

The trade-off between condition and growth shapes juveniles' survival of harvested demersal fish of the Mediterranean sea

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ABSTRACT

Fish body condition and growth are two interrelated traits closely associated with species life history and fitness, whose trade-off can ultimately impact population dynamics albeit seldom empirically demonstrated. They can intricately affect survival rates, which are particularly relevant for species under exploitation. Using individual spatiotemporal information in Northwestern Mediterranean, we document for the first time the existence of a trade-off between condition and growth in regulating survival dynamics in two important fish species for the Mediterranean fisheries that are characterized by contrasting life histories. For the European hake (*Merluccius merluccius*), a benthopelagic species, juveniles' body condition was detected to be positively linked to survival and negatively associated with the growth of this age group. For the red mullet (*Mullus barbatus*), the same pattern was observed for young adults. We also show that the observed patterns on a regional level have a clear spatial dependence as we found that observed body condition over a local scale had a broad effect on the population dynamics of the whole region, with the Ebro delta area emerging as the demographic engine of the two species. We discuss our results in the context of fisheries management and underline the importance of improving current stock assessment models and spatially based fishery management towards incorporating body condition and growth due to their influence on important parameters such as survival.

1. Introduction

Life history traits reflect species adaptations to the surrounding environment. They are known to modulate biodiversity-ecosystem functioning relationships and ecosystem services such as productivity or stability (Färber et al., 2020; Massol et al., 2017), but also species distributions and populations genetic differences and temporal dynamics (e.g. De Roos et al., 2003). Multiple linkages between life history strategies and body condition have been documented – such as the effect on reproductive output and breeding time (Brosset et al., 2016; Serrat et al., 2019). Body condition, as defined in Bolin et al. (2021), is an integrated measure of the physiological status of the fish. It constitutes an important and very informative attribute of a variety of organisms,

including fish, and has broadly been used to quantify individual health through the development and implementation of condition indices (Stevenson and Woods, 2006). In fisheries science, information on body condition of exploited marine taxa is associated with a plethora of biological traits and ecological processes such as survival, reproduction, and offspring quality though it is rarely integrated in operational management and assessment frameworks (but see Casini et al., 2016a). All these factors should render information on condition paramount for applied research aimed at fishery management (Lloret et al., 2014).

Fish body condition is governed by many factors such as food availability and trophic resources (Hidalgo et al., 2009; Rueda et al., 2019), fishing impacts (Hiddink et al., 2016; Rueda et al., 2015), density dependence (Casini et al., 2016b; Kjesbu et al., 2014; Rueda et al., 2015)

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in addition to a variety of environmental factors such as primary productivity (Rueda et al., 2015; Véron et al., 2020), sea surface and bottom temperature (Laurel et al., 2016; Rueda et al., 2014; Véron et al., 2020) and salinity (Rueda et al., 2015; Véron et al., 2020). As energy reserves directly affect essential biological functions, such as growth, survival and reproductive success, condition indices have been employed by various studies to assess individuals health and fitness as well as population health and their spatial and temporal patterns (Rueda et al., 2019; Véron et al., 2020). Numerous condition indices have been developed serving as proxies of the quantity of energy stored within an individual or of habitat quality (Lloret et al., 2014; Stevenson and Woods, 2006). The use of condition indices is becoming more and more frequent as they can provide essential information on the effects of environment and human perturbations on fish populations (Lloret et al., 2014).

Besides condition, growth is another important life history trait for organisms. Fish allocate the assimilated energy according to their physiological state and the trade-off between growth, survival and reproduction (Gunderson, 1997). Growth, for instance, is a fundamental physiological process influencing the state and dynamics of fish stocks by directly or indirectly affecting the maturity, fecundity as well as natural and fishing mortality of individuals (Lorenzen 2016 and references therein). Growth is indeed particularly relevant along the first stages of the life cycle when the natural mortality rate is higher. That is, young individuals that increase in length faster are more likely to survive. This is explained by the need of immature individuals to focus on maximizing their growth in length to avoid being preyed while individuals that have reached maturity mainly invest their energy to gamete production and reproductive behavior (Saborido-Rey and Kjesbu, 2005). Evidence suggests that there is a trade-off between body condition and growth, i.e. a decrease in growth rate occurring in return of an increase in condition and vice versa, but this is highly species-specific and has mainly been investigated in younger age classes (Rueda et al., 2015). This trade-off has been observed in several fish species (e.g. Kingsbury et al., 2020), although a positive correlation between growth and body condition has also been documented (Bentley and Schindler, 2013) with most studies, however, either addressing only one age class or only examining the growth accumulated over a short period of time (<1 year). With such discrepancies in the link between condition and growth among different species, often complemented by study-specific limitations, it can fairly be inferred that this link can be highly species-specific and should further be investigated across multiple age-classes as well.

One of the overarching goals of fisheries assessment has been to elucidate the mechanisms that regulate the abundance and persistence of wild populations in space and time (e.g. Minto et al., 2008). In this context, it is pivotal to understand temporal and spatial variability of survival (Minto et al., 2008), in which the influence of life history traits is also known to be central. This is particularly related to the natural mortality rate (M) currently used in fisheries assessment models which has been assumed to be constant with a temporally invariant age-based vector. Omitting the temporal variability of M or its impact on the under- and overestimation of fishing mortality (F) and the related reference points generates a considerable bias in stock assessments (Jørgensen and Holt, 2013; Punt et al., 2021). Recent research evidenced that spatiotemporal information of body condition can be related to the dynamics of natural mortality (Casini et al. 2016a), however this application has not been extended. Maternal effects such as female total length (TL) and condition on hake recruitment success have been documented (García-Fernández et al., 2020), but they have not been implemented in regular assessment schemes either. Although it has been speculated that body condition regulates juveniles' survival (Gronud-Colvert and Sponaugle, 2006), there still is limited information available for large commercial marine stocks.

The Mediterranean Sea has been witnessing elevated pressure from a variety of anthropogenic perturbations, including intense fisheries (Piroddi et al., 2017). A very high percentage (75%) of Mediterranean

stocks are currently overexploited (FAO, 2020). European hake, hereafter hake, (*Merluccius merluccius*) represents the most paradigmatic species of this alarming overexploitation trend along with other demersal species of high commercial value, such as the red mullet (*Mullus barbatus*), whose fishing mortality rates can be up to ten (hake) or eight (red mullet) times higher than the optimal value in some cases (e.g. Colloca et al., 2017). While great effort is currently invested in protecting both nursery (i.e. recruitment) and spawning areas of hake (Druon et al., 2015), juveniles, a highly fishery-impacted life stage, are not efficiently protected by regulations.

Fishing mortality and environmental factors are considered the primary drivers in the population dynamics of fish species, though there still is a knowledge gap regarding the relative effect of growth, condition, or environmental drivers in shaping juveniles' survival. In the present study, we explore the hypothesis that condition and growth affect the survival -expressed in two different metrics, as regular survival and recruitment success-of two of the most important commercial species in the Mediterranean Sea, hake and red mullet. We examined the relative effect of growth, condition, and environmental factors on survival, and whether the contribution of condition or growth can change in hake and red mullet, two species with starkly contrasting life histories and habitats. We further investigated the potential influence of condition at sub-regional level by examining whether the linkages between condition and demographic processes such as survival or recruitment success detected at regional scale are also observed at sub-regional scale in order to identify potential demographically important areas. We discuss the implications of our results in the context of stock assessment and spatially based fishery management.

2. Materials & methods

2.1. Selected species

The selected species, hake and red mullet, are of high commercial value for the Mediterranean demersal fisheries (e.g. Papaconstantinou and Farrugio, 2000; Piroddi et al., 2017; Sion et al., 2019). Though they are both demersal, they exhibit contrasting life history strategies, favorable habitats and trophic preferences and interactions. The continental shelf and coastal areas constitute the nursery sites for hake and red mullet, respectively (Druon et al., 2015; Paradinas et al., 2020). Hake exhibits daily vertical migrations in contrast to the red mullet which predominantly inhabits sandy and muddy bottoms and is characterized by a more benthic behavior (Bozzano et al., 2005; Tserpes et al., 2019). From an exploitation perspective, specific age groups of both species are targeted by commercial bottom trawls in the Mediterranean. Hake recruits (age-0) and juveniles (age-1) are the most impacted age classes while the catchability and fishing pressure on adults is comparatively lower (i.e. the known as 'spawning refugia', Caddy, 2015). All red mullet specimens older than age-1 are targeted by fisheries (Colloca et al., 2013).

2.2. Survey fish sampling and stock estimates

Data on the selected species were obtained from international MEDITS bottom trawl surveys that have been conducted on an annual basis between spring and early summer since 1994 (Spedicato et al., 2019). This study covers the trawlable waters off the coast of Northern Spain within the Geographic Sub-Area (GSA) 6 from 10 to 800 m depth (Fig. 1). Further specifications about the MEDITS sampling can be found in (Bertrand and Spedicato, 2017). Here we used individual weight and length information available from 1994 to 2017 for hake and from 2008 to 2017 for red mullet.

All individuals were grouped into age classes that are currently used in the GFCM stock assessment working groups (Anonymous 2017). These age-classes are time invariant but they are appropriate for the scope of this study as we overcome the challenges of otolith-based age

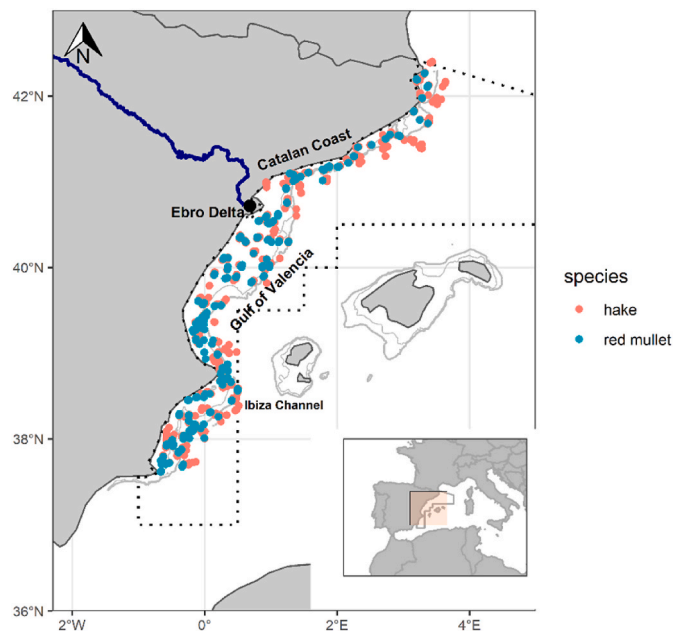


Fig. 1. Overview of the study area with the hauls that were carried out from 1994 to 2017. The dotted line represents the boundaries of the Geographic Sub Area (GSA) 6 and the blue line represents Ebro River.

determination described for both species (Belcari et al., 2006; Carbonara et al., 2018), and they will allow direct comparison with assessment reports and other studies that utilize data from MEDITS surveys and current fisheries assessment. For both species, age-slicing remains the preferred method for age determination in the GSA 6 as age-length keys have not yet officially established for the species in the area while great variability is documented across the Mediterranean with regard to age determination from annuli (e.g. Carbonara et al., 2018). For hake, age classes were determined as follows: recruits (age-0, less than 15.5 cm), juvenile males (age-1, between 15.5 and 29 cm) and juvenile females (age-1, between 15.5 and 32.5 cm) and adult males (age-2+, more than 29 cm) and adult females (age-2+, more than 32.5 cm) (García-Rodríguez and Esteban, 2002). Red mullet specimens were grouped as follows: recruits (age-0, less than 11.1 cm), young adults (age-1, between 11.1 and 17.9 cm), adults of age-2 (between 17.9 and 22.6 cm) and adults of age-3+ (more than 22.6 cm) (Demestre et al., 1997). These length-at-age relationships were used in the latest assessment of red mullet in the Western Mediterranean (Rodríguez, 2021). Due to limited data on age-2+ of hake and age-0 of red mullet, these age groups were excluded from the rest of the analyses. Data on abundance were standardised to number of individuals per km² (n/km²) using the swept area to obtain density estimates per haul, age class and year. The stratified mean equation by Souplet (1996) was employed to calculate the abundance indices per haul and age class and year. A mean length per haul, sex, age class and year was also calculated.

Data deriving from the regular assessments of the Geographic Sub Area (GSA) 6 (Northern Spain) were also used to retrieve information about spawning stock biomass (SSB) and recruitment (R) estimates (Gil et al., 2021; Rodríguez, 2021; <https://www.fao.org/gfcm/data/safs/en/>).

2.3. Mean length and condition indices

Specimens from both species captured in the surveys were counted, sexed, measured to the nearest 0.5 cm below and weighted to the nearest 0.1 g. Sex could not be determined only for a very small fraction of red mullet specimens which were excluded from the analyses. In regard to hake, the sex of the majority of recruits (age-0) could not be determined,

however, considering that both sexes in this age group have similar patterns on mean length (ML), abundance, survival and spatial patterns for the age classes considered herein (Hidalgo et al. 2019a), the two sexes were combined and treated as a single entity for the rest of the study.

We used the relative condition index (K_n ; Le Cren, 1951) as a proxy of body condition, which is widely utilized in fisheries science (Gubiani et al., 2020) and has previously been applied for the examined species (e.g. Gücü et al., 2021; Hidalgo et al., 2008). For each individual i , K_n was calculated as $K_n = 100(W_i/W'_i)$, where W_i is the actual weight and W'_i is the predicted weight from the length weight equation $W' = a \times (TL)^b$, with TL being the total length. We used Ordinary Least Squares (OLS) regression after detecting a very strong correlation between OLS and another applicable regression method (supplementary material). Preliminary analysis showed no statistical differences in condition between males and females of hake juveniles (age-1) and thus condition indices were estimated for all individuals of this age class together. Differences between the two sexes were detected, however, in preliminary analyses for the red mullet in all age classes. Therefore, the condition was estimated separately for each sex and then all specimens of the same age class were pooled together in the same data set for posterior analyses.

In addition to K_n , a second condition index was calculated by retrieving the residuals from the linearized regression of the length–weight relationship and standardising them by dividing each residual by the standard deviation of the predicted values ($SR_i = \text{residual}_i / \text{standard deviation}$) (Labocha et al., 2014).

2.4. Survival, growth, and recruitment success

Survival (S) per age class per year was calculated using the annual abundance indices from the surveys. Given two consecutive years, $t-1$ and t , we calculated an index of survival (S) between age a and the ensuing age $a+1$ as follows:

$$S_{(a \rightarrow a+1),t} = X_{(a+1),t} - X_{a,(t-1)} \quad (1)$$

where $X_{(a+1),t}$ and $X_{a,(t-1)}$ are the natural logarithms of the annual abundance index of age $a+1$ and age a , respectively.

An index of growth (G) per age class between years was calculated based on the mean length obtained by MEDITS as follows:

$$G_{(a \rightarrow a+1),t} = Y_{(a+1),t} - Y_{a,(t-1)} \quad (2)$$

where $Y_{(a+1),t}$ and $Y_{a,(t-1)}$ are the natural logarithms of ML of age $a+1$ and age a , respectively.

Finally, Recruitment Success (RS) index was obtained by dividing the recruitment R (young-of-the-year, age-0), in terms of recruit number, of a year t by the total Spawner Stock Biomass (SSB) of the preceding year $t-1$:

$$RS_t = R_t / SSB_{(t-1)} \quad (3)$$

2.5. Environmental data

To examine whether environmental variability exerts an additional or more robust effect than condition and growth do on survival, several environmental and hydroclimatic variables and indices were used. Two potential local environmental drivers from remote sensing were selected: primary productivity in terms of chlorophyll a (chl- a) concentration (E.U. Copernicus Marine Service Information, <https://doi.org/10.48670/moi-00300>) and sea surface temperature (SST) (E.U. Copernicus Marine Service Information, https://doi.org/10.25423/CMCC/MEDSEA_MULTYEAR_PHY_006_004_E3R1), whose effect on the two selected species and other demersal communities has already been shown in other studies (e.g. (Cook and Heath, 2005; Levi et al.,

2003; Rueda et al., 2014). Bottom temperature was not included in this study as it is generally more conservative than temperatures in the rest of the water column (Hiddink and Ter Hofstede, 2008) and thus it would not be expected to significantly affect survival and growth dynamic. These variables were previously found to be important as observed in species-specific responses and low trophic level effects (Hidalgo et al., 2019a; Puerta et al., 2014; Rueda et al., 2014). Seasonal averages of sea surface temperature and chl- α were calculated corresponding to a cool (including December of the previous year, January, and February of current year) and a warm season (May, June, and July of current year). The cool period average corresponds to the main phytoplanktonic bloom and to a delayed response of the model species to the physical variables they are subjected to; the warm period average lines up with the time that MEDITS trawl surveys are conducted. Averages were calculated over the whole study area from 1994 to 2017 for SST and from 1998 to 2017 for chl- α .

In addition, two climatic indices broadly applied in this region were used. The Regional Hydroclimatic Index (RHI) (Monserrat et al., 2008) has been documented to have a close relationship with the recruitment success of hake (Massutí et al., 2008a; Hidalgo et al., 2011; 2019a). RHI (also referred as IDEA index in other studies) is used as a proxy of Western Mediterranean Intermediate Water (WIW) formation in the Gulf of Lions during winter based on air-sea heat exchange anomalies in the North-Western Mediterranean, and has been related to the inter-annual variability of WIW characteristics as well as to the seasonal surface circulation and primary production patterns in the region (Balbín et al., 2014; Monserrat et al., 2008). Furthermore, the Local Climatic Index (LCI) (Molinero et al., 2005) was also applied. In particular, LCI quantifies an integrated hydroclimatic variability at the regional scale, synthesizing the air temperature, sea surface temperature, atmospheric sea level pressure, 500 hPa geopotential height, and precipitation rates at a monthly scale by means of the first axis of a Principal Component Analyses. High LCI values are associated with higher atmospheric sea level pressure and 500 hPa geopotential height, and negative values with high precipitation rate. It has been used in previous studies (Hidalgo et al., 2011; Puerta et al., 2014). LCI was also seasonally calculated for the cool and warm seasons.

2.6. Statistical analyses

For descriptive purposes, we employed Generalised Additive Models (GAMs) to reveal the mean geographic pattern for each age class of Kn and ML. Interannual differences in for Kn and ML for both species and all age classes were also explored.

Generalised Linear Models (GLMs) (Nelder and Wedderburn, 1972) with a Gaussian distribution and identity link were used to test the effect of explanatory variables on survival and growth while GLMs with a Gamma distribution and log link were used for the effects on the recruitment success. For an i response variable Y and j explanatory variables X , the model can be written as:

$$Y_i = \alpha + \sum_{j=1}^p \beta_j X_{ji} + \varepsilon_i \quad (4)$$

where α is the intercept, β_j are regression coefficients (slopes) and p is the number of explanatory variables included in the analysis.

The explanatory variables included the mean length (ML) and the condition index (K_n) for different age classes and all environmental variables described above. As growth directly derives from ML, the latter was not included in the models of growth. Additionally, growth was included as an explanatory variable in the models of survival and recruitment success for both species. To test for collinearity among the environmental variables, we estimated the Pearson's correlations among them. No strong correlation was detected in the set of the environmental variables (all $R^2 < |0.6|$). Model selection was based on Akaike's information criterion (AIC) minimization as well as model

diagnostics. Models with Delta AIC values (ΔAIC : difference in AIC from the single best model) of less than 2 were considered equally plausible (Burnham and Anderson, 2001). For every model, residuals were checked for variance homogeneity and absence of temporal autocorrelation in the residuals.

To identify small-scale areas that are closely associated with the processes indicated by the best model on regional scale, that is areas where the observed patterns are more pronounced and prevailing, we selected the best models in which ML or K_n were included as explanatory variables, and we replicated them spatially. To do that, we first divided our study area into cells of 0.5° and we fit the model with the same set of covariates as the best regional model, after having calculated ML and K_n for each age and grid cell. Following that, we replicated the best model for each cell using the ML or K_n information associated to the given cell and the environmental covariates of the best regional models. We retained the coefficient (i.e. slope) associated to K_n and/or ML effect and represented spatially as a measure of the strength of the effect. Only the cells with a p -value < 0.1 or p -value < 0.05 were plotted, representing areas of high prevalence of the effect and hotspots, respectively. This approach allowed us to reveal the areas where the relationship demonstrated by the respective GLM (Table 1) was prevailing spatially assuming that all the other regional covariates (e.g. environmental covariates) remain constant for the whole region.

All statistical analyses were performed in R version 3.6.2 (R Core Team 2020). In particular, the package "mgcv" (Wood, 2011) was used for the computation of GAMs.

3. Results

Overall, 37964 specimens of hake and 10677 specimens of red mullet were collected from 1994 to 2017 and from 2008 to 2017, respectively. Individuals were caught over a mean of $59.8 (\pm 17.2)$ and $50.1 (\pm 14.8)$ hauls in our study area per year (Fig. 1).

3.1. Mean spatial and temporal patterns of ML and K_n

Figs. 2 and 3 depict the mean spatial and temporal patterns of K_n and ML per age class. Hake recruits of better condition were found in coastal

Table 1

Covariates of the best GLMs obtained to model survival, growth and recruitment success as response variables for the three best models, when three models with significant covariates are available. Models were independently performed for all individuals. Signs in parentheses represent the direction of the effect in the response variable (positive effect, +, and negative effect, -). Adjusted R^2 (R^2_{adj}), AIC and ΔAIC for each model are also displayed. ***, $p < 0.001$; **, $p < 0.005$; *, $p < 0.05$. S_{01} , S_{12} , S_{23} and G_{01} , G_{12} , G_{23} represent the survival (S) and growth (G) from age-0 to age-1, from age-1 to age-2 and from age-2 to age-3, respectively. RS: recruitment success, K_n : body condition, ML: mean length, SST: Sea Surface Temperature, LCI: Local Climatic Index, RHI: Regional Hydroclimatic Index, _w: warm season, _c: cool season.

Response variable	Explanatory variable(s)	R^2_{adj}	AIC	ΔAIC
Hake				
S_{01}	$K_{n,age1}^{**}(+)$, $ML_{age0}^{*}(+)$	0.49	25.309	0
G_{01}	$RHI^{*}(+)$	0.18	-35.297	0
	$RHI^{*}(+)$, $LCI_{_w}(+)$	0.20	-35.024	0.27
	$K_{n,age1}(-)$, $LCI_{_w}(+)$	0.20	-34.946	0.35
RS	$G_{01}(+)$, $RHI^{*}(-)$	0.101	22.449	0
	$Chl_{_w}(-)$, $K_{n,age2(t-1)}(-)$	0.14	23.681	0.23
	$RHI(-)$, $K_{n,age0}(-)$	0.03	24.137	1.69
Red mullet				
S_{12}	$ML_{age1(t-1)}^{*}(+)$	0.45	11.280	0
	$G_{12}^{*}(-)$	0.39	12.256	0.98
	$ML_{age2(t-1)}^{*}(+)$	0.36	12.766	1.49
S_{23}	$LCI_{_c}^{***}(-)$	0.79	1.006	0
G_{12}	$K_{n,age2}^{**}(-)$	0.56	-41.825	0
G_{23}	$LCI_{_w}^{*}(-)$	0.38	-57.742	0
RS	$SST_{_c}(+)$	0.31	-5.965	0

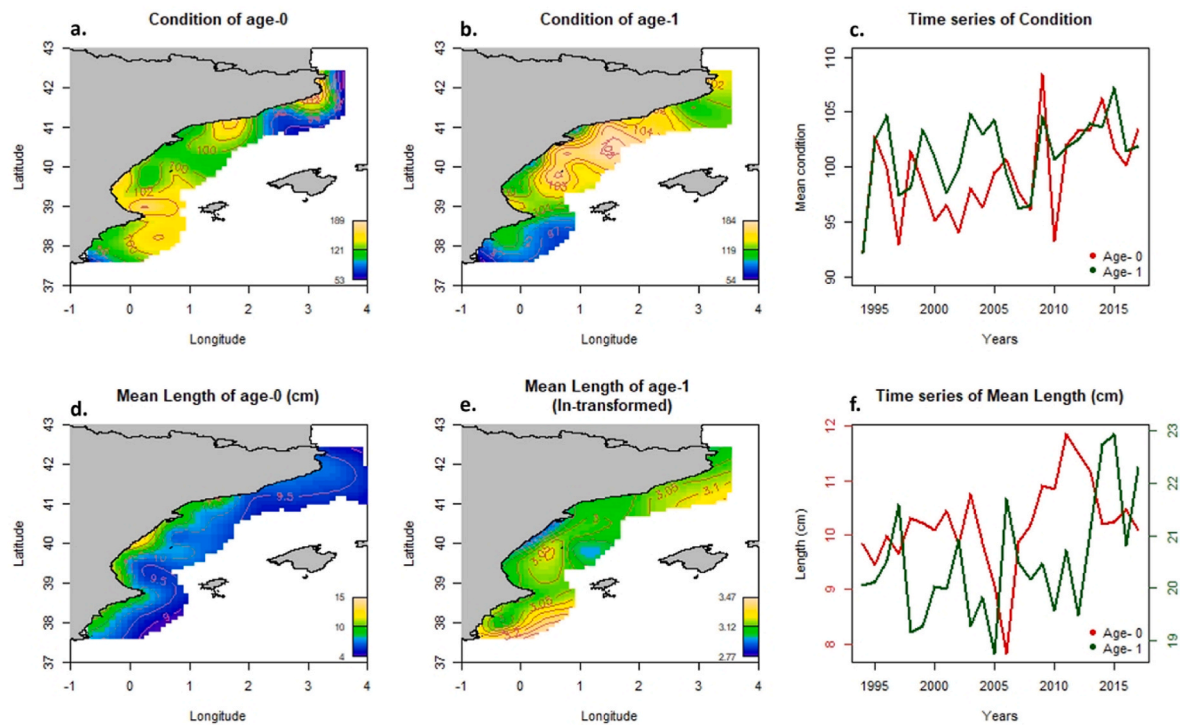


Fig. 2. Spatial and temporal variation of hake body condition (Kn, row above) and Mean Length (ML, row below). Condition of age-0 (a) and age-1 (b) specimens. Time-series of condition (c). Mean length of age-0 (d) and age-1 (e) specimens. Time series of mean length (f). Gaussian distribution with identity link was used for the GAMs in a, b and d and Gamma distribution with log link was used for the GAM in e.

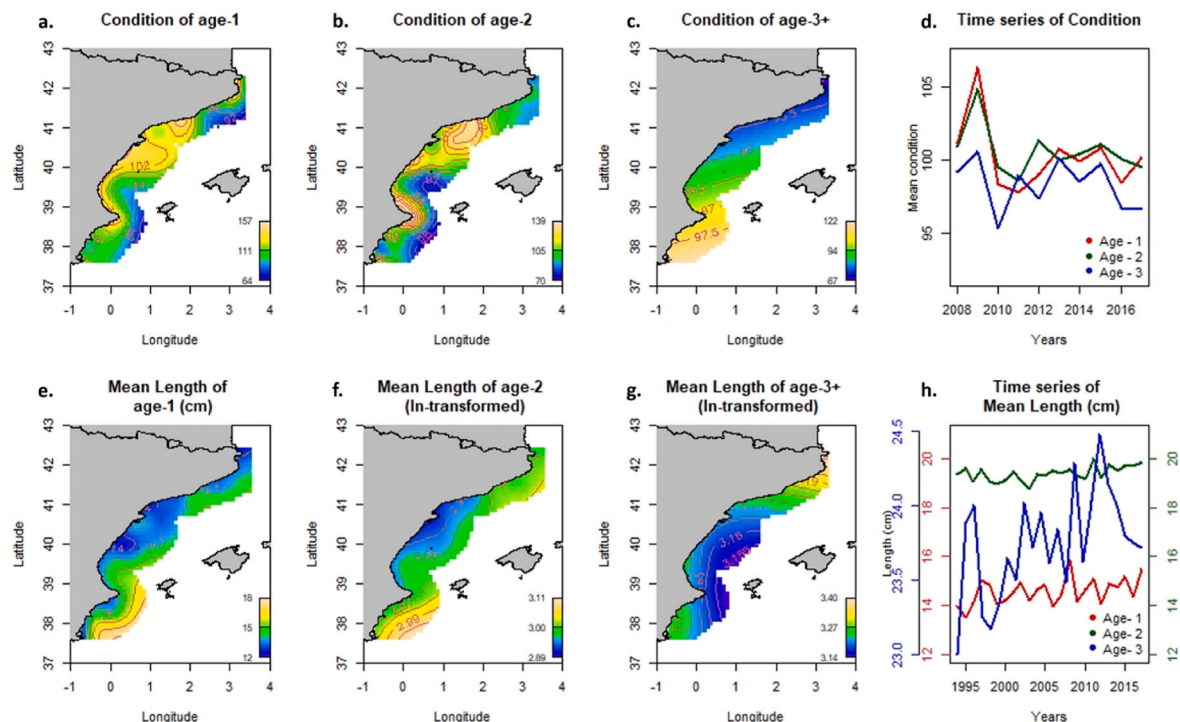


Fig. 3. Spatial and temporal variation of red mullet body condition (Kn, row above) and mean length (ML, row below). Condition of age-1 (a), age-2 (b) and age-3 (c) specimens. Time-series of condition (d). Mean length of age-1 (e), age-2 (f) and age-3 (g) specimens. Time series of mean length (h). Gaussian distribution with identity link was used for the GAMs in a, b, c and e and Gamma distribution with log link was used for GAMs in f and g.

waters where three distinct hotspots of high condition can be detected: the southern Gulf of Valencia, northeast of Ebro Delta, and off the Catalan Coast (Fig. 2a). Hake juveniles exhibited the highest K_n in

waters further offshore in front of Ebro Delta to an area extending from the north of the Gulf of Valencia to the southern Catalan Coast (Fig. 2b). The highest values of ML for hake recruits (Fig. 2d) were observed in

coastal waters near Ebro Delta, either southwards or northwards. Conversely, hake juveniles presented the highest values of ML in offshore waters and, particularly south of Ibiza Channel, with lower values observed in coastal waters (Fig. 2e). At a temporal scale, mean condition showed greater variation in the case of hake recruits (99.31 ± 4.27) and juveniles (101.20 ± 3.49) (Fig. 2c) compared to all age classes of red mullet which showed a more stable trend; age-1: 100.28 ± 2.41 , age-2: 100.63 ± 1.70 and age-3: 98.32 ± 1.72 (Fig. 3d). We found significant increasing trends in K_n of hake recruits and ML of juveniles across the time series (regression slope, $sl = 0.188$ and $sl = 0.075$, both $p < 0.05$). Large fluctuations in ML of recruits (10.19 ± 0.81) and juveniles (20.50 ± 1.11) (Fig. 2f) were detected with variations of up to 4 cm for both age classes. The lowest values for recruits and juveniles were observed in 2006 and 2005, respectively.

Red mullet young adults (age-1) and age-2 adults showed similar spatial patterns for K_n where the highest values were observed northeast of Ebro Delta (Fig. 3a and b). Age 3+ specimens had the highest values of K_n in the area south-southwest of Ibiza Channel (Fig. 3c). Young adults and age-2 adults exhibited similar spatial patterns of ML in our study area (Fig. 3e and f). Individuals with greater lengths preferred waters further offshore with higher concentrations on the south and southwest of Ibiza Channel. Lastly, age-3+ individuals with higher values of ML were associated to the northernmost part of the study area close to the French border (Fig. 3g). At temporal scale, all red mullet specimens showed the highest value of K_n in 2009 followed by a sharp decrease in 2010, when the minimum value for adult individuals was observed (Fig. 3d). Red mullet ML exhibited slighter fluctuations (young adults: 14.57 ± 0.55 , age-2 adults: 19.40 ± 0.30 , age-3+ adults: 23.75 ± 0.36) with the maximal difference between two separate years being approximately 2 cm observed in specimens of age-1 (Fig. 3h).

3.2. Temporal variations in survival, recruitment success and growth

Hake survival estimates from age-0 to age-1 ranged between -5.50 and -1.33 ($S_{01} = -2.57 \pm 0.87$) (Fig. 4a). For the red mullet, the survival estimates from age-1 to age-2 ranged between -2.23 and 0.23 ($S_{12} = -1.37 \pm 0.56$) while the one from age-2 to age-3 ranged from -2.19 to -0.37 ($S_{23} = -1.34 \pm 0.40$) (Fig. 4d). A positive value of survival observed in 2006 indicates that the number of age-2 specimens in 2006 was higher than the number of age-1 specimens in the preceding year.

This is linked to a sharp increase in abundance across all age classes of red mullet observed in 2006 (Appendix S11) which is possibly associated with an immigration of individuals from neighboring regions due to underlying connectivity processes or with an unknown to us peculiarity in the sampling procedure of that year.

Growth estimates for hake individuals fluctuated from 0.48 to 0.86 ($G_{01} = 0.69 \pm 0.1$) (Fig. 4b) while the same estimates for red mullet showed more limited fluctuations across the whole time series ($G_{12} = 0.30 \pm 0.03$, $G_{23} = 0.21 \pm 0.02$) (Fig. 4e). Finally, recruitment success (RS) estimate for hake ranged from 4.65 to 5.94 ($RS = 5.04 \pm 0.3$) across the years while the same estimate for red mullet only reached a plateau of 2.54 ($RS = 2.25 \pm 0.14$).

3.3. Drivers of survival, recruitment success and growth

Table 1 shows the three best models for the survival, growth and recruitment success for the two study species. For hake, the survival from recruit to juvenile stage is positively influenced by the body condition of juveniles and the mean length of the recruits. Growth from recruit to juvenile stage was found to be positively influenced by the Regional Hydroclimatic Index (RHI) although the condition of juveniles was found to exert a negative effect on the growth too. The best GLMs for RS revealed a positive association with the growth from recruit to juvenile stages, complemented by a negative effect of the condition of adults of the previous year, the RHI and the chl- α concentration in cool season.

For the red mullet, the survival from age-1 to age-2 was found to be positively affected by the mean length (ML) of the preceding year's young adults. A strong negative effect of the local climatic index (LCI_c) on the survival from age-2 to age-3 was also detected. Growth from age-1 to age-2 was negatively affected by the body condition of age-2 specimens while growth from age-2 to age-3 seems to be governed by the local climatic index but, in this case, with the warm season average (LCI_w). Finally, RS for the red mullet was found to be positively affected by the cool season sea surface temperature.

3.4. Spatial effect of the condition and mean length on survival

We considered all the best GLMs of Table 1 including the explanatory variables that were spatially variant (i.e. ML and/or K_n) for which we

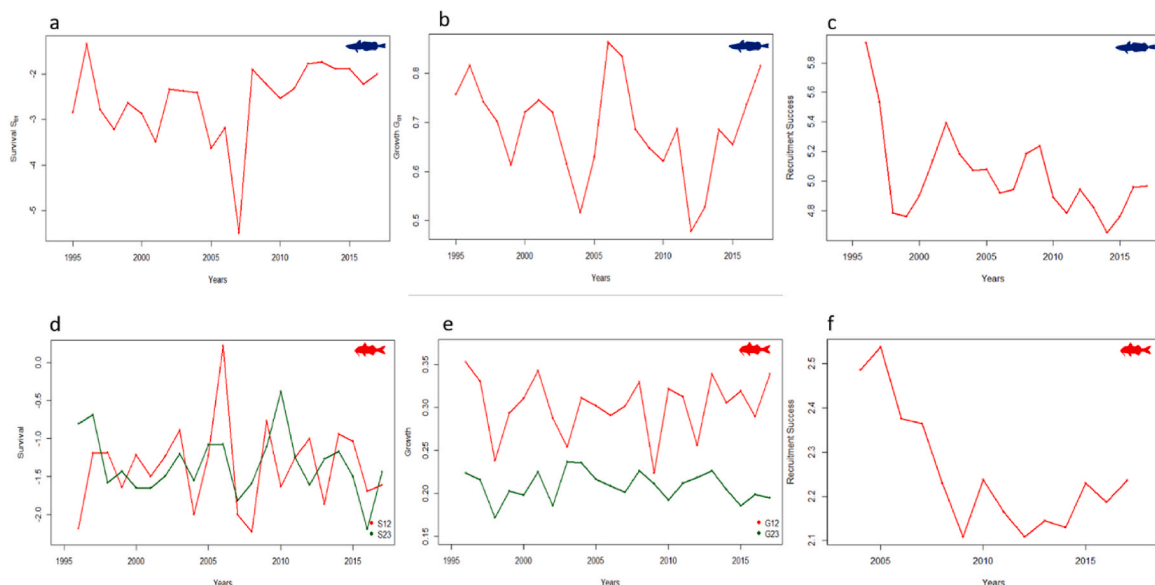


Fig. 4. Time-series of survival (a, d), growth (b, e) and recruitment success (c, f) for hake (above) and red mullet (below). S_{01} , S_{12} , S_{23} and G_{01} , G_{12} , G_{23} represent the survival (S) and growth (G) from age-0 to age-1, from age-1 to age-2 and from age-2 to age-3, respectively.

had information at a local scale (cells of 0.5°) to spatially analyse the effect we observed at regional scale. These models included: i) hake survival (S_{01}), hake growth (G_{01}) and red mullet survival (S_{12}) and red mullet growth (G_{12}) (Table 1). For hake, coastal waters adjacent to Ebro Delta were found to exhibit the strongest effect of juveniles' K_n on hake survival (Fig. 5a). Regarding the effect of ML of the recruits on the survival from the juvenile stage, it was found to be significant throughout the whole study area (Fig. 5b). The effect of hake juveniles' K_n on their growth (G_{01}) varied along the coastline of the mainland but it was found to be significant in grid cells near the Catalan coast, Ebro Delta and around Ibiza Channel (Fig. 5c).

In the case of the red mullet juveniles, a main positive influence of ML of specimens of age-1 of the preceding year on juveniles' survival (S_{12}) was observed in the south in the offshore areas of the Gulf of Valencia with coastal areas on the western area of Ibiza Channel displaying the strongest effect (Fig. 6a). Finally, the influence of spawners K_n on red mullet juvenile growth (G_{12}), was prevailing in the Gulf of Valencia as well as in the coastal water of the Catalan Sea (Fig. 6b).

4. Discussion

Our study shows that the survival in young stages of two of the most important commercial species of the Mediterranean Sea, hake and red mullet, is strongly regulated by a trade-off between the body condition and growth. That is, for both species, somatic growth was negatively related to condition and, at the same time, body condition and/or growth, were related to survival and recruitment success in addition to the influence of environmental variability in some cases (Table 1). The observed pattern for each of the two species was, however, different with the survival of hake mainly influenced by body condition variability while red mullet survival was mainly associated with growth and mean length variability. More specifically, we showed that hake survival

from recruit (age-0) to juvenile stage (age-1), S_{01} , is positively affected by the condition of juveniles and the mean length of recruits. This means that the greater the condition and the length of hake, the higher the chances are for its survival. However, as we also show that G_{01} is negatively linked to the condition of juveniles, it can be inferred that although both the condition and the growth are important parameters positively linked to survival, they are negatively associated with each other. As for red mullet, survival S_{12} was negatively affected by the growth G_{12} , while G_{12} was directly negatively affected by body condition of adults of age-2. Our study, thus, shows that the way each species regulates the trade-off between growth and condition is important to understand their survival dynamics. This is the first study revealing the direct and opposite effects of growth and body condition on the survival of two highly important Mediterranean species.

Complex links between body condition and other life-history parameters have been reported or speculated, such as the reproductive potential (Lloret et al., 2008) and survival (ICES, 2016) for the Mediterranean hake, with the latest not yet substantiated. Hence, beyond energetic dynamics, somatic growth and condition are critical to understand the variability of demographic rates such as survival (Casini et al., 2016a; Jensen et al., 2018). Hake survival from recruit to juvenile stage was positively related to the condition that was accumulated along this ontogenetic step in the form of energy reserves. This was ultimately measured as the juvenile body condition. It has been demonstrated that food availability affects the condition of hake (Lloret and Leonart, 2002) and can have a significant impact on the survival of juvenile specimens (Maynou, 2003). Additionally, environmental variability, apart from directly influencing fish condition, has also been shown to affect hake prey abundance and thereby exert an indirect effect on the condition and the survival of the species (Rueda et al., 2019). Hake juveniles -the most heavily fisheries-targeted age group-are also characterized by a size-dependent survival (Hidalgo et al., 2019a). This is

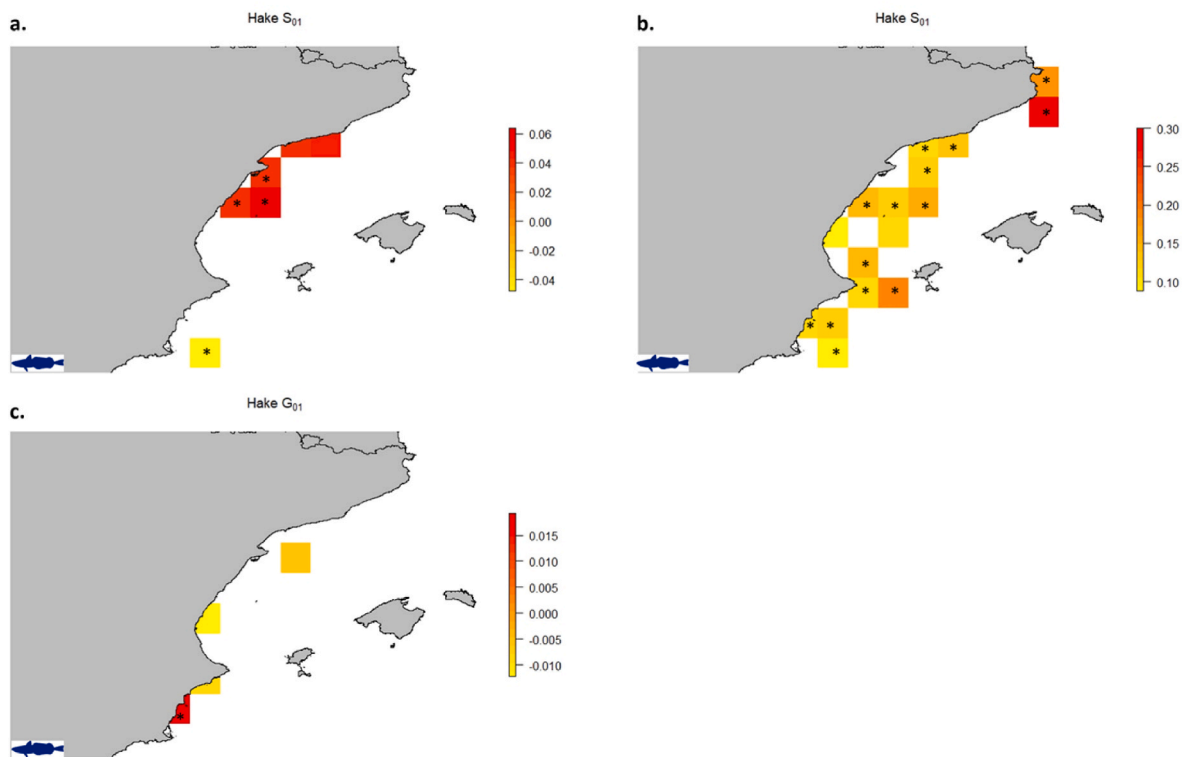


Fig. 5. Spatial effect of K_n and ML of the best GLMs in a $0.5^\circ \times 0.5^\circ$ grid where the coefficients of the models are given. (a, b) hake $S_{01} \sim K_{n,age1} + ML_{age0}$ and (c) hake $G_{01} \sim K_{n,age1} + LCI_w$. Cells with an asterisk (*) represent a high level of significance of the effect ($p < 0.05$); the rest of the cells represent a $p < 0.1$. Note that ML_{age0} in (a) and $K_{n,age1}$ in (b) are spatially invariant in order to explore the dynamic effect of $K_{n,age1}$ in (a) and that of ML_{age0} in (b). Also note that LCI_w in (c) remains spatially invariant. S_{01} , G_{01} represent the survival (S) and growth (G) from age-0 to age-1, respectively; LCI_w : Local Climatic Index during the warm season.

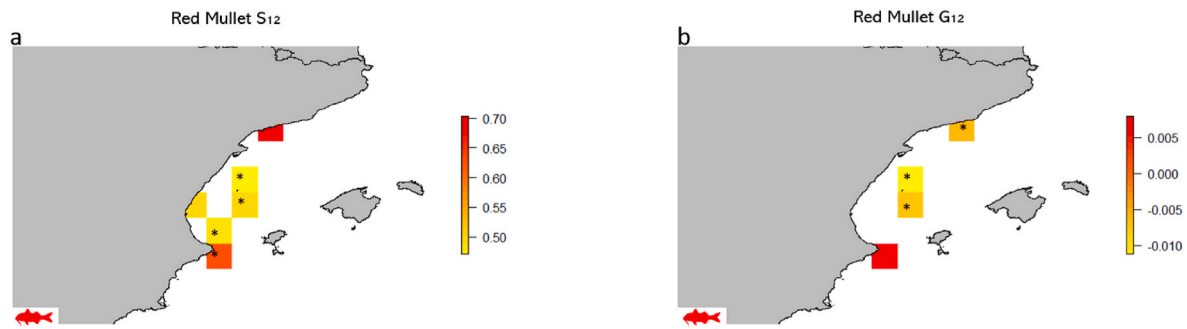


Fig. 6. Spatial effect of Kn and ML of the best GLMs in a $0.5^\circ \times 0.5^\circ$ grid. (a) Red mullet $S_{12} \sim ML_{age1(t-1)}$ and (b) red mullet $G_{12} \sim Kn_{age2}$. Cells with an asterisk (*) represent a high level of significance of the effect ($p < 0.05$); the rest of the cells represent a $p < 0.1$. S_{12} , G_{12} represent the survival (S) and growth (G) from age-1 to age-2, respectively.

consistent with our results, but we also found that the role of condition is equally important and therefore years in which hake is able to maximize condition from recruits to juveniles do favor the survival of the species. By contrast, for the red mullet, the survival from age-1 to age-2 was driven by the mean length of age-1 specimens of the previous year, suggesting that growth during the early life stages affects posterior survival. This is consistent with the general pattern ‘the bigger the better’ generally observed in nature, particularly in young stages (Bonner 2011), something that has also been documented for demersal fish species (Primo et al., 2021). Rueda et al. (2015) showed that there is a species-specific strategy in the growth regulation in length or weight during the first ontogenetic stages of gadoid species. Species that are highly dependent on mesopelagic behavior, such as blue whiting (*Micromesistius poutassou*), thereby more susceptible to being preyed, allocate their energy in growing faster in length to maximize survival. While this does not seem to be the case for red mullet juveniles, the recruits of this species undergo a relatively long phase of pelagic behavior before they settle to the bottom, during which growth in length should be maximized as a survival strategy (Carbonara et al., 2019).

Recruitment success, an indicator of recruits’ survival over the first stages of life, is typically presumed to be highly dependent on the environment. Previous studies have highlighted the contribution of environmental conditions to recruitment success of hake (Massutí et al., 2008b; Hidalgo et al., 2012; 2019a) and red mullet (Levi et al., 2003; Tserpes et al., 2019). Our results, however, demonstrate that, beyond environmental variability, both the condition of spawners and the growth of juveniles have a major effect in the temporal variability of this critical vital rate. Hake RS was negatively influenced by spawners condition of the previous year and positively influenced by juvenile growth. Although this is in contrast with the big old fat fecund female fish (BOFFFF) paradigm based on which the condition of spawners favors eggs production and recruitment (Marshall et al., 1998 and references therein) while ensuring reproductive success (Hixon et al., 2014), our study may have not a complete view of hake spawning stock as scientific surveys primarily captures recruits and juveniles of hake and not adult and large specimens. Furthermore, the spawning season that is associated to the recruits captured during spring in the surveys is autumn (Recasens et al., 1998). Given the clear phenology of energy allocation for hake (Hidalgo et al., 2008) and the period when the survey is conducted (i.e., late-spring/early summer), we likely miss an accurate signal of hake spawners’ condition. Red mullet RS was found to be positively influenced by the cool season sea surface temperature. Our results evidence that the morphometric condition of spawners is the main factor affecting the recruits’ survival (Carbonara et al., 2015). Recent studies evidence that connectivity processes in the early life stages and, particularly, self-recruitment off the Catalan coast play an important role in the hake recruitment dynamics off the Spanish coast (Hidalgo et al., 2019b). Here we add that the condition gained along these months is also critical to maximize the survival during the first year. Our results

are in line with Brosset et al. (2020) and Szuwalski et al. (2015) who maintain that extreme life stages mortality largely affects recruitment.

Limited resources in the environment prevent individuals from simultaneously allocating energy in all life-history traits and this generates trade-offs (Brosset et al., 2016). This is particularly evident in the Mediterranean Sea because, as it constitutes a generally oligotrophic system, the opportunities for favorable environmental conditions and productivity are temporally and spatially segregated (Piroddi et al., 2017; Russo et al., 2019). Previous studies have documented energy allocation trade-offs in Mediterranean gadoids between body size and lipid reserves (Hidalgo et al., 2009) or between lipid reserves and reproduction (Serrat et al., 2019). However, the existence of a trade-off has not yet been demonstrated for two important traits for recruits and juveniles such as the somatic growth and condition; a relationship that might differ among species (Rueda et al., 2015), as we observed in our study species. Although our two study species show evidence of a trade-off between somatic growth and condition, this is more evident in the case of red mullet for which we have a better coverage of the different ontogenetic stages until young adults (from age 1 to age 2) that provide a more complete display of the counterbalance of these two features. In the case of hake, this can also be identified in the transition from recruits to juveniles and we posit that it could be more evident with a better coverage of information for age-2 (adults), which is not currently available due to the high decrease of catchability of adults of this species by trawl. A recent study on tropical fishes showed that individuals occupying new cooler waters as a response to climate change, exhibit trade-offs between growth and condition (Kingsbury et al., 2020). This supports a more pronounced development of counterbalanced energy allocation as environmental conditions become less favorable and metabolic costs increase (Neuheimer et al., 2011). As of that and given the expected impacts of climate change on the Mediterranean fish species (FAO, 2018), the influence of the energetic dynamics on key vital rates as survival is likely to increase.

Environmental conditions also hold an important role in affecting survival, condition or growth in fish, including the two species examined in the present study (Clark et al., 2020; Rueda et al., 2019). The Regional Hydroclimatic Index (RHI) was the primary environmental variable that was found to be associated with hake juveniles’ growth and recruitment success. This implies that years with negative values of this index, that is higher convection and anomalously strong formation of intermediate waters in the Gulf of Lion forced by winter wind-driven vertical mixing (Balbín et al., 2014; Monserrat et al., 2008), will trigger a reduced growth and recruitment success. Assuming the trade-off discussed above, this scenario could favor the condition of recruits with more nutrient-rich waters flowing southwards and increasing biological productivity in the Balearic Sea (Balbín et al., 2014), ultimately affecting recruits’ survival. A similar influence on the condition of recruits was reported recently by Ordines et al. (2019), although it is known that this index can trigger contrasting geographic influence due to the different

local processes with which it is associated in different areas (Hidalgo et al., 2019a). In the case of red mullet, we detected a strong negative effect of the local climatic index associated with the cool season (LCI_c) on survival from age-2 to age-3, that is low values of the index favor the survival of this cohort and vice versa. Negative values of this index in winter are associated with higher temperatures, higher atmospheric sea level pressure while positive values are linked to higher precipitation rates (Puerta et al., 2014). This scenario can pose a risk for the red mullet which has been shown to be positively influenced by increased SST anomalies in different region of the Mediterranean (Levi et al., 2003). Furthermore, there have been studies maintaining that elevated temperatures may enhance red mullet populations locally such as in the case of Sicily (Fiorentino et al., 2008) and the Aegean Sea (Maravelias et al., 2007). However, this can be also related to the food availability to the red mullet specifically, as it has been shown that this index can also influence other species belonging to the benthic realm (e.g. Puerta et al., 2014). It is important to note that interacting (non-additive) effects between growth and environmental variables that might have an effect on survival and recruitment success of hake and red mullet were not explored in the present study.

Our study also revealed the existence of a spatial scale-dependence in some of the relationships afore described. This highlights the impact that a potential protection of certain areas can have on the dynamics of the whole population if protection is focused on critical demographic functions (i.e. survival and recruitment success) affecting species occurrence, abundance and biomass. European hake and red mullet are common species in the Mediterranean with differences in biological characteristics and suitable habitats and, consequently, different species-specific hotspots of abundance throughout the basin (Tserpes et al., 2019; Sion et al., 2019), although they often co-occur in certain areas. Our results illustrate that the Ebro Delta and its shallow shelf extending southwards in the Gulf of Valencia constitute a hotspot for the influence of body condition of young specimens on the survival of the two examined species, with secondary areas identified north in the Catalan coast and further south in the Ibiza Channel. The surrounding area, under the influence of the Ebro Delta runoff, is considered a biomass hotspot for hake (Druon et al., 2015; Sion et al., 2019), particularly associated with the occurrence of large nursery areas. Rueda et al. (2019) showed that the shelf off Ebro Delta is an important area for the influence of hake condition due to its high productivity. The same area has also been found to play another vital role for hake by constituting a key reproduction area for the species (Lloret-Lloret et al., 2020). Recent efforts have been made to protect Ebro Delta with spatiotemporal closures (Regulation (EU) 2019/1022, Jardim et al., 2019) or others recently proposed for the area (e.g. FRA proposal in the Ebro delta, Bastari et al., 2020). Our findings about the influence of condition on survival rates support this need by evidencing the key role of the Ebro Delta as demographic engine for the species harvested over the Spanish mainland coast of the Mediterranean Sea. Likewise, for the red mullet, all areas identified for the juvenile survival of this species are consistent with those identified by Paradinas et al. (2020), who demonstrated the existence of the same hotspot areas of abundance of larger individuals suggesting survival. Although the positive effect of condition on survival in hake is relevant for the whole study area and it is particularly important in the areas around Ebro Delta, we observe one area in the southernmost part of our study where the condition seems to have a negative effect on the survival of hake. This may be related to the decrease of recruitment success in secondary nursery areas (note that the main one is off Ebro Delta), as a consequence of the long-term recruitment production decrease of the species over the last two decades.

5. Implications and concluding remarks

Recruitment and natural mortality are the two main key ecological processes come into the stock assessment procedures and our results

demonstrate that both rates are impacted by the condition and growth dynamics in the Mediterranean Sea. Nowadays, the majority of marine stocks are assessed with age-based single species assessment models (e.g. age-based Assessment for All (a4a) tool, Jardim et al., 2019) which omit environmental and ecosystems complexities that are incorporated in other more integrated frameworks within Ecosystem Approach to Fisheries Management (EAFM) (Skern-Mauritzen et al., 2016). Moreover, only a handful of marine stocks are evaluated in a way that embodies condition as a biological component (e.g. Black Sea anchovy, Lloret et al., 2014), even though many stocks are suffering from condition distress, i.e. the reduction of individuals condition over the past years or decades (Brosset et al., 2016). Our results highlight that, in addition to implementing ecosystems and environmental information to spatial management and regular fisheries assessment, the dynamics of life history characteristics such as growth and condition need to be considered. For instance, natural mortality, a fundamental component of fish stocks, is generally assumed to be either a constant or a temporally invariant age-based vector (Casini et al., 2016a). However, recent studies illustrated the dynamic nature of natural mortality which can be size- and density dependent (Stige et al., 2019), related to fishing pressure (Jørgensen and Holt, 2013) and generate considerable biases in assessment models (Punt et al., 2021). It is important to note that density dependence was not explored in our study as we focused solely on somatic condition, mean length and environmental drivers. Specifically for hake, it has been documented that growth and survival relationship is mediated by density dependence (Hidalgo et al., 2019a). It is crucial that future studies investigate density dependence and how it affects the survival of red mullet. Our results, however, provide well-founded ecological support to further implement a dynamic influence of life history in the natural mortality information used for the assessment of the two species examined. It is deemed essential and practical to include condition and/or growth metrics in stock assessment protocols and this is of highlighted importance for the Mediterranean where fisheries target younger age classes in very high rates for most species (Colloca et al., 2013; Hidalgo et al., 2019a). The fact that we have found similar processes in two contrasting species support a fair suggestion that this important influence may be generalised to other species and regionalized to other areas of the Mediterranean Sea, and eventually outside of the basin.

For a sound and more comprehensive ecosystem-based management of fish stocks in the future, holistic and operational approaches need to be developed (Clark et al., 2020). It is essential to study and comprehend fish stocks biological processes and their various driving forces. In the present study, a trade-off between body condition and mean length as a growth proxy at given ages regulating survival and recruitment success is documented for two important Mediterranean resources for the first time. We also evidence that spatially based approaches are now necessary to consider in stock assessments and management as a few specific areas may be particularly important for the population dynamics of a species over regional scales. Important areas for such key biological processes for commercial species within a greater region are crucial for their demography and thus we advocate that such areas be considered in the designation of areas of special protection.

Author contributions

Conceptualization: MH; Methodology: GK, LR, MGP and MH; Validation: GK, LR and MH; Formal analysis: GK, LR and MH; Investigation: GK, LR and MH; Resources & Data Curation: GK, LR, JMB, AE, EG, LGS, MGP, JLPG and MH; Writing—original draft preparation: GK, LR and MH; Writing—review and editing: GK, LR, JMB, AE, EG, LGS, MGP, JLPG and MH; Visualization: GK, LR, MGP and MH; Supervision: LR and MH; Project administration: MH; Funding acquisition: GK, AE, EG, MGP and MH. All authors have read and agreed to the submitted version of the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2022.105844>.

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