). On the other hand, intragroup similarity, in other sub-sectors like the Tyrrhenian, the 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 sub-sectors is available in Table S2.

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 (Fig. 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 ($p < 0.001$).

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Finally the number of NES increased between 33 and 40 degrees of latitude, and remained stable at higher latitudes (Fig. 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 (Fig. 3, Table S3).

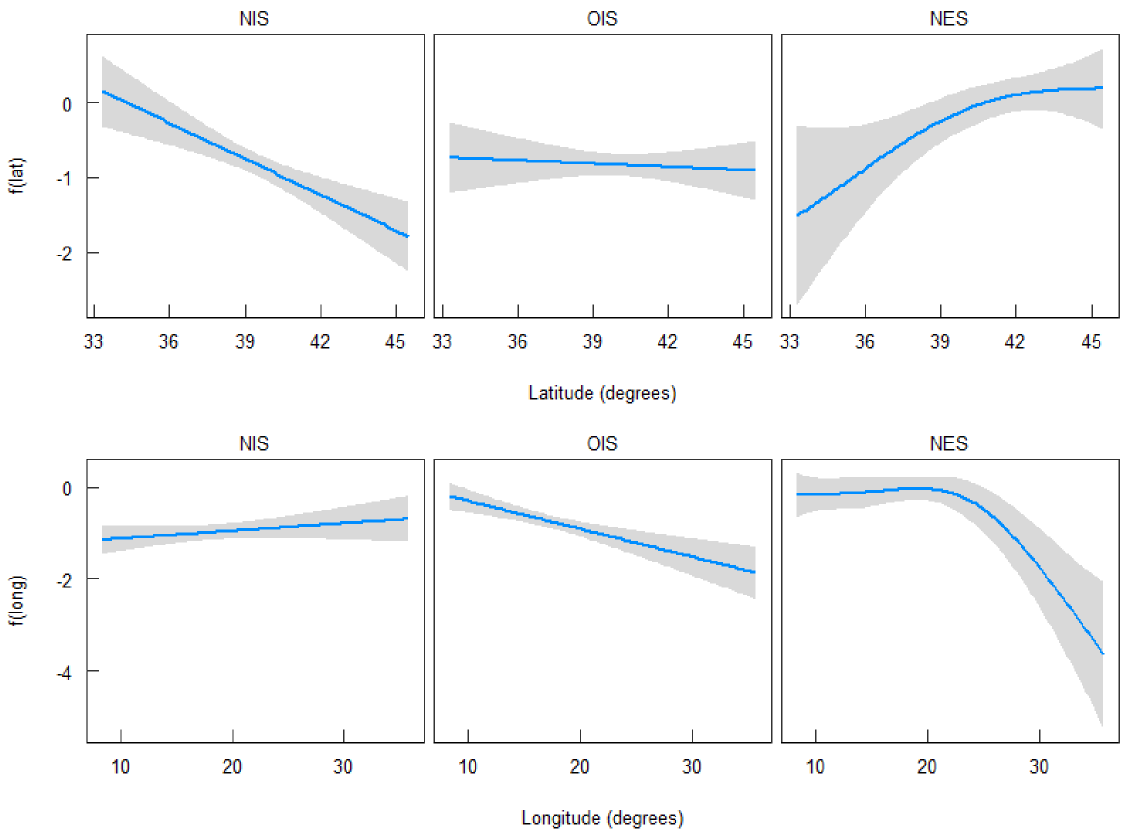

Figure 3 – Generalized Additive Model (GAM) smoothing effects of latitude and longitude on the total number of increasing species. Grey shaded area indicates standard errors above and below the estimates shown in solid blue lines.

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*)

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and the most cited NES (*P. saltatrix* and *S. viridensis*) (Fig. 4) we traced back their spatio-temporal 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.

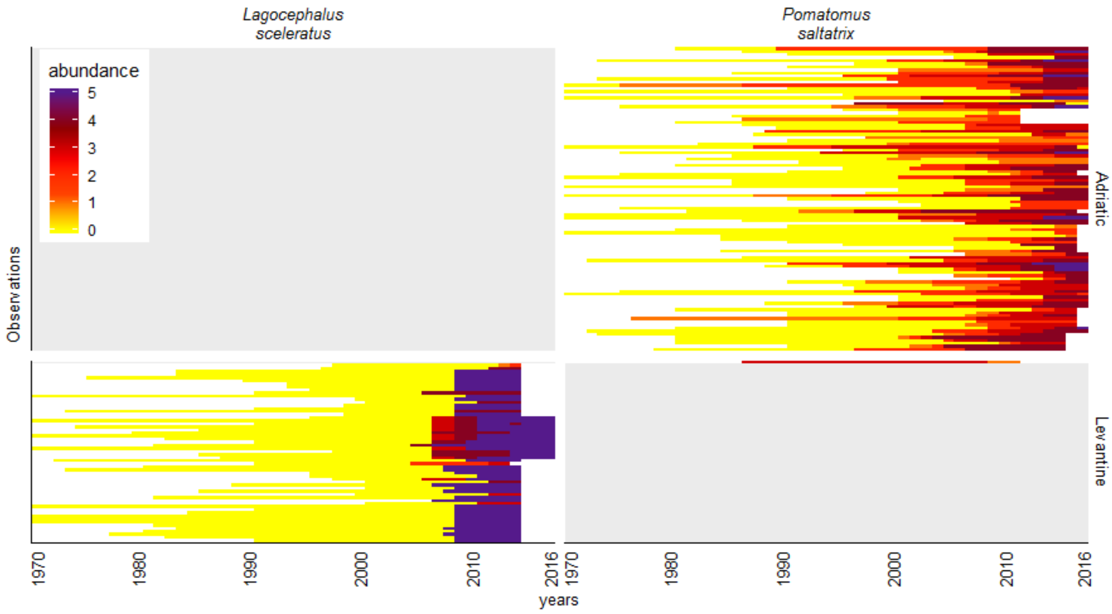

Figure 4 – A representative example of the reconstruction of historical abundances according to fisher’s knowledge for two species (*Lagocephalus sceleratus* and *Pomatomus saltatrix*) in two different geographical sectors (Adriatic and Levantine). A more complete dataset is presented in figure S2.

Concerning NIS, GAM indicated that at lower latitudes the years of break and arrival started soon after 2000 for *F. commersonii* and positively increased towards 2010 at higher latitudes (Fig. 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 (Fig. 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 (Fig. 6). On the contrary,

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the 57 breaks and arrivals of *L. sceleratus* were not modelled 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 South-Eastern area of the Mediterranean Sea (Latitude: 33.3 – 35.0; Longitude: 32.4 – 35.8).

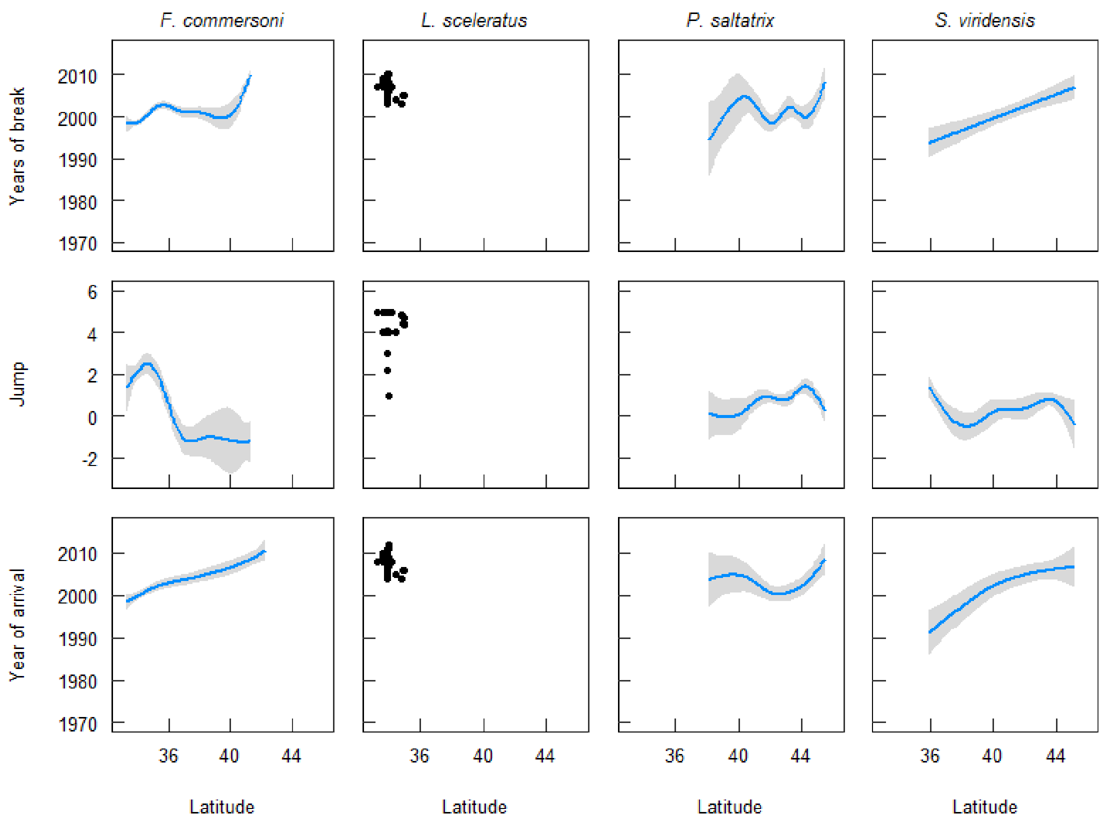

Figure 5 – Generalized Additive Model (GAM) smoothing effects of latitude on the years of break, jump and year of arrival for the most common species perceived in increase. Grey shaded area indicates standard errors above and below the estimates shown in solid blue lines.

Concerning NES, the smoothing effects of latitudes and longitudes on breaks and arrivals were weak or not significant for *P. saltatrix* (Fig. 5, 6 and 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 modelling indicated that in *S. viridensis* there was a significant smooth effect of latitude and

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the years of break and arrival started around 1995 at 36 degrees of latitude and then positively increased towards 2005 at higher latitudes (Fig. 5). Despite there were no clear pattern related to longitude, we did not detect significant breakpoints at longitudes higher than 26.0.

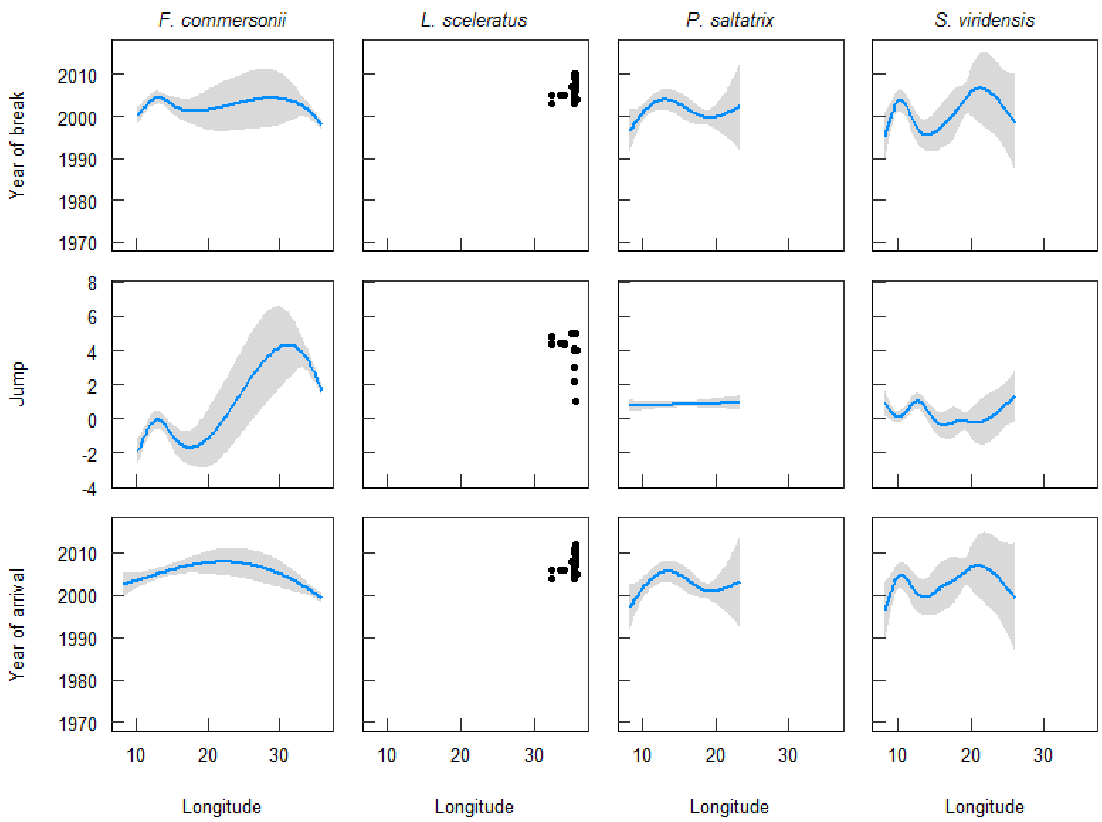

Figure 6 – Generalized Additive Model (GAM) smoothing effects of longitude on the years of break, jump and year of arrival for the most common species perceived in increase. Grey shaded area indicates standard errors above and below the estimates shown in solid blue lines.

Discussion

In this research we used for the first time Local Ecological Knowledge (LEK) to reconstruct distributional changes of 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

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to ensure effective collaboration among countries and tangible information on a specific ecological or societal phenomena (Nativi, Mazzetti, Santoro, Papeschi, Craglia *et al.*, 2015). By gathering and combining the experience of Mediterranean fishers and everyday knowledge across different countries and varying social settings (Papaconstantinou & Farrugio, 2016), 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, Steinberg, Hay, Poore, Campbell *et al.*, 2014).

Respondents, in almost all the sub-areas other than the Levantine, reported an increase of NES and GAM modelling 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 North-Western 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. saltarix*, which was reported to positively respond to seawater warming in both the North Western Mediterranean (Sabatés, Martín & Raya, 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. Whilst native fishes comprised a large number of species mentioned by a large number of fishers, non-indigenous 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 North western Mediterranean Sea (Golani *et al.*, 2018). Here GAM highlighted a latitudinal and a longitudinal effect over the number of reported NIS, and the change of the NIS pool across longitude reflect the geographical structure of the Lessepsian bio-invasion, whose importance progressively declines when we move to the west and to the north of the basin (Golani *et al.*, 2018).

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 of this species over large geographical areas. The increase of *S. aurata* all over the Mediterranean can be explained by its recent intensive and widespread mariculture and associated unintentional escapees (Dempster, Arechavala-Lopez, Barrett, Fleming, Sanchez-Jerez *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 (Fig. 3) and the plotted distances of reported observations shows that respondents from different subsectors of the Mediterranean might hold different experiences. For example, Levantine and Adriatic fishers did not overlap in term of cited species, and this is primarily explained by the great differences held by these sectors in terms of community composition.

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

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around year 2000 and then positively increased towards 2010 with lower strength, matching the strength and rates of its invasion history, as reconstructed through published observations (Azzurro, Soto, Garofalo & Maynou, 2013). On the other hand, the expansion of *P. saltatrix* was mostly reported from the North-West of the Mediterranean Sea, whilst any significant breaks and/or arrivals were recorded in the South-East sectors of the Mediterranean, where the species historically occurs (Sabatés, Martín & Raya, 2012).

Overall, the first evidences on the northward expansion of warm-water species were provided in the 1990s (e.g., Bianchi, 2007; Bianchi, Morri, Chiantore, Montefalcone, Parravicini *et al.*, 2012; Francour, Boudouresque, Harmelin, Harmelin-Vivien & Quignard, 1994), whilst 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 warm-water species at higher latitudes. For example, the dynamic 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 demographical 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 Mediterraenan, since 2003, hence, immediately after its detection.

Strengths and weaknesses of a large-scale LEK survey

The not-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

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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). Clearly, information obtained from interviews about fish distribution and abundance can be influenced by the attitude of respondents and 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, were not specifically tested in this study. To this regard, we might note that, only a restricted subset of Mediterranean NIS were mentioned, representing only the most recent invasions. Other invaders were not cited by the respondents, because not perceived as new or increasing in their fishing area. This is particularly evident in the Levantine sectors, where several invasive fishes settled in historical times, attaining commercial relevance and declining afterwards 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.

Conclusions

Accessing the knowledge of Mediterranean fishers, provided us with an improved understanding on the recent spatio-temporal 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 Mediterranean dimension of species redistributions, which will leave “winners” and “losers” in their wake (Pecl *et al.*, 2017). As other participatory efforts, our action is expected to empower the observational potential of local communities for adaptive management (Allen, Fontaine, Pope & Garmestani, 2011; Bennett, Roth, Klain, Chan, Christie *et al.*, 2017; Berkes, 2004; McGeoch, Genovesi, Bellingham, Costello, McGrannachan *et al.*, 2016) and to support robust and effective conservation policies in the Mediterranean region (Katsanevakis *et al.*, 2017). 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.

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Mediterranean fishers, which shared with us their observations as well as all the esteemed researchers which adopted the LEK protocol, contributing to foster the use of this methodology at the Mediterranean level.

We would like to thank all the researchers and field technicians, who were involved in data collection.

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.

Author Contributions

EA conceived and designed the LEK protocol, the experiments and the local trainings with the help of PM and NM; CA, MB, FP, GV, LG, GB, JBS, FG, PM, ETI, FG, LL, YSR, JT, SC, CM, JK, EA collected the data; JC and VS, analysed the data, EA, JC and VS wrote the paper.

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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

SUPPORTING INFORMATION

Table S1: Species that contributed the most to retrospective abundance estimates, in each sector of the Mediterranean Sea. Similarities were measured with the Bray-Curtis index

Sub-sector	Species	Average similarity	Average abundance	Sim/SD	Contribution (%)	Cumulative (%)
Levantine (average similarity = 44.79)	*Lagocephalus sceleratus*	0.84	39.74	1.19	88.70	88.70
	Fistularia commersoni	0.32	4.32	0.32	9.64	98.34
Adriatic (average similarity = 34.31)	*Pomatomus saltatrix*	0.74	30.75	0.88	89.60	89.60
	Caranx crysos	0.16	1.02	0.14	2.97	92.56
Thyrrenian (average similarity = 13.72)	*Pomatomus saltatrix*	0.41	6.83	0.39	49.79	49.79
	Sphyraena viridensis	0.26	2.27	0.24	16.57	66.36
	Caranx crysos	0.16	0.88	0.14	6.40	72.75
	Stephanolepis diaspros	0.13	0.76	0.12	5.52	78.28
	Sparisoma cretense	0.14	0.70	0.13	5.13	83.40
	Pomadasys incisus	0.11	0.48	0.09	3.49	86.89
	Sardinella aurita	0.09	0.30	0.08	2.20	89.09
	Lichia amia	0.09	0.27	0.08	1.98	91.06
Algero-Provencal (average similarity = 35.11)	*Sphyraena viridensis*	0.79	21.19	0.99	60.34	60.34
	Balistes capriscus	0.42	5.19	0.41	14.78	75.12
	Epinephelus marginatus	0.47	4.83	0.50	13.75	88.87
	Pomatomus saltatrix	0.32	2.57	0.30	7.33	96.20
Aegean (average similarity = 14.70)	*Sparisoma cretense*	0.32	5.70	0.31	38.78	38.78
	Coryphaena hippurus	0.24	2.90	0.22	19.73	58.50
	Sardina pilchardus	0.20	2.89	0.18	19.65	78.16
	Sardinella aurita	0.20	1.99	0.18	13.53	91.69
Ionian (average similarity = 26.57)	*Balistes capriscus*	0.58	13.33	0.67	50.19	50.19
	Thunnus thynnus	0.33	4.75	0.31	17.87	68.06
	Lagocephalus lagocephalus	0.33	3.69	0.31	13.88	81.94
	Sparisoma cretense	0.33	3.69	0.31	13.88	95.82
Strait of Sicily (average similarity = 32.41)	*Sphyraena viridensis*	0.71	13.83	0.89	42.67	42.67
	Caranx crysos	0.57	7.30	0.61	22.53	65.20
	Sparisoma cretense	0.43	3.97	0.39	12.24	77.44
	Diplodus sargus	0.29	1.90	0.22	5.88	83.32
	Diplodus vulgaris	0.29	1.90	0.22	5.88	89.19
	Siganus luridus	0.29	1.36	0.22	4.20	93.39

Table S2. Table showing whether each species was perceived as increasing or not, in each Mediterranean subregion: Adr = Adriatic; Aeg = Aegean; AlP = Algero Provencal; Ion = Ionian; Lev = Levantine; StT = Strait of Sicily and Tunisa; Thy = Thyrrenian. Values equal to '1' indicated that at least one respondent mentioned the species as increasing

Species Group	Species	Mediterranean sub-regions						
		Adr	Aeg	AlP	Ion	Lev	StT	Thy
NES	*Balistes capriscus*	1	1	1	1	1	1	1
	Caranx crysos	1	1	1	1	1	1	1
	Coryphaena hippurus	1	1	1	1	1	1	1
	Epinephelus aeneus	1	0	0	0	0	0	0
	Epinephelus costae	1	0	0	0	1	0	0
	Epinephelus marginatus	0	0	1	0	1	1	1
	Lichia amia	1	1	1	1	1	1	1
	Lobotes surinamensis	0	0	0	0	0	0	1
	Mycteroperca rubra	0	0	0	0	1	0	0
	Pomadasys incisus	1	1	1	1	1	1	1
	Pomatomus saltatrix	1	1	1	1	1	1	1
	Sardinella aurita	1	1	1	1	1	1	1
	Scomber colias	1	0	0	0	0	0	1
	Seriola dumerili	1	0	1	0	0	0	1
	Sparisoma cretense	1	1	1	1	1	1	1
	Sphoeroides pachygaster	1	0	0	0	0	0	0
	Sphyraena viridensis	1	1	1	1	1	1	1
	Talassoma pavo	0	0	1	0	1	0	0
	Trachinotus ovatus	1	0	0	0	0	1	1
NIS	*Fistularia commersonii*	1	1	1	1	1	1	1
	Hemiramphus far	0	0	0	0	0	0	1
	Lagocephalus lagocephalus	0	0	0	1	0	0	0
	Nemipterus randalii	0	0	0	0	1	0	0
	Plotosus lineatus	0	0	0	0	1	0	0
	Pterois miles	0	0	0	0	1	0	0
	Sargocentron rubrum	0	0	0	0	1	0	0
	Saurida lessepsianus	1	1	1	1	1	1	1
	Scomberomorus commerson	0	0	0	0	1	0	0
	Siganus luridus	0	0	0	0	0	1	1
	Siganus rivulatus	0	0	0	0	1	0	1
	Stephanolepis diaspros	1	1	1	1	1	1	1
OIS	*Aulopus filamentosus*	0	0	0	0	0	0	1
	Boops boops	0	0	0	0	0	0	0
	Chelidonichthys lucerna	1	0	0	0	0	0	0
	Chromis chromis	1	0	0	1	0	0	0
	Coris julis	0	0	0	0	0	0	1
	Dactylopterus volitans	0	0	1	0	0	0	0
	Dentex dentex	0	0	1	0	0	0	0
	Dentex gibbosus	0	0	0	0	0	0	0
	Dicentrarchus labrax	1	0	0	0	1	0	1
	Diplodus sargus	0	0	0	0	0	1	1
	Diplodus vulgaris	0	0	0	0	0	1	0
	Gymnothorax unicolor	0	0	1	0	0	0	0

	Labrus viridis	0	0	1	0	0	0	0
	Lagocephalus sceleratus	1	1	1	1	1	1	1
	Lampris guttatus	0	0	0	1	0	0	0
OIS	*Macroramphosus scolopax*	0	0	0	1	0	0	0
	Merlangius merlangus	0	1	0	0	1	0	0
	Muraena helena	1	0	0	0	0	0	0
	Oblada melanura	0	1	0	0	0	0	0
	Pagellus erythrinus	0	0	0	0	0	0	1
	Pagrus pagrus	1	0	0	0	0	0	0
	Regalecus glesne	0	0	0	1	0	0	0
	Sarda sarda	0	0	0	0	0	0	1
	Sardina pilchardus	0	1	0	0	0	0	0
	Sarpa salpa	1	0	0	0	0	0	1
	Sciaena umbra	0	0	1	0	0	0	0
	Scomber scombrus	0	1	0	0	0	0	1
	Serranus cabrilla	0	0	0	0	0	0	1
	Serranus scriba	0	0	0	0	0	0	1
	Sparus aurata	1	1	1	1	1	1	1
	Spicara maena	0	0	0	0	0	0	1
	Spondyliosoma chantarus	0	0	0	0	0	0	0
	Sprattus sprattus	0	0	0	0	0	0	1
	Synodus saurus	1	1	1	1	1	1	1
	Tetrapturus belone	0	0	1	0	0	0	0
	Thunnus thynnus	1	0	1	1	0	0	1
	Trachurus mediterraneus	1	0	0	0	0	0	1
	Trachurus trachurus	0	0	0	0	0	0	1
	Tylosurus acus imperialis	1	0	0	0	0	0	0
	Umbrina cirrosa	1	0	0	0	1	0	1
	Xiphias gladius	0	0	0	0	1	0	0
	Xyrichthys novacula	1	0	0	0	0	0	1
	Zu cristatus	0	0	1	0	0	0	0

Table S3 – Modelling results on the total amount of increasing species respect to latitude and longitude. Increasing species were classified in three different groups, according to their origin and spatial trend. We distinguished non-indigenous species (NIS), other-indigenous species (OIS), and native North expanding species (NES). Each model is represented together with the R squared adjusted values (R^2 Adj), the amount (%) of deviance explained (Dev), the Un-Biased Risk Estimator (UMBRE), the effective degrees of freedom (edf), the χ^2 statistic values and the corresponding *p* values for the smoothing term (*p*).

model	**R^2 Adj.**	**Dev.**	**UMBRE**	**Smooth terms**	**edf**	**χ^2**	***p***
Species ~ s(Lat, k=6) + s(Long, k=6)	0.54	33.5%	0.267	Lat-NIS	1.00	18.18	< 0.001
				Lat-OIS	1.00	0.17	0.667
				Lat-NES	1.67	11.20	< 0.001
				Long-NIS	1.00	1.46	0.227
				Long-OIS	1.00	16.06	< 0.001
				Long-NES	2.82	18.32	< 0.001

743 **Figure S1.** Distribution of the 886 observations across 75 species increasing species. These included 13 NIS, 46 OIS and 20 NES

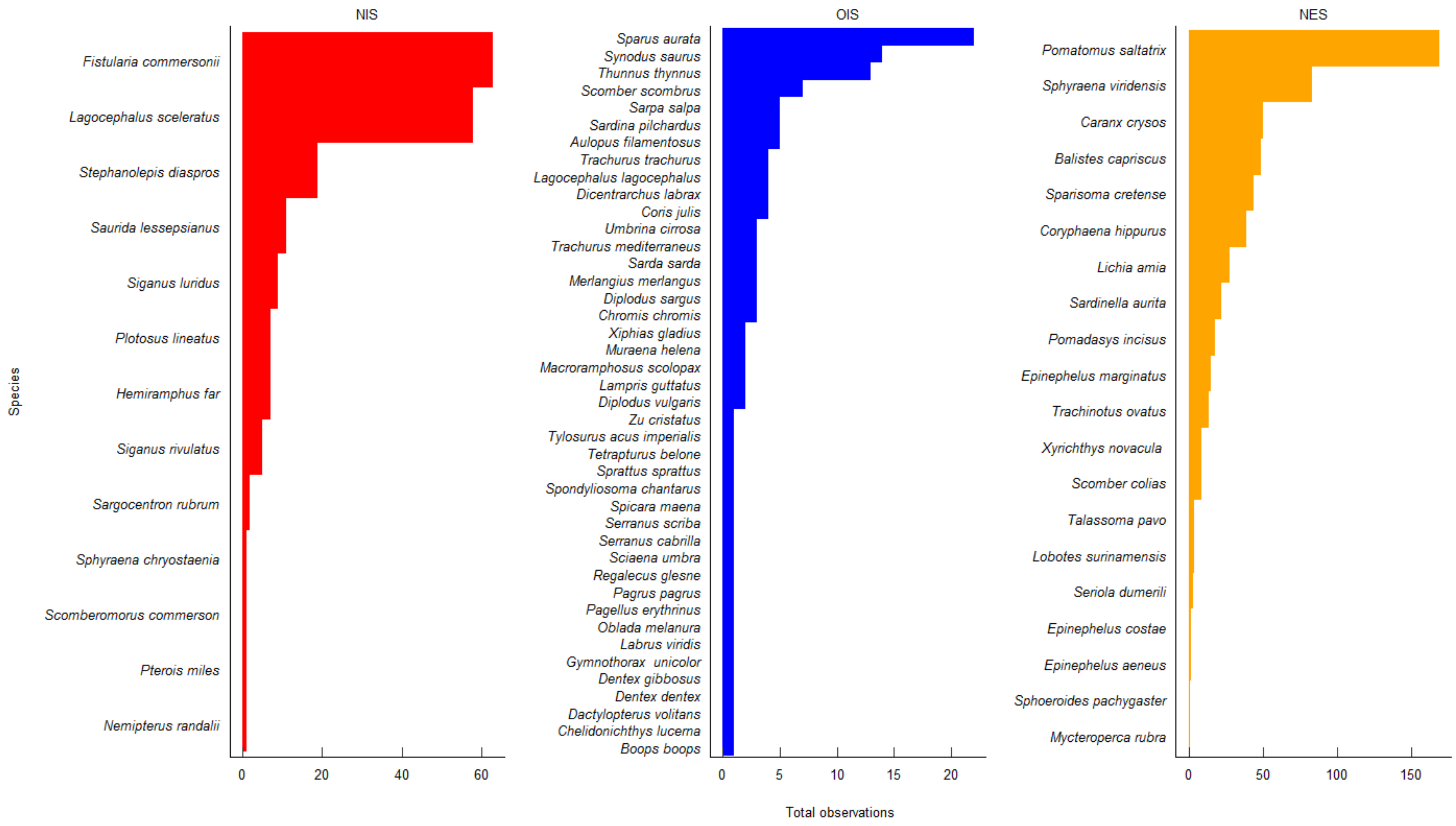

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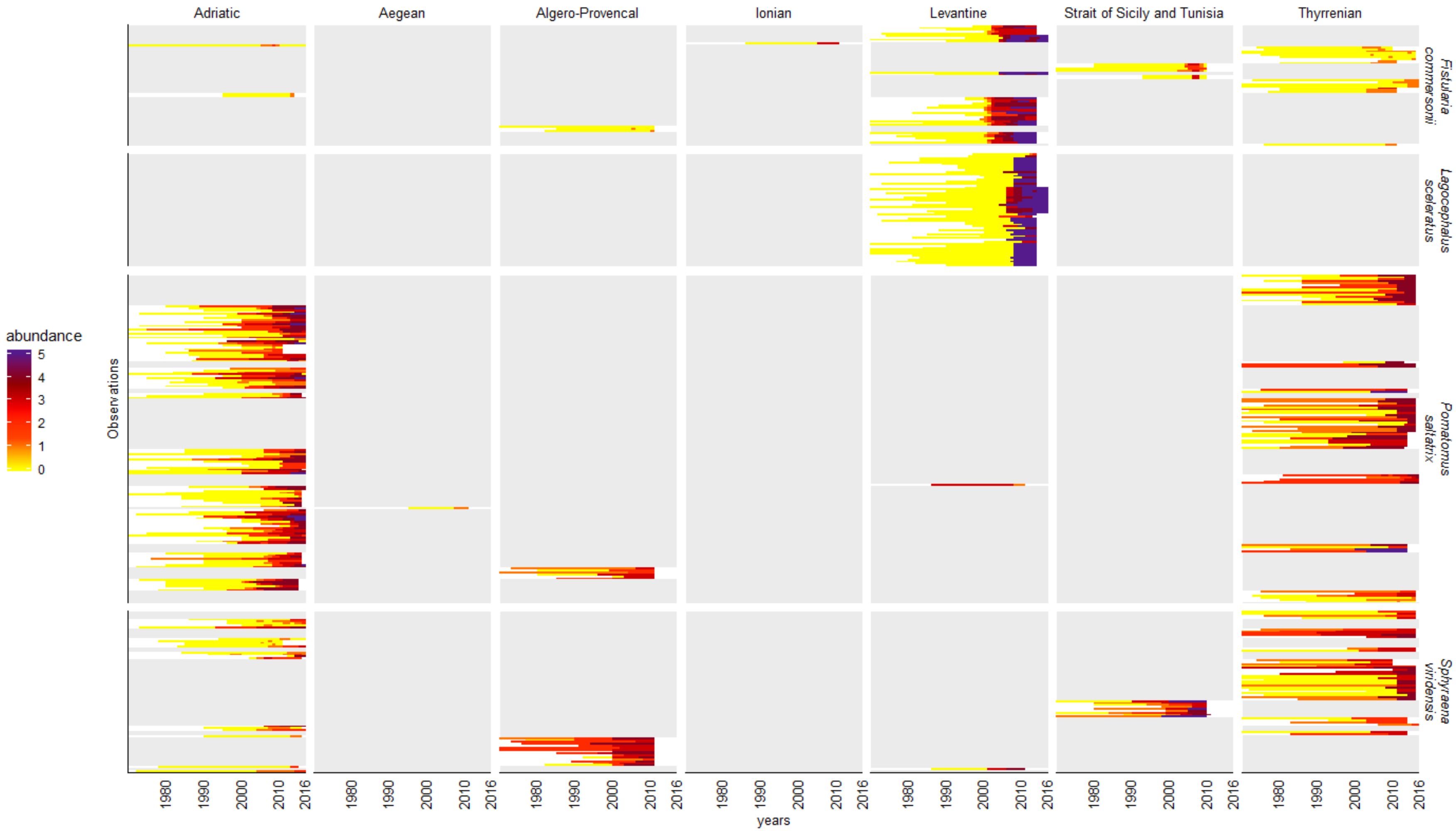
Figure S2. A complete reconstruction of historical abundances according to fisher's knowledge for four species (*Fistularia commersoni*, *Lagocephalus sceleratus*, *Pomatomus saltatrix* and *Sphyraena viridensis*) in the seven geographical sectors presented here.



749