

Accounting for ocean connectivity and hydroclimate in fish recruitment fluctuations within transboundary metapopulations

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Citation: Hidalgo, M., V. Rossi, P. Monroy, E. Ser-Giacomi, E. Hernández-García, B. Guijarro, E. Massutí, F. Alemany, A. Jadaud, J. L. Perez, and P. Reglero. 2019. Accounting for ocean connectivity and hydroclimate in fish recruitment fluctuations within transboundary metapopulations. *Ecological Applications* 29(5):e01913. 10.1002/eap.1913

Abstract. Marine resources stewardships are progressively becoming more receptive to an effective incorporation of both ecosystem and environmental complexities into the analytical frameworks of fisheries assessment. Understanding and predicting marine fish production for spatially and demographically complex populations in changing environmental conditions is however still a difficult task. Indeed, fisheries assessment is mostly based on deterministic models that lack realistic parameterizations of the intricate biological and physical processes shaping recruitment, a cornerstone in population dynamics. We use here a large metapopulation of a harvested fish, the European hake (*Merluccius merluccius*), managed across transnational boundaries in the northwestern Mediterranean, to model fish recruitment dynamics in terms of physics-dependent drivers related to dispersal and survival. The connectivity among nearby subpopulations is evaluated by simulating multi-annual Lagrangian indices of larval retention, imports, and self-recruitment. Along with a proxy of the regional hydroclimate influencing early life stages survival, we then statistically determine the relative contribution of dispersal and hydroclimate for recruitment across contiguous management units. We show that inter-annual variability of recruitment is well reproduced by hydroclimatic influences and synthetic connectivity estimates. Self-recruitment (i.e., the ratio of retained locally produced larvae to the total number of incoming larvae) is the most powerful metric as it integrates the roles of retained local recruits and immigrants from surrounding subpopulations and is able to capture circulation patterns affecting recruitment at the scale of management units. We also reveal that the climatic impact on recruitment is spatially structured at regional scale due to contrasting biophysical processes not related to dispersal. Self-recruitment calculated for each management unit explains between 19% and 32.9% of the variance of recruitment variability, that is much larger than the one explained by spawning stock biomass alone, supporting an increase of consideration of connectivity processes into stocks assessment. By acknowledging the structural and ecological complexity of marine populations, this study provides the scientific basis to link spatial management and temporal assessment within large marine metapopulations. Our results suggest that fisheries management could be improved by combining information of physical oceanography (from observing systems and operational models), opening new opportunities such as the development of short-term projections and dynamic spatial management.

Key words: ecosystem-based management; fish recruitment; fisheries conservation; hydroclimate variability; metapopulations; ocean connectivity; self-recruitment.

INTRODUCTION

Manuscript received 9 May 2018; revised 11 March 2019; accepted 19 March 2019. Corresponding Editor: Éva Plaganyi.

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Understanding the complex dynamics of large marine fish stocks is one of the most pressing challenges for

fisheries science, as it is the fundamental basis to improve the reliability of future projections of fish production (Cheung et al. 2013) and since species shift their distributions due to climate change, increasing the number of transboundary stocks (Pinsky et al. 2018). Besides, there is a general acceptance that the spatial and demographic structure of marine populations is more complex than currently accounted for in assessment and management frameworks (e.g., Stephenson et al. 2009; Kerr et al. 2017). Indeed, marine populations are often structured as a metapopulation, that is, a set of sub-populations connected through the exchange of individuals (Carson et al. 2011, Castorani et al. 2015) and whose spatial boundaries rarely coincide with management units (Kerr et al. 2017). This limitation comes along the contemporary challenge in fisheries assessment and management of making the best use of physical predictions (from earth-system models up to high-resolution biophysical ocean models) to include them in the short-term projections of abundance of fish stocks (Hinrichsen et al. 2011). Despite a recent expansion of spatially explicit fish stock assessment procedures to cope with the populations' complexity (e.g., adult movement; Goethel et al. 2011), they still overlook the dynamics of early life stages potentially connecting sub-populations. Apart from those species whose adults migrate substantially (Frisk et al. 2014), connectivity is largely driven by physical dispersion due to multi-scale oceanic currents (Cowen and Sponaugle 2009), and has a profound impact on fish recruitment success and fish population dynamics (Botsford et al. 2009a,b, Harrison et al. 2012, Huwer et al. 2016).

Recruitment success (i.e., survival of progeny that enters a population in a given year) is a pivotal ecological process in fisheries ecology that relates quantitative observations of young fish to a measure of spawning potential (stock–recruitment relationships). Most of the fish recruitment research is still co-opted by contemporary topics such as assessing the effects of global changes on marine ecosystems and fisheries by exploring how large-scale climatic variability influences key ecological processes like survival (Rice and Browman 2014). Most of these studies, however, do not take into account the stochastic and fine-scale structures of the seascape, which shape both larval dispersal and survival resulting in “realized” connective pathways (Carson et al. 2011). Incorporating realistic larval dispersal schemes into population dynamics and fisheries studies could improve our comprehension of population structuring and its temporal variability (Castorani et al. 2015). By embracing simultaneously connectivity and environmental processes, we test here whether the combination of high-resolution connectivity patterns with climate influences and biological factors improves our capability of reproducing fish recruitment dynamics in a ubiquitous harvested nekto-benthic species.

Empirical studies in the prominent field of ocean connectivity have largely concentrated on small scales,

particularly for the spatial design of Marine Protected Areas (MPAs) networks in coastal and coral-reef seascapes (e.g., Botsford et al. 2009a,b, Almany et al. 2017). Recent large-scale modeling studies linked connectivity, MPAs and fishery sciences (Botsford et al. 2009a,b, Dubois et al. 2016, Krueck et al. 2017) but they remained eminently theoretical and they mainly focused on the implications for spatial management at transnational scale and long dispersal organisms (e.g., Kough et al. 2013, Andreollo et al. 2017). However, they did not explore, nor provide observational evidence of, how connectivity temporally affects fishery assessment exercises. Indeed, the effects of broad-scale connectivity on the spatiotemporal population dynamics of large populations has received little attention (Hidalgo et al. 2017), mostly focused on nearshore systems, or sedentary and benthic species with reduced mobility (Siegel et al. 2008, Carson et al. 2011, Watson et al. 2012, Rochette et al. 2013, Castorani et al. 2015). In the meantime, numerical models are becoming mature enough to study the influence of environmental variability on recruitment success, to improve stock management frameworks (Hinrichsen et al. 2011), as well as to explore the spatiotemporal variability of larval connectivity over several years (e.g., Ospina-Alvarez et al. 2015). Daewel et al. (2015) recently documented a relative predictive ability of modeled larval survival for observed cod recruitment in the North Sea, but their entire time-series were not significantly correlated due to non-resolved trophic interactions. Simulated multi-annual connectivity estimates have been indirectly interpreted in the context of fisheries (e.g., Huwer et al. 2016, Andreollo et al. 2017) but, to our knowledge, there is no report of significant and coherent relationship between modeled connectivity proxies and observed population estimates (e.g., assessment outputs of segregated stocks). Many biophysical models are being developed by the community to address this challenge but they often use different formulations and they generate various connectivity indices, which are not necessarily harmonized or inter-comparable. Nevertheless, most recent research suggests that the mechanistic and deterministic models currently used in fisheries assessment can be substantially improved by including realistic information of physical processes related with both larval dispersal and survival.

The reliability of fish assessment and management strategies are often questioned worldwide because of the mismatch between biological and management scales (Kerr et al. 2017). In the Mediterranean Sea, this has been recently challenged as a priority to ensure sustainability of assessed fish stocks (Fiorentino et al. 2014), of which more than 90% are in overexploitation state (Fernandes et al. 2017). This urges for effective measures and population dynamics modeling that realistically capture the ecological complexity of harvested populations. Focusing on the European hake (*Merluccius merluccius*), which is the most overexploited nekto-benthic species of the Mediterranean Sea, the present study aims at

addressing the following specific objectives. First, we assess the potential larval connectivity within and among six discrete subpopulations of hake in the Western Mediterranean. Second, we evaluate whether the connectivity estimates help to explain the temporal dynamics of recruitment and survival (i.e., the rate of individuals that survived from birth to the age of recruitment) in three contiguous geographical areas (hereafter referred to as “management units”) that currently frame independent assessment procedures for this species. By combining ocean circulation models, time-series of regional climate and biological variables, we model the spatiotemporal dynamics of hake recruitment. We then quantify the relative influence of the regional circulation-driven dispersal and the hydroclimate as selective forces shaping recruitment and survival across the metapopulation sub-units. Our results are discussed to question whether connectivity estimates provided by ocean models are able to effectively capture the temporal dynamics of key biophysical processes shaping fish recruitment and how they can improve the ecological basis of fisheries assessment and management.

MATERIALS AND METHODS

Metapopulation system

This work focuses on the northwestern Mediterranean metapopulation of European hake (*Merluccius merluccius*), an exploited nekton-benthic species of high economic value. The study system is structured by recognized physical and environmental recognized boundaries, and the phenology of key ecological processes such as spawning and recruitment. On the southern border, the Almeria-Oran front represents a physical barrier of transport by ocean currents, which confines the population structure and act as a gene-flow barrier for many marine species (Galarza et al. 2009). In addition, the recruitment of hake in the southwestern Mediterranean occurs in autumn whereas it peaks in late winter / early spring in the study area (Rey et al. 2004, Recasens et al. 2008). In the north-east, the spawning phenology of hake in the Ligurian and Tyrrhenian seas is seasonally opposed to that in the Gulf of Lion, off the Iberian Peninsula and around the Balearic Islands, which occurs in autumn (Recasens et al. 2008, Hidalgo et al. 2009). Altogether, this allows us to simplify our metapopulation to six distinct eco-regions consistent with recent studies (Hidalgo et al. 2009, Puerta et al. 2016): Gulf of Lion, Catalan coast, Ebro delta, Valencia gulf, Northern and Southern Balearic Islands (Fig. 1). This structure of the metapopulation system implies that all larvae ending their dispersal phase outside of these regions are considered lost. Similarly, it presupposes that the potential arrival of dispersed larvae from other hake metapopulations is very unlikely and the effect minimal.

From now on and in the entire paper, we assumed that each of these eco-regions constitutes a metapopulation

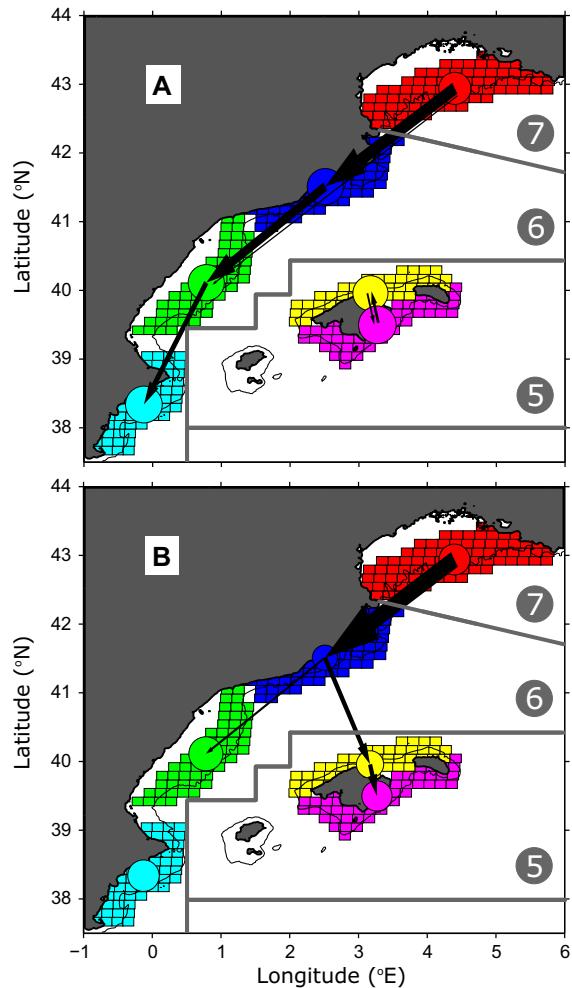


FIG. 1. Normalized estimates of larval exchanges (arrows) and retention (colored circles) among the different subpopulations of hake (colored clusters composed of several individual nodes of the transport network). To facilitate the interpretation, only fluxes greater or equal to 5% of the total annual exchanges are displayed. Two panels are examples illustrating the two contrasting scenarios of connectivity. (A) Year 1989 shows the main southwestward transport pattern along the mainland with almost no import into the Balearic archipelago. (B) Year 2005 exhibits a reduced southwestward transport and stronger connections with the Balearic Islands. The six subpopulations are Gulf of Lion (red), Catalan coast (dark blue), Ebro delta (green), Valencia gulf (light blue), northern Balearic Islands (yellow), and southern Balearic Islands (magenta). Widths of arrows and diameters of circles are proportional to the strength of larval Import (Imp) and Local Retention (LR), respectively. Gray thick lines represent the three Geographic Sub-Areas (GSAs) that correspond with management units used by the General Fisheries Commission of the Mediterranean: Gulf of Lion (GSA-7), Iberian Peninsula (GSA-6), and Balearic Archipelago (GSA-5). Black thin contours show the 200-m isobaths.

subunit. That is, a subpopulation of hake *sensu stricto* as defined by Cowen and Sponaugle (2009) “a set of individuals that live in the same habitat patch and interact with each other.” We consistently use the term

“subpopulation” throughout this study for clarity purpose while alternative semantic choices and their scientific implications are further discussed in the light of our results. Our six hypothesized subpopulations correspond to three of the 30 current Geographical Sub-Areas (GSAs, gray contours on Fig. 1), currently used for assessment and management purposes in the General Fisheries Commission for the Mediterranean (GFCM): Gulf of Lion (GSA-7), Iberian Peninsula (which includes Catalan coast, Ebro Delta, and Valencia gulf subpopulations; GSA-6) and the Balearic Islands (encompassing both northern and southern Balearic subpopulations; GSA-5; map *available online*).⁸ We consistently use the term “management unit” to refer to these areas in this study.

Lagrangian flow network and connectivity metrics

We evaluate the dispersion of hake’s larvae among those six subpopulations using the Lagrangian flow network (LFN) methodology that has been inspired from network theory and dynamical systems perspectives (Ser-Giacomi et al. 2015). This framework has been applied to depict connectivity patterns within the entire Mediterranean basin (Rossi et al. 2014, Dubois et al. 2016). The oceanic surface is subdivided in thousands of equal-area rectangular subregions that serve as nodes (small boxes in Fig. 1) in our transport network. These nodes, equivalent of discrete habitat patches, are interconnected by weighted and directed links that represent, using the most adequate numerical and biological parameters (Monroy et al. 2017), passive transport of hake’s propagules (eggs and larvae) by ocean currents. Those links are orientated by the oceanic flow and are weighted proportionally to the normalized larval fluxes occurring over the entire period of the pelagic phase. To characterize such links, Lagrangian particle trajectories are computed by integrating the horizontal (two-dimensional) flow field generated by an eddy-resolving hydrodynamical model implemented at $1/16^\circ$ horizontal resolution in the Mediterranean over years 1987–2011 (Oddo et al. 2009). A total of 100 particles were seeded evenly in each node of $1/8^\circ$ width (this means releasing about 1 particle/km²) at a fixed subsurface layer. We retained here the layer at 90 m depth, where hake larvae have been mostly observed (Olivar et al. 2003). The pelagic larval duration (PLD) simulated is 40 days (Hidalgo et al. 2009). We considered repeated spawning events each year during the main autumnal spawning period of the species with seven starting times (15 days apart) from 1 September to 30 November (Hidalgo et al. 2009). We also performed additional sensitivity tests to further support the robustness of our conclusions (see Appendix S1).

From several millions of virtual trajectories representing the transport of free-swimming propagules, LFN builds high-resolution connectivity matrices between all

possible origin and destination nodes (i.e., for each node, it stores the numbers and weights of all links emanating from it and entering it) of the region under study. Matrices are post-processed to discard specific sites (through an adequate selection of nodes) and to vary the scales of interest (through the grouping of selected nodes) without the need to recompute any trajectory. In particular, we consider as origin/destination sites only those with preferential habitats of hake (e.g., nodes inshore of the 300-m isobath). Within those nodes, local larval release and success of recruitment are homogeneous; they are null in the remaining nodes. Overall, 175 numerical experiments (seven spawning events per year over 25 years) generate 175 connectivity matrices that are then further analyzed to compute metrics, which measure larval retention and directional exchanges applying formulations derived from population dynamics concepts (Dubois et al. 2016). We assume that recruitment of a given subpopulation is at primary controlled by locally produced larvae and the immigration of distantly released larvae. Consequently, the three complementary connectivity metrics exploited here are: import, local retention and self-recruitment. Import (Imp) is the total number of incoming larvae from all origins (produced elsewhere only). Local Retention (LR) is the proportion of locally produced larvae that are locally retained. Self-Recruitment (SR) is the ratio of locally produced larvae retained in each area to the total number of incoming larvae (including those produced locally). In this respect, LR is only a local measure whereas SR encompasses information of both local (LR) and remote directional influences (Imp). LR and SR relate to the self-persistence of a given subpopulation while Imp and SR evaluate the network persistence of the whole metapopulation (Castorani et al. 2015, Dubois et al. 2016). Imp is expressed in absolute number of particles. LR and SR are probabilities with values between 0 and 1 (0 indicates no retention). While some authors suggested that SR can be a good predictor of LR under certain conditions (e.g., Lett et al. 2015), Dubois et al. (2016) generalized the formulations of these connectivity estimates applied to larval transport and showed that the relative difference between LR and SR provides insight into the source or sink behavior of the subpopulation of interest. We report here the annual averages of these three connectivity metrics with associated uncertainties (standard deviations), calculated among the successive spawning events within the main reproductive season.

The sensitivity and robustness of those connectivity metrics to the most relevant parameters of the LFN were extensively assessed (Dubois et al. 2016, Monroy et al. 2017; Appendix S1). In order to compare modeled connectivity estimates with fisheries assessment outputs (see also *Statistical Approach*), we calculated the metrics at two hierarchical scales: for the six aforementioned subpopulations of hake and at the scale of the three regional management units described previously. This lets us evaluate (1) which is the best connectivity metric to reproduce

⁸ <http://www.fao.org/gfcm/data/map-geographical-subareas/es/>

the fisheries assessment estimates and (2) at which spatial scale (subpopulation or management unit) the impact of larval retention and exchange is better captured.

Statistical approach

Prior to the modeling of fisheries-based information, we first assessed the relative contribution of LR and Imp on SR, applying general additive modeling (GAMs) on SR as response variable and LR and log(Imp) as nonlinear covariates.

We then statistically assessed and quantified the impact of our physical-dependent drivers on recruitment and survival (i.e., the ratio of recruitment at time t to the spawners biomass at time $t - 1$), which were obtained from GFCM fisheries assessment groups of the three corresponding management units that take into account information from scientific bottom trawl surveys (SAC-GFCM 2015). As physical covariates, we investigated the potential linear effects of the simulated connectivity metrics (LR, SR, and log(Imp)) along with the regional hydroclimatic index (RHI) that can capture biophysical processes not related to dispersal. Connectivity estimates included in the models were calculated at both “subpopulation” and “management unit” levels to assess the spatial scale at which including connectivity maximizes models’ performance (Metadata S1, Data S1). RHI is calculated attending to air–sea heat exchange anomalies in the northwestern Mediterranean, and has been related to the inter-annual variability of intermediate water mass formation in winter in the Western Mediterranean. Negative values of this index are associated to higher formation rate of winter intermediate water mass, which influences the seasonal surface circulation patterns resulting in greater regional primary production than average (Balbín et al. 2014), with a positive impact on the recruitment success of hake in the Balearic Islands (Massutí et al. 2008). While it suggests that the RHI captures biophysical processes mainly related to early life stages survival, it is not yet clear if and how they could be related to dispersal.

Besides physical drivers, we also accounted for density-dependent regulation in our statistical modeling. In the case of recruitment, we included the potential nonlinear effect of spawning stock biomass (SSB) applying a GAM framework (Hidalgo et al. 2012). If the density-dependent effect was not significant, the model resulted in a linear model. In the case of survival, we used the classic Ricker model extended to environmental drivers, $R_t = a_0 \text{SSB}_{t-1} e^{-b \text{SSB}_{t-1} + \sum_i^c \mathbf{P}_{i,t}} e^{\varepsilon_t}$, applying its transformation to a linear model, $\log(R_t/\text{SSB}_{t-1}) = \log(a_0) - b \text{SSB}_{t-1} + \sum_i^c \mathbf{P}_{i,t} + \varepsilon_t$, where R_t is the recruitment (age-0) at year t and $\log(R_t/\text{SSB}_{t-1})$ the survival, SSB_{t-1} the spawning abundance at year $t - 1$, $\mathbf{P}_{i,t}$ represent a vector of the i physical drivers, a_0 , b , and c_i are the estimated parameters, and ε_t the error term.

To account for the temporal lag induced by the successive spawning, dispersal, settlement and finally

recruitment process, connectivity metrics of year t were regressed against fisheries assessment variables of year $t + 1$. To test whether density dependence influences recruitment survival at larger spatial scales than expected in the meta-population, spawning biomasses of contiguous management units were combined. Given that the length of the time-series of fisheries assessment variables differs among areas, a final model with three, two and one covariate(s) were considered for the Balearic Islands, Gulf of Lion, and the Iberian Peninsula, respectively.

Prior statistical analyses, absence of correlation and collinearity among physical and biological covariates was confirmed by applying, respectively, Spearman correlations and the variance inflation factor test (Zuur et al. 2009). The best model was obtained by minimizing the Akaike information criterion (AIC). For every model, residuals were checked for variance homogeneity and absence of temporal autocorrelation applying the autocorrelation function (acf). To quantify the benefits of considering connectivity and climate proxies to model fish recruitment, we compare the percentage of deviance explained of models including those metrics with the standard models based solely on SSB. Once the best model was obtained for each management unit, all time-series were normalized to mean 0 and variance 1 and pooled in a unique and centered (i.e., intercept equals 0) linear model to compare the size (slope) of each effect (connectivity, hydroclimate, and spawning stock) for each management unit.

RESULTS

Connectivity estimates

Larval exchanges simulated by the Lagrangian flow network (LFN) among the six discrete subpopulations of hake suggest that the subsurface circulation in the northwestern Mediterranean, dominated by the Liguro-Provençal-Catalan current, drives a southwestward directional pattern of connectivity (Fig. 1). The Gulf of Lion is thus the main source of particles Import (Imp) into the Iberian Peninsula. While this southwestward connectivity prevails in all 25 years under study (see the annual mean patterns of connectivity over 1987–2011 in Appendix S2: Fig. S1), two distinct scenarios can be distinguished. The first connectivity pattern consists in a southwestward flux to the mainland, with a weak or null transport towards the Balearic Islands (Fig. 1a). The second one reveals a reduced transport towards the Iberian Peninsula shelf and an eastward retroflexion of the main transport pathways, resulting in stronger connections with the Balearic Archipelago (Fig. 1b). Larval Local Retention (LR) also displays consequent spatiotemporal variability, which seems less prominent than the changes of directional connectivity patterns (Fig. 1; Appendix S2: Fig. S1). The lowest LR values occur over the narrow shelves of the Catalan coast (0.32 ± 0.1

[mean \pm standard deviation]) and the northern Balearic Islands (0.33 ± 0.07). In contrast, relatively extended continental shelves tend to favor retention rates: the Gulf of Lion has intermediate LR (0.42 ± 0.07), while the highest LR values are obtained for the Ebro delta (0.46 ± 0.06), the Valencia channel (0.47 ± 0.06) and the southern Balearic Islands (0.47 ± 0.05 ; see pairwise comparisons in Appendix S2: Table S1).

The high variability of ocean currents is reflected in all modeled connectivity metrics; Imp (not shown), LR, and Self-Recruitment (SR) displayed consistent inter-annual (Fig. 2a) and geographical variations (Appendix S2: Figs S1, S2). The relative position of a given cloud of points in the scatter plot LR vs. SR (Fig. 2b) illustrates the different contributions of retention (LR) and exchange (Imp) processes in each subpopulation. In this sense, SR results in a synthetic index that integrates both local and distant connectivity processes. The inter-annual variability of SR is more dependent on Imp in the Ebro Delta, the Gulf of Valencia, and the southern Balearic Islands (Fig. 2b and Appendix S2: Figs S1, S2). In contrast, both the Catalan coast and the northern Balearic Islands show a more even contribution of LR and Imp variability on SR (Fig. 2b and Appendix S2: Fig. S2). Overall, the whole meta-population shows a balanced contribution of LR and Imp on SR, with relatively high SR at moderate LR. Following Dubois et al. (2016), who showed that the greater deviation between SR and LR, the more pronounced is the source or sink behavior, it indicates that the 6 subpopulations mostly behave as sources in which larval export dominates import (Fig. 2b). This further suggests a dynamical system in which both self-replenishment and exchanges among distant sub-populations (i.e., network persistence) play key roles in controlling its connectivity. While the inter-annual variability of SR is elevated, reflecting the variations of both LR and Imp, means of

SR for each subpopulation still show significant geographic discrepancies: high in the southern Balearic Islands (0.84 ± 0.07) and Gulf of Valencia (0.87 ± 0.06), medium in the Ebro delta (0.68 ± 0.1) and northern Balearic Islands (0.72 ± 0.09), and relatively low in the Catalan coast (0.53 ± 0.1 ; Fig. 2b; see also pairwise comparisons in Appendix S2: Table S2). Note that SR in the Gulf of Lion is always close to 1 (0.99 ± 0.003), demonstrating it is mostly influenced by local processes (LR) as Imp is very weak or null due to the dominant southwestward directional connectivity and its positioning on the north-eastern boundary of our simplified meta-population system.

We also evaluated LR and Imp contribution to SR variability for the three corresponding management units to match the scale used in fisheries assessment procedures (Fig. 3). The Iberian Peninsula shows that the rate of change of SR is similar to the positive effect of LR and the negative one of Imp. The LR and Imp components in SR variability for the Gulf of Lion are similar to the corresponding values presented above and computed at the subpopulation scale. The Balearic archipelago exhibits a connectivity behavior close to the one of the southern Balearic Islands with SR variability mostly controlled by Imp (Fig. 3 and Appendix S2: Fig. S2). This suggests that the local influence of LR inter-annual variability in the northern Balearic Islands becomes negligible in comparison with the growing external influences when the scale of study accounts for the whole management unit.

Sensitivity tests performed at both levels of analyses (six subpopulations and three management units) reveal that our connectivity metrics and their inter-annual variability are robust to variations of the three critical parameters (Appendix S1: pelagic larval duration, Fig. S1; spawning frequency, Fig. S2; and dispersal depths, Table S1 and S2).

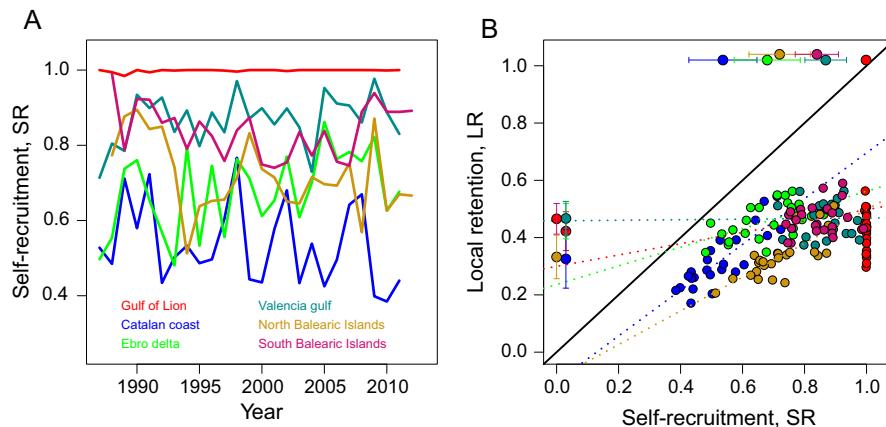


FIG. 2. Time-series of annual mean of Self-Recruitment (SR) in all subpopulations coded with the same colors as in Fig. 1. (A) Relationship between Self-Recruitment (SR) and Local Retention (LR) for all subpopulations over 25 years (1987–2011) (B) Dots with bars represent the mean and the standard deviation calculated over the 25 years, respectively, for the two connectivity metrics. Dotted colored lines represent the linear fits between SR and LR for each subpopulation.

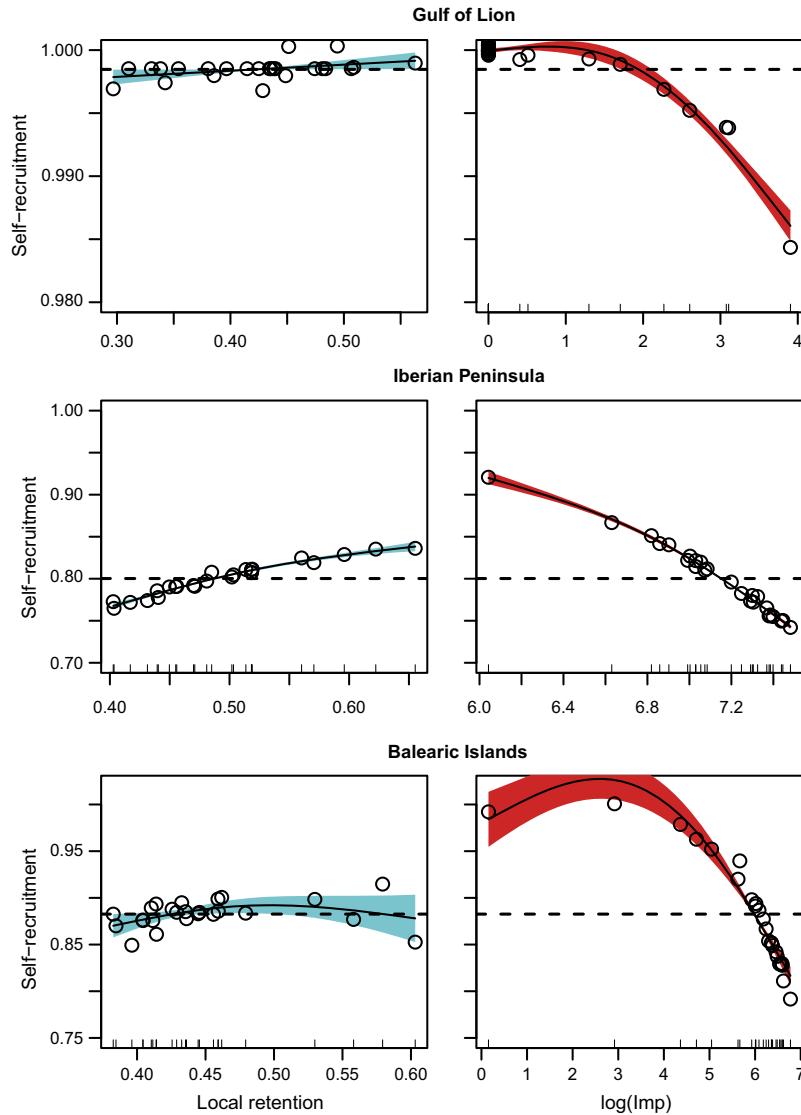


FIG. 3. Relative effects of Local Retention (LR, left column) and Import (Imp, log-transformed, right column) on the inter-annual variability of Self-Recruitment (SR) for each of the three management units: Gulf of Lion (upper), Iberian Peninsula (middle), and Balearic Islands (bottom). Data were fit with a nonlinear regression (GAM) with the two covariates being statistically significant ($P < 0.05$) in all models. The dashed line represents the mean value (i.e., model intercept) in each management unit. The solid black lines, shaded colored regions, and dots represent, respectively, fitted values of the partial effect, 95% confidence intervals, and partial residuals.

Recruitment dynamics

The best statistical model of recruitment for each management unit reveals the influence of SR and RHI as the most relevant drivers (Table 1). SSB was not significant in all models in which its effect was considered, including those in which SSB was the unique covariate (Table 1). There was a considerable increase of the deviance explained (DE) from models exclusively based on SSB to the best models obtained for each management unit (from 27.3% in the Gulf of Lions to 36.2% in the Balearic Islands, Table 1). An increase of 21.3% of

DE was observed in the model of Balearic Islands including RHI and SR from the model exclusively based on RHI. Besides the minimization of AIC, DE of models including SR were between 2.7% and 7.6% higher compared to those including the other connectivity metrics tested here, that is LR or IMP (Table 1).

As SR and RHI effects were linear and the most representative in all management units (Fig. 4a), they were standardized in a unique model for the whole metapopulation (DE = 37.6%; Appendix S3: Fig. S1) to compare these effects across areas. SR is a significant variable influencing the recruitment in both the Iberian Peninsula

and the Balearic Islands with a similar effect size (i.e., slope, Fig. 4b). However, in the model for the Iberian Peninsula management unit, SR calculated in the Catalan coast subpopulation emerges as the most relevant SR metric. For the Balearic Islands case, the most relevant SR metric turns out to be SR calculated at the management unit level (Table 1). None of our connectivity metrics was a significant predictor of recruitment in the Gulf of Lion. However, for the RHI, a clear directional change is observed from a negative significant effect on recruitment in the Balearic Islands (i.e., recruitment is favored under negative values of RHI) to a positive significant effect in the Gulf of Lion, and no effect observed in the Iberian Peninsula (Fig. 4c). The size of RHI effects were of the same order as those of SR (Fig. 4b, c).

The models applied to the recruitment survival (linearized Ricker model) return results that are consistent with the best models found for recruitment, including a negative effect of spawners' biomass (i.e., density dependence) of similar strength for the Balearic Islands and the Gulf of Lion (Appendix S3: Table S1, Fig. S2 and Fig. S3; DE = 38.1%). Concerning the Spanish mainland, although density dependence was not included in the best model, the effect of SR in the Catalan coast was only observed when the survival combines the density dependence of two contiguous management units (Spanish mainland and Gulf of Lion; Appendix S3: Table S2).

DISCUSSION

Our study demonstrates that, making reasonable assumptions, the inter-annual variability of recruitment

of large fish stocks can be modeled incorporating physics-dependent drivers related to dispersal and survival: the spatiotemporal connectivity estimates derived from a high-resolution circulation model and an index capturing the temporal variability of the regional hydroclimate. While nearshore connectivity is sometimes suggested to be heterogeneous at short time scales due to stochastic transport of pelagic larvae (Siegel et al. 2008, Watson et al. 2012), and although basin-scale models are known to poorly simulate complex coastal currents, our statistical analyses derived from such model provide signals consistent with both inter-annual variability and geographical discrepancies of LR associated with local topography and hydrodynamics (Dubois et al. 2016). Moreover, we demonstrate that our connectivity metrics integrate both larval retention and exchanges (Watson et al. 2012, Lett et al. 2015) and are able to capture recurrent annual circulation patterns (Dubois et al. 2016), that significantly affect the recruitment success of hake on larger spatial-scales (i.e., both at "subpopulation" and "management unit" levels). Given that recruitment dynamics is the main ecological basis and the unique mechanistic insight of fishery assessment, our study presents a novel framework to incorporate physical information into assessment procedures to improve stock–recruitment relationships and short-term predictions of fisheries production. The two main steps consist of (1) identifying the spatial scale at which the influence of connectivity processes on the population is prominent and (2) mechanistically comparing fisheries recruitment data and ad hoc connectivity metrics (namely import, local retention, and self-recruitment) adequately

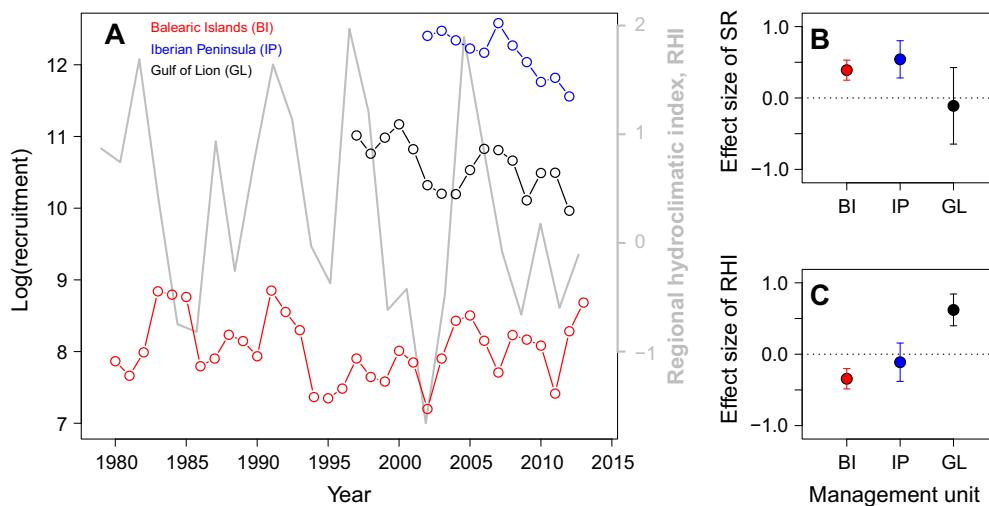


FIG. 4. Time-series of annual recruitments from fisheries assessment in the three management units (Balearic Islands, BA, red colors; Iberian Peninsula, IP, blue colors; Gulf of Lion, GL, black colors) and the regional hydroclimatic index (RHI, gray curve; Balbín et al. 2014). (A) Based on the covariates obtained of the best recruitment models (Table 1), a global linear model was constructed for the whole metapopulation with standardized time series (mean 0 and variance 1) to statistically compare the strength of connectivity (self-recruitment, SR) and hydroclimate (RHI) effects on recruitment for each management unit (Appendix S3: Fig. S1). The effect size (i.e., linear model estimates) of each management unit is presented for (B) SR and (C) RHI. No overlapping of vertical bars (standard errors of the model estimates) with zero horizontal lines reveals statistical significance of the effect.

TABLE 1. Best fisheries recruitment models obtained for each management unit.

Management unit and covariates	AIC	Delta AIC	DE (%)
Balearic Islands			
SSB ^{BS}	35.24	13.72	6.95
RHI	39.99	18.47	18.25
RHI + SR_{BI}	21.52	0	36.39
RHI + Imp _{BI}	22.44	0.92	34.02
RHI + SR _{NBI}	23.63	2.11	30.78
RHI + Imp _{NBI}	25.46	3.94	25.54
Iberian peninsula			
SSB ^{BS}	9.74	8.02	1
SR_{CC}	1.92	0	32.9
SR _{IP}	2.68	0.76	27.5
LR _{CC}	4.19	1.51	15.69
LR _{IP}	4.82	2.90	10.16
Gulf of Lions			
SSB ^{BS}	11.28	5.6	20.4
RHI	5.68	0	47.85

Notes: Covariates included are self-recruitment (SR), import (Imp), local retention (LR), regional hydroclimatic index (RHI), and spawning stock biomass (SSB). Akaike information criteria (AIC), delta AIC, and deviance explained (DE, %) are also presented. Connectivity metrics were calculated at two geographical levels: management unit and subpopulations (see *Materials and Methods*). CC and NBI refer, respectively, to Catalan coast and Northern Balearic Islands subpopulations. IP and BI refer, respectively, to Iberian Peninsula and Balearic Islands management units. An ns means nonsignificant ($P > 0.05$) effect of the SSB covariate, which is presented for comparison with other models in terms of DE. Note that information provided for models using SSB as unique covariate were fit applying general additive models, while the rest applies linear models. Bold values represent the best model.

computed over the region previously defined. Earlier studies have explored how estimates of larval dispersion could be integrated into fisheries or demographic models. They include theoretical perspectives (e.g., Botsford et al. 2009b, Castorani et al. 2015), but also studies for small regions and highly sedentary species (e.g., Rochette et al. 2013, Johnson et al. 2018). For large fish stocks, connectivity information derived from genetic, tagging and otolith is often used to spatially delineate subpopulations rather than to model temporal dynamics (e.g., Holmes et al. 2014). Here, we propose a framework to link dispersal simulations with temporal dynamics of recruitment data of open and large stocks such as the European hake with wide distribution and complex spatial structure.

Historically, marine populations tended to be classified as open or closed according to their replenishments being ensured primarily by immigrants or by local production (Hixon et al. 2002). While this dichotomy and its management implications could be applied in small metapopulation of littoral sedentary species (i.e., when connectivity processes are relatively well captured by local retention), it does not hold for most offshore fish stocks for which there is an increasing awareness that spatial and demographic structure is more complex than

currently accounted for (Cadrin and Secor 2009, Kerr et al. 2017). This inherently calls for indicators that properly parameterize the observed continuum between open and closed systems beyond stock boundaries and that are able to account for both local and distant connectivity processes. In this view, Self-Recruitment (SR), which was defined to take into account the influences of both local recruits and immigration from the surrounding subpopulations (Botsford et al. 2009a), seems best adapted. Indeed, our study shows that larval SR is, according to our statistical models, the best synthetic predictor of fisheries recruitment, as it constitutes the mechanistic link among the three management units of the European hake in the Western Mediterranean. Furthermore, to precisely assess the demographic role of each subpopulation (source/sink) and the global metapopulation persistence (Lett et al. 2015), we advocate for the simultaneous interpretation of both SR and local retention (LR). Dubois et al. (2016) indeed showed that the greater the relative difference between SR and LR, the more pronounced is the source or sink behavior. We found that SR of four hake subpopulations are mainly controlled by the inter-annual variations of import (Imp), emphasizing the role of network persistence. We also showed that variability in both LR and Imp in the Catalan Coast and in the northern Balearic Islands contribute to meaningful changes in their respective SRs, indicating the importance of both network and self-replenishment. Our model suggests that all subpopulations behave as sources, with stronger larval export than import. It is worth distinguishing the effective sources (e.g., Gulf of Lion, Catalan coast), whose exported larvae successfully sustain other identified subpopulations due to favorable dispersal pathways, as compared to the non-effective ones (e.g., north Balearic Islands) whose exported larvae are lost from the metapopulation system under its hypothesized geographical structure. While those larvae would be, in reality, lost in the open ocean with low likelihood of surviving, they could reach other subpopulations outside of our studied region. However, the phenology of reproduction and recruitment season of neighbored areas upstream (Ligurian and Tyrrhenian Seas [Recasens et al. 2008]) and southward Almeria–Oran front (Alboran Sea [Rey et al. 2004]) are seasonally opposed. In addition, the absence of favorable nursery habitats upstream from the “source” area of the Gulf of Lions makes the success of potential settlement very unlikely (Druon et al. 2015). From a spatial management perspective, the subpopulations whose SR represent a balanced contribution of local (LR) and remote (Imp) connectivity processes are of crucial importance for the global persistence of a metapopulation (Botsford et al. 2009a, Lett et al. 2015). In this view, SR emerges as a crucial variable to be properly estimated by scientists and to be adequately considered by managers for ensuring population persistence.

The spatial heterogeneity of climate effects on fish recruitment has been reported for global indices, but not yet at regional scales. Our study presents evidence of a

clear regional gradient with antagonist effects in nearby areas located only about 500 km away. Together with SR, the climatic index has an elevated explanatory power in two of the three management units. Our results reinforce the inverse relationship between this index and hake recruitment already documented in the Balearic Islands (Massutí et al. 2008). Low values of the index are related to anomalously intense formation of intermediate waters in the Gulf of Lion forced by winter wind-driven vertical mixing (Balbín et al. 2014). These nutrient-rich waters then flow further south and increase biological productivity in the Balearic sea, an area especially oligotrophic in the western Mediterranean, enhancing food availability for hake larvae and juveniles there (Massutí et al. 2008). In contrast, we also demonstrate for the first time a strong positive correlation between this index and hake recruitment in the Gulf of Lion. We hypothesize that stronger than average mixing events homogenize the water column down to several hundred meters' depth (and even down to the seabed in extreme events; Balbín et al. 2014) can trigger high mortality rates of locally produced hake larvae, negatively impacting recruitment success in the Gulf of Lion. Other indirect mechanisms could be that, under intense winter convection, hake larvae could entrain in water masses with no food supply and/or within unfavorable dispersal routes toward the open ocean. These findings reveal how the link between climate variability and its ecological impact is geographically structured at regional scales. In this case, the same local oceanographic event (winter wind-driven vertical mixing in the Gulf of Lion) has opposite impacts in close-by regions. Locally, strong mixing events considerably reduce the survival of hake larvae and recruitment in the Gulf of Lion, whereas they increase food availability over the northwestern Mediterranean region, affecting positively hake recruitment in the Balearic Islands.

Although climate indices are able to capitalize a broad spectrum of environmental processes with simplistic formulations (standardized air temperature anomalies in our case), they often integrate various processes acting over different time and space windows, with the potential risk of redundancy between drivers, dispersal, and hydroclimate. This suggests the need to complement the formulations of climatic indexes with additional information (e.g., from high-resolution ocean model simulations as well as observations gathered by ocean observing systems) that would parameterize adequately the local manifestation of large-scale climatic signals and its associated ecological response. Indeed, while the climate influence of fish populations has been largely demonstrated, it is rarely included in fisheries assessment due to the difficulty to link climate indices with a specific ecological process within age-structured modeling frameworks. Our study demonstrates that the combination of spatially structured connectivity and climatic effects could be applied in a simple and synthetic way (e.g., Rochette et al. 2013), beyond classic stock–recruitment relationships and

independently of the functional form of density dependence. The two physical-dependent drivers can be calculated in winter, increasing the short-term predictive ability of hake recruitment mainly concentrated during the following spring. This suggests that our approach could be of general applicability for many stocks recruiting to the fishery during their first year of life.

The population structure of marine species falls in a continuum from truly panmictic to numerous isolated subpopulations, and the majority exhibits complex structures within this range (often referred to as biocomplexity, e.g., salmon in Alaska [Hilborn et al. 2003], herring in the east Atlantic [Ruzzante et al. 2006], cod in the North Sea [Wright et al. 2006]). A growing concern among fishery scientists during the last decade is to understand how the loss of biocomplexity influences the resilience and stability of exploited marine populations. This general objective triggered an increasing consideration of complex metapopulation structures and combines in fact two current challenges: a historic questioning about fish stocks boundaries and also a more recent recognition of sub-structuring within management areas as a set of “sub-units” displaying different ecological or demographic functions. Although a panmictic scenario has been suggested for hake in the western Mediterranean (Morales-Nin et al. 2014), our study provides evidence that demographic connectivity is more relevant than genetic connectivity to provide scientific support for the management of hake's metapopulation in the Mediterranean Sea as it is able to explain a sizeable component of the inter-annual variability of the observed recruitment. The Gulf of Lion is linked to the Iberian Peninsula management unit mostly by a unidirectional south-westward connection that shapes the hake recruitment dynamics of the latter, consistent with recent research on small pelagic fish (Ospina-Alvarez et al. 2015). Furthermore, the Catalan coast emerges as the critical transitional subpopulation connecting both management units since its simulated larval SR significantly correlates to the observed recruitment of the entire Iberian Peninsula unit, questioning the current geographical delimitation for assessment and management. In contrast, Atlantic populations of the same species show a different scenario with documented gene flows between geographically separated management units but relative demographic independence (Pita et al. 2016), supporting the current management separation.

CONCLUDING REMARKS AND FUTURE CHALLENGES

Recognizing subpopulations and providing specific demographic metrics that reflect their heterogeneous contributions to the global dynamic of a metapopulation is a current but accessible challenge for fisheries ecologists (Kerr et al. 2017). Our study provides a methodological framework to calculate and compare these metrics, which acknowledge the complexity of marine populations and ecosystems in a relatively simple

manner, providing a research pathway alternative to the development of complex models (e.g., end-to-end ecosystem models). Efficient ways to embrace physics and fisheries assessment to improve management of large metapopulations include, as we showed here, the integrated analysis of a limited number of controlling ecological and environmental processes that are critical to understand and reproduce the functioning and dynamics of marine systems. In this sense, mechanistic modeling constitutes a valuable tool to circumvent the lack of observations and understanding of these processes. Further research also needs to assess the wider implications of our results for: the population dynamics (i.e., short- and long-term persistence at both sub- and meta-population levels) by incorporating our connectivity indices into population models; for the determination of biological reference points (e.g., maximum sustainable yield) obtained from stock assessment models; or for the design of dynamic and adaptive spatial management. To support the application of spatially and temporally pertinent conservation measures, future research also needs to include other elements such as the relevance of spatially structured ecological functions (e.g., spawning areas, nursery and feeding grounds) along with the impact of adult-mediated connectivity (Goethel et al. 2011). Finally, a more efficient use of the environmental information generated by ocean models and observing systems is required to pursue the fast development of “operational fisheries oceanography” (Alvarez-Berastegui et al. 2016). Besides the abundant research dedicated at including climatic influences in long-term projections of fish production (Rice and Browman 2014), a new paradigm should focus in those oceanographic and climatic processes that considerably affect short-term predictions, which are the relevant scales for management purposes. While our study supports the predictive power of SR in a fisheries assessment context, it generally calls for further effort to incorporate connectivity estimates and mesoscale climatic indexes derived from ocean observations and models into fisheries modeling, assessment and stewardship. Over longer time scales, human-induced climate change is projected to increase ocean temperature, affecting the distribution of fish stocks and increasing the number of transboundary stocks (Pinsky et al. 2018). In addition, climate change is also expected to modify circulation patterns and favor extreme events, influencing the transport and survival of marine planktonic larvae and, thus, altering connectivity (Lett et al. 2010). Our modelling framework, backed-up by decadal observations, could help to investigate those long-term effects toward the sustainable protection and management of marine ecosystems.

ACKNOWLEDGMENTS

We thank R. Balbin for helpful comments and suggestions on an earlier draft of the manuscript. M. Hidalgo acknowledges support of two contracts funded by the Spanish national program “Ramon y Cajal” (RYC-2015-18646) and by the regional

government of the Balearic Islands, the later co-funded by the European Social Fund 2014-2020. V. Rossi acknowledges support of a post-doctoral ‘Juan de la Cierva Incorporación’ fellowship (IJCI-2014-22343) provided by the Spanish MICINN and a networking grant through the HYDROGENCONNECT project funded by the French program MISTRALS ENVI-Med. E. Ser-Giacomi thanks French program “Investissements d’Avenir” (ANR-10-LABX-54 MEMOLIFE and ANR-11-IDEX-0001-02 PSL Research University). This work was also supported by the Spanish National projects LAOP (CTM2015-66407-P) P. Monroy and E. Hernandez-Garcia and CLIFISH (CTM2015-66400-C3-1-R) and to M. Hidalgo, B. Guijarro, and E. Massuti (AEI/FEDER, EU). P. Reglero and M. Hidalgo acknowledge funding of the H2020 PANDORA project (Nr. 773713). The authors thank two anonymous reviewers and the editor for their constructive comments that helped improve the original manuscript. Authors’ contributions: M. Hidalgo and V. Rossi co-designed and co-directed the study. They have equally contributed to this study; this co-first authorship implies that any correspondence should be addressed to both jm.hidalgo@ieo.es and vincent.rossi@mio.osupytheas.fr. P. Monroy, E. Ser-Giacomi, V. Rossi, and E. Hernández-García set up the Lagrangian modelling framework and performed the simulations. A. Jadaud, B. Guijarro, and J. L. Perez provided the recruitment data. M. Hidalgo and V. Rossi analyzed all data and interpreted the results. All authors discussed the results. M. Hidalgo and V. Rossi wrote the paper. M. Hidalgo, V. Rossi, E. Ser-Giacomi, E. Hernández-García, B. Guijarro, E. Massuti, F. Alemany, A. Jadaud, J. L. Perez, and P. Reglero commented on the manuscript.

LITERATURE CITED

- Almany, G. R., et al. 2017. Larval fish dispersal in a coral-reef seascape. *Nature Ecology and Evolution* 1:0148.
- Alvarez-Berastegui, D., et al. 2016. Pelagic seascape ecology for operational fisheries oceanography: modelling and predicting spawning distribution of Atlantic bluefin tuna in Western Mediterranean. *ICES Journal of Marine Science* 73:1851–1862.
- Andrello, M., F. Guilhaumon, C. Albouy, V. Parravicini, J. Scholtens, P. Verley, M. Barange, U. R. Sumaila, S. Manel, and D. Mouillot. 2017. Global mismatch between fishing dependency and larval supply from marine reserves. *Nature Communications* 8:16039.
- Balbín, R., M. M. López-Jurado, P. Reglero, P. Vélez-Velch, J. M. González-Pola, A. García, and F. Alemany. 2014. Interannual variability of the early summer circulation around the Balearic Islands: driving factors and potential effects on the marine ecosystem. *Journal of Marine Systems* 138:70–81.
- Botsford, L. W., J. W. White, M.-A. Coffroth, C. B. Paris, S. Planes, T. L. Shearer, S. R. Thorrold, and G. P. Jones. 2009a. Connectivity and resilience of coral reef metapopulations in marine protected areas: matching empirical efforts to predictive needs. *Coral Reefs* 28:327–337.
- Botsford, W., R. Brumbaugh, C. Grimes, B. Kellner, J. Largier, R. O’Farrell, S. Ralston, E. Soulanille, and V. Weststad. 2009b. Connectivity, sustainability, and yield: bridging the gap between conventional fisheries management and marine protected areas. *Reviews in Fish Biology and Fisheries* 19:69–95.
- Cadrin, S., and D. Secor. 2009. Accounting for spatial population structure in stock assessment: past, present, and future. Pages 405–426 in R. Beamish, and B. Rothschild, editors. *The future of fisheries science in North America*. Springer Publishing, Dordrecht, The Netherlands.
- Carson, H. S., G. S. Cook, P. C. López-Duarte, and L. A. Levin. 2011. Evaluating the importance of demographic connectivity in a marine metapopulation. *Ecology* 92:1972–1984.

- Castorani, M. C., D. C. Reed, F. Alberto, T. W. Bell, R. D. Simons, K. C. Cavanaugh, D. A. Siegel, and P. T. Raimondi. 2015. Connectivity structures local population dynamics: a long-term empirical test in a large metapopulation system. *Ecology* 96:3141–3152.
- Cheung, W. W. L., R. Watson, and D. Pauly. 2013. Signature of ocean warming in global fisheries catch. *Nature* 497:365–368.
- Cowen, R. K., and S. Sponaugle. 2009. Larval dispersal and marine population connectivity. *Annual Review of Marine Science* 1:443–466.
- Daewel, U., C. Schrum, and A. K. Gupta. 2015. The predictive potential of early life stage individual-based models (IBMs): an example for Atlantic cod *Gadus morhua* in the North Sea. *Marine Ecology Progress Series* 534:199–219.
- Druon, J. N., et al. 2015. Modeling of European hake nurseries in the Mediterranean Sea: an ecological niche approach. *Progress in Oceanography* 130:188–204.
- Dubois, M., V. Rossi, E. Ser-Giacomi, S. Arnaud-Haond, C. López, and E. Hernández-García. 2016. Linking basin-scale connectivity, oceanography and population dynamics for the conservation and management of marine ecosystems. *Global Ecology and Biogeography* 25:503–515.
- Fernandes, P. G., et al. 2017. Coherent assessments of Europe's marine fishes show regional divergence and megafauna loss. *Nature Ecology and Evolution* 1:0170.
- Fiorentino, F., et al. 2014. Stock units: Identification of distinct biological units (stock units) for different fish and shellfish species and among different GFCM-GSA. STOCKMED Deliverable 03: FINAL REPORT. 310 p. September 2014.
- Frisk, M. G., A. Jordaan, and T. J. Miller. 2014. Moving beyond the current paradigm in marine population connectivity: Are adults the missing link? *Fish and Fisheries* 15:242–254.
- Galarza, J. A., J. Carreras-Carbonell, E. Macpherson, M. Pascual, S. Roques, G. F. Turner, and C. Rico. 2009. The influence of oceanographic fronts and early-life-history traits on connectivity among littoral fish species. *Proceedings of the National Academy of Sciences USA* 106:1473–1478.
- Goethel, D. R., T. J. Quinn, and S. X. Cadrin. 2011. Incorporating spatial structure in stock assessment: movement modelling in marine fish population dynamics. *Reviews in Fisheries Science* 19:119–136.
- Harrison, H. B., et al. 2012. Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Current Biology* 22:1023–1028.
- Hidalgo, M., J. Tomás, T. Moranta, and B. Morales-Nin. 2009. Intra-annual recruitment events of a shelf species around an island system in the NW Mediterranean. *Estuarine, Coastal and Shelf Science* 83:227–238.
- Hidalgo, M., et al. 2012. Context-dependent interplays between truncated demographies and climate variation shape the population growth rate of harvested populations. *Ecography* 35:637–649.
- Hidalgo, M., D. M. Kaplan, L. A. Kerr, J. R. Watson, C. B. Paris, and H. I. Browman. 2017. Advancing the link between ocean connectivity, ecological function and management challenges. *ICES Journal of Marine Science* 74:1702–1707.
- Hilborn, R., T. P. Quinn, D. E. Schindler, and D. E. Rogers. 2003. Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences USA* 100:6564–6568.
- Hinrichsen, H.-H., M. Dickey-Collas, M. Huret, M. A. Peck, and F. B. Vikebo. 2011. Evaluating the suitability of coupled biophysical models for fishery management. *ICES Journal of Marine Science* 68:1478–1487.
- Hixon, M., S. W. Pacala, and S. A. Sandin. 2002. Population regulation: historical context and contemporary challenges of open vs. closed systems. *Ecology* 83:1490–1508.
- Holmes, S. J., C. P. Millar, R. J. Fryer, and P. J. Wright. 2014. Gadoid dynamics: differing perceptions when contrasting stock vs. population trends and its implications to management. *ICES Journal of Marine Science* 71:1433–1442.
- Huwer, B., H. H. Hinrichsen, K. Hüseyin, and M. Eero. 2016. Connectivity of larval cod in the transition area between North Sea and Baltic Sea and potential implications for fisheries management. *ICES Journal of Marine Science* 73:1815–1824.
- Johnson, D. W., M. R. Christie, T. J. Pusack, C. D. Stallings, and M. A. Hixon. 2018. Integrating larval connectivity with local demography reveals regional dynamics of a marine metapopulation. *Ecology* 99:1419–1429.
- Kerr, L., N. T. Hintzen, S. X. Cadrin, L. W. Clausen, M. Dickey-Collas, D. Goethel, E. M. C. Hatfield, J. P. Kritzer, and R. D. M. Nash. 2017. Lessons learned from practical approaches to reconcile mismatches between biological population structure and stock units of marine fish. *ICES Journal of Marine Science* 74:1708–1722.
- Kough, A. S., C. B. Paris, and M. J. Butler. 2013. Larval connectivity and the international management of fisheries. *PLoS ONE* 8:e64970.
- Krueck, N. C., G. N. Ahmadi, A. Green, G. P. Jones, H. P. Possingham, M. J. Butler, C. Riginos, E. A. Treml, and P. J. Mumby. 2017. Incorporating larval dispersal into MPA design for both conservation and fisheries. *Ecological Applications* 27:925–941.
- Lett, C., S. D. Ayata, M. Huret, and J. O. Irisson. 2010. Biophysical modelling to investigate the effects of climate change on marine population dispersal and connectivity. *Progress in Oceanography* 87:106–113.
- Lett, C., T. Nguyen-Huu, M. Cuif, P. Saenz-Agudelo, and D. M. Kaplan. 2015. Linking local retention, self-recruitment, and persistence in marine metapopulations. *Ecology* 96:2236–2244.
- Massuti, E., et al. 2008. The influence of oceanographic scenarios on the population dynamics of demersal resources in the western Mediterranean: hypothesis for hake and red shrimp off Balearic Islands. *Journal of Marine Systems* 71:421–438.
- Monroy, P., V. Rossi, E. Ser-Giacomi, C. López, and E. Hernández-García. 2017. Sensitivity and robustness of larval connectivity diagnostics obtained from Lagrangian Flow Networks. *ICES Journal of Marine Science* 74:1763–1779.
- Morales-Nin, B., S. Pérez-Mayol, M. Palmer, and A. J. Geffen. 2014. Coping with connectivity between populations of *Merluccius merluccius*: an elusive topic. *Journal of Marine Systems* 138:11–219.
- Oddo, P., M. Adani, N. Pinardi, C. Fratianni, M. Tonani, and D. Pettenuzzo. 2009. A nested Atlantic-Mediterranean Sea general circulation model for operational forecasting. *Ocean Science Discussions* 6:1093–1127.
- Olivar, M. P., G. Quilez, and M. Emelianov. 2003. Spatial and temporal distribution and abundance of European hake, *Merluccius merluccius*, eggs and larvae in the Catalan coast (NW Mediterranean). *Fisheries Research* 60:321–331.
- Ospina-Alvarez, A., I. A. Catalán, M. Bernal, D. Roos, and I. Palomera. 2015. From egg production to recruits: connectivity and inter-annual variability in the recruitment patterns of European anchovy in the northwestern Mediterranean. *Progress in Oceanography* 138:431–447.
- Pinsky, M. L., G. Reygondeau, R. Caddell, J. Palacios-Abrantes, and J. Spijkers. 2018. Preparing ocean governance for species on the move. *Science* 360:1189–1191.
- Pita, A., A. Leal, A. Santafé-Muñoz, C. Piñero, and P. Presa. 2016. Genetic inference of demographic connectivity in the Atlantic European hake metapopulation (*Merluccius*

- merluccius*) over a spatio-temporal framework. *Fisheries Research* 179:291–301.
- Puerta, P., A. Quetglas, and M. Hidalgo. 2016. Seasonal variability of cephalopod populations: a spatio-temporal approach in the Western Mediterranean Sea. *Fisheries Oceanography* 25:373–389.
- Recasens, L., et al. 2008. Spawning pattern and batch fecundity of the European hake (*Merluccius merluccius* Linnaeus, 1758) in the western Mediterranean. *Scientia Marina* 72:721–732.
- Rey, J., J. Árbol, and L. Gil de Sola. 2004. Seasonal recruitment of hake in the Alboran Sea (SW Mediterranean). *Rapports et Procès-Verbaux des Réunions de la Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée (CIEM)* 37:427.
- Rice, J., and H. I. Browman. 2014. Where has all the recruitment research gone, long time passing? *ICES Journal of Marine Science* 71:2293–2299.
- Rochette, S., O. Le Pape, J. Vigneau, and E. Rivot. 2013. A hierarchical Bayesian model for embedding larval drift and habitat models in integrated life cycles for exploited fish. *Ecological Applications* 23:1659–1676.
- Rossi, V., E. Ser-Giacomi, C. López, and E. Hernández-García. 2014. Hydrodynamic provinces and oceanic connectivity from a transport network help designing marine reserves. *Geophysical Research Letters* 41:2883–2891.
- Ruzzante, D. E., et al. 2006. Biocomplexity in a highly migratory pelagic marine fish, Atlantic herring. *Proceedings of the Royal Society B* 273:1459–1464.
- SAC-GFCM 2015. Scientific Advisory Committee on Fisheries (SAC). Report of the Working Group on Stock Assessment of Demersal Species (WGSAD). Rome, Italy, 23–28 November 2015. General Fisheries Commission of the Mediterranean (GFCM).
- Ser-Giacomi, E., V. Rossi, C. López, and E. Hernández-García. 2015. Flow networks: a characterization of geophysical fluid transport. *Chaos* 25:036404.
- Siegel, D. A., S. Mitarai, C. J. Costello, S. D. Gaines, B. E. Kendall, R. R. Warner, and K. B. Winters. 2008. The stochastic nature of larval connectivity among nearshore marine populations. *Proceedings of the National Academy of Sciences USA* 105:8974–8979.
- Stephenson, R. L., G. D. Melvin, and M. Power. 2009. Population integrity and connectivity in Northwest Atlantic herring: a review of assumptions and evidence. *ICES Journal of Marine Science* 66:733–1739.
- Watson, J. R., B. E. Kendall, D. A. Siegel, and S. Mitarai. 2012. Changing seascapes, stochastic connectivity and marine metapopulation dynamics. *American Naturalist* 180:990–1120.
- Wright, P. J., F. C. Neat, F. M. Gibb, I. M. Gibb, and H. Thorndarson. 2006. Evidence for metapopulation structuring in cod from the west of Scotland and North Sea. *Journal of Fish Biology* 69:181–199.
- Zuur, A. F., A. A. Saveliev, E. N. Leno, G. M. Smith, and N. Walker. 2009. *Mixed effects models and extensions in ecology with R*. Springer, New York, New York, USA.

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