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5 **Accounting for ocean connectivity and hydroclimate in fish**

6 **recruitment fluctuations within transboundary metapopulations**

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29

30 **Abstract**

31 Marine resources stewardships are progressively becoming more receptive to an
32 effective incorporation of both ecosystem and environmental complexities into the
33 analytical frameworks of fisheries assessment. Understanding and predicting marine
34 fish production for spatially and demographically complex populations in changing
35 environmental conditions is however still a difficult task. Indeed, fisheries assessment
36 is mostly based on deterministic models that lack realistic parameterizations of the
37 intricate biological and physical processes shaping recruitment, a cornerstone in
38 population dynamics. We use here a large metapopulation of a harvested fish, the
39 European hake (*Merluccius merluccius*), managed across transnational boundaries in
40 the northwestern Mediterranean, to model fish recruitment dynamics in terms of
41 physics-dependent drivers related to dispersal and survival. The connectivity among
42 nearby subpopulations is evaluated by simulating multi-annual Lagrangian indices of
43 larval retention, imports and self-recruitment. Along with a proxy of the regional
44 hydroclimate influencing early-life stages survival, we then statistically determine the
45 relative contribution of dispersal and hydroclimate for recruitment across contiguous
46 management units. We show that inter-annual variability of recruitment is well
47 reproduced by hydroclimatic influences and synthetic connectivity estimates. Self-
48 recruitment (i.e. the ratio of retained locally-produced larvae to the total number of
49 incoming larvae) is the most powerful metric as it integrates the roles of retained local
50 recruits and immigrants from surrounding subpopulations and is able to capture
51 circulation patterns affecting recruitment at the scale of management units. We also
52 reveal that the climatic impact on recruitment is spatially-structured at regional scale

53 due to contrasting biophysical processes not related to dispersal. Self-recruitment
54 calculated for each subpopulation explains between 19% and 32.9% of the variance of
55 recruitment variability, that is much larger than the one explained by spawning stock
56 biomass alone, supporting an increase of consideration of connectivity processes into
57 stocks assessment. By acknowledging the structural and ecological complexity of
58 marine populations, this study provides the scientific basis to link spatial management
59 and temporal assessment within large marine metapopulations. Our results suggest
60 that fisheries management could be improved by combining information of physical
61 oceanography (from observing systems and operational models), opening new
62 opportunities such as the development of short-term projections and dynamic spatial
63 management.

64

65 **Key words**

66 Ecosystem-based management, fish recruitment, fisheries conservation, hydroclimate
67 variability, metapopulations, ocean connectivity, self-recruitment

68 INTRODUCTION

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

91 Recruitment success (i.e., survival of progeny that enters a population in a
92 given year) is a pivotal ecological process in fisheries ecology that relates quantitative

93 observations of young fish to a measure of spawning potential (stock-recruitment
94 relationships). Most of the fish recruitment research is still co-opted by contemporary
95 topics such as assessing the effects of global changes on marine ecosystems and
96 fisheries by exploring how large-scale climatic variability influences key ecological
97 processes like survival (Rice and Browman 2014). Most of these studies, however, do
98 not take into account the stochastic and fine-scale structures of the seascape, which
99 shape both larval dispersal and survival resulting in ‘realized’ connective pathways
100 (Carson *et al.* 2011). Incorporating realistic larval dispersal schemes into population
101 dynamics and fisheries studies could improve our comprehension of population
102 structuring and its temporal variability (Castorani *et al.* 2015). By embracing
103 simultaneously connectivity and environmental processes, we test here whether the
104 combination of high-resolution connectivity patterns with climate influences and
105 biological factors improves our capability of reproducing fish recruitment dynamics in
106 a ubiquitous harvested nekto-benthic species.

107 Empirical studies in the prominent field of ocean connectivity have largely
108 concentrated on small-scales, particularly for the spatial design of Marine Protected
109 Areas (MPAs) networks in coastal and coral-reef seascapes (e.g., Botsford *et al.* 2009;
110 Almany *et al.* 2017). Recent large-scale modeling studies linked connectivity, MPAs
111 and fishery sciences (Botsford *et al.* 2009; Dubois *et al.* 2016; Krueck *et al.* 2017) but
112 they remained eminently theoretical and they mainly focused on the implications for
113 spatial management at transnational scale and long dispersal organisms (e.g., Kough
114 *et al.* 2013; Andrello *et al.* 2017). However, they did not explore, nor provide
115 observational evidence of, how connectivity temporally affects fishery assessment
116 exercises. Indeed, the effects of broad-scale connectivity on the spatio-temporal
117 population dynamics of large populations has received little attention (Hidalgo *et al.*

118 2017), mostly focused on nearshore systems, or sedentary and benthic species with
119 reduced mobility (Siegel *et al.* 2008; Carson *et al.* 2011; Watson *et al.* 2012; Rochette
120 *et al.* 2013; Castorani *et al.* 2015). In the meantime, numerical models are becoming
121 mature enough to study the influence of environmental variability on recruitment
122 success, to improve stock management frameworks (Hinrichsen *et al.* 2011), as well
123 as to explore the spatio-temporal variability of larval connectivity over several years
124 (e.g., Ospina-Alvarez *et al.* 2015). Daewel *et al.* (2015) recently documented a
125 relative predictive ability of modeled larval survival for observed cod recruitment in
126 the North Sea, but their entire time-series were not significantly correlated due to non-
127 resolved trophic interactions. Simulated multi-annual connectivity estimates have
128 been indirectly interpreted in the context of fisheries (e.g., Huwer *et al.* 2016;
129 Andrello *et al.* 2017) but, to our knowledge, there is no report of significant and
130 coherent relationship between modeled connectivity proxies and observed population
131 estimates (e.g., assessment outputs of segregated stocks). Many biophysical models
132 are being developed by the community to address this challenge but they often use
133 different formulations and they generate various connectivity indices, which are not
134 necessarily harmonized or inter-comparable. Nevertheless, most recent research
135 suggest that the mechanistic and deterministic models currently used in fisheries
136 assessment can be substantially improved by including realistic information of
137 physical processes related with both larval dispersal and survival.

138 The reliability of fish assessment and management strategies are often
139 questioned worldwide because of the mismatch between biological and management
140 scales (Kerr *et al.* 2017). In the Mediterranean Sea, this has been recently challenged
141 as a priority to ensure sustainability of assessed fish stocks (Fiorentino *et al.* 2014), of
142 which more than 90% are in overexploitation state (Fernandes *et al.* 2017). This urges

143 for effective measures and population dynamics modeling that realistically capture the
144 ecological complexity of harvested populations. Focusing on the European hake
145 (*Merluccius merluccius*), which is the most overexploited nekto-benthic species of the
146 Mediterranean Sea, the present study aims at addressing the following specific
147 objectives. First, we assess the potential larval connectivity within and among six
148 discrete subpopulations of hake in the Western Mediterranean. Second, we evaluate
149 whether the connectivity estimates help to explain the temporal dynamics of
150 recruitment and survival (i.e., the rate of individuals that survived from birth to the
151 age of recruitment) in three contiguous geographical areas (hereafter referred to as
152 “management areas”) that currently frame independent assessment procedures for this
153 species. By combining ocean circulation models, time-series of regional climate and
154 biological variables, we model the spatiotemporal dynamics of hake recruitment. We
155 then quantify the relative influence of the regional circulation-driven dispersal and the
156 hydroclimate as selective forces shaping recruitment and survival across the
157 metapopulation sub-units. Our results are discussed to question whether connectivity
158 estimates provided by ocean models are able to effectively capture the temporal
159 dynamics of key biophysical processes shaping fish recruitment and how they can
160 improve the ecological basis of fisheries assessment and management.

161

162 **MATERIALS AND METHODS**

163 *Metapopulation system*

164 This work focuses on the northwestern Mediterranean metapopulation of European
165 hake (*Merluccius merluccius*), an exploited nekton-benthic species of high economic
166 value. The study system is structured by recognized physical and environmental
167 recognized boundaries, and the phenology of key ecological processes such as

168 spawning and recruitment. On the southern border, the Almeria-Oran front represents
169 a physical barrier of transport by ocean currents, which confines the population
170 structure and act as a gene-flow barrier for many marine species (Galarza *et al.* 2009).
171 In addition, the recruitment of hake in the south-western Mediterranean occurs in
172 autumn whereas it peaks in late winter / early spring in the study area (Rey & Gil de
173 Sola 2004; Recasens *et al.* 2008). In the north-east, the spawning phenology of hake
174 in the Ligurian and Tyrrhenian seas is seasonally opposed to that in the Gulf of Lion,
175 off the Iberian Peninsula and around the Balearic Islands which occurs in autumn
176 (Recasens *et al.* 2008, Hidalgo *et al.* 2009). Altogether, this allows us to simplify our
177 metapopulation to six distinct eco-regions consistent with recent studies (Hidalgo *et*
178 *al.* 2009; Puerta *et al.* 2016): Gulf of Lion, Catalan coast, Ebro delta, Valencia gulf,
179 Northern and Southern Balearic Islands (Fig. 1). This structure of the metapopulation
180 system implies that all larvae ending their dispersal phase outside of these regions are
181 considered lost. Similarly, it presupposes that the potential arrival of dispersed larvae
182 from other hake metapopulations is very unlikely and the effect minimal.

183 From now on and in the entire paper, we assumed that each of these eco-
184 regions constitutes a metapopulation subunit. That is, a subpopulation of hake *sensu*
185 *stricto* as defined by Cowen *et al.* (2009) ‘a set of individuals that live in the same
186 habitat patch and interact with each other’. We use consistently the term
187 ‘subpopulation’ throughout this study for clarity purpose while alternative semantic
188 choices and their scientific implications are further discussed in the light of our
189 results. Our six hypothesized subpopulations correspond to three of the thirty current
190 geographic subareas (GSAs, grey contours on Fig. 1), currently used for assessment
191 and management purposes in the General Fisheries Commission for the
192 Mediterranean (GFCM, <http://www.fao.org/gfcm/data/map-geographical->

193 [subareas/es/](#)): Gulf of Lion (GSA-7), Iberian Peninsula (which includes Catalan coast,
194 Ebro Delta and Valencia gulf subpopulations; GSA-6) and the Balearic Islands
195 (encompassing both northern and southern Balearic subpopulations; GSA-5). We use
196 consistently the term ‘management unit’ to refer to these areas in this study.

197

198 *Lagrangian Flow Network and connectivity metrics*

199 We evaluate the dispersion of hake’s larvae among those six subpopulations using the
200 *Lagrangian Flow Network* (LFN) methodology that has been inspired from Network
201 Theory and Dynamical systems perspectives (Ser-Giacomi *et al.* 2015). This
202 framework has been applied to depict connectivity patterns within the entire
203 Mediterranean basin (Rossi *et al.* 2014, Dubois *et al.* 2016). The oceanic surface is
204 subdivided in thousands of equal-area rectangular sub-regions that serve as nodes
205 (small boxes in Fig. 1) in our transport network. These nodes, equivalent of discrete
206 habitat patches, are interconnected by weighted and directed links that represent,
207 using the most adequate numerical and biological parameters (Monroy *et al.* 2017),
208 passive transport of hake’s propagules (eggs and larvae) by ocean currents. Those
209 links are orientated by the oceanic flow and are weighted proportionally to the
210 normalized larval fluxes occurring over the entire period of the pelagic phase. To
211 characterize such links, Lagrangian particle trajectories are computed by integrating
212 the horizontal (2-dimensional) flow field generated by an eddy-resolving
213 hydrodynamical model implemented at $1/16^\circ$ horizontal resolution in the
214 Mediterranean over years 1987-2011 (Oddo *et al.* 2009). 100 particles were seeded
215 evenly in each node of $1/8^\circ$ width (this means releasing about 1 particle per km^2) at a
216 fixed subsurface layer. We retained here the layer at 90 m depth, where hake larvae
217 have been mostly observed (Olivar *et al.* 2003). The Pelagic Larval Duration (PLD)

218 simulated is 40 days (Hidalgo *et al.* 2009). We considered repeated spawning events
219 each year during the main autumnal spawning period of the species with seven
220 starting times (15 days apart) from September, 1st to November, 30th (Hidalgo *et al.*
221 2009). We also performed additional sensitivity tests to further support the robustness
222 of our conclusions (see below and Appendix S1).

223 From several millions of virtual trajectories representing the transport of free-
224 swimming propagules, LFN builds high-resolution connectivity matrices between all
225 possible origin and destination nodes (i.e., for each node, it stores the numbers and
226 weights of all links emanating from it and entering it) of the region under study.
227 Matrices are post-processed to discard specific sites (through an adequate selection of
228 nodes) and to vary the scales of interest (through the grouping of selected nodes)
229 without the need to re-compute any trajectory. In particular, we consider as
230 origin/destination sites only those with preferential habitats of hake (e.g., nodes
231 inshore the 300 m isobath). Within those nodes, local larval release and success of
232 recruitment are homogeneous; they are null in the remaining nodes. Overall, 175
233 numerical experiments (7 spawning events per year over 25 years) generate 175
234 connectivity matrices that are then further analyzed to compute metrics, which
235 measure larval retention and directional exchanges applying formulations derived
236 from population dynamics concepts (Dubois *et al.* 2016). We assume that recruitment
237 of a given subpopulation is at primary controlled by locally-produced larvae and the
238 immigration of distantly-released larvae. Consequently, the three complementary
239 connectivity metrics exploited here are: Import, Local Retention and Self-
240 Recruitment. Import (Imp) is the total number of incoming larvae from all origins
241 (produced elsewhere only). Local Retention (LR) is the proportion of locally
242 produced larvae that are locally retained. Self-Recruitment (SR) is the ratio of locally

243 produced larvae retained in each area to the total number of incoming larvae
244 (including those produced locally). In this respect, LR is only a local measure whereas
245 SR encompasses information of both local (LR) and remote directional influences
246 (Imp). LR and SR relate to the self-persistence of a given subpopulation while Imp
247 and SR evaluate the network-persistence of the whole metapopulation (Castorani *et*
248 *al.* 2015; Dubois *et al.* 2016). Imp is expressed in absolute number of particles and,
249 LR and SR are probabilities with values between 0 and 1 (0 indicates no retention).
250 While some authors suggested that SR can be a good predictor of LR under certain
251 conditions (e.g. Lett *et al.* 2015), Dubois *et al.* (2016) generalized the formulations of
252 these connectivity estimates applied to larval transport and showed that the relative
253 difference between LR and SR provides insight into the source or sink behavior of the
254 subpopulation of interest. We report here the annual averages of these three
255 connectivity metrics with associated uncertainties (standard deviations), calculated
256 among the successive spawning events within the main reproductive season.

257 The sensitivity and robustness of those connectivity metrics to the most
258 relevant parameters of the LFN were extensively assessed (Dubois *et al.* 2016;
259 Monroy *et al.* 2017) (Appendix S1). In order to compare modeled connectivity
260 estimates with fisheries assessment outputs (see below), we calculated the metrics at
261 two hierarchical scales: for the six aforementioned subpopulations of hake and at the
262 scale of the three regional management units described previously. This lets us
263 evaluate i) which is the best connectivity metric to reproduce the fisheries assessment
264 estimates and ii) at which spatial scale (subpopulation or management unit) the impact
265 of larval retention and exchange is better captured.

266

267 *Statistical approach*

268 Prior to the modeling of fisheries-based information, we first assessed the
269 relative contribution of LR and Imp on SR, applying General Additive Modeling
270 (GAMs) on SR as response variable and LR and log(Imp) as non-linear covariates.
271 We then statistically assessed and quantified the impact of our physical-
272 dependent drivers on recruitment and survival (i.e., the ratio of recruitment at time t to
273 the spawners biomass at time $t-1$), which were obtained from GFCM fisheries
274 assessment groups of the three corresponding management areas that take into
275 account information from scientific bottom trawl surveys (SAC-GFCM 2015). As
276 physical covariates, we investigated the potential linear effects of the simulated
277 connectivity metrics (LR, SR and log(Imp)) along with the Regional Hydroclimatic
278 Index (RHI) that can capture biophysical processes not related to dispersal.
279 Connectivity estimates included in the models were calculated at both
280 “subpopulation” and “management unit” levels to assess the spatial scale at which
281 including connectivity maximizes models’ performance (Metadata S1, Data S1). RHI
282 is calculated attending to air-sea heat exchange anomalies in the northwestern
283 Mediterranean, and has been related to the inter-annual variability of intermediate
284 water mass formation in winter in the Western Mediterranean (Monserrat *et al.* 2008).
285 Negative values of this index are associated to higher formation rate of winter
286 intermediate water mass, which influences the seasonal surface circulation patterns
287 resulting in greater regional primary production than average (Balbín *et al.* 2014),
288 with a positive impact on the recruitment success of hake in the Balearic Islands
289 (Massutí *et al.* 2008). While it suggests that the RHI captures biophysical processes
290 mainly related to early life stages survival, it is not yet clear if and how they could be
291 related to dispersal.

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

302 To account for the temporal lag induced by the successive spawning, dispersal,
303 settlement and finally recruitment process, connectivity metrics of year t were
304 regressed against fisheries assessment variables of year $t+1$. To test whether density
305 dependence influences recruitment survival at larger spatial scales than expected in
306 the meta-population, spawning biomasses of contiguous management areas were
307 combined. Given that the length of the time-series of fisheries assessment variables
308 differs among areas, a final model with three, two and one covariate(s) were
309 considered for the Balearic Islands, Gulf of Lion and the Iberian Peninsula,
310 respectively.

311 Prior statistical analyses, absence of correlation and collinearity among physical
312 and biological covariates was confirmed by applying, respectively, Spearman
313 correlations and the variance inflation factor test (Zuur et al. 2009). The best model
314 was obtained by minimizing the Akaike Information Criterion (AIC). For every
315 model, residuals were checked for variance homogeneity and absence of temporal
316 autocorrelation applying the auto-correlation function (acf). To quantify the benefits

317 of considering connectivity and climate proxies to model fish recruitment, we
318 compare the percentage of Deviance Explained of models including those metrics
319 with the standard models based solely on SSB. Once the best model was obtained for
320 each management area, all time-series were normalized to mean 0 and variance 1 and
321 pooled in a unique and centered (i.e., intercept equals 0) linear model to compare the
322 size (slope) of each effect (connectivity, hydroclimate and spawning stock) for each
323 management area.

324

325 **RESULTS**

326 *Connectivity estimates*

327 Larval exchanges simulated by the Lagrangian Flow Network (LFN) among the 6
328 discrete subpopulations of hake suggest that the subsurface circulation in the
329 northwestern Mediterranean, dominated by the Liguro-Provencal-Catalan current,
330 drives a southwestward directional pattern of connectivity (Fig. 1). The Gulf of Lion
331 is thus the main source of particles Import (Imp) into the Iberian Peninsula. While this
332 southwestward connectivity prevails in all 25 years under study (see the annual mean
333 patterns of connectivity over 1987-2011 in Appendix S2: Fig. S1), two distinct
334 scenarios can be distinguished. The first connectivity pattern consists in a
335 southwestward flux to the mainland, with a weak or null transport towards the
336 Balearic Islands (Fig. 1a). The second one reveals a reduced transport towards the
337 Iberian Peninsula shelf and an eastward retroflexion of the main transport pathways,
338 resulting in stronger connections with the Balearic Archipelago (Fig. 1b). Larval
339 Local Retention (LR) also displays consequent spatiotemporal variability, which
340 seems less prominent than the changes of directional connectivity patterns (Fig. 1;
341 Appendix S2: Fig. S1). The lowest LR values occur over the narrow shelves of the

342 Catalan coast (0.32 ± 0.1) and the northern Balearic Islands (0.33 ± 0.07). In contrast,
343 relatively extended continental shelves tend to favor retention rates: the Gulf of Lion
344 has intermediate LR (0.42 ± 0.07), while the highest LR values are obtained for the
345 Ebro delta (0.46 ± 0.06), the Valencia channel (0.47 ± 0.06) and the southern Balearic
346 Islands (0.47 ± 0.05) (see pair-wise comparisons in Appendix S2: Table S1).

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

367 southern Balearic Islands (0.84 ± 0.07) and Gulf of Valencia (0.87 ± 0.06), medium in
368 the Ebro delta (0.68 ± 0.1) and northern Balearic Islands (0.72 ± 0.09), and relatively
369 low in the Catalan coast (0.53 ± 0.1) (Fig. 2b; see also pair-wise comparisons in
370 Appendix S2: Table S2). Note that SR in the Gulf of Lion is always close to 1
371 (0.99 ± 0.003), demonstrating it is mostly influenced by local processes (LR) as Imp is
372 very weak or null due to the dominant south-westward directional connectivity and its
373 positioning on the north-eastern boundary of our simplified meta-population system.

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

385 Sensitivity tests performed at both levels of analyses (6 subpopulations and 3
386 management units) reveal that our connectivity metrics and their inter-annual
387 variability are robust to variations of the three critical parameters (Appendix S1:
388 pelagic larval duration, Fig. S1; spawning frequency, Fig. S2; and dispersal depths,
389 Table S1 and S2).

390

391 *Recruitment dynamics*

392 The best statistical model of recruitment for each management unit reveals the
393 influence of SR and RHI as the most relevant drivers (Tab. 1). SSB was not
394 significant in all models in which its effect was considered, including those in which
395 SSB was the unique covariate (Tab. 1). There was a considerable increase of the
396 Deviance Explained (DE) from models exclusively based on SSB to the best models
397 obtained for each management area (from 27.3% in the Gulf of Lions to 36.2% in the
398 Balearic Islands, Tab. 1). An increase of 21.3% of DE was observed in the model of
399 Balearic Islands including RHI and SR from the model exclusively based on RHI.
400 Besides the minimization of AIC, DE of models including SR were between 2.7 %
401 and 7.6% higher compared to those including the other connectivity metrics tested
402 here, that is LR or IMP (Tab. 1).

403 As SR and RHI effects were linear and the most representative in all
404 management areas (Fig. 4a), they were standardized in a unique model for the whole
405 metapopulation (DE = 37.6 %; Appendix S3: Fig. S1) to compare these effects across
406 areas. SR is a significant variable influencing the recruitment in both the Iberian
407 Peninsula and the Balearic Islands with a similar effect size (i.e., slope, Fig. 4b).
408 However, in the model for the Iberian Peninsula management unit, SR calculated in
409 the Catalan coast subpopulation emerges as the most relevant SR metric. For the
410 Balearic Islands case, the most relevant SR metric turns out to be SR calculated at the
411 management unit level (Tab. 1). None of our connectivity metrics was a significant
412 predictor of recruitment in the Gulf of Lion. However, for the RHI, a clear directional
413 change is observed from a negative significant effect on recruitment in the Balearic
414 Islands (i.e., recruitment is favored under negative values of RHI) to a positive
415 significant effect in the Gulf of Lion, and no effect observed in the Iberian Peninsula

416 (Fig. 4c). The size of RHI effects were of the same order as those of SR (Figs. 4b and
417 4c).

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

427

428 **DISCUSSION**

429 Our study demonstrates that, making reasonable assumptions, the inter-annual
430 variability of recruitment of large fish stocks can be modeled incorporating physics-
431 dependent drivers related to dispersal and survival: the spatiotemporal connectivity
432 estimates derived from a high-resolution circulation model and an index capturing the
433 temporal variability of the regional hydroclimate. While nearshore connectivity is
434 sometimes suggested to be heterogeneous on short time-scales due to stochastic
435 transport of pelagic larvae (Siegel *et al.* 2008; Watson *et al.* 2012), and although
436 basin-scale models are known to poorly simulate complex coastal currents, our
437 statistical analyses derived from such model provide signals consistent with both
438 inter-annual variability and geographical discrepancies of LR associated with local
439 topography and hydrodynamics (Dubois *et al.* 2016). Moreover, we demonstrate that
440 our connectivity metrics integrate both larval retention and exchanges (Watson *et al.*

441 2012; Lett *et al.* 2015) and are able to capture recurrent annual circulation patterns
442 (Dubois *et al.* 2016), that significantly affect the recruitment success of hake on larger
443 spatial-scales (i.e., both at “subpopulation” and “management” levels). Given that
444 recruitment dynamics is the main ecological basis and the unique mechanistic insight
445 of fishery assessment, our study presents a novel framework to incorporate physical
446 information into assessment procedures to improve stock-recruitment relationships
447 and short-term predictions of fisheries production. The two main steps consist in: 1)
448 identifying the spatial scale at which the influence of connectivity processes on the
449 population is prominent; and 2) mechanistically comparing fisheries recruitment data
450 and ad-hoc connectivity metrics (namely import, local retention and self-recruitment)
451 adequately computed over the appropriate region previously defined. Earlier studies
452 have explored how estimates of larval dispersion could be integrated into fisheries or
453 demographic models. They include theoretical perspectives (e.g., Botsford *et al.*
454 2009b; Castorani *et al.* 2015), but also studies for small regions and highly sedentary
455 species (e.g., Rochette *et al.* 2013; Johnson *et al.* 2018). For large fish stocks,
456 connectivity information derived from genetic, tagging and otolith is often used to
457 spatially delineate subpopulations rather than to model temporal dynamics (e.g.,
458 Holmes *et al.* 2014). Here, we propose a framework to link dispersal simulations with
459 temporal dynamics of recruitment data of open and large stocks such as the European
460 hake with wide distribution and complex spatial structure.

461 Historically, marine populations tended to be classified as open or closed
462 according to their replenishments being ensured primarily by immigrants or by local
463 production (Hixon *et al.* 2002). While this dichotomy and its management
464 implications could be applied in small metapopulation of littoral sedentary species
465 (i.e., when connectivity processes are relatively well captured by local retention), it

466 does not hold for most offshore fish stocks for which there is an increasing awareness
467 that spatial and demographic structure is more complex than currently accounted for
468 (Cadrin *et al.* 2009; Kerr *et al.* 2017). This inherently calls for indicators that properly
469 parameterize the observed continuum between open and closed systems beyond stock
470 boundaries and that are able to account for both local and distant connectivity
471 processes. In this view, Self-Recruitment (SR), which was defined to take into
472 account the influences of both local recruits and immigration from the surrounding
473 subpopulations (Botsford *et al.* 2009a), seems best adapted. Indeed, our study shows
474 that larval SR is, according to our statistical models, the best synthetic predictor of
475 fisheries recruitment, as it constitutes the mechanistic link among the three
476 management areas of the European hake in the Western Mediterranean. Furthermore,
477 to precisely assess the demographic role of each subpopulation (source/sink) and the
478 global metapopulation persistence (Lett *et al.* 2015), we advocate for the simultaneous
479 interpretation of both SR and Local Retention (LR). Dubois *et al.* (2016) indeed
480 showed that the greater the relative difference between SR and LR, the more
481 pronounced is the source or sink behavior. We found that SR of four hake
482 subpopulations are mainly controlled by the inter-annual variations of Import (Imp),
483 emphasizing the role of network persistence. We also showed that variability in both
484 LR and Imp in the Catalan Coast and in the northern Balearic Islands contribute to
485 meaningful changes in their respective SRs, indicating the importance of both
486 network- and self-replenishment. Our model suggests that all subpopulations behave
487 as sources, with stronger larval export than import. It is worth distinguishing the
488 effective sources (e.g., Gulf of Lion, Catalan coast), whose exported larvae
489 successfully sustain other identified subpopulations due to favorable dispersal
490 pathways, as compared to the non-effective ones (e.g., north Balearic Islands) whose

491 exported larvae are lost from the metapopulation system under its hypothesized
492 geographical structure. While those larvae would be, in reality, lost in the open ocean
493 with low likelihood of surviving, they could reach other subpopulations outside of our
494 studied region. However, the phenology of reproduction and recruitment season of
495 neighbored areas upstream (Ligurian or Tyrrhenian Seas, Recasens *et al.* 2008) and
496 southward Almeria-Oran front (Alboran Sea, Rey *et al.* 2004) are seasonally opposed.
497 In addition, the absence of favorable nursery habitats upstream the ‘source’ area of the
498 Gulf of Lions makes the success of potential settlement very unlikely (Druon *et al.*
499 2015). From a spatial management perspective, the subpopulations whose SR
500 represent a balanced contribution of local (LR) and remote (Imp) connectivity
501 processes are of crucial importance for the global persistence of a metapopulation
502 (Botsford *et al.* 2009a; Lett *et al.* 2015). In this view, SR emerges as a crucial variable
503 to be properly estimated by scientists and to be adequately considered by managers
504 for ensuring population persistence.

505 The spatial heterogeneity of climate effects on fish recruitment has been
506 reported for global indices, but not yet at regional-scales. Our study presents evidence
507 of a clear regional gradient with antagonist effects in nearby areas located only about
508 500 km away. Together with SR, the climatic index has an elevated explanatory
509 power in two of the three management units. Our results reinforce the inverse
510 relationship between this index and hake recruitment already documented in the
511 Balearic Islands (Massutí *et al.* 2008). Low values of the index are related to
512 anomalously intense formation of intermediate waters in the Gulf of Lion forced by
513 winter wind-driven vertical mixing (Balbín *et al.* 2014). These nutrient-rich waters
514 then flow further south and increase biological productivity in the Balearic sea, an
515 area especially oligotrophic in the western Mediterranean, enhancing food availability

516 for hake larvae and juveniles there (Massutí *et al.* 2008). In contrast, we also
517 demonstrate for the first time a strong positive correlation between this index and
518 hake recruitment in the Gulf of Lion. We hypothesize that stronger than average
519 mixing events homogenize the water column down to several hundred meters' depths
520 (and even down to the seabed in extreme events, Balbín *et al.* 2014) can trigger high
521 mortality rates of locally produced hake larvae, negatively impacting recruitment
522 success in the Gulf of Lion. Other indirect mechanisms could be that, under intense
523 winter convection, hake larvae could entrain in water masses with no food supply
524 and/or within unfavorable dispersal routes toward the open-ocean. These findings
525 reveal how the link between climate variability and its ecological impact is
526 geographically structured at regional scales. In this case, the same local
527 oceanographic event (winter wind-driven vertical mixing in the Gulf of Lion) has
528 opposite impacts in close-by regions. Locally, strong mixing events considerably
529 reduce the survival of hake larvae and recruitment in the Gulf of Lion, whereas they
530 increase food availability over the north-western Mediterranean region, affecting
531 positively hake recruitment in the Balearic Islands.

532 Although climate indices are able to capitalize a broad spectrum of
533 environmental processes with simplistic formulations (standardized air temperature
534 anomalies in our case), they often integrate various processes acting over different
535 time and space windows, with the potential risk of redundancy between drivers,
536 dispersal and hydroclimate. This suggests the need to complement the formulations of
537 climatic indexes with additional information (e.g., from high-resolution ocean model
538 simulations as well as observations gathered by ocean observing systems) that would
539 parameterize adequately the local manifestation of large-scale climatic signals and its
540 associated ecological response. Indeed, while the climate influence of fish populations

541 has been largely demonstrated, it is rarely included in fisheries assessment due to the
542 difficulty to link climate indices with a specific ecological process within age-
543 structured modeling frameworks. Our study demonstrates that the combination of
544 spatially structured connectivity and climatic effects could be applied in a simple and
545 synthetic way (e.g., Rochette et al. 2013), beyond classic stock-recruitment
546 relationships and independently of the functional form of density dependence. The
547 two physical-dependent drivers can be calculated in winter, increasing the short-term
548 predictive ability of hake recruitment mainly concentrated during the following
549 spring. This suggests that our approach could be of general applicability for many
550 stocks recruiting to the fishery during their first year of life.

551 The population structure of marine species falls in a continuum from truly
552 panmictic to numerous isolated subpopulations, and the majority exhibits complex
553 structures within this range (often referred to as biocomplexity, e.g., salmon in
554 Alaska, Hilborn *et al.* 2003, herring in the east Atlantic, Ruzzante *et al.* 2006, cod in
555 the North Sea, Wright et al. 2006). A growing concern among fishery scientists during
556 the last decade is to understand how the loss of bio-complexity influences the
557 resilience and stability of exploited marine populations. This general objective
558 triggered an increasing consideration of complex metapopulation structures and
559 combines in fact two current challenges: a historic questioning about fish stocks
560 boundaries and also a more recent recognition of sub-structuring within management
561 areas as a set of ‘sub-units’ displaying different ecological or demographic functions.
562 Although a panmictic scenario has been suggested for hake in the western
563 Mediterranean (Morales-Nin *et al.* 2014), our study provides evidence that
564 demographic connectivity is more relevant than genetic connectivity to provide
565 scientific support for the management of hake’s metapopulation in the Mediterranean

566 Sea as it is able to explain a sizeable component of the inter-annual variability of the
567 observed recruitment. The Gulf of Lion is linked to the Iberian Peninsula management
568 unit mostly by a unidirectional south-westward connection that shapes the hake
569 recruitment dynamics of the latter, consistent with recent research on small pelagic
570 fish (Ospina-Alvarez *et al.* 2015). Furthermore, the Catalan coast emerges as the
571 critical transitional subpopulation connecting both management units since its
572 simulated larval SR significantly correlates to the observed recruitment of the entire
573 Iberian Peninsula unit, questioning the current geographical delimitation for
574 assessment and management. In contrast, Atlantic populations of the same species
575 show a different scenario with documented gene flows between geographically-
576 separated management units but relative demographic independence (Pita *et al.* 2016),
577 supporting the current management separation.

578

579 *Concluding remarks and future challenges*

580 Recognizing subpopulations and providing specific demographic metrics that
581 reflect their heterogeneous contributions to the global dynamic of a metapopulation is
582 a current but accessible challenge for fisheries ecologists (Kerr *et al.* 2017). Our study
583 provides a methodological framework to calculate and compare these metrics, which
584 acknowledge the complexity of marine populations and ecosystems in a relatively
585 simple manner, providing a research pathway alternative to the development of
586 complex models (e.g., end-to-end ecosystem models). Efficient ways to embrace
587 physics and fisheries assessment to improve management of large metapopulations
588 include, as we showed here, the integrated analysis of a limited number of controlling
589 ecological and environmental processes that are critical to understand and reproduce
590 the functioning and dynamics of marine systems. In this sense, mechanistic modeling

591 constitutes a valuable tool to circumvent the lack of observations and understanding
592 of these processes. Further research also needs to assess the wider implications of our
593 results for: the population dynamics (i.e. short- and long-term persistence at both sub-
594 and meta-population levels) by incorporating our connectivity indices into population
595 models; for the determination of biological reference points (e.g. maximum
596 sustainable yield) obtained from stock assessment models; or for the design of
597 dynamic and adaptive spatial management. To support the application of spatially and
598 temporally pertinent conservation measures, future research also needs to include
599 other elements such as the relevance of spatially structured ecological functions (e.g.,
600 spawning areas, nursery and feeding grounds) along with the impact of adult
601 mediated-connectivity (Goethel *et al.* 2011). Finally, a more efficient use of the
602 environmental information generated by ocean models and observing systems is
603 required to pursue the fast development of ‘operational fisheries oceanography’
604 (Álvarez-Berastegui *et al.* 2016). Besides the abundant research dedicated at including
605 climatic influences in long-term projections of fish production (Rice & Browman
606 2014), a new paradigm should focus in those oceanographic and climatic processes
607 that considerably affect short-term predictions, which are the relevant scales for
608 management purposes. While our study supports the predictive power of SR in a
609 fisheries assessment context, it generally calls for further effort to incorporate
610 connectivity estimates and mesoscale climatic indexes derived from ocean
611 observations and models into fisheries modeling, assessment and stewardship. Over
612 longer time-scales, human-induced climate change is projected to increase ocean
613 temperature, affecting the distribution of fish stocks and increasing the number of
614 transboundary stocks (Pinsky *et al.* 2018). In addition, climate change is also expected
615 to modify circulation patterns and favor extreme events, influencing the transport and

616 survival of marine planktonic larvae and, thus, altering connectivity (Lett *et al.* 2010).
617 Our modelling framework, backed-up by decadal observations, could help to
618 investigate those long-term effects toward the sustainable protection and management
619 of marine ecosystems.

620

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635

636 **AUTHORS’ CONTRIBUTIONS:**

637 M.H. and V.R. designed and directed the study. P.M., E.S.-G., V.R. and E.H.-G. set
638 up the Lagrangian modelling framework and performed the simulations. A.J., B.G.
639 and J.L.P. provided the recruitment data. M.H. and V.R. analyzed all data and
640 interpreted the results. All authors discussed the results. M.H. and V.R. wrote the

641 paper. M.H., V.R., E.S.-G., E.H.-G., B.G., E.M., F.A., A.J., J.L.P. and P.R.
642 commented on the manuscript.

643

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790

791

792 **Table 1.** Best fisheries recruitment models obtained for each management area.

793 Covariates included are Self-Recruitment (SR), Import (Imp), Local Retention (LR),

794 Regional Hydroclimatic Index (RHI) and Spawning Stock Biomass (SSB). Akaike

795 Information Criteria (AIC), delta AIC and Deviance Explained (DE, %) are also

796 presented. Connectivity metrics were calculated at two geographical levels:

797 management area and subpopulations (see Materials and Methods). CC and NBI refer,

798 respectively, to Catalan coast and Northern Balearic Islands subpopulations. IP and BI

799 refer, respectively, to Iberian Peninsula and Balearic Islands management units. Ns

800 mean non-significant ($p > 0.05$) effect of the SSB covariate, which is presented for

801 comparison with other models in terms of DE. Note that information provided for

802 models using SSB as unique covariate were fit applying general additive models,

803 while the rest applies linear models.

804

Management area	Covariates	AIC	Delta AIC	DE (%)
Balearic Islands	SSB ^{ns}	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 ^{ns}	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 ^{ns}	11.28	5.6	20.4
	RHI	5.68	0	47.85

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809 **FIGURE LEGENDS**

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

826

827 **Figure 2.** Time-series of annual mean of Self-Recruitment (SR) in all subpopulations
828 coded with the same colors as in Fig. 1 **(a)**. Relationship between Self-Recruitment
829 (SR) and Local Retention (LR) for all subpopulations over 25 years (1987-2011) **(b)**.
830 Dots with bars represent the mean and the standard deviation calculated over the 25
831 years, respectively, for the two connectivity metrics. Dotted lines represent the linear
832 fits between SR and LR for each subpopulation.

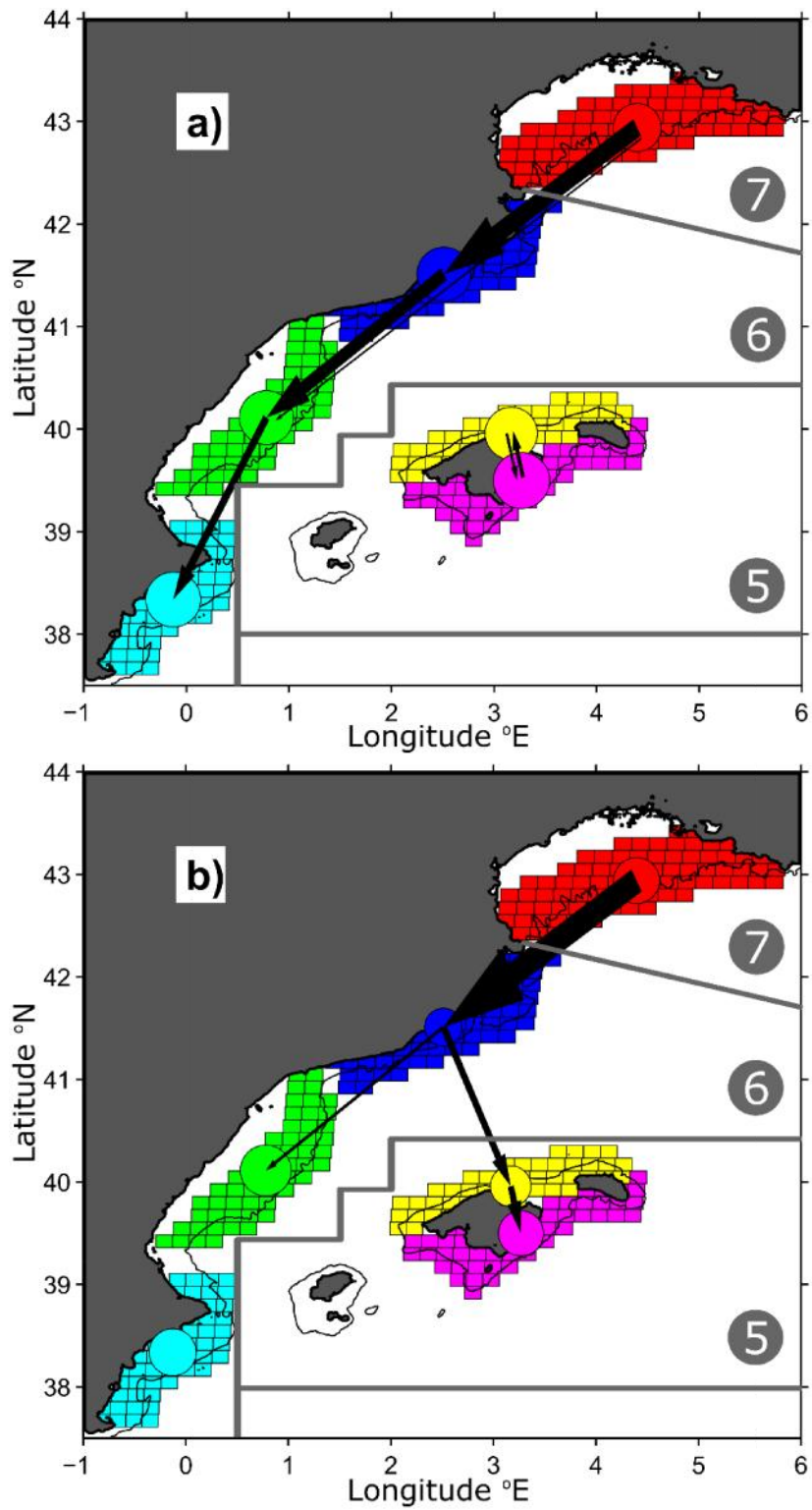
833 **Figure 3.** Relative effects of Local Retention (LR, left column) and Import (Imp, in
834 log scale, right column) on the inter-annual variability of Self-Recruitment (SR) for
835 each of the three management areas: Gulf of Lion (upper), Iberian Peninsula (middle)
836 and Balearic Islands (bottom).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

841

842 **Figure 4.** Time-series of annual recruitments from fisheries assessment in the three
843 management areas (Balearic Islands, BA, red colors; Iberian Peninsula, IP, blue
844 colors; Gulf of Lion, GL, black colors) and the Regional Hydroclimatic Index (RHI,
845 grey curve, Balbín *et al.* 2014) (a). Based on the covariates obtained of the best
846 recruitment models (Table 1), a global linear model was constructed for the whole
847 metapopulation with standardized time series (mean 0 and variance 1) to statistically
848 compare the strength of connectivity (Self-Recruitment, SR) and hydroclimate (RHI)
849 effects on recruitment for each management area (Appendix S3: Fig. S1). The effect
850 size (i.e., linear model estimates) of each management area is presented for SR (b)
851 and RHI (c). No overlapping of vertical bars (standard errors of the model estimates)
852 with zero horizontal lines reveals statistical significance of the effect.

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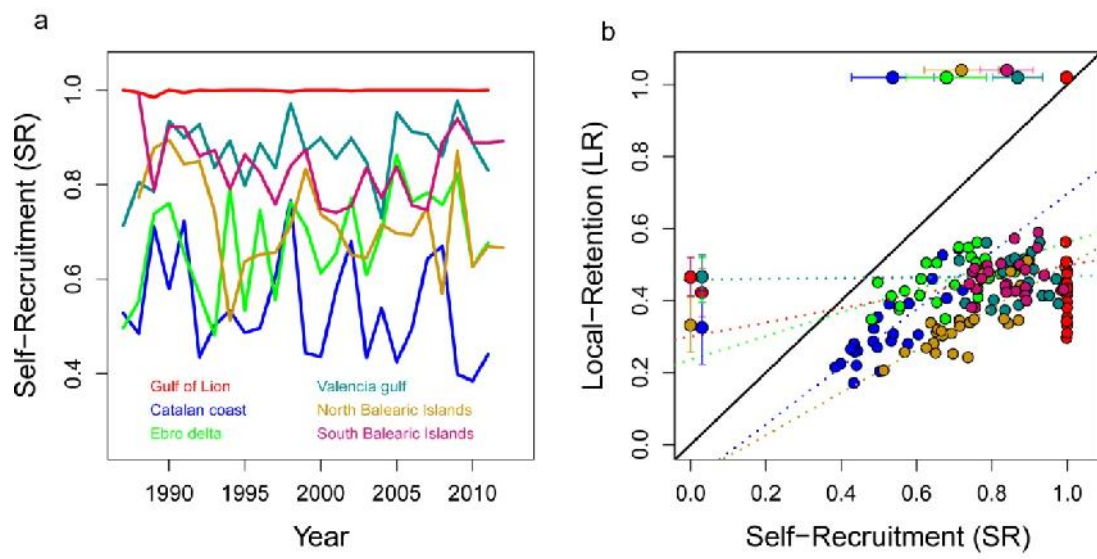
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858 Figure 1

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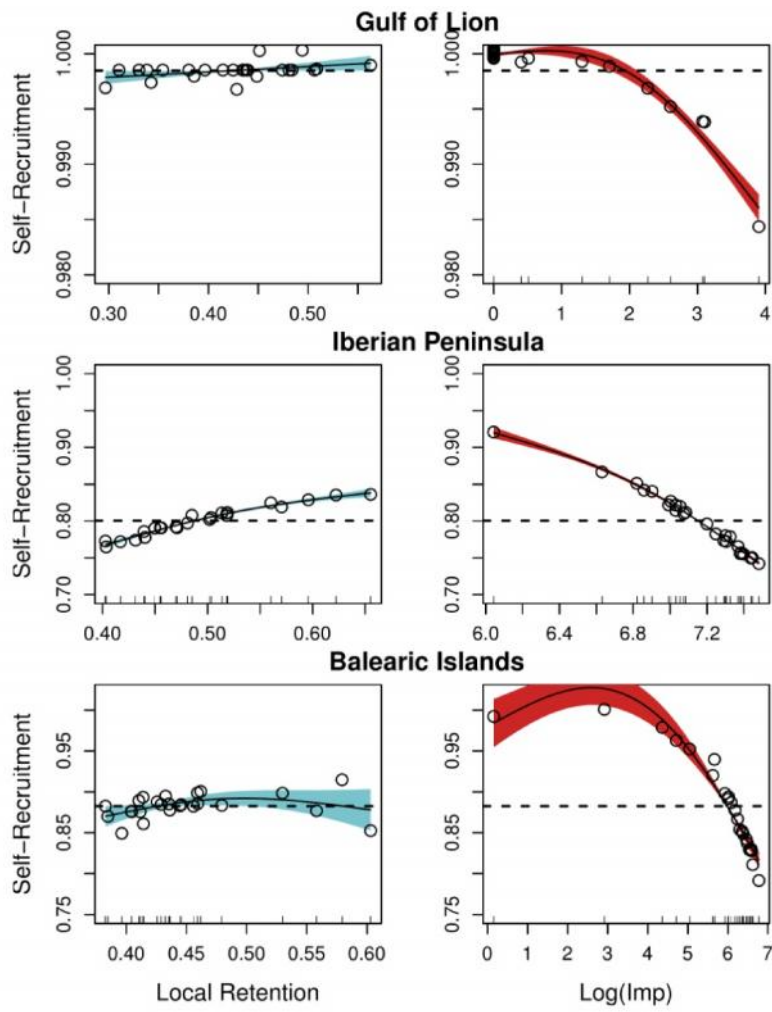
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863 Figure 2.

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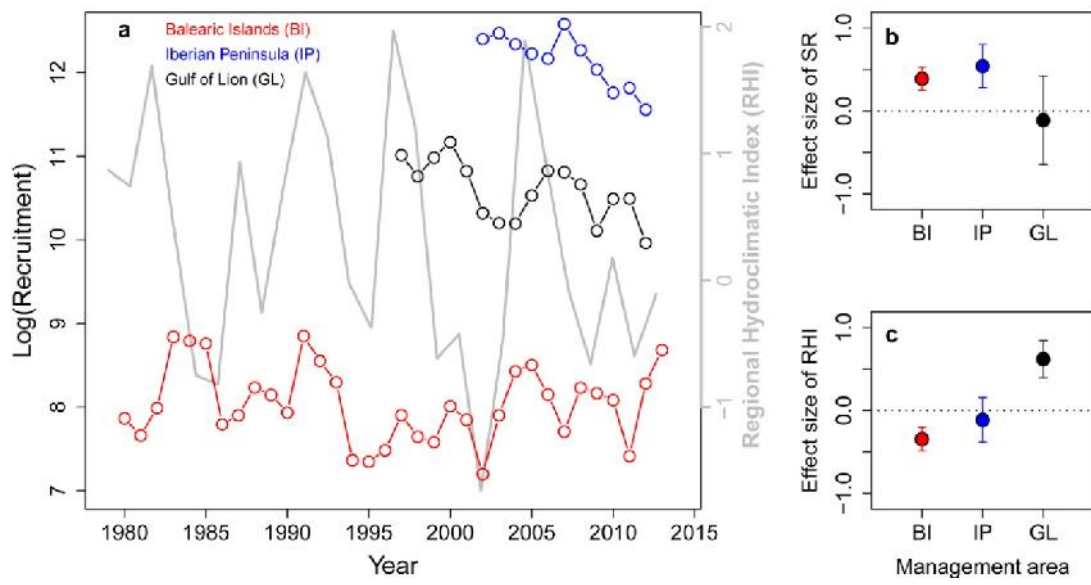
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869 Figure 3

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874 Figure 4

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Appendix S1: Sensitivity analysis of connectivity metrics to critical life history parameters.

While the global sensitivity of the LFN modeling framework was already assessed (Monroy et al. 2017), the robustness of the present results is here more specifically tested for three key parameters: the duration of the Pelagic Larval Duration (PLD), the number and frequency of spawning events, and the depth of dispersion. The primary factor that would affect dispersal patterns is the PLD. As such, three potential PLDs were evaluated: 30, 40 and 50 days. Note that these analyses serve also as a test to evaluate the influence of a pre-competency period of ± 10 days for the settling of hake larvae. In addition, we tested the robustness of our results to more frequent spawning events by comparing periodicities of 5 and 15 days evenly distributed over the same 2-month period (September 1st to 30th November), i.e. a total of 19 and 7 (respectively) spawning events per year. Last, although hake larvae are mainly found at depths of around 90 m, suggesting it is a fair approximation of its dispersal depths (Olivar et al. 2003, Sabates, 2004), it may vary in nature. We thus assessed the robustness of our results to three different depths (60, 90 and 120 m).

Our sensitivity tests reveal that, although the absolute means of three connectivity proxies (chosen arbitrarily) slightly differ among the three tested PLDs (changes concern, in average over all years and across all diagnostics, about $\pm 10-15\%$ of the reference values obtained with PLDs of 40 days), their inter-annual patterns remain consistent in three distinct regions (chosen arbitrarily, Appendix S1 - Figure S1). All connectivity diagnostics in any subpopulation or management area return the same consistent inter-annual variability. The spawning frequency tests demonstrated that the annual averages of LR and SR do not differ, while minimal differences are observed in the yearly means of Imp (Appendix S1 - Figure S2). The inter-annual variability remains consistent between the two tested periodicities and the connectivity diagnostics in any subpopulations return the same robustness. While the depth of dispersal seems to be the most sensitive parameter of the three tested here, we found no consistent trend of its impact among our six subpopulations or over time. This is due to the unpredictable nature of the vertical structuring of ocean currents: in a given region and period (e.g. Gulf of Lion in winter) currents may be nearly homogeneous in the vertical (barotropic) while they may be substantially heterogeneous (baroclinic) in other regions and periods. It is also due to the fact that the surfaces of each sub-region are not comparable across the sensitivity experiments testing depth since the bathymetric mask is specific to each horizontal layer of the model. Despite these isolated small differences, non-parametric Friedman tests showed that both retention and exchange indices computed at those three depths are statistically equivalent, except in rare occasions (Appendix S1 - Tables S1 and S2).

In summary, sensitivity tests showed that the main spatial and temporal connectivity patterns are robust against small changes of LFN parameters such as PLD, periodicity of spawning and depth of dispersal. The inter-annual variability of

connectivity metrics was always conserved while the mean values displayed, as expected, certain but negligible differences (apart from the specific cases sensitive to the dispersal depth). Note that the most important element in the present study is to ensure that the inter-annual fluctuations of our connectivity metrics are preserved despite slightly different parameter choices, as it was shown unambiguously for different PLDs (Appendix S1: Figure S1), frequencies of spawning (Appendix S1: Figure S2) and dispersal depths (Appendix S1: Tables S1 and S2).

References:

- Monroy, P., Rossi, V., Ser-Giacomi, E., López, C. & Hernández-García, E. Sensitivity and robustness of larval connectivity diagnostics obtained from Lagrangian Flow Networks. *ICES J. Mar. Sci.* **74**, 1763–1779 (2017).
- Olivar, M.P., Quilez, G. & Emelianov, M. Spatial and temporal distribution and abundance of European hake, *Merluccius merluccius*, eggs and larvae in the Catalan coast (NW Mediterranean). *Fish. Res.* **60**, 321–331 (2003).
- Sabatés, A. Diel vertical distribution of fish larvae during the winter-mixing period in the North-western Mediterranean. *ICES J. Mar. Sci.* **61**, 1243–1252 (2004).

Appendix S1 – Tables

Table S1. List of p-values resulting from Friedman tests comparing the annual averages of retention metrics (LR and SR) obtained from 7 dispersion experiments at 60, 90 and 120 m with PLD = 40 days over 1992. Significant p-values (bold, applying a 1% significant level) indicate that the mean LR/SR among those dispersal depths are

significantly different, which is only the case for LR in the southern Balearic Islands and SR in the northern Balearic Islands. The remaining values suggest statistical equivalence (i.e. there are no statistical differences in the median values obtained with different depths).

Connectivity metric	Gulf of Lion	Catalan coast	Ebro delta	Valencia gulf	North Balearic Islands	South Balearic Islands
LR	0.156	0.07	0.01	0.052	0.18	0.002
SR	0.368	0.02	0.056	0.06	0.002	0.368

Table S2. List of p-values resulting from Friedman tests comparing the annual mean numbers of particles exchanged among (and, in the diagonal, retained within) 6 subpopulations computed from 7 dispersion experiments at 60, 90 and 120 m using PLD = 40 days over 1992. The significant p-values (bold, applying a 1% significant level) indicate that the numbers of particles exchanged at those dispersal depths are significantly different; this is the case for only 6 directional connections over 21 effective larval fluxes. The remaining non-significant values suggest statistical equivalence. Na indicates the absence of connection (i.e. no larval flux).

	Gulf of Lion	Catalan coast	Ebro delta	Valencia gulf	North Balearic Islands	South Balearic Islands
Gulf of Lion	0.0009	0.004	0.22	Na	Na	Na
Catalan coast	0.368	0.011	0.002	Na	0,074	Na
Ebro delta	Na	0.135	0.012	0.035	0.66	0.22
Valencia gulf	Na	Na	0.076	0.651	0.004	0.004
North Balearic Islands	Na	Na	Na	Na	0.276	0.368
South Balearic Islands	Na	Na	Na	0,368	0.05	0.002

Appendix S1 - Figures

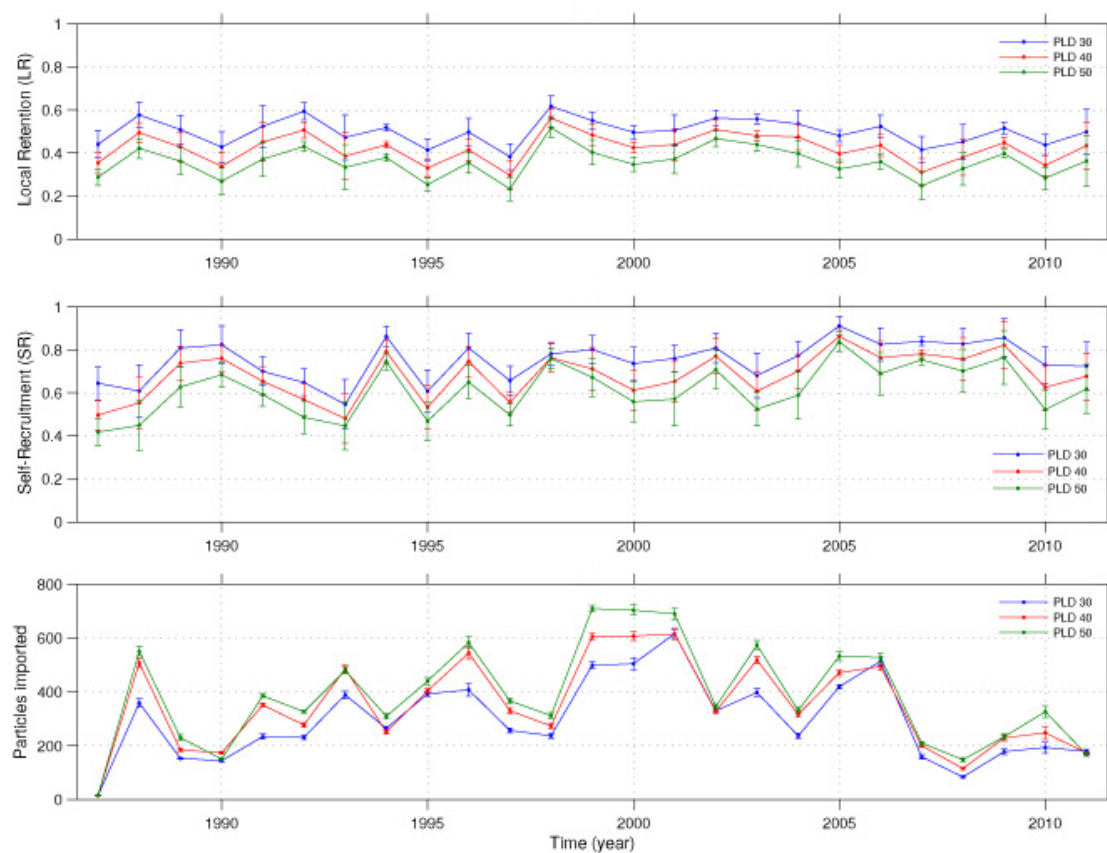


Figure S1. Time-series of regional connectivity metrics. Local Retention (LR) in the Gulf of Lion (top), Self-Recruitment (SR) over the Ebro delta (center), and particles imported (Imp) into northern Balearic Islands (bottom) for three different PLD values: 30 days (blue curves), 40 days (red curves) and 50 days (green curves). Error bars indicate the standard deviations among several spawning events.

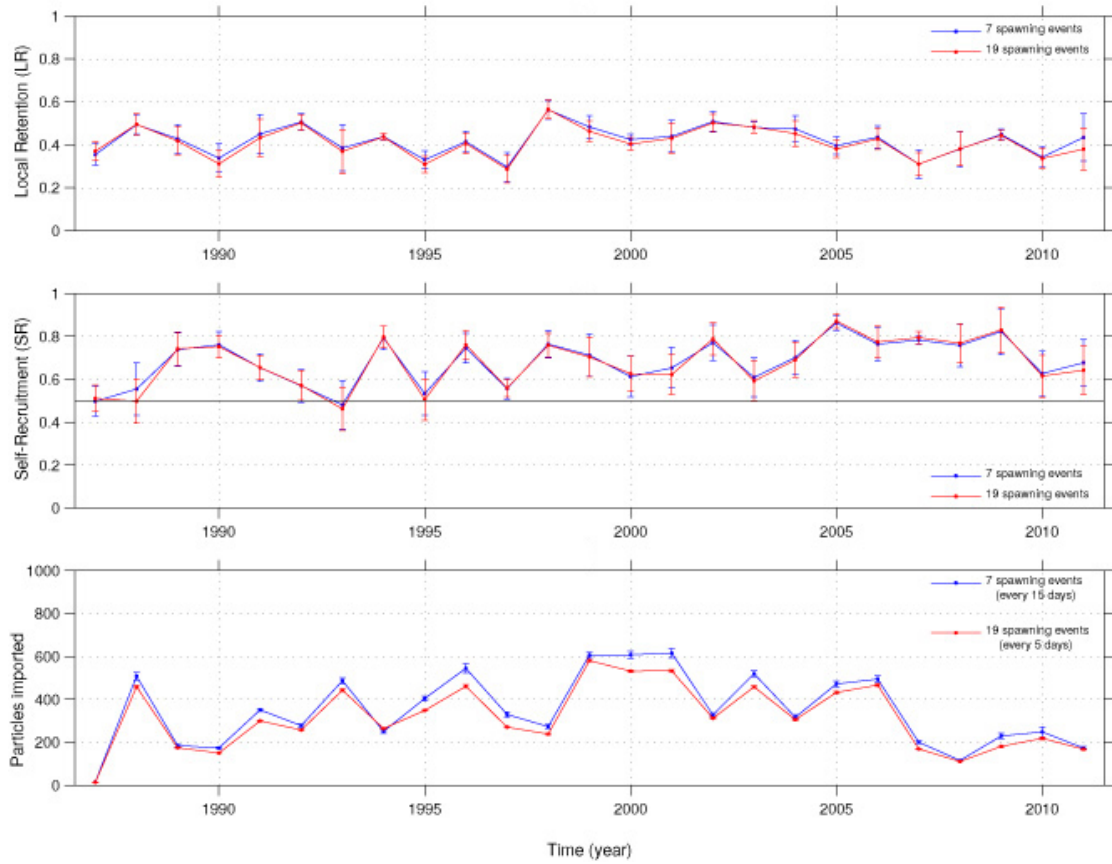


Figure S2. Time-series of regional connectivity metrics. Local Retention (LR) in the Gulf of Lion (top); Self-Recruitment (SR) over the Ebro delta (center); and particles imported (Imp) into northern Balearic Islands (bottom) for two frequencies of spawning over the same autumnal period: 7 spawning events (15 days apart, blue curves) and 19 spawning events (5 days apart, red curves). Error bars indicate the standard deviation among several spawning events.

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Appendix S2: Connectivity estimates for different subpopulations.

Appendix S2 - Tables

Table S1. List of p-values resulting from the non-parametric Friedman tests comparing the annual averages of LR computed over 7 spawning events for years 1987-2011 among our 6 subpopulations using a PLD of 40 days. The significant p-values (bold, applying a 5% significant level) indicate that mean LR of those two subpopulations are significantly different.

Local Retention (p-values)	Gulf of Lion	Catalan coast	Ebro delta	Valencia gulf	North Balearic Islands
Catalan coast	0.0093				
Ebro delta	0.31	2.7 10⁻⁵			
Valencia gulf	0.02	2.7 10⁻⁵	0.84		
North Balearic Islands	0.6 10⁻³	0.54	2.7 10⁻⁵	4.2 10⁻⁶	
South Balearic Islands	0.31	2.6 10⁻⁴	0.84	0.31	4.2 10⁻⁶

Table S2. List of p-values resulting from the non-parametric Friedman tests comparing the annual averages of SR computed over 7 spawning events for years 1987-2011 among our 6 subpopulations using a PLD of 40 days. The significant p-

values (bold, applying a 5% significant level) indicate that mean SR of those two subpopulations are significantly different.

Self-Recruitment (p-values)	Gulf of Lion	Catalan coast	Ebro delta	Valencia gulf	North Balearic Islands
Catalan coast	5.7 10⁻⁷				
Ebro delta	5.7 10⁻⁷	0.0027			
Valencia gulf	5.7 10⁻⁷	5.7 10⁻⁷	5.7 10⁻⁷		
North Balearic Islands	5.7 10⁻⁷	2.7 10⁻⁵	0.31	6.7 10⁻⁴	
South Balearic Islands	5.7 10⁻⁷	5.7 10⁻⁷	2.7 10⁻⁵	0.07	2.7 10⁻⁵

Appendix S2 – Figures

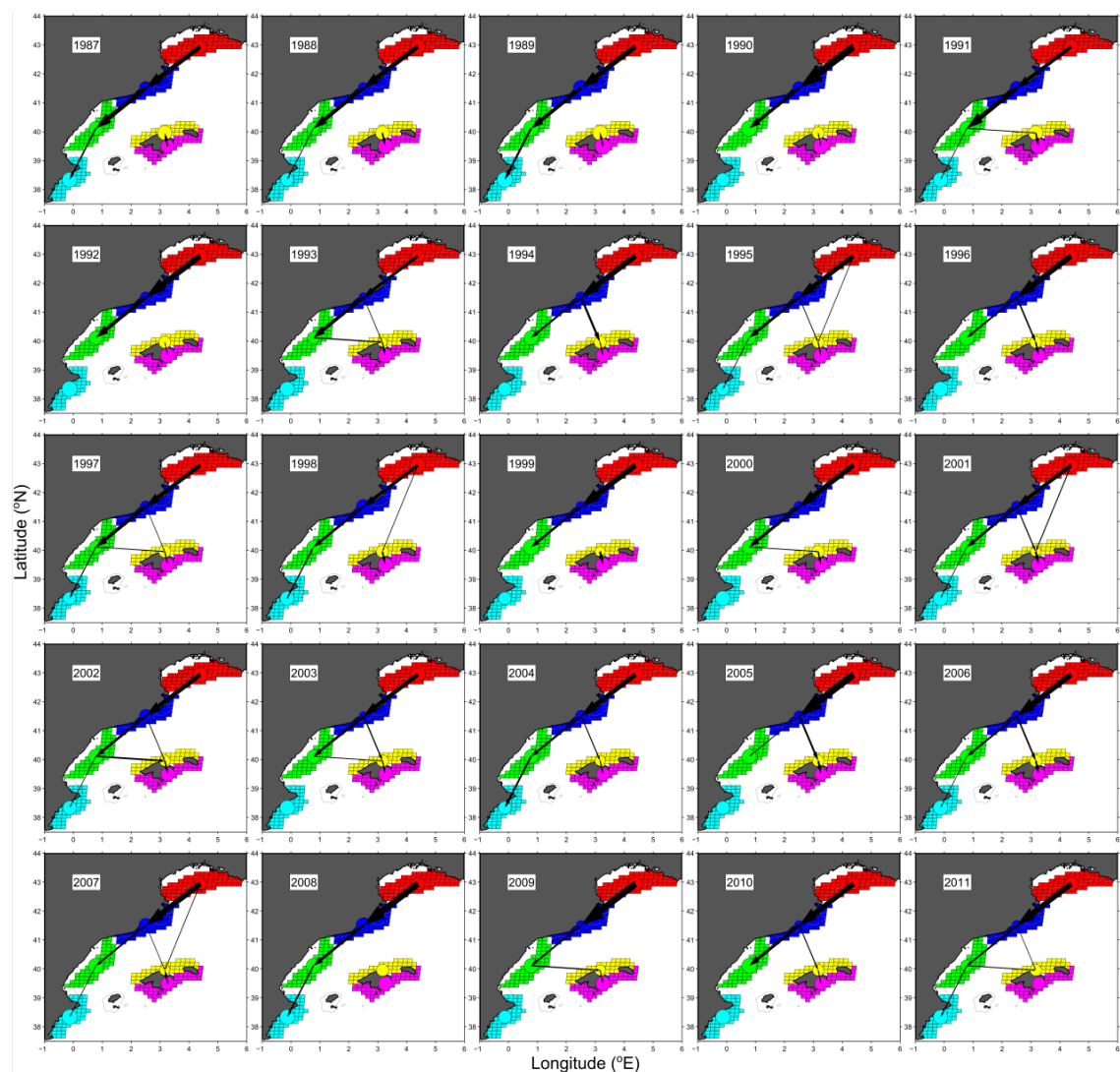


Figure S1. Normalized estimates of larval exchanges (arrows) and retention (circles) among the 6 subpopulations of hake from 1989 to 2011: Gulf of Lion (red), Catalan coast (dark blue), Ebro delta (green), Valencia gulf (light blue), northern Balearic Islands (yellow) and southern Balearic Islands (magenta). Widths of arrows and diameters of circles are proportional to the strength of larval Import (Imp) and Local Retention (LR), respectively. To facilitate the interpretation, only fluxes greater or equal than 5% of the total annual exchanges are displayed.

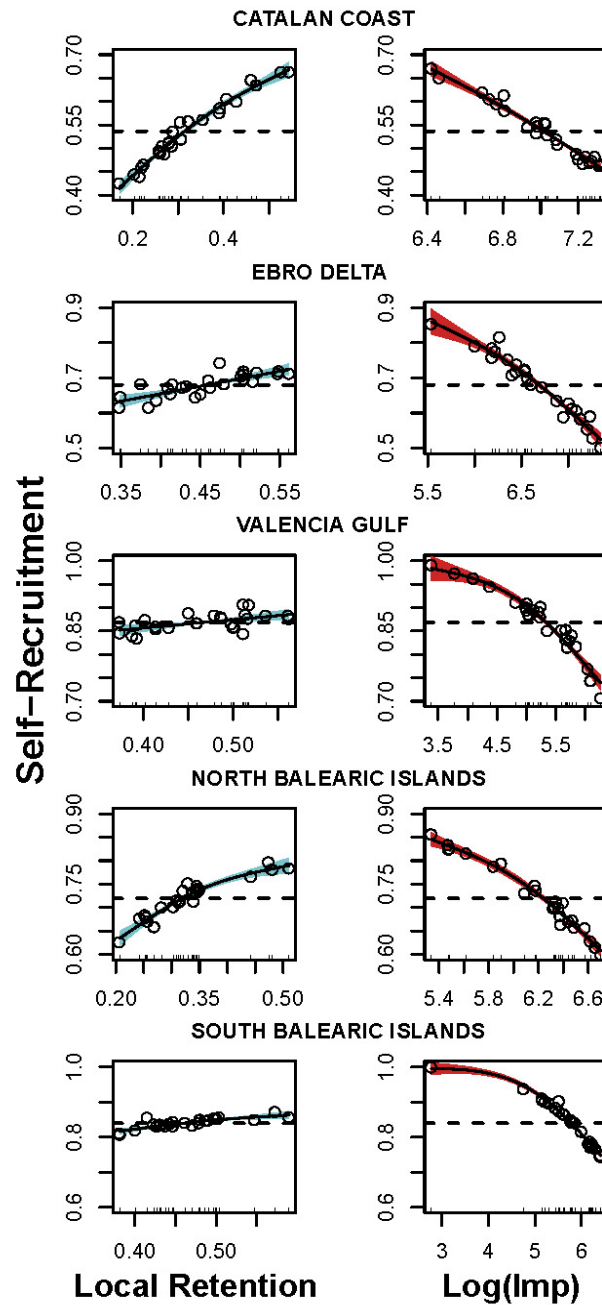


Figure S2. Relative effects of Local Retention (LR, left column) and Import (Imp, in log scale, right column) on the inter-annual variability of Self-Recruitment (SR) for each subpopulation. The plots for Gulf of Lion are presented in the Fig. 3 of the main document since it coincides with a management unit. Data were fit with a non-linear regression (General Additive Modeling, GAM) with the two covariates being statistically significant ($p < 0.05$) in all models. The dashed line represents the mean SR value (i.e. model intercept) in each subunit. The solid black lines, shaded colored

regions and dots represent, respectively, fitted values of the partial effect, 95% confidence intervals and partial residuals.

Supporting Information. M. Hidalgo, 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 variability in fish recruitment fluctuations within large transboundary metapopulations. *Ecological Applications*.

Appendix S3: Statistical analyses of recruitment time-series of the three management areas.

Appendix S3 - Figures

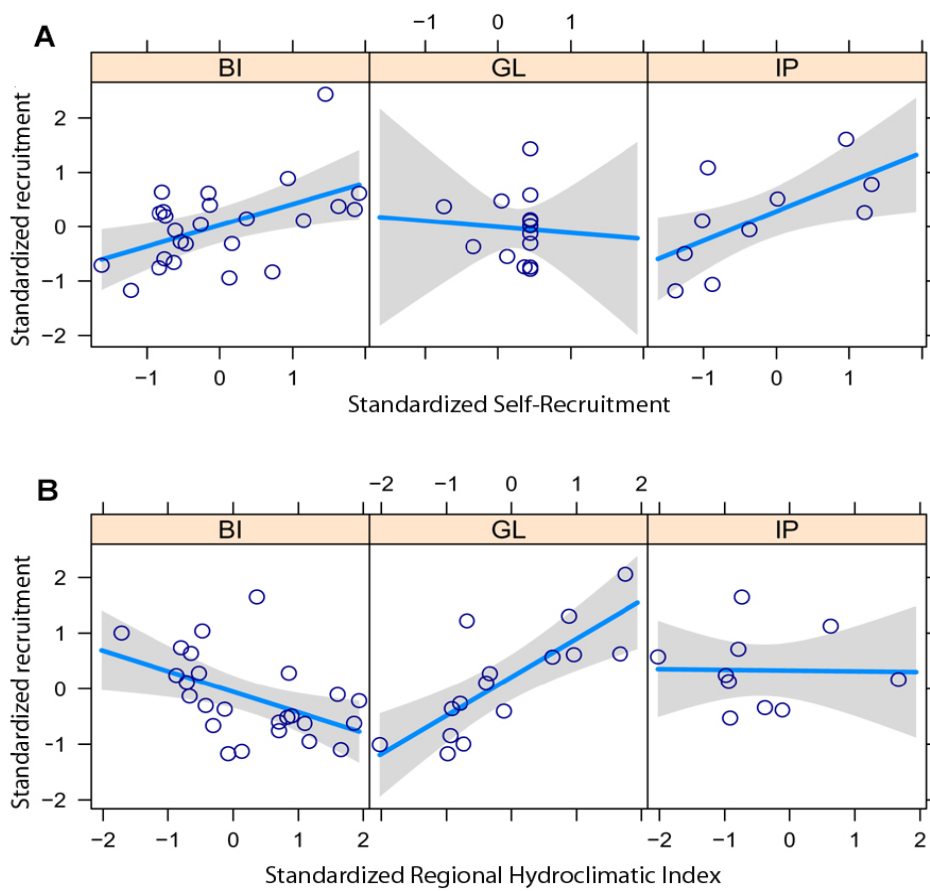


Figure S1. Partial effects of the global linear model of fish recruitment constructed for the whole metapopulation with all variables standardized to statistically compared the strength of Self-Recruitment (SR, A) and the Regional Hydroclimatic Index (RHI, B) on the fisheries recruitment estimates for each management area. Partial effects for Balearic Islands (BI), Gulf of Lion (GL) and the Iberian Peninsula (IP) appear in the left, center and right sides respectively. Blue dots represent the partial residuals and the gray shadows the 95% confidence intervals.

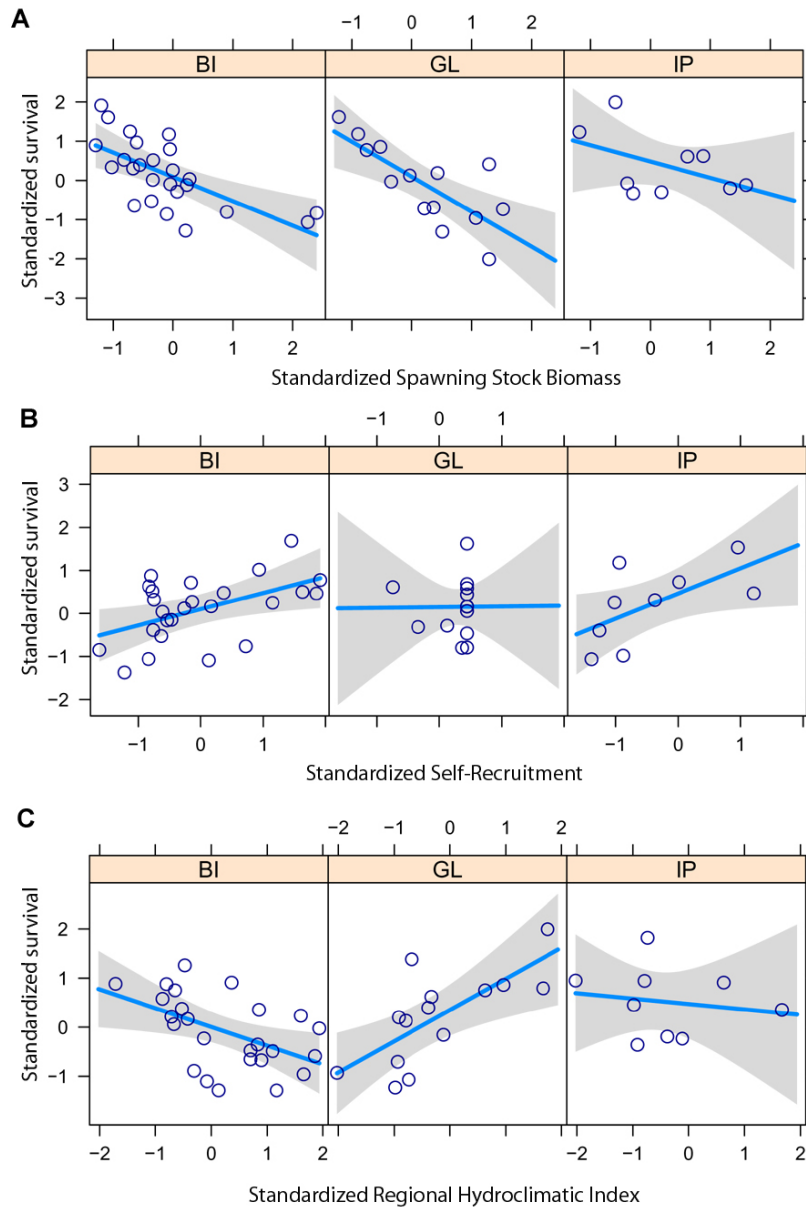


Figure S2. Partial effects of the global linear model on fish survival constructed for the whole metapopulation with all variables standardized to statistically compared the strength of the effects of spawning stock biomass (SSB, A), Self-Recruitment (SR, B) and Regional Hydroclimatic Index (RHI, C) on survival for each management area. Partial effects for Balearic Islands (BI), Gulf of Lion (GL) and the Iberian Peninsula (IP) appear in the left, center and right sides respectively. Blue dots represent the partial residuals and the gray shadows the 95% confidence intervals.

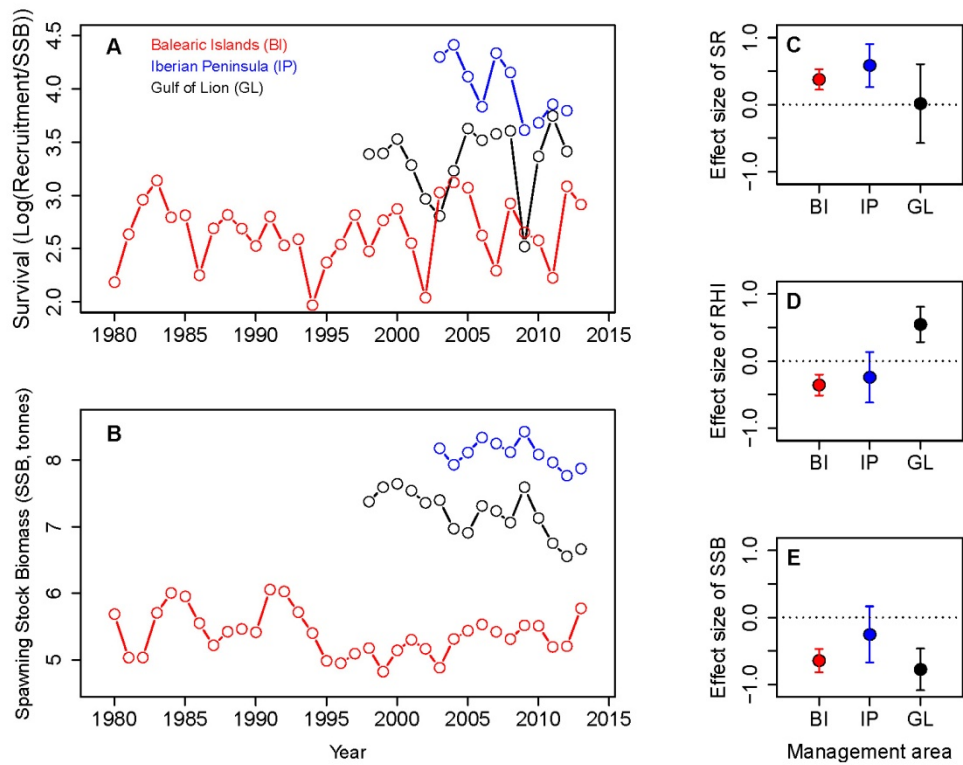


Figure S3. (A) Annual survival and (B) spawning stock biomass (SSB) for the three management areas (Balearic Islands, BA; Iberian Peninsula, IP; Gulf of Lion, GL). With the covariates of the best survival models (Appendix S2: Table S1), a global linear model was constructed for the whole metapopulation with all variables standardized to statistically compare the strength of the effect of Self-Recruitment (SR), the Regional Hydroclimatic Index (RHI) and spawning stock biomass (SSB) on survival for each management area (Appendix C: Fig. C2). The effect size (i.e. linear model estimates) is presented for SR (B), the RHI (C) and SSB (D): no overlapping of vertical bars (standard errors of the model estimates) with zero horizontal lines reveals statistical significance of the effect.

Appendix S3 - Tables

Table S1. Best four linear models for survival obtained for each management area. Covariates included are the Spawning Stock Biomass (SSB), Regional Hydroclimatic Index (RHI), Self-Recruitment (SR), Import (Imp) and Local Retention (LR). In the case of the Gulf of Lion and Iberian Peninsula, less than four models had significant covariates. Note that connectivity metrics were calculated at two geographical levels: management area and subpopulations (see *Materials and Methods*). CC, VG and NBI refer, respectively, to Catalan coast, Valencia gulf and Northern Balearic Islands subpopulations. GL, IP and BI refer, respectively, to Gulf of Lion, Iberian Peninsula and Balearic Islands management units. Akaike Information Criteria (AIC), delta AIC and Deviance Explained (DE, %) are also presented. Models for the Iberian Peninsula are presented attending to two different spawning stock biomass (SSB) estimates, one including only SSB of the IP and other combining SSB of IP and GL.

Management area	Covariates	AIC	Delta AIC	DE (%)
Balearic Islands	SSB	48.98	25.51	19.86
	SSB+RHI + SR_{BI}	23.47	0	49.21
	SSB+RHI + SR _{NBI}	27.26	3.79	40.89
	SSB+RHI + LR _{BI}	27.91	4.44	39.65
	SSB+RHI + LR _{NBI}	28.82	5.35	37.09
Iberian peninsula SSB= SSB-IP	SSB ^{ns}	9.74	6.02	2.3
	Imp_{CC}	3.76	0	41.6
	Imp _{VG}	5.53	1.77	25.4
Iberian peninsula SSB= SSB-IP+SSB-GL	SSB ^{ns}	7.3	3.15	4.25
	SR_{CC}	4.25	0	30.7
	SR _{IP}	5.28	1.03	20.8
	SR _{VG}	5.33	1.08	20.3
Gulf of Lion	SSB ^{ns}	11.28	5.41	13.98
	SSB + RHI	5.87	0	43.1