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2 Using larval dispersal simulations for
3 Marine Protected Area design: application
4 to the Gulf of Lions (NW Mediterranean)

5 K. GUIZIEN ^{1,*}, M. BELHARET ¹, P. MARSALEIX ², and J.M. GUARINI ¹

6 ¹ Laboratoire d'Ecogéochimie des Environnements Benthiques, CNRS, Université Paris
7 VI, Avenue du Fontaulé - F-66651 Banyuls-sur-Mer (FRANCE)

8 ² Laboratoire d'Aérologie de Toulouse, CNRS, Université de Toulouse, 14 avenue E.
9 Belin - F-31400 Toulouse (FRANCE)

10 **RUNNING TITLE: Marine Protected Area design based on larval dispersal**
11 **simulations**

*E-mail: guizien@obs-banyuls.fr

ABSTRACT: The design (location and size) of sustaining, no-take reserves was investigated by combining realistic numerical simulations of larval dispersal from a sedentary marine species with a population dynamics model. The method explored, *a priori*: (1) the Planktonic Larval Duration (PLD) of self-persistent populations within no-take reserves with radii from 1 to 20 kms, (2) the size of a no-take reserve reaching self-persistent recruitment of the reserve population, and (3) offspring spillover to adjacent fisheries for PLDs from one to six weeks. In the Gulf of Lions (NW Mediterranean), as the radius of a no-take reserve increased to 20 kms, the median PLD of a self-persistent species within the reserve increased from 2 to 6.5 days. No unique relation between PLD and sustaining no-take reserve size could be established due to large spatial and temporal variabilities, thus precluding any general guidelines for marine protected area sizes. For species with mass spawning lasting < 3 days, variability due to spawning timing yielded twice the spatial variability, reflecting strong wind variability. In contrast, when spawning lasted more than 10 days, the spawning location became more important. This pinpoints how a biological process (spawning duration) can trigger deterministic and stochastic effects of environmental variability. Finally, some unprotected areas (Narbonne to Agde and the Camargue) clearly appeared as better locations than the existing no-take reserves for maximizing biodiversity persistence within a reasonable no-take reserve size (10 to 20 kms), and for producing offspring spillover important for regional fisheries (80 %).

INTRODUCTION

During the 10th meeting of the Conference of the Parties of United Nations Convention on Biological Diversity, held in October 2010 in Nagoya (Japan), the Strategic Plan for Biodiversity 2011-2020 formulated a conservation objective of 10% of coastal and marine areas by 2020. Such an objective clearly imposes a scientific basis for designing new Marine Protected Areas (MPAs) to sustain biodiversity and ecosystem services inside and outside the protected area (Palumbi, 2004). Most existing MPAs were not designed to fulfill these needs, but aimed instead at protecting habitats presumed to host high biodiversity and were created without any ecological foundation. Furthermore, the use of species surrogates measures to position an MPA is not supported by existing ecological theories that may be used to forecast the efficiency of protection measures for conservation of local and regional biodiversity (Sætersdal & Gjerde, 2011).

Amongst existing ecological theories, neutral theory (which ignores the role of biological constraints in biodiversity distribution) is a tempting scientific framework for MPA designers because its simplicity supports its operationality. According to neutral theory, local species richness S^* has a power-law relationship with surface area A following $S^* \propto A^z$ with $z > 0$ at intermediate spatial scales (Rosindell et al., 2011). Taking $z = 0.25$, any MPA covering 10% of any region should thus protect 56% of its regional diversity.

Yet, *a posteriori* assessment of protection efficiency for some taxonomic groups showed that even if overall positive effects on both biomass and species diversity for fish in no-take reserves exist, protection efficiency is less clear for invertebrates and algae (Lester et al., 2009). Differential effects of protection efficiency have been attributed to trophic cascade effects in relation to fish grazing pressure increase (Halpern, 2003; Lester

et al., 2009), pinpointing the importance of species interactions in shaping local
diversity. Conflicting results were also reported about the expected relation between
biological response and no-take reserves size arising from the neutral theory (Claudet et
al., 2008; Lester et al., 2009). Reasons invoked to explain these discrepancies were either
differences in statistical methods or shifts in Planktonic Larval Duration (PLD) range
due to temperature differences between temperate and tropical regions that would affect
dispersal distance.

Most marine sedentary species and particularly 70 % of invertebrates, (Thorson, 1946)
exhibit a planktonic larval phase which can last from a few hours (ascidians, Olson,
1985) to several months or years (Strathmann & Strathmann, 2007). Offspring released
into the water column are transported and dispersed more or less passively by the flow
due to limited motility ability compared to horizontal flow speed (Chia et al., 1984;
Scheltema, 1986). Dispersal distance thus increases with the PLD because of both
advection and diffusion processes when the current field is spatially uniform and
permanent (Siegel et al., 2003). This basic finding has been implicitly extended to the
global scale (Kinlan & Gaines, 2003) with declarations like the larger the reserve, the
broader range of PLDs, i.e. species, will be protected (Botsford et al., 2003). However,
postulating hydrodynamic steadiness and spatial uniformity at a global scale is
obviously incorrect. Dispersal distances differing by one order of magnitude for the same
PLD were already related to hydrodynamic transport variability for the same species in
different areas (Shanks et al., 2003). Hydrodynamic variability, in both time and space,
will easily blur any relationship between PLD and dispersal distance (Siegel et al., 2008),
and may explain the absence of correlation between PLD and genetic connectivity as
well (Weersing and Toonen, 2009). Hence, there is no reason for the biological response

79 to protection and protected area size to be correlated at a global scale.

80 Ocean modelling works well for hindcasting realistic coastal circulation (Dufaud-Julliand
81 et al., 2004; Estournel et al., 2003; Leredde et al., 2007) and provides a comprehensive
82 description of current variability useful for improving dispersal distribution and
83 population connectivity estimates (Tremblé et al., 2008). Without overlooking the
84 ultimate role of species' interaction to shape local diversity, ensuring marine sedentary
85 species' self-persistence within a no-take MPA would require that the design accounts
86 for a dispersion period during reproduction.

87 In this study, we propose a methodology using larval dispersal simulations and
88 population dynamics traits to design (in terms of location and size) sustainable no-take
89 reserves for sedentary species with a planktonic larval stage. Offspring spillover from the
90 no-take reserve to adjacent fished areas is also quantified and the best compromise
91 between no take reserve size and maximum benefit for resources management solved for
92 (Pauly et al., 2002; Halpern and Warner, 2003). The methodology was applied to the
93 Gulf of Lions: a broad continental shelf in the NW Mediterranean Sea with high
94 primary production ($\text{Chl}_a > 1 \mu\text{g L}^{-1}$) compared to the generally oligotrophic
95 Mediterranean sea (Durrieu de Madron et al., 2011) and intense fishery activities
96 (40,000 tons per year, Demaneche et al., 2009) (16,000 km², Fig. 1). Two MPAs with
97 no-take zones were implemented 37 and 15 years ago in this region: the first is located
98 at its southeastern and the second, at its western extremity (Mabile & Pianté, 2005).

99 These MPAs cover only 0.66% of the Gulf of Lion surface and include no-take areas with
100 a maximum radius of 0.9 km. Recently, in October 2011, protection was dramatically
101 increased by the creation of a Natural Marine Park 4,000 km², representing about 25 %
102 of the Gulf of Lions surface. Using our method, we selected locations optimizing both

conservation potential and spillover benefit for adjacent fisheries along the 300-long
coastline segment which remains unprotected.

MATERIAL AND METHODS

Methodology for No-Take reserve design based on larval dispersal simulations

We consider the design of a no-take marine reserve ensuring the local persistence of a
sedentary species with a pelagic larval stage and maximizing offspring spillover to
adjacent fished area. Even if generally, the larger the no-take reserve, the higher the
retention rate, such criteria are not acceptable to stakeholders. Thus, being able to
determine the minimal dimensions of a sustainable no-take reserve and then follow how
these minimal dimensions evolve at a regional scale appears crucial. Sustainability is
taken here to mean that the reserve population is self-persistent.

Criteria for self-persistence of a population were derived from a simplified generic
population dynamics model for a species with two sedentary stages (adult and juvenile)
and a dispersive pelagic larval stage (Fig. 2). The time required by offspring to reach
their first reproduction is ΔT and PLD is the pelagic larval stage duration. The
sedentary population includes N_0 adults which reproduce at time t_0 . Sedentary
reproducers abundance exponentially decays through time as a result of many loss
processes (predation, starvation, ...) represented by a global mortality rate m .

Reproducers' mortality rates can be related to life expectancy $T_{0.99}$ assuming cohort
abundance had decreased by 99 % after $T_{0.99}$, i.e. $m = -\ln(0.01)/T_{0.99}$. Losses of
reproducers over the ΔT days are $\Delta N^- = N_0(1 - \gamma)$ where $\gamma = \exp(-m\Delta T)$.
After each reproduction, the number of larvae N_1 released in the water reads:

$$N_1 = FS_RfN_0 \quad (1)$$

where F is female fertility (number of eggs per female), S_R is the proportion of female within the sedentary population and f is the fertilization success rate. During the pelagic larval stage lasting PLD days, larvae are dispersed by currents and turbulence and some die as a result of biotic processes (predation, starvation, unsuccessful development, ...). The number of competent larvae remaining in the surroundings of the sedentary population after PLD days reads:

$$N_2 = \mathcal{R}(x, PLD)\mathcal{M}N_1 \quad (2)$$

where $\mathcal{R}(x, PLD)$ is the retention rate of larvae after PLD days as a function of the distance x around the sedentary population and $\mathcal{M} = \exp(-\mu PLD)$ where μ is the natural mortality rate during pelagic larval stage due to biotic processes, excluding dispersal.

At the end of larval stage, competent larvae settle as a benthic juvenile stage. Even if no recruitment failure due to substrate unsuitability occur in an area where adults already exist, young juveniles generally have higher mortality rates than adults due to enhanced competition and predation on smaller organisms. The number of benthic juveniles thus drastically decreases to N_3 during the growth period δt after settlement:

$$N_3 = N_2 \exp(-m'\delta t) \quad (3)$$

where m' is the enhanced mortality rate of post settlement juvenile stages.

141 Finally, the reproductive gain ΔN^+ reaching their first reproduction after ΔT days
 142 reads:

$$\Delta N^+ = \exp(-m(\Delta T - PLD - \delta t))N_3 \quad (4)$$

143 The population will be stable if the losses of sexually matured individuals between two
 144 reproductions ΔN^- are compensated by the reproductive gains reaching their first
 145 reproduction ΔN^+ . Self-persistence condition describes the offspring retention rate
 146 $\mathcal{R}(x, PLD)$ within a distance x and after a pelagic larval duration PLD is larger than
 147 $\mathcal{R}_0(PLD)$:

$$\mathcal{R}_0(PLD) = \frac{(1 - \gamma)}{\gamma F S_R f \exp[-(\mu - m)PLD] \exp[-(m' - m)\delta t]} \quad (5)$$

148 Offspring retention rate can be quantified using Lagrangian larval dispersal simulations.
 149 Lagrangian larva track consists of the successive positions of one larva released at a
 150 given time, at a given location accounting for current advection, turbulent dispersion
 151 and when relevant, specific swimming behaviour (Guizien et al., 2006). In the case no
 152 specific locomotion behaviour is accounted for (passive dispersal), the same track can be
 153 analysed for different PLDs. Lagrangian dispersal, as opposed to Eulerian dispersal,
 154 enables us to analyse independantly tracks originating from different locations at
 155 different times (even though they were computed in the same model run) and to account
 156 for age-varying motility of the larvae. However, in order to investigate tracks' sensitivity
 157 to the hydrodynamics variability, the Lagrangian approach requires computing a large
 158 number of tracks varying with the spawning location and timing, each of these being

159 replicated thirty times to account for turbulent dispersion.
 160 Larvae tracks were analyzed first for the offspring dispersal distance after PLD days.
 161 For each spawning location assigned as the center of a no-take reserve and for the PLD
 162 of the species for which persistence is desirable, two cumulative frequency distributions
 163 of offspring dispersal distance (cumulative dispersal kernel) were built for the two
 164 half-planes defined by the right and the left sides of the spawning location in the along
 165 shore direction. Drift associated to directional dispersion was removed by ensuring that
 166 each larvae dispersed to the left was compensated by one larvae dispersed to the right.
 167 For any given PLD, retention rate $\mathcal{R}_{PLD}(x)$ was calculated as twice the minimum value
 168 of between larvae proportion dispersed within distance x from the spawning site, in one
 169 or the other half-plane. And finally, the radius $b(PLD)$ of the smallest no-take reserve
 170 ensuring the persistence of a species with pelagic larval duration PLD was the distance
 171 at which retention rate $\mathcal{R}_{PLD}(b)$ yielded the threshold value $\mathcal{R}_0(PLD)$ defined by
 172 equation (5) for the species demographic parameters (Fig. 3a).
 173 Larvae tracks were also analyzed for offspring age within a fixed distance around a
 174 spawning location in order to scan persistent species within an existing no-take reserve.
 175 Two age frequency distributions were built up by counting the proportion of larvae of a
 176 given age remaining within the left or the right half part of a no-take reserve of radius b .
 177 Again, care was taken to remove any drift and retention rate $\mathcal{R}_b(t)$ as a function of larvae
 178 age t since spawning was twice the minimum value between larvae proportion of a given
 179 age t dispersed within the distance b in one or the other half plane. Persistent PLDs
 180 within a no-take reserve of radius b were identified when retention rate for the species
 181 PLD $\mathcal{R}_b(PLD)$ was larger than the species persistence threshold $\mathcal{R}_0(PLD)$ (Fig. 3b).
 182 Finally, larvae tracks were also used to estimate the offspring spillover to adjacent fished

183 area for any PLD, $\mathcal{R}_s(PLD)$, that is, the proportion of larvae dispersed to fished areas.

184 **Application to diversity conservation in the Gulf of Lions**

185 The methodology described above was applied in the Gulf of Lions to design a no-take
186 reserve fulfilling a double objective of global biodiversity conservation and fisheries
187 support. The Gulf of Lions is a micro-tidal, wide continental shelf (< 200 m depth,
188 Fig. 1), mainly covered by soft, sandy sediment down to 30 m depth. Hard-bottom
189 substrates mostly occur at the very eastern (Marseille) and western (Banyuls) tips of the
190 gulf. Two other small hard bottom locations exist in the central part of the Gulf of
191 Lions (Leucate, Agde). Fisheries in the Gulf of Lions are divided between artisanal
192 methods targeting demersal fishes and benthic invertebrates in the nearshore (up to
193 three nautical miles from the coast) and intense benthic trawling targeting small pelagic
194 and demersal fishes further offshore (Demaneche et al., 2009).

195 We postulate that maximizing the number of self-persistent polychaete populations in a
196 no-take reserve located anywhere along the coast and their corresponding offspring
197 retention at the regional scale should contribute to global biodiversity conservation and
198 fisheries support in the Gulf of Lions. Indeed, polychaetes dominate soft-bottom benthic
199 invertebrates biomass and diversity in the Gulf of Lions (Grémare et al., 1998), demersal
200 fishes feed on them and the polychaetes suffer collateral damage during trawling
201 activities. Moreover, other benthic invertebrate families and fish species will display life
202 traits similar to polychaetes and thus, our results should also be relevant for these
203 species.

204 Realistic three-dimensional simulations of the Gulf of Lions circulation were carried out
205 over two nested domains with increasing spatial resolution from 1500 m to 750 m

(Fig. 1) and using meteorological forcings of the Météo-France weather forecast model
 (Marsaleix et al., 2006). Simulations covered the reproductive period of most
 polychaetes and fish species in this area (January to June, Bhaud, 1972; Charles et al.,
 2003; Macpherson & Raventos, 2006). The circulation in the Gulf of Lions results from
 the interaction between the large-scale northern current (1 to $2 \cdot 10^6 \text{ m}^3 \text{ s}^{-1}$) flowing from
 east to west along a steep jagged shelf-break (Petrenko et al., 2005) and local hydrology
 (Reffray et al., 2004) and meteorology (Petrenko et al., 2008). Strong winds blow with
 speeds higher than 10 m s^{-1} and on average 30% of time from the North in the eastern
 part, and 60% of time from the North-West in the western part without a marked
 seasonal difference from January to June but showing strong daily to weekly variability
 (Millet, 1990; Guénard et al., 2005). The Rhône River flows at the eastern tip of the
 Gulf of Lions (average discharge is $1,700 \text{ m}^3 \text{ s}^{-1}$, Ludwig et al., 2003) while the many
 Mediterranean rivers bordering the Gulf of Lions reach significant discharges of
 hundreds of $\text{m}^3 \text{ s}^{-1}$ only during flooding events (Guizien et al., 2007).

We considered two years with contrasted hydrological forcings. First, in 2004, the Rhône
 River discharge was high in January but remained lower than $1,000 \text{ m}^3 \text{ s}^{-1}$ from March
 to June while recurrent flooding of small rivers occurred. In 2006, flooding of small
 rivers was minimal and the Rhône River discharged more than $2,000 \text{ m}^3 \text{ s}^{-1}$ during most
 of January through June.

Simulations of Lagrangian larval dispersal in the Gulf of Lions used the
 three-dimensional currents and turbulent kinetic energy computed at a resolution of
 $750 \text{ m} \times 750 \text{ m}$ after interpolation between hourly outputs (Guizien et al., 2006). As a
 Lagrangian dispersal track stops when the larva reach the domain boundary,
 computational domain design was of paramount importance to avoid any biases due to

larvae returning into the domain. The offshore boundary was thus located in the large-scale northern current, ensuring an insignificant number of larvae could return (Cianelli et al., 2007). Dispersal's role in conservation of polychaete populations was studied for two test cases: a generic passive species (neutrally buoyant, no locomotion behaviour) with PLD of one to six weeks (most frequently reported PLDs of temperate coastal species, Levin & Bridges, 1995); and the annelid polychaete *Owenia fusiformis* (three week PLD, with settling behaviour, Guizien et al., 2006) which is the dominant species within the gulf's muddy sands (Labrune et al., 2007).

Thirty-three spawning locations, representing potential no-take reserve locations, were tested along the 20 m isobath (Fig. 1). Continuous spawning was simulated by releasing thirty eggs every hour from January 5 at 0h until April 13 at 23h and larvae positions were stored every thirty minutes (72000 tracks per spawning location). The dispersal of generic passive larvae was simulated over six week periods in 2004 and 2006, and for *Owenia fusiformis* during three weeks in 2004.

Demographic parameters values for the seven test cases and corresponding retention rate threshold value within a no-take area are summarised in Table 1. Natural mortality rates during larval dispersal due to biological processes were the most difficult parameter to estimate. Values for mortality rates derived from monitoring larval cohorts in the plankton (thus including losses and gain through larval dispersa) have been reported as ranging from 0.016 up to 0.8 day⁻¹ (Rumrill, 1990). In our study, low larvae mortality rates were accounted for ($m' = 0.06$ to 0.1 day⁻¹, Table 1), by assuming that larval losses measured in the field were mainly due to dispersal. This latter hypothesis leads to the minimal size for the sustainable Marine Protected Area as a higher larval mortality would increase the minimum retention rate required for local population sustainability.

254 Statistical methods

255 For each of the thirty-three spawning locations (labeled i) and for four spawning
 256 durations (labeled j), descriptors of dispersal (regional retention rate $\mathcal{R}_s^{i,j,k}(PLD)$,
 257 retention rate after PLD days as a function of distance x $\mathcal{R}_{PLD}^{i,j,k}(x)$ and retention rate
 258 within a distance b as a function of larvae age $\mathcal{R}_b^{i,j,k}(t)$) were computed for
 259 $N_j = 98, 91, 31$ and 11 spawning periods (labeled k) of duration three, ten, thirty and
 260 ninety days, respectively. Thus, for each spawning duration j , each dispersal descriptor
 261 was an ensemble of thirty-three by N_j values.

262 The potential for biodiversity conservation of a no-take reserve with radius b ranging
 263 from 1 to 20 kms was screened by seeking PLD for which retention rate within the
 264 no-take reserve $\mathcal{R}_b^{i,j,k}(PLD)$ was larger than the persistence retention rate $\mathcal{R}_0(PLD)$.
 265 Overall potential biodiversity conservation of the no-take reserve was indicated by the
 266 shortest non-persistent pelagic larval duration, $PLD_{SNP}^{i,j,k}(b)$ defined as:

$$PLD_{SNP}^{i,j,k}(b) = \min[t \text{ such as } \mathcal{R}_b^{i,j,k}(t) < \mathcal{R}_0(t)] \quad (6)$$

267 The persistence probability $PP(PLD, b)^{i,j}$ of a species with a PLD and spawning
 268 duration j within the same no-take reserve centered on spawning site i and with radius b
 269 was computed as the proportion of spawning periods for which retention rate after PLD
 270 days exceeded the persistence condition:

$$PP(PLD, b)^{i,j} = Prob[\mathcal{R}_b^{i,j,k}(PLD) > \mathcal{R}_0(PLD), k \in (1, N_j)] \quad (7)$$

271 Persistent PLDs were defined as PLDs for which this probability was larger than 0.5.

For each spawning location i and spawning period k of duration j , the minimum radius $b(PLD)^{i,j,k}$ of a sustainable no-take reserve for a generic species with a pelagic larval duration PLD or for *Owenia fusiformis* were computed. Regional retention rate $R_r(PLD)^{i,j,k}$ defined as the number of larvae remaining over the Gulf of Lions continental shelf were also computed. The three quantities (shortest non-persistent PLD, minimum radius of sustainable no-take reserve, regional retention rate) were presented as boxplots for each spawning duration ensemble at the regional (whatever the reserve location) and local (for each reserve location) scales.

For each of the spawning durations (3, 10, 30 and 90 days) and each of the five reserve radii (1, 2, 5, 10 and 20 kms), the temporal variability of any quantity, $X^{i,j,k}$, was computed by averaging over all reserve locations (labeled i) the coefficient of dispersion (variance-to-mean ratio) of the quantity between spawning periods (labeled k). Spatial variability was computed by averaging over all spawning periods, the coefficient of dispersion of the quantity between reserve locations.

RESULTS

Planktonic larval duration of persistent populations within no-take reserves

For all spawning durations and reserve locations studied, median values of shortest, non-persistent PLDs increased from 2 to 6.5 days when the radius of protection increased from 1 to 20 kms (Figure 4a). Concurrently, the variability of the shortest, non-sustainable PLD also increased with no-take reserve radius as the 25 % quantile increased less (from 1 to 2 days) than the 75 % quantile (from 2 to 20.5 days). This means that large no-take reserves can protect longer PLDs than shorter ones, but they can also have as low biodiversity conservation potential as a small reserve, depending on

294 the location or on the spawning timing or duration. Median value of shortest
 295 non-persistent PLDs increased less for a short spawning duration (from 1 to 2 days,
 296 Fig.4b), than for a long spawning duration (from 2 to 21.5 days, Fig.4d) when no-take
 297 reserve radius increased, while the range of shortest non-persistent PLDs varied little
 298 with spawning duration. Thus, a no-take reserve's potential for conservation will be
 299 higher in the Gulf of Lions for species displaying long spawning duration compared to
 300 those having short spawning duration (Figure 4).

301 This property of conservation potential was not uniformly distributed along the Gulf of
 302 Lions coastline. Persistent PLDs within five no-take reserve sizes displayed large
 303 variability amongst the thirty-three reserve locations tested along the Gulf of Lions, and
 304 spatial variability increased with the spawning duration (Figure 5). In each location and
 305 for each spawning duration, the range of persistent PLDs increased with reserve size.

306 No-take reserves with radii of 2 km still have a very low potential for biodiversity
 307 conservation with persistent PLDs shorter than 3.5 days, whatever the location or the
 308 spawning duration. When reserve radius was increased to 5 km, persistent PLDs range
 309 increased only in a few locations for a spawning duration of three days (Figure 5a) while
 310 it increased everywhere for spawning duration larger than 10 days (Figure 5b). Spatial
 311 variability in conservation potential was further amplified when reserve radius increased
 312 from 5 to 10 kms and with spawning duration. Again using a three day spawning
 313 duration in the central part of the Gulf of Lions (position 16), the persistent PLDs
 314 range was already three times wider compared to locations in the western part of the
 315 Gulf of Lions (positions 3 to 8) and conservation potential increased not only for short
 316 but also for long PLDs (Fig. 5a). For spawning duration larger than 10 days,
 317 conservation potential increase was even more marked in the central part of Gulf of

Lions (positions 12 to 20, Fig.5b to d), up to six times larger than in the western part of the Gulf of Lions. Finally, it was necessary to increase the reserve radius to 20 kms to reach a persistence probability larger than 50 % for all PLDs from 0 to 6 weeks. Such wide conservation potential occurs in only a few locations (positions 14 and 24 to 26) when spawning duration lasted less than 10 days. For the same 10 day spawning duration and reserve radius of 20 kms, a no-take reserve in the western part of the Gulf of Lions would reach a similar probability of conservation potential only for species with PLDs less than 6 days. No-take reserve location became more important than spawning timing during the reproductive season in determining conservation potential only when spawning durations were longer than 30 days. This is because temporal variability of conservation potential was comparable to or dominated over spatial variability whatever the no-take reserve radius for spawning durations up to 10 days (Table 2).

Minimum size of sustainable no-take reserve

Including all spawning durations and reserve locations, sustainable no-take reserve could only be defined in less than 10% of spawning periods (Figure 6). Radial median values of the smallest sustainable no-take reserve that could be defined increased from 5 to 20 kms when the targeted species' PLD increased from 1 to 4 weeks (Figure 6). The statistical distribution of smallest sustainable no-take reserve radius were comparable for species with five or six week PLDs and two week PLDs. Losses due to longer dispersal were compensated by lower persistence threshold due to the higher fertility attributed to species with large PLDs. The proportion of spawning periods for which a sustainable no-take reserve could be defined increase from 6 to 14 % when spawning duration increased from 3 to 90 days, whatever the species PLD. Smallest no-take reserve radii

required to ensure species persistence were also more variable for shorter spawning durations than for a longer spawning duration (as shown for a species with a 3 week PLD in Fig. 7). Temporal variability due to spawning timing was larger than spatial variability due to spawning location for a spawning duration of 3 days (Fig.7a), while it was reversed for the spawning duration of 30 days (Fig.7c). Median values of the smallest sustainable no-take reserve radius displayed large variations along the Gulf of Lions. In the western part (positions 1 to 10) and the extreme eastern part (positions 31 to 33) of the Gulf of Lions, the self-persistence threshold for a neutrally buoyant larvae drifting passively during 3 weeks was not reached, whatever the no-take reserve size (Fig.7).

In the eastern part of the Gulf of Lions (positions 21 to 30), sustainable no-take reserves could always be defined, while in the central part of the Gulf of Lions (positions 11 to 20), spawning duration triggered the probability to define a sustainable no-take reserve. For example, a spawning duration of 3 days, this probability reached 50% in 5 locations and 25 % in others; durations longer than 30 days had a probability greater than 50 % in all locations. Including all spawning durations, median values of sustainable no-take reserve radius ranged from 9 to 40 km along the Gulf of Lions, while the same values only ranged from 5 to 20 km for PLDs ranging from one to four weeks for all spawning durations *and* locations (Fig.6).

Conservation potential clearly varies with location in the Gulf of Lions. For a neutrally buoyant larvae drifting passively during 3 weeks, smallest values for sustainable no-take reserve radii were found between Narbonne and Agde (positions 12 to 16 for spawning duration larger than 10 days and only positions 13 and 14 for spawning duration of 3 days) and off the Camargue (positions 24 to 26) (Fig.7). In these locations, median

values of sustainable no-take reserve radii were about 10 km. For the same three week PLD, median values for the smallest no-take reserve radius required for *Owenia fusiformis* persistence were generally larger than the ones defined for passive drifting larvae in most locations along the Gulf of Lions. Larvae settling behaviour had the largest effect on sustainable no-take reserve radius in the central part of the Gulf of Lions, doubling its value in positions 11 to 13 and in positions 17 to 20. The settling larvae of *O. fusiformis* were only less far dispersed in the eastern part of the Gulf of Lions (positions 31 to 33) where the persistence threshold was reached in additional locations.

Spatial and temporal variability of regional retention rates

Including all spawning durations and reserve locations, median values of regional retention rate decreased from 100% to 38% when the targeted species PLD increased from 1 to 6 weeks. Yet, regional retention rates could vary from 0 to 100% whatever the species PLD, since spatial structure dominating over temporal variability or PLD biological constraints (Fig.8). For neutrally buoyant larvae drifting passively during 3 weeks, median regional retention rate varied from less than 10% in the western part of the Gulf of Lions (positions 1 to 9, Fig.8) to more than 90% in the eastern part of it (positions 20 to 28, Fig.8), whatever the spawning duration. However, temporal variability due to spawning timing decreased when spawning duration increased. While temporal coefficient of dispersion was three times larger than spatial coefficient of dispersion for a spawning duration of 3 days (Fig.8a), it had decreased to half the spatial coefficient of dispersion for a spawning duration of 90 days (Fig.8d). Larvae settling behaviour increased retention rates by 10% on average, except at the western

388 tip of the Gulf of Lions where regional retention rates were increased by 20 (35 %,
389 respectively) in position 1 (2, respectively).

DISCUSSION

390 Dispersal simulations in the Gulf of Lions showed that on average at the regional scale,
391 the longest persistent PLDs increased with no-take reserve size, and the smallest
392 sustainable no-take reserve size increased with the PLD of the targeted species. This
393 seemingly agrees with a dispersal distance increase with species PLD. However, both the
394 shortest non-persistent PLD and smallest sustainable no-take reserve size had temporal
395 and spatial variabilities of more than 300 %, ruling out any proportional relationship
396 between dispersal distance and species PLD at the regional scale. This result weakens
397 the argument about the presence or the absence of a relationship between reserve size
398 and effects on biodiversity conservation at a global scale which are based on the
399 existence of a proportional relationship between dispersal distance and species PLD
400 (Claudet et al., 2008; Lester et al., 2009). In fact, our results confirm that temporal and
401 spatial variability of water circulation directly shapes dispersal kernels (Aiken et al.,
402 2007), which in the general case are not gaussian as would arise from diffusion only
403 (Gerber et al., 2003; Moffitt et al., 2011). Dispersal distance strongly depends on the
404 relative strength of advective and diffusive transport and on the permanence of its
405 directionality which may also display spatial variability (Gaines et al., 2003).

406 Temporal variability of circulation in the Gulf of Lions is mainly driven by the two
407 regional winds (northerly Mistral and northwesterly Tramontane) which intensely blow,
408 generally together, during repeated periods of one day to a week, whatever the season
409 (Guénard et al., 2005). This wind-induced temporal circulation dynamic explains how in
410 our results, persistence conditions were triggered in dispersal kernels by spawning

411 duration: transport drift dominated over diffusion in species dispersal for spawning
 412 durations less than 10 days and led to very low retention rates. For a spawning duration
 413 longer than 30 days it was reversed, except in the western part of the Gulf of Lions
 414 where directional transport prevailed. Thus, in most locations, the longer the spawning
 415 duration, the higher the probability to reach a persistent retention rate. These results
 416 also suggest that the probability to find a relationship between dispersal distance and
 417 PLD increases, when spawning duration is longer than the hydrodynamics' temporal
 418 stability scale.

419 Marine invertebrates are mostly free-spawning species (Barnes et al., 1988) which require
 420 reproduction synchronicity of neighbours to increase fertilization probability (Levitan,
 421 1995). Synchronized spawning seems to dominate among marine invertebrates species,
 422 presumably resulting from a fitness selective process (Barnes et al., 1988). In tropical
 423 regions, reduced spawning duration makes a relationship between dispersal distance and
 424 PLD not likely, considering the high stability of meteorological forcings in these regions.

425 Short mass spawning events of a few days have also been recorded for temperate
 426 gorgonians (Coma et al., 1995) and for the two dominant polychaetes species of the Gulf
 427 of Lions, *Owenia fusiformis* (Koh, 2002) and *Ditrupa arietina* (Charles et al., 2003). Yet,
 428 spawning duration tends to be longer due to synchronizing difficulty in a highly variable
 429 environment and may display large inter-annual variability (from a few days to a month
 430 for *Owenia fusiformis*, Koh, 2002). Thus, the design of no-take reserves in the Gulf of
 431 Lions for protecting benthic invertebrates and particularly polychaetes, should account
 432 for short and long spawning durations with variable timing within the spawning season.

433 More generally, we know that spawning timing varies between species and within the
 434 same species, presumably due to complex interactions between ultimate (endogeneous

435 cycle, food availability, temperature,...) and proximate (day/night, pressure,
436 temperature,...) factors which are far from being elucidated (Morgan, 1995). As a
437 result, spawning timing in temperate regions could be at best related to the season. In
438 the present study, dispersal was only computed for spawning in late winter/spring,
439 which is the main reproductive period in the Gulf of Lions, including temperate
440 polychaetes species (Bhaud, 1972) and most labridae and sparidae fish species
441 (Macpherson & Raventos, 2006). Moreover, as dispersal distance is expected to be
442 larger in spring than in the summer (second most important reproductive period) when
443 weaker wind speed favours higher retention (Milot, 1990), the present study analyzed
444 the more constraining dispersal situation for no-take reserve design.

445 Despite the strong temporal variability for the short 3 days spawning duration, potential
446 conservation requirement displayed a spatial structure with more favourable locations
447 along the Gulf of Lions where sustainable no-take reserves could be defined with a
448 median radius lower than 20 km and its temporal variability could be minimized. This
449 contradicts one of the basic assumptions underlying the neutral theory which states that
450 regional dispersal probability is spatially uniform. In the gulf, these sites are located
451 between Narbonne and Agde and off the Camargue, in two of the six frequent upwelling
452 areas (Milot, 1990). The existence of anticyclonic eddies between these upwelling areas
453 was early suggested by Milot (1990) after he identified one large anticyclonic gyre in the
454 southwestern part of the Gulf of Lions associated to the Tramontane upwelling between
455 Narbonne and Agde. Such wind-driven spatial structures are well represented in
456 circulation numerical simulations (Estournel et al., 2003) and may potentially increase
457 larvae retention. However, neither the locations nor the sizes of the best no-take reserves
458 locations identified in the present study agreed with the location and size of mesoscale

459 structures identified in a recent analysis of anticyclonic eddies of realistic numerical
 460 simulations of the Gulf of Lions hydrodynamics (Hu et al., 2009). It is more probable
 461 that submesoscale eddies (smaller than 20 km) created by coastline promontories (Agde
 462 and Beauduc Cape) would explain the more favourable locations for biodiversity
 463 conservation identified between Narbonne and Agde and off the Camargue. Yet, the
 464 large mesoscale structures identified in the Gulf of Lions shelf may explain the strong
 465 regional retention rate of larvae released along the eastern and central parts of the Gulf
 466 of Lions shoreline (Cianelli et al., 2007).
 467 Conversely, strong export through the canyons in the western part of the Gulf of Lions
 468 has been attributed to frequent cascading of negatively buoyant water formed after wind
 469 cooling (Dufaud-Julliand et al., 2004; Ulses et al., 2008). Climatic forecasts indicate a
 470 drastic reduction of dense water cascading in the region for the next century (Herrmann
 471 et al., 2008). The regional retention rate is thus likely to increase with probable positive
 472 consequence on regional fish populations' maintenance, even in the absence of any
 473 management measure.
 474 Existing no-take reserves (Cerbère-Banyuls and Carry-le-Rouet, Fig. 1) are not located
 475 in the best locations identified and their radius (smaller than 1 km) is less than the
 476 smallest radius for a sustainable no-take reserve anywhere in the Gulf of Lions. Thus,
 477 these no-take reserves should not be very efficient for global biodiversity conservation.
 478 For example, a protection effect of the Cerbère-Banyuls reserve has only been
 479 demonstrated for the emblematic dusky grouper *Epinephelus marginatus* (Ludwig et al.,
 480 2003) and some commercial fish species (although not all, Dufour et al., 1995). Habitat
 481 protection was clearly the primary motivation behind establishing these no-take
 482 reserves. The Cerbère-Banyuls reserve targeted rocky reefs, corraligenous habitats and

the emblematic *Posidonia oceanica* beds, which are known to support higher fish diversity (Guidetti, 2000), while the more recent Carry-le-Rouet reserve also included sandy beds. Bearing in mind the interest for the specific habitats that motivated existing reserves establishment, it should be necessary to increase the reserve radius up to 20 kms to conserve efficiently species with larvae passively dispersed during three weeks in Carry-le-Rouet. In contrast, in Cerbère-Banyuls, no sustainable reserve could be defined for the same species. Moreover, even if a sustainable wider reserve could be settled there, impact on regional fisheries sustainability would be low due to current low regional retention rates. The recent creation of a Natural Marine Park extending the protection area around the Cerbère-Banyuls reserve in the western part of the Gulf of Lions highlights once again, the underappreciation for the dispersal process when planning marine protected areas.

Our results stress that marine protection spatial planning requires dedicated studies accounting for not only species biological traits but also local hydrodynamics. Guidelines for MPA size and spacing established in one area should not be transposed to other places. For example, in California (USA), a pioneering American state in terms of MPA implementation, the design of MPA network was recommended. Current guidelines describe recommendations for size (5 to 20 kms along shore) and spacing (50 to 100 km apart, CDFG, 2009). These recommendations are based on dispersal distance estimates ranging from 50 to 100 kms and yielding unacceptable size for isolated sustainable no-take reserve. Yet, spatially explicit population dynamics have shown that these recommendations would not guarantee persistence of targeted species along the California coast when exploitation pressure was high outside the MPAs and that a large MPA of the size of the dispersal distance would be preferable (Moffitt et al., 2011).

Returning to the Gulf of Lions, the reasonable radius (10 to 20 kms, compared to dispersal distance of hundreds of kms estimated from Shanks et al., 2003)) of sustainable no-take reserve for species with the most frequent PLD (3 weeks) is encouraging for the implantation of reserves. Moreover, extension of protection measures targeting the central or the eastern part of the Gulf of Lions would combine benefits for both biodiversity conservation and fisheries sustainability. However, it is clear that convincing fishermen that protection measures in this part of the Gulf of Lions will benefit them will not be easy as these areas are currently supporting 45% of the regional fishing effort (Demaneche et al., 2009). From the dispersal point of view, implementing conservation measures off the Camargue would have the largest effect on fisheries while conservation measures between Narbonne and Agde would probably contribute more to regional biodiversity conservation as these areas include diverse habitats, including rock reefs, *Posidonia oceanica* beds and sandy beds. Next step will be to discuss MPA design as a framework for optimizing the potential for biodiversity conservation in an ecosystem-based approach.

The importance of using a methodology like that proposed in this paper is that it enables pre-screening of locations at a regional scale. Our estimates showed discrepant values for both passive drifting and settling larvae in upwelling areas, highlighting the interaction between three dimensional physical structure and biological traits. Our approach offers a scientific basis for decision-making using the dispersal process, and a reasonable no-take reserve size (about 300 km², 2 % of the Gulf of Lions surface) could become a reality under the new marine park and existing Natura 2000 initiatives. However, even if the approach presented in this paper allowed us to detect best locations for protection implementation at the regional scale, it should be complemented by local

531 dispersal studies accounting for more detailed hydrodynamic features and species
532 motility behaviour (Guizien et al., 2006) and species interactions, which can potentially
533 reshape diversity patterns within communities (Moriz et al., 2009), should not be
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766		<i>between January and June 2004 within no-take reserves of increasing radius</i>	
767		<i>b from 2 kms to 20 kms (see greyscale on plot) along the Gulf of Lions and</i>	
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772		<i>be defined versus Planktonic larval duration (PLD) whatever the spawning</i>	
773		<i>duration between January and June (2004 and 2006) and the reserve loca-</i>	
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775		<i>periods for which a sustainable no-take reserve could be defined is reported</i>	
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778		<i>reserve location computed for four spawning durations of (a) 3 days, (b) 10</i>	
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780		<i>neutrally buoyant passive larvae and <i>Owenia fusiformis</i> larvae(both 3 weeks</i>	
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782		<i>on Figure 1 and numbered from the west (Banyuls) to the East (Marseille).</i>	46
783	8	<i>Boxplots of regional retention rate versus no-take reserve locations com-</i>	
784		<i>puted for four spawning durations of (a) 3 days, (b) 10 days, (c) 30 days</i>	
785		<i>and (d) 90 days between January and June 2004 for a neutrally buoyant</i>	
786		<i>passive larvae and <i>Owenia fusiformis</i> larvae(both 3 weeks PLD). No-take</i>	
787		<i>reserves were centered on the 33 spawning locations shown on Figure 1 and</i>	
788		<i>numbered from the west (Banyuls) to the East (Marseille).</i>	47

PLD (weeks)	Generic passive species						<i>Owenia</i>
	1	2	3	4	5	6	<i>fusiformis</i>
F	10^4	10^4	10^4	10^4	10^5	10^5	10^4
m' (% day $^{-1}$)	10	10	6	6	6	6	6
R_0 (%)	5.9	6.6	9.8	14.4	2.1	3.15	9.8

Table 1: *Demographic parameters (female fertility F and larval mortality rate m') and subsequent minimum retention rate for population persistence R_0 for *Owenia fusiformis* and generic species with passive larval dispersal durations increasing from one to six weeks. Most restrictive condition on adult mortality rate $m = 0.0042 \text{ day}^{-1}$ for population stability was applied based on shortest life expectancy (three years, McHugh & Fong, 2002). Female fertility in the oligotrophic Mediterranean sea was taken in the lower part of female fertility range (Charles et al., 2003; Koh, 2002) and was assumed to increase with species PLD (McHugh & Fong, 2002). Sex ratio S_R in the adult population and fertilization success rate f were taken equal to 0.5 and 0.1 respectively, for all species (Eckman, 1996). The mortality rate of young, small juveniles was one order of magnitude greater than the adult mortality rate and applied during one-tenth of the time between two reproduction events ($m' = 0.042 \text{ day}^{-1}$ during $\delta t = 36 \text{ days}$).*

No-take reserve radius	1 kms	2 kms	5 kms	10 kms	20 kms
Spawning duration					
3 days	1.5	1.4	1.3	1.3	1.3
10 days	1.2	1.2	0.9	0.8	0.8
30 days	1.0	0.8	0.4	0.4	0.4
90 days	0.5	0.3	0.1	0.2	0.3

Table 2: *Ratio of the averaged coefficient of dispersion between different spawning events to the averaged coefficient of dispersion between spawning location of the shortest sustainable PLD for no-take reserve radii increasing from 1 to 20 kms and spawning durations increasing from 3 to 90 days.*

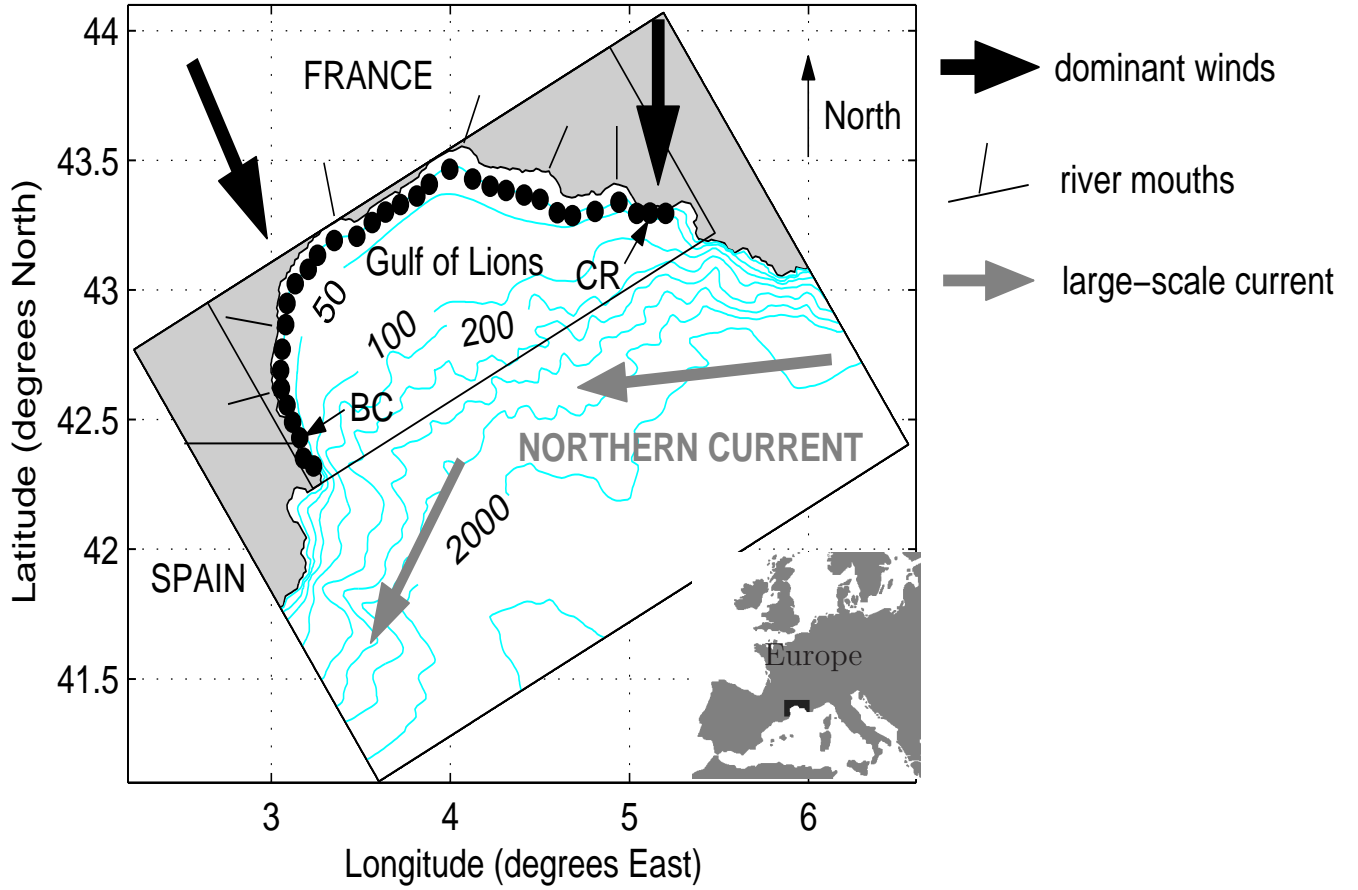


Fig. 1: *Gulf of Lions (NW Mediterranean Sea) bathymetric map with depth contour in meters (depth contour spacing is 200 m below 200m deep). Locations for potential no-take reserves are shown as filled circles. Arrows indicate the location of existing no-take reserve, CR stands for Carry-le-Rouet and BC stands for Cerbère-Banyuls. Boxes show the extension of the two nested computational domains (1500 m and 750 m resolution grids).*

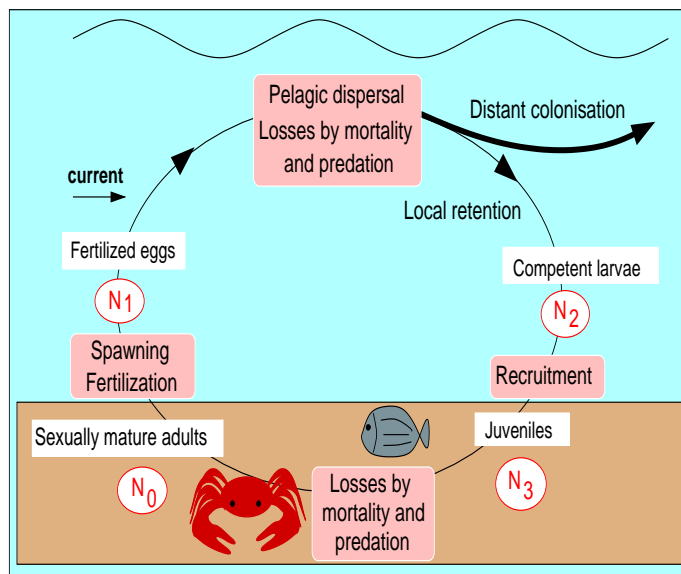


Fig. 2: *Simple population dynamics model for benthic species with a pelagic larval stage*

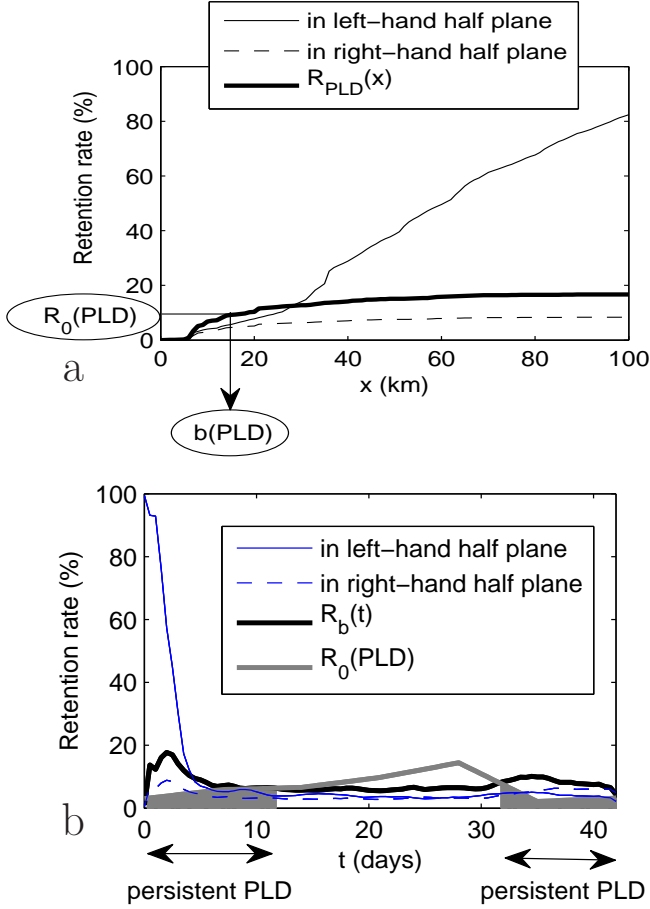


Fig. 3: (a) Definition of the minimum size $b(PLD)$ of sustainable no-take area for a species with pelagic larval duration equal to PLD days based on retention rate $R_{PLD}(x)$ after transport drift has been removed from dispersal kernels; (b) Exploration of the pelagic larval duration PLD of persistent populations within a no-take area with radius b defined as pelagic larvae age t for which retention rate $R_b(t)$ after transport drift has been removed from age frequency distribution is larger than population persistence retention rate $R_0(PLD)$.

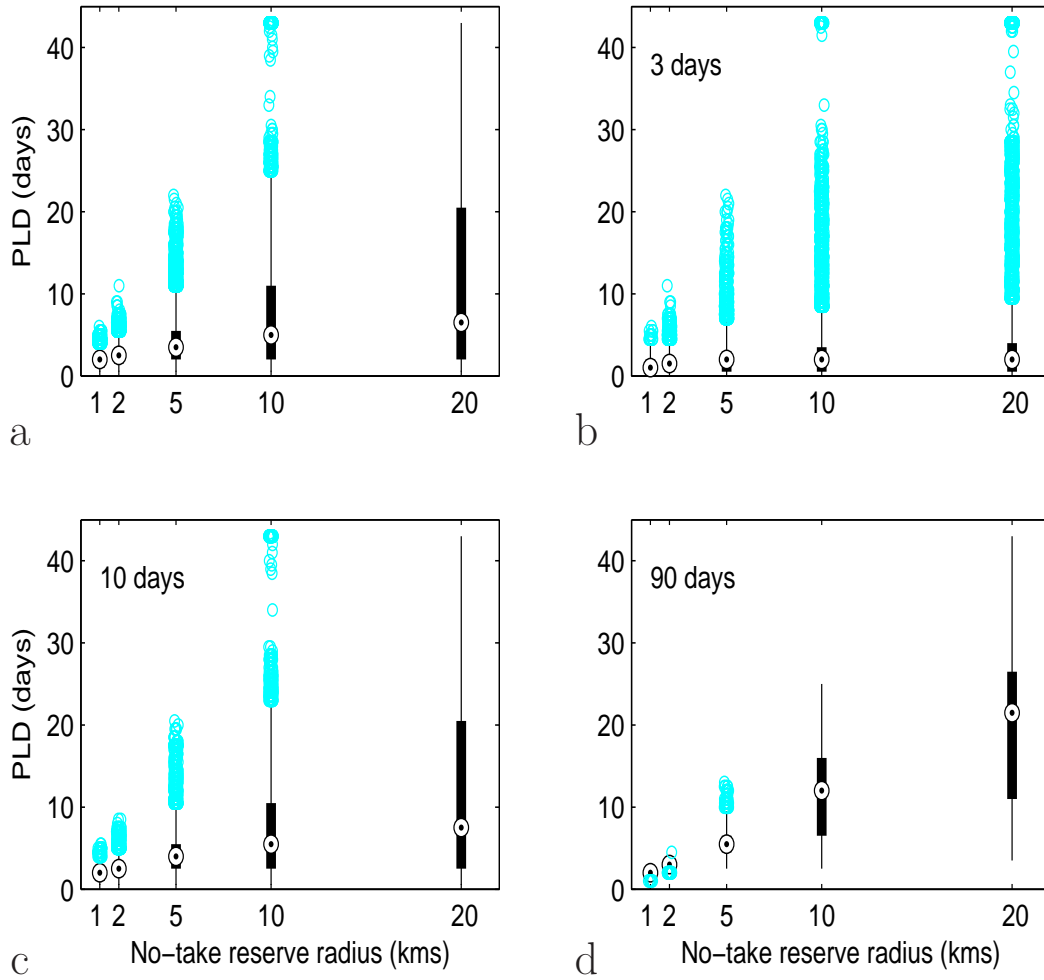


Fig. 4: Boxplots of shortest non-persistent Planktonic larval duration (PLD_{SNP}) between January and June (in 2004 and 2006) versus no-take reserve radius for four spawning durations of (a) 3 days, (b) 10 days, (c) 30 days and (d) 90 days, whatever the reserve locations along the Gulf of Lions (see Figure 1).

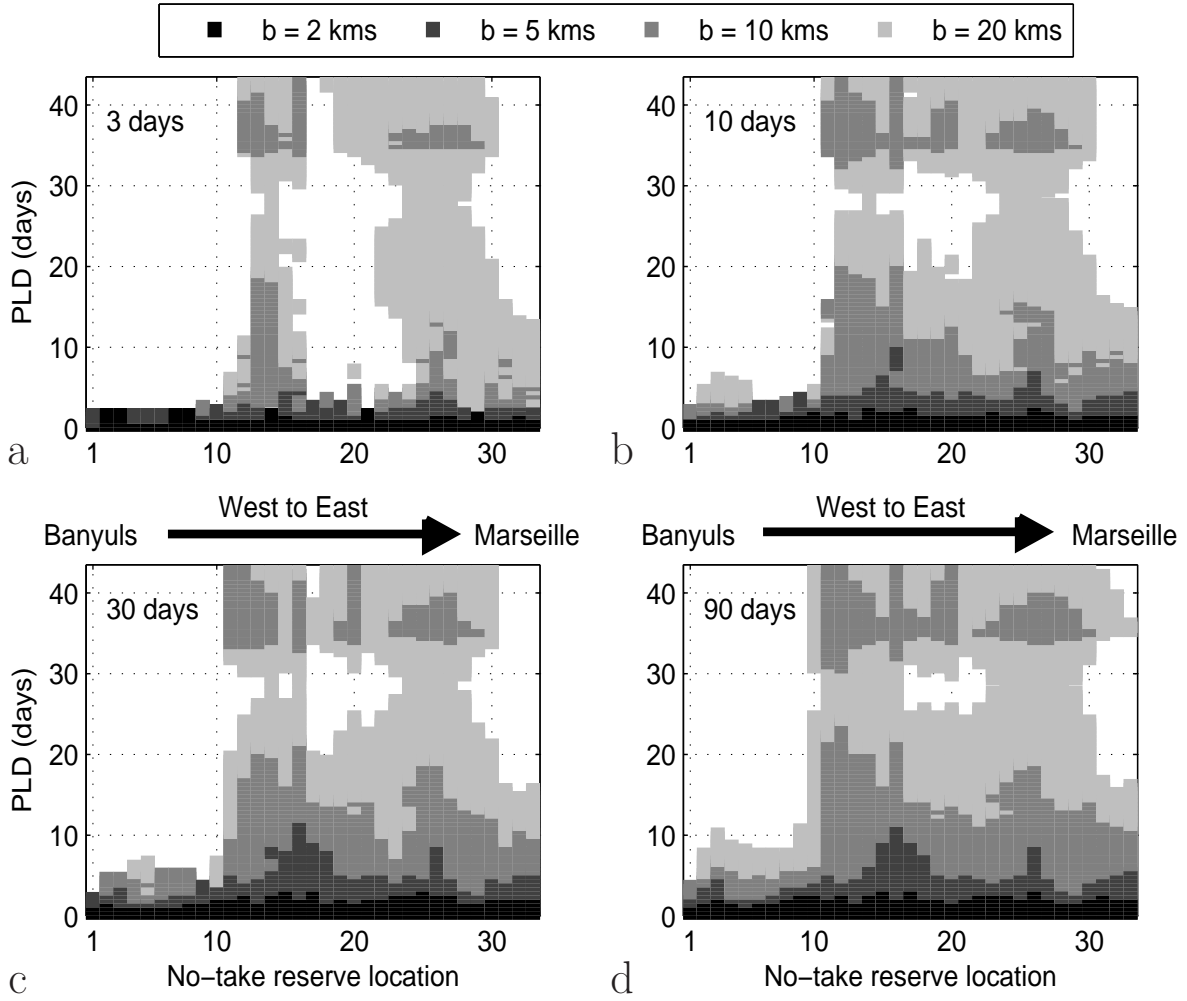


Fig. 5: *Persistent PLDs (see definition in the text, displayed with grey shading) between January and June 2004 within no-take reserves of increasing radius b from 2 kms to 20 kms (see greyscale on plot) along the Gulf of Lions and for four spawning durations of (a) 3 days, (b) 10 days, (c) 30 days and (d) 90 days. No-take reserves were centered on the 33 spawning locations shown on Figure 1 and numbered from the west (Banyuls) to the East (Marseille).*

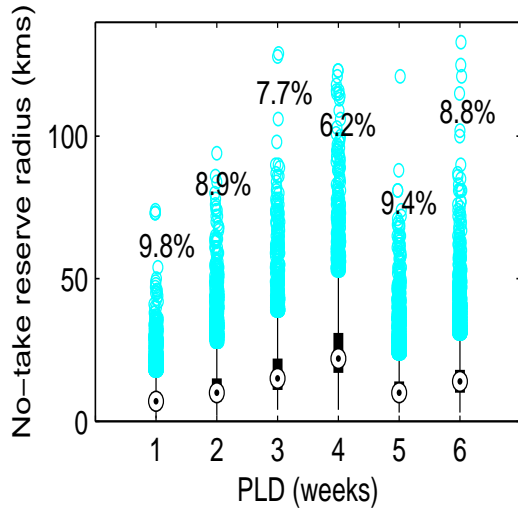


Fig. 6: Boxplots of minimum radius of sustainable no-take reserve when it could be defined versus Planktonic larval duration (PLD) whatever the spawning duration between January and June (2004 and 2006) and the reserve locations along the Gulf of Lions (see Figure 1). The proportion of spawning periods for which a sustainable no-take reserve could be defined is reported above each boxplot.

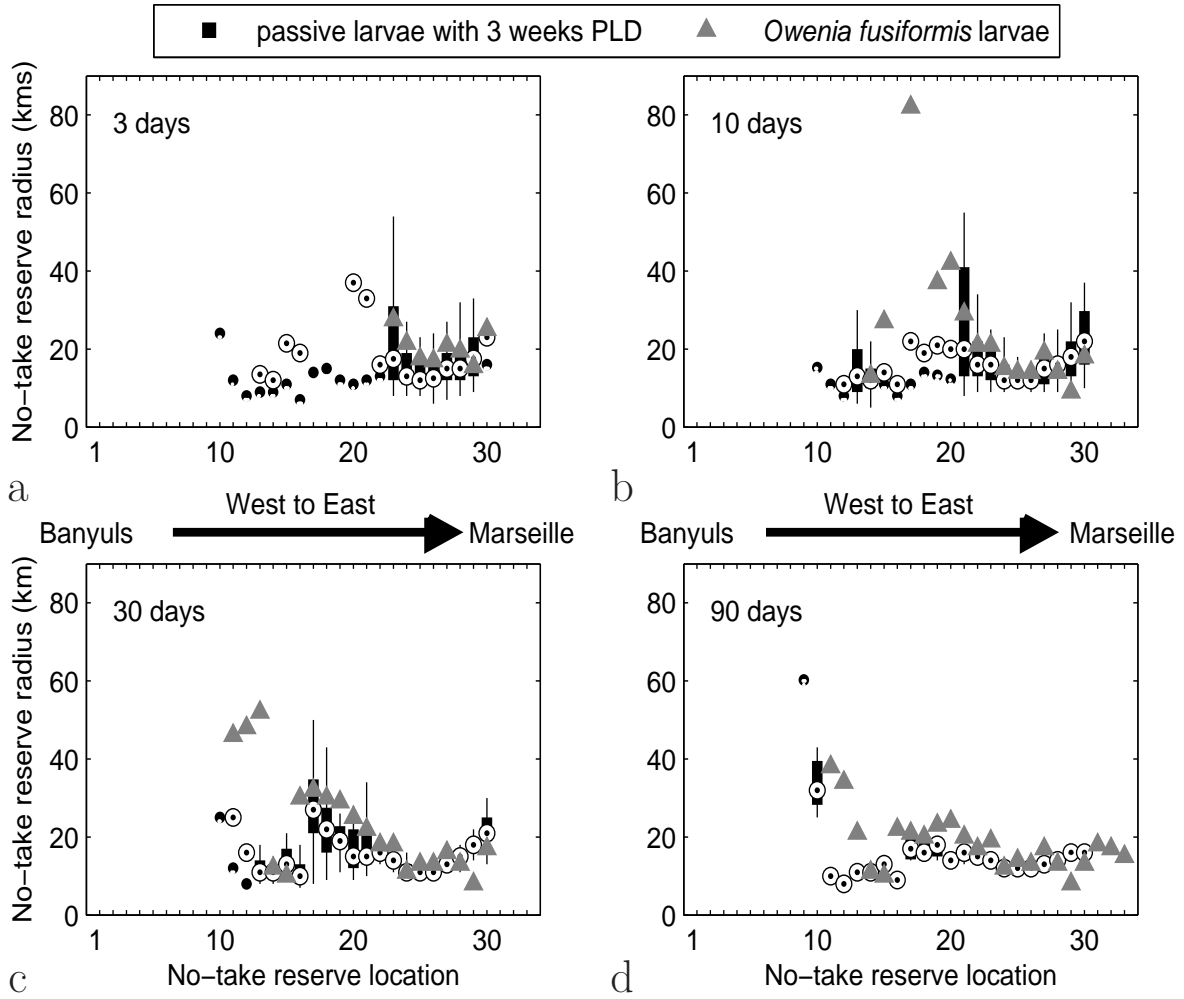


Fig. 7: Boxplots of minimum radius of sustainable no-take reserve versus no-take reserve location computed for four spawning durations of (a) 3 days, (b) 10 days, (c) 30 days and (d) 90 days between January and June 2004 for a neutrally buoyant passive larvae and *Owenia fusiformis* larvae (both 3 weeks PLD). No-take reserves were centered on the 33 spawning locations shown on Figure 1 and numbered from the west (Banyuls) to the East (Marseille).

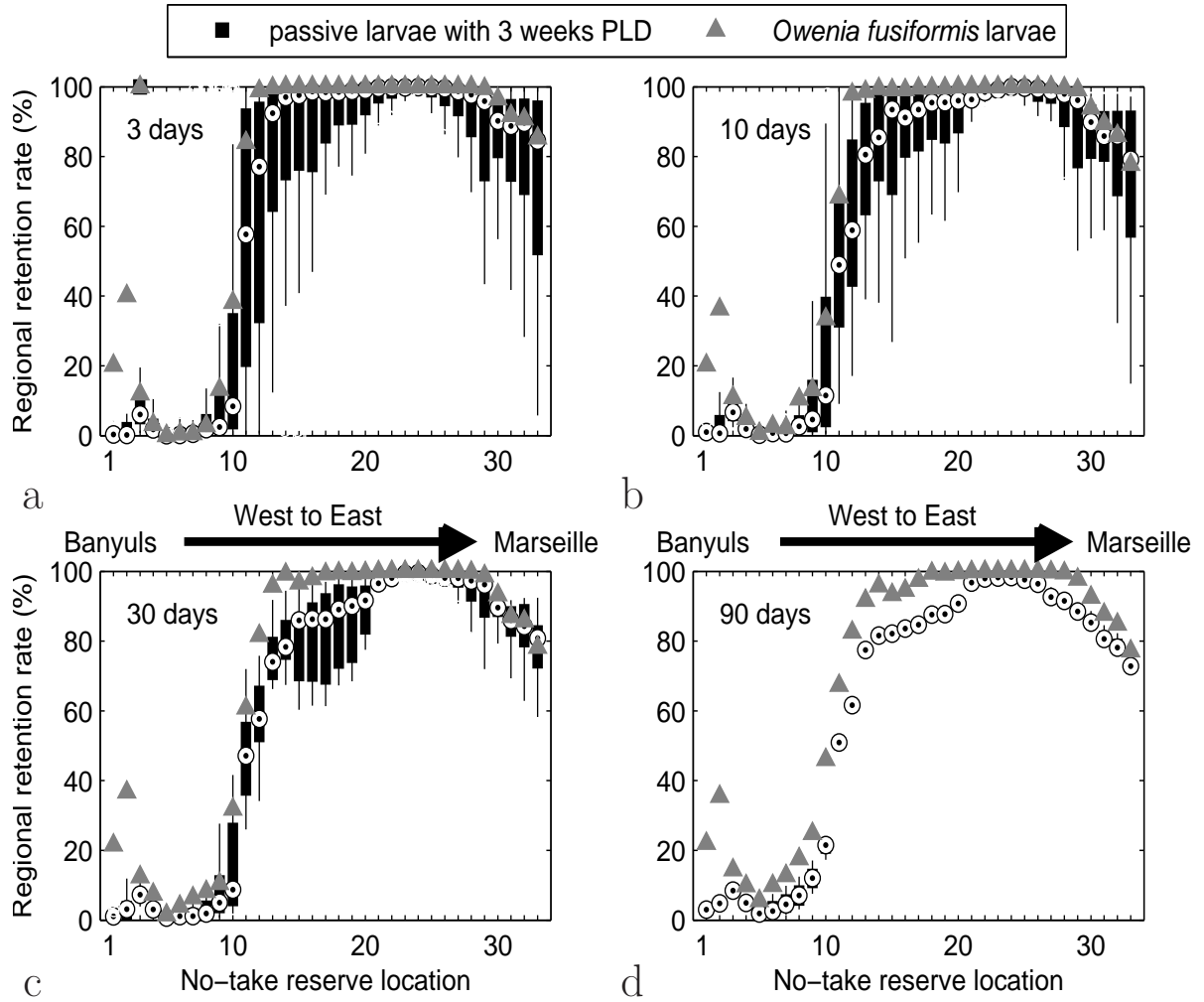


Fig. 8: Boxplots of regional retention rate versus no-take reserve locations computed for four spawning durations of (a) 3 days, (b) 10 days, (c) 30 days and (d) 90 days between January and June 2004 for a neutrally buoyant passive larvae and *Owenia fusiformis* larvae (both 3 weeks PLD). No-take reserves were centered on the 33 spawning locations shown on Figure 1 and numbered from the west (Banyuls) to the East (Marseille).