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Modeling larval dispersal for the gilthead seabream in the northwestern Mediterranean Sea

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Abstract

To investigate dispersal and connectivity between spawning and lagoon nursery habitats of the
15 gilthead seabream, *Sparus aurata*, in the Gulf of Lions (northwestern Mediterranean), we modeled
the potential transport of the species' larvae between its supposed main spawning site in the region
(the Planier Island) and two of its main local nursery areas (the coastal lagoons of Thau and Salses-
Leucate). Passive larval drift simulations using a dispersal biophysical model showed a large
variability in the possible trajectories from spawning to nursery areas and in the predicted ages for
20 larvae arrival on the two nursery sites. The most common ages at arrival obtained in the simulations
(20-60 days) are broadly consistent with previous modeling studies but contrast with the actual ages
of the *S. aurata* post-larvae collected in 2016 and 2017 at time of the lagoon entrances (60-90 days,
from otolith readings). The period between 25 and 70 days being critical for gilthead seabream
larvae to acquire sufficient swimming, osmoregulatory, and olfactory abilities to enter coastal
25 lagoons, we argue that ontogenic development plays a crucial role in the transport and local

retention of *S. aurata* larvae in the studied region, explaining the discrepancy between simulation results and observed data.

Keywords

30 *Sparus aurata*, Gulf of Lions, Fish, Larvae, Models-hydrodynamic, Biophysical model,
Connectivity, Otolith

1. Introduction

Dispersal is the process by which living organisms expand actively or passively the space or range
35 where they live and is one of the fundamental life-history traits affecting the dynamics of spatially
structured populations (Cote et al., 2010). Collecting information on dispersal patterns at the
population level is critical not only in terms of basic ecological knowledge, but also for
management issues such as marine spatial planning (Costello et al., 2010; Grüss et al., 2011; Di
Franco et al., 2012; Magris et al., 2014). The identification of fish spawning and nursery habitats is
40 equally critical to marine population management and conservation (Erisman et al., 2017). When
spawning and nursery areas are distinct, the dispersal of individuals from the former to the latter is
referred to as connectivity. Connectivity is defined as “the exchange of individuals among
geographically separated subpopulations” (Cowen et al., 2007) and it is “often measured at some
point after settlement” (Pineda et al., 2007). Marine population connectivity is an area of active
45 research (Bryan-Brown et al., 2017) and is best assessed using multiple, complementary approaches
(Levin, 2006; Cowen and Sponaugle, 2009; Leis et al., 2011) in order to encompass the complexity
(Pineda et al., 2009) and uncertainty (Kaplan et al., 2017; Nolasco et al., 2018) of the larval life.

The overarching context of this work is to investigate the dispersal and connectivity between
50 spawning and lagoon nursery habitats of gilthead seabream (*Sparus aurata*) in the Gulf of Lions
(GoL), in the northwestern Mediterranean Sea. The GoL is the biggest continental shelf of the

northwestern Mediterranean basin. It stretches from Marseille to the Creus cape and has a semicircular shape with an area of 250 km from East to West and 150 km from North to South and an average depth of 90 m (Millot, 1990). Except for the area directly influenced by the Rhône river plume, the GoL is mainly oligotrophic (Lochet and Leveau, 1990). However, its coastline is punctuated by a chain of highly productive estuarine lagoons, many of which are recurrently used as nursery sites by marine fish species, including the gilthead seabream (Mercier et al., 2012; Tournois et al., 2017). This is a marine and brackish water finfish distributed along the coasts of the northeastern Atlantic Ocean and the Mediterranean Sea. It has been economically important since the Roman Empire, and has undergone a drastic increase in aquaculture production in Mediterranean countries during the last few decades. It is also one of the most important commercial species for the French artisanal fishery with an estimate of 690 t landed in 2018, representing almost 19 M€ of income for this fishing sector (Weiss et al., 2019).

In the GoL, almost 85% of the adult *Sparus aurata* captured have spent most of their first year growing in a local lagoon (Tournois et al., 2017). Seabream post-larvae enter the lagoons in the spring (Lasserre, 1976) to feed and grow during the warm season (Escalas et al., 2015; Isnard et al., 2015). Then, at the beginning of the reproductive period in late autumn, yearly individuals migrate back to the sea to avoid cold waters until the next feeding season (Audouin, 1962; Lasserre, 1976; Zohar et al., 1978; Mosconi and Chauvet, 1990). Although the number and the exact location of the spawning sites for the gilthead seabream are still unknown in the area, the mature individuals that exit the Thau lagoon in autumn have been reported to migrate massively towards the East (Audouin, 1962; Lasserre, 1976), the last ripe females being captured in front of the Rhône river delta in October (Lasserre, 1976). Then *S. aurata* adults leave the shallow coastal zone of the GoL, where they massively reappear only in March. Because aggregations of ripe females are repeatedly observed in the winter around the Planier Island, off Marseille (i.e. further East than the Rhône river mouth), we currently consider this area to be the main potential source of *S. aurata* larvae for the

coastal lagoons of the GoL. However, the connectivity between this spawning site and the local lagoons used as nursery areas by the species still has to be assessed.

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Three-dimensional explicit biophysical modeling of larval dispersal is a good way to investigate the respective roles of physical and biological drivers on larval connectivity (Miller et al., 2006) and their influence on marine populations (Daewel et al., 2008). Biophysical models to describe the larval drift in the Mediterranean were scarce ten years ago (Calò et al., 2013) but have flourished since then (e.g., Andrello et al., 2013; Catalan et al., 2013; Koeck et al., 2015; Ospina-Alvarez et al., 2015; Bray et al., 2017; Calò et al., 2018; Faillettaz et al., 2018). Numerical studies focusing on the connectivity between coastal lagoons and the adjacent sea areas have also appeared recently (Ghezze et al., 2015; Fiandrino et al., 2017; Pérez-Ruzafa et al., 2019). However, no biophysical model of larval dispersal has been applied to the gilthead seabream in the Mediterranean Sea so far. The main objectives of this study were to set up such a model in the GoL and to confront its results on the spatio-temporal variation in the duration and success of dispersal at sea with actual data on the spawning dates and ages of *Sparus aurata* post-larvae captured at the time of their spring arrival at lagoon entrance. This investigation of the value of three-dimensional biophysical modeling for predicting larval connectivity patterns for the species in the GoL is a prerequisite to its use to help locating the species' regional spawning areas, with potentially high implications for local marine spatial planning and coastal lagoon management.

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2. Material and methods

For this first modeling attempt, we chose to focus on the potential transport of *S. aurata* larvae between the species supposed main spawning site in the GoL, the Planier Island, and two of its main local nursery areas: the coastal lagoons of Thau and Salses-Leucate (Isnard et al., 2015; Tournois et al., 2017; Figure 1). The trajectories followed by the passive larvae dispersing from the spawning site at sea were modeled for four consecutive years using a Lagrangian tool coupled to a

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hydrodynamic model driven by realistic meteorological forcings. The results obtained were then
105 confronted to the biological information gathered through the structural analysis of the otoliths of
local seabream post-larvae collected in both lagoons.

2.1. Study area

Like the whole northwestern Mediterranean Sea, the GoL hydrodynamics is mainly influenced by
110 the two dominant winds (Mistral and Tramontane), by the inputs of the Rhône river (Naudin et al.,
1997) and by the Mediterranean Northern Current (Barrier et al., 2016). The Mistral is a North wind
coming from the Rhône river valley and blowing from the GoL eastern side. The Tramontane comes
from the North too but blows in the GoL western side (Millot, 1990). The main source of freshwater
inputs to the area is the Rhône river discharge, which varies from 500 to 10,000 m³ s⁻¹, with a 1,715
115 m³ s⁻¹ annual mean flow. For the last 20 years, the highest monthly mean flow (2,355 m³ s⁻¹)
occurred in February and the lowest (1,047 m³ s⁻¹) in August (Naudin et al., 1997). The Northern (or
Liguro-Provencal) Current (NC) is part of the large-scale ocean circulation of the Mediterranean
Sea. It is the northern branch of the cyclonic gyre circulation occurring in the northwestern
Mediterranean (Millot, 1999). This current is, at first order, in geostrophic balance, and globally
120 flows westwards along the continental shelf, with a seasonal modulation in current amplitude and
eddy activity (Guihou et al., 2013). The NC is known to often act as a barrier between the fresh
nutrient-rich coastal waters and the salty oligotrophic offshore waters (Ourmières et al., 2011). As
evidenced in observations and numerical modeling, the NC occasionally penetrates within the GoL
(Barrier et al., 2016), causing drastic changes in the biogeochemistry and in turn in the primary
125 productivity along its shelf (Ross et al., 2016).

The main source of larvae retained for this study, the Planier Island, is located at about 8.6 km from
the south-west coast of the city of Marseille (Figure 1). This rocky islet has a very small area (2 ha)
and its altitude is not exceeding 5 m. It is worth noting that this island is located on the episodic NC

130 intrusion path. The two arrival sites retained for *S. aurata* larvae, the Thau and Salses-Leucate lagoons, have similar surface areas, environmental conditions, and number of connections with the sea. However, otholith microchemical analyses revealed that the two lagoons have contrasted importance for the multi-annual renewal of the local population: Thau is the lagoon nursery contributing most to the local exploited stock (18%) while the contribution of Salses-Leucate (7%)
135 is among the lowest in the area (Mercier et al., 2012; Tournois et al., 2017).

2.2. Hydrodynamic model

High resolution simulations from the NEMO-GLAZUR64 configuration performed by Ourmières et al. (2011) over the GoL were used to model local hydrodynamic circulation at sea over the years of
140 interest (2014-2017). GLAZUR64 is based on the primitive equation ocean circulation model of the “Nucleus for European Modelling of the Ocean” (NEMO) modeling framework (Madec and the NEMO team, 2016). The resolution on the horizontal is $1/64^\circ$ (about 1.3 km) on a regular grid with 130 vertical z-levels. The vertical resolution ranges from 1 m near the surface to 30 m near the bottom. Ocean boundary conditions used to force the model came from the NEMO-based
145 operational configuration developed by MERCATOR-OCEAN (<http://www.mercator-ocean.fr>) PSY2V4R1.

Daily averages of the PSY2V4R1 velocity and mass fields were used at the GLAZUR64 open boundaries, and the typical damping coefficients for inflow and outflows adjusted consequently to 1
150 and 10 days, respectively (Guihou et al., 2013). Surface boundary conditions used to force the simulation were retrieved from the Météo-France operational regional model ARPEGE, with a horizontal resolution of around 9.5 by 9.5 km and files provided every 3 h. This atmospheric model features data assimilation and state-of-the-art atmospheric physics (Fischer et al., 2005).

155 **2.3. Larval dispersal model**

Water velocity fields provided by daily stored simulations of GLAZUR64 over the period 2014-2017 were used to simulate the larval dispersal of gilthead seabream in the GoL. We used the Lagrangian tool Ichthyop (<http://www.ichthyop.org/>), an individual-based model (IBM) designed to study the effects of physical and biological factors on the dynamics of fish eggs and larvae (Lett et al., 2008). In the IBM, the velocity fields were interpolated in space to provide values at any individual location, and in time to feed the IBM time step (here taken as 15 min). Simulations consisted in releasing randomly 5,000 particles representing virtual larvae in the neighborhood of the Planier Island. For this, the release zone was defined as a cylinder of 5 km radius centered on the Planier Island (43.198855°N, 5.23064°E) and extending from 0 to 20 m depth (other depth range tested: 80 to 100 m). Particle releases for each year were scheduled every 5 days during the main local spawning season for *S. aurata*, from November to February (Audouin, 1962; Lasserre, 1976), and their locations in the GoL were subsequently tracked during 120 days (i.e. four months), the maximum duration for seabream larval life in the area (Isnard et al., 2015). We covered three consecutive reproductive seasons fully (Nov. 2014 to Feb. 2015, Nov. 2015 to Feb. 2016, and Nov. 2016 to Feb. 2017) and the last two months of the 2013-2014 reproductive season (Jan. to Feb. 2014). Overall we released $5,000 * 3.5 \text{ (years)} * 4 \text{ (months)} * 6 \text{ (releases per month)} = 420,000$ particles.

Ichthyop outputs files gathered all possible larval locations for every hour within the 120-days of simulated dispersal. From these, we plotted the larval dispersal trajectories and histograms of ages for larvae reaching the Thau or Salses-Leucate lagoons. In the simulations, virtual larvae were considered to have reached the Thau or the Salses-Leucate lagoon when they arrived at a minimum distance of 5 km from their main connection with the sea, the “Port des Quilles” (43.3920126°N, 3.665203°E) or the “Port Leucate” (42.872259°N, 3.049062°E) harbor, respectively (Figure 1). An additional run of simulations was also made with a minimum distance of 10 km to both lagoon

entrances for larval arrival. In each case, the number of larvae reaching each lagoon along the whole simulated period was computed.

2.4. Oceanographic drifters

185 To confront simulated results with actual oceanographic data, we used the Global Drifter Program (GDP) database (<https://www.aoml.noaa.gov/phod/gdp/>) and the Coriolis database (<http://www.coriolis.eu.org>) to find oceanographic drifters trajectories passing within the GoL. We found one such drifter in each database, drifter id 2442647 from the GDP, an Argos-2 Surface Velocity Profiler (SVP) with a drogue centered at 15 m released October 6th 2005, and drifter id
190 61794 from the Coriolis database, another SVP released October 28th 2014.

2.5. Otolith data

To confront simulated results with actual biological data, *Sparus aurata* post-larvae were sampled at the time of their first arrival at the entrance of local coastal lagoons (in February-March), for two
195 successive years (in 2016 and 2017). The right sagittal otoliths of these individuals were extracted, washed and prepared for daily ring counts following Tomás and Panfili (2000). They were embedded in Polyester resin and transversal sections of approximately 1 mm, including the central nucleus, were made with a precision saw (Buehler, Isomet 1000). Otolith cuts were polished to
200 approximately 10 µm depth with the nucleus exposed on the surface. These sections were photographed with a digital camera system (Olympus ProgRes C5) and ProRes Capture pro 2.5 software linked to a microscope (Olympus BX41, x400). All pictures were imported into Perfect Image software.

Examination of the otolith sections revealed multiple concentric rings from the nucleus to the edge,
205 clearly visible on all otoliths. In accordance with previous literature validating their daily deposition (Morales-Nin et al., 1995; Isnard et al., 2015), these increments were counted to assess fish age (in

days). For this, each otolith was read twice by two independent readers, from the first visible increment corresponding to mouth opening, 3 days after hatching (Bodinier et al., 2010) to the edge of otolith, namely the capture date. Otoliths were read again if the two estimated ages in days
210 differed by more than 5%, to achieve a consensual age estimate between the two readers. The two separate readings of otolith daily increments were compared by paired t-tests after checking normality and homoscedasticity and when there were non-significant differences, the mean of the two readings was used. This allowed estimation of the age (in days) of the post-larvae at their arrival at the lagoon entrances and back-calculation of the date of spawning for each individual,
215 with an average potential error in otolith reading of ± 3.2 days.

3. Results

3.1. Larval dispersal model

Among the 420,000 virtual gilthead seabream larvae released around the Planier Island (5,000 for
220 84 dates), 13,531 reached a distance < 5 km of the Thau lagoon entrance “Port des Quilles” at some time along their 120-day drift, i.e. a mean transport success of 3.2%. Transport success varied greatly with release date, though, ranging from 0% for five dates, all in November (2014/11/05, 2015/11/15, 2015/11/20, 2015/11/25, 2016/11/10), to 31.6% for a release on 2015/02/25 (Figure 2, standard deviation SD = 4.8%, median = 1.7%, and interquartile range (IQR) = 3.2%). There were
225 two periods of one month, from 2015/11/05 to 2015/11/30 and from 2016/12/05 to 2017/01/05, when particles releases led to transport successes constantly below 0.5%. Conversely, release periods with high subsequent transport success were short (< 5 days) irrespective of the year, and represented by only a single release date (e.g. 2016/11/25 and 2017/01/25, Figure 2).

230 Virtual larvae from the Planier Island followed a great variety of trajectories to reach the Thau lagoon along the simulated period (Figure 3). There were direct transport trajectories following the coastline and generally reaching “Port des Quilles” quickly (within 10–20 days), either from the

East or from the West (Figure 3a). We also found longer transport trajectories entering the GoL from mid-shelf (Figure 3b), and a few trajectories following the continental shelf offshore before entering the GoL coastal zone from its western side (Figure 3c). There were also many indirect trajectories, e.g. some following the coast to pass offshore the “Port des Quilles” toward the western side of the GoL, and then crossed back the GoL to arrive to “Port des Quilles” from mid-shelf, or larvae entering and leaving the GoL several times (Figure 3d). Overall, possible larval dispersal routes from the Planier Island to “Port des Quilles” spread over the entire GoL, but were mostly concentrated along the coast, with most larvae reaching the lagoon entrance from the West, an unexpected result (Figure 4).

The age at which the virtual larvae reached “Port des Quilles” in the simulations was also very variable, ranging from 8 to 120 days (the total duration of the simulations). However, a clear mode was observed between 10 and 60 days (Figure 5, mean = 46.7 days, SD = 23.9 days, median = 41.2 days, IQR = 31.2 days).

Among the same 420,000 virtual larvae, 23,060 reached a distance < 5 km to the Salses-Leucate lagoon entrance “Port Leucate”, i.e., a mean transport success of 5.5%. Unexpectedly, transport success to “Port Leucate” was therefore higher, on average, than to “Port des Quilles”. Like for “Port des Quilles”, transport success to “Port Leucate” was very variable according to the release date (Figure 6a, min = 0%, max = 45.7%, SD = 8.1%, median = 3.4%, IQR = 4.8%). Lowest and highest transport successes occurred generally for the same release dates for the two lagoons (Figure 2, Figure 6a). As for Thau, virtual larvae were mostly transported to the Salses-Leucate lagoon by currents following the coastline, but they generally reached “Port Leucate” from the East (Figure 6b). The age distribution of the virtual larvae reaching “Port Leucate” was bimodal, with modes between 20–30 and 50–60 days (Figure 6c, min = 10.5 days, max = 120 days, mean = 50.9 days, SD = 24.6 days, median = 49.6 days, IQR = 37.2 days). Interestingly, the 30–40 days peak in

the age distribution of larvae reaching “Port des Quilles” (Figure 5) was a trough in the age
260 distribution of larvae reaching “Port Leucate” (Figure 6c).

Among the 420,000 virtual dispersal trajectories simulated for this work, only 4,080 (< 1%) reached
distances < 5 km to both “Port Leucate” and “Port des Quilles” within the 120 days of larval drift
modeling. Most of these trajectories (4,010) reached “Port des Quilles” before “Port Leucate”,
265 spending on average 18.5 days at sea traveling between the two sites. Unsurprisingly, increasing the
distance area around the lagoon main entrances, from 5 to 10 km, for considering larval arrival to
both lagoons, increased the transport success of virtual larvae to 9.3% and 13.0% on average for
“Port des Quilles” and “Port Leucate”, respectively. However, it also changed the age distribution of
larvae reaching “Port des Quilles”, which tended to become bimodal with peaks at age 10–20 and
270 30–40 days (Appendix Figure Aa), while for larvae reaching “Port Leucate” it remained unchanged
with two peaks at age 20–30 and 50–60 days (Appendix Figure Ab). Conversely, releasing particles
deeper, i.e. at 80-100 m instead of 0-20 m, decreased the transport success of virtual larvae to 0.5%
and 1.1% on average for “Port des Quilles” and “Port Leucate”, respectively, and delayed the ages
at which they reached the lagoon entries by ~10 days (Appendix Figure Bb).

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3.2. Oceanographic drifters

The trajectory followed within the GoL by the oceanographic drifter 2442647 from the GDP is
shown in Figure 1 with locations every 6 hours. It passed ~ 20 km south of the Planier Island then
drifted westwards off the coast passing ~ 30 km from “Port des Quilles” after ~ 5 days and ~ 20 km
280 from “Port Leucate” after ~ 8 days, before leaving the GoL from its southwestern part after ~ 14
days. The trajectory of Coriolis drifter 61794 is shown in Figure 1 with locations every 1/2 hour. It
came very close to the Planier Island then drifted westwards passing ~ 10 km from “Port des
Quilles” after ~ 14 days and eventually drifted southwards along the coast, passing very close to
“Port Leucate” after ~ 24 days.

3.3. Otolith data

Otolith reading (N = 145, Appendix Table) revealed large variation in the age of the *S. aurata* post-larvae collected at their time of first arrival at lagoon entrances (in February-March for both 2016 and 2017, Figure 7). However, the minimum and maximum ages observed were of 60 days (for a post-larva captured in mid-February 2016) and 121 days (for a post-larva captured in late March 2017), respectively. Moreover, most of the post-larvae collected (88%) had ages between 60 and 90 days (Figure 7), including 80% of the individuals sampled at their arrival in Thau and 100% of those caught at their arrival in Salses-Leucate. Interestingly, the oldest larvae were all caught in March (Figure 7), irrespective of the year or the lagoon, suggesting similar spawning dates for all fish, irrespective of their final age at lagoon entrance. As a matter of fact, estimated spawning dates for all lagoons and both sampling years ranged between November 23rd (for an individual caught in 2015) and December 29th (for an individual caught in 2017), with a majority (> 51%) of fish spawned in early December (1–15th) irrespective of the year of capture (Figure 8). However, small differences in fish spawning dates could be observed between the two sampling years. Thus, the percentage of fish spawned in November was close to zero (2 individuals only) in the post-larvae collected in 2016, but reached 14% in those captured in 2017, especially at the Salses-Leucate entrance (29%). Conversely, the percentage of post-larvae spawned after December 20th was greater in the fish collected in 2016 (14%) than in those collected in 2017 (6.5%). This suggests that the peak of spawning of *S. aurata* and/or the most favorable time for the dispersal of its larvae at sea occurred later in 2015-16 than in 2016-17, but with no major influence on fish age at lagoon entrance.

4. Discussion

Information on the location of fish spawning grounds and the scale of dispersal towards their

310 nursery areas is crucially important for elucidating connectivity patterns between populations, and
for providing the optimal background knowledge in order to design efficient protection and
management strategies (Fogarty and Botsford, 2007; Erisman et al., 2017). The method used here
combining model simulations with information on otolith age-reading of gilthead seabream larvae
in the Gulf of Lions (GoL) is a first attempt to fill information gaps on the species potential
315 spawning areas, larval drift duration, larval dispersal pathways, and age at recruitment.

The large variability in simulated trajectories found for the virtual larvae transported from the
Planier Island to “Port des Quilles” corresponds to different well-documented conditions. Coastal
simulated trajectories (Figure 3a) are consistent with the trajectories observed for the two
320 oceanographic drifters (Figure 1) and can correspond to two types of events, either a classical
Northern Current (NC) intrusion on the shelf (for causes and consequences, see Barrier et al., 2016),
or a current induced by strong easterlies, pushing the Rhône river plume to the coast, creating a
light water current along the GoL coast. Mid-shelf trajectories (Figure 3b) also correspond to
classical NC intrusions. This place of the shelf is favorable to water intrusion into the GoL, as
325 shown by hydrological data, drifters and models (Petrenko et al., 2005; Leredde et al., 2007;
Poulain et al., 2012). Some intrusions are forced by easterlies, through either Ekman transport or a
shoreward displacement of the NC. Both the Mistral and Tramontane winds may further favor
intrusions through the associated positive wind stress curl. This curl would provide a source of
vorticity to the NC that may drive intrusions (Gatti, 2008). In the eastern part of GoL, intrusions are
330 also likely to occur after the relaxation of upwelling-favourable winds, as shown by Millot and
Wald (1980). When the wind relaxes, the frontal zone between the cold upwelled waters and warm
water originating from the NC tends to move northwestward and to penetrate over the shelf. Using
analytical model and numerical simulations, Echevin et al. (2003) suggested that Ekman transport
associated with south-easterlies induces downwelling, which in turn generates a westward coastal
335 current that transports NC waters onto the shelf. There are also meanders and eddies allowing

waters to flow into the shelf. Estournel et al. (2003) showed an anticyclonic eddy located at the center of the GoL continental shelf. On its eastern part, eddies are generated by local winds (Allou et al., 2010). Backloops identified on many of our simulated trajectories reaching “Port des Quilles” from the West are likely induced by the presence of an eddy preventing the water to flow southwards, called the Latex eddy (Hu et al., 2011; Petrenko et al., 2017). Trajectories entering from the western side of the GoL (Figure 3c) can be due to a current flowing northwards from the Creus cape when the Tramontane blows homogeneously over the GoL (Petrenko et al., 2008), or are possibly trapped by the Latex eddy onshore branch (Hu et al., 2011; Petrenko et al., 2017).

The high diversity in the hydrodynamic conditions that larvae face in the GoL explains the large variability obtained in our simulations for their transport success to the vicinity of “Port des Quilles” (Figure 2) or “Port Leucate” (Figure 6a), as well as for their age at arrival (Figure 5, Figure 6c). The most common ages predicted for larval arrival (20 to 60 days) are broadly consistent with previous modeling studies. Indeed, using a Lagrangian approach for the whole Mediterranean Sea based on a NEMO model configuration at $1/16^\circ$ horizontal resolution, Rossi et al. (2014) identified the GoL as a more coherent hydrodynamic province (i.e., well connected internally and with limited external exchanges) for a larval life duration of 30 days than for a duration of 60 days. Similarly, Nicolle et al.’s (2009) results using a configuration of the MARS model at 1.2 km resolution predicted residence time of 1 to 2 months for the GoL shelf waters. Possibility for diel vertical migration from 0 to 50 m in the larvae, as tested for anchovy larvae in the GoL, was not shown to significantly affect this result (Nicolle et al., 2009). Possibly, however, the resolution and forcing of the hydrodynamic models used so far may not have been sufficient to reproduce adequately small retentive coastal structures that may play a crucial role in larval retention (Briton et al., 2018). In addition, the simulated currents used are typically daily averaged, which means that a part of the information regarding the currents modulation might have been lost by the averaging process, though being important for the larvae trajectory computing (Blanke et al., 2012). With high-

resolution (200 m) and high-frequency (3 h) currents simulated with a configuration of the MARS-3D model covering the Bay of Marseille, Thibaut et al. (2016) showed that particles released around the Planier Island could reach sites located 20 km away ($\sim 15\%$ of the distance to the Thau lagoon) in 12 h under strong wind conditions.

The most common ages predicted for larval arrival at the coastal lagoons in the simulations (20 to 60 days) are also consistent with the gilthead seabream pelagic larval duration (45 days in Chaoui et al., 2009; 50 days in Franchini et al., 2012) and the ages over which the species fins develop (20 to 50 days; Chatain, 1994; Patruno et al., 1998; Moretti et al., 1999). However, they contrast with the ages actually observed in the post-larvae collected in 2016 and 2017 (60 to 90 days, Figure 7).

Endurance tests of raised gilthead seabream larvae of age 50 days showed that they could swim at a constant 12 cm s^{-1} speed during $42.2 \pm 11.1 \text{ h}$, covering a mean distance of nearly 20 km (Faria et al., 2011). The critical swimming speed of larvae of ages 58 to 96 days collected at sea was recently estimated as $10.4 \pm 1.7 \text{ cm s}^{-1}$ (Rossi et al., 2019). The individuals collected here had similar ages and therefore probably also a significant capacity of movement, which they may have used to depart from drifting currents and swim to the coast and/or to remain close to the lagoon entrances, until they have developed sufficient ability to osmoregulate and sense lagoon waters. Bodinier et al. (2010) showed that seabream larvae increase their osmoregulatory ability sharply from age 30 to 70 days. Morais et al. (2017) reported that young (< 25 days) seabream larvae had insufficient swimming capacity to response to water cues and that older larvae (25 to 57 days) were still predominantly unresponsive. Overall, ages from 25 to 70 days appear to be critical for seabream larvae to acquire sufficient swimming, osmoregulatory, and olfactory abilities to enter the coastal lagoons. The full morphological development of seabream larvae takes approximately 90 days in aquaculture (Chatain, 1994). The fact that the larvae collected at the lagoon entrances in March were generally older than those collected earlier (in February, Figure 7) suggests that they actually stayed offshore for some time once arrived in front of the lagoon entrance, possibly in order to

complete their development. It is also possible that larvae younger than 60 days did arrive at the lagoon entrances but were missed in the sampling due to their small size, or quickly died because they were not developed enough either to successfully feed on coastal prey or escape local predators.

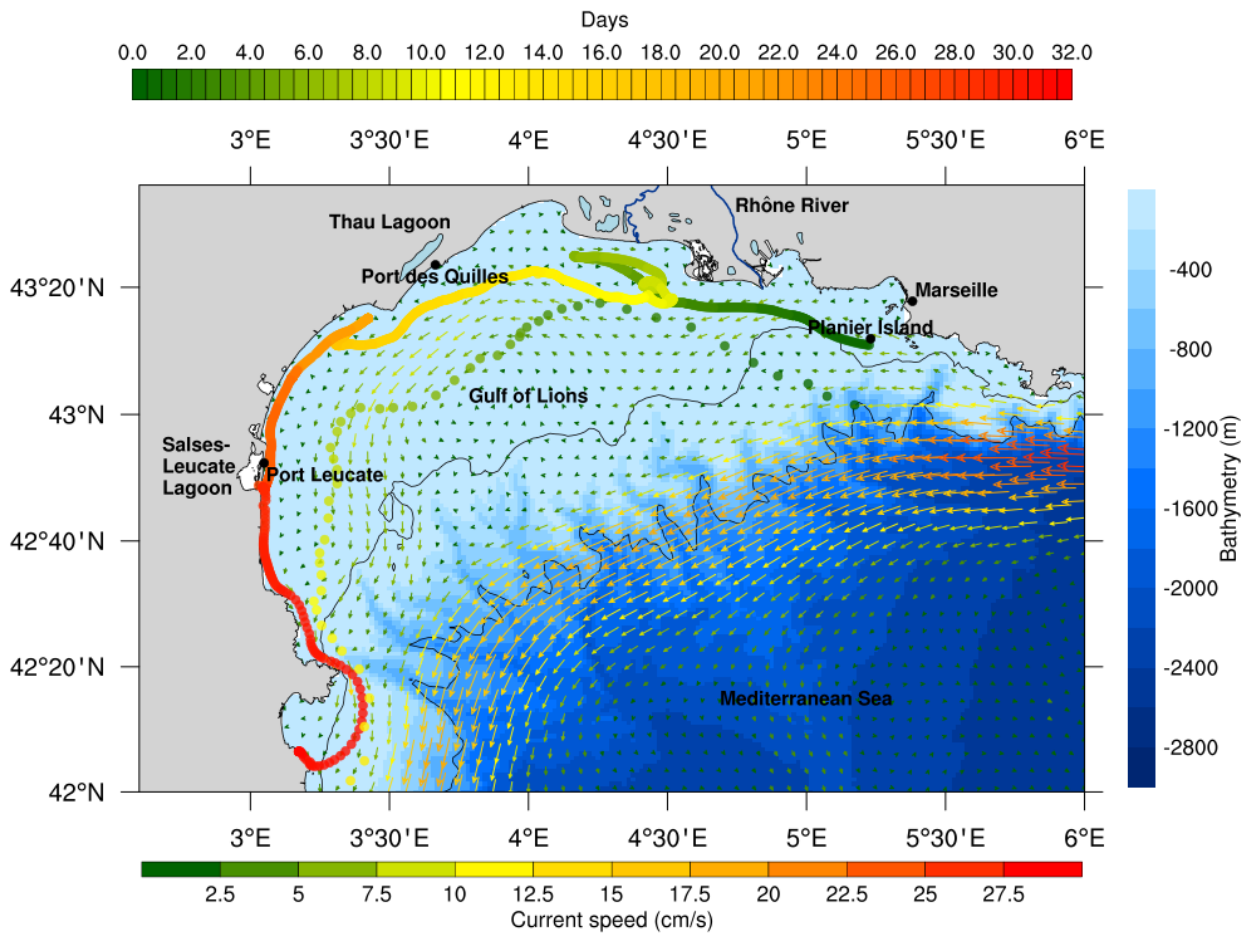
To conclude, we believe that horizontal swimming plays a critical role in the transport and retention of seabream larvae within the GoL, explaining the discrepancy between our observed data and simulation results. Recently, Faillettaz et al. (2018) showed that including shoreward swimming in their model of Sparidae larvae dispersal in the northwestern Mediterranean Sea increased the simulated coastal settlement significantly. Another explanation would be that the larvae we collected come from spawning grounds located further East than the Planier Island. Contrasting results concerning the genetic structure of the gilthead seabream in the western Mediterranean were reported, with a strong genetic differentiation obtained between samples collected from the GoL and from Algerian waters (Chaoui et al., 2009), but low levels of structure along the Italian coast (Franchini et al., 2012). Comparing samples from the GoL and the Ligurian Sea could indicate if a Ligurian origin of the GoL larvae is plausible. More broadly, there is a crucial need to better identify where the key reproduction sites of the seabream found in the coastal lagoons of the GoL are located. If biotelemetry is now widely used to study the spatial ecology of large migratory marine species (Block et al., 2011; Hussey et al., 2015), we believe that acoustic telemetry is the best approach for a small coastal migratory fish such as the gilthead seabream in order to avoid affecting its natural behavior (Forin-Wiart et al., 2019). Acoustic telemetry is widely used to study the spatial ecology of fish (Donaldson et al., 2014; Abecasis et al., 2018) and it has already helped following the movements of seabream adults within a coastal lagoon in Portugal (Abecasis and Erzini, 2008). By using a large network of hydrophones deployed at lagoon entrances along the GoL coastline as well as around expected offshore reproduction sites such as the Planier Island, and by putting acoustic tags on seabream adults while in their lagoon feeding grounds, we expect to

obtain valuable information on these fish movement from foraging areas to spawning sites in the
415 near future.

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Figures



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Figure 1: Map of the Gulf of Lions in the northwestern Mediterranean Sea showing the bathymetry (right colorbar), the current speed averaged over the period 2014-2017 and depth range 0-20 m from GLAZUR64 daily outputs (bottom colorbar), trajectories of two oceanographic drifters (top colorbar) and locations cited in the text.

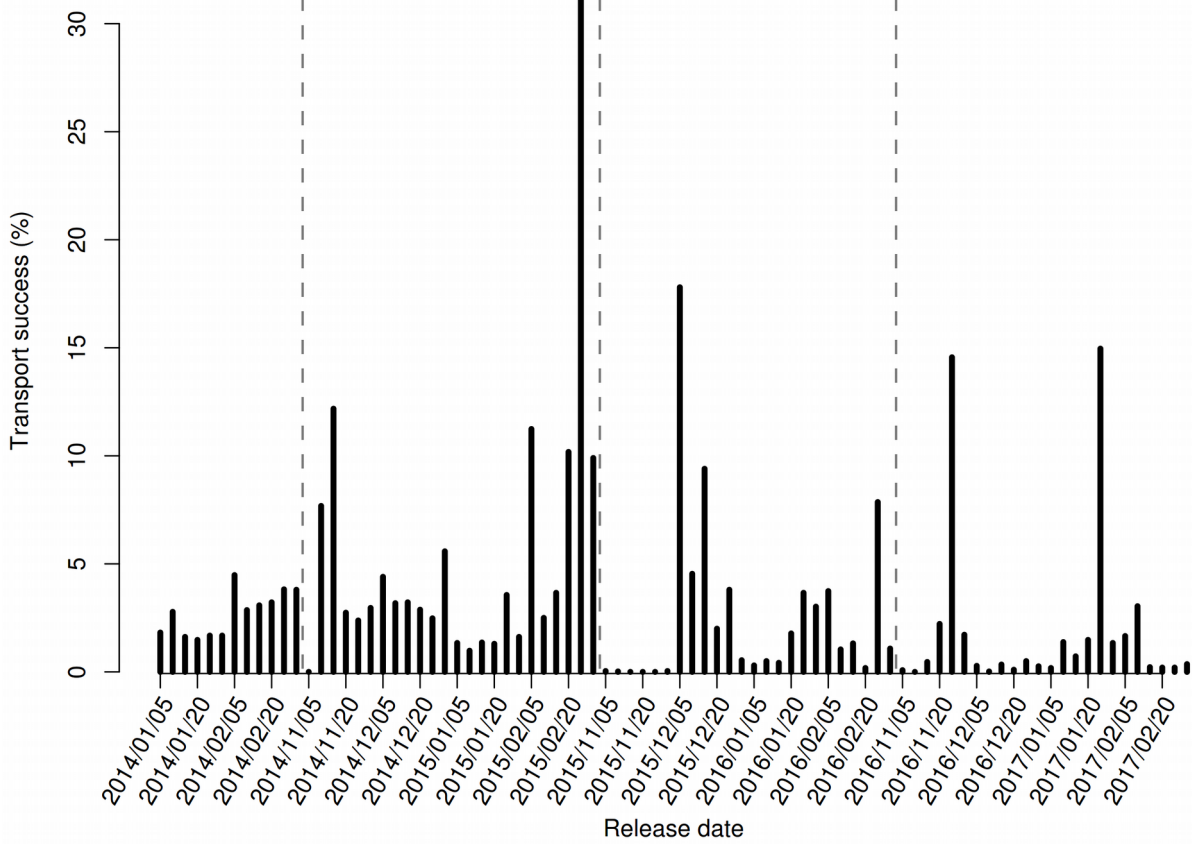
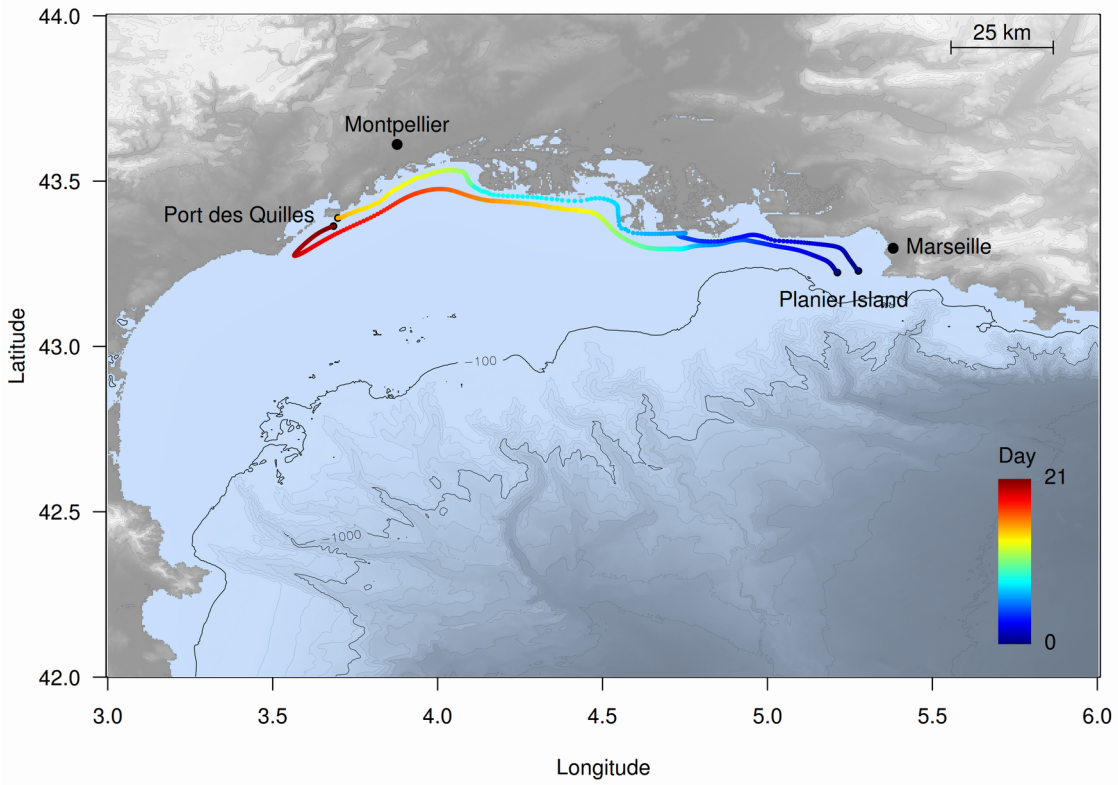
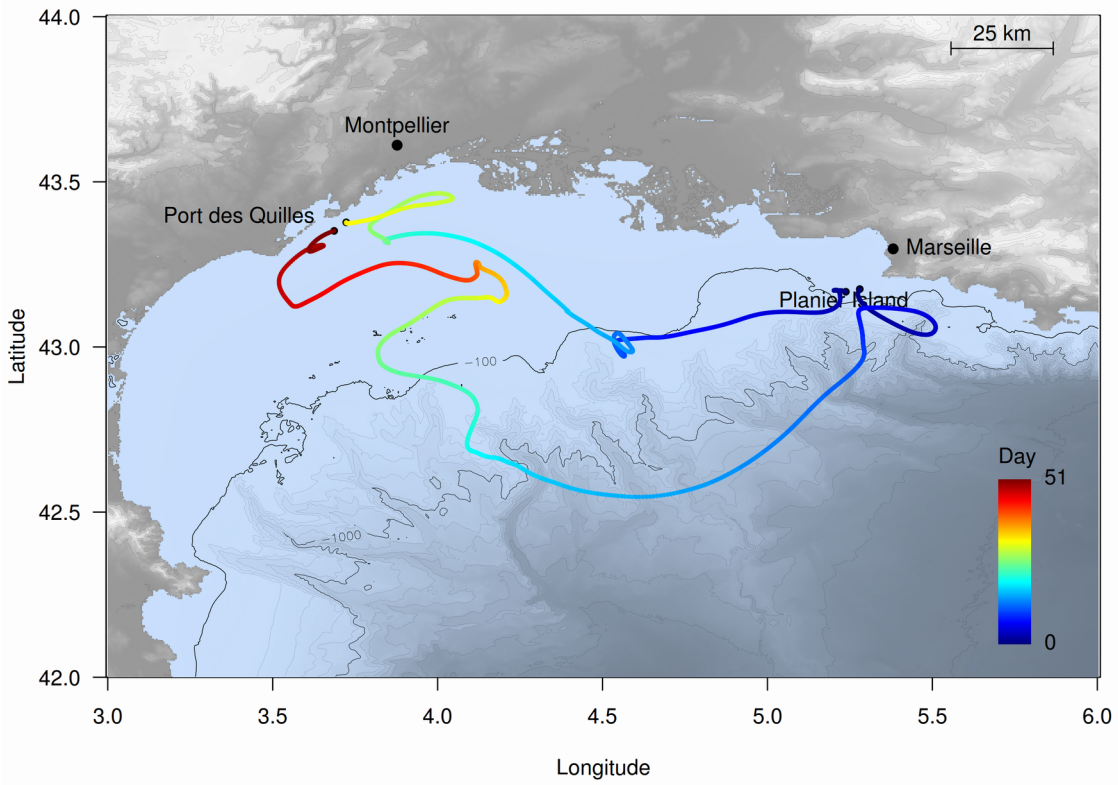


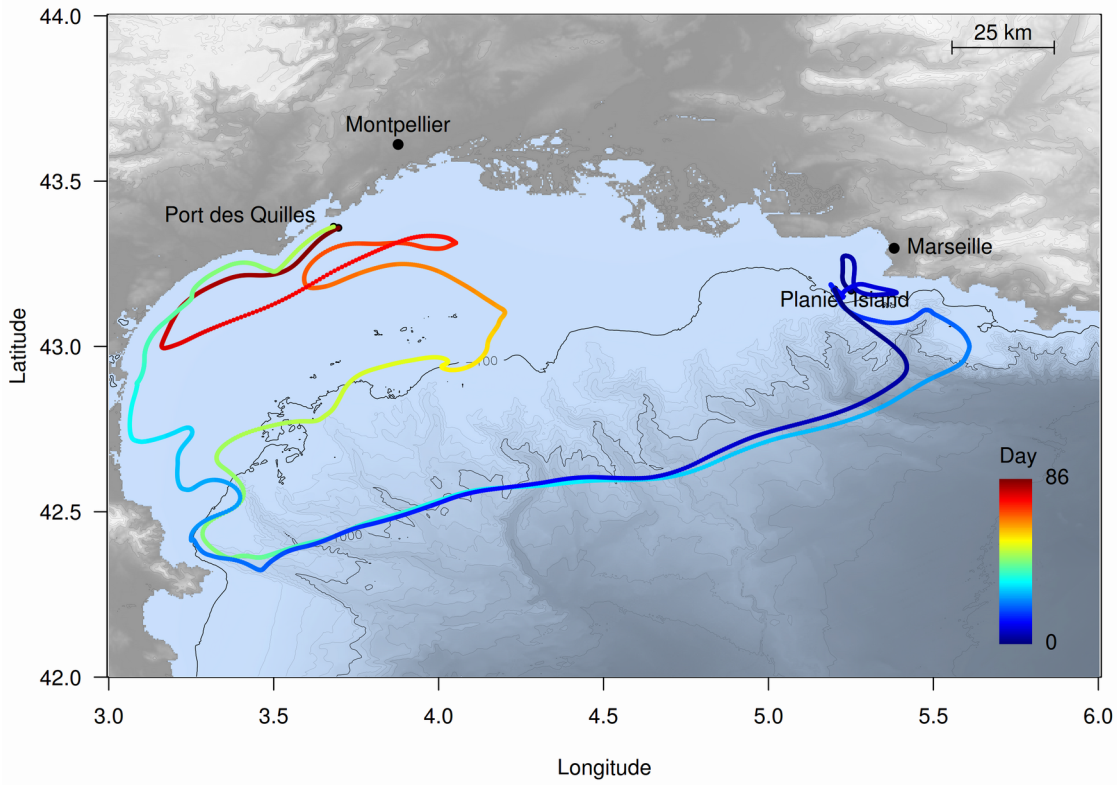
Figure 2: Percentage of the virtual gilthead seabream larvae released around the Planier Island and successfully transported to the Thau lagoon entrance “Port des Quilles”, for each release date. Dashed grey lines separate breeding seasons (Nov.-Feb.).



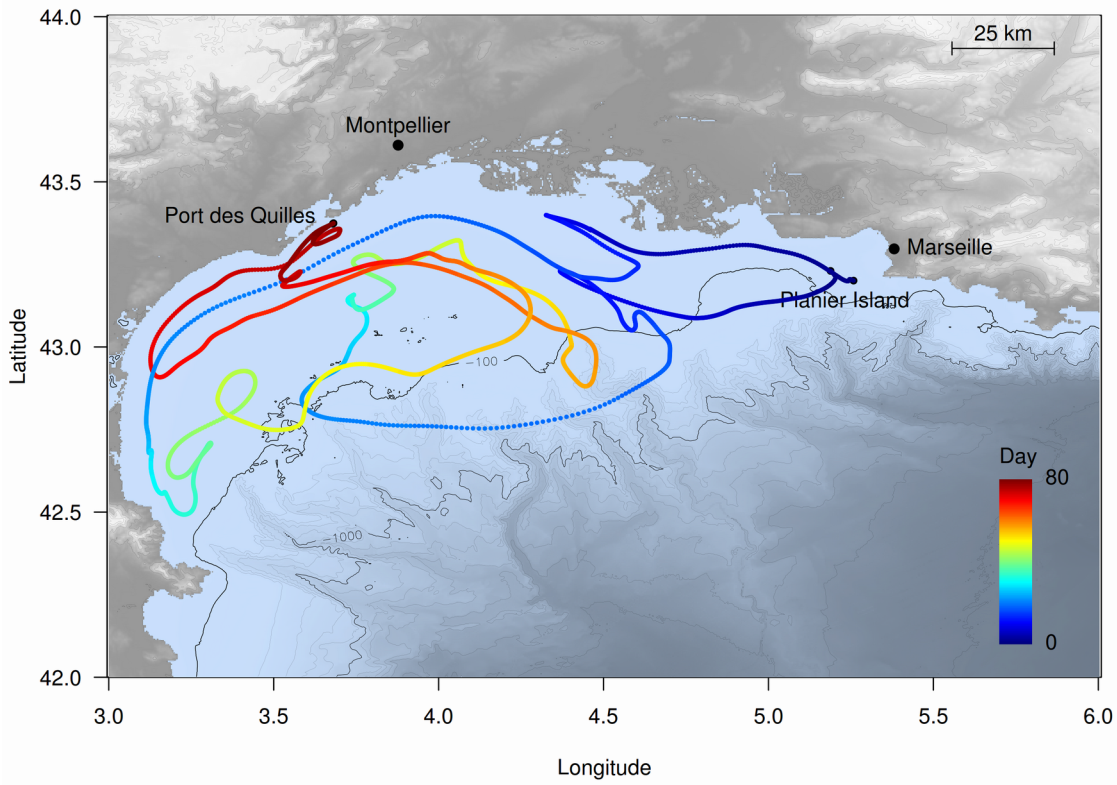
(a)



(b)



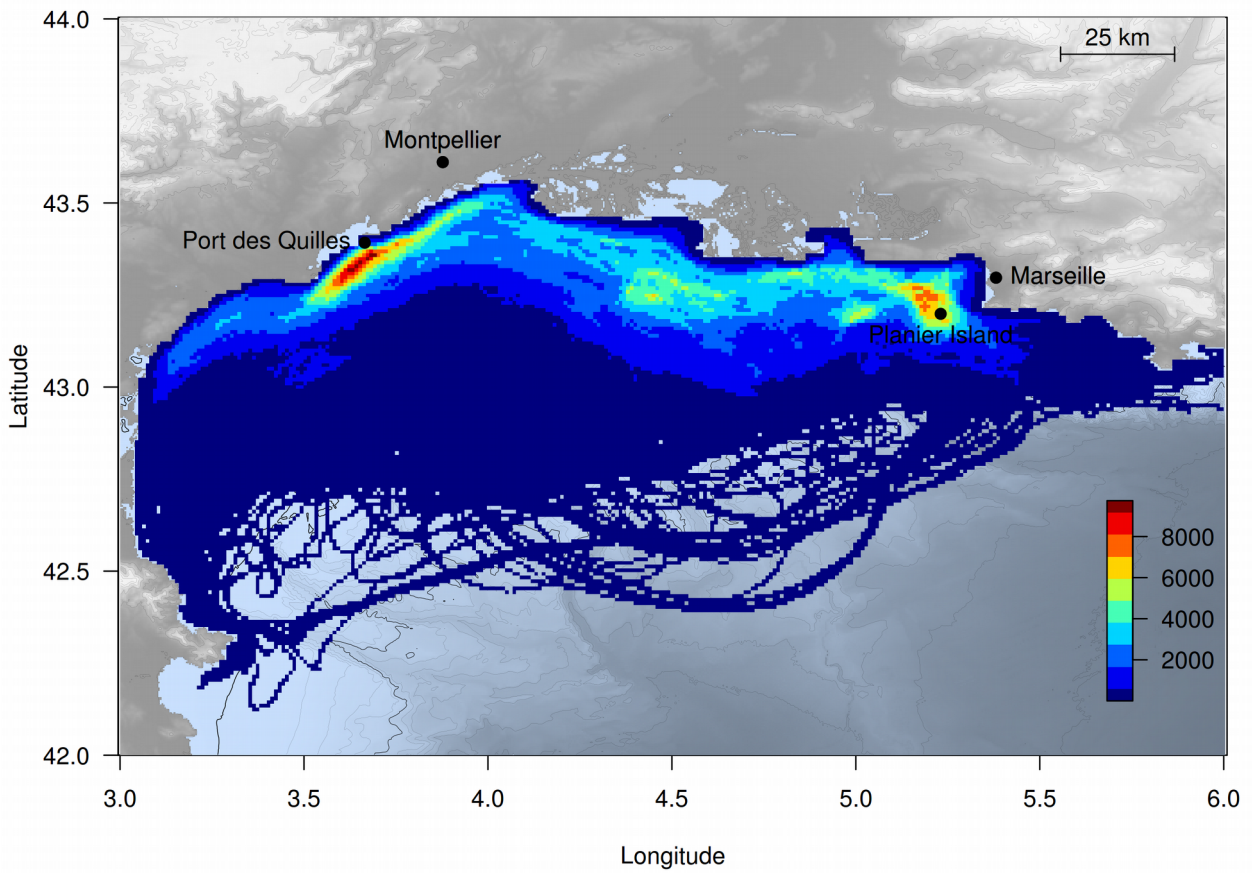
(c)



(d)

Figure 3: A few illustrative trajectories of virtual gilthead seabream larvae released around the

Planier Island and successfully transported to the Thau lagoon entrance “Port des Quilles”.



*Figure 4: Spatial distribution of the virtual gilthead seabream larvae released around the Planier Island and successfully transported to the Thau lagoon entrance “Port des Quilles”. Locations were summed along the simulated trajectories and among all release dates on a $0.01^\circ * 0.01^\circ$ map.*

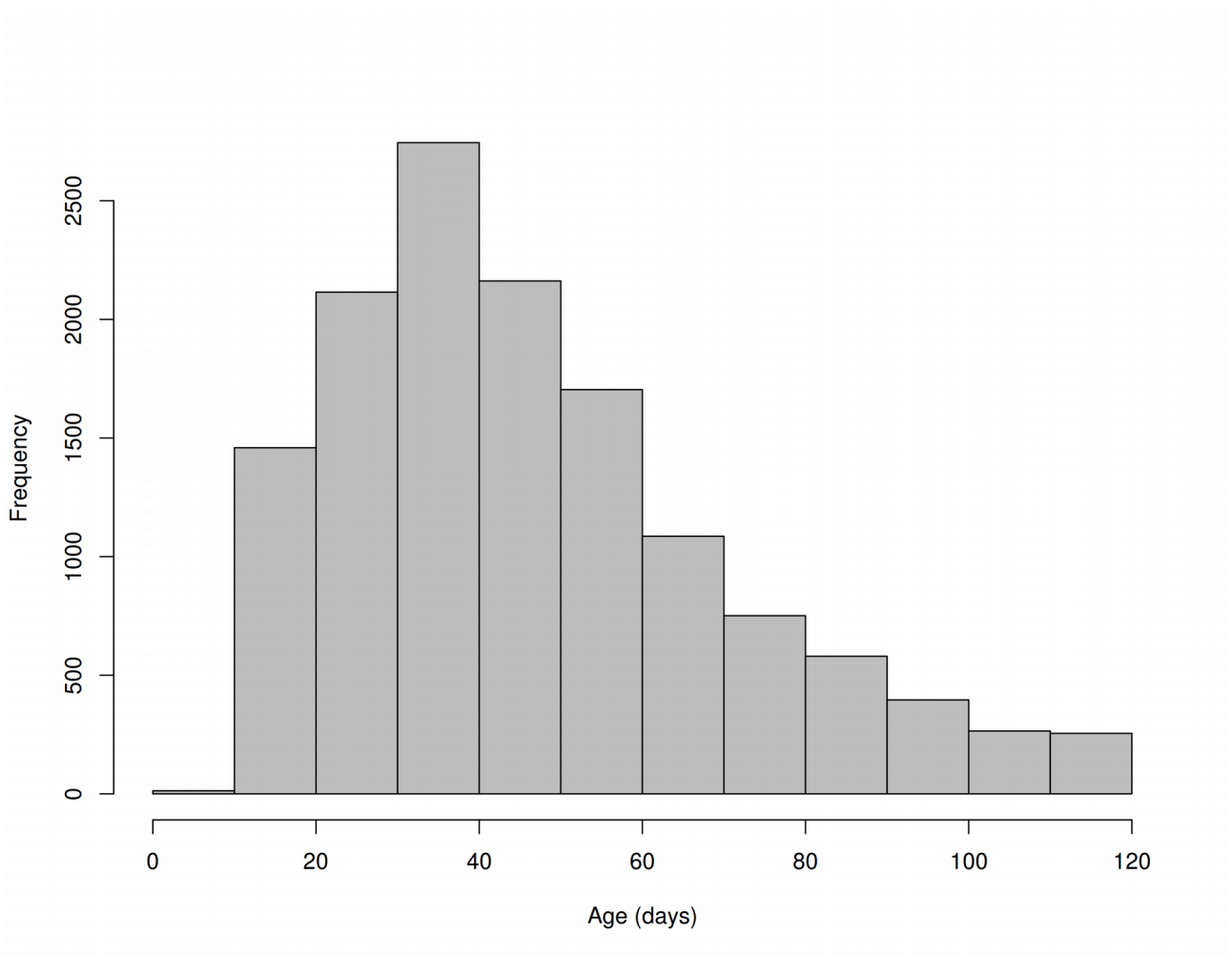
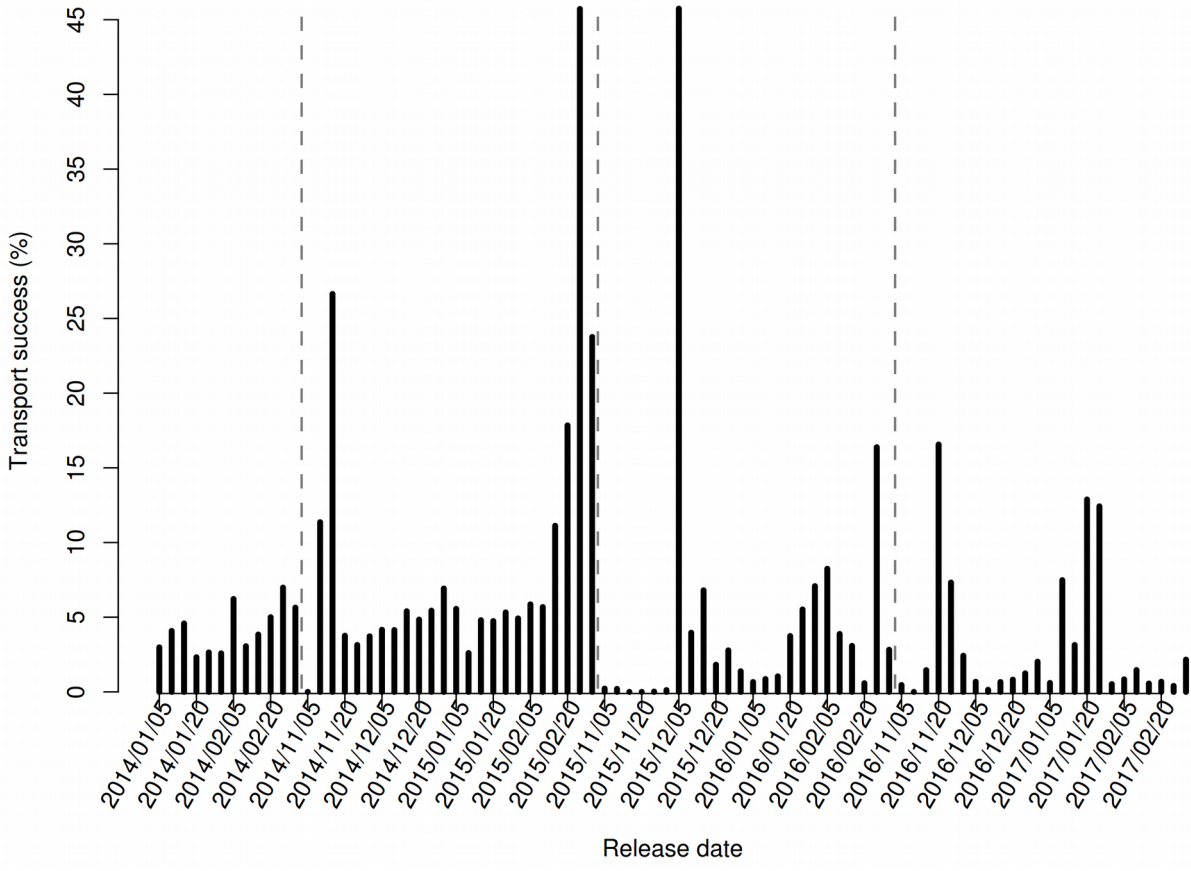
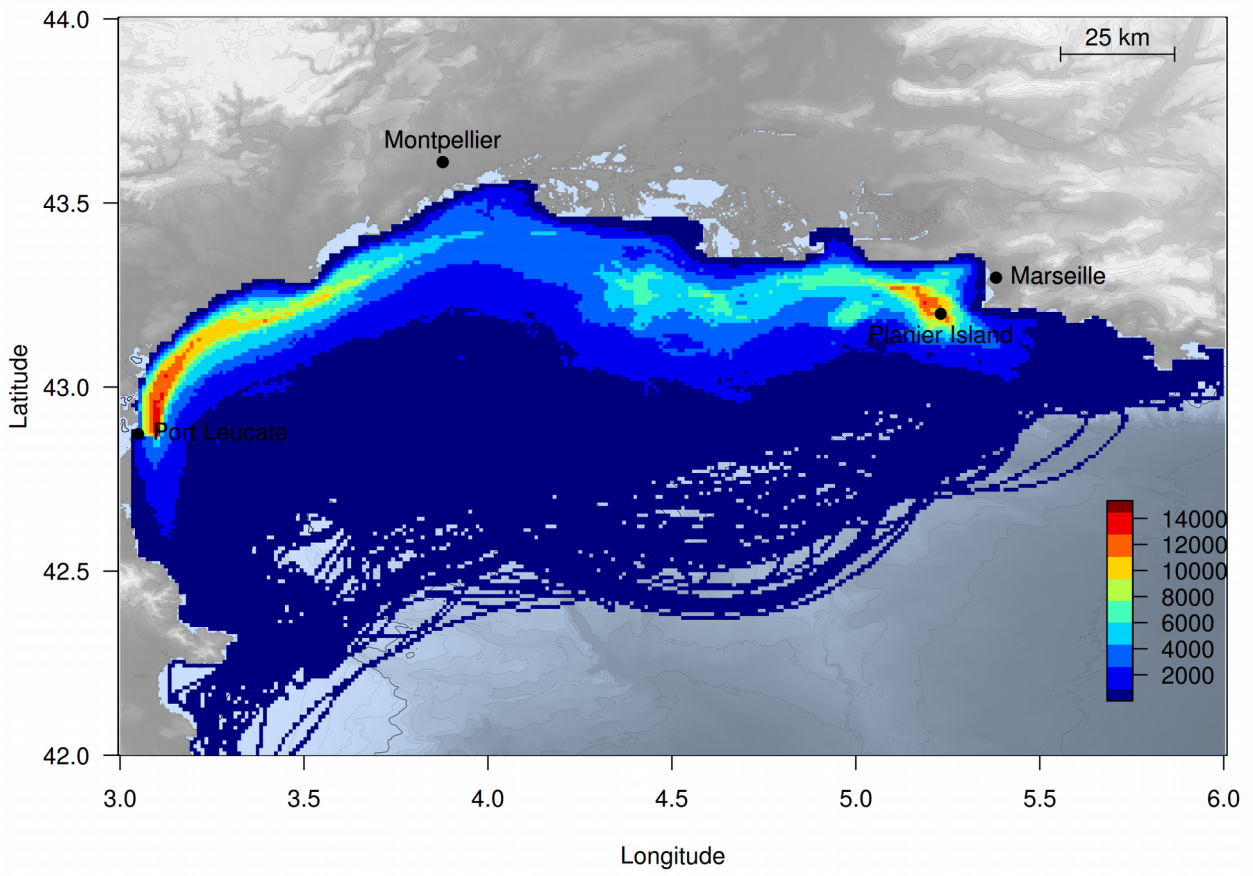


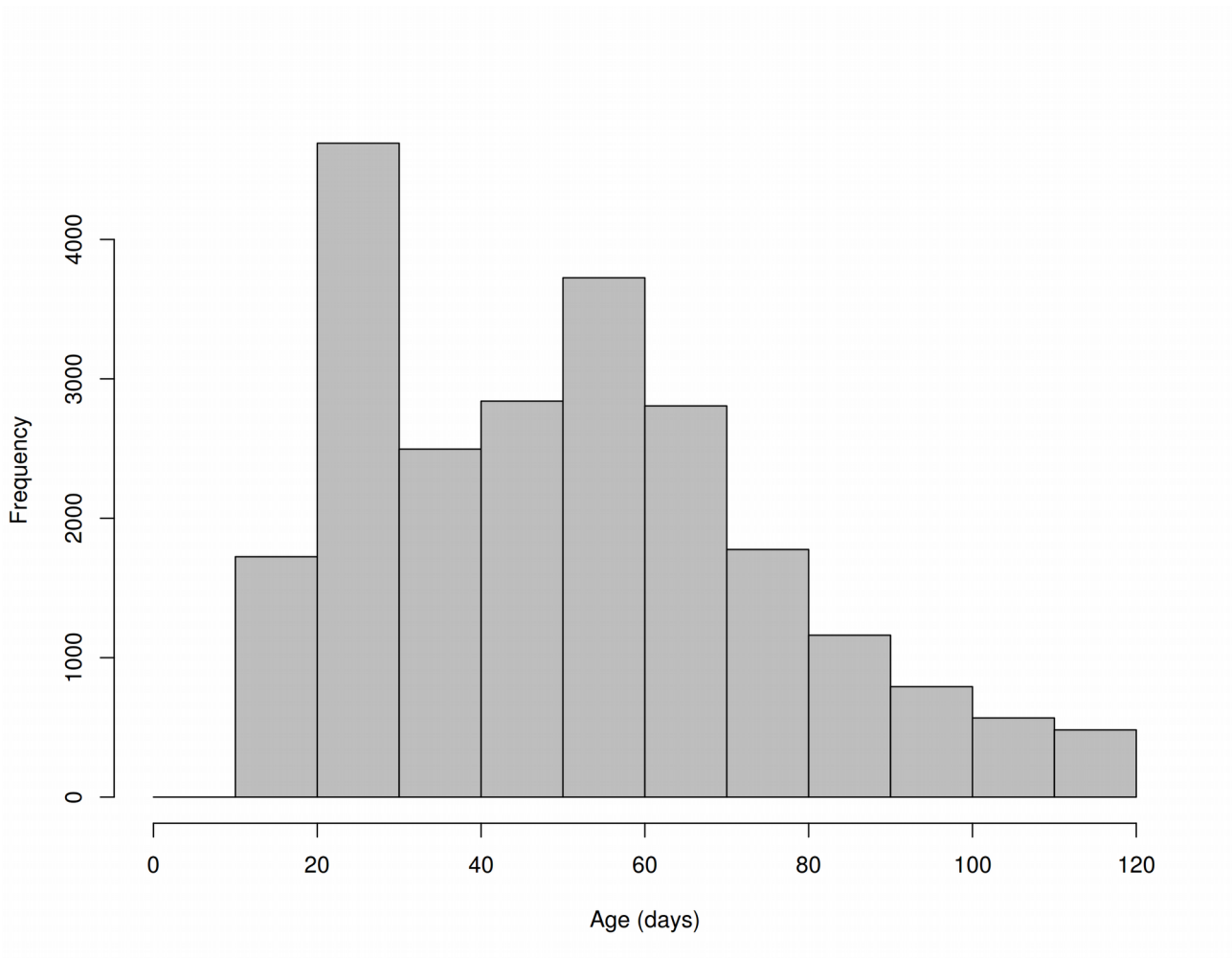
Figure 5: Age distribution of the virtual gilthead seabream larvae released around the Planier Island and successfully transported to the Thau lagoon entrance “Port des Quilles” for all release dates combined.



(a)



(b)



(c)

Figure 6: Same as (a) Fig. 2 (b) Fig. 4 and (c) Fig. 5 for the virtual gilthead seabream larvae released around the Planier Island and successfully transported to the Salses-Leucate lagoon entrance "Port Leucate".

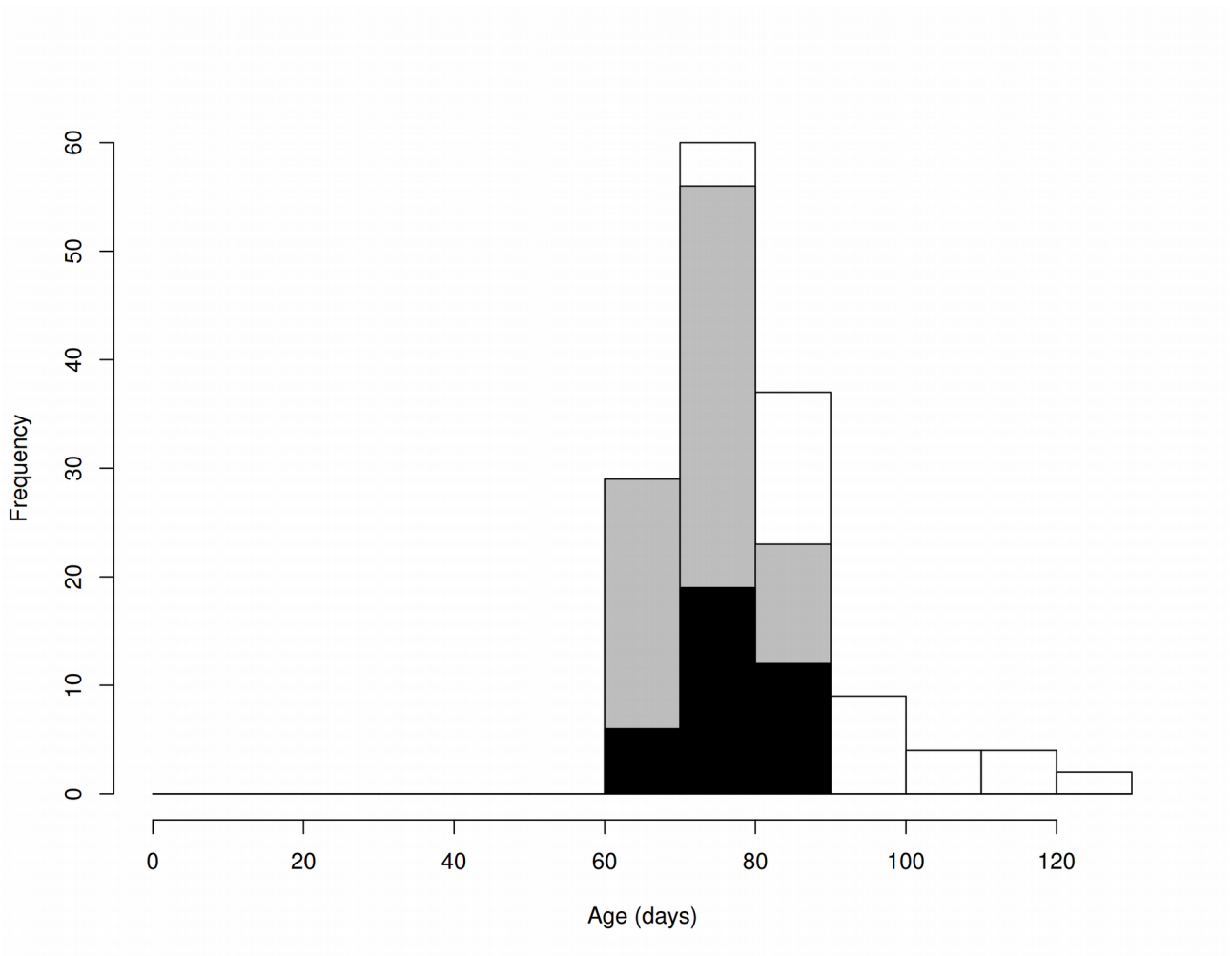


Figure 7: Age distribution of 145 gilthead seabream larvae collected at the entrance of four lagoons in February-March 2016-2017. Grey bars are for the 108 larvae collected in February. Black bars are for the 37 larvae collected in February at the Thau and Salses-Leucate lagoon entrances “Port des Quilles” (16 larvae) and “Port Leucate” (21 larvae) combined.

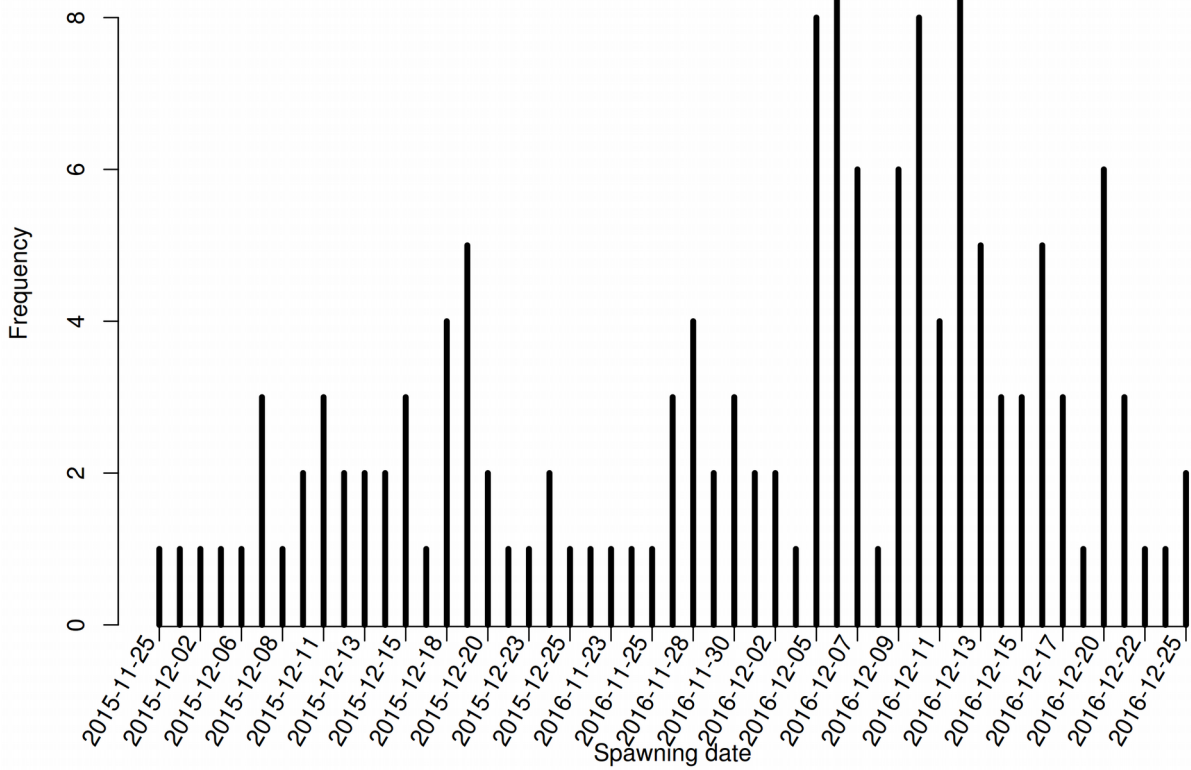


Figure 8: Distribution of estimated spawning dates for 145 gilthead seabream larvae collected at the entrance of four lagoons in February-March 2016-2017.

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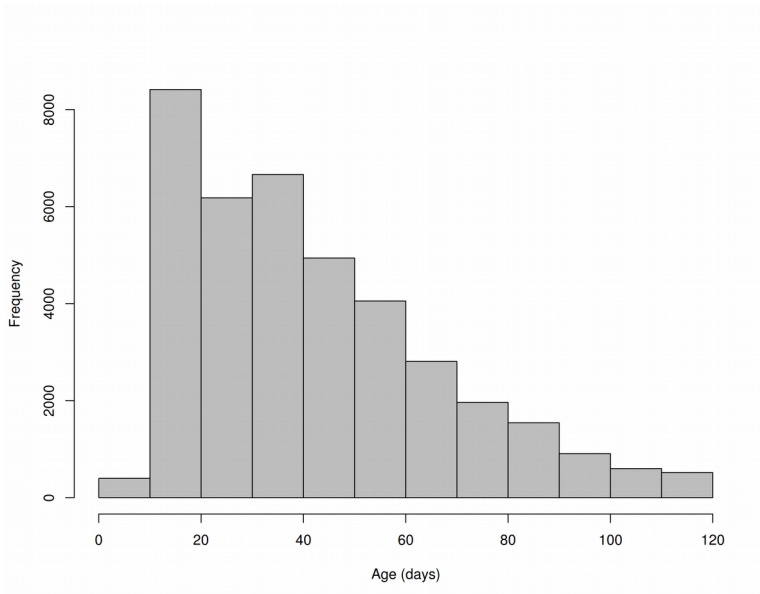
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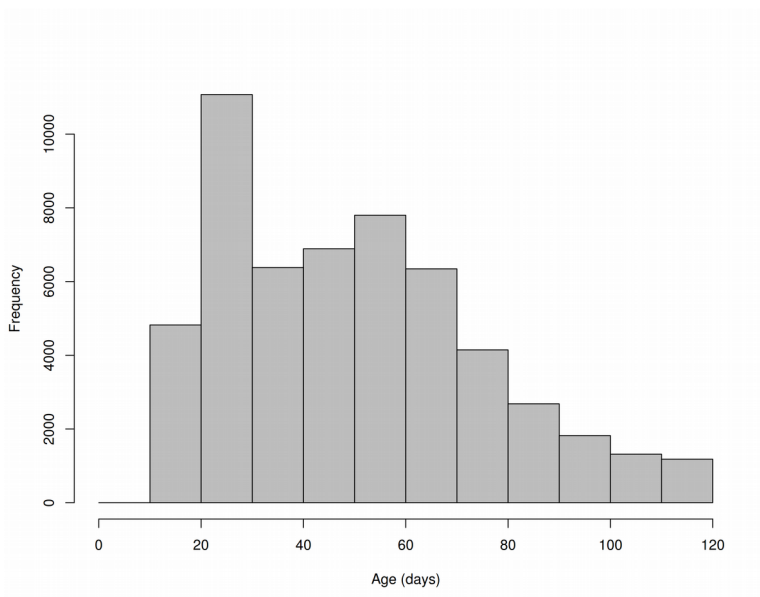
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Appendix figures

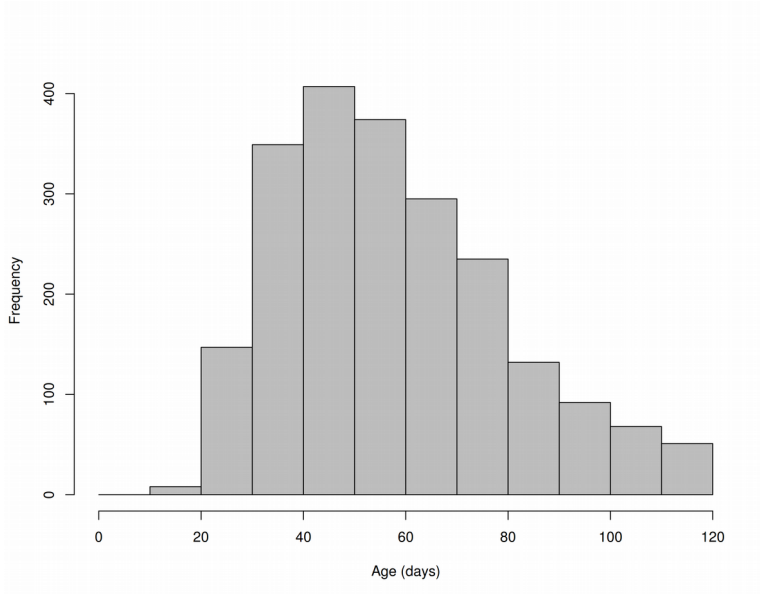


435 (a)

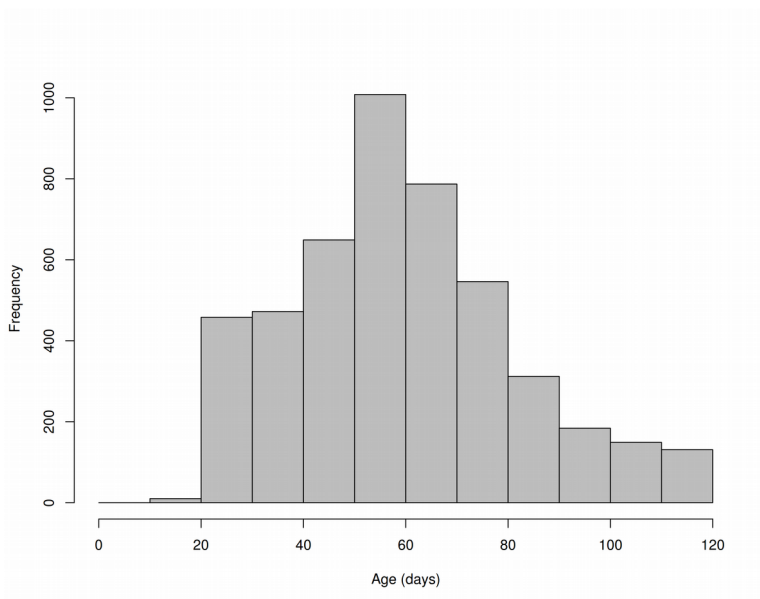


(b)

Figure A: Age distribution of the virtual gilthead seabream larvae released around the Planier Island reaching a distance < 10 km to (a) the Thau lagoon entrance “Port des Quilles” (min = 7.8 days, max = 120 days, mean = 41.8 days, SD = 24.5 days, median = 36.3 days, IQR = 34.33 days); (b) the Salses-Leucate lagoon entrance “Port Leucate” (min = 10.5 days, max = 120 days, mean = 50.0 days, SD = 25.0 days, median = 47.3 days, IQR = 36.8 days).



440 (a)



(b)

Figure B: Age distribution of the virtual gilthead seabream larvae released at 80 to 100 m depth around the Planier Island reaching a distance < 5 km to (a) the Thau lagoon entrance “Port des Quilles” (min = 18.6 days, max = 120 days, mean = 57.5 days, SD = 22.1 days, median = 54.0 days, IQR = 30.6 days); (b) the Salses-Leucate lagoon entrance “Port Leucate” (min = 17.5 days, max = 120 days, mean = 59.4 days, SD = 21.9 days, median = 57.1 days, IQR = 27.0 days).

Appendix table

Lagoon	Date of capture	Estimated age at capture (days)	Back-calculated spawning date	Total length (mm)
Mauguio	18/02/2016	68	15/12/2015	18
Mauguio	18/02/2016	81	02/12/2015	16
Mauguio	18/02/2016	63	20/12/2015	16
Mauguio	18/02/2016	69	14/12/2015	18
Mauguio	18/02/2016	65	18/12/2015	16
Mauguio	18/02/2016	65	18/12/2015	16
Mauguio	18/02/2016	64	19/12/2015	16
Mauguio	18/02/2016	76	07/12/2015	17
Mauguio	18/02/2016	70	13/12/2015	18
Mauguio	18/02/2016	72	11/12/2015	20
Mauguio	18/02/2016	68	15/12/2015	20
Mauguio	18/02/2016	68	15/12/2015	17
Mauguio	18/02/2016	88	25/11/2015	19
Mauguio	18/02/2016	65	18/12/2015	18
Mauguio	18/02/2016	74	09/12/2015	17
Mauguio	18/02/2016	71	12/12/2015	17
Mauguio	18/02/2016	65	18/12/2015	16
Mauguio	18/02/2016	78	05/12/2015	17
Mauguio	18/02/2016	69	14/12/2015	17
Mauguio	18/02/2016	60	23/12/2015	16
Mauguio	18/02/2016	76	07/12/2015	16
Thau	10/03/2016	85	19/12/2015	18
Thau	10/03/2016	80	24/12/2015	19
Thau	10/03/2016	93	11/12/2015	17
Thau	10/03/2016	85	19/12/2015	18
Thau	10/03/2016	97	07/12/2015	19
Thau	10/03/2016	88	16/12/2015	19
Thau	10/03/2016	85	19/12/2015	20
Thau	10/03/2016	80	24/12/2015	19
Thau	10/03/2016	104	30/11/2015	19
Thau	10/03/2016	84	20/12/2015	20
Thau	10/03/2016	82	22/12/2015	18
Thau	10/03/2016	79	25/12/2015	18

Thau	23/02/2016	80	08/12/2015	18
Thau	23/02/2016	82	06/12/2015	18
Thau	23/02/2016	79	09/12/2015	18
Thau	23/02/2016	77	11/12/2015	18
Thau	22/03/2016	87	29/12/2015	19
Thau	22/03/2016	104	12/12/2015	20
Thau	22/03/2016	97	19/12/2015	20
Thau	22/03/2016	103	13/12/2015	20
Mauguio	29/03/2017	99	23/12/2016	20
Mauguio	29/03/2017	97	25/12/2016	19
Mauguio	29/03/2017	110	12/12/2016	18
Mauguio	29/03/2017	117	05/12/2016	20
Mauguio	29/03/2017	116	06/12/2016	18
Mauguio	29/03/2017	106	16/12/2016	17
Mauguio	29/03/2017	121	01/12/2016	19
Mauguio	29/03/2017	121	01/12/2016	18
Mauguio	29/03/2017	112	10/12/2016	18
Mauguio	15/02/2017	70	10/12/2016	16
Mauguio	15/02/2017	72	08/12/2016	17
Mauguio	15/02/2017	70	10/12/2016	17
Mauguio	15/02/2017	75	05/12/2016	16
Mauguio	15/02/2017	70	10/12/2016	16
Mauguio	15/02/2017	73	07/12/2016	16
Mauguio	21/02/2017	75	11/12/2016	20
Mauguio	21/02/2017	73	13/12/2016	19
Mauguio	21/02/2017	76	10/12/2016	18
Mauguio	21/02/2017	80	06/12/2016	20
Mauguio	21/02/2017	71	15/12/2016	16
Mauguio	21/02/2017	65	21/12/2016	17
Mauguio	21/02/2017	72	14/12/2016	20
Mauguio	21/02/2017	65	21/12/2016	19
Mauguio	21/02/2017	66	20/12/2016	18
Mauguio	21/02/2017	72	14/12/2016	18
Mauguio	21/02/2017	75	11/12/2016	18
Mauguio	21/02/2017	74	12/12/2016	17
Mauguio	21/02/2017	71	15/12/2016	16
Mauguio	21/02/2017	74	12/12/2016	17

Mauguio	21/02/2017	66	20/12/2016	16
Mauguio	21/02/2017	70	16/12/2016	16
Mauguio	21/02/2017	66	20/12/2016	17
Mauguio	21/02/2017	68	18/12/2016	16
Mauguio	10/02/2017	68	07/12/2016	17
Mauguio	10/02/2017	82	23/11/2016	19
Thau	21/02/2017	87	29/11/2016	19
Thau	21/02/2017	70	16/12/2016	18
Thau	21/02/2017	76	10/12/2016	20
Thau	21/02/2017	73	13/12/2016	15
Thau	21/02/2017	69	17/12/2016	17
Thau	21/02/2017	73	13/12/2016	18
Thau	21/02/2017	75	11/12/2016	17
Thau	21/02/2017	79	07/12/2016	20
Thau	21/02/2017	70	16/12/2016	20
Thau	21/02/2017	74	12/12/2016	19
Thau	21/02/2017	81	05/12/2016	17
Thau	21/02/2017	80	06/12/2016	18
Thau	07/03/2017	80	20/12/2016	19
Thau	07/03/2017	78	22/12/2016	19
Thau	07/03/2017	83	17/12/2016	18
Thau	07/03/2017	75	25/12/2016	17
Thau	07/03/2017	88	12/12/2016	21
Thau	07/03/2017	85	15/12/2016	17
Thau	07/03/2017	90	10/12/2016	20
Thau	07/03/2017	93	07/12/2016	22
Thau	07/03/2017	79	21/12/2016	16
Thau	07/03/2017	88	12/12/2016	19
Thau	07/03/2017	93	07/12/2016	20
Thau	07/03/2017	91	09/12/2016	18
Salses	16/02/2017	69	12/12/2016	-
Salses	16/02/2017	79	02/12/2016	-
Salses	16/02/2017	76	05/12/2016	-
Salses	16/02/2017	83	28/11/2016	-
Salses	16/02/2017	83	28/11/2016	-
Salses	16/02/2017	81	30/11/2016	-
Salses	17/02/2017	73	09/12/2016	-

Salses	17/02/2017	77	05/12/2016	-
Salses	16/02/2017	86	25/11/2016	-
Salses	16/02/2017	74	07/12/2016	17
Salses	16/02/2017	68	13/12/2016	18
Salses	16/02/2017	67	14/12/2016	18
Salses	16/02/2017	75	06/12/2016	18
Salses	16/02/2017	75	06/12/2016	17
Salses	16/02/2017	75	06/12/2016	19
Salses	16/02/2017	84	27/11/2016	18
Salses	16/02/2017	69	12/12/2016	19
Salses	16/02/2017	84	27/11/2016	18
Salses	17/02/2017	85	27/11/2016	20
Salses	17/02/2017	62	20/12/2016	15
Salses	17/02/2017	73	09/12/2016	16
Bages	17/02/2017	83	29/11/2016	20
Bages	17/02/2017	77	05/12/2016	19
Bages	17/02/2017	72	10/12/2016	17
Bages	17/02/2017	88	24/11/2016	16
Bages	17/02/2017	65	17/12/2016	18
Bages	17/02/2017	69	13/12/2016	20
Bages	17/02/2017	62	20/12/2016	15
Bages	17/02/2017	71	11/12/2016	19
Bages	17/02/2017	82	30/11/2016	20
Bages	17/02/2017	70	12/12/2016	17
Bages	17/02/2017	84	28/11/2016	19
Bages	17/02/2017	84	28/11/2016	20
Bages	17/02/2017	82	30/11/2016	17
Bages	17/02/2017	73	09/12/2016	20
Bages	17/02/2017	73	09/12/2016	19
Bages	17/02/2017	77	05/12/2016	18
Bages	17/02/2017	76	06/12/2016	20
Bages	17/02/2017	80	02/12/2016	21
Bages	17/02/2017	79	03/12/2016	19
Bages	17/02/2017	66	16/12/2016	16
Bages	17/02/2017	76	06/12/2016	21
Bages	17/02/2017	76	06/12/2016	17
Bages	17/02/2017	73	09/12/2016	18

Bages	17/02/2017	77	05/12/2016	16
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Appendix Table: Estimated age, length and spawning date for 145 gilthead seabream larvae collected at the entrance of four lagoons in February-March 2016-2017.