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Exploration of the inter-annual variability and multi-scale environmental drivers of European spiny lobster, *Palinurus elephas* (Decapoda: Palinuridae) settlement in the NW Mediterranean

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Abstract

Determining the drivers of key ecological processes of commercial marine species is important to acquire basic and essential knowledge for fisheries management and conservation. Here we report on a long-term monitoring of the settlement of the European spiny lobster, *Palinurus elephas*, the most commercially important spiny lobster species in the Mediterranean and north-eastern Atlantic. Densities of recently settled individuals (early benthic juveniles – EBJs) were recorded annually, as an approximation to annual settlement, from 2000 to 2016 (17 years) in three zones of the north-western Mediterranean: Catalonia (CAT), the Columbretes Islands (COL), and the Balearic Islands (BAL). Settlement, the end point that integrate most of the variability occurred during dispersion, is a complex ecological process governed by the interaction of biotic and abiotic factors that can be in turn influenced by the atmospheric and oceanographic conditions. Using linear regression of the size structure of EBJs, we demonstrate that settlement occurs synchronously in the three study zones. Densities of EBJs were handled as time series, and regression analysis revealed that CAT and COL covaried significantly, but none of them with BAL. Therefore, CAT and COL were analysed together using generalized linear model and much of their joint variability was explained by the mesoscale oceanographic index IDEA. Settlement in BAL showed a different pattern, explained by the joint effect of the atmospheric oscillations NAO and WEMO. Complexity of *P. elephas* settlement cannot be fully accounted neither for CAT-COL nor for BAL because settlement seems be driven by more complex unknown multi-factorial processes. Therefore, further studies are necessary to gain insight into other factors that allow short- or medium-term predictions of settlement. Expanding the study area across the Mediterranean would also allow establishing a complete knowledge of the ecology of the species applicable to the management of the fishery.

KEYWORDS
ecological processes, environmental drivers, long-term monitoring, *Palinurus elephas*, settlement, spiny lobster

1 | INTRODUCTION

Many harvestable marine species have metapopulation dynamics where individuals are spatially structured and divided into several sub-populations connected by dispersive phases (Fogarty et al., 2007; Kritzer & Sale, 2004). Most of the benthic sedentary species are characterized by developing a meroplanktonic larva with multiple capabilities and behaviours adapted to maximize dispersion and/or survival (Pineda et al., 2007) which allows the exchange of individuals among sub-populations (Cowen & Sponaugle, 2009; Kritzer & Sale, 2006). Taking into account the difficulties to track and monitor larvae, valuable information can be gained from the study of settlement (Bertness et al., 1996), end point that integrate most of the variability occurred during dispersion. In ecology, the process by which pelagic stages cease swimming and take up residence on a substrate is known as settlement.

It is well established that settlement is a complex ecological process governed by the interaction of biotic factors and the atmospheric and oceanographic conditions (Rodriguez et al., 1993), and the longer the dispersive phase the greater their potential leverage (Queiroga & Blanton, 2004). Large-scale climate indices such as the North Atlantic Oscillation index (NAOI) or the Southern Oscillation index (SOI) may be relatively more important than local and small-scale environmental factors as sea surface temperature (SST) or precipitation in determining settlement magnitude (Pineda et al., 2010).

The Palinuridae family (spiny lobsters) has a highly dispersive larva called phyllosoma (Cunningham, 1891). To maximize dispersion and facilitate connectivity between populations, this larva has a leaf-like morphology and develops through multiple instars typically in oceanic waters, beyond the continental shelf. Larval duration of palinurids lasts from 4 to 7 months, as in *Panulirus ornatus* (Dennis et al., 2001) and up to 24 months as in *Jasus edwardsii* (Booth & Phillips, 1994). The final phyllosoma stage metamorphoses into a non-feeding, highly mobile nektonic post-larva known as *puerulus* that migrates across the continental shelf to settle in shallow coastal waters, becoming the first-instar *post*-puerulus (Jeffs & Holland, 2000; Phillips et al., 2006), hereafter called EBJ (early benthic juvenile). In several spiny lobster species, correlation between settlement and environmental conditions has been identified (e.g., Briones-Fourzán et al., 2008; Pearce & Phillips, 1988), which helps explaining the annual variability of settlement.

Palinurus elephas (Fabricius, 1787) is a temperate, deep-water, slow-growing and long-lived palinurid species (Díaz et al., 2016). It reproduces once a year during the summer, starting in July, and ovigerous females have been observed until February. Females produce up to 230,000 eggs and have a single spawning event per year (Goñi et al., 2003). In 1998, *P. elephas* was successfully cultured in the laboratory from egg to puerulus by Kittaka and Ikegami. Metamorphosis into the puerulus phase occurred 132 days after hatching; however, the range in larval duration of palinurids under controlled laboratory conditions is usually shorter than that estimated from the field (Booth & Phillips, 1994) due to the great difference in food availability, among other factors. Based on the breeding, post-hatching and settlement seasons, phyllosomes have, in the wild, an estimated duration of 5–6 months and up to 10–12 months depending on the region (Groeneveld et al., 2013). Therefore, in the present study a larval duration of 8 months will be considered. Settlement of post-larvae occurs once a year distributed in three peaks (June, July and August (Díaz et al., 2001)). During their first year at the bottom, individuals increase their carapace by 28 mm in average (from 7, at the moment of settlement, to 35 mm carapace length – CL) by moulting once a month with a growth rate of 2 mm per moult (Díaz, 2010), similar to other palinurid species (e.g., *Panulirus japonicus*, Norman et al., 1994).

Palinurus elephas has been a major target of artisanal fisheries in the Mediterranean Sea since ancient times (Spanier et al., 2015). At present, it is overexploited throughout its range, depleted in the Atlantic and listed as threatened by the IUCN (Goñi, 2014). However, it continues to be targeted by artisanal fleets in the western Mediterranean and is considered the most commercially important spiny lobster in the Mediterranean and north-eastern Atlantic (Groeneveld et al., 2013). Despite its economic importance going back many centuries (Spanier et al., 2015), no study has yet explored the environmental cues driving the settlement of this species.

As suggested in other spiny lobster species (Booth et al., 2000; Linnane et al., 2010), we hypothesize that annual strength of the settlement of *P. elephas* can be accounted by the influence of environmental factors that affect the distribution and the influx of post-larvae into coastal areas. A metapopulation model with a common larval pool has been proposed for *P. elephas* in the north-western (NW) Mediterranean (Díaz, 2010) and genetic studies verified the high larval connectivity (Elphie et al., 2012), detecting no clear differentiation among adult populations (Palero et al., 2011). The present study shows the results of the longest *P. elephas* settlement monitoring (17 years) existing in the Mediterranean Sea, undertaken in 13 sites located in three Mediterranean zones. Here we assess (a) synchrony of settlement across the NW Mediterranean, (b) spatial and temporal variability of settlement, and (c) correlation between the strength of annual settlement and several environmental factors operating at different spatial scales. Our main goal is revealing the effects of annual environmental scenarios over the population dynamics of the species.

2 | MATERIAL AND METHODS

2.1 | Study area and biological data

This study was conducted in the NW Mediterranean, where three zones along a 400km latitudinal gradient in the Catalan-Balearic sub-basin (Catalonia – CAT, the Columbretes Islands – COL, and the Balearic Islands – BAL) (Figure 1) were sampled from 2000 to 2016 in summer. Like all ecological processes in nature, settlement has temporal variability, so to ensure that post-larvae had already settled at the moment of sampling, surveys were carried out in July, August and September. Settlement was quantified once a year in

13 sites and local variability was captured by sampling 4 stations per site >500 m apart from each other. At each station, a minimum of nine 50 m^2 random transects were performed by underwater visual census following nearly the same track over the years. In the transects, suitable habitats for EBJs of *P. elephas* – date mussel (*Lithophaga lithophaga*) holes and crevices in rocky and coralligenous habitats at 10 to 25 m depth (Díaz et al., 2001) – were surveyed. Number of lobsters and sampled area were recorded in each transect.

Carapace length of the sampled lobsters was measured underwater using plastic callipers whenever their capture was possible. Only lobsters smaller than 25 mm CL, before their ontogenetic migration, were considered EBJs and taken into account in the study, since bigger lobsters were considered juveniles belonging to the settlement in previous years (Díaz, 2010). After being manipulated, every lobster was returned to its shelter as soon as possible to minimize stress.

Annual time series of settlement index were calculated for each zone by averaging densities (number of EBJs /m^2) of the correspondent sites.

2.2 | Environmental data

We selected, according to previous studies, 12 representative physical factors encompassing both the regional- and the large-scale environmental conditions of the study area (Table 1). We assumed that the strength of the settlement at a sub-basin scale can be influenced by physical factors operating during the dispersion of larvae rather than local factors operating at the time of settlement (Briones-Fourzán et al., 2008). Therefore, annual average of each environmental factor was calculated from October (year-1) to May (year) to match the phyllosoma duration period (Goñi & Latrouite, 2005).

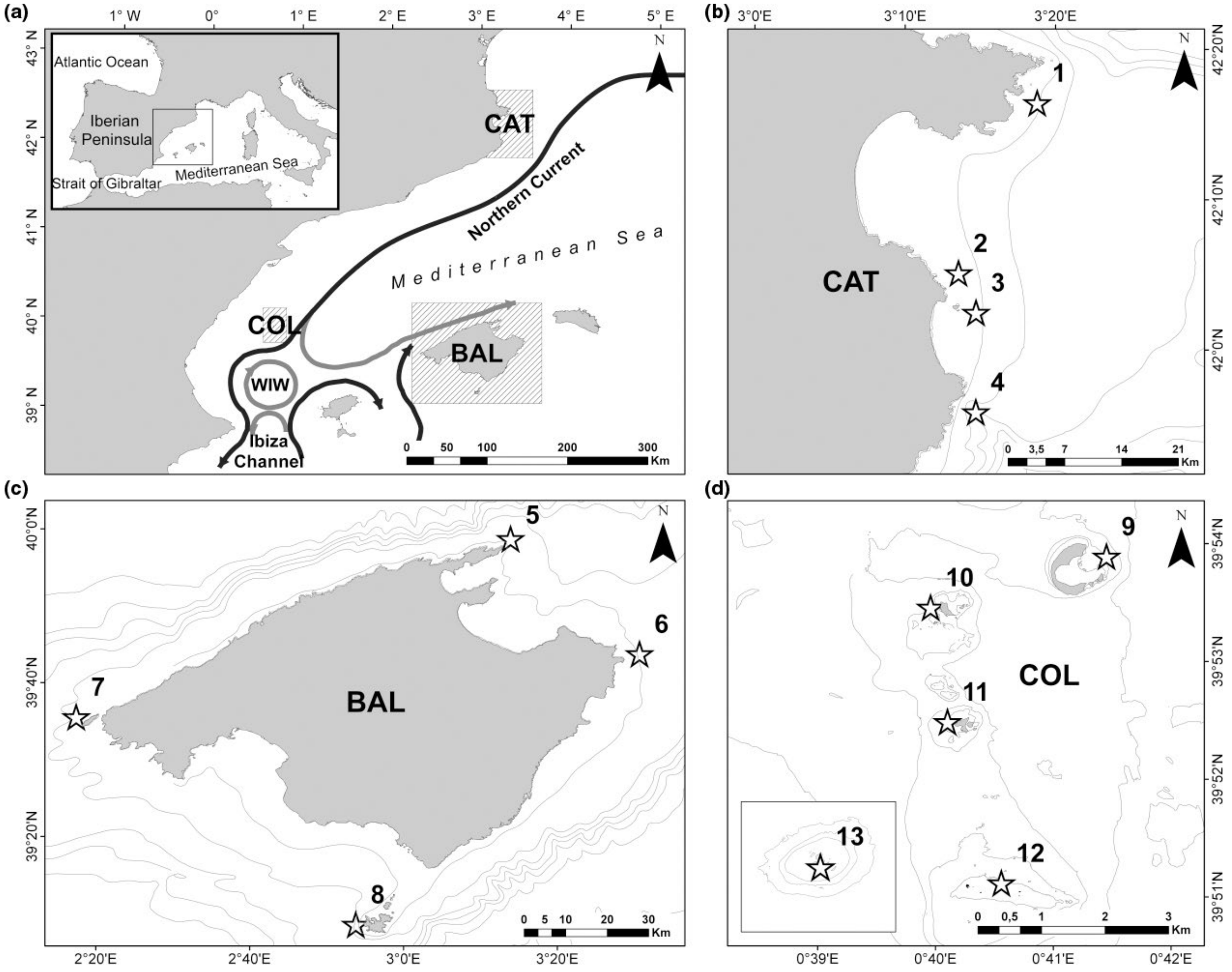


FIGURE 1 General view of the study area where the main ocean circulation (in black) and circulation after very cold winters (in grey) are represented (a) and study zones (b–d). The sampling sites are indicated by stars on the map of each zone. In Catalonia (b), Cape of Creus (1), Montgrí (2), Medes Islands (3), Begur 4). In the Balearic Islands (c), Formentor (5), Cala Ratjada (6), Dragonera Island (7), Archipelago of Cabrera (8). In the Columbretes Islands (d), Illa Grossa (9), Ferrera (10), Foradada (11), Carallot (12), Placer (13)

TABLE 1 Initial data set of environmental factors. The type, spatial scale, range, standard deviation (*SD*) and units are also indicated

Name of the environmental factor	Abbreviation	Type	Scale	Range	*SD*	Units
North Atlantic Oscillation	NAOI	Index	Global	−1.162–1.140	0.530	-
Atlantic Multi-decadal Oscillation	AMOI	Index	Global	−0.069–0.240	0.091	-
Southern Oscillation	SOI	Index	Global	−1.587–3.250	1.308	-
Arctic Oscillation	AOI	Index	Global	−1.633–0.879	0.689	-
Western Mediterranean Oscillation	WEMOI	Index	Regional	−1.430–0.196	0.408	-
-	IDEAI	Index	Regional	−1.660–2.117	1.092	-
Zonal wind	ZW	Weather variable	Regional	0.8–2.9	0.567	m/s
Meridional wind	MW	Weather variable	Regional	−2.7–−0.2	0.464	m/s
Sea level pressure	SLP	Weather variable	Regional	1,014–1,020	1.788	Mb
Sea air temperature	SAT	Weather variable	Regional	12.0–13.7	0.487	°C
Sea surface temperature	SST	Weather variable	Regional	13.2–14.4	0.358	°C
Precipitation	PPT	Weather variable	Regional	0.8–2.1	0.289	mm/day

Large-scale environmental conditions were represented by four climate indices: (a) the NAOI (Hurrell, 1995), based on the difference in the normalized sea level pressure (SLP) of the Azores Islands and Iceland that modifies the paths of the storms crossing the North Atlantic (Woolf et al., 2002); (b) the Arctic Oscillation index (AOI) (Thompson & Wallace, 1998), expressed as an opposing pattern of pressure between the Arctic and the northern-middle latitudes; (c) the Atlantic Multi-decadal Oscillation index (AMOI) (Schlesinger & Ramankutty, 1994), which is identified as a coherent pattern of variability in sea surface temperature (SST) centred in the North Atlantic Ocean, and (4) the Southern Oscillation index (SOI) (Chen, 1982), a periodic fluctuation of 2–7 years in the SST and the SLP of the overlying atmosphere across the equatorial Pacific Ocean. The NAOI and AOI time series are available on: http://www.cpc.ncep.noaa.gov; the AMOI and SOI time series are available on: http://www.esrl.noaa.gov.

Regional-scale environmental conditions were represented by the following climate indices and weather parameters: (a) the Western Mediterranean Oscillation index (WEMOI) (Martín-Vide & López-Bustins, 2006), based on the difference in the SLP of Padova (Italy) and San Fernando (Spain) (http://www.ub.edu/gc/English/wemo.htm); (b) the IDEA index (IDEAI – influence of oceanographic structure and dynamics on demersal populations in waters of the Balearic Islands) (López-Jurado et al., 2008), based on air–sea heat fluxes during the winter that defines the inter-annual variability of the regional circulation around the Balearic Islands during the late spring; (c) zonal wind (ZW), east-west component at sea level; (d) meridional wind (MW), north-south component at sea level; (e) surface air temperature (SAT); (f) SST; (g) SLP; and (h) precipitation (PPT). The six weather parameters (ZW, MW, SAT, SST, SLP and PPT) were obtained from the NOAA/OAR/ESRL PSD (Boulder, CO, USA) website (https://psl.noaa.gov/).

2.3 | Data analyses

Since settlement activity of *P. elephas* takes place in three discrete peaks during the summer (Díaz, 2010) and individuals grow in average 2 mm per monthly moult, synchrony of settlement across the NW Mediterranean was assessed using size of the lobsters sampled. Lobster size was evaluated using linear regression (a) to compare growth rates between months (July, August and September) and (b) to compare size structures between zones (CAT, COL and BAL) each month.

Differences between zones in terms of densities were assessed using Kruskal–Wallis test, as data were not normally distributed, and subsequent Dunn's post hoc test was performed.

To assess spatial variability of settlement, generalized linear mixed model was used. To prevent temporal variability loss, abundance of lobsters in each transect (per zone and year) was used as dependent variable assuming a negative binomial distribution error to account for overdispersion of the data. An offset term was defined as log of the sampled area because the sampling effort was not homogeneous. Sampling zone was set as fixed factor and sampling year as random factor. Post hoc pairwise comparisons of the estimated marginal means test (EMMs) were used to assess differences between years.

Annual settlement index of each zone was transformed to time series, and covariation between zones was investigated by cross-correlation function (CCF) and measured by the Pearson's product-moment correlation coefficient. Annual settlement index of CAT and COL was significantly correlated at lag 0 ($r = 0.58$, $p < .05$), but none of them with BAL (CAT-BAL: $r = -0.31$, $p > .05$ and COL-BAL: $r = 0.12$, $p > .05$). As settlement of CAT and COL showed common patterns, data of these zones were gathered and were analysed separately from BAL to assess temporal variability of settlement and its correlation with the environmental variables.

To assess temporal variability of settlement, generalized linear models was used and two models were performed (CAT-COL and BAL). To prevent spatial variability loss, abundance of lobsters in each transect (per zone and year) was used as dependent variable assuming a negative binomial distribution error. The offset term of the models was defined as log of the sampled area, and the sampling year was set as independent variable. Post hoc pairwise comparisons of EMMs were used to assess differences between years. Coefficients of variation of the settlement index time series were also computed.

TABLE 2 Results of linear regression model of lobster size (carapace length (CL) in mm) per sampling month

Independent variable	Estimated coefficient	SE	z	*p*
(Intercept)	11.10	0.15	75.31	$<.01^{**}$
August CL	1.80	0.16	10.87	$<.01^{**}$
September CL	4.21	0.21	20.24	$<.01^{**}$

$^{**}p < 0.01$

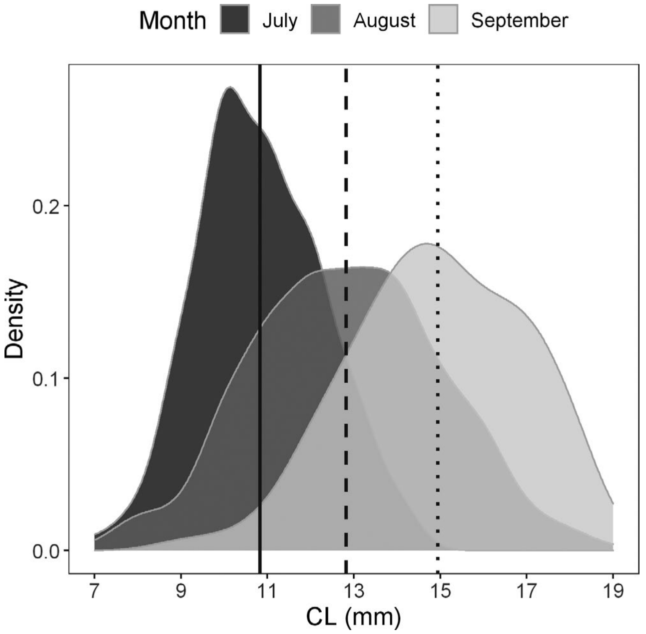


FIGURE 2 Size structure of the measured EBJs by sampling month. Mean carapace length (CL) is also indicated (July: solid line, August: dashed line, September: dotted line)

Environmental variables may not affect settlement individually, but jointly. Therefore, two multiple linear regression models were performed (CAT-COL and BAL) where settlement indices were set as dependent variables and environmental variables, as independent term. Both settlement and environment (handled as time series) were previously detrended to ensure that correlation only reflects shared time series variation independent of any underlying trend. A backward model selection based on the Akaike information criterion (AIC; Buhrnham & Anderson, 2002) procedure was applied to get the most parsimonious model. For the final model, residuals were plotted and checked for normality and homoscedasticity.

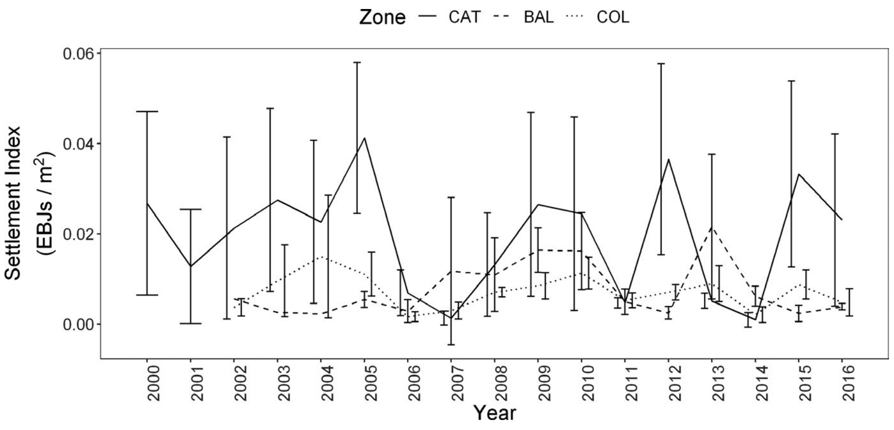
The existence of collinearity inflates the variance of the regressions and leads to a biased result. Therefore, variance inflation factor (VIF) with a cut-off of 2 (Naimi, 2015) was used to remove collinearity between environmental variables previously scaled. Strong relationships were found between seven variables (AOI, AMOI, ZW, MZ, SLP, SAT and SST). Consequently, the full regression models testing the environmental effects contained the five non-correlated explanatory variables (NAO, SOI, WEMOI, IDEAI and PPT).

All statistical analyses were carried out using R software (v 3.6.2) and RStudio (v 1.2.5001).

3 | RESULTS

A total of 2,986 EBJs of *P. elephas* were sampled within 42,500 m^2 of suitable settlement habitat in three zones of the NW Mediterranean between 2000 and 2016. Carapace length of the 1,426 individuals measured (47.76% of the total sampled) ranged from 7 to 24 mm and differed between sampling month ($F_2 = 207.66$, $p < .01$). Based on the estimates of the linear regression, mean size showed increments of around 2 mm per month (Table 2 and Figure 2). When grouped by sampling month, mean lobster size did not show significant differences between zones (July: $F_1 = 6.264$, $p > .01$; August: $F_2 = 2.944$, $p > .01$; September: $F_2 = 1.444$, $p > .01$).

FIGURE 3 Annual settlement index of *P. elephas* (EBJs/m^2) in the three study zones (Catalonia – CAT, the Columbretes Islands – COL and the Balearic Islands – BAL) with 95% confidence intervals



Densities of EBJs showed differences between zones (Chi-squared = 47.27, *df* = 2, $p < .001$), being significantly higher in CAT than those in COL ($p < .01$) and BAL ($p < .01$) (Figure 3 and Table 3). No significant differences were found between COL and BAL ($p > .05$). Despite these results, settlement index time series of COL and CAT showed a significant correlation and both zones were different from BAL (*see results of CCF in material and methods*).

Time series of CAT-COL and BAL presented, in general, high temporal variability with coefficients of variation of 54.25% and 80.05%, respectively. However, EMMs pairwise comparison revealed that both time series showed three groups of years: (a) years with above-average densities and high *SD*, (b) years with around-average densities and high *SD*, and (c) years with below-average densities and low *SD* (Table 4).

TABLE 3 Summary of the annual settlement index of *P. elephas* (EBJs/m^2) by sampling zone averaging densities of all the monitoring years

Zone	Min	Max	Mean (*SD*)
Catalonia	0.000	0.056	0.019 (0.018)
Balearic Islands	0.000	0.043	0.008 (0.009)
Columbretes Islands	0.000	0.035	0.007 (0.005)

TABLE 4 Summary of the annual settlement index of *P. elephas* (EBJs /m^2) by groups of years according to the results from the post hoc analysis: (A) years with above-average densities and high *SD*, (B) years with around-average densities and high *SD*, and (C) years with below-average densities and low *SD*

Settlement zone	Group	Years	Min	Max	Mean (*SD*)
Catalonia + Columbretes Islands	A	2005	0.004	0.053	0.019 (0.016)
	B	2000, 2001, 2002, 2003, 2004, 2008, 2009, 2010, 2011, 2012, 2013, 2015, 2016	0.001	0.056	0.015 (0.015)
	C	2006, 2007, 2014	0	0.120	0.002 (0.003)
Balearic Islands	A	2008, 2009, 2010	0.002	0.03	0.014 (0.007)
	B	2000, 2001, 2002, 2004, 2005, 2006, 2007, 2011, 2012, 2013, 2014	0	0.04	0.009 (0.01)
	C	2003, 2015, 2016	0	0.005	0.003 (0.001)

Note: Mean (*SD*) density of lobsters along the study period was 0.013 (0.014) and 0.008 (0.009) for CAT-COL and BAL, respectively.

TABLE 5 Model selection procedure based on AIC assessing the relationship between settlement of *P. elephas* and the environmental factors

Dependent variable	Independent variables		*df*		AIC
Catalonia + Columbretes Islands (Settlement index)	NAOI + WEMOI + IDEAI + SOI + PPT		11		−134.18
	NAOI + WEMOI + IDEAI + SOI		12		−136.12
	NAOI + **IDEAI** + SOI		13		−137.80
	NAOI + **IDEAI**		14		−135.95
	IDEAI		15		−135.50
	Independent variable	**Estimated coefficient**	***SE***	***t***	***p***
	(Intercept)	−5.426e−19	9.734e−04	0.000	1.000
	IDEAI	−5.038e−03	1.103e−03	4.568	<.001***
Dependent variable	**Independent variables**		***df***		**AIC**
Balearic Islands (Settlement index)	**NAO** + **WEMOI** + IDEAI + SOI +PPT		9		−50.63
	NAO + **WEMOI** + IDEAI + PPT		10		−52.54
	NAO + **WEMOI** + PPT		11		−52.58
	NAO + **WEMOI**		12		−52.29
	Independent variable	**Estimated coefficient**	***SE***	***t***	***p***
	(Intercept)	0.003015	0.009401	0.321	.754
	NAOI	−0.051471	0.022645	−2.273	.042*
	WEMOI	0.085307	0.030437	2.803	.016*

Note: Procedures of CAT-COL and BAL are presented separately. Significant explanatory variables are indicated in bold. Results of the final models are also shown.

$^{*}p < 0.05$.

$^{***}p < 0.001$.

Multiple linear regression procedures showed that settlement of CAT-COL can be accounted by a single environmental variable, the IDEAI ($p < .001$), which had a negative effect and explained 58.3% of the total variability. Conversely, settlement of BAL was negatively correlated with the NAOI ($p < .05$) and positively correlated with the WEMOI ($p < .05$), which jointly explained 51.3% of the total variability. Details on the backward model selection procedure and the final models are provided in Table 5.

4 | DISCUSSION

Larval survival and settlement processes are directly and strongly affected by climate conditions (Pineda et al., 2007). The effects of environmental conditions over demographic parameters are more pronounced in species with long larval duration (Macpherson & Raventos, 2006). Marine decapod crustacean metapopulations are characterized by having aggregate distributions of adults linked to restricted habitats, long duration of the larval phase which connects sub-populations, poorly differentiated genetic structure and synchronized settlement fluctuations (Fogarty & Botsford, 2006). In this study, we have sampled densities of first-benthic-stages of *P. elephas* in their natural habitat during 17 consecutive years as an approximation to annual settlement.

We found that size of EBJs did not differ between zones when grouped by sampling month regarding the discrete peaks of settlement described for the species (Díaz, 2010). Independently of the sampling zone, EBJs presented a growth rate of 2 mm CL per month (Figure 2) in agreement with Díaz, 2010, who demonstrated that the European spiny lobster moults once a month during its first year of life with increments of around 2 mm per moult. Synchronized temporality of settlement in the NW Mediterranean could explain why lobster sizes were not significantly different between zones at each peak. Synchrony of settlement has been described in many marine invertebrates (e.g., *Dascyllus albisella*, Booth, 1995; *Chthamalus spp*, Valencia-Gasti & Ladah, 2016; *Callinectes sapidus*, Rabalais et al., 1995), including spiny lobsters (e.g., *J. edwardsii*, Hinojosa Toledo, 2015). The three hypotheses commonly used to explain synchrony are dispersal (Kendall et al., 2000), Moran effect (Sheppard et al., 2019) and predator–prey system (Bjørnstad et al., 1999). In the case of *P. elephas*, egg incubation lasts 7 months (Goñi et al., 2003) and dispersion takes around 8 months, but settlement synchronizes throughout the NW Mediterranean and concentrates in only 3 months. The long-lasting dispersal phase in combination with common environmental drivers at a mesolarge spatial scale are the most plausible factors that explain synchrony of *P. elephas* settlement.

Densities of EBJs varied between the three sampling zones (Figure 3 and Table 3), being higher in CAT. In 2001, Díaz et al. found higher densities of EBJs in calcareous rocks, where empty *L. lithophaga* holes offered an optimal shelter for the individuals. In our study, all samplings were performed on calcareous rock, but substrates around sites of CAT consist of metamorphic slate rocks (Díaz et al., 2001), where *L. lithophaga* is not present. We believe that the high densities observed in CAT are probably due to an *oasis effect* that agglutinates lobsters from the unsuitable surrounding grounds. In addition, we must take into account that the north-eastern continental shelf of the Iberian Peninsula, where CAT is located, is an end point of the western Mediterranean currents (Millot, 1999) which collect larvae around the whole basin. This probably leads, after an average of 8 months of dispersion, to higher accumulations of larvae in CAT than in the Balearic promontory, where BAL is located. Despite the differences between CAT and COL in terms of densities of EBJs, these are significantly linearly correlated, indicating the existence of common settlement patterns in both zones. Probably, the environmental drivers equalize the strength of settlement over this region, but the absolute abundances of settlers are modulated by local conditions. On the other hand, settlement in BAL has apparently its own dynamics, probably due to the presence of two main currents around the island, the Northern Current and the Algerian Current. This can be a source of variability in the dynamic of settlement success (Millot, 2005).

Correlation between settlement and environment has been identified in several spiny lobster species. Pearce and Phillips in 1988, and Caputi in 2008, found that the strength of the Leeuwin Current, which is influenced by El Niño-Southern Oscillation (ENSO) events, correlates positively with variations in the spatial distribution of western rock lobster (*Panulirus cygnus*) EBJs in the west coast of Australia. Settlement of the Caribbean spiny lobster (*Panulirus argus*) is highly influenced by sea level variations, although extreme settlement pulses appear to be associated with hurricane seasons that could maximize onshore transport of pueruli (Briones-Fourzán et al., 2008). It has been suggested that storm events in combination with onshore surface drifts are the main physical mechanisms affecting the settlement patterns of *J. edwardsii* in the south coast of Australia and Tasmania; specifically, high settlement has been observed during winter, when the wind-driven Ekman Currents are strong (Linnane et al., 2010). By contrast, settlement of *J. edwardsii* across New Zealand has been suggested to be linked to the ENSO, with differing patterns between North and South Islands (Hinojosa et al., 2017).

Our results indicate that dynamic of annual settlement of *P. elephas* is not homogeneous across the whole study area, distinguishing two regions (CAT-COL and BAL) where settlement behaves differently and responds to extreme values of different environmental indices. Settlement of CAT and COL, both located in the north-eastern continental shelf of the Iberian Peninsula, was negatively correlated with the IDEAI, whereas settlement of BAL correlated negatively with the NAOI and positively with the WEMOI (Figure 4 and Table 5).

The qualitative index IDEA reflects two different scenarios in the ocean circulation of the western Mediterranean (López-Jurado et al., 2008) (Figure 1a). (a) Positive values reflect the average ocean circulation. In this scenario, the Northern Current (NC) runs strongly and continuously along the east coast of the Iberian Peninsula flowing throughout the sampling sites of CAT and COL (Millot, 1999). Part of the NC continues southwards to the Ibiza Channel (between the Balearic Islands and the Iberian Peninsula) losing energy gradually.

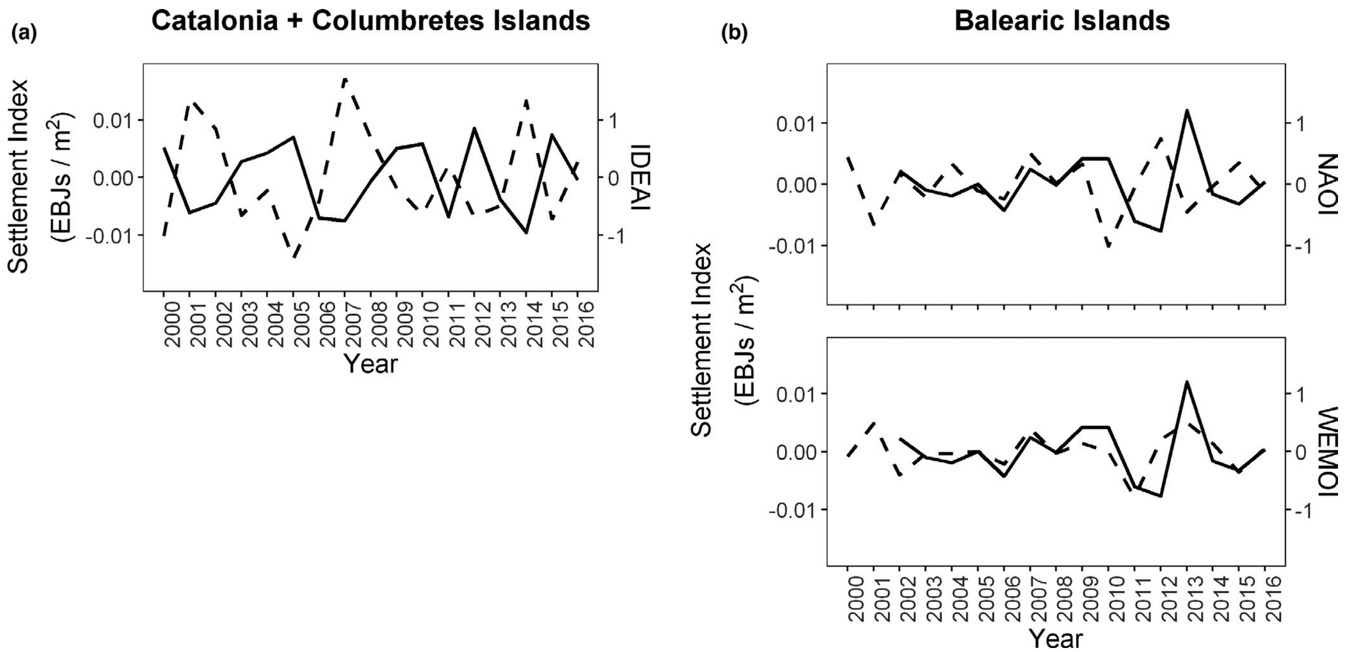


FIGURE 4 Evolution of the annual settlement index of *P. elephas* (EBJs/m^2) in Catalonia and the Columbretes Islands (a) and the Balearic Islands (b) against the significant environmental variables from the multiple linear regression. Both settlement (in solid lines) and environment (in dashed lines) series have been detrended

(b) Negative values of the index occur when, after cold winters, cold western intermediate water (WIW) is formed in the Gulf of Lions and moves southward blocking the Ibiza Channel. When this occurs, the NC splits and one of its branches redirects toward the northern slope of the Balearic Islands (Monserrat et al., 2008). The existence of WIW could favour regional retention of larvae in the NW Mediterranean through recurrent anti-cyclonic eddies that retain the old modified Atlantic water and reduce the incoming Atlantic water, which is poor in phyllosomes of *P. elephas* (Groeneveld et al., 2013).

The North Atlantic Oscillation (NAO) is the dominant mode of the climate variability in the North Atlantic region, and the Mediterranean is not isolated from its effects (Tsimplis & Josey, 2001). Positive phases of the NAO induce higher than average westerly winds across northern mid-latitudes with a dry climate around the Iberian Peninsula, whereas the negative phases of the NAO induce major precipitation in southern Europe. It was found that the NAO, in its positive phase, favours the entrance of migratory species to the Mediterranean through the Strait of Gibraltar owing to the high westerly winds (e.g., Abella et al., 2008; Muñoz-Expósito et al., 2017). The negative correlation between settlement of BAL and the NAOI represents that the positive phase of the NAO is detrimental to settlement in the Balearic Islands. Due to its geographical location, the Balearic Islands are considered a transition zone between the NW Mediterranean sub-basin, with old modified Atlantic waters from the Ligurian Sea, and the Algerian sub-basin, with newcomer Atlantic waters that could move northwardly through the Balearic Channels. The intensified westerly winds during the positive phase of the NAO enhance transport of Atlantic waters to the Mediterranean which could reach the Balearic Islands, resulting in low settlement events in BAL. By contrast, winters with negative NAOI have shown higher values of water transport by the East Corsica Current (Central Mediterranean) (Astraldi et al., 1999). These conditions could promote the transport of larvae from southern spawning areas (e.g., Tunisia), causing higher densities of EBJs carried by the NC which could reach the Balearic Islands. Abella et al., (2008) found the existence of a negative correlation between winter NAOI and 1-year-old hake (*Merluccius merluccius*) density in the Northern Ligurian Sea.

The Western Mediterranean Oscillation (WEMO) is a low frequency variability pattern of atmospheric circulation through the NW Mediterranean (Martín-Vide & López-Bustins, 2006). Positive phase of the WEMO, which represents a strong surface pressure gradient and offshore winds from north, north-west and west (Azorín-Molina & López-Bustins, 2008), was correlated with above-average annual settlement of *P. elephas*. Northerly winds promote water and nutrient mixing (Millot, 1979; Salat, 1996), causing the intrusion of cooler waters that enhance phyto- and zooplankton productivity in the region (Fernández de Puelles & Alemany, 2007). Low SST and strong wind mixing are favourable conditions for the overall biological productivity in the NW Mediterranean, which is beneficial for larval survival, and the higher the survival of phyllosomes the higher the potential settlement. Positive WEMO periods have been also associated to high abundance of red shrimp (*Aristeus antennatus*) in BAL due to increased productivity (Massutí et al., 2008). By contrast, negative WEMO phase is associated with strong surface pressure gradients and onshore synoptic flows from the east, southeast and south (Azorín-Molina & López-Bustins, 2008). These conditions would favour the intrusion of phyllosoma-poor water from the Algerian sub-basin (Groeneveld et al., 2013) and originate low settlement events in BAL.

This study is a first and necessary step toward understanding the complex ecological processes that govern the settlement of *P. elephas*. Our results reveal that absolute densities of EBJs vary between zones, presumably due to small-scale differences between sites. However, the strength of settlement behaves similarly in both zones of the north-eastern continental shelf of the Iberian Peninsula and its dynamic can be explained by the influence the oceanographic index IDEA. Settlement in the Balearic Islands showed its own dynamics, influenced by the NAO and the WEMO. In any case, settlement might be driven by more complex processes which probably include environmental and biotic factors not examined here, and therefore a large amount of settlement variability remains unexplained. Thus, further studies are necessary to gain insight into other factors that allow accurate short- or medium-term predictions of settlement. Also, collaborative work across the whole Mediterranean would expand our study area allowing to establish a complete and comprehensive knowledge of the ecology of the species, being useful in the management of the fishery.

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