The role of larval transport on recruitment dynamics of red mullet (*Mullus barbatus*) in the Central Mediterranean Sea

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Abstract

Recruitment success depends on external forcing mechanisms such as ocean currents that affect the transport of eggs and larvae to favorable habitats. In this study, we investigated the role of larval transport in the recruitment of *Mullus barbatus* in the Central Mediterranean Sea by modeling the recruits' abundance as a function of both spawning stock size and dispersal rates of the species' early life stages. Our analysis involved twenty years of data on recruits and spawners abundance obtained from scientific trawl surveys, and data on larval dispersal rates derived from a combination of actualized published sources and original data. By calculating in the Sicilian nurseries, the estimates of retention, import and uniformity of the contribution of the spawning areas distributed among different Geographical Sub Areas (GSAs), we assessed their contribution to recruitment using modified Ricker stock size-recruits models. In particular, our results show that a higher uniform contribution from spawning areas within GSA16, mainly related to the oceanographic patterns promoting larval retention, together with spawners abundance, significantly reduced the variability of red mullet recruitment. We further highlighted that when switching from a higher to a lower level of evenness of contribution to the recruit population from different spawning areas in the GSA16, the expected spawning stock abundance per recruit for a given fishing pattern can suffer a rapid short-term decline, which is likely to have negative consequences for stock assessment and management decisions. Our results suggest that larval transport plays a crucial role in explaining the interannual variability of recruitment, thereby contributing to a better understanding of stock size variation. Additionally, our study enhances the understanding of the spatial dynamics involved in the recruitment of this species, which is of increasing interest within fisheries management frameworks.

Keywords: fish recruitment; ocean connectivity; larval transport; larval retention; stock–recruitment

1. INTRODUCTION

The recruitment (i.e. the number of new young fish entering a population) and its rate is a crucial process in determining the evolution in size of fish populations (e.g., King, 2013; Cadrin *et. al* 2020 and references therein). Since the beginning of the last century, fluctuations in the size of fished stocks have captured the interest of many marine scientists (Hjort, 1914), leading to extensive research to identify, evaluate, and quantify the causes of the recruitment variability. Even today, significant effort is directed towards understanding the relationship between the spawners population size (S) and the recruitment (R) due to its critical role for management strategies of sustainable fisheries (Walters and Martell, 2004; Barbieri et al. 2017). Despite the spawning stock-recruitment relationship is fundamental in marine population management, relying solely on adult abundance as a predictor of recruitment, as classically done in S-R relationships, may not always be a reliable approach (Barbieri et al. 2017; Cury et al. 2014). This is because in most exploited marine species, the effective breeding population often diverges from the number of reproducing individuals due to reproductive strategies (Barbieri et al. 2017). In fact, external fertilization is the main reproductive strategy of most exploited marine fish, involving the release of a large number of eggs into the water, which are inevitably subject to fluctuation of environmental factors (e.g. Barbieri et al. 2017) and physical dispersion due to oceanic current patterns (Cowen and Sponaugle 2009; Houde, 2016). However, attempts to incorporate external factors to reduce the degree of unexplained variation in the spawning stock-recruitment relationship have sometimes yielded inadequate results, because S-R are basically linear approximations of non-linear environmental effects (Subbey et al. 2014). Thus, understanding and assessing the factors regulating the recruitment dynamics remains one of the most complex issues in fishery science (Szuwalski et al. 2015). Various environmental factors can modulate the recruitment success, especially for broadcast spawning species, by influencing the survival of their pelagic early life stages (ELS) (Cushing, 1990; Agostini and Bakun, 2002). To improve the understanding of the interannual recruitment variability, some studies have explored various predictors, in addition to spawning stock size, to assess the abundance of recruits. These predictors include sea water temperature and its anomalies, either separately or together with zooplankton abundance (Levi *et al.*, 2003; Planque *et al.*, 2003; Olsen *et al.*, 2011; Perretti *et al.*, 2017), salinity values (Akimova *et al.*, 2016), and proxies for changes in the patterns of temperature, wind, and precipitation, expressed in terms of climatic indices such as the North Atlantic oscillation index (Brander and Mohn, 2004; Perretti *et al.*, 2017). All of these factors, although with different effects depending on the species, proved to be important in reducing unexplained interannual variability when relating parental stock size to recruits. Concurrently with these ecological factors, physical oceanographic processes associated with the advection, retention, or transport of eggs and larvae to favorable or unfavorable habitats undoubtedly contribute to variability in ELS survival and thus to variation in recruitment (Huwer *et al.*, 2014, 2016; Houde, 2016 and references therein). Therefore, spatial structure and related connectivity between spawners and recruits mediated by the larval dispersal, from the areas of eggs release to nurseries, cannot be neglected when investigating factors influencing recruitment dynamics (Cadrin, 2020). In other words, identifying self-sustained populations requires understanding the space-time patterns of larval dispersal, as well as the migration of juveniles and adults. Based on the hypothesis that the dispersal and retention patterns of ELS contribute to the recruitment variability, we expect that, by modeling recruitment as a function of larval transport estimates and spawners abundance, it is possible to achieve a more comprehensive understanding of the renewal dynamics of marine populations.

A better understanding of eggs and larval transport is crucial for fishery management because it aims to maintain the persistence of the population of a harvested species, by defining a sustainable yield that assumes a self-sustained stock. This property mainly consists of the replacement of one adult with at least one offspring that must reach the favorable habitat to survive and subsequently reproduce (Burgess *et al.*, 2014). So, assessing the role of both parental stock size and larval dispersal pattern in recruitment success is essential for the conservation and management of fished populations (Fogarty and Botsford, 2007). Well-established tools for exploring dispersal patterns and connectivity are the *Lagrangian* transport models, which are able to simulate eggs and larvae drifting as passive particles in a modeled biophysical environment (Miller, 2007). The estimated number of particles that arrive or are retained in the examined area can be related to recruitment to quantitatively assess the role of the pelagic transport, also offering the possibility to discern the effects of local factors from regional ones on the renewal of the population. Recently, estimates of larval transport across transnational boundaries have been explicitly applied to model fish population fluctuations in the Northwestern Mediterranean Sea (Ospina-Álvarez et al. 2015, Hidalgo et al. 2019) and the Strait of Sicily (Patti et al.2020), as well as in in the North Sea (Romagnoni et al. 2020).

Based on this premise, we focused on the role that the larval drift has on the recruitment of the red mullet (*Mullus barbatus*, L., 1758) in the southern coast of Sicily (Geographical Sub Area GSA 16; FAO 2009) within the Strait of Sicily (SoS). *M. barbatus* is one of the main target species for coastal bottom trawl and small-scale fisheries in the Mediterranean Sea (Tserpes *et al.*, 2019) reaching in the GSA16 an average value of about 550 ± 171 tons of landing in 2006-2018 (Scannella et al., 2019). As measures of larval transport, we used the annual upgraded estimates, adopting the revised projection of 'Copernicus Monitoring Environment Marine Service (CMEMS)' velocity fields (Escudier et al 2020), of the *Lagrangian* dispersal simulations from 1999 to 2012 reported in Gargano et al. (2017) and to extend the time series until 2019, we employed the same *Lagrangian* model and its parametrization. Gargano et al. (2017) simulated and quantified particles passive drifting from the known red mullet spawning areas (*sources*) located on the northern (Sicilian-Maltese) and southern (African) shelves of the Strait of Sicily to the potential nursery areas (*sinks*) identified off the Sicilian, Maltese and African coasts. The authors found a low exchange of particles between the Sicilian–Maltese and the African sides of the SoS and a high degree of retention of larvae in all the respective shelves. In the present study, we were interested in the recruitment processes occurring in the GSA 16, i.e. the fraction of particles released in different spawning areas across the entire SoS that reach the nurseries off the Sicilian coasts. Starting from the annual *Lagrangian* estimates of particle arrivals in GSA 16 from the different release areas in the SoS, we calculated estimates of retention within the GSA16, and estimates of eggs and larvae import from the African and Maltese Shelf. Furthermore, we analyzed the degree of uniformity in terms of eggs and larvae provenience from the different spawning zones in each continental shelf considered. The resulting interannual patterns of variability, discriminated in terms of the magnitude of egg and larval input and spatially in terms of equal or inhomogeneous contribution from the different zones, reflects the ocean current dynamics that influence larval dispersal and could ultimately serve as a proxy for the oceanographic conditions favouring larval settlement and recruitment on the shelf within the studied GSA.. Then, by using a fishery-independent dataset of red mullet abundance in the GSA16 from 2000 to 2019, we modeled the abundance of recruits as function of the spawning population size using traditional parametric stock-recruitment model formulation, and compared this formulation with models including estimates of retention within GSA16, import from the two different continental shelves, and the related homogeneity of retention/import eggs and larvae from the different areas.. Overall, our primary objective was to assess whether larval transport patterns contribute to explaining the temporal dynamics of red mullet recruitment within GSA 16. Additionally, we explored the effects of larval transport variability on the interannual variation of red mullet recruitment and the subsequent spawner abundance (i.e., the replacement line; Goodyear, 1993) in GSA16, and its implications for stock assessment and fishery management.

MATERIAL AND METHODS

2.1 Study area

The study area is the GSA 16 which corresponds to the North sector of the Strait of Sicily, a large and dynamically active area that connects the western and eastern Mediterranean Sea. The GSA 16 is characterized by a narrow shelf along the central part of the Southern coast of Sicily and by a wide and shallow bank extending in the western part, the Adventure Bank (Fig. 1). In the middle of the area, there are deep canyons, trenches, and steep slopes. In the southernmost part, the shallower bottoms North East of the island of Lampedusa belong to the northern edge of the African platform. Both the northern (Sicilian-Maltese) and southern (African) continental shelves of the SoS host discrete and persistent spawning and nursery areas of red mullet (Fig. 1a; Garofalo et al., 2004, 2008, 2011; Colloca et al., 2013). The predominant surface current in the region is the Atlantic Ionian Stream (AIS), formed by the Modified Atlantic Water (MAW) entering the SoS and flowing eastwards. The main path of the AIS crosses the Adventure Bank, circulating around a semi-permanent cyclonic vortex, and follows the shelf along the central part of the southern coast of Sicily (Beranger et al., 2004). The AIS is more intense during the spring-summer season, which coincides with the red mullet spawning period, thus influencing the transport and dispersal of the larval stages of the species (Gargano et al., 2017).

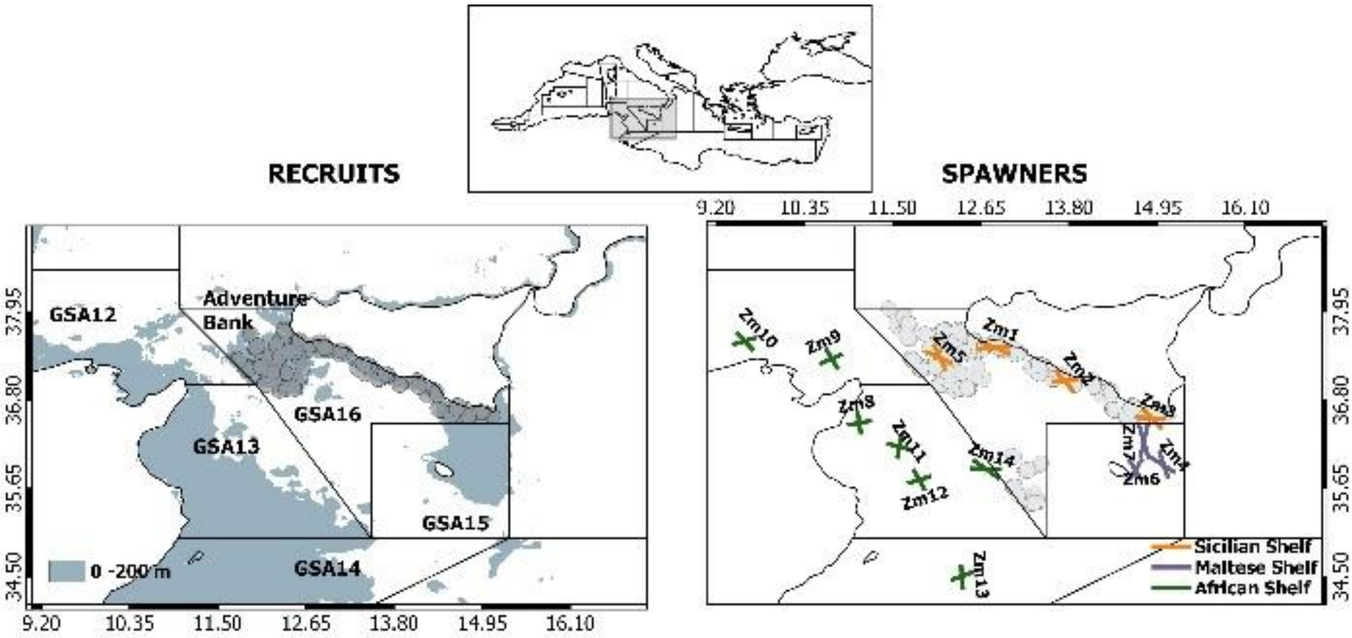

Figure 1. Study area (GSA16) and the positions of the hauls (gray circles) used to calculate the density index (N/km²) of red mullet spawners and recruits. The spawning areas (Zm1-Zm14) where Lagrangian particles were released in the study by Gargano et al. 2017 are indicated, color-coded based on their location on the Sicilian (orange), Maltese (purple), or African (green) shelf.

2.2 Data sources

2.2.1 *Red mullet data*

Fishery-independent data of red mullet spatial distribution, abundance, and length structure were obtained from the bottom trawl surveys carried out annually in the GSA16 from 2000 to 2019, during spring/summer, within the International Bottom Trawl-Surveys in the Mediterranean (MEDITS; Bertrand et al., 2002; Spedicato et al., 2019). The MEDITS survey is based on a depth-stratified sampling design with five depth strata, i.e. 10-50, 51-100, 101-200, 201-500, and 501-800 m, where the number of hauls per stratum is proportional to the area of each stratum. According to literature red mullets in the SoS spawn in spring and recruit in August-September of the same year, reaching full maturity by the following spring at the age of 1 year (Levi 1991, Levi *et al.* 2003). Therefore, we used the 1-year-old individuals caught at time $_{t}$ as a proxy of recruitment, while as spawners we considered all the individuals from 1 year onwards caught at time $_{t-1}$. Firstly, the age distribution by year and depth stratum was estimated by the length distribution through the inverse of the von Bertalanffy's growth curve (VBGC), using the deterministic approach, i.e. the “age slicing”, described by Kell and Kell (2011). Specifically, we used the parameters of the VBGC for combined sexes as set in the General Fishery Commission for the Mediterranean (GFCM) stock assessment for the GSA16 (Scannella et al., 2019), being the asymptotic mean length L_∞ = 24.1, the growth rate coefficient K= 0.42, and the time when the average length is zero t_0 = -0.8. Then, annual abundance estimates of recruits in terms of the number of individuals per km^2 were obtained as the total abundances observed in the sampling stations located on the Sicilian shelf and Adventure Bank until a depth of 200 m. These estimates were standardized with respect to the yearly total swept area, considering that from settlement to one year of age, M. barbatus extends its distribution across the entire shelf. The standardized Density index (N/ km^2) was used for the spawners abundance.

2.2.2 *Oceanographic-dependent driver*

Dispersion rates of red mullet eggs and larvae in the SoS have been calculated by adopting the Lagrangian model and associated parametrization published by Gargano et al. (2017),and on the updated CMEMS velocity field projections (Escudier et al. 2020) for the period 2000-2019.

Here, we provide a brief description of the simulations and refer the reader to the original paper for further details. The model adopted by Gargano et al. (2017) is based on the hypothesis that eggs and larvae are particles passively transported. The simulations of transport were performed using the quasi-Lagrangian model proposed by Palatella et al. (2014). This model restores the 3D vertical mixing and the unresolved sub-mesoscale motions by superimposing suitable extra velocity fields on the real main large scale 3D current field. In our new analysis the 3D current field time series was obtained, for the spawning period, from the MyOcean Project (https://marine.copernicus.eu/). Specifically, we acquired the daily means of the northward and eastward current velocity components at 72 vertical levels (from 1.4 to 5000 m depth), with a horizontal resolution of 1/24° × 1/24° from the MEDREA system (Escudier et al. 2020). The initial setup for Lagrangian particles is the same as outlined by Gargano et al. (2017), and is based on previously identified spawning and nursery areas. Specifically, the particles were equally distributed within the Sicilian (Zm1 to Zm3, Zm5), Maltese (Zm4, Zm6, Zm7), and African (Zm8 to Zm14) spawning areas to examine connectivity between the northern and southern continental shelves of the SoS in terms of larval supply to the potential nurseries in the investigated area (Fig 1). These nurseries are the Sicilian (SN), Maltese (MN), and African coastal areas (AN), defined by extracting the 60-m bathymetric contour levels. In each year, the simulations were performed from May 1 to July 31. In June, a total of 800 drifting particles per day were equally distributed among the spawning areas, while in May and July, the number of particles was decreased according to $N=N_0e^{-(d/15)^{\wedge}2}$, where d is the time lapse in days between a day in May and June 1, or a day in July and June 30. The total number of particles for the entire series from 2000 to 2019 is 912,120, and the trajectories were followed up to 45 days from the initial release of particles. The depth of the particles' release was randomly chosen between 3 and 10 meters. In red mullet, the pre-settlement and settlement stages occur at 30 and 45 days, respectively. Accordingly, the transport success (i.e., the fraction of larvae arriving in the nursery areas) was evaluated by considering the particles staying within the nurseries during this time range.. From the dispersion model outputs, we built a multivariate dataset of the total number of *Lagrangian* particles passively transported per years from the different spawning areas across the SoS to the GSA16 nursery area. Since no particles from GSA14 (Zm13) reached the nurseries of the GSA16, it was excluded from further analyses (Fig. 1). The total number of particles arriving from the various areas reflects the oceanographic conditions conducive to the transport of eggs and larvae toward the GSA16 red mullet nursery area. By considering the annual arrivals from the release areas situated in the different shelves of the SOS, we can differentiate between oceanographic spatial patterns that promote larval retention and immigration. This allows us to infer the relative contribution of various larval sources to population replenishment in GSA16. Specifically, we calculated the annual local retention as the mean number of eggs and larvae spawned and retained in GSA 16 (RES), while the import from the African (IAF) and Maltese (IMA) shelves was calculated as the mean number of arrivals from the different spawning areas situated within the two continental shelves. Furthermore, to evaluate whether differences in the contribution of each spawning zone influenced recruitment success, we assessed the inhomogeneity of contributions from each zone of the different shelves using Camargo's index of evenness (Camargo, 1995) : $IndEv = 1 - [\sum_{i=1}^{s}\sum_{j=i+1}^{s}\left(\frac{|p_{i-}p_j|}{s}\right)]$

where p_i is the proportion of particles coming from the spawning zone i; p_j is the proportion coming from the spawning zone j; and s is the total number of spawning zones of the considered shelf (inRES, inIAF and inIMA, for the Sicilian, African and Maltese shelf respectively). Index values range from 0 (inhomogeneous) to 1 (even). An index of 1 indicates that the contributions are homogeneous across spawning zones, suggesting that favorable oceanographic conditions promote either the retention or the import of eggs and larvae from all spawning areas, depending on the shelf considered. Conversely, a lower index indicates greater inequality among the contributions from the different spawning zones of the considered continental shelf.

2.2.3 Data analysis

We used the Ricker model to describe the relationship between spawning stock and recruitment (S-R) (Ricker, 1954), as this formulation has already been successfully used to describe the red mullet spawning stock-recruits relationship in the SoS (Levi *et al.* 2003).

The Ricker model describes a dome-shaped relationship, where the peak of recruitment (R_t) occurs at intermediate spawning stock size SS_{t-1}. One of the parametrizations of this model is:

$$R_t = aSS_{t-1}e^{-bSS_{t-1}}$$

a is the density-independent parameter and b is the density-dependent parameter. R_t is the abundance of red mullet of age class 1 at the year *t*, while SS_{t-1} is the spawning stock abundance of the year *t-1*. A multiplicative error structure was used as suggested by Hilborn and Walters (2001) and the significance of the parameters was obtained deriving the 95% confidence intervals. The comparison of Ricker model with the assumption of a linear relationship between R and SS, i.e. $R_t = aSS_{t-1}$ was assessed using the extra sum of squares F-test (Ritz and Streibigg, 2008).

To test the contribution of larval dispersal pattern to S-R relationship, we introduced the different estimates of retention, import and evenness -which capture the oceanographic conditions for eggs and larval transport- in the Ricker model, once at time, as follows:

$$R_t = aSS_{t-1}e^{-bSS_{t-1}+cX_{t-1}}$$

Where X_{t-1} represents the estimate of larval transport (i.e. one of RES, IAF, IMA, inRES, inIAF and inIMA) and c is the parameter to be estimated summarizing the relationship between R_t and X_{t-1}. The significance of the parameters was obtained extracting their confidence intervals. When the parameter resulted significant the extra sum of squares was instead used to compare the model with the classical Richer model.

To investigate whether changes in oceanographic conditions can affect not only recruitment but also the population under study—specifically, the adult population size—and consequently the assessment of fishing mortality for sustainable exploitation, we superimposed the curve of the best model explaining recruitment variability with the replacement line. This line, calculated according to Goodyear (1993), is characterized by a slope directly dependent on fishing and natural mortality and describes the potential contribution of the recruitment to the mature fish population size. For each annual spawner abundance, the amount of recruitment required to replace the spawners is determined by a given specific fishing (F) and natural mortality (M) and proportion of mature at age (*pa*), assuming that the replacement occurs in a given year rather than over the lifespan of the cohort (Gabriel et al. 1989). Specifically, we calculated the spawning stock abundance per recruits (SPR), using vectors of *pa,* M and F at age (considering the last year of the studied series, i.e., 2019) obtained by the more recent available stock assessment of red mullet in GSA 16 (Scannella et al., 2021) (Tab 1) as follows:

$$\mathrm{SPR}_j = \sum_i (MF_i * pa_i)$$

where SPR_j is an estimate of the annual replacement, and pa_i the proportion of mature at age respectively, and MF_i is the cumulative product of the survival rate for all the age classes (*i*) computed as

$$MF_i = \prod^i e^{-(F+M)}$$

Being the spawning stock abundance per recruit for a given fishing and natural mortality designated by $\mathrm{SPR} = \mathrm{Spawner} / \mathrm{Recruits}$, in number, then the slope of the replacement line passing through the origin is 1/SPR (Gabriel et al. 1989). By examining a simulated evolution of recruitment and replacement, this approach highlights how transitions from favorable to adverse oceanographic conditions, and vice versa, can impact on replacement levels at specific levels of fishing mortality and biological characteristics of the stock. All the analyses were performed using the R statistical software (R Core Team, 2019).

Table *1*. Parameters used to calculate the replacement line. *The* gray col*umns show* the parameters by age obtained from the GFCM – SAF report (Scannella et al. 2021)*: p*a= proportion of mature *individuals* at ages, M= natural mortality, F = fishing mortality

age	pa	M	F
1	1	0.9	0.07
2	1	0.67	0.34
3	1	0.57	0.21
4	1	0.5	0.41
5	1	0.47	0.41

2. Results

The density index of $Recruits_t$ and $Spawners_{t-1}$ increased during the years, peaking in 2014 and in 2015 respectively (Fig. 2). There was a clear increasing pattern until the 2014, after which both the abundance series experienced wide fluctuations (Fig. 2).

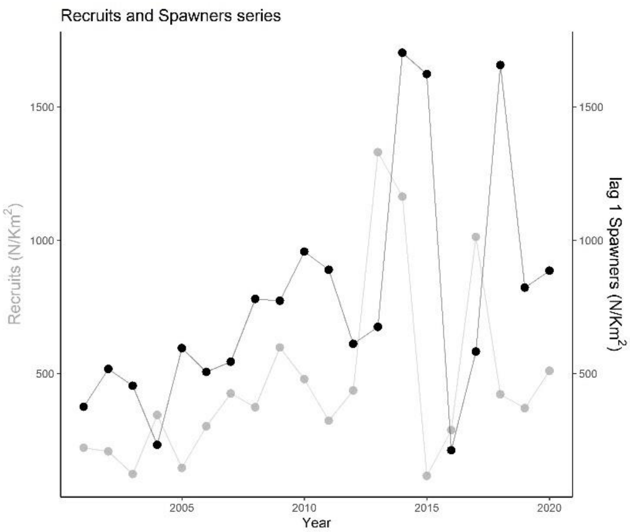

Figure 2. Temporal series of Recruits and Spawner Densities (N/Km^2).

The highest values of eggs and larvae were those produced and retained on the GSA16 shelf (mean = 242.125 ± sd 266.68) Fig 3, Fig. S1). Retention in GSA 16 fluctuated throughout the considered period, with the highest value observed in 2012. Evenness remained close to its mean (0.48), with lower values during the first part of the series and a peak in 2016, when the mean number of retained eggs and larvae was slightly below the long-term average. This indicates an equal contribution from the different zones to total retention within GSA 16. In contrast, the lowest evenness coincided with the lowest retention values, indicating that low retention was unevenly distributed among the various spawning areas within GSA 16 (Fig. 3, Fig S1). Arrivals from the Maltese Shelf had a mean percentage value lower than 0.001, and evenness remained low, regardless of arrival values (Fig. 3, Fig S1). The lowest evenness was observed for particles originating from the African Shelf, suggesting that in certain years, only one or two spawning zones contributed to the arrivals from the African Shelf (Fig. 3, Fig S1).

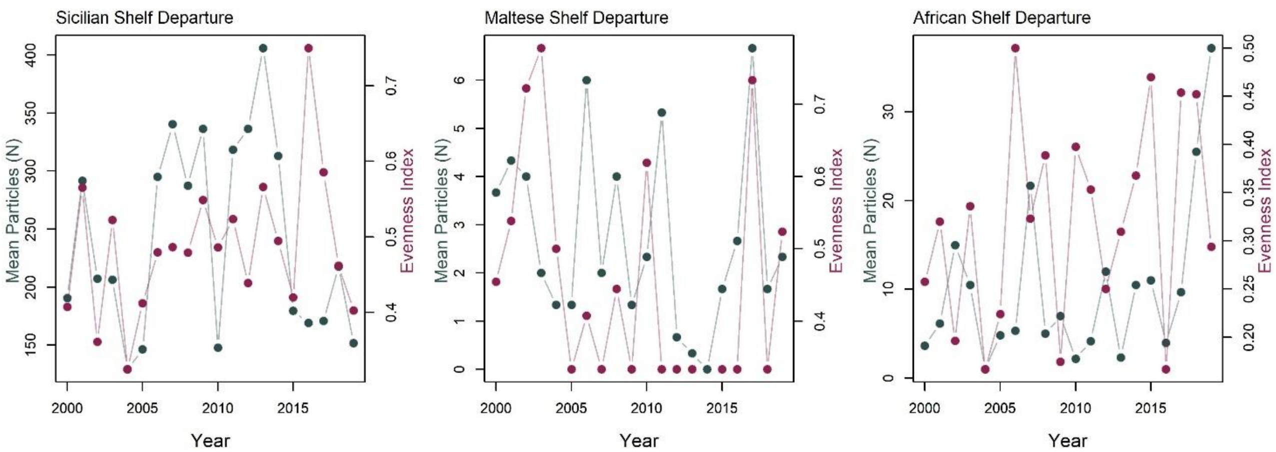

Figure 3. Temporal series of the mean number of eggs and larvae arriving in the GSA16 nurseries differentiated based on the continental shelf of origin, and the associated evenness index.

The best model selected based on significance of coefficient was the one including spawner abundance and inRES (adjusted R2 from the linearized form of Ricker model = 0.39) which reduced significantly the Residual sum of square compared to the classical Richer model (adjusted R2 from the linearized form of Ricker model = 0.24) (Fig 4, Tab 2). This model highlights the synergistic influence of spawner abundance and oceanographic conditions, which affect the contribution of larval transport from each spawning zone in GSA16, in explaining recruitment dynamics (Fig 4, Tab 2). Specifically, a positive linear relationship was observed between recruits abundance and evenness, suggesting that a more homogeneous contribution to retention across different spawning zones favors recruitment (fig 4).

Table 2. Richer models with the different covariates (a,b and c are the parameter estimates of the Ricker models together with their 95% confidence intervals).

	Coefficient (CI)			F-test	R2 from linear transformed Ricker model
	a	**b**	**c**		
Ricker	51,76741 (29,95-85,05)	0,05367 (0,018-0,09)		vs Ind model F=7,05 p=0,01 *	0.24
Extended Ricker inRES	0.23 (0,095-0.89,22)	0.0012 (0,005-0,0017)	3.635 (0,88-5,85)	vs Ricker F=5,52 p=0,03 *	0.39
Extended Ricker RES	0.72 (0,26-1.98)	0.001 (0,0003-0,0017) NS	0.002 (-0,001-0,0065) NS		0.26
Extended Ricker IMA	1.24 (0.52-2.99)	0,53 (0,0001-0,0017)	-0,02 (-0.20-0.158) NS		0.17
Extended Ricker inIMA	1.84 (0.67 -5.01)	0,0005 (-0,0001-0,001)	-1,52 (-3.35-0.29) NS		0.20
Extended Ricker IAF	1.17 (0.55-2.51)	0,0009 (0,0001-0,0017)	-0,02 (-0.39-0.034) NS		0.19
Extended Ricker inIAF	1.035 (0.32 -3.29)	0,0009 (0,0001-0,002)	0.35 (-2.89-3.30) NS		0.19

The best and statistically significant model, which included the spawner abundance and iRES, was used to illustrate the impact of transitioning between conditions of high to low evenness on the replacement line. The parameters listed in Table 1 were employed for this purpose (see Figure 4). The positive effect of the interaction between spawner abundance and oceanographic conditions, which promote higher evenness of larvae born along the spawning areas of the Sicilian coast, leads to a greater number of recruits. These recruits contribute to replenish the spawning stock at a given level of fishing mortality (refer to Figure 4, numbers 1 to 4). However, when transitioning from higher to lower evenness, recruitment can significantly decrease, resulting in a decline in the expected abundance of spawners per recruit for red mullet for a given level of fishing mortality (refer to points 4 and 5 in Figure 4).

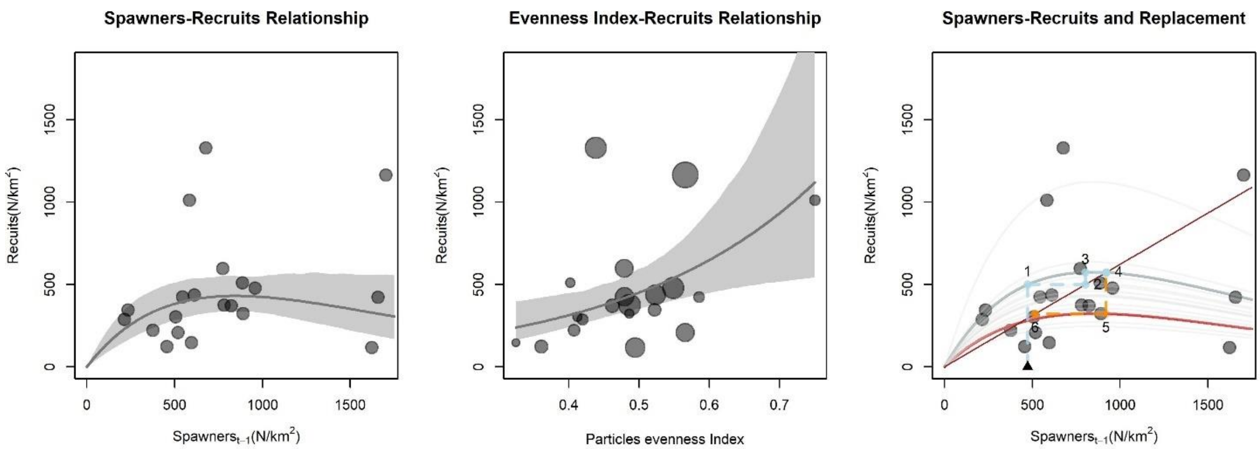

Figure 4. Results of the best model including spawner abundance (left panel) and inRES (evenness of the retained eggs and larvae in the Sicilian shelf coming from the different spawning zones of the GSA16) in the central panel. Point size are the average retained particles in the GSA16. Right Panel: Replacement line superimposed on the predictions of the best model, demonstrating the shift in abundance when the transition occurs from favorable conditions promoting high evenness to not-favorable conditions.

Discussion

In this study, we combined twenty years of indices of spawner and recruit abundance of red mullet with estimates of larval transport by ocean currents across the SoS, to demonstrate the synergistic effect they have on recruitment in GSA 16. Our results showed that more uniform contributions of larval arrivals from the different spawning areas within the GSA16 play a critical role in shaping recruitment success and acts synergistically with spawner abundance in years characterized by a high evenness level. Additionally, by enlarging the examined time series, we confirmed the results obtained by Gargano et al. (2017) indicating that larval arrivals to GSA 16 from adjacent areas are negligible. These findings provide new insights into the complex interplay between spawner abundance, larval transport, local retention, and recruitment dynamics in GSA 16.

Since the first half of the twentieth century, Hjort (1914; 1926) proposed the transport of eggs and larvae in favorable or unfavorable areas as a key mechanism generating interannual variability of recruitment success. So, various investigations have been carried out with the aim to test the effects of environmental factors often used as proxies for ELS transport on recruitment. Recruitment success has been related to wind speed (e.g. Hinrichsen *et al.*, 2001; Köster *et al.*, 2003), or large scales environmental processes such as gyres or coastal currents (e.g. Trenkel *et al.*, 2014; Zimmermann *et al.*, 2019) directly involved on the pre-recruits survival for the Atlantic stocks. Similarly, in the Mediterranean Sea climatic indexes associated with changes in wind speed and mesoscale circulation have been linked to the population dynamic of demersal resources (e.g. Lloret et al. 2001, Levi et al., 2003; Massutí *et al.*, 2008; Ligas *et al.*, 2011). Although not as numerous as studies based on environmental parameters and climate indices, there have been studies based on the hypothesis that ELS transport could be one of the factors influencing the unclear relationship between spawner stock size and recruitment (Baumann et al. 2006; Zimmermann, Claireaux, & Enberg, 2019). Some of these studies use proxies for larval transport, while only a few studies utilize direct estimates of larval transport (e.g. Hidalgo et al. 2019; Romagnoni et al 2020). In particular, in the Atlantic Ocean, the estimates of retention processes were used to weight the spawning stock biomass of the North Sea cod enhancing the explained variability of the stock recruitment relationships (Romagnoni et al. 2020). In the Western Mediterranean Sea, an improvement in the stock recruitment relationship for European hake has been achieved by explicitly introducing both immigrants and local recruits into the analytical relationship (Hidalgo et al, 2019). In the SoS, Patti et al. 2020 have shown the crucial role of eggs and larvae retention in promoting anchovy recruitment.

By analyzing the spawning stock-recruitment relationship, we found that recruitment of red mullet in GSA 16 was significantly related to parental stock size. However, the variation in recruits abundance explained by the model including only the parental stock size expressed as goodness of fit (R^2) was only 0.24 , indicating limited usefulness for management purposes. This result aligns with the findings of Cury et al. (2014), who examined 211 marine stocks worldwide. They reported that parental stock size is a predictor that only accounts for between 5% (for demersal species) and 15% (for small pelagic species) of the recruitment variability. No significant increase in explained recruits' variation was observed when the estimates of import and retention of egg and larvae transport from the different spawning zones within and outside the GSA16 were incorporated into the model formulation together with the spawners' stock size. Instead, we found that by incorporating the evenness index of the eggs and larvae contribution of the spawning zones from the GSA16 (inRES), enhanced the degree of explained variation in recruitment. This indicates a stronger link between recruitment of red mullet in GSA 16 and spawning stock size when oceanographic currents force the retention of eggs and larvae spawned from different areas of the GSA16 shelf. In other words, for the same abundance of spawners, the relationship with recruits can change depending on the evenness of the contribution of the different spawning zones, regulated by oceanographic currents. Specifically, by modeling recruitment as a function of both spawner abundance and the variation in oceanographic current patterns driving retention of eggs and larvae from all the spawning areas within the GSA16, the explained variability in recruitment was enhanced by 64%, compared to using spawning stock abundance alone (R2 of classical Ricker model 0.24, R2 of Ricker model including Evenness =0.39). The evenness index (inRES), which indicates the oceanographic conditions that favor the retention of eggs and larvae from different spawning areas in GSA16, reflects the AIS jet, which represents a semi-permanent and partially stable barrier between the southern and northern parts of the SOS (Quattrocchi et al. 2019). Years with high inRER reflect conditions in which this current retains a fraction of eggs and larvae in the vicinity of the nursery area, regardless of the spawning zone considered. At the same time, this current could increase and concentrate primary productivity on the continental shelf, as described by Patti et al. 2018. Considering the highly oligotrophic waters surrounding the Sicilian shelf, this could increase the survival of early life stages (Patti et al. 2018) and consequently favor recruitment. Conversely, the presence of a high average retention of eggs and larvae may represent conditions favouring the arrival from one of the spawning areas, while preventing the arrival from the other areas, thus representing a condition where the barrier created by AIS is not stable and also far from the one favoring high primary productivity. These results are in line with those obtained by Levi et al. (2003), who found that at a given level of spawning stock size of red mullet off the Southern Sicilian coasts the recruitment success was higher when the water's temperature in the pre-recruitment period (July-August) was warmer than the average SST. The Authors associated these results with a weaker upwelling of deep waters in coastal waters off southern Sicily and a consequent lower offshore transport of early life stages.

Our results highlight that oceanographic currents, which contribute to larval dispersal, along with spawner abundance, can enhance the explained variation in red mullet recruitment compared to the model that includes only the spawner stock size. Focusing on the metrics of larval transport from adjacent areas, the results indicated that the larval arrivals from other GSAs were extremely low, never exceeding 1% of the released particles, in the examined time series. This suggests that they are unlikely to significantly influence recruitment within GSA 16. On the contrary, its fluctuations appear to be driven by both the spawner abundance and the changing currents patterns, which affect the homogeneous arrivals of eggs and larvae from the different spawning zones of the GSA16. Additionally, it is noteworthy that the Lagrangian simulations in Gargano et al. 2017 assume that larvae are particles passively transported during the dispersal phase, which generally overestimate dispersal distance while underestimating the local retention (e.g. Shanks, 2009; Faillettaz *et al.*, 2018; Corell and Nissling, 2019; Pires et al. 2021) considering also the capacity of larvae of *Mullus barbatus* of displacing in areas with a high productivity compared to the neighborhood areas (Sabates et al. 2015) therefore able to perform active behavior. Consequently, it is likely that the synergic effect oceanographic condition and parental stock abundance on recruitment could be much greater than that shown by our results if Lagrangian experiments simulated the active behavior of larvae and pre-recruits, while the contribution to recruitment from sources external to the GSA 16 would be even lower.

According to the origin of the recruits, marine populations can be classified as ranging from entirely closed to fully open, and one of the processes underlying this distinction is the interaction of various biophysical mechanisms (e.g. currents and coastal topography) that can counteract or enhance the dispersion of eggs and larvae, favoring, in the first case, their retention in the natal area and the maintenance of the spatial structure of the populations (e.g. Cowen *et al.*, 2000; Sponaugle *et al.*, 2002). In our study, we observed that red mullet recruitment within GSA16 is not significantly dependent upon larval import from external spawning areas. This result suggests that within GSA 16, where the red mullet reproduces in the summer season characterized by intense AIS (Sorgente et al. 2003), the mesoscale circulation associated with the coastal bathymetry represents a powerful larval retention mechanism (Garcia La Fuente et al., 2002; Falcini et al. 2015; Quattrocchi et al., 2019; Patti et al., 2020). In summary, our results are consistent with the stock unit assumption for assessment and management purposes of red mullet in the GSA 16 adopted the GFCM, being a quite self-sustained population with a low degree of demographic exchanges with the adjacent GSAs covering the waters around the Maltese Islands and the African shelves.

However, the current study is based on the current distribution of spawning and nursery areas in the region. Considering the possible shifts in species distribution due to climate change (Cheung et al. 2013; Pinsky et al. 2013), solutions for addressing such shifts (e.g., re-evaluating spatial patterns of nursery and spawning areas and the stock unit boundaries) should be taken into account to avoid mismatches between biological populations and management units (Kerr et al., 2017; Cadrin, 2020).

The multidimensionality of the recruitment process, with numerous biotic and abiotic factors involved in its variability, is well recognized (Jakobsen *et al.*, 2016 and references therein; Sharma *et al.*, 2019). Environmental processes, such as the oceanographic conditions involved in the ELS drift, can rapidly cause changes in recruitment rates and, consequently, stock size, affecting the dynamics of exploited populations (e.g., Fogarty et al. 1991). Here we showed that since the parental stock size is a measure of the cumulative contribution of each year class, the expected spawners per recruit, calculated according to the classical replacement line for a given fishing mortality, varies when the evenness level of larval transport from different areas change. Specifically, we showed that for a given fishing mortality, when there is a switch from high to low evenness on the GSA16 shelf, recruitment can be inadequate to maintain the spawning stock size, leading to a short-term stock decline. These concerns are particularly relevant in relation to future changes of ocean conditions predicted in the Mediterranean Sea, i.e. an increase in mixing and a decrease of boundary strength between regions, with potential effects on drifting organisms such as plankton, eggs, and larvae (Ser-Giacomi *et al.*, 2020). Numerical ocean simulations in the Mediterranean are refined enough to explore the spatiotemporal variability of larval transport over several years (e.g. Gargano et al. 2017; Quattrocchi et al. 2019; Palmas et al., 2017; Celentano *et al.*, 2020; Clavel-Henry *et al.*, 2021; Patti *et al.,* 2020; Melaku Canu et al., 2021). However, results of dispersal patterns are rarely incorporated into fisheries assessment and management (Hidalgo et al. 2019; Romagnoni et al. 2020). Understanding and predicting recruitment is an important part of the stock assessment mainly in those cases such as the Mediterranean fisheries in which most of the catch is based on youngest year classes (Levi et al., 2003). The number of recruits entering the fishery and their prediction are needful for understanding future biomass and catch and defining a reference points framework based on the relationship between parental stock size and recruitment (Gabriel & Mace, 1999; Sharma et al. 2019). A model framework which accounts for the interdependence of parental stock size and larval transport estimates has proved to improve the understanding of the recruitment dynamics and support the stock units identification for management purposes, which is still a main scientific challenge for sustainable management of fisheries (e.g. Cadrin et al., 2020).

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