Vulnerability of marine benthic metapopulations: implications of spatially structured connectivity for conservation practice in the Gulf of Lions (NW Mediterranean Sea)

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Vulnerability of marine benthic metapopulations: implications of spatially structured connectivity for conservation practice

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ABSTRACT:

Aim: Connectivity is currently considered to essential to enhance biodiversity conservation efforts and benefit adjacent areas. We evaluate the spatial structure of vulnerable marine benthic invertebrate populations based on connectivity to improve the placement of marine protected areas.

Location: Gulf of Lions, NW Mediterranean Sea.

Methods: We used a spatially explicit metapopulation model to explore how larval dispersal affects marine benthic invertebrate dynamics at local and regional scales. Minimum recruitment success (the proportion of larvae that settle in a site and survive between spawning and first reproduction, which is required to ensure species persistence) is proposed as a measure of vulnerability. Three contrasting simulations were constructed: closed versus connected populations, habitat loss versus recruitment failure disturbances, and varying patterns of oceanographic connectivity. The rescue factor (the ratio of minimum recruitment success in connected and closed populations) quantified the decrease in vulnerability due to oceanographic connectivity.

Results: In the Gulf of Lions, connectivity reduced population vulnerability by a rescue factor of 5.3. The minimum recruitment success for regional persistence decreased from 3 % to 0.2 % when species' life expectancies increased from 2 to 50 years. Connectivity enabled the spread of individuals over the entire region, but there were higher densities in sink sites, where low retention rates do not allow for local persistence (western tip of the gulf). Source sites, defined as those sites bringing metapopulation resistance to recruitment failure and stresses from habitat loss, were located in the center of the gulf.

Main conclusions: Connectivity drives the spatial structure of regional adult distribu-

tions and population vulnerability in the absence of any other structuring factor. In the Gulf of Lions, marine protected areas are located in the western tip, where there are population sink; however, if protection measures were taken in the central part, populations would benefit throughout the region via the rescue effect.

INTRODUCTION

Landscape connectivity is considered an essential factor for enhancing the resilience of biodiversity and ecosystem services in the face of climate change (Heller & Zavaleta, 2009; Morecroft et al., 2012). The role of connectivity in biodiversity resilience (defined as the long-term persistence of a species) has been extensively examined theoretically in conservation biology and population ecology. Connectivity alters biodiversity in many ways, with both negative and positive outcomes. On the one hand, connectivity linked to anthropogenic actions (e.g. the opening of commercial routes, species introductions) has enabled the spread of alien species (Hulme, 2009; Katsanevakis et al., 2013), which has been identified as one of the major drivers of biodiversity loss (MEA, 2005). On the other hand, connectivity associated with propagule dispersal during reproduction has favored the wide geographical distribution of sessile species, which are dependent on the availability of suitable habitat downstream (Scheltema, 1986). Connectivity has also been recognized as a process that can reduce extinction threats due to invasive species by linking species refuges (Gilbert & Levine, 2013). Despite the adaptive disadvantage represented by dispersal to new sites, larval dispersal is also a way for sessile populations to recover following disturbances, such as extreme meteorological events or anthropogenic

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stresses (Baker et al., 2008; Miller et al., 2009; Kendrick et al., 2012; Bernhardt & Leslie, 2013).

Since the earliest metapopulation model of Levins (1969), a wealth of stochastic patch occupancy models have been used to address the fundamental question of the consequences of habitat fragmentation on the persistence of individual (Quinn and Hastings, 1987; Hanski, 1989, 1994) and multiple species (Mouquet & Loreau, 2002). Increased satellite imaging capabilities have enabled the production of high-resolution maps of species' habitats in terrestrial environments, which have improved the spatially explicit modeling of species distribution (Schnell et al., 2013). Such an approach is limited in the marine environment, where habitat mapping is still incomplete. Conversely, dispersal is often described simplistically in terrestrial environments and is based solely on the distance between patches of a species' habitat (Roy et al., 2008; Dornier et al., 2011; Skelsey et al., 2013; Johansson et al., 2013). Yet in the case of propagule dispersal (pollen in the air, larvae in the ocean), transport mediated by an unsteady and non-uniform flow will often be asymmetrical (Aiken & Navarrete, 2011) and can cover long distances. In the marine environment, larval transfer between sites has been calculated from larval dispersal simulations and summarized by oceanographic connectivity matrices (Melbourne-Thomas et al., 2011; Thomas et al., 2012; Jacobi et al., 2012; Morecroft et al., 2012; Moritz et al., 2013). Such connectivity matrices have been analyzed to elucidate population persistence using either graph theory methods (Treml et al., 2008) or eigenvalue decomposition (Hastings and Botsford, 2006). However, local demography may mitigate oceanographic connectivity (Moilanen, 2011); thus, assessing population persistence requires the integration of oceanographic connectivity and local demography into models of metapopulation dynamics (Watson et al., 2012; Williams & Hastings, 2013). Of the local demographic pa-

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rameters, recruitment success (the proportion of settling larvae that survive from spawning to the adult stage) ultimately drives the persistence of a population, although flow does bring larvae to a settling area. Persistence requires a 'minimum recruitment success' to compensate for the loss of adults in the population during the same period. The order of magnitude of recruitment success is virtually unknown for most species due to limitations in observing the supply of settled larvae (Grüss et al., 2012), and this parameter is the missing link between dispersal and local demography. Integrating demographic connectivity in spatially explicit metapopulation models is a challenge for the practical design of conservation strategies for the marine environment (Kaplan et al., 2009; Moffitt et al., 2011). It would be particularly interesting to identify sites, by considering the functional connections within self-persistent sites or between sites, where protection efforts aimed at minimizing adult loss would ensure persistence (Berumen et al., 2012; Olds et al., 2014). Furthermore, if persistence is achieved within the protected network, then dispersal export may further benefit populations in non-protected areas (Harrison et al., 2012).

In this paper, we present the results of numerical simulations of the spatio-temporal dynamics of soft-bottom worm populations in the Gulf of Lions driven by oceanographic connectivity. The generic metapopulation model of Hastings and Botsford (2006), which incorporates spatially structured parameters for survival, fecundity and dispersal was modified to account for density-dependent recruitment (Roughgarden et al., 1985) and time-varying connectivity. A set of twenty different connectivity matrices were estimated from larval dispersal simulations and were randomly picked in the simulations of the metapopulation dynamics to reflect the inter-annual variability in dispersal that arises from the conjunction of environmental (currents) and biological (spawning timing) variability (Guizien et al., 2012). 'Minimum recruitment success', which is required to ensure

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^{105} populations persistence under each oceanographic connectivity scenario was used as a

^{106} measure of population vulnerability. Simulations were designed to test three hypotheses:

^{107} (1) Connectivity decreases population vulnerability at the regional scale, (2) population

^{108} vulnerability to stresses is spatially structured by connectivity and (3) adult spatial dis-

^{109} tribution allows for the identification of sink sites but not sites essential for regional

^{110} persistence (source). The findings were also used to propose an extension of the current

^{111} protection measures in the Gulf of Lions.

METHODS

^{112} **The generic metapopulation model for benthic invertebrates**

^{113} The spatio-temporal dynamics of benthic invertebrate populations with a dispersive

^{114} pelagic larval stage were simulated after modifying the generic metapopulation model of

^{115} Hastings and Botsford (2006). The model describes explicitly, in discrete times and for a

^{116} set of sites with different areas connected by larval transfer, the spatial density dynamics

^{117} of only the sedentary adult stage (Fig.1). Density dynamics at a given site result from spa-

^{118} tially structured local survivorship and reproductive success input potentially contributed

^{119} by all the other sites in the system. The original model of Hastings and Botsford (2006)

^{120} was modified to account for (1) recruitment limitation due to space availability at the

^{121} destination site (computed as the proportion of free space based on the saturating density

^{122} of adults $N_{max} = 1/\alpha_A$, where α_A is the mean cross-sectional area of one adult), and (2)

^{123} the variability in propagule transfer rate. The model in matricial form is as follows:

$$N(t + \Delta t) = min(G(t)N(t), N_{max}) \tag{1}$$

^{124} with a time step of Δt and a transfer matrix G defined by:

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$$G_{ji} = b_j C_{ji}(t) a_i + s_{jj} \delta_{ji} \qquad (2)$$

where $N(t)$ is a vector $\in R^p$ containing the spatial density of adults at each site $i \in [1, p]$ at time t, a_i [larva per adult] is the propagule production rate in site i, C_{ji} **[no units] is the propagule transfer rate from site i (column) to site j (row)** multiplied by the ratio of the areas of origin A_i to settling A_j sites, b_j [adult per larva] is the recruitment success in site j, s_{jj} [no units] is the adult survivorship rate at settling site j, δ_{ij} is the Kronecker symbol (1 when $i = j$, 0 otherwise) and N_{max} is the site's carrying capacity. The propagule production rate is equal to the number of larvae produced by each adult female $FS_R f$ where F is the fecundity rate, S_R is the sex ratio in the adult population, and f is the probability of an egg being fertilized. The adult survivorship rate can be related to species life expectancy L_E as $s_{jj} = exp(ln(0.01) \, \Delta t / L_E)$, where life expectancy is the age at which 99% of the individuals of the same generation have died.

Propagule transfer rates are the elements of a square connectivity matrix C and are defined as the proportion of larvae coming from an origin site (columns) and arriving at a settlement site (rows), multiplied by the ratio of the areas of the origin to the settlement sites.

Recruitment success is the proportion of larvae settling in one site that has survived dispersal and will finally reach sexual maturity. This parameter, with values of between 0 and 1 and accounting for all mortality losses since egg release until the first reproduction by the new recruits, is unknown for all species and is very difficult to measure. An alternative approach is to seek a minimum value of this parameter that would avoid either population (based only on local retention) or metapopulation (allowing for transfer

within the network of populations) extinction. The minimum recruitment success of a population corresponds to the recruitment success that yields a population growth rate equal to 1. Thus, the minimum recruitment success co-varies with the fecundity value; when the fecundity value is increased by a factor of 10, the minimum recruitment success is decreased by a factor of 10. Such a minimum recruitment success provides a measure of population vulnerability: the lower the minimum recruitment success, the lower the population vulnerability. The minimum recruitment success is independent of the saturating capacity choice because the site carrying capacity is not reached. The rescue factor was defined as the ratio between the recruitment success required to maintain individuals in any connected site in the region (regional persistence) and the minimum recruitment success required to maintain individuals in at least one isolated site in the region (local persistence). The rescue factor is, by definition, independent of species fecundity.

Application to the Gulf of Lions soft-bottom polychaete populations

The Gulf of Lions is a wide, micro-tidal continental shelf, dominated by soft-bottom habitat and it is delimited along the shore at its two extreme tips by rocky beds extending to a depth of 40 m (Aloisi et al., 1973). Polychaetes dominate the soft-bottom benthic communities of the gulf and their community composition is related to the grain size distribution and organic matter content, which is strongly related to water depth in this region except for some restricted areas at the river outlets (Labrune et al., 2007a). In the simulations, demographic parameters were assumed to be spatially uniform for the 10-30 m depth range to more clearly reveal the effect of connectivity on spatial structure. Species were differentiated by their life expectancy (ranging from 2 to 50 years) and their

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mean fecundity (averaged over the duration of their reproductive life). According to the review of demographic parameters of 200 polychaete species by McHugh & Fong (2002), no trade-off can be found between fecundity and life-expectancy, but fecundity is related to larval development mode. Fecundity values for polychaete species with dispersive larval stages range from 10^3 to 10^6 (McHugh & Fong, 2002). As fecundity can be related to food availability, fecundity in the oligotrophic Mediterranean sea is expected to be in the lower part of the range. Fecundity was thus varied between 10^3 and 10^5 eggs per female in the simulations, resulting in a propagule production rate of $5\ 10^1$ to $5\ 10^3$ larvae per female (using a sex ratio of $1:1$ and a fertilization rate of 10%), independent of species life expectancy. As site saturating capacity is an upper limit introduced to avoid unrealistic population explosion when population growth rate is greater than 1 and is not expected to be reached at equilibria, this parameter, by definition, should be larger than the natural density. Furthermore, to avoid the introduction of an artificial trade-off between life expectancy and site saturating density, site saturating density was overestimated and set to 25,000 ind m^{-2}, which corresponds to a value larger than any density observed in the area (Labrune et al., 2007a). Given these demographic parameters, recruitment success was also considered to be spatially uniform and varied from 10^{-6} to 1 (10 regular steps within each $\log_{10}$-interval) to detect the minimum value R at which either local or regional persistence was reached (see above).

The continuous sand facies bed spanning the 10 to 30 m isobaths along the gulf was discretized into thirty-two contiguous sites to describe the spatial distribution of the different worm species living in this habitat (Fig. 2). Site boundaries were placed according to the natural coastline features forming bays or approximately every 20 km along the rectilinear shoreline, which yielded sites ranging in area from 6.2 to 121 km^2. Connectivity

matrices, with local retention rates on the diagonal, and transfer rates between distant sites off of the diagonal, were quantified from Lagrangian larval dispersal simulations. Simulations of larval dispersal in the gulf used three-dimensional currents and turbulent kinetic energy computed at a resolution of 750 m × 750 m following interpolation between the hourly outputs (Guizien et al., 2006). Spawning was simulated by releasing thirty neutrally buoyant larvae in the center of each of the 32 sites, on the 20 m isobath, every hour during the reproductive season. As temperate polychaetes reproduce in late winter-early spring in the NW Mediterranean Sea (Bhaud, 1972), a 100-day reproductive season (from January 5 at 0h until April 13 at 23h) was considered and divided into ten consecutive 10-day spawning events in 2004 and 2006 (see details in Guizien et al., 2012). In the absence of knowledge regarding sinking behavior that might differentiate species' dispersal capabilities (Guizien et al., 2006), connectivity was set as the same for all species in this study because most benthic invertebrates have a similar competency period of between 3 and 5 weeks (Mc Edward, 1995). Three connectivity matrices corresponding to three different pelagic larval durations (3-, 4- and 5-week) were built for each spawning period, and the proportion of larvae coming from the center of any site and arriving in each of the thirty-two sites was multiplied by the ratio of the areas of origin to the destination sites. A composite connectivity matrix was then calculated as the weighted sum of the 3- (1/4), 4- (1/2) and 5- (1/4) week pelagic larval duration connectivity matrices. In total, twenty variant composite matrices were used to describe the interannual variability in connectivity arising from a conjunction between meteorological variability and the timing of spawning during a reproductive season, and this variability was assumed to affect all polychaete species. Then, the average and standard deviation of these twenty variant matrices were computed, and used as the average conditions matrix

in some of the simulations described in the next section.

Simulation groups and statistical methods

Three groups of spatio-temporal simulations over a duration of 50 life-expectancy cycles were carried out, starting with a low uniform spatial density of 0.4% of the site's carrying capacity. Asymptotic stable equilibrium was defined as the average of the population density between the 45 and 50 life-expectancy cycles. Connectivity was either set deterministically (the same matrix repeated every year) or stochastically (a random matrix picked up every year among the twenty variants). When connectivity was set stochastically, ensembles of 500 simulations were performed for each set of the other parameters in order to evaluate the variability arising from the connectivity sequence. Redundant patterns among the ensemble of 500 stochastic simulations in the regional spatial distribution were sought by grouping spatial distributions that deviated by less than 20% (square root of the sum of normalized squared deviations in each site). **The spatial distribution of population density was described by the mean and standard deviation of the 500-simulation asymptotic stable equilibrium. The spatial distribution of relative density was described by the ratio between the population density in each site and the regional average of population density. The average regional coverage was defined as the ratio between the regional average of population density and the saturating capacity.**

Simulation settings are summarized in Table 1. Simulation groups 1 and 2 explored the effect of connectivity on population persistence and spatial distribution. Simulation group 3 explored the resistance of a short lived species to two types of scenarios (Fig.1B and C). By gradually increasing the number of unsuitable sites starting from each port,

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group 3A aimed to quantify the resistance of the metapopulation to habitat loss around the four main ports: Port-Vendres, Port La Nouvelle, Sète and Marseille (Fig. 2). Group 3B aimed to quantify the resistance of the **metapopulation** to different return periods of recruitment failure affecting either the Roussillon or the Languedoc Coasts. Recruitment failure is typically caused by extreme meteorological events (e.g. swell or heat waves, Durrieu de Madron et al., 2011) that affect populations over larger spatial scales than the scales affected by anthropogenic stresses.

RESULTS

Minimum recruitment success for local and regional persistence: the connectivity effect (group 1)

Connectivity matrices for the Gulf of Lions display a strong but highly variable spatial structure with variation coefficients for each connection spanning from 40 to 450 % (Fig. 3A and B). Amongst the twenty variants, three main connectivity structures could be identified and ranked according to drift direction: 65% with a dominant westward drift, 30% without dominant drift (diffusive connectivity) and 5 % with a dominant eastward drift. On average, the local retention rates (matrix diagonal terms) were higher in the central gulf (ranging from 0.2 % to 1.41 %) than in the eastern and western tips ($<$ 0.05%). Sites located in the central gulf were also major larvae exporters, and can be split into two groups. Sites 10 to 13 predominantly exported individuals to the west, whereas sites 20 to 25 exported to both the east and the west (Fig. 3A). Larval transfer within and between the two groups of sites was also strong.

The spatial structure of local retention rates along the gulf coastline is depicted by the minimum recruitment successes required for the local persistence of species with life-

expectancies ranging from 2 to 50 years and a fecundity of 10^4 eggs per female (Fig. 4 A). The minimum recruitment success would be multiplied by a factor of 10 for species with a fecundity of 10^3 eggs per female or divided by a factor of 10 for species with a fecundity of 10^5 eggs per female, but their relative values along the Gulf of Lions would be the same. In the nine sites along the western tip of the gulf (Roussillon coast, region of Port-Vendres) and also for three sites at its very eastern tip (region of Marseille), local retention rates were too small to achieve persistence for a species with a life expectancy of up to 10 years (up to 50-year life span in the five sites at the western tip). In contrast, the larger local retention rates in the central part of the gulf ensure the local persistence of the shortest-lived species (2-year) and of the longest-lived species (50-year) if recruitment success is larger than 70 % and 6 %, respectively. In fact, the recruitment success required for regional persistence without (in one isolated population with a maximum retention rate) and with connectivity decayed exponentially as species life expectancy increased, as it was divided by a factor of 2 between 2- and 7-year life expectancies (Fig. 4B).

Connectivity decreased vulnerability independently of the species life expectancy (Fig. 4B). The rescue factor was independent of species life expectancy and varied from 1 to 6.6 among the twenty connectivity matrix variants (3.8 on average). When a connectivity matrix was picked randomly every year from the twenty variants, the minimum recruitment success required for regional persistence was the same in the 500 simulations and was slightly higher or equal to the value when the averaged connectivity was repeated every year (data not shown). The rescue factor was 5.3 for the averaged connectivity and 5.0 when the connectivity matrix was variable every year.

Connectivity between distant sites (i.e. larval import) tended to decrease the sensitivity of the persistence thresholds to the variability of the hydrody-

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namics. The minimum recruitment success required for regional persistence was highly variable among the twenty different hydrodynamic periods when only local retention was included, which reflected the large variability in local retention rates (Fig. 4 B, without connectivity). In contrast, the minimum recruitment success required for regional persistence was less variable among the connectivity matrix variants when larval import from distant sites was included, with the exception of one matrix characterized by very low transfer rate values (Fig. 4 B, with connectivity).

Connectivity and spatial distribution of population density at equilibrium (groups 1 and 2)

The relationship between connectivity matrix structure and the spatial distribution of population density at equilibrium is illustrated in this section for a species with a 2-year lifespan but would be the same for any other life expectancy provided that recruitment success was set to the minimum value required to ensure regional persistence. When the same connectivity matrix was used every year and regional persistence was ensured, the spatial distribution of population density was significantly correlated with the spatial distribution of cumulated import rates in the settlement sites of the corresponding connectivity matrix (on average, $R = 0.78$, $p < 0.05$). When larval transfer drifted to the east, density was much lower in the western part of the gulf (Fig. 5 A). When larval transfer drifted to the west, individuals were mainly distributed in the western part of the gulf (Fig. 5B). As larval transfer rates were of the same order of magnitude regardless of the different connectivity structures, regional persistence was ensured by similar values of minimum recruitment success. Interestingly, in both cases, individuals were not only

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present in the sites with the highest retention rates but also in sites where local retention was far too low to ensure local population persistence. When the averaged connectivity matrix was repeated every year in a simulation (deterministic case) with recruitment success set to its minimum value for regional persistence, density distribution was uneven in the gulf, which reflected the average spatial distribution of the cumulative import rates along the gulf ($R = 0.94$, $p < 0.05$). Individuals, although present everywhere, accumulated in the western half of the gulf with the highest densities in sites 13 to 17 and in sites 1 and 2 at the very western tip (Fig. 5C).

When connectivity was variable each year (conserving the averaged connectivity during the 100-year simulation) and recruitment success was set to the minimum value for regional persistence, density spatial distribution displayed the same accumulation pattern as in the deterministic case, whereas the relative density disequilibrium between the eastern and western part of the gulf was smoothed (Fig. 5D). **It was not possible to identify a dominant pattern for the spatial distribution of population density, as the redundancy of the asymptotic equilibria density spatial distribution reached 4% at the maximum among the 500 simulations.** In fact, spatial distribution of population density displayed higher variability among the 500 simulations than among years in each simulation. This variability was also spatially structured, and was larger in the locations identified as the accumulation sites of the averaged connectivity matrix (Fig. 5D) as these locations also correspond to the areas of highest transfer rate variability (Fig. 3A and B). When recruitment sucess was increased, densities increased and their spatial distribution became more even (data not shown).

Connectivity and resistance to habitats loss or periodic recruitment failure of

a 2-year lifespan species (groups 3A and 3B)

The spatial structure of vulnerability to stresses affecting habitat availability or recruitment occurrence is described in this section only for a 2-year lifespan species, because the vulnerability of such short-lived species was already highest in the absence of any stress. Wherever habitat loss was occuring (western, central or eastern part of the Gulf of Lions), the average regional coverage decreased with habitat availability and reached metapopulation extinction before all of the suitable habitats were lost (Fig. 6A and B). However, resistance to habitat loss displayed a strong spatial structure. Applying a recruitment success value of 3% (which was the minimum value required for regional persistence in the absence of stress), resistance to habitat loss was much lower in Sète (central part of the Gulf of Lions, where extinction occurred as soon as 3 sites were lost) than in Marseille (western tip, where extinction occurred when 10 sites were lost) and Port La Nouvelle (central part, where extinction occurred when 12 sites were lost) or finally Port-Vendres (eastern tip, where extinction occurred when 16 sites were lost, Fig. 6A). Yet ultimately, the spatial structure of the resistance to habitat loss can be shaped by the recruitment success value (Fig. 6A and B). When recruitment success was doubled, resistance to habitat loss was increased globally but the spatial structure of vulnerability to habitat loss was modified. For example, Port La Nouvelle became as resistant as Port-Vendres (Fig. 6B). The spatial structure of vulnerability to habitat destruction was not sensitive to the history of the connectivity sequence, as variability lead to less than a 5% standard deviation in species average regional coverage amongst the 500 simulations, irrespective of where habitat loss started.

When recruitment failure affected the western part of the Gulf of Lions (Roussillon coast), populations never went extinct and average regional coverage was insensitive to

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recruitment failure frequency (Fig. 7A and B). In contrast, when recruitment failure affected the northern part of the Gulf of Lions (Languedoc coast), the species with a 2-year lifespan would go extinct with a recruitment failure return period greater than 4 years if recruitment success was the minimum required to ensure metapopulation persistence in the absence of stress (Fig. 7A). However, the metapopulation could resist recruitment failure of up to every other year (species life expectancy) when compensated by a higher recruitment success (Fig. 7B). In contrast to habitat loss, metapopulation resistance to recruitment failure was strongly dependent on the history of the connectivity sequence, when the northern part of the Gulf of Lions was impacted (the standard deviation in average regional coverage amongst the 500 simulations reaching approxiamtely 50%).

DISCUSSION

The role of population connectivity in species persistence is currently emphasized in conservation biology and is translated into policy in the current Strategic Plan for Biodiversity $2011-2020$ which formulated a conservation goal for the marine environment through 'ecologically representative and well connected systems of protected areas, and integrated into the wider seascapes' (https://www.cbd.int/decision/cop/?id=12268). At the same time, the openness of marine populations is being reconsidered using numerical simulations of larval dispersal that suggest that the scales of dispersal may not be as large as previously thought, with drastic reductions in realized long-distance connectivity due to larval mortality (Cowen et al., 2000). However, this concept does not imply that the closed-population hypothesis is valid (Cowen & Sponaugle, 2009). By subdividing the nearshore area of the Gulf of Lions into consecutive sites of tens of kilometers in width, we showed that local persistence would require different values of local recruitment success to compensate for different retention rates along an unfragmented uniform soft-

bottom habitat. This spatial structure was already identified in an earlier study concerned with the definition of self-persistent no-take reserves in this region (Guizien et al., 2012). The findings of the present study confirm the very low or non existent potential for the conservation of soft-bottom species with a dispersive larval phase and a life span of up to 50 years in existing isolated marine protected areas located in the extreme tips of the Gulf of Lions (e.g. Parc Marin de la Côte Bleue, Réserve Naturelle Marine de Cerbère-Banyuls). These MPAs mainly target the conservation of hard-bottom species, which may experience higher retention rates in the boundary layer that develops around coralligeneous three-dimensional structures (Moulin et al., 2007). Of greater concern is the location of the recently created Parc Naturel Marin du Golfe du Lion (PNM, Fig.2) which explicitly targets soft-bottom species as part of its sustainability goals for fisheries, while, according to our simulations, only including sink populations. The location of these sink populations is confirmed by the recurrent but transient extirpations of the 2-year life span serpulid *Ditrupa arietina* in Banyuls Bay followed by rapid recovery over the last 15 years (Grémare et al., 1998; Medernach et al., 2000; Labrune et al., 2007a, F. Charles, Pers. Comm.). Furthermore, the presence of many soft-bottom polychaete spawners in the western part of the Gulf of Lions (Labrune et al., 2007a), where local retention rates are too low to ensure species persistence as isolated populations, also indicate the existence of efficient larval transfer at the meso-scale. The rescue factor is proposed as a metric to rank the decrease in population vulnerability due to connectivity (regional persistence is not achieved by local persistence at any site, but implies a larval flux between sites) in different regions and for different species. In the Gulf of Lions, the rescue factor for species with a 4-week planktonic larval duration reached a value of 5.3 on average. Interestingly, this value was only 6% less when connectivity was variable among years, in contrast to

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findings reported by Watson et al. (2012).

In the present study, scenarios of spatially structured disturbances based on existing meteorological and anthropogenic threats to a short-lived species were used to identify source sites that promote resistance to disturbances and thus are essential for regional persistence. As an example, *Ditrupa arietina*, which displays high densities in the absence of stress, is subject to local extirpations following successive recruitment failures due to mechanical disturbances and resuspension during swell events in Banyuls Bay (Charles et al., 2003; Labrune et al., 2007b). In the Gulf of Lions, swells impact different parts of the coast according to their origin: southerly swells impact the Languedoc coast whereas easterly swells impact the Roussillon coast (Fig. 2, Guizien, 2009). The recruitment failure scenario applied to *Ditrupa arietina* indicates that there is no risk of regional extirpation linked to the easterly swells impacting the Roussillon coast, which is consistent with the recolonization observed after two successive years of recruitment failure in Banyuls Bay (Roussillon coast). Another potential threat to species persistence in the Gulf of Lions is habitat loss due to boat traffic hazards spreading from ports (oil spill, invasive species). The present study identified source sites essential for metapopulation persistence around Sète. Our findings suggest that a re-evaluation of the boundaries of the Parc Naturel Marin should include the center of the Gulf of Lions and more generally account for connectivity when evaluating the ecological cost of habitat destruction.

This study showed that the few essential sites for regional persistence could not be depicted from the spatial distribution of population density along the gulf because, in the absence of disturbances, connectivity will enable individuals to spread to all importing sites. Consequently, traditional methods based on species inventories may fail to guide the design of protection measures to target source sites. Indeed, for a short-lived species,

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connectivity patterns lead to a spatial distribution in the Gulf of Lions with a higher relative abundance in the western part than in the eastern part. Such disequilibrated spatial distribution is also present in long-lived species. These findings, which only account for the dispersal process in homogeneous habitat, are consistent with the community diversity throughout the muddy shelf sediment in the Gulf of Lions, which is separated into two clusters corresponding to the eastern and western parts of the gulf (Labrune et al., 2007a). These two clusters were originally differentiated by organic matter content, i.e., a habitat descriptor. In fact, the spatial distribution of organic matter in the gulf is likely to be driven by oceanographic dispersal as well. Such a result highlights the existence of co-variations among factors affecting the spatial distribution of individuals that may blur the assessment of connectivity using statistical inferences (Moritz et al., 2013).

In light of our findings, consideration should be given, when setting local protection measures to the oceanographic connectivity at the meso-scale (from tens to hundreds of kilometers) which drives regional distribution of population density and population vulnerability. In the Gulf of Lions, our results indicate that MPAs in the western tip are located in population sink for the soft-bottom species and establishing local protection measures in the central part of the gulf would benefit soft-bottom species over the entire region through the rescue effect. We highlight that metapopulation modeling integrating oceanographic connectivity, local demography and habitat mapping is a powerful tool that enables the inclusion of scenarios in the *a priori* design of conservation measures.

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Biosketch: The research interests of the LECOB concern the ecogeochemistry, which is the integration of the interactions among the biotic and abiotic components of benthic ecosystems (http://lecob.obs-banyuls.fr/). K.G., J.M.G. and M.B. conceived the ideas; K.G. and M.B. performed the simulations; K.G. and M.B. analyzed the data; and K.G. and C.M. took the lead in writing the paper.

30

	Group 1	Group 2	Group 3 A	Group 3 B
Connectivity	D	S	S	S
Fecundity	10^3-10^5	10^3-10^5	10^4	10^4
Life expectancy	2-50 years	2-50 years	2 years	2 years
Disturbance	NO	NO	habitat loss	recruitment failure
Number of simulations per life expectancy	21	500	500	500

Table 1: *Settings for the three simulation groups. Connectivity was set either deterministically using the same matrix every year (either one of the twenty variants or the averaged value D) or stochastically picking a different matrix among the twenty variants every year with a uniform probability in order to conserve the averaged connectivity during the simulation (S).*
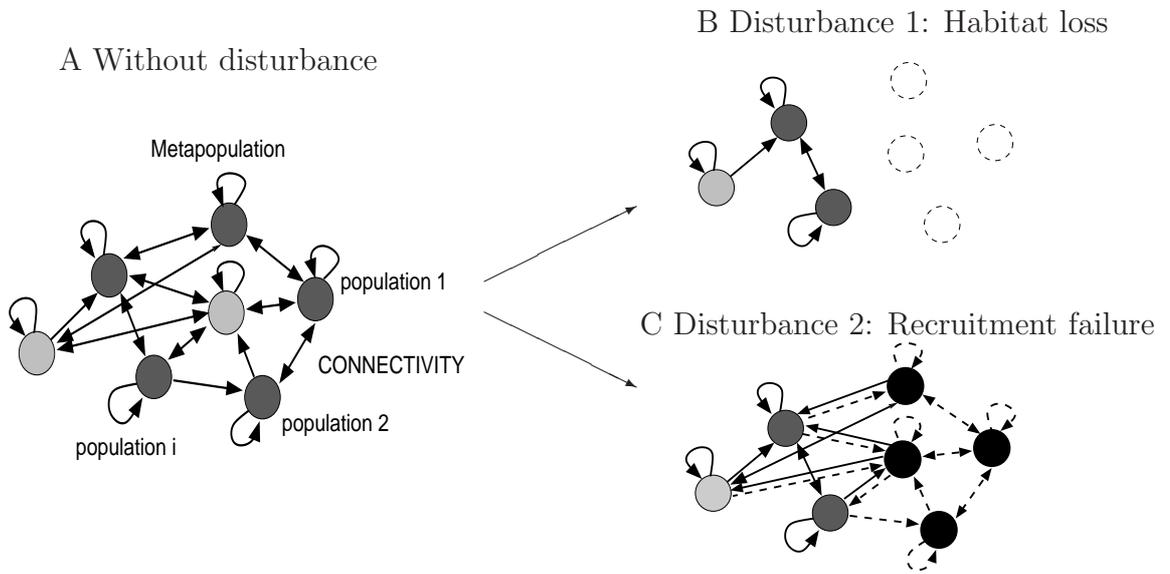
A Without disturbance

B Disturbance 1: Habitat loss

C Disturbance 2: Recruitment failure

Fig. 1: *(A) Schematic diagram for a spatially explicit model of a metapopulation, where gray intensity indicates adult abundance per unit area in each population and solid arrows indicate larval fluxes in the absence of disturbance. (B) Habitat loss disturbance: adult abundance in dashed sites is set to zero. (C) Recruitment failure disturbance: dashed arrows indicate useless larval transfers due to recruitment failure in sites diplayed in black.*
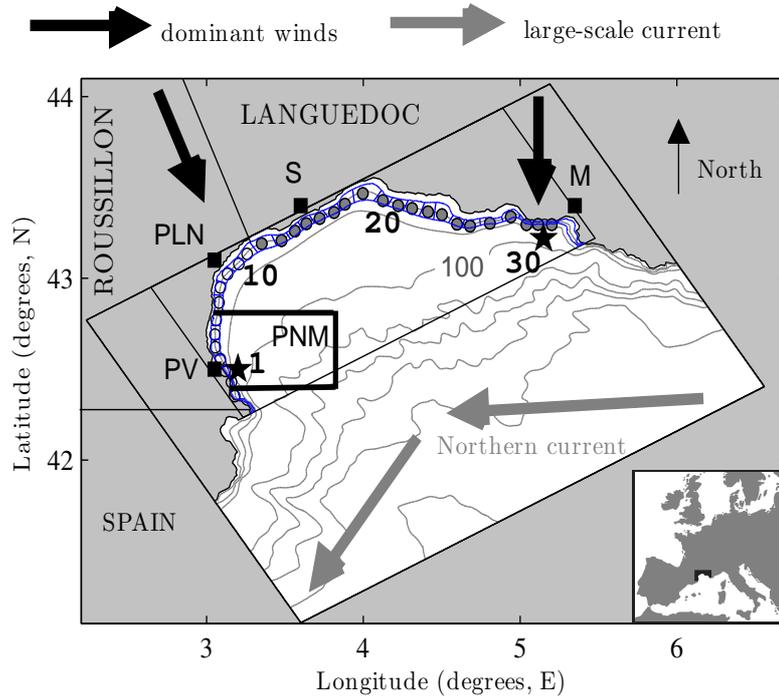
Fig. 2: *Gulf of Lions (NW Mediterranean Sea) bathymetric map with depth contours displayed in gray lines (depth contours are 20, 50, 100, 500 m and spacing is 500 m below 500 m deep). The nearshore sandy habitat (depth between 10 and 30 m) was meshed into 32 sites from the center of which (indicated by circles and numbered from west to east) larvae were released for dispersal simulations. Hollow circles indicate the release points off the Roussillon coast and filled circles indicate the release points off the Languedoc coast used in the simulations, group 3B. Solid boxes show the extension of the two nested computational domains (1500 m and 750 m resolution grids) and the thick-lined box displays the extent of the Parc Naturel Marin du Golfe du Lion (PNM). The two stars indicate the location of the two other marine protected areas (Parc Marin de la Côte Bleue in the West and Réserve Naturelle Marine de Cerbère-Banyuls in the East). The four trade ports of the Gulf of Lions for the simulations group 3A are indicated by a filled square and a letter. From east to west, M stands for Marseille, S for Sète, PLN for Port La Nouvelle and PV for Port-Vendres. Banyuls Bay (not depicted) is located 10 km south of Port-Vendres.*
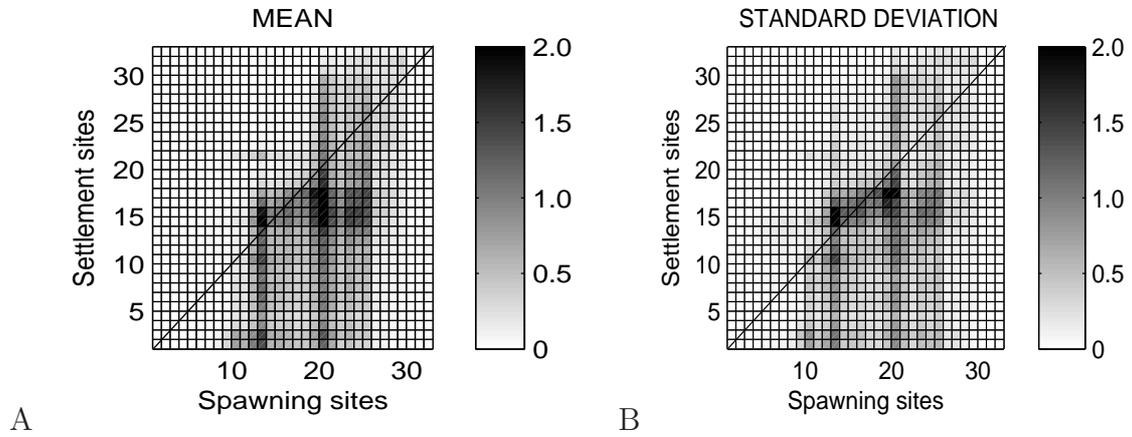
Fig. 3: *(A) Mean and (B) standard deviation of the twenty connectivity matrices computed for twenty 10-day spawning periods and a 4-week pelagic larval duration.*
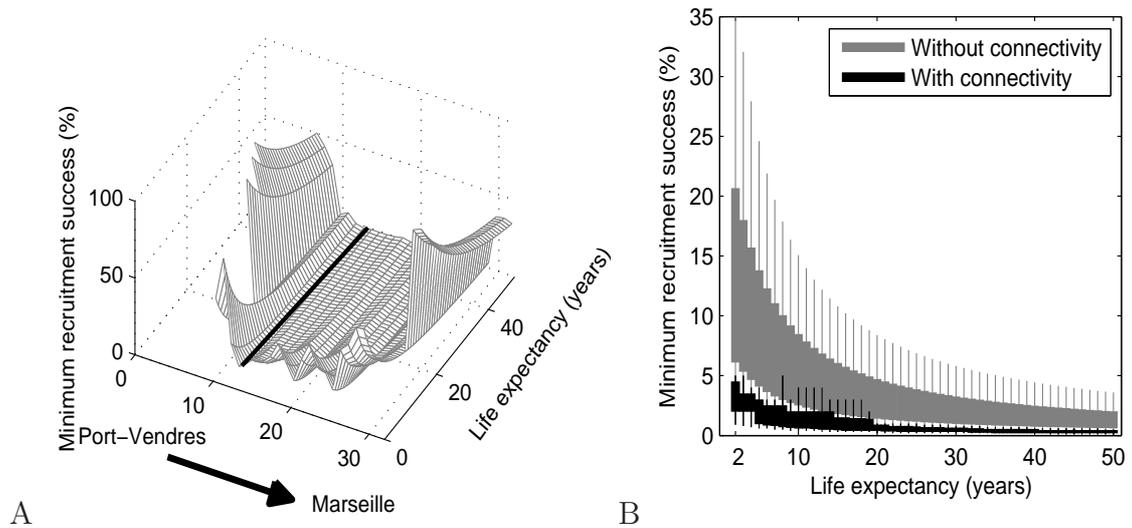

Fig. 4: *Simulation group 1: (A) Minimum recruitment success required to ensure local persistence considering only average local retention rates (without connectivity). The black line displays the location where recruitment success for local persistence was at a minimum along the Gulf of Lions, and this section is plotted in B. (B) Minimum recruitment success required to ensure regional persistence (persistence in at least one site of the region) with and without connectivity for each of the twenty connectivity variants.*
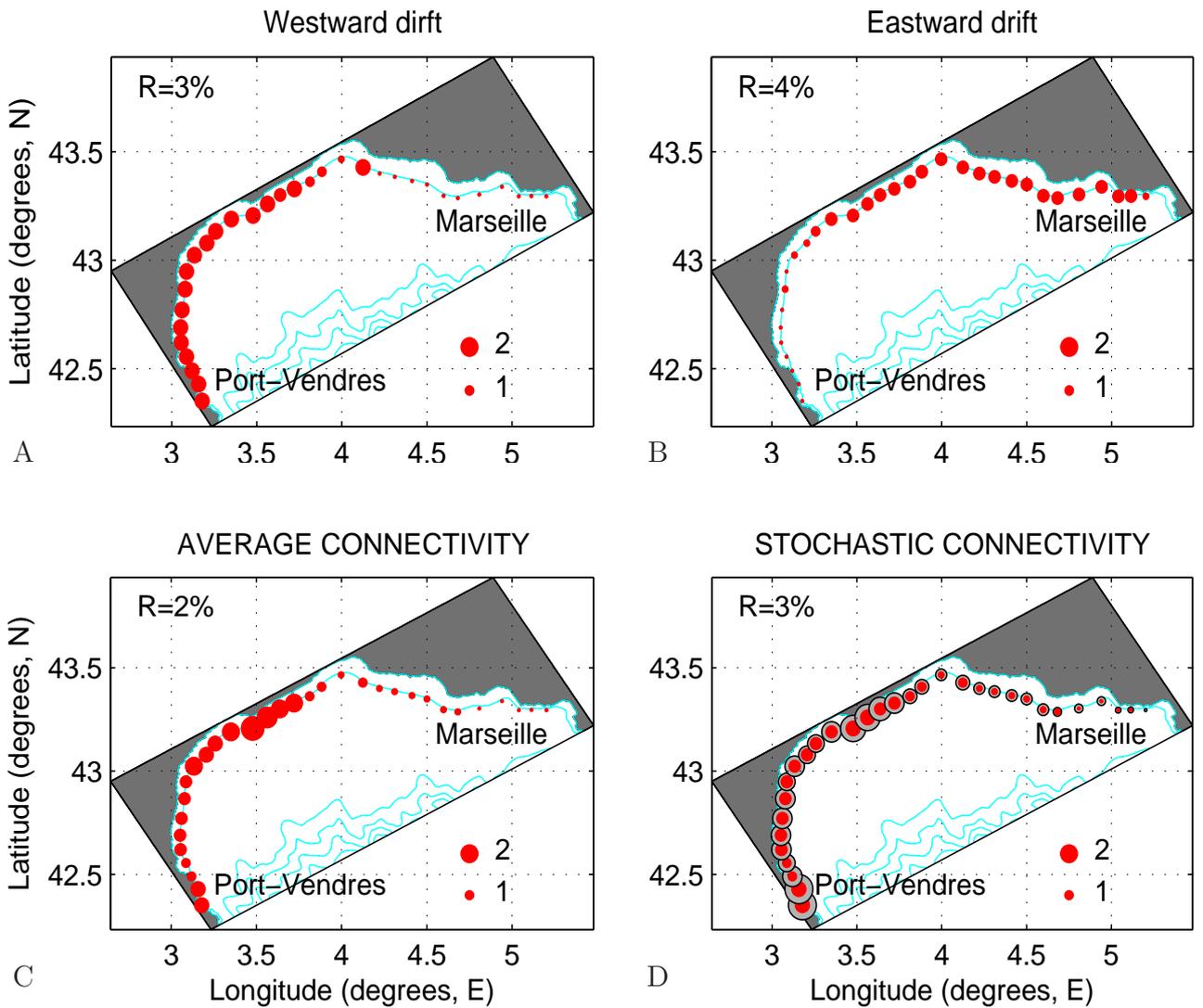
Fig. 5: *Spatial distribution of the relative population density (ratio between the site popu-
lation density and the regional average of population densities) of a 2-year lifespan species
computed between 91 and 100 years and repeating the same connectivity matrix every year
(simulations group 1): (A) for a connectivity matrix displaying a westward drift, (B) for a
connectivity matrix displaying an eastward drift, (C) for the average connectivity matrix,
and (D) for an ensemble of 500 simulations in which connectivity was picked every year
with uniform probability amongst the 20 connectivity variants (simulation group 2). Black
circles display the standard deviation of the 500 simulations replicated when connectivity
was stochastic. R is the minimum recruitment success value to ensure species persistence
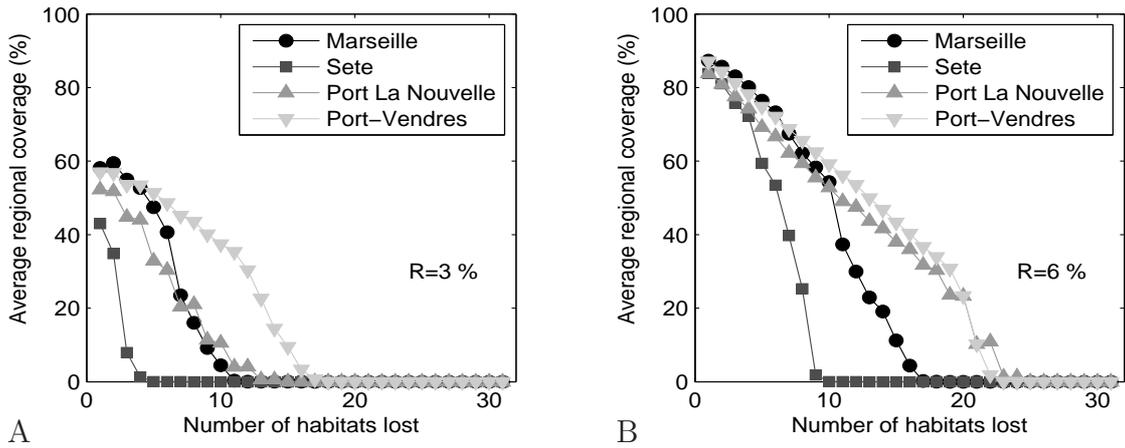in each connectivity case.*

Fig. 6: *Average regional coverage of a 2-year lifespan species between 91 and 100 years for the ensemble of 500 simulations of group 3A. Connectivity was picked every year with uniform probability amongst the 20 connectivity variants and the number of habitat sites destroyed was increased from 1 to 32. Recruitment success R was set to (A) 3% and (B) 6%. The errorbars displaying variability among the 500 simulations are smaller than the symbols.*
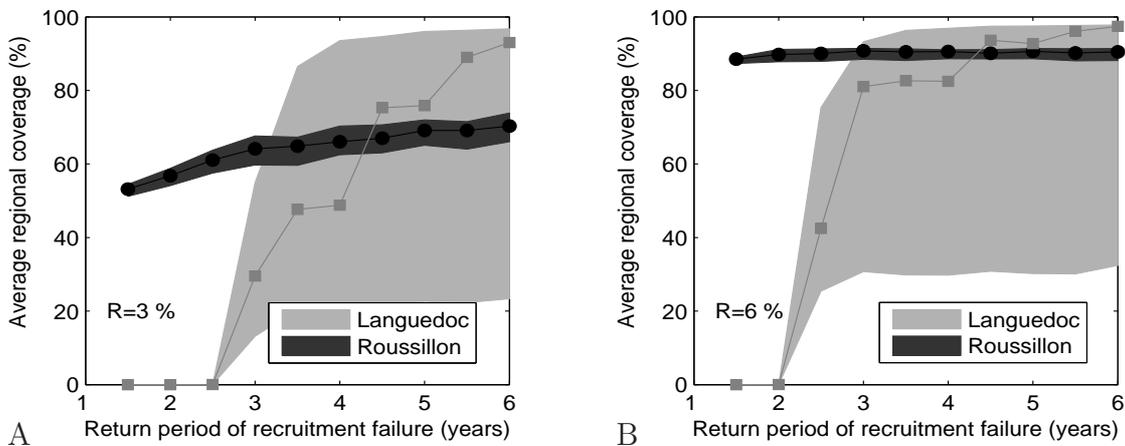

Fig. 7: *Median of the average regional coverage of a 2-year lifespan species between 91 and 100 years for the ensemble of 500 simulations of group 3B. Connectivity was picked every year with uniform probability amongst the 20 connectivity variants and the return frequency of recruitment failure in the northern (Languedoc) and western (Roussillon) part of the Gulf of Lions varied from every ten years to every year. Recruitment success R was set to (A) 3%, and (B) 6%. The shaded area is delimited by the 5% and 95% quantiles of the average regional coverage between 91 and 100 years.*