



Contribution to the Theme Section 'Latest advances in research on fish early life stages'

Spatio-temporal patterns of larval fish settlement in the northwestern Mediterranean Sea

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ABSTRACT: Most coastal fish species spend their early life stages in the pelagic environment, before settling in coastal habitats. The variability in the arrival of larvae to coastal habitats provides information on the species' biology and recruitment potential. To explore the dynamics of larval fish supply to coastal habitats in the NW Mediterranean Sea, 13 sites were monitored using light-traps, from July 2012 to December 2015. Most variation in catches per unit effort (CPUE) among topographic basins and species were statistically significant for high (quantile 75%) and very high (quantile 90%) catches only. At the yearly scale, CPUE displayed strong seasonality, and 3 main species assemblages were detected in late spring-early summer, summer and late autumn-early winter. At the monthly scale, CPUE were higher around the new moon for all quantiles and temporally autocorrelated at a lag of ~28 d. Larval supply also varied spatially with site-specific associations and with riverine influence. Altogether, these results confirm that the previously described patterns of larval supply observed in tropical and subtropical environments (e.g. the high variability at all spatial and temporal scales and the strong influence of the moon) also apply to Mediterranean fish assemblages. Our quantile-based approach demonstrated that the larval supply in the NW Mediterranean Sea is a solid candidate for monitoring the state of the marine ecosystems, highlighting the need to continue such time series.

KEY WORDS: Fish larvae · Larval supply · Light-traps · NW Mediterranean Sea · Monitoring time series

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1. INTRODUCTION

By the end of their pelagic phase, coastal fish larvae switch from a pelagic to a demersal lifestyle and need to reach a habitat on the coast to settle. While mortality after this settlement phase can be high (Planes et al. 1998, Almany & Webster 2006), the bulk of the mortality still occurs during the larval phase, with mortality rates ranging from 10 to >70% d⁻¹ (Houde 2008, White et al. 2014, Johnson et al. 2015). The intensity of larval supply to coastal habitats at settlement often largely determines recruitment success (i.e. settlers that survive and metamorphose into

juveniles; Félix-Hackradt et al. 2013a) and local population dynamics (Victor 1986b). Monitoring the intensity of settlement may therefore provide valuable information to anticipate the abundance of future fish stocks, for fisheries management and conservation efforts in general (Doherty & Fowler 1994, McLeod & Costello 2017).

The main factors known to influence the intensity of settlement, at a given time in a given location, are (1) the reproductive periods of adults, often conditioned by temperature, lunar phase, and photoperiod (Robertson 1992, Dixon et al. 1999, D'Alessandro et al. 2007, Tsikliras et al. 2010); (2) hydrodynamics, at

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all scales (from 1000s km to <10 m), which can favour retention through inshore-flowing currents, stable eddies, and low flow zones or favour dispersal through offshore-flowing currents and impair settlement in some areas because of fast-paced currents (reviewed by Pineda et al. 2010); (3) survival of the pelagic stages, including predation pressure that may drastically reduce the larval pool (Planes & Lecaillon 2001, Lecchini et al. 2014); and (4) larval behaviour, as fish larvae can sense their environment and use several cues to select a settlement site and time (Victor 1986a, Dufour & Galzin 1993, Leis et al. 2011, Barth et al. 2015).

Marine protected areas (MPA) have been established worldwide to protect habitats, biodiversity or emblematic species (Fernandes et al. 2005). Protected habitats often support higher species richness and diversity (Edgar et al. 2014) and may, in turn, present attractive signals for new settlers. However, whether larval supply differs between protected and unprotected sites is poorly known, with contrasting results (Valles et al. 2001, Grorud-Colvert & Sponaugle 2009).

Settlement-stage fish larvae of Perciformes species have particularly strong swimming abilities (Leis 2006, Domenici & Kapoor 2010, Faillettaz et al. 2017) and may avoid standard plankton nets (Choat et al. 1993, Carassou & Ponton 2009, Catalan et al. 2014). Since most larval supply to settlement habitats occurs at night (Dufour & Galzin 1993, Mwaluma et al. 2014) and larvae of the majority of species are positively phototactic, light-traps have been developed to selectively sample the settlement-stage larvae of coastal species (Doherty 1987a, McLeod & Costello 2017) and provided consistent results across various locations and conditions, such as Australia (Doherty 1987a, Fisher & Bellwood 2002), Florida (D'Alessandro et al. 2007, Grorud-Colvert & Sponaugle 2009), Caribbean (Sponaugle & Cowen 1996), North-East Atlantic (Chícharo et al. 2009), and the Mediterranean Sea (Félix-Hackradt et al. 2013b).

In the Mediterranean Sea, reproduction is typically seasonal and usually occurs in spring-summer. During this period, the water column is mostly stratified, with low plankton abundance in the surface layer and high phytoplankton and zooplankton biomass around the deep chlorophyll maximum (Sabatés et al. 2007). In offshore waters, the succession of assemblages of young fish larvae is characterised by high abundance and low species richness in late spring followed by lower abundance along with higher species richness in summer (Álvarez et al. 2012). For later life stages, recruitment intensity, evaluated by visual census of young settlers, was found to be corre-

lated with the abundance of juveniles in some species (García-Rubies & Macpherson 1995, Macpherson et al. 1997, Vigliola et al. 1998, Félix-Hackradt et al. 2013a) but not in all (Di Franco et al. 2013).

Less information is available regarding the crucial stage of settlement for Mediterranean fishes. A single study quantified larval supply to coastal habitats in the South of Spain, on a monthly basis for 1 yr (Félix-Hackradt et al. 2013b). Higher larval supply (80% of total catches) and diversity were measured during warmer months, from June to September, which is consistent with seasonal patterns of ichthyoplankton abundance described above (e.g. Álvarez et al. 2012). However, because of the high variability in recruitment at all temporal and spatial scales, in all habitats where it was studied (Victor 1986b, Doherty 1987b, D'Alessandro et al. 2007, White & Caselle 2008, Félix-Hackradt et al. 2013a), the description of the dynamics of larval supply in the northwestern Mediterranean Sea remains largely incomplete. The present study aims to fill this gap by monitoring and describing the seasonal and basin-scale patterns of larval supply at 13 sites distributed along the northwestern Mediterranean coast, over >3 yr (2012–2015).

2. MATERIALS & METHODS

2.1. Study sites

A total of 13 sites were sampled, covering most of the French Mediterranean coast (Fig. 1). Five sites were located in the Ligurian Sea (3 in Corsica, 2 on the French Riviera), while 8 were in the Gulf of Lion (5 on the eastern side of the Rhône, 3 on the western side; Fig. 1). The sites covered different ecosystems and levels of anthropogenic impact (see Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m650p153_supp1.pdf): Bastia and Leucate were close to large coastal lagoons (Biguglia and Leucate, respectively) and over sandy bottoms while all other sites were over rocky bottoms; Port-Vendres, Carry, Les Embiez, Port-Cros, Saint-Florent, and Bonifacio were located within or close to (<5 km) a marine protected area (MPA); Agde, Villefranche, La Ciotat, and Cassis were located in areas of limited urbanisation; Marseille and Carry were located within the bay of Marseille, a city of 2 million inhabitants, which is the most urbanised area along the coast.

The main hydrographical structure of the region is the Liguro-Provençal current, flowing along the 200 m isobath from a few to ~30 km from the shore (Fig. 1b) and between the surface and 150–200 m depth. It is

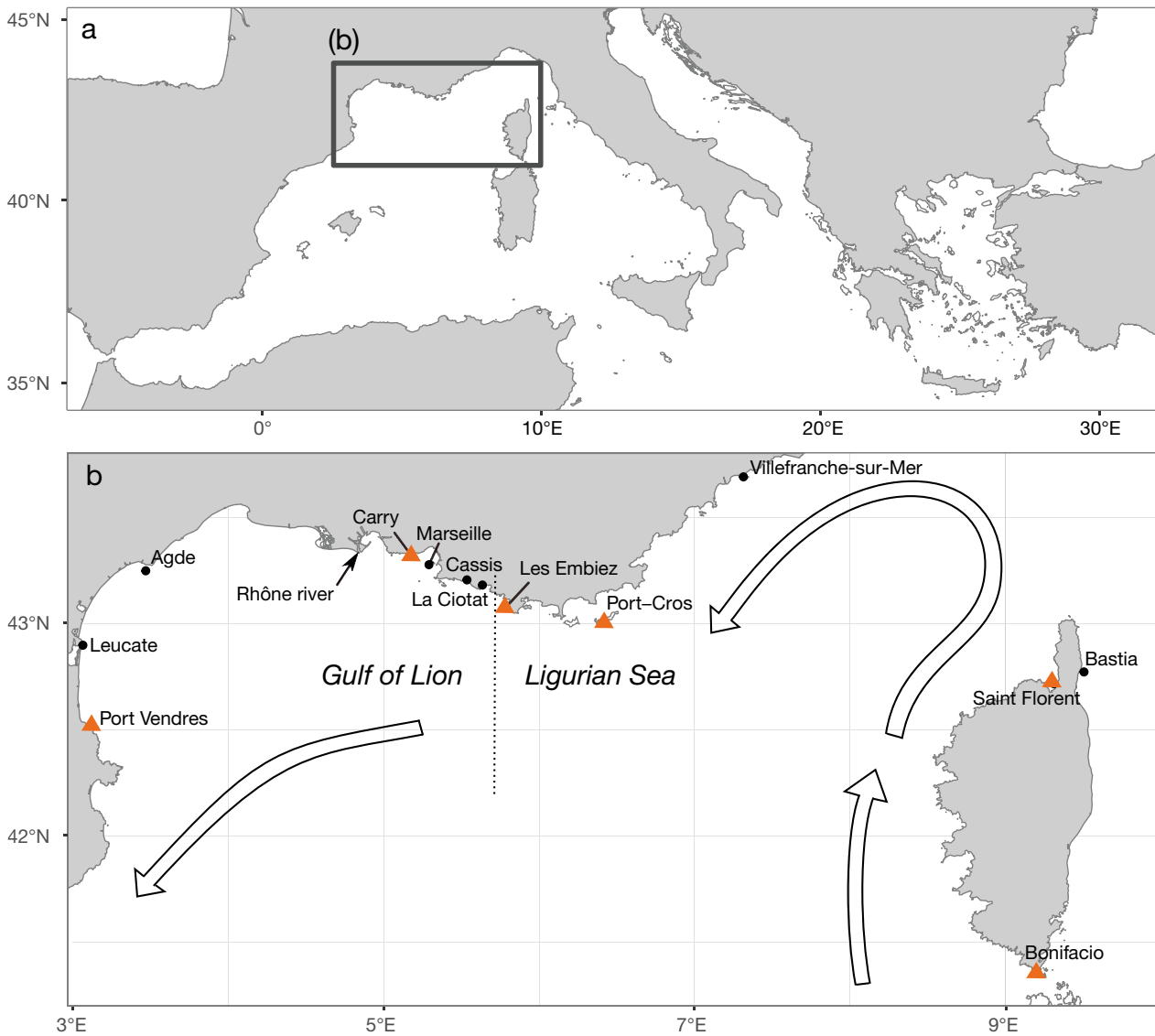


Fig. 1. (a) Sampling region within the Mediterranean Sea and (b) detailed position of the 13 sampling sites. Orange triangles indicate sites located within or close to MPAs. The 2 main topographic regions (Gulf of Lion and Ligurian Sea) are indicated, along with the average path of the Liguro-Provençal current (arrows)

25 km wide on average and flows at $25\text{--}35\text{ cm s}^{-1}$ towards the south-west (Béthoux & Prieur 1983, Stemmann et al. 2008). The current is present throughout the year and creates a marked hydrological front that may act as a barrier to offshore dispersal of coastal organisms, as do other Mediterranean fronts (Galarza et al. 2009), along with a near-shore, stochastic counter-current (Pedrotti & Fenaux 1992).

2.2. Fish larvae collection

Settlement-stage fish larvae (hereafter referred to as larvae, for brevity) were collected with ‘Collect

by Artificial Reef Eco-friendly’ (CARE) light-traps (Lecaillon 2004). Today, light-traps have become a standard tool to quantify the larval supply of many taxa (Doherty 1987a, Thorrold 1992, McLeod & Costello 2017). The efficiency of light traps may be reduced by the intensity of ambient moonlight (Hernandez & Shaw 2003), water turbidity, and strong currents (Lindquist & Shaw 2005, Chícharo et al. 2009). Predation of fish larvae may also take place inside the light-traps (Vilizzi et al. 2008). These biases, however, seem to be low enough for fish larvae to be caught at all lunar phases and to display clear, species-specific patterns (Hernandez & Shaw 2003).

The CARE light-traps have proven to be effective at capturing fish larvae in the Mediterranean Sea (Catalan et al. 2014, Félix-Hackradt et al. 2013b) and elsewhere (Carassou et al. 2009). The traps are composed of a buoyant block with a 55 W LED light floating at the surface, above a 2 m long conical net made of 2 mm PVC mesh with a funnel in the middle (see Fig. S1). Settling larvae are first attracted to the light and then descend in the net in search of a settlement substrate, in this case, the net; these traps are therefore quite selective (Lecaillon 2004). Still, the traps occasionally caught fish larvae in the pre-flexion or flexion stages, i.e. that are not ready to settle, as well as juveniles and young adults of strictly pelagic species (e.g. Belonidae, Carangidae, Centrolophidae, Clupeidae, Engraulidae, Myctophidae, and Scombridae). Their occurrences are reported in the full database for completeness (Table S2 in Supplement 2 at www.int-res.com/articles/suppl/m650p153_supp2.csv) but were excluded from all analyses below to focus on settlement-stage larvae of demersal species only.

Sampling was performed as part of multiple projects with different objectives and the sampling effort was not equivalent at all sites. Many sites were mostly sampled around the new moon (e.g. Bastia, Saint-Florent, and Port-Vendres), while others were homogeneously sampled throughout the year (e.g. Villefranche and Leucate). Sampling occurred between July 2012 and December 2015, yet not at all sites, spanning a period of >3 yr and almost 4 summers (see Fig. S2), i.e. the main spawning season in the Mediterranean Sea (Tsikliras et al. 2010). Overall, the total sampling effort amounted to 7036 light-trap-nights (1 light-trap-night stands for 1 light-trap set to fish for 1 night).

Apart from this heterogeneity in sampling schedule, sampling was strictly comparable among sites: the exact same model of light-trap was used everywhere (same dimensions, net, mesh, led light bulb, etc.); they were set at sea from small motor boats, 1 to 2 h before sunset; in the morning, light-traps were retrieved as soon as possible, usually within 1 h after sunrise.

After collection, fish larvae were stored in >30 l white buckets or coolers. In most locations, larvae were caught to be raised in aquaria and later released to reinforce adult populations. Larvae were visually identified and separated per species and night of capture, then raised for a few months. A second identification of the juvenile stages, based on Louisy (2015), allowed correction of any early misidentification. When possible, and after formal identification, juveniles were released alive. In other locations (Port-Vendres, Agde, Port-Cros, Villefranche,

Bonifacio and Saint-Florent), larvae were euthanized following ethical standard procedures by cooling their water down (following Mittal & Whitear 1978, Collymore et al. 2014). Each specimen was identified under a stereomicroscope to the lowest taxonomic level, usually species, based on Lo Bianco (1931), Fahay (2007), and Crec'hriou et al. (2015).

2.3. Ancillary data

The list of species caught by CARE light-traps was compared with the list of potentially catchable teleost species along French Mediterranean coasts (Louisy 2015). The moon phase and theoretical illumination at midnight were computed for each sampling night using the date, longitude, and latitude of sampling (Meeus 1988).

2.4. Statistical analyses

2.4.1. Standardisation of catches

Raw abundances were standardized into catch per unit of effort (CPUE), with 'effort' being both number of traps and time fished (e.g. in Doherty 1987b, Félix-Hackradt et al. 2013b, Strydom 2003); this CPUE is used in all analyses and always computed as the number of larvae in a trap per night at a site.

2.4.2. Exploration of taxonomic diversity

The standardisation in CPUE cannot compensate for the underestimation of taxonomic richness at sites with low sampling effort. To compare species richness among sites, species accumulation curves were therefore computed. For each site, these curves represent the cumulative number of species found for increasing numbers of nights sampled. The curves were computed from 1000 random permutations of the full dataset, to homogenise the effect of effort along the series (Gotelli & Colwell 2001). Species richness was then compared among sites and MPA proximity, i.e. within or <5 km to a MPA vs. > 5 km from a MPA, for a fixed sampling effort (20, 50, and 150 nights), and p-values for the comparisons among pairs of sites were computed based on the result of the 1000 permutations.

Diversity indices focusing on the relative abundance of species, such as Shannon's entropy (H) and Pielou's evenness (J) were computed and compared

among sites, regions, and MPA proximity using non-parametric tests since the distribution of residuals was never normal. We also computed regional (β) diversity using the Whittaker formulation and tested the different factors (east vs. west of the Rhône, topography, and MPA vs. no-MPA) with an ANOVA on the dissimilarity matrices. Because most sites were sampled during summer months only, data were restricted to catches between May to September to test for east vs. west and topographic differences and between June and August for protection-based analyses, when MPAs were sampled.

To explore assemblage composition among sites, years, or months, assemblage matrices were represented graphically using a correspondence analysis. Groups of species displaying similar settlement patterns were objectively delimited through hierarchical clustering, based on chi-squared distance matrices to focus on relative rather than absolute abundances and still be comparable with the correspondence analysis. Yet, even with the chi-squared distance, which is appropriate for abundances and accounts for rare species, results were dominated by the effect of the numerous rare species in the dataset. A subset of 19 species was therefore constituted for such assemblage analyses, using the 12 species with highest CPUE and 7 less abundant species but that were present in at least 7 of the 13 sites, hereafter referred as 'meaningful species'. This subset represented 96 % of the total catches and 26.4 % of the total species richness and was considered representative of the dominant species in the assemblage.

To compare assemblage composition among sites, multivariate analyses of variance by permutations (PERMANOVAs) were performed. They were also based on chi-squared distance matrices, and p-values were calculated based on 1000 random permutations (Anderson 2001). Two 1-way PERMANOVAs were performed to compare sites located (1) in proximity vs. away from an MPA, (2) to the east vs. west of the Rhone river and (3) in the Ligurian sea vs. the Gulf of Lion. The first comparison enables to test for an effect of protection measures on larval supply, while the two latter reflect the most obvious geomorphological and hydrographical shifts in the region. Sites on the west of the Rhône are mostly over sandy bottoms, under the influence of the plume of sediment of this major river, while rocky shores and clearer waters dominate in the east. Sites in the Ligurian Sea are under strong influence of the Liguro-Provençal current, which can flow close to the coast due to the absence of a continental shelf, while sites in the Gulf of Lion are more remote from the current.

2.4.3. Exploration of abundances

Fish recruitment, and subsequently settlement, has long been known to be highly variable among years (Hjort 1914) and clustered in time and space within a year (Doherty 1987b). This pattern was also the case here, and the data were dominated by null or low catches, with few events of high catches distributed along the series. These rare events may, however, be the most important for the replenishment of coastal populations (Hedgecock 1994). Classic statistical approaches considering only variance around the mean (i.e. parametric) or ranks around the median (i.e. non-parametric) are useless in this situation because the central tendency only (i.e. the mean or median) is not relevant. Therefore, we chose to base our entire approach on quantile regression (Koenker 2005), with a focus on low catches (25 % quantile, q_{25}), median catches (50 % quantile, q_{50}), high catches (75 % quantile, q_{75}), and extraordinary catches (90 % quantile, q_{90}). Tests on q_{50} will provide results relatively similar to non-parametric tests on the median, but the consideration of several quantiles enables extraction of additional information from the same data. For example, even if no difference is found in the median larval supply between 2 sites, significant differences in q_{25} would indicate that the 2 sites still receive a different baseline supply (i.e. events of low larval supply), while differences in the upper quantiles (q_{75} and q_{90}) indicate that one site receives more exceptional events of larval supply than the other.

The relationships between quantiles of CPUE and continuous variables (i.e. classic regressions) were tested, and 95 % confidence intervals were calculated by bootstrapping with 1000 repetitions. The variance of CPUE quantiles among levels of a categorical variable (i.e. ANOVA) were tested by comparing the model with the explanatory variable included in a null model; significance was computed through an analysis of weighted absolute residuals (Chen et al. 2008), with 1000 repetitions.

Time series of the target quantiles were fitted by locally linear non-parametric regressions: 200 dates were regularly spread across the range of the data. For each date, a linear quantile regression model was fitted with normally distributed weights centred on the date of interest and spanning a neighbourhood of 20 d; the fitted value was extracted at the point of interest and a 95 % confidence interval was computed through bootstrapping with 1000 repetitions.

The influence of the moon phase was tested by computing the mean CPUE per lunar day (i.e. the number of days since the last new moon) for each

species. This index of CPUE per lunar day was scaled to the maximum CPUE among all species to remove differences in total abundance. The target quantiles of these scaled CPUE were linearly regressed against the absolute number of days to or since the new moon (e.g. data from 5 d before or after the new moon provide 2 data points for the fifth absolute lunar day), hence assuming a symmetric response of larval supply intensity around the new moon and homogenising differences in sampling effort among sites.

To assess the variability in CPUE at multiple temporal scales, quantile-based autocorrelograms (also named 'quantilograms') were computed based on Linton & Whang (2007). While classic autocorrelograms consider the pairwise correlations of anomalies to the mean for each temporal lag, quantilograms consider the pairwise correlations of the signs of the anomaly to the selected quantiles (here 25%, 50%, 75%, and 90%) at each temporal lag. Quantilograms can be interpreted like classic autocorrelograms, e.g. if the correlation values for the 90% quantile of CPUE are high until a lag of 5 d, it means that, when an extraordinary catch occurs, there is a high probability that another one will occur again within the next 5 d. We computed quantilograms at the 3 sites with the highest and most systematic sampling effort (Leucate, Villefranche, and Bastia) for the following lags: every day from 1 to 7 d, every 2 d from 8 d to 1 mo, and every 5 d from 1 mo to 1.2 yr.

The characteristic arrival date of each species at each site was computed as the mean of the numbers of days since 1 January, weighted by the CPUE of those days. For species settling in winter, with settlement peaks spanning over 1 January, dates were shifted by half a year, providing the mean of the number of days since 1 July for computation. This allowed us to correctly fit settlement peaks or to centre the date in the middle of the settlement period for species with a broader settlement phenology, regardless of their settlement period. Then synchronicity among sites was tested with Wilcoxon tests on the characteristic day of arrival. Anomalies were computed by subtracting the average date of arrival, for each species; this way, all species can be represented on the same plot, where 0 means 'the usual date of arrival'. These statistics were computed for the meaningful species plus all other species common enough across sites to warrant a computation (27 species). *Sarpa salpa* was not considered because it has 2 reproduction periods (Tsikliras et al. 2010) that would bias the test.

All p-values of pairwise tests were corrected within the tests with the Holm's statistical correction for multiple testing, and p-values of multiple tests based

on the same data were corrected with the Bonferroni correction.

2.4.4. Implementation

All analyses were conducted in R (3.5.1) (R Core Team 2018) with packages *tidyverse* (Wickham et al. 2019) for data manipulation and plotting, *oce* (Kelley & Richards 2019) for moon phase calculations, *pastecs* (Grosjean & Ibanez 2018) for time series analyses, *vegan* (Oksanen et al. 2019) for species composition comparisons, and *quantreg* (Koenker 2019) for quantile regression. All code and data are freely available, under GNU General Public License v3 and Creative Commons Attribution-ShareAlike 4.0 International license, respectively, at <https://github.com/jiho/medplanet>.

3. RESULTS

3.1. General description of catches

A total of 27 800 settlement-stage fish larvae of demersal species were caught over the course of the study. When zeros were excluded (42% of the sampling events), the usual CPUE were still very low, often ~1 larvae per trap per night at a site. However, in terms of total number of fishes supplied to the coast, it was the rare, very high CPUE events that contributed the most. Overall, 1073 'sampling events' (1 event = 1 night fished at 1 site, regardless of the number of light-traps) were recorded in the dataset, and >50% of the 27 800 larvae were caught during only 23 of those fishing events (2% of the effort); 90% of the catch was reached for only 32% of the sampling effort. In particular, 2 nights in Corsica resulted in extremely high catches of *Spicara smaris* (CPUE > 800 larvae per trap per night at a site), which dominated everything else.

Among the 51 families, 123 genera, and 218 species of demersal fishes living along the Mediterranean coast of France (Louisy 2015), 59% of families (n = 29), 39% of genera (n = 48), and 33% of species (n = 72) were caught in CARE light-traps. The most abundant and frequent families among sites were Sparidae (58% of total CPUE), Pomacentridae (16%), Blenniidae (10%), Mullidae (6%), Mugilidae (4%), Atherinidae (2%), and Gadidae (1%), which altogether, represent 97% of the total CPUE. The 12 dominant species retained for several analyses accounted for 93% of the total CPUE: *S. smaris*

(44%), *Chromis chromis* (18%), *Mullus surmuletus* (7%), *Diplodus annularis* (5%), *Parablennius pilicornis* (4%), *Pagellus bogaraveo* (4%), *Sarpa salpa* (3%), *Pagellus acarne* (2%), *Oblada melanura* (2%), *Atherina hepsetus* (2%), *Gaidropsarus mediterraneus* (2%), and *Boops boops* (1%).

3.2. Spatial patterns

3.2.1. Total larval supply among sites and regions

Overall, the average larval supply was 4.5 ± 30 larvae per trap per night, with particularly high mean CPUE in Saint-Florent and Bonifacio (mean \pm SD CPUE of 17.6 ± 51.0 and 29.7 ± 152 , respectively) due to several events of very intense settlement. The highest local taxonomic richness was observed in Villefranche-sur-Mer (46 taxa) and the lowest in Carry (7 taxa).

The distribution of CPUE among sites (Fig. 2) highlights that 5 sites yielded high catches (Saint-Florent, Villefranche, Port-Cros, Les Embiez, and La Ciotat) and 6 sites received consistently low larval supply (Bastia, Marseille, Carry, Agde, Port-Vendres, and Leucate). While Bonifacio and Cassis seemed to pres-

ent above-average CPUE, they showed no statistical differences, probably because of a lower sampling effort at those sites. In detail, the 25% quantile of CPUE (q25, i.e. the CPUE when catches were low) was significantly higher in Saint-Florent than in Bastia, Marseille, and Carry (quantile-based ANOVA: qAOV, all $p < 0.05$). St-Florent and Villefranche had significantly higher q50 than Bastia, Marseille, and Carry (qAOV, all $p < 0.05$). For higher catch levels, q75 was significantly lower in Bastia compared to several other sites, while q90 was significantly higher in Villefranche than in Bastia, Marseille, Carry, Agde, Port-Vendres, and Leucate. Finally, Saint Florent, Bonifacio, Villefranche, Port-Cros, Les Embiez, La Ciotat, and Cassis, the group of sites with high supply, were never significantly different from each other at any level of catches (qAOV, all $p > 0.05$).

On a broader scale, this pattern is translated in the fact that high (q75) and extraordinary (q90) catches were significantly larger at sites located in the Ligurian Sea (q75 = 3 CPUE, q90 = 9.9 CPUE) compared to those located in the Gulf of Lion (q75 = 2 CPUE, q90 = 5.4 CPUE; qAOV both $p < 0.01$); and also larger for sites located to the east of the Rhone river (q75 = 3 CPUE, q90 = 9.2 CPUE) compared to

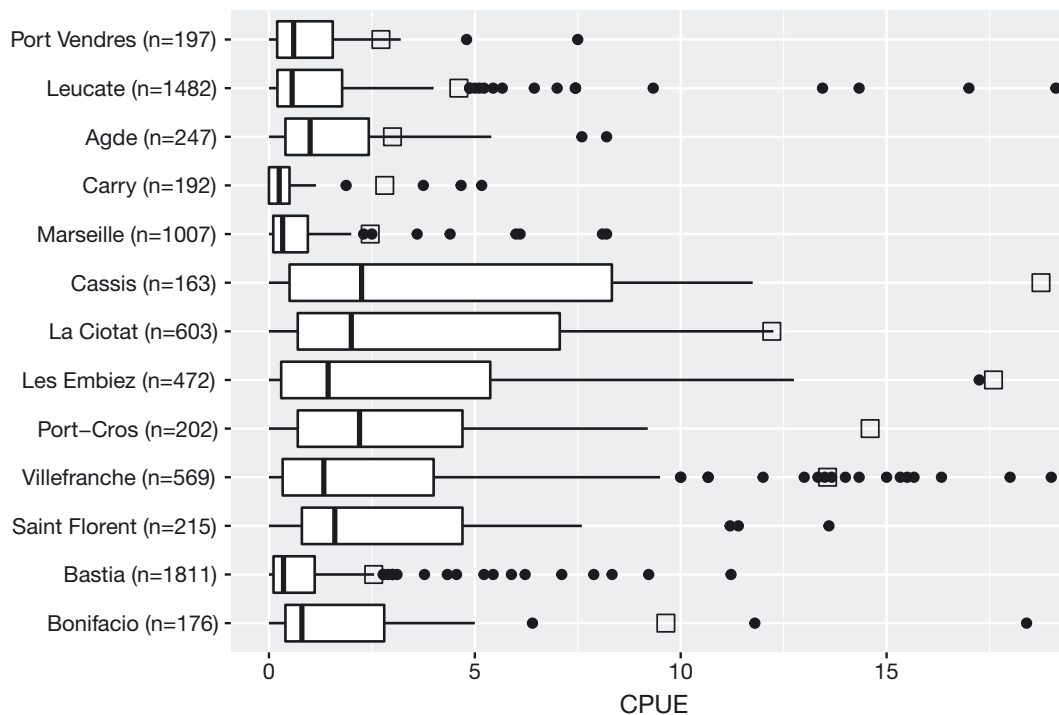


Fig. 2. Distribution of CPUE per site. CPUE is displayed using standard boxplots (central bar: median, box: 25% to 75% quantiles, whiskers: 95% confidence interval for the median, dots: points outside this interval) and an empty square for the 90% quantile. The plot is truncated at CPUE 18.5 to focus on the most common events, which still encompass >90% of the data for 9 of the 13 sites

the west side ($q_{75} = 2$ CPUE, $q_{90} = 3.8$ CPUE; q_{AOV} both $p < 0.001$).

3.2.2. Taxonomic diversity among sites and regions

On the species accumulation curves (Fig. 3), Carry showed significantly lower species richness than many other sites ($p < 0.05$ for 6 sites) at an effort of 20 nights sampled (the largest effort level at which all stations could be compared). At the more meaningful effort levels of 50 and 150 nights, species richness was significantly lower in Bastia compared to Leucate and Villefranche. Besides these differences, other sites did not significantly differ in terms of species richness, when they were comparable.

Diversity indices were not different between sites located in the Ligurian Sea and in the Gulf of Lion ($H = 1.16 \pm 0.6$, $J = 0.76 \pm 0.2$ and $H = 1.12 \pm 0.5$, $J = 0.82 \pm 0.2$, respectively; Wilcoxon, all $p > 0.05$; Table 1) nor between the west and east of the Rhône ($H = 1.22 \pm 0.5$, $J = 0.84 \pm 0.1$ and $H = 1.11 \pm 0.6$, $J = 0.77 \pm 0.2$, respectively; Wilcoxon, all $p > 0.05$). Similarly, few differences in diversity indices were found among sites: Pielou's evenness was significantly different for at least 1 site, when tested against all sites (Kruskal,

$c^2 = 21$, $p = 0.05$), but it was not possible to identify which one, because the difference was too slight for the less powerful pairwise tests (pairwise Wilcoxon, all $p > 0.05$). No pattern of β -diversity emerged at the regional scale (Whittaker formulation of β -diversity and 3 ANOVA, each with $p > 0.05$).

3.2.3. Species assemblages among sites and regions

Sites were separated into 7 groups according to their assemblage composition (Fig. 4a). Villefranche was characterised by the relative abundance of *O. melanura*, Leucate of *P. bogaraveo*, Marseille of *D. annularis* and *B. boops* and Carry of *P. pagrus* and *Scorpaena porcus*. While most clusters matched geographical patterns, Agde and Port-Cros were associated (Fig. 4).

On a broader spatial scale, species assemblages were different between the east and west sides of the Rhône river (PERMANOVA, $F = 3.8$, $R^2 = 0.25$, $p = 0.001$) but not between the Ligurian Sea and the Gulf of Lion ($F = 1.4$, $R^2 = 0.09$, $p > 0.05$). At the species level, the median CPUE in the Gulf of Lion and the Ligurian Sea were significantly different for a few species only, mostly in the lower and upper quantiles (quantile-ANOVA, p -values < 0.05 for q_{25} : 8 of 12

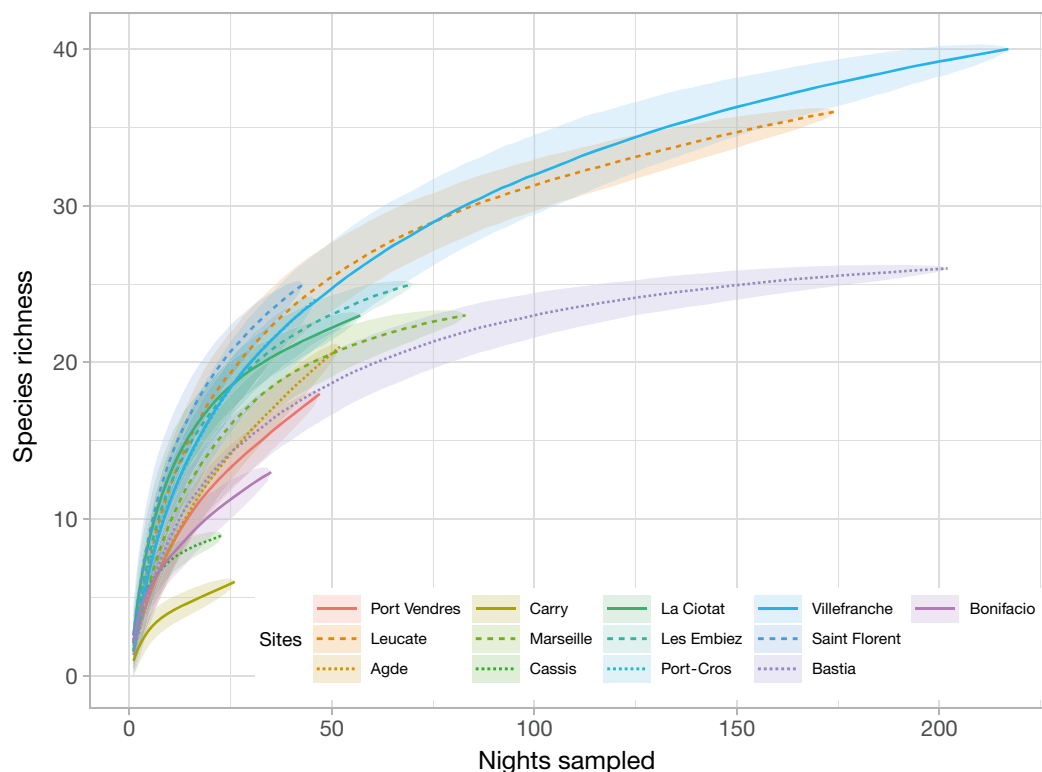


Fig. 3. Species accumulation curves per site (lines) and standard deviation around them (shaded areas)

species, median: 3 of 12 species, q75: 3 of 12 species, q90: 8 of 12 species). Differences between each side of the Rhône were more consistent, with differences in the median catches of all most abundant species, yet only in 5 of 12 species for most extreme quantiles (Table 2). Overall, *A. hepsetus*, *B. boops*, *C. chromis*, *O. melanura*, and *S. smaris* were more abundant in the Ligurian Sea, while *P. bogaraveo* and *P. pilicornis* were more abundant in the Gulf of Lion.

3.2.4. Synchronicity among sites

The date of arrival of the species at each site highlighted a geographical pattern (Fig. 5). On the eastern side, larvae arrived early at several sites (La Ciotat, Villefranche, and Bastia; Wilcoxon, all $p < 0.05$), except at Port-Cros where they arrived significantly late (Wilcoxon, $W = 285$, $p < 0.05$). On the western side, the only significant difference is at Port-Vendres, where arrivals were late (Wilcoxon, $W = 120$, $p < 0.01$). At larger scale, this difference translated into earlier arrivals east of the Rhône compared to west of the Rhône (mean lag east = -6.5 d vs. mean lag west = $+9.1$ d; Wilcoxon, $W = 1130$, $p < 0.01$). In contrast, once again, the timing of arrivals did not differ between the Ligurian Sea and the Gulf of Lion (Wilcoxon, $W = 1263$, $p = 0.23$).

3.2.5. Larval supply to MPAs

Total larval supply was significantly higher around MPAs than away from them for the intense events (q75 = 20.8 CPUE close to MPAs while q75 = 8.7 CPUE away from MPAs, qAOV, $F = 44.6$, $p < 0.05$). The difference only approached significance for quantile 90% (q90 = 54.3 vs. 24.8 CPUE; qAOV, $F = 70.2$, $p = 0.074$). Low and median larval supply events were never significantly different (median, qAOV, $F = 3.69$, $p = 0.37$; q25, qAOV, $F = 0.4$, $p = 0.61$). No clear pattern was found for events of median or high intensity of the meaningful species, with some species present at higher abundances around MPAs (e.g. *G. mediterraneus* and *S. smaris*) and others in unprotected sites (e.g. *S. salpa* and *P. bogaraveo*). Taxonomic richness in larval supply was never significantly different close or away from

MPAs, regardless of the sampling effort considered (species accumulation curves with 1000 permutations for 20 and 50 nights sampled, all $p > 0.05$). Similarly, diversity indices were comparable (Piélou's evenness: Wilcoxon, $W = 846$, $p = 0.7$; Shannon's diversity, $W = 750$, $p = 0.06$; β -diversity, ANOVA, $F = 0.27$, $p = 0.61$).

3.3. Temporal patterns

3.3.1. Larval supply among years

While summer 2013 was marked by the most extreme catch events of the time series (>100 larvae per trap per night at a site), over the whole year, catches were higher in 2014 and 2015 for almost all catch levels (pairwise quantile-ANOVA, all $p < 0.05$; except q50 compared to 2015 and q75 to 2014 with both $p > 0.05$). Contrastingly, CPUE were never significantly different between 2014 and 2015, at all levels (pairwise quantile-ANOVA, all $p > 0.05$). These differences should not be regarded as an interannual trend (and were not tested as such) because the 3.5 yr time series was likely too short for such an interpretation.

3.3.2. Seasonality of larval supply

Unsurprisingly, catches were very seasonal (Fig. 6a, Fig. S3). All particularly high catch events (CPUE > 30 larvae per trap per night at a site) occurred between the end of May and mid-August. High and extraordinary catches (quantiles 75% and 90%) dis-

Table 1. Diversity indices (*H*: Shannon's diversity, *J*: Piélou's evenness) of the sampling sites, computed over the entire period. The mean \pm SD and the median \pm median absolute deviation (MAD) are provided for each site

| Site | <i>H</i> | | <i>J</i> | |
|---------------|----------------|------------------|----------------|------------------|
| | mean \pm SD | median \pm MAD | mean \pm SD | median \pm MAD |
| Port Vendres | 1.13 \pm 0.4 | 1.07 \pm 0.5 | 0.91 \pm 0.1 | 0.93 \pm 0.1 |
| Leucate | 1.56 \pm 0.3 | 1.55 \pm 0.1 | 0.81 \pm 0.1 | 0.82 \pm 0.1 |
| Agde | 0.95 \pm 0.5 | 1.1 \pm 0.3 | 0.82 \pm 0.1 | 0.86 \pm 0.1 |
| Carry | 1 \pm 0.3 | 1.05 \pm 0.2 | 0.85 \pm 0.1 | 0.84 \pm 0.1 |
| Marseille | 0.99 \pm 0.5 | 1.05 \pm 0.4 | 0.83 \pm 0.2 | 0.94 \pm 0.1 |
| Cassis | 0.98 \pm 0.4 | 1.12 \pm 0.2 | 0.64 \pm 0.2 | 0.52 \pm 0 |
| La Ciotat | 0.97 \pm 0.6 | 1.16 \pm 0.5 | 0.62 \pm 0.3 | 0.61 \pm 0.3 |
| Les Embiez | 1.08 \pm 0.5 | 1.13 \pm 0.6 | 0.73 \pm 0.2 | 0.75 \pm 0.2 |
| Port-Cros | 1.18 \pm 0.4 | 1.14 \pm 0.3 | 0.7 \pm 0.1 | 0.72 \pm 0.1 |
| Villefranche | 1.41 \pm 0.6 | 1.48 \pm 0.5 | 0.86 \pm 0.1 | 0.9 \pm 0 |
| Saint Florent | 1.11 \pm 0.6 | 1.05 \pm 0.9 | 0.69 \pm 0.3 | 0.85 \pm 0.1 |
| Bastia | 1.06 \pm 0.6 | 0.85 \pm 0.3 | 0.77 \pm 0.3 | 0.91 \pm 0.1 |
| Bonifacio | 1.03 \pm 0.7 | 1.29 \pm 0.5 | 0.78 \pm 0.3 | 0.86 \pm 0.1 |

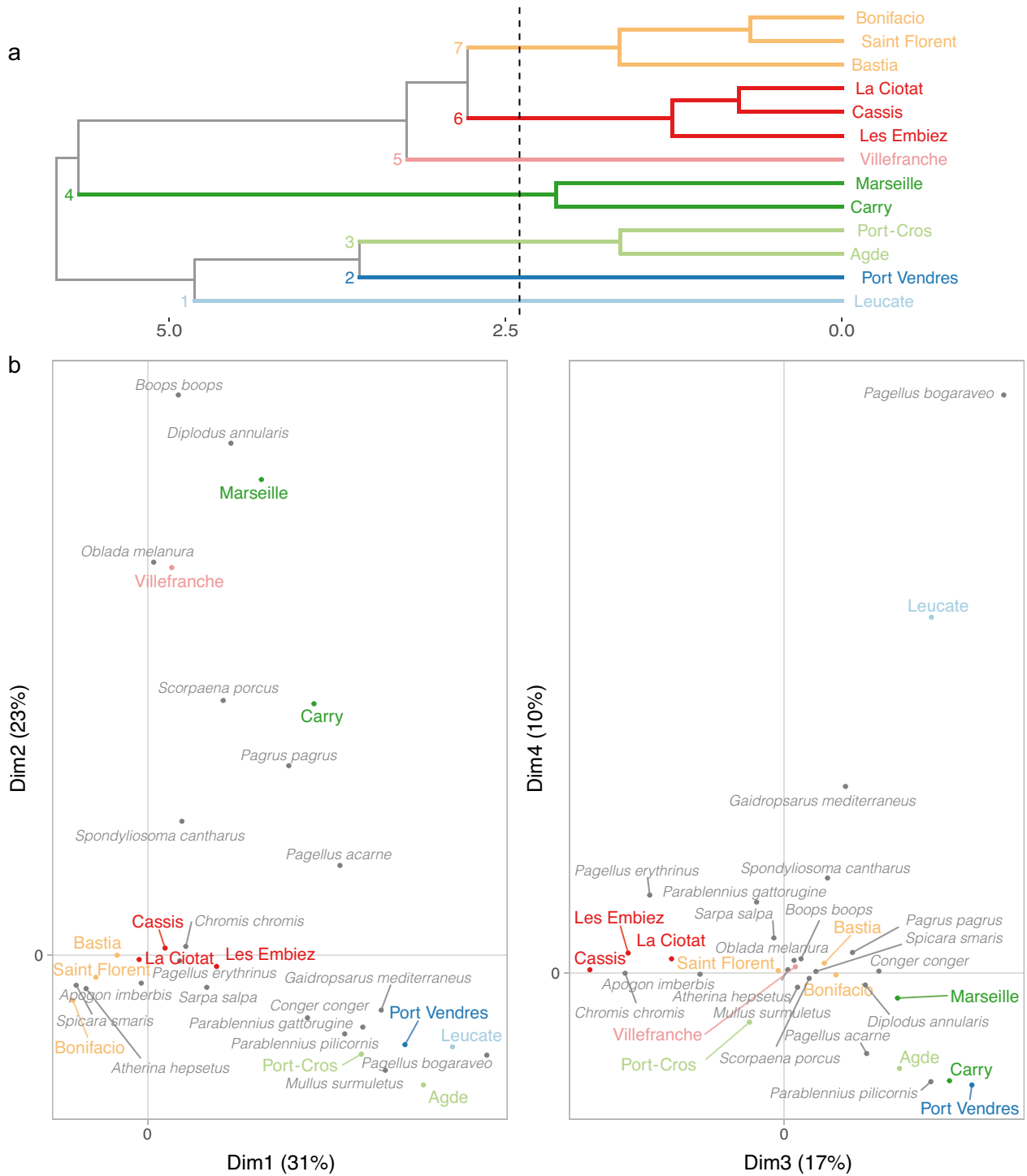


Fig. 4. (a) Tree of the hierarchical clustering and (b) plots in the 4 first dimensions of the correspondence analysis computed per site, on species assemblages considering the meaningful species and for summer months only. The proportion of variance explained is given for each dimension (%). Colors indicate sites displaying similar assemblages according to the hierarchical clustering

play the most marked seasonality but, overall, all quantiles follow the same seasonal pattern (Fig. 6a). The timing of arrival of the species was also very seasonal, with 3 main temporal assemblages (Fig. 6b,

Fig. S5): the first in late spring-early summer with low diversity and high abundances, the second in summer with high diversity and decreasing abundances, and the third in late autumn-early winter

Table 2. CPUE of the dominant species between West and East of the Rhône river. Mean \pm SD of CPUE are given for each species in each region, as well as the adjusted p-values of the quantile-PERMANOVA test for differences between regions for each target quantile. **Bold**: significant at $p < 0.05$

| Species | CPUE West of Rhone (mean \pm SD) | CPUE East of Rhone (mean \pm SD) | p-value of difference per quantile | | | |
|-------------------------|---------------------------------------|---------------------------------------|------------------------------------|------------------|------------------|------------------|
| | | | q25 | q50 | q75 | q90 |
| <i>A. hepsetus</i> | 0 \pm 0 | 0.09 \pm 1.5 | <0.001 | <0.001 | <0.001 | 0.26 |
| <i>B. boops</i> | 0 \pm 0 | 0.15 \pm 1.2 | <0.001 | <0.001 | <0.001 | 0.94 |
| <i>C. chromis</i> | 0.02 \pm 0.1 | 0.85 \pm 4.8 | 0.001 | 0.002 | 0.003 | <0.001 |
| <i>D. annularis</i> | 0.02 \pm 0.3 | 0.32 \pm 2.1 | <0.001 | <0.001 | 0.12 | <0.001 |
| <i>G. mediterraneus</i> | 0.04 \pm 0.1 | 0.05 \pm 0.3 | <0.001 | <0.001 | <0.001 | <0.001 |
| <i>M. surmuletus</i> | 0.34 \pm 1.5 | 0.23 \pm 2.3 | <0.001 | <0.001 | <0.001 | 0.001 |
| <i>O. melanura</i> | 0 \pm 0 | 0.2 \pm 2.3 | <0.001 | <0.001 | <0.001 | 0.59 |
| <i>P. acarne</i> | 0.12 \pm 0.6 | 0.11 \pm 0.7 | <0.001 | <0.001 | <0.001 | 0.94 |
| <i>P. bogaraveo</i> | 0.16 \pm 1 | 0.04 \pm 0.4 | <0.001 | <0.001 | <0.001 | <0.001 |
| <i>P. pilicornis</i> | 0.33 \pm 1.2 | 0.1 \pm 0.8 | <0.001 | <0.001 | <0.001 | <0.001 |
| <i>S. salpa</i> | 0.1 \pm 0.9 | 0.11 \pm 0.7 | 0.001 | <0.001 | <0.001 | 0.27 |
| <i>S. smaris</i> | 0 \pm 0 | 0.89 \pm 6.2 | <0.001 | <0.001 | 0.07 | <0.001 |

with low diversity and low abundances. Some species consistently settled over just few weeks (e.g. *Epinephelus marginatus* and *Dentex dentex*), many

over 1 or 2 mo (e.g. *Spondyliosoma cantharus* and *Scorpanea notata*), and some for up to 4 mo (e.g. *G. mediterraneus* and *P. pilicornis*).

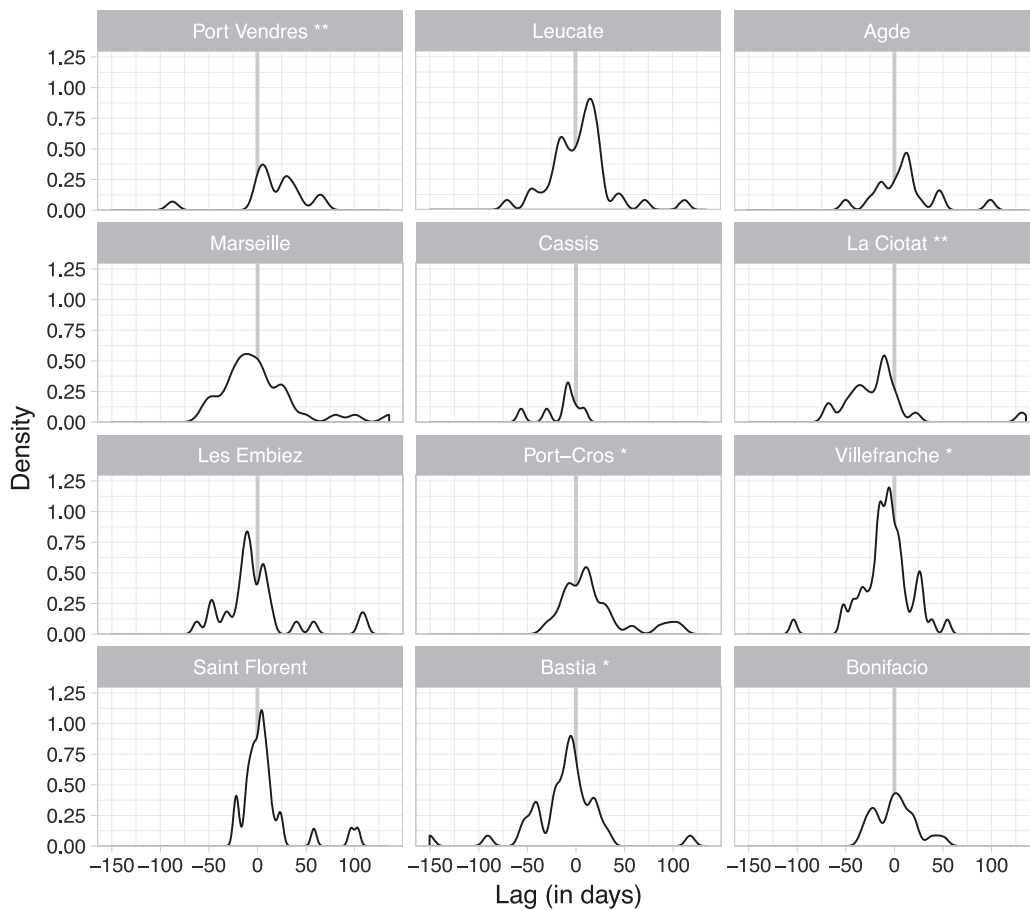


Fig. 5. Anomalies in the timing of arrival at each site. Smoothed probability density curves of the anomalies in the arrival dates, computed for each species, year, and site. Asterisks in the panels' titles indicate whether lags are significantly different from 0 (i.e. significant early or late arrival at this site; *adjusted $p < 0.05$, **adjusted $p < 0.01$). Site 'Carry' was removed from the plot since it provided limited information (only 5 species could be considered, which were caught in a single year)

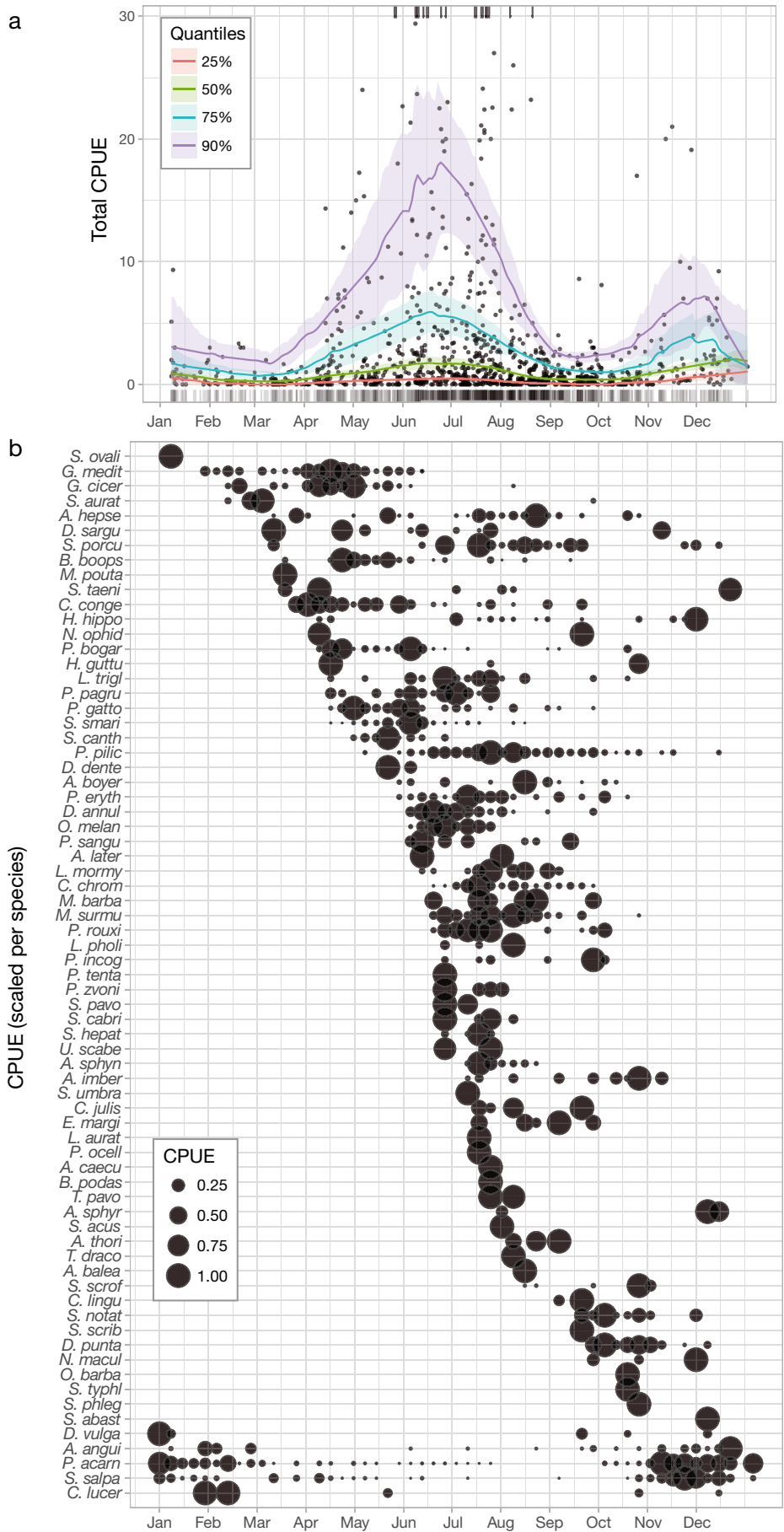


Fig. 6. (a) Seasonality in total CPUE. Points are observed CPUEs; lines display the local quantile regressions for quantiles 25%, 50%, 75% and 90%, along with their 95% confidence interval (shaded areas). Catch events with CPUE >30 fish larvae per trap per night at a site are cropped for plotting and indicated by ticks at the top of the figure. (b) Intensity of larval supply for each species, per week averaged across years. To allow comparison of arrival times among species, irrespective of their relative abundances, CPUE was scaled between 0 and 1 for each species

Abundances and diversity were low between January and April. Then abundances increased but diversity stayed low during early spring, from April to late May. In June, diversity and abundance started to increase, before both decreased in August. Abundances were low during the summer-autumn transition (i.e. mid-August to late October), even though larval diversity remained much higher than during the winter period (i.e. January to April). Finally, the November–December peak in CPUE was characterised by few species present in high abundance.

3.3.3. Influence of the moon

Catches were higher around the new moon, for all levels of catches considered (quantile regression, $p < 0.001$ for all quantiles). Still, the influence of the moon was most marked for the highest quantiles (75% and 90%), which display the steepest slopes (Fig. 7).

3.3.4. Temporal scales of variability in larval supply

Quantilograms were computed for the 3 sites where sampling effort was the highest and most homogeneously distributed (Bastia, Villefranche-sur-Mer, and

Leucate; Fig. S2). Larval supply is positively autocorrelated on the scale of a week for q25, q50, and q75 (Fig. 8). When catches are high, they are thus likely to stay high for 1 wk; when they are low, they are likely to stay low for 1 wk. Extraordinary catches (quantile 90%) are significantly autocorrelated at a lag of 1 d only, which is expected since these events typically do not last long. The influence of the moon, highlighted above, translates into frequent positive autocorrelation around 1 lunar month. Some seasonal patterns are apparent at larger time scales but not as consistently as the ones described above.

3.3.5. Species assemblages among years and seasons

The correspondence analysis of the fish larvae assemblage among years shows that 2013 was mostly characterised by the high relative abundance of a single species of Sparidae, *S. smaris* (Fig. S4), whose abundance peaks were the highest of the series. The year 2014 was associated with a more diverse assemblage mostly composed of sparids (e.g. *B. boops*, *D. annularis*, and *O. melanura*), while 2015 presented higher relative abundances of *C. chromis*, *G. mediterraneus*, and *Pagellus erythrinus*. The same analysis performed per month highlighted 3 main periods

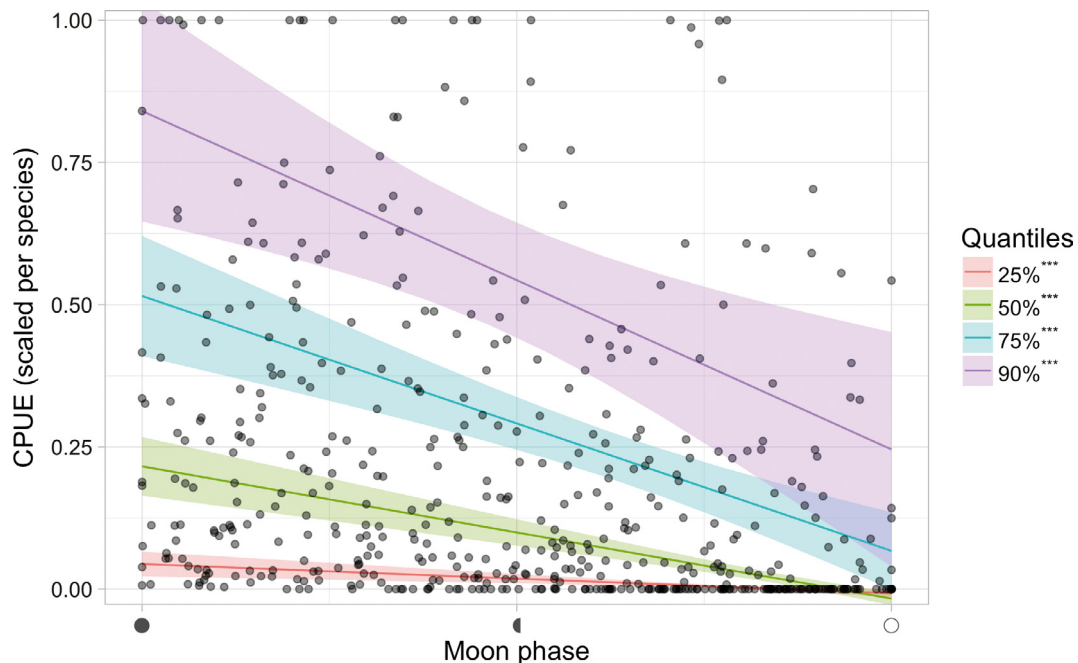


Fig. 7. Quantile regressions of CPUE on moon phase. CPUE were normalized between 0 and 1 per species to use all species together. They were binned per day since/to the new moon to simplify the plot. Points were slightly jittered horizontally (width = 0.5) to avoid overlap. The solid lines and shaded areas represent the quantile regressions and their 95% confidence interval for quantiles 25%, 50%, 75% and 90%. All regressions were significant (***) $p < 0.001$

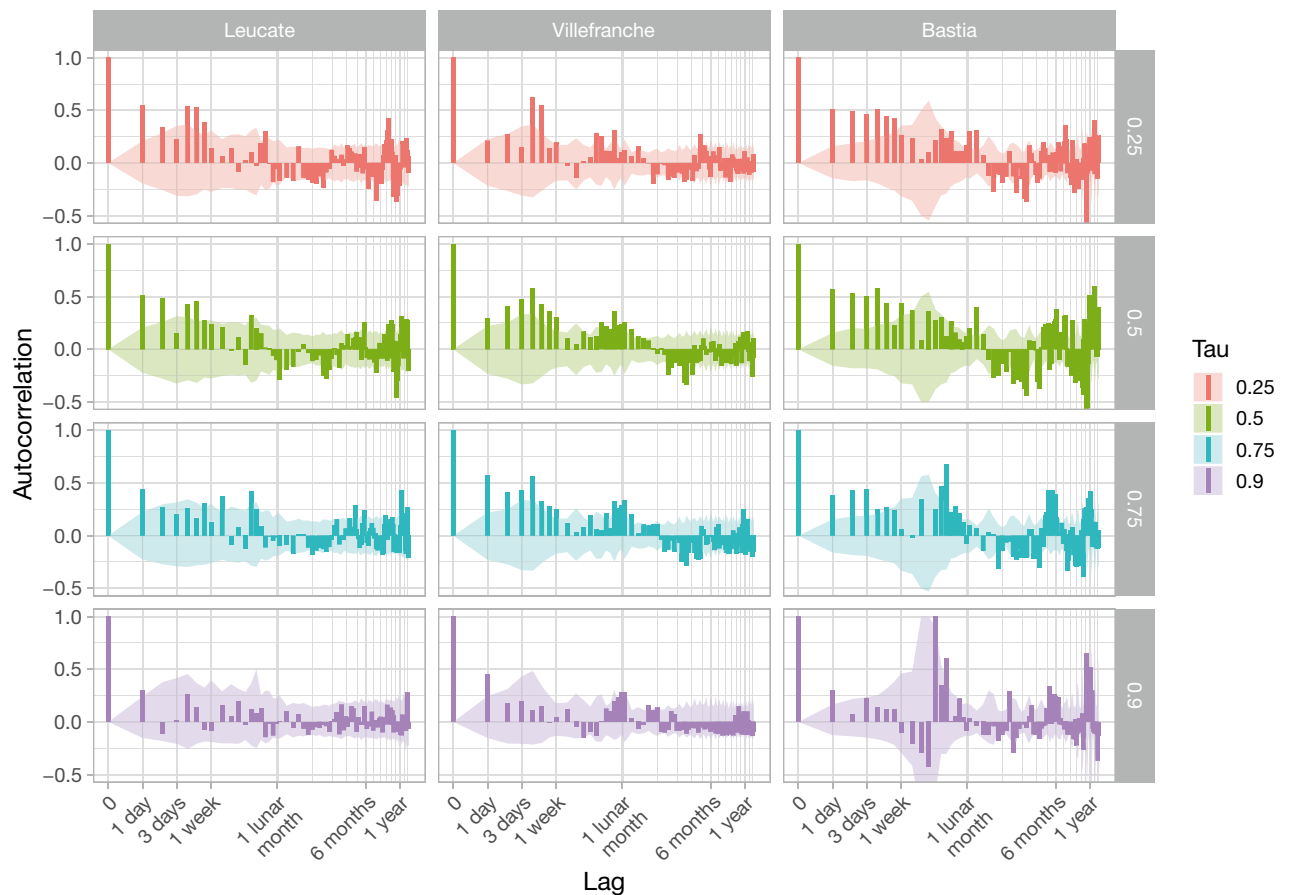


Fig. 8. Quantilograms (i.e. quantile-based correlograms) at the 3 most sampled sites for lags from 1 d to 1.2 yr. Autocorrelation is significant when higher (or lower) than the 95% confidence interval (shaded area). The periodic patterns in the confidence interval are due to sampling: when sampling occurs mostly at regular intervals (Villefranche: 1 wk, Bastia: 1 lunar month), some lags are rarely observed and uncertainty increases

and assemblages: (1) November to February, characterised by high relative abundance of *P. acarne* and *S. salpa*; (2) April to June, with a more diverse, less characteristic pool of species; (3) July to September, characterised by high relative abundances of *C. chromis*, *M. surmuletus*, *P. pilicornis*, *A. hepsetus*, *P. erythrinus*, and *S. porcus*. Other months were in between these 3 poles (Fig. S5).

4. DISCUSSION

4.1. Comparison with adult assemblages

In this study, 5 families constituted 94% of the larval fish assemblages: Sparidae, Pomacentridae, Blenniidae, Mullidae, and Mugilidae which constituted 94% of the catch. This is in general accordance with the assemblages of adults in coastal habitats of the north-western Mediterranean Sea (Guidetti 2000, 2004, García-Charton & Pérez-Ruzafa 2001). Still,

there were a few exceptions. For example, the family Gadidae was quite abundant in the larval pool while rarely observed as adults. Four species (*Dicentrarchus labrax*, *Sparus aurata*, *Diplodus vulgaris*, and *Diplodus sargus*) were seldom caught as larvae while adults are frequently observed in the region. These species are known to migrate to sandy lagoons during the pelagic phase (Abecasis et al. 2009, Mercier et al. 2012), and here, only 2 sites were located close to lagoons, therefore reducing the chances of catching these lagoon-associated species. The fact that few sampled sites were located over sandy bottoms may also explain the limited catches of species associated with sandy substrates, like Soleidae, Bothidae, and Schophtalmidae, which are common as adults (Letourneur et al. 2001).

Light-traps are selective for phototactic larvae only, and within a few families such as Labridae and Scariidae, this may lead to a taxonomic bias and possibly lower sampling efficiency compared to other methods (Meekan et al. 2000). This may further explain

the discrepancies between adults and larvae abundances. For example, the *Labrus* and the *Symphodus* genera of the Labridae family are abundant over hard substrates throughout the French Mediterranean coast (Guidetti 2000, 2004, García-Charton & Pérez-Ruzafa 2001, Guidetti et al. 2002), and the fact that only 16 specimens were caught in the light-traps over the 27 800 larvae collected is evidence of their selectivity. The global absence of labrids in light-traps may be attributed to the low mobility of their larvae, which have a short pelagic larval duration and do not undertake ontogenic migrations (Raventos & Macpherson 2005). Unless light-traps are set close to spawning sites, larvae of labrids may therefore be less easily captured than other fish taxa.

4.2. Spatial patterns of larval supply

4.2.1. Larval supply in and away from MPAs

The establishment of MPAs generally increases fish diversity (Rodrigues et al. 2004). Here, intense events of larval supply were >2-fold stronger at sites around MPAs, but taxonomic richness and diversity indices were comparable among protection levels. Both MPAs' locations and habitat quality within MPAs may favour higher (Gorud-Colvert and Sponaugle 2009) or lower (Valles et al. 2001) larval supply compared to fished areas. Such differences have also been observed in the NW Mediterranean Sea (Lopez-Sanz et al. 2009) yet only at local scale. In this region, the positive influence of MPAs on the intensity of larval supply may therefore occur at both local and larger scale. It is unknown, however, whether the larvae settling close to any of these MPAs originate from the nearby MPA, although such information is critical to enforce and develop the current network of MPAs along the French Mediterranean coast, where connectivity patterns are largely overlooked (Faillettaz et al. 2018b).

4.2.2. Larval supply among sites

The similarity in larval assemblages among sites can generally be explained by their geographic proximity (Fig. 4). The rates of larval supply (Fig. 2), the Shannon's diversity, and species evenness indices (Table 1) are also likely to be more similar when sites are closer to each other. However, when considering β -diversity only (i.e. regardless of the spatial patterns of abundance), the diversity appears relatively

homogeneous at the regional scale. Larval dispersal may thus occur more frequently as patches at local scale, while at the scale of the study, mixing may be high enough for most species to occur throughout the region.

While most sites were associated based on their geographic proximity, Port-Cros and Agde were associated based on high relative abundances of *Mullus surmuletus* and parablenniids (Fig. 4b), which is surprising because the 2 sites are distant, geomorphologically different (rocks surrounded by sand in Agde vs. mostly rock in Port-Cros), and Agde is an area open to fishing while the Port-Cros MPA was created in 1963 and is the oldest in France. Nevertheless, their relatedness may be explained by their potential function as refugia concentrating biodiversity, Port-Cros as an MPA and Agde as the rare rocky substrate within kilometres of sandy bottoms.

Carry and Marseille are located in the highly anthropised bay of Marseille, the second-largest city of France, and show the lowest diversity, species evenness, and larval supply (Table 1, Fig. 3; both median CPUE < 0.35 larvae per trap per night at site; Fig. 2). However, this cannot be explained by a biased sampling strategy. Habitat loss and pollutants are known to reduce the quality of marine habitats (Azzurro et al. 2010, Coll et al. 2012), which may result in poor larval supply and diversity in this bay, even in protected areas like the MPA of Carry (Hackradt et al. 2014). Given that larvae of Mediterranean Perciformes possess remarkable behavioural abilities at the settlement stage (Faria et al. 2011, Faillettaz et al. 2015, 2017), this finding also lends support to the active selection of their supply areas and not just of their settlement site (e.g. at the scale of meters; Carr 1991); if larval supply was driven by passive advection, they would be unaffected by the level of development and habitat degradation.

4.2.3. Larval supply at basin scale

Larval fish assemblages and the timing of larval supply were both different between the east and west of the Rhône river, but not between the topographic regions defined as the Gulf of Lions and Ligurian Sea. Larval supply was higher, with more exceptional events (quantiles 75% and 90%), in the east compared to the west of the study region, while fisheries are considered more productive in the west (Ifremer SIH 2016). Further data are required to compare adults with larvae abundance from the fisheries, yet sites located under the Rhône's influence may

experience higher variability due to the changing riverine inputs (Gatti et al. 2006) and may display higher seasonal and interannual variability (Thibaut et al. 2005) to which early larval stages of coastal species may be particularly sensitive. The Rhône may therefore induce a major shift in the longitudinal gradient of larval supply observed along the French Mediterranean coast.

4.3. Temporal patterns of larval supply

A strong seasonality was detected with 2 peaks of particularly high catches from mid-April to mid-August and from November to December (Fig. 6a). Species richness increases from March until July (48 species) and remains high until September (≥ 34 species mo^{-1} from June to September); it decreases from October onwards and remains low throughout the winter (≤ 12 species mo^{-1}). These seasonal patterns of larval supply are consistent as most larvae were caught within 1 to 2 mo of their reported spawning period in the NW Mediterranean or Adriatic Sea (Tsikliras et al. 2010). Such patterns had already been observed, albeit over shorter periods, in previous studies conducted in the region on settlement-stage fish larvae (Félix-Hackradt et al. 2013b) and on younger ichthyoplankton (Álvarez et al. 2012). Omitting pelagic species, the peak of larval supply occurred in the same months, from May to July. These seasonal patterns in larval supply are thus consistent throughout the western Mediterranean Sea.

It has long been suggested that fish larvae are strongly predated upon by visual predators during settlement and that settlement around the new moon, when light levels are lowest, has been evolutionarily selected because it increases survival (Johannes 1978, Leis & Carson-Ewart 1998, Planes & Lecaillon 2001, Doherty et al. 2004). The influence of the moon phase on larval supply is well described (Doherty 1987b, Milicich 1994, Sponaugle & Cowen 1996, Wilson 2001, Mwaluma et al. 2014) but had never been assessed explicitly in the Mediterranean. Félix-Hackradt et al. (2013b) sampled around the 1st and 3rd quarter moons only and still detected a slight preference towards lower illumination levels. With extensive sampling throughout the lunar month, our results confirm that larval supply is higher around the new moon (Fig. 7). This relationship was significant for all quantiles, which was rare in the rest of our analyses, and was the strongest for the higher quantiles (75% and 90%), indicating that massive supply

events are much more likely to occur around the new moon than during other lunar phases. While tides and lunar phase interact with larval supply in tropical environments (D'Alessandro et al. 2007), tides are negligible in the NW Mediterranean Sea. Unlike elsewhere, fish larvae may rely on signals other than tidal cues to trigger their transition from the pelagic environment to coastal habitats. A 1 wk, high-frequency sampling experiment at one of the sites (Villefranche-sur-Mer) showed that fish larvae settled primarily during the moonless hours of darkest night (Faillettaz 2015), further supporting that active selection in the timing of settlement may also occur in temperate fish larvae.

Light-trap efficiency may be reduced during moonlit nights (Hernandez & Shaw 2003) and this could have contributed to the above observed effect. However, the influence of the moon on settlement patterns has been confirmed by other sampling methods (Dufour & Galzin 1993). Catalan et al. (2014) compared the CARE light traps with other sampling methods in the NW Mediterranean Sea and found them efficient, but all tests were conducted around the new moon. Even if unlikely, a direct influence of external light on the catching efficiency cannot be ruled out.

Quantilograms enabled us to explore the variability of catches at multiple temporal scales, from which 3 main patterns have emerged. Over the longer time scale, the positive correlations at 6 mo and 1 yr lags, and the negative correlations at 3 mo lag (Fig. 8), are caused by the 2 seasonal peaks of settlement, in summer and winter (Fig. 6). At finer scale, the influence of the moon is visible at 1 lunar month. Yet, the strongest and most systematic positive correlations occurred within the first 7 d, while correlation vanished in the following 2 wk; for high quantiles, the positive correlations are significant over even shorter periods, indicating that high settlement events are very transient. With the 5% richest events yielding >50% of the total catch, larval supply in the NW Mediterranean Sea is dominated by pulses of high settlement occurring over a couple of days, around the new moon, in spring and to a lesser extent winter. In tropical environments, the replenishment of coral fish populations is also driven by local pulses of settlement (Doherty 1987b). The causes of such events are not known and likely result from the spawning patterns, hydrodynamic processes and the active control of their arrival time by larvae through swimming (Victor 1984), since several of these species have this potential (Faillettaz et al. 2015, 2017). While we cannot distinguish the causes of the spatio-temporal variability in larval supply, the 'sweepstakes

reproductive success' hypothesis, which states that the replenishment of marine populations and their gene flow are driven by extreme events (Hedgecock 1994, Christie et al. 2010, Riquet et al. 2017), may apply to demersal fish populations in the western Mediterranean Sea. This hypothesis could be tested by comparing the genetic structure of our largest cohorts to the genetic pool of a reference population in the northwestern Mediterranean Sea.

4.4. Emblematic species

Maintaining this type of sampling over long-term studies can also be used to monitor relative changes in the settlement of some endangered or managed species. For example, 23 dusky grouper larvae *Epinephelus marginatus* were caught: in 2013 in the MPA of Port-Cros (n = 10), in 2014 in Villefranche (n = 2) and the MPA of Les Embiez (n = 2), and in 2015 in La Ciotat (n = 1) and Cassis (n = 9; Table S2). Dusky groupers are emblematic, large top-predators which were highly targeted by spearfishers in the French Mediterranean until a moratorium was established in 1993 (Prato et al. 2013). No successful reproduction was observed in the region until 1990 (Chauvet & Francour 1990), and the recurrent presence of larvae of this rare species in the settlement pool, both inside and outside MPAs (Faillettaz et al. 2018a), likely results from the recovery of adult populations observed along the French coast (Ganteaume & Francour 2007).

European eels *Anguilla anguilla* and gilthead seabreams *S. aurata* migrate towards lagoons to settle (Mercier et al. 2012). The sampling site in Leucate, which is located near the entrance of the large 'Étang de Leucate' lagoon, was the only one where those species were regularly collected (44 glass eels and 15 *S. aurata* larvae; Table S2). Both species suffer intense fishing pressure due to their high commercial value and are the focus of numerous studies (e.g. Koumoundouros et al. 2009, Faria et al. 2011, Díaz-Gil et al. 2017, Naisbett-Jones et al. 2017, Cresci et al. 2017). The site in Leucate therefore appears to be a good candidate to study the early life stages of these species in the region.

5. CONCLUSION

This study describes the spatio-temporal patterns of larval supply of 72 demersal fish species to 13 sites distributed throughout the French Mediter-

anean coast, over >3 yr. Thanks to a novel quantile-based analysis, it highlights higher supply to the regions located east of the Rhône river, which is surprising because fisheries yield is lower there, and around MPAs. No large-scale patterns in species diversity indices emerge but the composition of the larval pool is strongly linked to geographical locations and their geomorphological characteristics. While the connectivity within the Ligurian Sea is high (Faillettaz et al. 2018b), further studies focusing on the connectivity both within and among the Gulf of Lion and the Ligurian Sea, using the patterns of larval supply described here, would enable conclusive analyses of the potential role of source or sink of these sites and regions. Temporally, settlement is extremely sporadic with frequent null to low catches and few short events of very high supply, often around the new moon and in the spring; these events are likely to have sweepstakes consequences for future populations. The timing of settlement seems to be controlled by climatic events at the scale of the basin, with clear synchronicity among sites. Incidentally, it also shows that quantile-based analysis is an efficient tool to detect patterns in such episodic data, where large events can have disproportionate importance. Quantile-based approaches also provide a solid alternative when time series are too short to detect spatio-temporal patterns using solely the mean larval supply.

These results can serve to guide further studies: fishing effort should focus around the new moon if the goal is to catch more larvae (for population replenishment purposes, for example; e.g. Bell et al. 1999), but monitoring studies should cover various locations and moon phases to correctly represent the full diversity of Mediterranean coastal fishes. The monitoring larval fish settlement could provide a relevant, relatively cheap, and actionable (for fisheries) indicator of ecosystem state as demanded by the Marine Strategy Framework Directive to European countries (MSFD 2008/56/EC). Because of the episodicity of larval supply and the long-term fluctuations that have been known to occur in fisheries for over a century (Hjort 1914), only continued monitoring will allow us to detect and understand temporal fluctuations in marine fish populations (Giron-Nava et al. 2017). Although still too short to address inter-annual differences in larval supply (only 3 yr sampled), monitoring at such high intensity had to be stopped at most sites, due to lack of long-term funding on this spatio-temporal scale. Fortunately, it continued for 4 more years in the bay of Villefranche-sur-Mer and still goes on around Marseille.

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