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Insights into the spatio-temporal variability of spawning in a territorial coastal fish by combining observations, modelling and literature review

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Abstract

In bipartite life cycle fishes, spawning represents the onset of propagules dispersal, with eggs and larvae experiencing anisotropic transport and high mortality rates, before eventually metamorphosing and settling. Hence, early-life stages operate as bottlenecks for population demography by strongly constraining recruitment. Despite its significance, spawning is rarely explicitly considered in ecosystem management due to a lack of knowledge, for many species, about where and when spawning occurs. Previous evidences suggest that temperature is among the main drivers of spawning in Teleosts. Using the ecologically and economically relevant white seabream *Diplodus sargus* in the central Mediterranean Sea as a case study, we assess the abiotic factors that regulate the onset and duration of spawning and subsequent dispersal. Lagrangian backtracking simulations fed with early-life observations allow locating 11 spawning events, which are then associated to simulated temperatures ranging from 14.8  C to 20.6  C, in close agreement with previous estimates. Based on this range of suitable temperatures, we model the spatio-temporal variability of spawning success at broad-scale over 10 years (2005–2014) following the backtracking approach with hypothetical constant settlement areas. It highlights a prominent inter-annual variability in the Adriatic and Siculo-Tunisian strait driven by oceanographic processes. Moreover, a powerful clustering method uncovers relatively stable spawning areas in the Ligurian and Tyrrhenian seas with both early (January to Mid-February) and late (April to June) spawning peaks. Our methodology can be applied to other species and oceanic systems to investigate how oceanic processes impact spawning success, enabling the design of sound management strategies.

KEYWORDS

Diplodus sargus, ecosystem management, lagrangian backtracking model, Lagrangian flow network, larval dispersal, marine connectivity, Mediterranean Sea, oceanic variability, spawning event

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1 | INTRODUCTION

The Mediterranean is one of the most over-exploited sea in the world with about 75% of the assessed fish stocks being currently overfished, mostly by large scale fisheries (FAO, 2018; Tsikliras et al., 2015). Moreover, among coastal species, which are essentially targeted by small scale and recreational fisheries, many are currently not assessed despite declining catches (Lloret & Planes, 2003). While local conservation initiatives (e.g., Marine Protected Areas, MPAs) have been shown to have positive effects on such coastal species locally (Abecasis et al., 2015; Di Franco et al., 2016; Giakoumi et al., 2017; Sala et al., 2012), their large-scale protection and management remain challenging because of complex life cycles and high environmental variability (Cadrin & Secor, 2009). Due to the current lack of information to design sound management strategies and fisheries restrictions for coastal fish at basin scale, there is an urgent need to develop research and management for a more sustainable exploitation of fish stocks in this semi-enclosed and densely populated sea.

In this context, determining the location and onset of spawning now represents a key element for fishery science (Sadovy de Mitcheson, 2016). Indeed, spawning aggregations are often targeted by fisheries as it represents relatively easy and lucrative catches in a first place, but these activities ultimately lead to a rapid decrease in stocks and to long-term reduction of fishery activities (Sadovy & Domeier, 2005). Moreover, spotting spawning areas is crucial to appraise the dispersal of propagules (i.e., eggs and larvae) and hence understand population connectivity (Bauer et al., 2014; Calò et al., 2018; Dubois et al., 2016; Legrand et al., 2019), especially for bipartite life cycle for which the spatial scales of ecological connectivity are mainly determined by the dispersal of early-life stages by currents across the seascape (Burgess et al., 2016; Gaines et al., 2007; Nathan et al., 2003). These early-life stages start with the spawning process, when fish aggregates and gametes are released into the water column, and then, eggs hatch into larvae, which, after a first stage mostly passive, will acquire the capability to actively swim, just before metamorphosing in juveniles and settling in coastal habitats (Thresher et al., 1989). Enormous amounts of propagules are generally assumed to have the potential to disperse over large distances, spanning tens to hundreds of kilometres (Cowen et al., 2006) while exhibiting high mortality (Pineda et al., 2007). Nevertheless, by introducing migrants into a population, dispersal can impact growth and mortality rates, a process called demographic connectivity (Cowen & Sponaugle, 2009). Demographic connectivity is fundamental in fishery and conservation science as it has been shown to influence dynamics and persistence of spatially structured populations (Burgess et al., 2014; Hidalgo et al., 2019). Few management tools have already been considering demographic connectivity explicitly, thus limiting their efficiency (Fogarty & Botsford, 2007) and pointing out the necessity of a change in the management approach to a more sustainable exploitation of marine living resources (Carr et al., 2019).

However, the location and timing of spawning events and their eventual stability/variability in space and time remain major unknowns of the fish life cycle (Calò et al., 2018). Since field

observations of spawning events are very sparse and fragmentary, they do not provide sufficient quantitative information about when and where spawning occurs. Moreover, monitoring the spawning activity of a given fish species over broad-scale would be overly costly, if not impossible. As such, indirect methodologies must be considered. One approach, which we follow here, consists in using field observations of just-settled juveniles (i.e., post-settlers) as indirect evidence of the successful occurrence of one or multiple spawning events. Then, backtracking larvae trajectories from settlement sites to putative spawning areas and identifying the abiotic conditions that prevail during these spawning events may help gain insights into which abiotic conditions favour spawning. By extrapolating these relationships and thanks to constant monitoring of abiotic conditions, one could then predict future events and use this information to design sound management strategies enabling the protection of these propagules' sources, contributing to the replenishment of both local and distant sub-populations (Di Franco et al., 2012; Erisman et al., 2015; Pelc et al., 2010; Pittman & Heyman, 2020). Development of hydrodynamical models backtracking larvae from settlement areas to potential spawning areas is actively trying to fill this gap (Bauer et al., 2014; Calò et al., 2018; Legrand et al., 2019; Torrado et al., 2021). Combining these models with the variability of environmental factors, known to control the onset of fish spawning in favourable areas, could improve the simulation of the spawning process and thus enhance scientific-based knowledge of this event (Huret et al., 2010; Werner et al., 2007).

Among all potentially relevant abiotic factors, previous findings suggest seawater temperature playing a key role as a trigger of fish spawning, both in freshwater (King et al., 2016) and in marine species (Gill et al., 1996; Hereu et al., 2006; Winters & Wheeler, 1996). In the Mediterranean sea, temperature as a spawning cue has been already reported for Sparids: changing temperatures seem to trigger the onset of spawning for this family (Gonçalves, 2000; Mouine et al., 2011; Pajuelo et al., 2003, 2006, 2008). Here, we focus on a demersal fish of the Sparid family, the white sea bream *Diplodus sargus* (Linnaeus, 1758) as it is a relatively data-rich case study in the Mediterranean. *D. sargus* is known to spawn once a year (Mouine et al., 2007). More precisely, the rise of seawater temperature from the winter minimum throughout spring has been related with the onset and the duration of the spawning period for this species (Aspillaga et al., 2016; Di Lorenzo et al., 2014; Morato et al., 2003; Mouine et al., 2007, 2012; Potts et al., 2014). The white seabream is a keystone species as it feeds on sea urchins *Paracentrotus lividus*, and regulates their grazing pressure on algae, therefore potentially controlling regime shifts (from vegetated to bare rocky coastal habitats) in the Mediterranean ecosystem (Hereu et al., 2005). Moreover, *D. sargus* is economically relevant in the Mediterranean Sea as targeted by both recreational and professional fisheries (Sala et al., 1998), despite the lack of stock assessment for this species (FAO, 2006).

Our objectives here are to understand how abiotic factors influence the timing and location of spawning events for *D. sargus* in order to appraise the locations and periods that are potentially favourable for spawning, hence delivering useful inputs to design sound

management and conservation strategies. We first determine a range of temperatures that triggers spawning by building a backward-in-time particle tracking model fed with early life traits and settlement locations for the investigated species. Based on this range, we use multi-year outputs of a regional ocean model to simulate and analyse the inter-annual variability / stability of dispersal and spawning over 10 recent years at large scale. We finally discuss our results against the published literature and interpret them in the context of dynamic spatio-temporal management.

2 | MATERIAL AND METHODS

2.1 | Modelling the dispersal stages using the Lagrangian flow network

The Lagrangian Flow Network (LFN) model, which combines network theory tools and a particle-tracking model, has been successfully applied to study marine connectivity (Dubois et al., 2016; Hidalgo et al., 2019; Legrand et al., 2019; Rossi et al., 2014, 2020) thanks to robust theoretical foundations (Ser-Giacomi et al., 2015) and comprehensive sensitivity studies (Monroy et al., 2017). It simulates the

dispersal of fish early-life stages (eggs and larvae) by calculating passive horizontal trajectories at a given depth for predetermined starting times and durations.

Here, the LFN is coupled offline with a hydrodynamical model, the Adriatic-Ionian REGIONal configuration (AIREG; Ciliberti et al., 2015; Oddo et al., 2006; Figure 1), which is based on the NEMO kernel (Madec & the NEMO team, 2008). We use the high-resolution ($1/45^\circ$) AIREG outputs that consist in daily three-dimensional velocity and temperature fields on 121 depths for years ranging from 2005 to 2014. The LFN first discretizes the AIREG domain in a non-regular mesh of equal-area boxes, called nodes, and computes a land ratio for each of them (e.g., a node with a land ratio of 0/1 is considered fully covered by sea/land, respectively). The node size is set to a horizontal resolution of $1/16^\circ$ to properly consider the typical intricate coastlines and small islands found in the full AIREG domain. In total, the LFN builds 48,839 nodes, which are quasi-squared boxes of about 6 km width and a surface of around 40 km². Just-released eggs and subsequent larvae are represented as passive particles drifting at a fixed depth of about 10 m, following the few available evidences for Sparid larvae dispersal (Olivar & Sabatés, 1997). While changing in buoyancy or ontogeny of larvae could potentially modify the vertical positioning of some species, hence modifying trajectories (Pineda et al., 2007), no

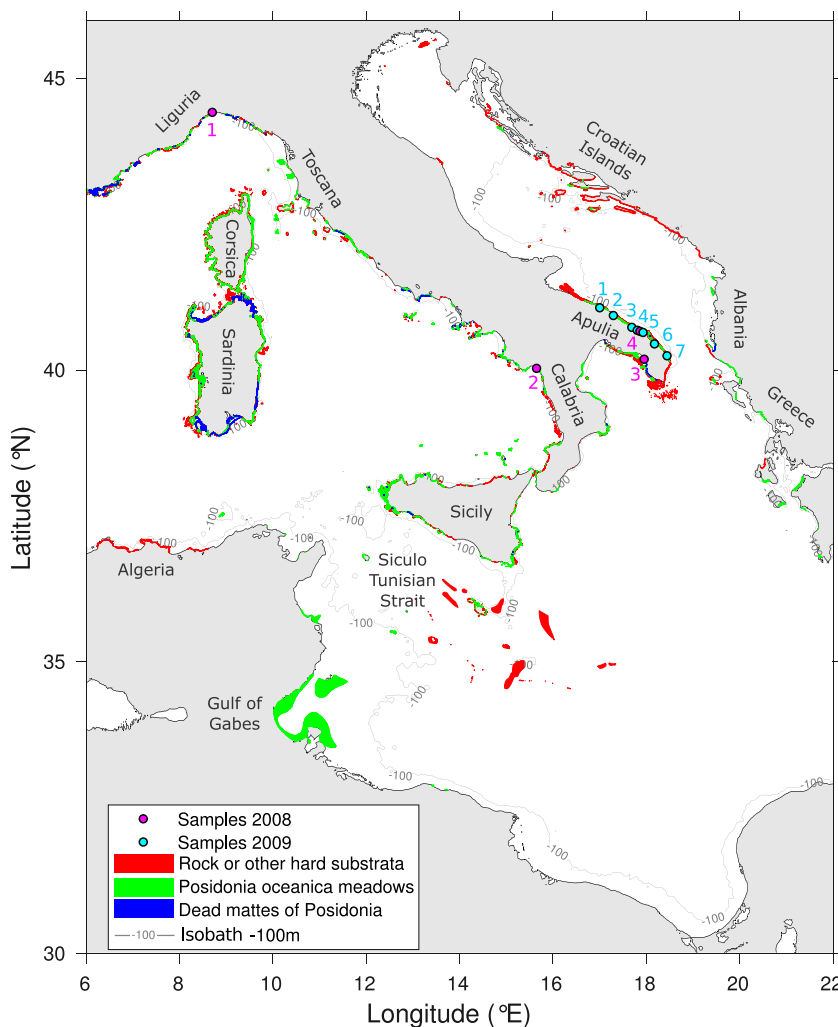


FIGURE 1 Seabed substrates downloaded from the EMODnet portal (European Marine Observation and Data Network, EMODnet, 2013) and 100 m isobath (dark thin line) used to determine the spawning habitat in Section 2.2 and the spawning and settlement habitat in Section 2.3, in accord with the literature concerning *D. sargus* (Aspillaga et al., 2016; Di Lorenzo et al., 2014; Guidetti, 2000; Giacalone et al., 2018). The sites of 2008 are in pink colour: 1. Genova, 2. Maratea, 3. San Isidoro, 4. Torre Guaceto. The sites of 2009 are light blue: 1. Bari, 2. Monopoli, 3. Hotel La Darsena, 4. Torre Guaceto MPA, 5. Punta Penne, 6. Casalabate, 7. San Andrea. Those sites represent the settlement habitat in Section 2.2.

study has documented this effect for *D. sargus* yet. Moreover, small vertical displacements (e.g., tens of metres) within the surface mixed layer (which ranges from 30 to 100 m or more in the Mediterranean Sea) would return similar trajectories as modelled near-surface currents are mostly barotropic. Another potentially relevant biological behaviour occurs at the end of the larval stage, when competent larvae gain swimming abilities to move toward more suitable settlement sites located 1 or 2 km away (Clark et al., 2005; Faillettaz et al., 2018; Staaterman et al., 2012). Our model indirectly includes the effect of such behaviour since such small nearshore movements are clearly imperceptible in nodes of 40 km². In addition, note that this coarse-graining procedure allows the consideration of adult movements in our simulations since the home range of adult individuals is, on average, smaller than 1 km² (Aspillaga et al., 2016; Di Lorenzo et al., 2014), while individuals can display longer distance movement (for 1 or 2 km) during spawning. For each numerical experiment, about 100 Lagrangian particles (for full-sea node; otherwise slightly less, proportionally to the land ratio) are homogeneously seeded in each node, representing around 2.5 million particles for the entire AIREG domain. The Runge-Kutta time step used to integrate Lagrangian trajectories is 30 min, fulfilling the Courant-Friedrichs-Lewy condition (Courant et al., 1928; Legrand et al., 2019). Each experiment is characterized by specific starting dates and particle-tracking durations, which are chosen according to *D. sargus* spawning dates and Pelagic Larval Durations (PLD, here assumed to be the time comprised between spawning and settlement) determined through otoliths' reading (Di Franco et al., 2011; Di Franco & Guidetti, 2011; see Table S1).

Finally, the LFN builds a connectivity matrix that encodes the particles exchanged between any pairs of nodes and retained within them. Such a connectivity matrix contains all the dispersal information: each element of the raw matrix is the number of particles exchanged between the departure node, corresponding to the row, and the arrival node, corresponding to the column.

2.2 | Identification of successful spawning areas and determination of favourable temperatures using observation-constrained simulations

The first part of the study consists in spatially delimiting successful spawning areas associated with settlement areas previously identified and for which specific information on early life traits is available (Di Franco et al., 2011; Di Franco & Guidetti, 2011). To do so, we track early-life stages from their settlement sites back to their spawning areas (Legrand et al., 2019) using our dispersal model and fine-tuned parameters following the biological observations collected at each site (see Table S1 and Figure S2). Then, we determine and compile all the modelled temperatures found within these discrete spawning areas over well-defined temporal periods. This range of spawning suitable temperatures is finally used as a parameter of the second modelling exercise (see Section 2.3).

Along the Italian coasts, 10 *D. sargus* juveniles per site were caught at four sites in June 2008 and 20 juveniles per site at seven

sites in June 2009 (Di Franco et al., 2011; Di Franco & Guidetti, 2011; Figure 1). Since the timing of the sampling has been chosen in accord with the supposed settlement peak of each region (Di Franco et al., 2011; Di Franco & Guidetti, 2011), these observations should provide reliable information about the maximum spawning activities associated with each site and year. For each site, we derive a range of spawning dates (minimum and maximum) obtained by keeping 95% of a normal probability distribution adjusted on the spawning dates obtained thanks to otoliths' reading (see Table S1). We consider this range of spawning dates as the temporal duration of that distinct spawning event: as such, we run as many daily LFN experiments (characterized by a connectivity matrix attributed to each spawning date) as the number of days comprised within this period. For the LFN tracking-time, we retain the median of all observed PLDs (see Table S1) that have been also determined by otolithometry (Di Franco et al., 2011; Di Franco & Guidetti, 2011).

Based on the analytical framework developed by Legrand et al. (2019), the full dispersal information contained in the raw connectivity matrices must be pre-processed for our purpose. The first filter is applied on arrival nodes (note that in backward-in-time dynamics, they act as departure nodes) to consider only the surveyed settlement sites. To account for the coastal processes non-resolved by the AIREG model and to limit the impacts of 'beaching' artefacts, we retain here four nodes encompassing each sampled site and its vicinity (note that the mean land ratio of the retained four nodes is low and similar between sampling sites). The second filter, applied on departure nodes (becoming the arrival nodes in backward-in-time), simulates the suitable habitat of low-moving adult stage of *D. sargus*. Adults are generally associated to rocky substrate and *Posidonia oceanica* meadows (Guidetti, 2000) and have been observed at least until 80 m depth during the spawning period (Aspillaga et al., 2016; Giacalone et al., 2018). The filter is thus constructed by keeping all nodes that encompass those substrates and a conservative bathymetric limit that is shallower than 100 metres depth (see Figure 1). To do so, we exploit the hand-made corrected habitat maps published in Legrand et al. (2019) and the ETOPO1 Global Relief Model (National Geophysical Data Center, 2021). After applying both filters, each element of the filtered matrices represents the number of particles sent by the effective spawning habitat toward the surveyed settlement site.

The elements of such matrices can be readily transformed into dispersal probabilities thanks to a column-normalization of the number of particles, hence approximating backward-in-time dynamics (Legrand et al., 2019; Rossi et al., 2014; Ser-Giacomi et al., 2015). With this normalization, the diagonal elements of these matrices represent in our case the self-recruitment of the surveyed sites, described by Dubois et al. (2016) (based on Botsford et al., 2009). After the spatial filtering and the column-normalization, all daily matrices (i.e., 6 to 31 matrices, depending on the site considered) representative of a given surveyed site are weighted averaged into a unique composite matrix to obtain the total probability of all spawning nodes to send larvae into the surveyed settlement site during the entire spawning period (spanning 6 to 31 days). More specifically, the weight attributed to each daily matrix is determined according to the position

of the corresponding spawning date in the Gaussian distribution fitted on the total spawning period of each site (see Figure S1 and Table S1). Only non-zero elements of the composite matrix are kept, meaning that the retained spawning areas effectively deliver larvae to the settlement site. Overall, we delineate 11 spawning events composed of several nodes representing the spawning areas during their corresponding spawning period for each of the 11 surveyed settlement sites.

Finally, we gather all the temperature values simulated by the AIREG model (Ciliberti et al., 2015; Oddo et al., 2006) for depths ranging from 0 to 50 m within each previously identified spawning area for the entire effective spawning period. All those temperatures values are compiled into a single dataset while taking into account the larval contributions of each spawning node (e.g., dispersal probabilities are interpreted as proportion of larvae) to the settlement sites they replenished. Quantile values are then estimated using a kernel density estimation method (Simonoff, 1996). It allows retaining a 95% temperature interval that controls the spawning outbreak of *D. sargus* in the north western Mediterranean Sea. These favourable seawater temperatures are then used as a threshold for the broad-scale modelling exercise of spawning success (Figure 2; see Section 2.3).

2.3 | Inverse simulations of spawning success at broad scale

Building on the range of temperatures suitable for spawning, determined through a combination of modelling and field observations (see Section 2.2), we now investigate the spatio-temporal variability of spawning over the entire model domain over 10 years (2005 to 2014). In our inverse approach that considers non-varying habitats, the sources of variability affecting early-life stages are ocean currents, which control the backward-in-time dispersal from settlement to spawning areas, and seawater temperature, which governs where and when spawning occurs.

We performed LFN experiments every 5 days (Monroy et al., 2017) from 5 January to 29 June each year from 2005 to 2014 (available data of AIREG model; Ciliberti et al., 2015; Oddo et al., 2006). Consequently, we compute 36 connectivity matrices per year. The

conservative choice of the spawning period relies on the information gathered from the literature (Table 1), revealing that *D. sargus* spawning may occur as early as January and until June. Since Monroy et al. (2017) showed little to none effects of small PLD changes, we fix the PLD to 16 days, equal to the median PLD from individuals collected at all settlement sites (see Table S1; Di Franco et al., 2011; Di Franco & Guidetti, 2011). Note that some output files of the AIREG model are corrupted; as such, a few connectivity matrices (10/01, 15/01, 20/01, 25/01 and 30/01/2012) cannot be modelled so that year 2012 has only 31 matrices.

For each connectivity matrix, we apply the same habitat filter (e.g., *Posidonia oceanica*, rocks and maximum 100 m depth; see Section 2.2 and Figure 1) on both departure (i.e., spawning areas) and arrival (i.e., settlement areas) nodes to consider all possible spawning and settlement connections across the full domain (Figure 2). The habitat filter used for settlement is the same as the spawning one whereas, in nature, literature specifies that juveniles recruit between 0 and 2 m deep in sandy bays and rocky shores (Harmelin-Vivien et al., 1995; Lenfant & Planes, 1996). However, there is no continuous and reliable information about marine micro-habitats at basin-scale. Moreover, the spatial resolution of our approach is too coarse and the node surface too wide to allow distinguishing settlement sites at this scale. Therefore, based on data constraints we operate this choice to perform a filter of the potential settlement sites based on these depth and habitat. Then, we sum all the columns of each matrix into a vector (i.e., all the settlement nodes are now represented as one global settlement area). Each element of this vector gives the total number of particles sent by a given spawning node to the total settlement area over one spawning event. This vector is column-normalized to transform its elements into backward-in-time probabilities of 'physical connectivity', co-varying only with the oceanic circulation. They are interpreted as the probabilities for any node pertaining to the spawning habitat to send larvae into any of the favourable settlement sites for a given spawning event.

Then, for each non-zero element of a vector (meaning a physical connection exists between the corresponding pair of spawning and settlement nodes), we evaluate if surface and subsurface temperatures (from 0 to 50 m) encompassed in a given spawning node fall into the reference range of spawning favourable temperatures. More

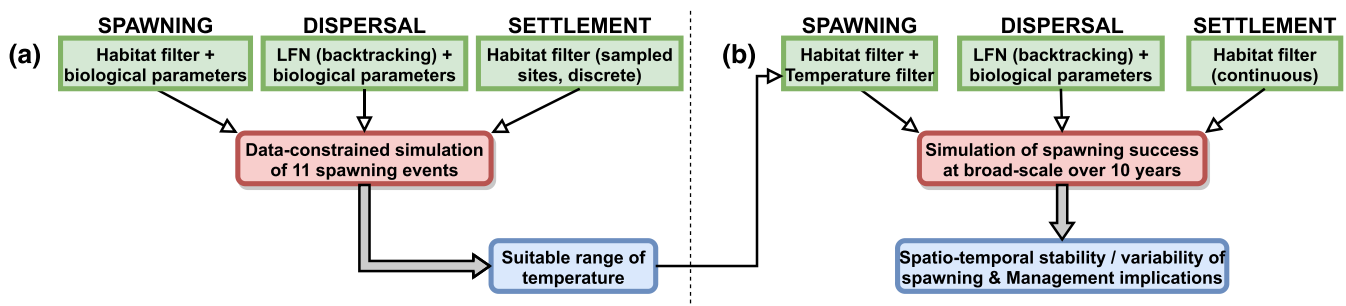


FIGURE 2 Schematic representation of the modelling approach for (a) the data-constrained simulation and (b) the inverse simulations of spawning success at broad scale. Green boxes identify the inputs of the numerical experiments represented by the red boxes. Blue boxes represent the analysed outputs of the study. A more detailed version of this figure is available in the supporting information (see Figure S2).

TABLE 1 Literature review reporting the minimum and maximum values of temperature (in °C) suitable for spawning and the favourable period (in month) for spawning documented for *Diplodus sargus* in the Mediterranean Sea.

Article	Minimum temperature	Maximum temperature	Minimum spawning date	Maximum spawning date
Aspillaga et al. (2016)	13	14.5	March	April
Di Lorenzo et al. (2014)	13	18	April	May
Mouine et al. (2007)	15	18	March	May
Mouine et al. (2012)	14.8	15.6	March	June
El Maghraby et al. (1982)	17	20	January	April
Benchalel and Kara (2010)	15	18	February	April
Man-Wai (1985)	14	16	April	May
Present study	14.8	20.6	January	June

Note: The last line reports the values derived from the present study.

specifically, we determine the ‘thermal niche’ probability as follows: a kernel density estimation has been fitted over the temperature distribution of each node and integrated between the bounds of the reference thermal range (i.e., we calculate the surface under the estimator, bounded by the temperature range; see Figures S2 and S3).

Finally, the ‘successful spawning probability’ for each node and for the 2005–2014 period/each spawning event is obtained by multiplying the ‘physical connectivity’ probability vector and the ‘thermal niche’ probability vector (Figure 2), considered independent (not shown). For each year over 2005–2014, we thus compute 36 vectors of probability of successful spawning (31 vectors for 2012), each of them representing a spawning event. Note that the range of successful spawning probabilities depends on the total number of nodes of the studied domain. Hence, our subsequent analyses disregard absolute probabilities but rather focus on highlighting and interpreting the relative differences among node probabilities. Note also that our ‘successful spawning probabilities’ comprehend how ocean temperatures control spawning and how ocean currents influence dispersal while it neglects the time and space variability of early-life stages natural mortality.

These vectors are further exploited by first averaging all events and all years and computing associated standard deviations to highlight spatial differences between regions potentially due to interannual or seasonal variability (see Figure 6). To dig into the origins of this variability, the ‘successful spawning probability’ vectors are also exploited by computing seasonally averages and associated standard deviations to observe if the variability is seasonal or if there are interannual differences in the spawning process according to the season and the region (see Figures S4 and S5). Moreover, the ‘successful spawning probability’ vectors are yearly averaged and their standard deviations computed to highlight spatio-temporal patterns between regions, according to the year without considering the seasonal aspect (see Figure S6). With all the ‘successful spawning probability’ vectors of all years, we run a non-normalized Principal Component Analysis on a data table composed with nodes as observations (1,500 nodes × 10 years) and 36 dates as variables (FactoMineR package/library on R version 3.6.0 by Lê et al., 2008). The 2D mapping of the principal components (coordinates of each node) allows to display the different years (yearly mean of the node coordinates). Note that the

unfavourable nodes with probabilities equal to zero for all years and events were removed from the Principal Component Analysis.

Finally, a model-based clustering (R package mclust by Scrucca et al., 2016) is implemented using the 10 first principal component coordinates accounting for about 80% of the entire variability. The selection of a small number of node clusters in which spawning is expected to have the same pattern over time is operated using a BIC criterion. These clusters highlight the dynamical behaviour of spawning probabilities through years and thus show potential interannual stability of some areas (Figure 2). Our objective is to highlight and categorize the spatio-temporal windows suitable for spawning. Consequently, the unfavourable nodes with probabilities equal to zero for all years and events were removed from the analysis.

3 | RESULTS

3.1 | Data-constrained simulation

Discrete spawning areas are simulated, along with the respective larval contribution of each node to the total larval pool, through backtracking experiments using the LFN model for each of all settlement sites sampled in 2008 (Figure 3) and 2009 (Figure 4). In the Adriatic Sea, our model suggests that Apulian juveniles settled in 2009 (light blue dots for sites 1 to 7 in Figure 1 and red-edged nodes in Figure 4) originated mostly (90% to 100% of the larval contribution) from nearby spawning areas located along the Apulian shores, more or less north-westward of each settlement site. The same pattern occurred in 2008 for Torre Guaceto, with few additional larvae (less than 10%) coming from the south (Figure 3d). In the Ligurian sea, our model simulates that the spawning areas situated south-eastward of Genova are the main contributors ($\approx 75\%$) of this settlement site in 2008, while a relatively small proportion ($\approx 25\%$) of propagules were released westward of Genova (Figure 3a). In the Tyrrhenian sea, the Maratea settlement site was replenished equally by the northern ($\approx 50\%$) and southern ($\approx 50\%$) spawning areas surrounding the settlement site (Figure 3b). For San Isidoro, the larvae would have been released from Southern Apulia following the coastline (Figure 3c).

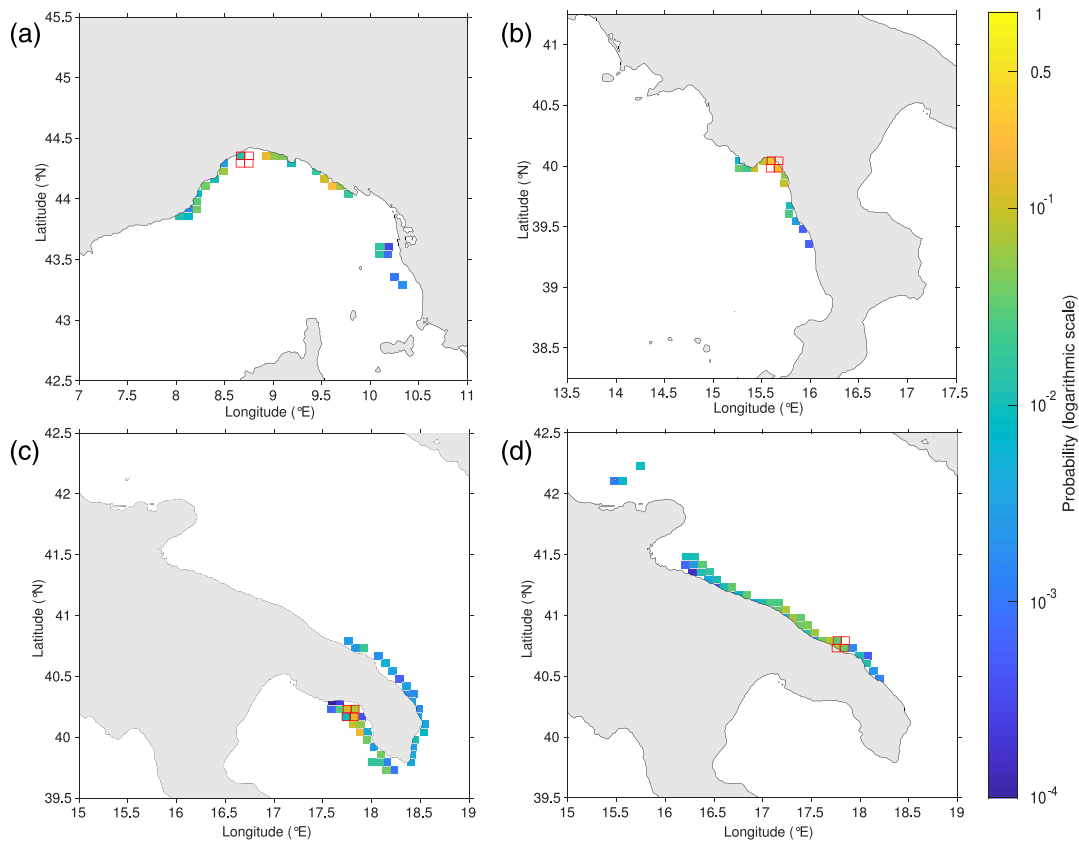


FIGURE 3 Backtracked spawning areas and associated probabilities of larval replenishment for four spawning events inferred from the post-settlers sampled in 2008 around (a) Genova; (b) Maratea; (c) San Isidoro; and (d) Torre Guaceto (see also Figure 1). The red-edged nodes represent the settlement sites.

Concerning the node-specific probabilities of larval replenishment, which can also be interpreted as larval contribution, the minimum is 10^{-4} , and the maximum is around 0.5 for both years while probabilities are not equally distributed over space. For most sites, a few nearby nodes constitute the main suppliers (probabilities spanning 0.1 to 0.5, yellowish colours; Figures 3 and 4) while a large proportion of widespread nodes act as minor but significant contributors (probabilities lower than 0.1). Note that some rather distant nodes constitute non negligible suppliers despite their weak contribution (from $\approx 10^{-3}$ to 3.10^{-1}). For instance, the Tremiti Islands (42.1° N, 15.6° E) and the inner Gulf of Manfredonia (41.5° N, 16.3° E) significantly replenish the Apulian sites (Figures 3d and 4). Similarly, the distant contributors localized on the Eastern side of Apulia contributes noticeably to the replenishment of San Isidoro (Figure 3c). Overall, the spawning contribution of the settlement nodes to themselves, which is equivalent to self-recruitment (Botsford et al., 2009; Dubois et al., 2016), is usually low ($<10^{-2}$), especially in 2009. Note however that the self-recruitment of Maratea and San Isidoro in 2008 (Figure 3b,c) is notably high (around 0.1). Furthermore, the locations of the main spawning areas (nodes with higher probabilities) replenishing Torre Guaceto vary among years, as this site was sampled twice (Torre Guaceto, Figure 3d for 2008 and Figure 4d for 2009). It shows that the spatial extent and larval replenishment probabilities of spawning

areas vary among eco-regions, exemplifying a substantial spatio-temporal variability of the spawning process.

When compiling all the modeled temperatures extracted from the specific dates and locations defined by the 11 backtracked spawning areas for depth spanning 0 to 50 m, we find a range of temperature with a minimum around 13°C and a maximum of 24°C (Figure 5a). A total of 95% of temperature values that are suitable for spawning range between 14.8°C and 20.6°C (Figure 5b). This data-constrained range of seawater temperatures is then used as a threshold triggering spawning in the following section.

3.2 | Simulated spawning success at broad-scale

3.2.1 | Inter-annual variability

Adopting an inverse modelling approach, we now identify spawning areas and their associated larval contributions at broad-scale over a 10-year period for all potential *D. sargus* populations inhabiting our domain of interest (see Figure 1). The 10-year averages of spawning success (Figure 6a) are analysed along with the standard deviation (Figure 6b) to highlight spatial patterns and assess their inter-annual variability.

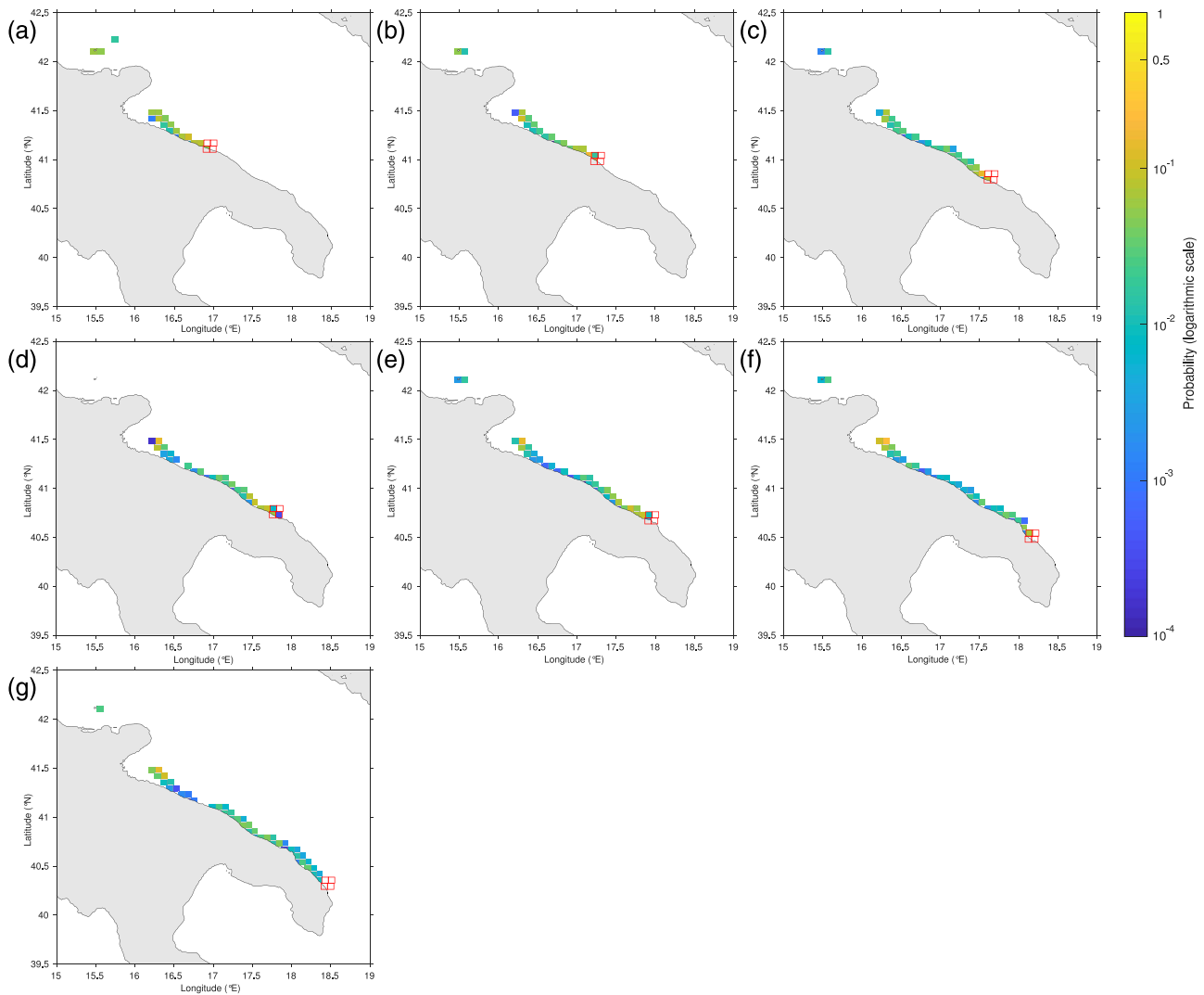


FIGURE 4 Backtracked spawning areas and associated probabilities of larval replenishment for seven spawning events inferred from the post-settlers sampled in 2009 around (a) Bari; (b) Monopoli; (c) Hotel La Darsena; (d) Torre Guaceto; (e) Punta Penne; (f) Casalabate; and (g) San Andrea (see also Figure 1). The red-edged nodes represent the settlement sites.

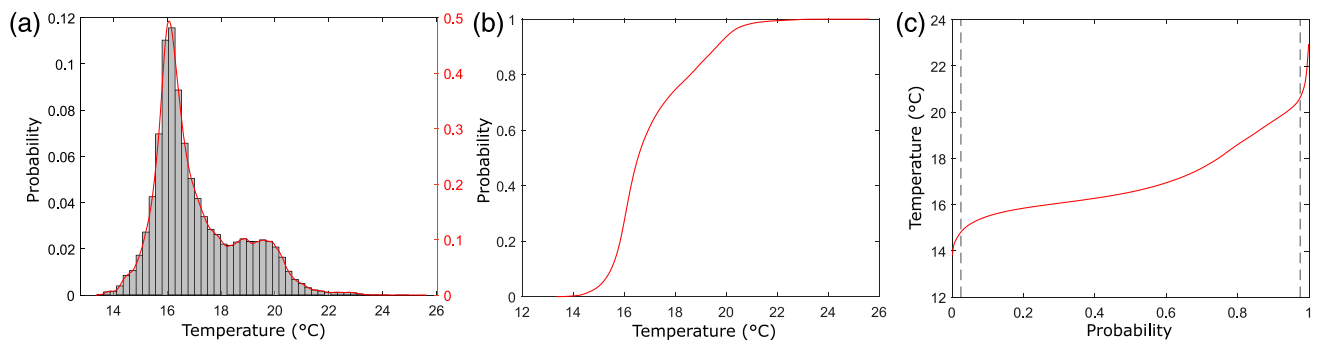


FIGURE 5 (a) Kernel density function (red line) fitted on the histogram (grey bars) of modelled temperatures extracted from the 11 discrete spawning areas. (b) Corresponding cumulated probability distribution function (red line). (c) Corresponding quantile function (red line) with the 2.5th and 97.5th quantiles (dotted dark lines) used to determine the temperature range triggering spawning.

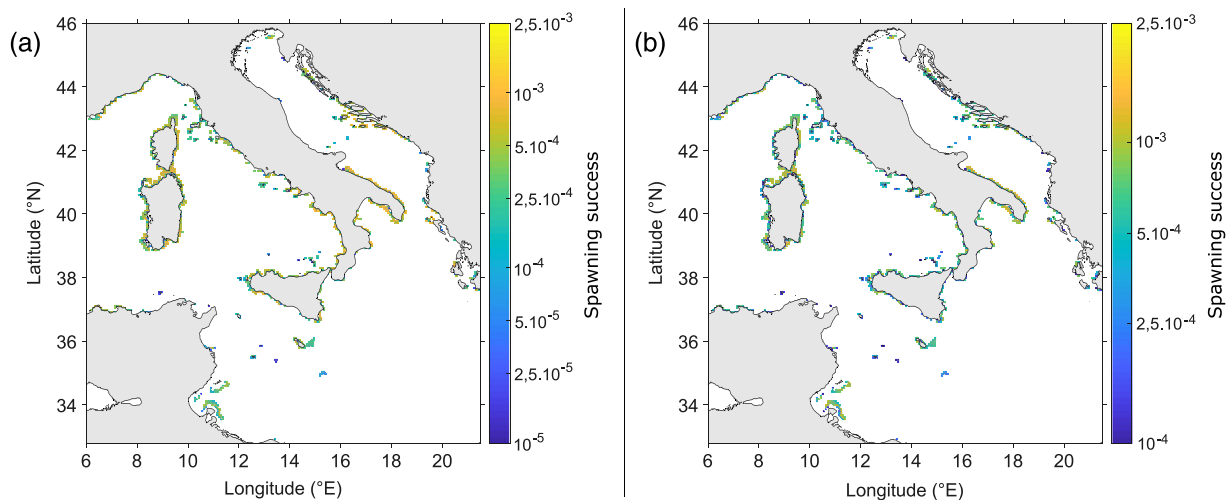


FIGURE 6 Total (10-year) (a) average and (b) standard deviation of successful spawning probabilities (logarithmic scale) over 2005–2014 considering all 36 spawning events simulated each year from January to June.

High averaged probabilities of larval replenishment (around 10^{-3}) are modelled in the Croatian Islands and on both sides of Calabria (Figure 6a) with moderate variability (around 5.10^{-4} , Figure 6b). Similar mean values are visible on both sides of Apulia, in Eastern Corsica and Eastern Sardinia, combined with high variability (standard deviation around $2.5.10^{-3}$, Figure 6b). Low probabilities (from 10^{-5} to 10^{-4}) appear around the islands of the Siculo-Tunisian Strait (Figure 6a), associated with very little variability around 10^{-4} (Figure 6b). Thus, the situation is rather contrasted with the emergence of high (low, respectively) means that are not necessarily associated with high (low, respectively) variability. This conclusion highlights the necessity of disentangling further the temporal variability into seasonal and interannual signals to better evaluate how they manifest themselves over space.

The Principal Component Analysis run on the spawning success probabilities of 36 yearly events over 10 years reveals that both first axes explain 54% of the inter-annual variability of spawning success (Figure 7a). 2007 and 2012 emerge as the most contrasted years while a sub-group encompasses 2008/2014 and another larger one concerns 2005/2006/2009/2010/2013. 2007 appears as a very particular year and seems to represent, along with 2012 that is closer to the other sub-groups, a great part of the variability of both first and second dimensions. The main reason behind this interannual structuring could be the magnitudes of probabilities, 2007 being a year with particularly high mean probabilities across the entire domain and the whole studied period (around 10^{-3} , Figure 7b) as compared with other years such as 2012 (Figures 7c and S6).

3.2.2 | Intra-annual variability

Intra-annual variability of spawning success is analysed using climatological averages (see Figure S4) and associated standard deviations (see Figure S5) by considering the 10 yearly replicates for each of the

36 events spanning January–June. Overall, the probability associated to an area is strongly dependent on the date (see Figure S4). In fact, average probabilities over most of the domain are quite high in January ($\approx 5.10^{-4}$) and then decrease to the lowest values around February and March ($\approx 2.5.10^{-5}$), except in Apulia where it remains elevated in late winter. Then, spawning success probabilities rise nearly everywhere from April until mid-June (up to $2.5.10^{-3}$) and then decrease rapidly, especially in Apulia, Gulf of Gabes and Toscana. Apulia, Eastern Calabria, Corsica and Sardinia are the sub-regions where intra-annual variability is the highest ($\approx 10^{-3}$; see Figure S5). March appears as a stable month with the lowest variability on the whole domain (less than $2.5.10^{-4}$). On the contrary, there is a high variability from April to mid-June (around 10^{-3}) and then this variability decreases.

3.2.3 | Clustering of spawning areas

The Model-Based Clustering methodology defines in an objective manner 4 clusters, that are sub-groups of nodes sharing similar magnitude and intra-annual variability of the spawning success probabilities. Each cluster is described by a specific intra-annual cycle of the spawning success on the studied period (Figure 8). For each year, all the nodes with the cluster they belong to are represented in the Figure S7. Clusters 1 and 4 characterize areas with elevated spawning potential from late March to the end of June, peaking at mean values of around 10^{-3} from mid-April to the end of May. Cluster 4 is unimodal with a unique spawning peak in late season, contrarily to the bi-modality of cluster 1 that also presents an early spawning peak in winter (January to mid-February). As both previous clusters, cluster 3 characterizes areas with a late spawning success, peaking from the end of March to the end of July but with weaker probabilities (mean of about $2.5.10^{-4}$). Moreover, it is worth noting that the seasonal cycles reported in Figure S4 are consistent with those revealed by

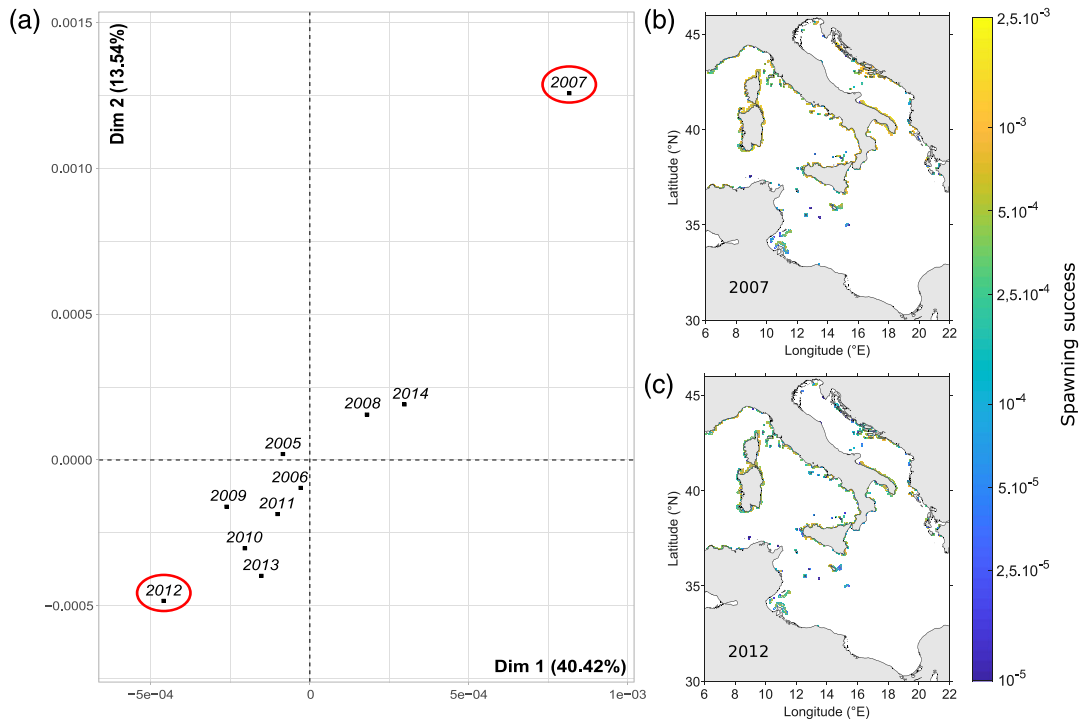


FIGURE 7 (a) 2D-mapping of the Principal Component Analysis of the spawning success probabilities. Displayed years correspond to the mean coordinates of all nodes belonging to a given year. Spatial representation of the yearly mean spawning success probabilities (logarithmic scale) for the most contrasted years: (b) 2007 and (c) 2012. Yearly mean maps for the remaining years are reported in Figure S6.

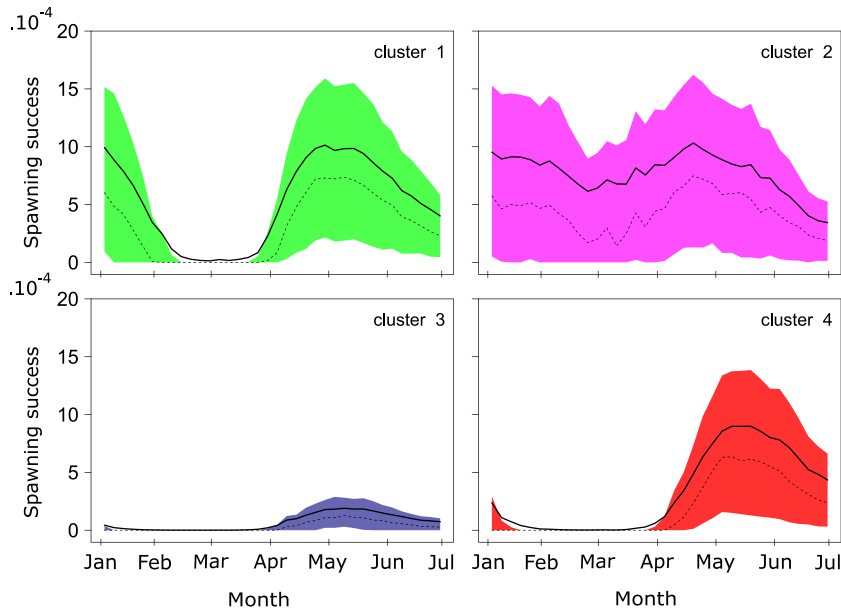


FIGURE 8 Intra-annual cycles of the spawning success probabilities for the four clusters obtained thanks to the Model-Based Clustering. The coloured shading represents the 0.25 and 0.75 quantiles, the black dot line is the median and the black bold line is the mean. The colours are used in the following to identify the clusters.

clusters 1, 3 and 4 with very weak to null spawning success around February to April and very low variability (see Figure S5), followed by high spawning success, with high variability, until the end of June. Cluster 2 represents areas characterized by elevated spawning potential pretty much over the whole studied period (January to June average is around 10^{-3} ; Figure 8) but with high variability throughout the

spawning season. The probabilities and the variability are decreasing from about early May to the end of June, but the exact duration of the spawning period is too difficult to forecast for this cluster due to its high variability over the studied period.

We now analyse the spatial distribution of the four clusters, representative of four seasonal modalities of spawning success. Each

node belonging to a given cluster, one can investigate at which frequency a node is objectively characterized by the same cluster across years. We set an arbitrary threshold to distinguish the discrete spawning areas whose seasonal behaviour is consistent from one year to another, from those whose seasonality varies at inter-annual time scales. In other words, the nodes whose cluster frequency is lower than 0.7 are subjected to prominent inter- and intra-annual variability; conversely, nodes characterized by cluster frequency greater or equal to 0.7 can be considered with relatively stable seasonal behaviour across years. The coloured nodes displayed in Figure 9 represent the spawning areas whose simulated success is highly stable across years, representing about 50% of all discrete spawning areas. Northern Sicilia, Western Calabria and Apulia are characterized by cluster 1. Cluster 2 describes the coastal areas of Albania and Greece with high variability over the entire studied period. Corsica, Sardinia, Liguria and Toscana are mainly represented by both clusters 3 and 4, thus sharing the same seasonal cycle of late spawning success with low or high probabilities, respectively.

4 | DISCUSSION

4.1 | Abiotic and biotic factors affecting spawning

Using the white seabream *Diplodus sargus* in the central Mediterranean Sea as a case study, we investigate the role of seawater temperature in controlling broad-scale spawning onset and duration of coastal fish by identifying the suitable temperature range for spawning while ensuring that spawning and settlement areas are effectively connected by oceanic dispersal. The key role of

temperature for triggering spawning has been indeed already documented in previous research (Table 2; see 'Temperature' row). Literature also suggests that spawning can be affected by multiple other abiotic or biotic factors (Table 2). Some papers focus primarily on abiotic factors (Table 2), such as oceanic temperature, upwelling, photoperiod, solar irradiance, lunar cycle (also linked to tides) and daylight/dark diurnal alternation. These studies often discuss the physiological internal processes (feeding status, gonad maturation) which would explain how environmental forcing somehow indirectly control fish spawning behaviour. Other studies focus on biotic factors (Table 2) at both population, such as demography and inter-specific competition, and individual levels, such as feeding status through lipid storage.

Here, we specifically focus on temperature as this abiotic factor has been predominantly reported as crucial in the compiled literature, comparatively with other factors (see Table 2). While this overrepresentation might originate from a publication bias, it is easily ruled out by some multi-factorial studies that reported major influences of seawater temperature on spawning as compared to other factors, such as photoperiod or lunar cycle, especially in the Mediterranean (De Vlaming, 1972; Hereu et al., 2006; Potts et al., 2014; Sheaves, 2006). More generally, this is consistent with the key role of seawater temperatures in driving major ecological patterns in the global ocean, such as fish biodiversity and dynamics (Burrows et al., 2019; Tittensor et al., 2010). The current warming trend of the coastal ocean due to climate change (Lima & Wethey, 2012; Liao et al., 2015) thus raises concerns about possible temporal and spatial shifts of spawning for coastal fishes, as already observed in demersal fish such as cod *Gadus morhua* and sole *Solea solea* (Auth et al., 2017; Fincham et al., 2013; McQueen & Marshall, 2017). Our modelling framework, which has been especially designed to consider the full environmental

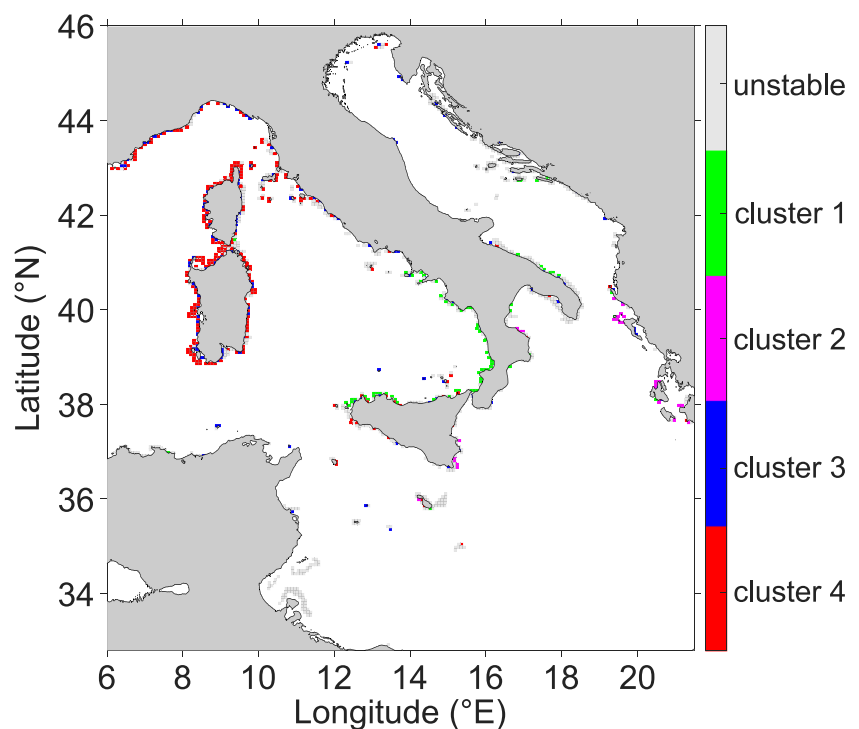


FIGURE 9 Spawning areas whose intra-annual variability (see also Figure 8) is stable across years (i.e., whose cluster frequency is greater or equal to 0.7) are coloured according to the cluster they belong to. Light grey nodes represent the overly variable spawning areas (i.e., whose cluster frequency is lower than 0.7).

TABLE 2 List of factors influencing the spawning process of Teleosts (in blue: of Sparids only) according to a literature review

Factors	Species	Areas	Articles
Temperature	Teleosts	Victoria, Australia	King et al. (2016)
	<i>Clupea harengus</i>	Newfoundland, Canada	Winters and Wheeler (1996)
	<i>Pseudogobius olorum</i>	Western Australia, Australia	Gill et al. (1996)
	Teleosts	Oregon, USA	Auth et al. (2017)
	<i>Solea solea</i>	Irish sea, North Sea, Channel	Fincham et al. (2013)
	<i>Epinephelus marginatus</i>	Medes Islands MPA, Catalonia, Spain	Hereu et al. (2006)
	<i>Gadus morhua</i>	North Sea, Scotland	McQueen and Marshall (2017)
	<i>Thunnus thynnus</i> , <i>Auxis rochei</i> , <i>T. alalunga</i>	Balearic archipelago, Spain	Reglero et al. (2012)
	Sparidae	Meta-analysis	Sheaves (2006)
	<i>D. sargus</i> subspecies	Meta-analysis	Potts et al. (2014)
	<i>D. sargus</i> , <i>D. annularis</i> , <i>D. puntazzo</i> , <i>D. vulgaris</i>	Gulf of Tunis, Tunisia	Mouine et al. (2011)
	<i>D. cervinus cervinus</i>	Canarian archipelago, Spain	Pajuelo et al. (2003)
	<i>D. vulgaris</i>	Canarian archipelago, Spain	Pajuelo et al. (2006)
	<i>D. puntazzo</i>	Canarian archipelago, Spain	Pajuelo et al. (2008)
	<i>D. vulgaris</i>	South Western Portugal	Gonçalves (2000)
	<i>D. sargus</i>	Azores archipelago, Portugal	Morato et al. (2003)
<i>D. sargus sargus</i>	Gulf of Tunis, Tunisia	Mouine et al. (2007)	
<i>D. sargus sargus</i>	Torre Guaceto MPA, Puglia, Italia	Di Lorenzo et al. (2014)	
<i>D. sargus</i>	Medes Islands MPA, Catalonia, Spain	Aspillaga et al. (2016)	
Photoperiod	Teleosts	Meta-analysis	De Vlaming (1972)
	<i>Lepomis macrochirus</i>	Story County, Iowa, USA	Mischke and Morris (1997)
	<i>Dicentrarchus labrax</i>	West Coast of Portugal	Vinagre et al. (2009)
	<i>D. vulgaris</i>	South West Coast of Portugal	Gonçalves (2000)
	Sparids	Meta-analysis	Sheaves (2006)
Irradiance	<i>D. vulgaris</i>	South West Coast of Portugal	Gonçalves (2000)
Moon / Tide	<i>Cheilinus undulatus</i>	Republic of Palau	Colin (2010)
	<i>Paracirrhites forsteri</i>	Kuchierabu-jima Island, Japan	Kadota et al. (2010)
	<i>Takifugu niphobles</i>	Kyushu Island, Japan	Yamahira (1997)
	<i>Epinephelus marginatus</i>	Medes Islands MPA, Catalonia, Spain	Hereu et al. (2006)
	<i>Thalassoma bifasciatum</i>	Puerto Rico	Appeldoorn et al. (1993)
	<i>Acanthopagrus pacificus</i>	Queensland, Australia	Sheaves and Molony (2013)
	<i>Acanthopagrus berda</i>	Kosi estuary, South Africa	Garratt (1993)
Dark / Night	<i>Osmerus mordax</i>	Newfoundland, Canada	Bradbury et al. (2004)
	<i>Acanthopagrus berda</i>	Kosi estuary, South Africa	Garratt (1993)
Upwelling	<i>Centroberyx gerrardi</i>	South-Western Australia	Coulson et al. (2019)
	Sardinops, Engraulis	California, USA	Lluch-Belda et al. (1991)
Demography	Teleosts	Meta-analysis	Wright and Trippel (2009)
Lipid storage	<i>Gambusia affinis</i>	Illinois, North Carolina, New Jersey, USA	Reznick and Braun (1987)
Competition	<i>D. annularis</i> , <i>D. sargus</i> , <i>D. puntazzo</i> , <i>D. vulgaris</i> , <i>Oblada melanura</i> , <i>Sarpa salpa</i>	Marseille, France	Harmelin-Vivien et al. (1995)
	<i>D. puntazzo</i> , <i>D. sargus</i> , <i>D. vulgaris</i>	North-West Mediterranean Sea	Planes et al. (1999)

variability of both ocean temperatures and currents in evaluating spawning success, could be used to predict future changes as well as to guide future sampling efforts.

Our findings highlight a range of seawater temperatures suitable for spawning (14.8–20.6° C; see Section 3.1) that is consistent with

the ranges compiled from the literature, especially for the minimum temperature (Table 1). The small mismatches between our range derived from modelled temperatures over multiple depths and those already published (Table 1) may result from their exclusive use of Sea Surface Temperature, despite the fact that the vertical distribution of

coastal fishes when living and/or spawning is much higher than just the sea surface (Aspillaga et al., 2016; Giacalone et al., 2018). Moreover, the surprisingly good agreement for the lower temperature threshold that triggers spawning may be partly explained by the fact that the spawning onset and associated temperatures are often derived from observational studies of juveniles targeting especially the supposed settlement peak (Table 1; Di Franco & Guidetti, 2011). On the other hand, the upper thermal range is slightly higher than previous estimates, suggesting that our approach may slightly overestimate the spawning duration. While this flaw would especially concern the warmer eco-regions (e.g., Gulf of Gabes) during the late spawning season (May/June), observations show that some spawning events have indeed occurred in these space/time windows (Benchalel & Kara, 2010; Morato et al., 2003). It is worth noting that the cessation of spawning could also be related to a combination of both external (environmental) and internal (biological) factors. In fact, some fishes could have stopped spawning after a certain duration of active spawning not necessarily due to non-favourable abiotic factor but rather due to biological limitations such as spent gonads (Mouine et al., 2012) or behavioural cessation of spawning aggregation (Aspillaga et al., 2016; Colin, 2010). Overall, it suggests that the control exerted by oceanic temperature on the spawning process may be more relevant to simulate the spatio-temporal variations of its onset rather than its termination.

Furthermore, detailed analyses of temperatures for 2008 and 2009 spawning events point out different suitable temperatures: mean optimal temperatures are around 18° C for all the sites of 2008 and around 16° C for all those of 2009. This could be explained by the different sampling design between 2008 (four sites relatively well scattered across the studied domain) and 2009 (seven sites, all located in Eastern Apulia). These regional differences of triggering temperatures could suggest local adaptation (Takahashi et al., 2012) but the small statistical samples prevent any further analyses. Considering PLD, some studies also highlight differences in dispersal time for *Diplodus sargus*. In fact, analysing early-life traits of *D. sargus* settlers in Marseilles (France) in 1994 and 1995, Vigliola (1998) find a mean PLD that is considerably higher than the one used in the present study (i.e., 28 vs. 16 days). Rossi et al. (2019) observe even higher PLD with a mean of 40 ± 5 days and ranging from 32 to 56 days in Corsica but explain this difference by the length of the fish at sampling (longer than 1 cm). In Spain, Macpherson and Raventos (2006) and Raventos et al. (2021) find PLD ranging from 19 to 37 days (mean 27.6 ± 4.3 days) and from 14 to 32 days, respectively. The last study points out the effect of temperature in reducing the larval dispersal time. It is worth noting that other biological and environmental conditions, such as the saturation of the settlement habitat by juveniles from a same batch of larvae, a limited intra-specific competition for settlement (Di Franco et al., 2013) and local hydrodynamics (Cuadros et al., 2018), could also be responsible for the variations of observed PLDs between these studies. Finally, the differences between the PLD ranges found in literature and ours could be linked to the number of samples collected. Hence, expanding our study to other areas and other years with more numerous observations could help studying the spatio-temporal variability of these early-life traits.

4.2 | Disentangling the spatial and temporal variability of spawning

4.2.1 | Spatial variability of backtracked spawning areas

Backtracking model experiments constrained by settlers observations (Calò et al., 2018; Legrand et al., 2019) allow us to characterize several discrete spawning events by well-delineated areas associated with their respective contribution to the larval replenishment of 11 settlement areas, considered here (Di Franco et al., 2011; Di Franco & Guidetti, 2011). Their spatial locations and relative larval contributions can be reasonably well explained by both local and regional hydrodynamics and topography.

Our model identifies the spatial locations of the major spawning areas (i.e., highest probabilities) within the pathways of surface currents prevailing in the region (Millot & Taupier-Letage, 2005; Poulain et al., 2013), generally upstream from their settlement locations. Once released off Livorno and La Spezia, fertilized eggs and larvae tend to follow the Liguro-Provençal current toward the Genova settlement site (Figure 3a). In the Tyrrhenian Sea, the influx of Atlantic Water entering from the Sardinia Channel (Iacono et al., 2021) carries propagules in a counter-clockwise direction following the shorelines of western Calabria up to Maratea (Figure 3b). In the Gulf of Taranto, the San Isidoro settlement site is replenished thanks to a coastal current that originates from the southern Adriatic Sea and then circles around the Salento peninsula while being pushed westward by the North Ionian Gyre (Crisciani & Masetti, 2016; Gačić et al., 2010; Figure 3c). Finally, the south-westward coastal current in the Adriatic Sea is the main contributor to the Apulian settlement sites sampled in 2008 and 2009 (Figures 3d and 4), which is in good agreement with Pujolar et al. (2013), Bray et al. (2017) and Legrand et al. (2019).

Counter-intuitively, some minor spawning areas (i.e., lowest probabilities) are found downstream for Genova, Maratea and Torre Guaceto in 2008. These more complex patterns can be caused by seasonal slowdowns of the main currents, by the presence of mesoscale eddies creating turbulent and anisotropic dispersal or by coastal counter-currents creating small-scale recirculation patterns (Millot & Taupier-Letage, 2005; Poulain et al., 2013). The remarkably elevated self-recruitment modelled in Maratea and San Isidoro (Figure 3b,c) could thus be linked to local hydrodynamics causing high residence times (Hernández-Carrasco et al., 2013). Moreover, the settlement site of Torre Guaceto was sampled in both 2008 and 2009 (Figures 3d and 4d), returning different spawning dates and spatial distribution of backtracked spawning areas. It exemplifies the substantial inter-annual variability of hydrodynamics that could be linked to the current reversal of the North Ionian Gyre occurring between these years (Crisciani & Masetti, 2016; Gačić et al., 2010).

Concerning the levels of contribution, a general pattern is that the closest to the settlement area, the highest the larval contribution for Maratea and San Isidoro in 2008 (Figure 3b,c). It can be related to the relatively short PLDs of *D. sargus* and the sluggish circulation in these regions, resulting in limited dispersal. Note that the probabilities

reported here must be interpreted with caution as we assumed similar larval production in each spawning area. In other words, the spatial heterogeneity of larval contributions originates essentially from the effective connectivity (controlled by ocean currents) between spawning and settlement areas. Since the mean number of fish eggs produced by mature adults is proportional to the size of the individuals (Lester et al., 2009), spatially explicit quantitative information about adult biomasses, or directly about eggs production (Blanco et al., 2017), could help improving the accuracy of our simulations in the future. Even without this valuable information, a more affordable improvement could be to scale the larval production of each spawning node according to its protection status, as done in Legrand et al. (2019). Indeed, current MPAs are expected, when effectively managed and enforced, to host bigger individuals producing large number of eggs (Di Franco et al., 2012; Marshall et al., 2019) that could act as effective sources of propagules for surrounding unprotected populations. Some distant sources highlighting weak but non negligible larval supply to the settlement site, such as Tremiti Islands (42.1° N, 15.6° E; Figures 3d and 4), could thus contribute to a higher level of larval replenishment than what is initially expected because they are protected by an effective MPA.

4.2.2 | Spatio-temporal variability of simulated spawning success

The results of Section 3.1 are constrained by data (different PLDs and spawning periods); thus, they are more likely to represent various spatial extents and larval contributions of the spawning areas. Hence, in Section 3.2, we decide to fix the PLD (median of all the data) and the spawning period (based on literature) to avoid the effect of intra-individual variability of these traits on the modelling. In fact, one of the overarching goals of this study is to evince how the variability of oceanographic processes, namely, hydrodynamics and seawater temperatures, affects the simulated spawning success in order to draw more general conclusions applicable to other oceanic systems.

Globally, our model suggests that there are two peaks of favourable conditions for spawning to occur: January to early/mid-February and from April to June for all clusters, primarily due to suitable temperatures for spawning during these periods. Beyond too simplistic latitudinal patterns, note that the early occurrence of suitable conditions for spawning concerns not only the most southern locations (e.g., Gulf of Gabes, also backed-up by observations of mature spawners during winter by Benchalel & Kara, 2010 or Mouine et al., 2007 in Algeria) but also more septentrional locations (such as Sicily and Southern Italy), suggesting the need to collect field observations earlier in the season in these regions. For clusters 1, 3 and 4 (as well as for cluster 2, to a lesser extent), our results suggest weak to null spawning success from early February to March, which seems to be due to seawater temperature lower than the suitable range (i.e., <14.8° C) in these areas. This bi-modality of the simulated spawning success could be explained by the general seasonal cycle of oceanic temperatures that is slightly delayed as compared to air temperatures: coldest sea

temperatures occur in late winter/early spring while air temperatures are already warming up. The non-favourable conditions simulated from February to April are probably linked to deep convection and dense water formation events that have been documented in the southern Adriatic and the Ligurian sea (Millot & Taupier-Letage, 2005).

More specifically, south-eastern Sicily, Greece and Albania are represented by cluster 2. For this cluster, the period between February and April exhibits lower spawning success (but still positive) than the early and late peaks. It suggests that temperature rarely goes below the prescribed threshold in these regions (far from the deep water formation areas) and that the small variations could be due to the variability of ocean currents. These areas are indeed characterized by highly turbulent mesoscale circulation such as the North Ionian Gyre and the Mid-Ionian Jet (Millot & Taupier-Letage, 2005; Poulain et al., 2012).

Cluster 4 represents areas in Ligurian Sea, Corsica, Sardinia, Toscana and French Riviera, which seem more impacted by temperature due to higher latitudes. The Ligurian sea is characterized by the Northern Current and is also known for deep-water formations (Poulain et al., 2012) which, along with the latitude, could explain why cluster 4 prevails in the Ligurian sea whereas cluster 1 predominates in the Tyrrhenian Sea (e.g., North Sicily, Calabria and Campania). In fact, this relates to the influx of warmer Atlantic waters coming from the Algerian Current: a major part, known as the Atlantic-Ionian stream, goes through the Siculo-Tunisian Strait to warm-up the southernmost locations (e.g., Gulf of Gabes) while another smaller contribution invades the Northern Sicily coastlines and the rest of the Tyrrhenian Sea (Iacono et al., 2021; Millot & Taupier-Letage, 2005; Poulain et al., 2012). Note that the large variability of the Atlantic-Ionian stream may also explain why the spawning success is characterized by unstable clusters in the Siculo-Tunisian Strait.

In fact, the Siculo-Tunisian Strait region is known to present particularly high eddy kinetic energy due to the presence of the particularly unstable Atlantic-Ionian stream (D'Ovidio et al., 2004), explaining why the spawning success probability is very low due to non-favourable dispersal routes that poorly connect spawning and settlement areas (Cuttitta et al., 2016; Figure 6a). Moreover, the regular coastal upwelling occurring on the western coast of the Sicily (Piccioni et al., 1988) could play a role too but its effect on the spawning success probability is difficult to disentangle from the influence of the Atlantic-Ionian stream in this region. More local analyses on spawning and larval dispersal, as realized by Cuttitta et al. (2016), could help to further understand the coupled bio-physical processes occurring in the region. On the other hand, the high variability of the spawning success in the Gulf of Gabes (unstable interannual clusters; see Figures 9 and S7) could be explained by a quick rise of the temperature and the large air-sea interactions (e.g., evaporation and heat fluxes) enhanced by the very shallow bathymetry in this region.

Finally, cluster 3 is found around some islands of the Siculo-Tunisian Strait and in Aeolian Islands (38.7° N, 15° E), which are highly turbulent areas. This cluster is represented by a very weak peak from April to June, however temperature is in the good range in the concerned regions (Figure 8), but the high variability of currents in these areas could be responsible of the limited connectivity among

spawning and settlement areas. On the other hand, clusters 3 and 4 are interlocked in the same areas (Ligurian Sea, Corsica, Sardinia, French Riviera, Toscana; see Figure 9) with cluster 3 appearing regularly in similar nearshore areas. These patterns could be a methodological artefact and must be interpreted with caution as these nodes present a mean land ratio of 0.75 (i.e., meaning that three quarter of the node is represented by land) due to the poor resolution of the ocean model around these complex coastlines.

Despite intricate spatio-temporal variations, we also highlight high probabilities and high variability of spawning success in the Adriatic, especially in Apulia and in Croatian Islands (Figure 6), supported by the unstable interannual clustering (Figures 9 and S7). For the Croatian Islands, this pattern can be explained by a shallow bathymetry (<100 m depth) and sluggish circulation probably implying a quick rise of temperature in these areas. Concerning Apulia, Gačić et al. (2014) studied the BiOS (Adriatic-Ionian Bimodal Oscillating System), which is a regime-shift of the North Ionian Gyre occurring at inter-annual/decadal time scales, modifying the regional-scale currents, including at the entrance of the Adriatic Sea (Crisciani & Masetti, 2016; Gačić et al., 2010). Those circulation changes could partly explain the inter-annual variability of spawning highlighted here. In fact, the path of the waters entering the Adriatic through the Strait of Otranto can considerably vary from one year to another as a function of the BiOS regime, leading to large variations in temperature and salinity (Gačić et al., 2013). When the gyre is anticyclonic (e.g., 2007–2008), the waters come from the Atlantic-Ionian stream and the Levantine waters originate from the west. When the regime is cyclonic (e.g., 2012–2013), the waters are directly coming from the Levantine Sea located to the South-East of the Adriatic Sea (Gačić et al., 2010). Consequently, it could be more or less favourable for spawning, depending on the BiOS regime.

Moreover, Gačić et al. (2014) observe a transition from cyclonic to anticyclonic circulation during 2005–2006, which is consistent with the central positions of both years in Figure 7a. In accord with the prominence of anticyclonic circulation during 2007–2008, years 2007 (and 2008, to a lesser extent) appear in the upper right corner of Figure 7a. It is characterized by extreme positive values for both dimensions and by the highest probabilities over the entire domain (Figure 7b). Thereafter, a second reversal of the basin-wide circulation occurs in 2009/2011, potentially explaining why these years are close to the centre of Figure 7a. Years 2012/2013 are characterized by negative values for both dimensions (lower left corner, Figure 7a), which is coherent with the prevailing cyclonic circulation during this period. Moreover, 2012 has been described as a very harsh winter by Gačić et al. (2014), probably explaining the lowest negative values for both dimensions (Figure 7a) and the very low probabilities of spawning success (Figure 7c). While the very specific position of year 2012 could have been slightly affected by the lack of five dates in January, it is likely that the main conclusions still hold since these dates are characterized by very low probabilities during the other years (see Figure S4).

Overall, our results suggest that colder and longer winters than average, as monitored by the BiOS index, are deleterious for the spawning success in our studied domain while warmer and milder winters than average are favouring spawning success at regional scale. In

fact, cluster 2, characterized by favourable spawning success over the entire season, is predominant over year 2007 (see Figure S7), which seems to be a warmer year than average due to a particularly short winter in comparison with the extreme 2012 winter (Gačić et al., 2014). The opposite behaviour of both years (Figure 7a) confirms the particularly high spawning success probability over the entire domain during 2007 (see Figure S6). Hence, 2014 must be a mild year too, mainly represented by the cluster 2 (see Figures S6 and S7) and by positive values for both dimensions on Figure 7, such as 2007.

Note that the variability of spawning success in the Adriatic Sea could also reflect local rather than regional oceanographic dynamics. It is indeed a semi-enclosed sea with its own intrinsic variability associated to local oceanographic processes such as coastal cooling/warming due to sporadic upwelling/downwelling events forced by Bora winds and/or fine-scale circulation changes (Magaldi et al., 2010). However, additional temperature analyses (not shown) highlight a change in the general dynamic of the temperature at regional scale, consistent with the BiOS regime. In fact, from 2005 to 2008, the warming of the waters is realized from the North-East to the South-West (i.e., Adriatic first, Liguria second, Tunisia last) contrary to the period 2009–2014 for which the warming of the waters occurs from the South-East to the North-West (from the Eastern Mediterranean sub-basin to the Adriatic and the Western Mediterranean sub-basin).

Overall, seawater temperature seems to be a preponderant factor of the triggering and intensity of spawning success, whereas currents act like a ‘background noise’ of the spawning success, except in places where highly turbulent currents have a major impact on the spawning success due to limited connectivity.

4.3 | Implications for management

Despite the fact that stocks of *Diplodus sargus* are not currently assessed by the General Fisheries Commission for the Mediterranean (FAO, 2006), coastal fishes like Sparids are targeted by small scale and recreational fisheries with reports of declining catches (FAO, 2004). In this context, the specific variability of the spawning success demonstrated by our results could help selecting the most adapted management tools and best spatially allocating restrictions, as advised by Erisman et al. (2015) and Sadovy de Mitcheson (2016). Note that while Hussein et al. (2011) report that permanent fishing closures appear more efficient on juveniles habitat (e.g., settlement) than on spawning areas, these conclusions need revisions as the ISIS-Fish model neglects the dispersal of early-life stages.

By assuming that any management initiative should be consistent over several years to be worth implementing, all nodes whose cluster frequency is lower than 0.7 (Figure 9) could be excluded since they exhibit too much inter-annual variability. In contrast, all nodes whose simulated spawning success and intra-annual evolution are relatively stable across years are good candidates following the current trend of spatially fixed management measures such as the Fisheries Restricted Areas (FAO, 2021). Areas characterized by clusters 1 and 4 consistently across years with favourable spawning success in late season

could be managed by restricting fishing when spawning potential is the highest (e.g., through April–June; see Figure 8). These measures represent useful management tools to protect and rebuild populations of exploited as well as patrimonial species (Di Franco et al., 2012, 2018; Guidetti et al., 2014). Note that the relevance of considering the early spawning peak (early January to mid-February) of cluster 1 for management could be questioned as Mouine et al. (2007) and Mouine et al. (2012) document in the Gulf of Tunis that gonads of *D. sargus* are not mature for spawning during this period. Using a gonado-somatic index, they state that spawning onset is linked to temperature increase, whereas in January it generally decreases or stabilizes in Western Mediterranean, except in places where winter is briefer like Tunisia or Algeria (see spawning period of Benchalel & Kara, 2010 in Table 1). Thus, the regions of North Sicily, Western Calabria and Apulia represented by cluster 1 could probably be protected during the late season only, such as cluster 4. In this study, we only look at external factors triggering spawning, but they could be favourable in periods where the gonado-somatic index is not, so it would be important to consider biotic processes in future studies. Such as clusters 1 and 4, cluster 3 presents a spawning potential late in the season but the weakness of the spawning success peak questions the relevance of a protection for the concerned areas, which require more information to be correctly managed. Finally, the spawning success of the areas typified by cluster 2 (south-eastern Sicily, Albania and Greece in Figure 9) is very stable and elevated over time, which requires long-term measures. In fact, these areas could be protected all year long with 'static' measures like MPA allowing the resilience of neighbouring exploited areas thanks to larval export (Fogarty & Botsford, 2007; Gaines et al., 2010; Jones et al., 2007).

Furthermore, dynamic measures could be required in order to adapt management with the oceanic variability. Some regions, highly dependent on oceanic temperature (areas represented by clusters 1 and 4 such as Corsica, Sardinia or North Sicily), could be ideal places to test implementing flexible protected areas and adaptive measures of protection or regulation, based on the variation of this environmental trigger of spawning (Maxwell et al., 2015). It is worth mentioning that, in the coming years, fishes are more likely to move to higher latitudes due to climate change and ocean warming, especially exacerbated near the coast (Lima & Wetthey, 2012; Liao et al., 2015; Perry et al., 2005), and dynamic management measures could thus be a standard in the future.

However, planning management measures at this scale could be challenged by the political context of the Mediterranean Sea, with potential straddling fish stocks encompassed by multiple jurisdictions or multiple countries (Hidalgo et al., 2019), for instance between Greece and Albania, making these measures difficult to apply without the concertation and collaboration of the various stakeholders.

Nevertheless, the methodology of this study could be used for other species with a bipartite life cycle in any other oceanic system for which an operational ocean model exists. Our results could help considering the interannual variability of spawning in the management of resources, and more especially in a context of adaptive and dynamic management (Maxwell et al., 2015). As future perspective, even more

effective recommendations could probably be achieved by considering an ecosystem-based approach that would study together multiple key species of an ecosystem to enhance their sustainability and reduce the negative impacts of human activities on these resources (Levin & Lubchenco, 2008). While our modelling approach could be well-adapted to guide these efforts, the accuracy and reliability of its outcome still rely on the performance levels of operational ocean models (Reglero et al., 2018). Finally yet importantly, it is worth noting that the forecast lead-time of operational ocean models does not currently exceed a few days. It implies that historical analyses such as this one are promising while future projections at these scales are still out-of-reach.

5 | CONCLUSION

In this study, we use backward-in-time particle tracking model from juveniles' settlement observations to delineate 11 spawning events and to determine a range of suitable temperatures for spawning. With this range that is consistent with the literature, we model and analyse the intra- and inter-annual variability of spawning locations and duration over ten years, from 2005 to 2014. Thanks to a Model Based Clustering method, we disentangle the different levels and sources of variability in the simulated spawning success, putting the emphasis on the role of oceanographic processes. The approach and tools developed in this study could guide future efforts that aims at evaluating when and where spawning occurs for other territorial fish species to help managers and conservationists.

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CONFLICT OF INTEREST

All authors have no conflict of interest to declare.

AUTHOR CONTRIBUTIONS

The authors confirm contribution to the paper as follows: the study conception and design was realized by M.D.S., T.L. and V.R.; A.D.F. provided data and critical feedback on the experiments; the statistical models were performed by D.N. and M.D.S.; M.D.S. analysed and interpreted the results, with contribution from T.L., V.R., A.D.F. and D.N.; M.D.S. led in writing the manuscript; T.L., V.R., A.D.F. and D.N. reviewed it and provided critical feedback.

DATA AVAILABILITY STATEMENT

Sharing observed data is not applicable to this article as no new data were created or analysed in this study (original published in Di Franco et al., 2011 and; Di Franco & Guidetti, 2011). Simulated results are available upon reasonable request to the authors.

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SUPPORTING INFORMATION

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