1 **SOS small pelagics: a Safe Operating Space for small**
2 **pelagic fish in the Western Mediterranean Sea**

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Abstract

Sustainable fishing practices must ensure human wellbeing by safeguarding the integrity of marine life-supporting systems. Unfortunately, a significant challenge to fisheries management is that sustainable fishing levels can decline, often synergistically, by co-occurring with climate-driven environmental stressors. Within one of the most impacted marine areas in the world, and encompassing a number of highly targeted commercial species, the small pelagic fish community of the western Mediterranean Sea has recently shown signs of collapse. In this study, we identify a worrying coincidence where fishing hotspots for the commercially valuable European sardine *Sardina pilchardus* and anchovy *Engraulis encrasicolus* occur in marine areas mostly affected by climate change. To identify these areas, we overlayed detailed, spatially explicit measurements of fishing pressure with the finest-scale maps of cumulative climate change impacts onto these species. According to our results, doubly impacted marine areas largely occur in the north-western Mediterranean Sea, with climate and fisheries mostly affecting European sardine. Reducing local stressors (i.e., fishing pressure) in highly impacted areas may contribute to maintain these communities within a “safe operating space” (SOS), where they remain resilient to climate change. Accordingly, the redistribution and/or reduction of fishing intensity may alleviate pressure in those areas already affected by climate change. Sustainable fishing strategies may benefit, therefore, from the SOS concept and the spatial assessments provided in this study.

Keywords: anchovy, sardine, fisheries, Mediterranean Sea, ocean warming, sustainability.

41 1. Introduction

42 There is now increasing evidence that human activities are driving rapid changes
43 on a scale similar to past events that resulted in hostile conditions leading to ecosystem
44 collapses (Rockström et al., 2009; Steffen et al., 2011). Among Earth's biomes, oceans
45 are of particular concern because of their complex nature and the number of stressors
46 simultaneously impacting marine life-supporting systems (Halpern et al., 2015; Hoegh-
47 Guldberg and Bruno, 2010; IPCC, 2014; Ramírez et al., 2017). Oceans are serving as a
48 sink for excess CO₂ and heat from the atmosphere, with ultimate consequences for
49 marine productivity that propagates through marine food webs up to top-predators
50 (Doney et al., 2012, 2009; Gregg et al., 2003; Ramírez et al., 2017).

51 Fisheries are also putting a severe burden on marine ecosystems, and are making
52 marine communities more sensitive to climate fluctuations (Berkeley et al., 2004; Coll
53 et al., 2020; Ottersen et al., 2006). Fishing pressure has increased over the last decades,
54 with recent assessments showing that approximately 60% of fish stocks worldwide are
55 completely exploited, whereas 34% are overexploited and just the 6% are underfished
56 (Food and Agriculture Organization -FAO-, 2020). Fisheries constitute, however, an
57 important socio-economic sector that, in addition to providing a major food source for
58 humanity, provide employment and economic benefits to those engaged in the activity
59 (FAO, 2020; Pinello et al., 2017). Models for sustainable fisheries should ensure,
60 therefore, the wellbeing of associated social sectors and stakeholders while safeguarding
61 the integrity of marine life-supporting systems (i.e., "Doughnut" fisheries, *sec.* Raworth,
62 2017; see also FAO, 2020). Unfortunately, this is a challenging objective within the
63 current scenario of climate change since sustainable fishing levels can decline, often
64 synergistically, by co-occurring, climate-driven environmental stressors.

The concept of a “safe operating space” (SOS), first coined by Rockström et al., (2009) to identify nine planetary boundaries that must not be transgressed to preserve the Earth’s systems, has recently been adapted as a framework to guiding management of highly impacted marine systems (Ramírez et al., 2018). SOS can be defined as an n-hypervolume, with climate and human impacts (e.g., fisheries) as axes or dimensions, where natural ecosystems should be retained to maintain a desirable state of conservation (Fig. 1). A central element of the SOS concept is that critical levels/thresholds for ecosystem collapse are lowered by interacting stressors (Fu et al., 2018; Lejeusne et al., 2010; Norström et al., 2016). Accordingly, climate and fishing stressors should be integrated as drivers of ecosystem changes to provide a more reliable and holistic framework for the management and conservation of marine systems (and associated ecosystem services, Coll et al., 2016, 2012). For instance, suitable management actions, i.e., those aimed at maximizing environmental benefits and minimizing socio-economic costs, might be based on the spatial redistribution and/or reduction of fisheries to alleviate pressure at those areas that are already affected the most by climate change (Ramírez et al., 2018, 2017).

Effective solutions and suitable management measures depend, therefore, on a better understanding of the spatial distribution of climate impacts and fishing pressure (Coll et al., 2016). In this regard, satellite remote-sensing environmental data, together with advances in modelling techniques based on Automatic Identification Systems (AIS) track data for fishing vessels, now provide a uniquely detailed insight into the spatial distribution of climate and fishing stressors threatening marine communities. Combined with the SOS framework, these data can inform effective management of commercial fisheries that takes into account the synergy with increasing climate impacts (Ramírez et al., 2018).

90 Surrounded by one of most densely populated areas in the world, and with a long-
91 standing natural, cultural and economic heritage, the Mediterranean Sea has experienced
92 a long history of anthropogenic perturbations. Only considering the contemporary era,
93 human impacts have exponentially grown since the Second World War with the
94 Mediterranean area population explosion and the fossil fuel-dependent industrialization
95 of socio-economic activities, including fisheries. Indeed, the Mediterranean and Black
96 Seas include the highest percentage (approximately 62%) of stocks fished at
97 unsustainable levels in the world (FAO, 2020). In addition to the human-induced loss of
98 habitat and biodiversity through direct exploitation (Coll et al., 2015, 2012), climate
99 change poses an additional threat that will certainly increase in severity in the future, in
100 line with world-wide predictions (Burrows et al., 2011; Coll et al., 2012; Micheli et al.,
101 2013; Ramírez et al., 2017). However, the Mediterranean Sea is considered a global
102 hotspot of marine biodiversity (accounting for 7% of known marine species, while only
103 representing the 0.8% of the Earth's ocean surface), and continues to serve as an
104 important fishing ground, particularly in its central and western sides (Coll et al., 2012;
105 Fernandes et al., 2017; Ramírez et al., 2018).

106 Because of their commercial value and ecological role within marine
107 communities, small pelagic fish are important species in the Mediterranean Sea, albeit
108 “under siege” (Coll et al., 2019; FAO, 2018a; Palomera et al., 2007; Ramírez et al.,
109 2018). Overall declines of commercially important small pelagic fish populations have
110 been observed in the Mediterranean Sea (Pennino et al., 2020; Piroddi et al., 2017; Van
111 Beveren et al., 2016). Population declines have been mostly attributed to the combined
112 effects of climate impacts and fishing pressure (Pennino et al., 2020; Coll et al., 2019;
113 Saraux et al., 2019, and references therein). However, fine-scale, spatially explicit
114 assessments of the co-occurring distributions of these two main stressors are noticeably

lacking, thus prohibiting the implementation of potentially effective management actions within the SOS framework.

Here, we developed a spatially explicit assessment where climate and fishing impacts were combined within an SOS framework to contribute to sustainable fisheries in the face of climate-driven environmental changes (Fig. 1). We focused on European sardine (*Sardina pilchardus*) and European anchovy (*Engraulis encrasicolus*) because they are the most important small pelagic species in terms of biomass and catches in the Mediterranean Sea (FAO, 2018a), and because their populations have shown signs of collapse (Coll and Bellido, 2020; Fernandes et al., 2017; Palomera et al., 2007). This is particularly the case for sardine that is also heavily impacted by ocean warming (Palomera et al., 2007; Pennino et al., 2020; Ramírez et al., 2018), and has shown sharper declines in key parameters such as body condition, length at age, and size at first maturity over the last decades (Albo-Puigserver et al., 2018; Saraux et al., 2019). By quantitatively combining long-term (1987-2018), spatially-explicit measurements of environmental features likely driving the dynamics of these two species, with their biomass distributions (2003-2016; based on acoustic surveys) and optimal environmental conditions for spawning (Palomera et al., 2007), we provided the first finest-scale assessments on climate-driven environmental shifts for these two species. We then combined these assessments with available data on fishing pressure to identify doubly impacted marine areas in the western Mediterranean Sea, where fisheries require management within a SOS framework to enhance resilience to climate change and ensure their long-term sustainability. Because of their different relationships with environmental features (Coll and Bellido, 2020; Palomera et al., 2007; Pennino et al., 2020), we predicted that the combination of climate and fishing impacts will differently affect sardine and anchovy. We also predicted that climate and fishing stressors will be

unevenly distributed spatially (Ramírez et al., 2018). Accordingly, we argue that our approach could be useful for implementing suitable spatially explicit management strategies from local to regional scales.

2. Material and methods

Data analyses and GIS procedures were conducted in R version 3.6.2 (R Core Team, 2019), whereas mapping designs and displays were performed with ArcGIS 10.5 (ESRI, Redland, USA).

2.1. Study area

Our study area, as shown in Fig. 2, represents the pelagic system of the western Mediterranean Sea, from the Alboran Sea in the south, through the Iberian coast up to the Gulf of Lion in the north (Geographical Sub-Areas GSA01, GSA06 and GSA07, as defined by the General Fisheries Commission for the Mediterranean, FAO, 2018b). This relatively large area includes contrasting mesoscale and sub-mesoscale processes that drive marine productivity patterns. For instance, the Alboran Sea is a highly productive area (Huertas et al., 2012), where marine productivity is largely driven by an intense eastward current that replenishes the Mediterranean basin with Atlantic waters through the Strait of Gibraltar, and that influence oceanographic features up to the Almeria-Oran front (García Lafuente, 2002). Northwards, marine productivity is weaker as a result of the combination of the Northern current, a counter-clock oceanographic circulation that brings nutrients to the upper slope and shelf areas, and runoff from the Ebro and Rhône rivers (Bosc et al., 2004; Estrada, 1996).

The Western Mediterranean Sea is an important fishing ground of sardine and anchovy (Giannoulaki et al., 2013; Maynou et al., 2020; Tugores et al., 2010).

Important landings of these two species have been reported in the region since the 60s-70s, with a substantial drop in captures during the last three decades (Coll et al., 2019; Van Beveren et al., 2016). This is particularly the case for sardines, while a moderate recovery for anchovies has been observed in recent years in the southern parts of the GSA06 (Coll et al., 2019; Maynou et al., 2020; Pennino et al., 2020).

Sardines and anchovies in our study area are likely genetically structured, with two distinct populations separated by the Almeria-Oran front that acts as a barrier to gene flow (Coll and Bellido, 2020; Kasapidis et al., 2012; Viñas et al., 2014). This genetic segregation is consistent with some distinct phenotypic traits, such as the relatively low body condition, gonadosomatic index, length at age or length at first maturity as found in individuals northwards the Almeria-Oran front (Albo-Puigserver et al., 2018; Brosset et al., 2017; Silva et al., 2006; Ventero et al., 2017). This segregation roughly matches with that for the westernmost GSAs (between GSA01 and GSA06) included in this study.

2.2. *Environmental, fishing and biological data sources*

We considered net primary productivity (NPP), sea surface temperature (SST) and sea surface salinity (SSS) as the main environmental factors impacting sardines and anchovies (Pennino et al., 2020). Environmental data was obtained online from the EU Copernicus Monitoring Environment Marine Service (<https://marine.copernicus.eu/>; accessed on March 2020, see Table S1). NPP, the mole concentration of particulate organic matter expressed as carbon in sea water due to net primary production ($\text{mol}\cdot\text{m}^{-3}$) was taken from the Mediterranean Sea Biogeochemical Reanalysis Product (MEDSEA_REANALYSIS_BIO_006_008; Teruzzi et al., 2019) as monthly mean composites at 0.0625° spatial resolution for the 1999-2018 time period. SST ($^\circ\text{C}$) and

SSS (PSU) were extracted as daily composites at a 0.063° spatial resolution for the 1987-2018 period from the Mediterranean Forecasting System, physical reanalysis component (MEDSEA_REANALYSIS_PHYS_006_004, Simoncelli et al., 2019).

Fishing effort estimates were obtained from Global Fishing Watch (GFW, <http://globalfishingwatch.org/>; accessed on August 2018, see Table S1). Our analysis focused on 2012-2016 GFW data for purse seiners, the main fishing gear targeting small pelagic fish; and bottom trawlers, that may impact small pelagic fish both directly through catches of these species (Sbrana et al., 2010) and indirectly through deterioration of interacting communities (Coll et al., 2016).

Biomass distributions for sardines and anchovies were obtained from the Mediterranean International Acoustic Survey (MEDIAS, <http://www.medias-project.eu/medias/website/>), as reanalyzed in Pennino et al., (2020) and Coll and Bellido (2020), for 2003-2016 (see Table S1). Pelagic acoustic surveys sampling design in the Mediterranean Sea was homogenized in 2009 under the MEDIAS project (Anonymus, 2008; see details in Pennino et al., 2020, for procedures prior to 2009). Acoustic samplings are performed during daytime each July by means of scientific split-beam echosounders working at 38 kHz (Saraux et al., 2014), and across parallel transects perpendicular to the coastline at a constant speed of 8–10 nmh⁻¹ (Doray et al., 2010).

2.3. *Climate impacts on small pelagic fish*

Small pelagic populations are highly impacted by changes in temperature, salinity and/or marine productivity (Agostini and Bakun, 2002; Checkley et al., 2009; Katara et al., 2011). This is particularly the case for the study area, where the population dynamics of small pelagic fish are likely driven by environmental factors directly influencing their spawning – larval growth, survival and hence recruitment - and

biomass (Coll et al., 2019; Maynou et al., 2014; Palomera et al., 2007; Pennino et al., 2020; Saraux et al., 2019). We used a multidisciplinary approach to provide a holistic view on the distribution of climate impacts on sardines and anchovies throughout our study area (Fig. 1 and Table S1). To investigate direct climate effects on sardine and anchovy biomasses, we first evaluated their responses to contrasting environmental conditions through Generalized Additive Mixed Models (GAMMs) using a Gaussian distribution with identity link, and thin plate regression splines for non-linear covariates. As explanatory variables we included annual averages for NPP, SST and SSS (2003-2016). We also considered the year as a covariable to account for the inter-annual variability of data; whereas the GSAs were included as a random factor to account for potential, spatial differences in biomass and other GSA-specific confounding factors.

Before modelling, all covariates were examined for a Pearson's correlation coefficient below 0.70 to avoid overfitting. The degrees of freedom of the smooth functions were restricted for each explanatory variable to avoid additional overfitting. Thus, the number of basis functions (k) associated with each smooth term was set to a maximum of k=6. Obtained functional responses were subsequently used to derive optimal environmental ranges and relationships between considered environmental features and fish biomass (Fig. S1).

Based on the available time series (1987-2018) for the chosen environmental variables, we produced spatially-explicit assessments of the long-term trends for optimal environmental ranges and relationships as a proxy to climate effects on fish biomass (Table S1). In the case of sardine, which biomass responded linearly and negatively to increasing annual SST (see Results and Fig. S1), we considered the long-term trend in SST as a suitable proxy for climate impacts. We then used pixel-basis, least-square linear regressions on average annual SST to derive the significance of this

240 temporal trend (α -values >0.05) and its magnitude (slopes; i.e. annual changes in SST;
241 see Ramírez et al., 2018, 2017). For anchovy, we identified optimal environmental
242 ranges for SST and SSS that resulted in biomass increases (see Results and Fig. S1).
243 Marine areas with optimal environmental conditions were identified for every year in
244 the 1987-2018 period. As a proxy for climate-driven environmental effects on
245 anchovy's biomass we quantified the persistency of these areas by counting how many
246 years each pixel/cell was identified as optimal. Marine areas ranged, therefore, from
247 permanently optimal (higher persistency) to permanently sub-optimal (lower
248 persistency).

249 Fish are particularly constrained by environmental conditions and habitat
250 requirements while spawning (Ciannelli et al., 2015). In our study area, optimal
251 environmental conditions for spawning of sardine and anchovy were defined by
252 Palomera et al., (2007). Sardines reproduce from October to March in water
253 temperatures typically below 19°C. In contrasts, anchovies spawn from April to
254 September in water temperatures between 17°C and 24°C (see also Maynou et al., 2020,
255 2014). As ocean warming progresses, spawning conditions for sardine and anchovy in
256 our study area are expected to be affected (Erauskin-Extramiana et al., 2019; Maynou et
257 al., 2020; Palomera et al., 2007). As a proxy to climate effect on the spawning of these
258 two species, we first estimated, for each year, the number of days outside optimal
259 spawning temperatures. We then used pixel-based least-square linear regressions
260 through Generalized Linear Models with a Poisson distribution for deriving the
261 significance of temporal trends in the number of days outside optimal spawning
262 temperatures (α -values >0.05) and their magnitudes (slopes) over the 1987-2018 time
263 period (Table S1).

Climate impacts on early life stages can generate order-of-magnitude fluctuations in annual recruitments (Houde, 2008), thus profoundly affecting fish stocks and population dynamics. In turn, reductions in spawning stock biomass and size of individuals will affect fecundity and the consecutive spawning successes (Brosset et al., 2016b; Maynou et al., 2020; Somarakis et al., 2004). Such circular, multi-faceted interactions support a strategy where multiple stressors must be considered in conjunction to obtain an integrated and more holistic picture of the climate effects on small pelagic fish communities. To this end, we considered a cumulative climate effect based on the equally weighted combinations of our multiple proxies. To compute cumulative climate effects impacts, we excluded areas with non-significant trends, rescaled our multiple proxies to their maximum value, and added them on a per-pixel basis (Ramírez et al., 2018).

2.4. *The overlapping impact of fisheries*

First, we summed daily fishing records to spatially explicit annual totals for the 2012-2016 period. Then, we averaged the entire time series to obtain an overview of the spatial distribution of fishing pressure, which allowed us to highlight those marine areas that have been particularly impacted by human fisheries over recent years. We considered purse-seiners separately (as the main fishing gear targeting small pelagic fish), along with a combination of purse-seiners and trawlers, to investigate the spatial congruence between fishing pressure and our proxies for the cumulative impact of climate on sardines and anchovies. Owing to the uneven distribution of our proxies for cumulative climate effects, and because fisheries management in our study area is undertaken at the GSA level, we divided each GSA into four subareas - each representing a quartile of magnitude of cumulative climate effects (Q1 to Q4; Fig 6).

Then, we extracted the magnitude of our proxy for fishing pressure for each Q1 to Q4 sub-areas.

3. Results

Sardines and anchovies showed contrasting trends in their biomass in our study area (Fig. 2). Overall, the biomass of sardines decreased from 2003 to 2016 with a partial recovery in GSA01 after 2012, whereas anchovy biomass remained roughly constant in GSA07, slightly increased in GSA06 and notably increased in GSA01 after 2012. Our GAMMs explained 45% and 75% of observed deviance for sardine and anchovy biomass, respectively. Both species responded differently to SSS and SST (Table S2). In addition to the temporal trend for sardine biomass, we observed a significant and linear partial effect of SST, with increasing annual temperatures resulting in decreasing biomasses (Fig. S1). In the case of anchovies, significant partial effects were observed for SST and SSS (Table S2). Response curves suggested enhanced biomasses for anchovies above the 19°C threshold and within a salinity range of 36.7 to 37.5 PSU (Fig. S1).

To understand climate impacts on sardine biomass, we therefore evaluated the long-term trend in annual SST. SST progressively increased throughout the 1987-2018 period (Fig. 3a, b). However, this warming was spatially heterogeneously distributed (as revealed by the pixel basis, least-square linear regressions), with the most striking changes occurring in the north of GSA01 and in central offshore areas in GSA06 and GSA07 (Fig. 3a). In the case of anchovy, the optimal ranges of SST and SSS largely occurred in the north of GSA01 and the south of GSA06 (and in the areas of influence of the Ebro and the Rhône rivers, particularly for optimal ranges of SSS), with optimal areas increasing in surface from 1987 to 2018 (Fig. 3c-f).

Average SST during sardine and anchovy spawning periods also increased progressively from 1987 to 2018 (Fig. S2). However, potential impacts on the spawning also contrasted between species. Our proxies for climate impacts on fish spawning revealed that, overall, sub-optimal conditions for spawning increased in the case of sardines (particularly after 1995); and remained relatively constant for anchovies (Fig. 4b,d). However, these general trends showed also large spatial variation. In the case of sardines, the most striking climate impacts (i.e., decreasing optimal environmental conditions) were observed in GSA01, the north of GSA06, and the west of GSA07 (Fig. 4a). Contrastingly, only a few areas experienced significant changes in the optimal environmental conditions for anchovy spawning. Most significant changes occurred in GSA1, the north of GSA6 and the offshore areas of GSA07 (Fig. 4c); and generally consisted of a slightly increase in the number of days under optimal environmental condition (Fig. 4c,d).

By combining our proxies for climate impacts on fish biomass and spawning, we found that the cumulative effect of these multiple stressors distributed heterogeneously throughout our study area. The most striking impacts for sardines occurred in GSA01 and at the border between GSA06 and GSA07 (Fig. 5a). In contrast, the enhanced optimal environmental conditions for anchovies occurred in the Gulf of Alicante, i.e. central area of the Mediterranean Iberian coast, encompassing water masses in the north of GSA01 and the south of GSA06 (Fig. 5b). No relevant changes were observed in GSA07.

Analogously, fishing pressure was unevenly distributed across our study area, with contrasting patterns between purse-seiners and trawlers (Fig. S3). Trawlers were more widely distributed throughout our study area, whereas purse-seiners were nearly absent in GSA07. Overall, fishing pressure was higher in GSA06.

Interestingly, we found a high overlap between fishing pressure and our proxy for the cumulative climate effect on sardines. In particular, those marine areas within GSAs showing the highest impacts from climate-driven environmental changes (i.e., those categorized as Q4), were also those most impacted by overall fishing pressure (i.e., accounting for purse-seiners and trawlers, Fig. 6). This spatial congruence was also observed when exclusively considering purse-seiners as the main fishing gear targeting this species (Fig. S4). Areas highly impacted by both climate impacts and fishing pressure for sardine largely occurred in the west of GSA01 and GSA07 and at the north of GSA06 (Fig. 6).

Similarly, we also observed a high spatial similarity between climate effects and fisheries for anchovies. In this case the areas that environmentally improved the most (Q4), which occurred along the central Iberian coast, also showed the lowest impacts from fisheries (Fig. 6; see also Fig. S4 for estimates that exclusively consider purse-seiners' fishing pressure). Therefore, those areas with less environmental improvements (Q1) where the areas that also supported the largest impacts of fishing.

4. Discussion

Our study provides the finest-scale, spatially-explicit assessments to date of climate and fishing impacts on two species of high commercial value in the Mediterranean Sea, i.e., the European sardine and European anchovy. Overall, our results concurred with previous findings showing that these two species are likely simultaneously impacted by changing environmental conditions (i.e., temperature and salinity) and fisheries, which, ultimately, might be responsible for recent declining trends in their biomasses (Coll et al., 2019; Maynou et al., 2020; Pennino et al., 2020; Van Beveren et al., 2016). However, these stressors apparently affect both species

differently and, even, the genetically distinct populations occurring West and East from the Almeria-Oran front (Kasapidis et al., 2012). These results highlight the importance of studying the life-history traits of species at different spatial scales in order to assess their resilience capacity, since organisms could present different phenotypic adaptations to local oceanographic conditions (Stange et al., 2020).

4.1. *The dual impact of climate and fisheries on small pelagics*

Based on the SOS framework, our results point to the worst of the potential scenarios, where the high spatial congruence between these stressors suggests that the small pelagic community is simultaneously threatened by climate and fishing impacts. However, the heterogeneous spatial distribution of stressors and the possibility to enforce fisheries limitations provide opportunities to recover small pelagic populations.

Increasing water temperatures across the study area broadly concur with general global trends (Halpern et al., 2015; Hoegh-Guldberg and Bruno, 2010; Ramírez et al., 2017) and regional and local assessments in the Western Mediterranean Sea (Ramírez et al., 2018; Salat et al., 2019; Skliris et al., 2012). In turn, the increase in water temperature has been identified as an important environmental driver of decreasing population dynamics for the small pelagic fish community (Coll et al., 2019; Pennino et al., 2020). These impacts could be mediated through a direct effect on these fish species (e.g., a physiological effect on individuals or an impact on egg quality and larval growth and survival, Coll et al., 2019; Ganas, 2009; Garrido et al., 2016; Maynou et al., 2020; Somarakis et al., 2019). Indirectly, small pelagic populations could be also impacted through the expansion of thermophilic and competing species (Albo-Puigserver et al., 2019; Maynou et al., 2020; Sabatés et al., 2018), as well as, through changes on food abundance or quality (Brosset et al., 2017; Coll et al., 2019; Feuilloley et al., 2020; Saraux et al., 2019; Vargas-Yáñez et al., 2020). For instance, it has been hypothesized

that ocean warming may prompt the development of small phytoplankton (Brosset et al., 2016a; Calvo et al., 2011; Queiros et al., 2019) and benefit fish species relaying largely on this food resource. This could be the case for sardines that comparatively feed more on smaller prey than anchovies (Bachiller et al., 2020; Brosset et al., 2016a). However, phytoplankton represents a minor fraction of dietary intake by both species at our study area (Bachiller et al., 2020; Costalago and Palomera, 2014; Queiros et al., 2019), and recent experimental assessments suggested that feeding on small-sized prey may have also deleterious consequences for small pelagics (see Queiros et al., 2019 for the particular case of sardines). In part, ocean warming may explain, therefore, dietary shifts by small pelagics towards smaller prey at our study area (Brosset et al., 2017), with ultimate impacts on their dynamics through a bottom-up control (Saraux et al., 2019).

In addition to climate impacts, fisheries also exert an important pressure on small pelagic species in the study area (Coll and Bellido, 2020; FAO, 2018a). Fishing pressure could have been particularly intense on anchovies of our study area, as fisheries preferably target this species (Coll et al., 2019; Pertierra and Lleonart, 1996). In part, this could explain the past drop in anchovy's biomass/captures even under relatively favourable environmental conditions (i.e., enhanced water temperatures and salinity, Fernández-Corredor, 2018; Pennino et al., 2020). Once the stocks are relatively low, as in the current case, then environmental factors dominate small pelagic dynamics (Essington et al., 2015; Planque et al., 2010). The apparent improvement in environmental conditions for anchovies at the transitional area between GSA01 and GSA06 may explain, therefore, the increase in anchovy's biomass from 2010 onwards (see also Coll et al., 2019; Maynou et al., 2020; Pennino et al., 2020) and an observed spatial expansion of the GSA06 population (Pennino et al., 2020). However, this may

414 just indicate that the increase in water temperature and salinity in our study area has not
415 been severe enough to affect anchovies significantly. As species or ecosystems often
416 react in non-linear ways to climate impacts (Bland et al., 2018; Durant et al., 2005) the
417 definition of numerical thresholds of environmental variables from which anchovies
418 may be drastically affected is still necessary (Maynou et al., 2014; Pennino et al., 2020).

419 Intense fishing pressure can modify the ability of populations to respond to
420 climate changes through demographic erosion, i.e., selective mortality of larger
421 individuals (Albo-Puigserver et al., 2018; Hidalgo et al., 2011; Planque et al., 2010).
422 This could be particularly the case for the populations in the north of GSA06 and
423 GSA07, where the most severe climate impact and the fishing pressure co-occur. These
424 results complement recent assessments of major life-history traits for these species,
425 which identified a truncated length-at-age pattern (due to size-selective mortality
426 induced by fishing) and the poorer conditions of northern populations, compared to the
427 central and the southern populations in our study area (Albo-Puigserver et al., 2018;
428 Coll and Bellido, 2020; Van Beveren et al., 2014). The southernmost population may
429 also benefit from contrasting phenotypic responses to environmental forcing factors as
430 well as an influx from the Atlantic population (Albo-Puigserver et al., 2018; Kasapidis
431 et al., 2012; Quintanilla et al., 2015; Ventero et al., 2017). Complementarily, the
432 northernmost area, which productivity is largely driven by runoff from the Ebro and
433 Rhône rivers (Bosc et al., 2004; Estrada, 1996), might be affected by an additional,
434 climate-driven reduction of river discharges (Lloret et al., 2004). In part, this could
435 explain the relatively low sensitivity of the southernmost small pelagic community to
436 the simultaneous impacts of climate and fisheries, which co-occur in this area with
437 similar magnitudes to those we observed northward. Again, this may suggest that the
438 system has not yet reached critical climate and fishing pressure that could conduct to

collapse, albeit recent declines in body condition for sardines and anchovy could be a possible early warning sign for future declines also in the south (Albo-Puigserver et al., 2018).

Identifying areas that are most likely to persist under adverse climate change conditions in the future, the so-called “climate refuges” is important for anticipating the complex impacts that climate change will have on ecosystems and societies (Monsarrat et al., 2019). Interestingly, climate refuges recently identified in GSA06 and GSA07 for anchovy and sardine occurred around the Rhône and the Ebro river mouths and the Gulf of Alicante (Pennino et al., 2020), where we observed comparatively low magnitudes of cumulative impacts. One may argue that preserving these slightly impacted areas might be key from a socio-ecological perspective and a “low-hanging fruit” for conservation, as they can act as seed areas for re-expansions and recolonizations (Pennino et al., 2020). However, further interacting stressors (e.g. pollution, aquaculture, biological invasions, Coll et al., 2010) may complicate preservation efforts based on marine spatial planning (Coll et al., 2019; Micheli et al., 2013), as do additional socio-economic considerations associated to seafood provisioning.

4.2. *A SOS framework for sustainable fisheries*

The SOS framework can incorporate as many dimensions as potential threats (Ramírez et al., 2018), while potentially considering the wellbeing of social sectors associated with ecosystem services. Models for sustainable development must optimize the trade-off between exploitation of natural resources to ensure human wellbeing and the conservation of Earth’s life-supporting services (i.e. Doughnut, Raworth, 2017). Currently, stock assessments in the Mediterranean Sea are provided on a GSA basis and are exclusively based on statistical extrapolations of observed catches and biomass accounting for estimated life-history parameters (e.g., growth or mortality), without

considering environmental factors (GFCM, 2019). However, the uneven distribution of fishing pressure, combined with environmental stressors makes particular areas and fish communities within GSAs more prone to collapse. Our results illustrate that sustainable fishing practices could be partially based on a spatial redistribution and reductions of fisheries in order to alleviate pressure in those areas mostly impacted by climate change. Management and conservation strategies may benefit, therefore, from SOS and fine-scale, spatially-explicit assessments on the distribution of climate and human stressors such as those provided in this study. In addition, management and conservation actions based on the SOS framework are fully compatible with the identification and protection of key marine areas that may act as climate refuges (Pennino et al., 2020), while contributing to the sustainability of fishing practices in non-protected areas.

A thorough comprehension of the thresholds of interacting stressors and the patterns and mechanisms by which these stressors are impacting marine systems synergistically is still required for anticipating and preventing ecosystem collapses (Montoya et al., 2018; Ramírez et al., 2018). In this regard, SOS promotes caution when considering (1) the uncertainty surrounding thresholds for climate and fishing stressors that cause ecosystem collapse when exceeded, and (2) the manner in which climate thresholds are lowered by fishing pressure (and vice versa, Ramírez et al., 2018). Our SOS framework could be considered as an “achievable” way for alleviating the consequences of climate change and overfishing, while the international community finds solutions for the global challenge posed by the greenhouse gas emissions (Green et al., 2017; Ramírez et al., 2018; Scheffer et al., 2015). SOS can also provide an adaptable framework that can be continuously updated by incorporating up to date information on potential threats or finer-scaled data on oceanographic features (Gissi et al., 2021). Satellite remote sensing records for key environmental features that are

presumed to drive fish abundances, along with spatially-explicit quantifications on fishing effort, are now provided at the global scale and for a long time period (e.g., Kroodsma et al., 2018; Ramírez et al., 2017). Accordingly, our SOS approach could also be potentially extended to other key ecologically and economically relevant regions or fish communities worldwide, whenever information on optimal environmental conditions for target species is available.

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Author contributions

FR, MGP and MC conceived the work; MC and JMB provided the funding; FR, JS and MGP extracted and analysed the data. FR drafted the paper. All authors contributed substantially to the writing, reviewing and editing of the work.

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Figure captions

Figure 1. Workflow and work concept. Based on spatially-explicit measurements for main environmental forcing factors and relevant biological information for sardines and anchovies, we first evaluated the optimal ranges and relationships between environmental conditions and fish biomass and spawning at the western Mediterranean Sea. As proxies to climate impacts on the small pelagic fish community, we then used the longest time series (1987-2018) for these environmental variables to evaluate the long-term trends for these optimal environmental ranges and relationships. Finally, we combined our spatially-explicit assessments with available data on fishing pressure to identify doubly impacted marine areas, where fisheries require management within a SOS framework to enhance resilience to climate change and ensure the long-term sustainability of these fisheries.

Figure 2. Our study area represents the pelagic system of the western Mediterranean Sea, from the Alboran Sea in the south, through the Iberian coast up to the Gulf of Lion in the north (a). Our study includes three different Geographical Sub-Areas: GSA01, GSA06 and GSA07. We show temporal trends (2003-2016) in the biomass of sardine (b) and anchovy per GSA (c). Raw data on biomass are represented along with smoothing lines and their 95% confident intervals (Wickham, 2009).

Figure 3. Proxies for climate-driven environmental effects for sardine (a-b) and anchovy biomasses (c-f). In the case of sardine, which biomass responded linearly and negatively to increasing annual SST (Fig. S1), we represent the pixel-basis, least-square linear regressions on average annual SST for the 1987-2018 period as a suitable proxy for climate impacts (a). Colours indicate the estimated slopes for these linear regressions and gridded areas include those water masses in which observed trends were not significant (α -value > 0.05). We also show the long-term (1987-2018) trends in annual SST per GSA (b); showing raw data, smoothing lines and their 95% confident intervals (Wickham, 2009). For anchovy, we represent the number of years within the 1987-2018 with optimal conditions of (c) SST ($>19^{\circ}\text{C}$) and (e) SSS (36.7 to 37.5 PSU). In this case, colours range from permanently optimal (blueish) to permanently sub-optimal (reddish) environmental conditions. We also show the long-term (1987-2018) trends in the surface of areas encompassing optimal environmental conditions for (d) SST and (f) SSS per GSA (note that environmental conditions at GSA07 were permanently out of the optimal range except for the mouth of the Rhône river). Different colours for sardines and anchovies refer to contrasting climate effects on both species (i.e., deteriorating and improving conditions, respectively).

Figure 4. Long term trends in optimal environmental conditions for sardine (a, b) and anchovy spawning (c, d). We considered that optimal environmental conditions for sardine spawning were below the 19°C threshold for water temperature, whereas anchovies mostly reproduce within the 17° - 24° range (Palomera et al., 2007). Colours in maps represent the slope of derived least-squares linear regressions for the number of days per spawning period with SST $>19^{\circ}\text{C}$ and within 17° - 24°C range, as suitable proxies to climate impacts on sardine and anchovy spawning, respectively. Gridded areas include those water masses in which observed trends were not significant (α -value > 0.05). We also show the long-term (1987-2018) trends for our proxies to climate impacts on (b) sardine and (d) anchovy spawning per GSA.

Figure 5. Cumulative climate effect on (a) sardine and (b) anchovy. Following Ramírez et al., (2018), we considered a cumulative climate effect based on the equally weighted combinations of our multiple proxies for climate effects on fish biomass and spawning (see Fig. 3 and 4). Different colours for sardines and anchovies refer to contrasting climate effects on both species (i.e., deteriorating and improving conditions, respectively).

Figure 6. The overlapping impact of fisheries on the cumulative climate impacts for sardines (a, b) and anchovies (c, d). Cumulative climate impacts accounted for estimated impacts on fish biomass and spawning (Figure 5). Four different subareas within each GSA were defined by quartiles (Q1; slightly impacted to Q4; highly impacted) for the magnitudes of the cumulative climate impacts (a, c). Different colours for sardines and anchovies refer to contrasting climate effects on both species (i.e., deteriorating and improving conditions, respectively). From these sub-GSAs, we extracted the magnitude of our proxy to overall fishing pressure (accounting for purse-seiners and trawlers) (b, d). Note that no changing environmental conditions for anchovies were observed at GSA07.

973 **Figure 1.**

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990 **Supporting information, Table S1.** Summary of datasets and their specific application in the study to evaluate climate effects on small pelagic
 991 fish and the overlapping impact of fisheries

Datasets used in the study

Variable	Units	Product	Time period	Resolution		Specific application	Source
				Temporal	Spatial		
Fish biomass	tons	Mediterranean International Acoustic Survey (MEDIAS)	¹ 2003-2016	Annual	GSA	To investigate climate effects on sardine and anchovy biomass	http://www.medias-project.eu/medias/website/
Net Primary Productivity (NPP)	mol·m ⁻³	MEDSEA_REANALYSIS_BIO_006_008	² 1999-2018	Monthly	0.0625°	To investigate climate	https://marine.copernicus.eu/

				l y		effects on sardin e and ancho vy bioma sses
Sea Surface Temperature (SST)	°C	MEDSEA_REANAL ³ YSIS_PHYS_006_00 4	1987-2018	D ai l y	0.063°	To https://marine.copernicus.eu/ investi gate climat e effects on sardin e and ancho vy bioma sses and spawn ing
Sea Surface Salinity (SSS)	PSU	MEDSEA_REANAL ³ YSIS_PHYS_006_00 4	1987-2018	D ai l y	0.063°	To https://marine.copernicus.eu/ investi gate climat e effects

Fishing effort	h·km ⁻²	Fishing Vessels	⁴	2012-2016	Daily	0.1°	on sardine and anchovy biomass. To investigate the overlapping impact of fisheries
							http://globalfishingwatch.org/

Climate effects on pelagic fish

	Environmental relationships		Our proxy to climate effect on small pelagic fish
European sardine	Optimal spawning SST < 19°C	⁵	Pixel-basis trend (1987-2018) in the number of days outside optimal spawning temperatures
	Biomass linearly and negatively affected by increasing annual SST	⁶	Pixel-basis trend (1987-2018) in average annual SST
European	17°C <	⁵	Pixel-basis trend (1987-2018) in the number of days outside optimal spawning temperatures

anchovy	Optimal spawning SST < 24°C		
	Enhanced biomass when: SST >19°C	⁶	Number of years (1987-2018) each pixel was identified as optimal (i.e. persistency of optimal conditions)
	Enhanced biomass when: 36.7 PSU < SSS <37.5 PSU	⁶	Number of years (1987-2018) each pixel was identified as optimal (i.e. persistency of optimal conditions)
¹ reanalyzed from Pennino et al., 2020			
² Teruzzi et al., 2019			
³ Simoncelli et al., 2019			
⁴ Kroodsma et al., 2018			
⁵ Palomera et al. 2007			
⁶ Current study; based on GAMMs (2003-2016) to evaluate fish responses to NPP, SST and SSS; see Results and Fig. S1			

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Supporting information, Table S2. Numerical summary of the Generalized Additive Mixed Models (GAMMs) we fit for European sardine (*Sardina pilchadurs*) and anchovy's (*Engraulis encrasicolus*) biomasses. GAMMs included as explanatory variables annual averages for Net Primary Production (NPP), Sea Surface Temperature (SST) and Sea surface Salinity (SSS). We also considered the year as a covariable; as well as the GSAs (GSA01, GSA06 and GSA07) as a random factor to account for potential, inter-annual and spatial differences in biomass and other GSA-specific confounding factors. Statistic acronyms are: edf= degree of freedom; Ref.edf = relative, F = F statistic. Note that f(covariable) means that such variable has been introduced in the model through a spline function.

Approximate significance of smooth terms:

European sardine				
	edf	Ref.edf	F	p-value
f(NPP)	1	1	0.073	0.79
f(SST)	1	1	5.04	0.03*
f(SSS)	1	1	3.56	0.07
f(Year)	2.267	2.267	3.58	0.04*

European anchovy				
	edf	Ref.edf	F	p-value
f(NPP)	1	1	3.826	0.06
f(SST)	3.786	3.786	3.096	0.04*
f(SSS)	5.777	5.777	15.618	<0.001**
f(Year)	1	1	3.605	0.07

Supporting information, Figure S1. GAMM plots showing the partial effects of NPP, SST and SSS on the biomass of sardines (top panels) and anchovies (bottom panels). The tick marks on the x-axis are observed data points. The y-axis represents the partial effect of each variable. The shaded areas indicate the 95% confidence intervals.

Supporting information. Figure S2. Long term changes in temperature for the spawning periods of sardines and anchovies. Increase in surface water potential temperature during the 1987-2018 period at the GSAs included in our study area. We considered the annual averages for the spawning periods of sardines (October to March -included-) and anchovies (April to September -included-, Albo-Puigserver et al. submitted).

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Supporting information, Figure S3. Spatial patterns on fishing pressure for purse-seiners (a) and trawlers (b). Based on data on fishing pressure from Global Fishing Watch (Kroodsma et al., 2018).

Supporting information, Figure S4. The overlapping impact of purse-seiners on the cumulative climate impacts for sardines (a, b) and anchovies (c, d). Cumulative climate impacts accounted for estimated impacts on fish biomass and spawning (Figure 5). Four different subareas within each GSA were defined by quartiles (Q1; slightly impacted to Q4; highly impacted) for the magnitudes of the cumulative climate impacts (a, c). Different colours for sardines and anchovies refer to contrasting climate effects on both species (i.e., deteriorating and improving conditions, respectively). From these sub-GSAs, we extracted the magnitude of our proxy to purse-seiners' fishing pressure (b, d). Note that no changing environmental conditions for anchovies were observed at GSA07.