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Connectivity of populations of the seaweed *Cystoseira amentacea* within the Bay of Marseille (Mediterranean Sea): genetic structure and hydrodynamic connections

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Abstract – The brown alga *Cystoseira amentacea* (Phaeophyceae, kingdom Stramenopiles) constitutes an extensive belt in the shallowest horizon of the infralittoral (the infralittoral fringe), in the Mediterranean Sea. Hydrodynamic modelling was used to infer connectivity between populations of *C. amentacea* of the Bay of Marseille (Provence, France, NW Mediterranean) and to test the correlation between genetic and hydrodynamic connectivity. We genotyped 183 individuals from six populations at six microsatellite loci. Current fields were computed at a fine resolution by a 3D numerical model simultaneously utilizing the local winds, the Rhone River inputs and offshore circulation. The Lagrangian trajectories of the propagules (zygotes, or rafts) were computed with the ICHTHYOP software, for both NW and SE strong wind forcing (11-12 $m \cdot s^{-1}$). *Cystoseira amentacea* displayed a strong and significant genetic structure, not correlated with the geographic distance, i.e. a lack of isolation by distance (IBD). The pairs of sites with the lowest F_{ST} were those connected by the current patterns. The time needed for a zygote or a raft to travel from one location to another ranged from 4 to 18 h (i.e. within the survival time of a zygote) and for distances of up to 23 km. Despite the very low dispersal capability of the zygotes, long-distance dispersal is therefore possible. Several non-exclusive processes can account for the genetic structure of *C. amentacea* populations, such as step-by-step local dispersal, long-distance dispersal of zygotes and rafts by currents, during storms, and the "priority effect", i.e. the importance of the timing of arrival of the propagules.

Hydrodynamic modelling / Lagrangian transport / connectivity / genetic differentiation / *Cystoseira amentacea* / Mediterranean Sea

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Résumé – *Cystoseira amentacea* (Phaeophyceae, Stramenopiles) se développe en ceintures au niveau de la mer le long du littoral rocheux méditerranéen. Une modélisation hydrodynamique a été utilisée pour étudier la connectivité génétique et hydrodynamique entre des populations de *C. amentacea* de la Baie de Marseille (Provence, France, Méditerranée nord-occidentale). 183 individus de six sites ont été génotypés avec six locus microsatellites. Les champs de courants, modélisés à grande échelle par un modèle numérique 3D, ont été forcés par l'influence des vents locaux, du Rhône et de la circulation du large. Les trajectoires lagrangiennes des propagules (zygotes ou radeaux) ont été modélisées avec le logiciel ICHTYOP sous les deux régimes de vents dominants dans la baie ; un vent de Sud-Est et un vent de Nord-Ouest (11-12 $m{\cdot}s^{-1}$). Les populations de *Cystoseira amentacea* sont significativement et fortement structurées et ne sont pas corrélés avec les distances géographiques ; il n'y a donc pas d'isolation par la distance (IBD). Les couples de populations ayant les F_{ST} les plus faibles sont celles connectés les courants. Le temps mis par des propagules pour voyager entre certains sites de la baie varie entre 4 et 18 h (ce qui correspond au temps de survie d'un zygote), avec une distance maximale de 23 km. En dépit de la faible capacité supposée de dispersion des zygotes, des dispersions lointaines apparaissent probables. Plusieurs hypothèses non-exclusives peuvent expliquer la structure génétique des populations de *C. amentacea*, telles que la dispersion de proche en proche, la dispersion lointaine de zygotes ou de radeaux par les courants pendant des coups de vents et le "priority effect" (*i.e.* la priorité au premier arrivant).

Modélisation hydrodynamique / transport lagrangien / connectivité / différenciation génétique / *Cystoseira amentacea* / Méditerranée

INTRODUCTION

Coastal ecosystems are deeply affected by the cumulative effects of exploitation, habitat destruction, pollution, biological invasions and climate change (e.g. Worm *et al.,* 2006; Halpern *et al.,* 2008; Jackson, 2008; Waycott *et al.,* 2009; Boudouresque & Verlaque, 2012). This global trend is visible in various ecosystems from tropical coral reefs to temperate kelp and fucoid habitat-forming stands (Jackson, 2008) and is linked to the increasing demographic pressures on these areas. This trend could have significant ecological and socio-economic consequences as these ecosystems are of major direct and indirect economic value (Balmford *et al.,* 2002; Barbier *et al.,* 2010; De Groot *et al.,* 2012). Efficient conservation and management of coastal ecosystems are therefore needed.

Connectivity is a major factor that shapes the evolution of species and communities. Population connectivity corresponds to the exchange of individuals among geographically separated populations, whereas genetic connectivity implies dispersal and reproduction (Cowen & Sponaugle, 2009). Connectivity has important consequences with regard to population demography and genetic evolution (Lowe & Allendorf, 2010). For most marine species, the larval or zygotic phase is the main dispersal stage, especially for sessile organisms. The small size of the propagules (larvae and zygotes, eggs) and the vast fluid environment makes it difficult to make direct assessments of connectivity for many marine species (Cowen & Sponaugle, 2009). Genetic data can however be used to estimate the scale of population connectivity. The study of oceanographic transport is an alternative approach that can be integrated with seascape genetics (e.g. Galindo *et al.,* 2006; Foster *et al.,* 2012). This strategy allows the identification of barriers and vectors of dispersal and can integrate the biological properties of the dispersal phase (life duration of larvae or zygotes, spawning date, swimming behaviour; Cowen *et al.,* 2006). Conversely, a discrepancy between genetic data and hydrodynamic modelling could be due to specific behaviour of the propagules, to local limits to recruitment or to the effect of chaotic genetic patchiness (Arnaud-Haond *et al.,* 2008). Estimating connectivity for ecologically key species will provide information on the potential responses of the associated ecosystems to environmental fluctuations and will help in management choices. The spatial genetic structure is a key parameter in conservation biology, especially when dealing with threatened, long-living, habitat-forming species (e.g. Procaccini *et al.,* 2002; Arnaud-Haond *et al.,* 2007; Coleman *et al.,* 2009; Alberto *et al.,* 2010; Ledoux *et al.,* 2010a, 2010b; Serra *et al.,* 2010; Mokhtar-Jamaï *et al.,* 2011). Genetic connectivity is important as it sustains local genetic diversity and can help in recolonization following disturbances. As a consequence, genetic structure and connectivity should be taken into account in management strategies and in the design of marine protected areas (e.g. Palumbi, 2003; Sale *et al.,* 2010; Andrello *et al.,* 2013).

Along the temperate rocky coasts, the large canopy-forming kelps (Laminariales, Phaeophyceae, Stramenopiles) and fucoids (Fucales, Phaeophyceae, Stramenopiles) represent the dominant species in pristine environments (Dayton, 1985; Steneck *et al.,* 2002; Schiel & Foster, 2006). Kelp and fucoids are autogenic ecosystem engineers (*sensu* Jones *et al.,* 1994) forming three-dimensional habitats that provide shelter, food and nursery for a wide range of species; they provide high primary production, which plays a role in supporting diversified functional compartments and trophic levels; they attenuate wave action in the case of the largest shallow-water species (e.g. Foster & Schiel, 1985; Harrold & Pearse, 1987; Komatsu & Murakami, 1994; Steneck et al., 2002; Estes *et al,* 2004; Schiel & Foster, 2006). The decline of kelps and fucoids is a worldwide phenomenon due, directly or indirectly, to human activities (e.g. Steneck *et al.,* 2002; Diez *et al.,* 2003; Helmuth *et al.,* 2006; Worm & Lotze, 2006; Airoldi & Beck, 2007; Coleman *et al.,* 2008; Hawkins *et al.,* 2008; Wernberg *et al.,* 2010; Phillips & Blackshaw, 2011; Schiel, 2011; Wernberg et al., 2011; Lamela-Silvarey *et al.,* 2012; Raybaud *et al.,* 2013; Filbee-Dexter & Scheibling, 2014).

In the Mediterranean Sea, the species of the genus *Cystoseira* C. Agardh are habitat-forming plants, dominating several benthic assemblages, from the sea surface (infralittoral fringe, the shallowest level of the infralittoral zone) down to the circalittoral zone (sensu Pérès, 1982) (e.g. Feldmann, 1937; Molinier, 1960; Pignatti, 1962; Boudouresque, 1971a, 1971b; Verlaque, 1987; Ballesteros, 1988, 1990a,b; Giaccone *et al.,* 1994). Loss of Mediterranean fucoid algae has been reported throughout the basin, as a consequence of habitat destruction, eutrophication and overgrazing by sea urchins and fish, leading to a shift to environments of lesser structural complexity, such as algal turfs and barren grounds dominated by filamentous and encrusting species, where sea urchin density is a driver of habitat homogenization (e.g. Munda, 1974, 1982, 1993; Cormaci & Furnari, 1999; Thibaut *et al.,* 2005; Devescovi & Iveša, 2007; Airoldi *et al.,* 2008; Falace *et al.,* 2010; Fraschetti *et al.,* 2011; Giakoumi *et al.,* 2012; Sala *et al.,* 2012; Bianchi *et al.,* 2014; Thibaut *et al.,* 2015a,b; but see Thibaut *et al.,* 2014, 2016). These shifts are associated with a loss of species diversity, ecosystem diversity and ecosystem functions and services (Sala & Knowlton 2006).

Along the whole of the French Mediterranean coast, two closely related Mediterranean *Cystoseira* species, closely related genetically, are restricted to the infralittoral fringe, from the mean sea level down to less than 1 m depth):

C. mediterranea Sauvageau, in the western part, along the French Catalonian coast, and *C. amentacea* (C. Agardh) Bory de Saint-Vincent (synonym: *C. amentacea* var. *stricta* Montagne) in Provence, French Riviera and Corsica (Sauvageau, 1912; Feldmann, 1937; Epiard-Lahaye *et al.,* 1987; Thibaut *et al.,* 2005; Susini, 2006; Draisma *et al.,* 2010; Robvieux, 2013; Thibaut *et al.,* 2014). *Cystoseira amentacea*, which is widely distributed in the Mediterranean (Ribera *et al.,* 1992, Cormaci *et al.,* 2012, Guiry & Guiry, 2016), is considered to have an important ecological role within the framework of the European Union (EU) Water Framework Directive (WFD, 2000) (e.g. Orfanidis *et al.,* 2001; Ballesteros *et al.,* 2007; Orfanidis *et al.,* 2011; Blanfuné *et al.,* 2016, 2017). *Cystoseira amentacea* is currently listed as a "strictly protected species" under the Bern Convention (1979: Annex I), and "endangered or threatened species" in the Barcelona Convention (2013: Annex II).

The species, which possesses a caespitose vegetative apparatus, up to 40 cm high, with a basal holdfast a few centimetres wide, forms extensive stands on shallow wave-exposed rocky substrates (Bellan-Santini, 1963; Robvieux, 2013; Thibaut *et al.,* 2014) and is one of the most productive Mediterranean seaweeds (Susini, 2006).

Cystoseira amentacea is slightly declining, at the scale of the French Mediterranean coast, but it has undergone its most severe decline, with a loss of ~54% of the historical populations at least since the1960s, around the city of Marseille (western Provence), because of an episode of heavy eutrophication and habitat destruction that led to the fragmentation and isolation of its populations (Bellan-Santini 1968; Bellan & Bellan-Santini, 1972; Soltan *et al.,* 2001; Thibaut *et al.,* 2014). The water circulation in the Bay of Marseille is mainly controlled by the wind regimes, but also by the Rhône River seasonal floods (Fraysse *et al.,* 2014) and periodic incursions on the continental shelf of the Northern Current, which flows westward along the continental slope from the Ligurian Sea to the Balearic Sea (Petrenko, 2003; Pairaud *et al.,* 2011; Pinazo *et al.,* 2013). The availability of knowledge on water circulation, along with the presence of *C. amentacea* in several places in this area, make the Bay of Marseille an interesting case study to test the correlation between hydrodynamics and genetic differentiation. The Bay of Marseille is an area where a significant and complex genetic structure has been observed for various benthic species (e.g. Ledoux *et al.,* 2010a, 2010b; Mokhtar-Jamaï *et al.,* 2011). The population genetics of *Cystoseira* species has been poorly studied. Only a preliminary study using RAPDs, and needing confirmation with more reliable markers, has focused on *C. amentacea.* It suggested a long-distance pattern of dispersal in spite of a putative low dispersal capability (Susini *et al.,* 2007). Genetic differentiation may not solely depend on geographic distance, but also on the orientation and strength of currents, which can promote or prevent gene flow (Engelen *et al.,* 2001; Billot *et al.*, 2003). Therefore, studying the potential link between hydrodynamics and genetic differentiation is required for a better understanding of the genetic structure of this species.

The aims of this work were (i) to use hydrodynamic modelling to infer connectivity between populations of *C. amentacea* around Marseille, and (ii) to test the correlation between genetic and hydrodynamic connectivity.

MATERIAL AND METHODS

Study site

The study site is the Bay of Marseille (western Provence, southern France) (Fig. 1). The study of the distribution of *C. amentacea* was completed in May 2008 (Thibaut *et al.,* 2014). The species occupies 45 km of coast (at 1/2 500 scale), mainly forming fragmented populations.

Population genetics

Six locations from the Bay of Marseille and nearby locations were sampled in May 2008 for genetic analyses (Table 1; Fig. 1). One hundred and eighty three individuals have been genotyped at six microsatellite loci (number 24, 27, 33, 35, 51, 58), as described in Robvieux *et al.* (2012). The parameters describing the genetic diversity were computed with FSTAT v2.9.3.2 (Goudet, 2001): observed and expected heterozygosity, and the fixation index F_{IS} were computed with the estimator of Weir & Cockerham (1984). The deviation from panmixia was tested with an exact test performed in GENEPOP 4.0 (Rousset, 2008) with default parameters.

Pairwise F_{ST} were computed with GENEPOP with the estimator of Weir & Cockerham (1984). Their significance was tested with an exact test as implemented

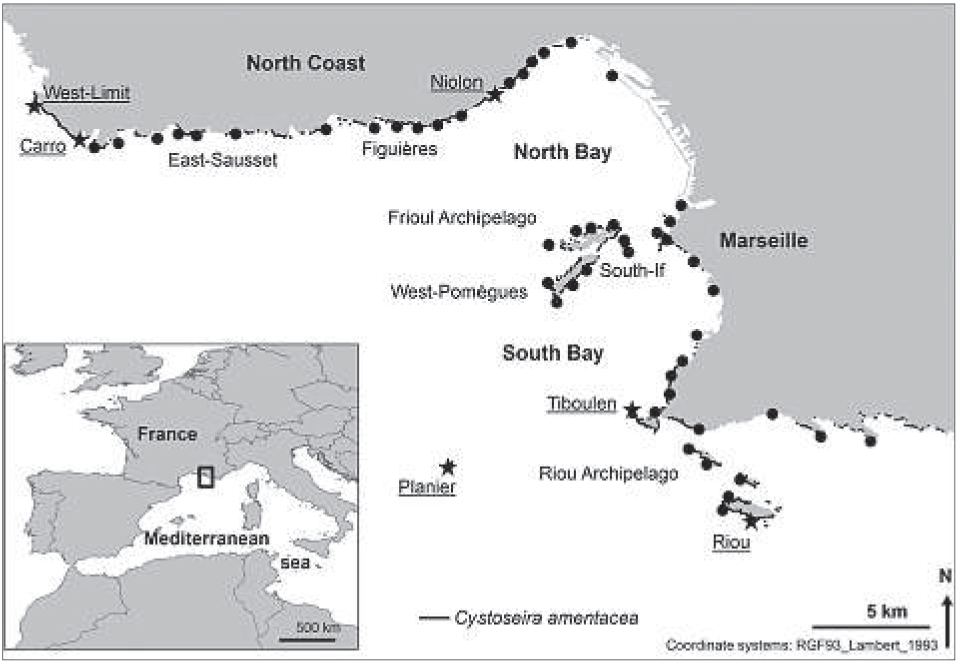

Fig. 1. Map of location of the 54 stations (dots) located around and near the Bay of Marseille and taken into account in the ICHTHYOP computations (modelling); *C. amentacea* can be present (black line) or absent at these modelling stations. Stars refer to the six sampling sites for genetic analyses of *C. amentacea* and underlined names correspond to the names of the sampling sites, as in Table 1.

in GENEPOP with default parameters. A clustering analysis was performed with the STRUCTURE software (Pritchard *et al.,* 2000), with the admixture model, independent allelic frequencies, a burn-in of 500 000 iterations followed by 200 000 iterations with K varying from 1 to 8 and 20 runs for each K value. The number of clusters was estimated on the basis of the method of Evanno *et al.* (2005) and the results of the different runs were combined in STRUCTURE HARVESTER (Earl & vonHoldt, 2012). As a complementary approach to STRUCTURE, and in order to take into account the possible effect of inbreeding or selfing, we studied the genetic structure of populations with the INSTRUCT software (Gao *et al*., 2007). We used the model for the inference of population structure only with admixture and then the model with inference of population inbreeding coefficients. We used five chains with 1 000 000 generations and a burn-in of 500 000 generations and with K varying from 1 to 8. The analysis of the results was performed with the CLUMPAK software (Kopelman *et al*., 2015).

We first tested the correlation between genetic and geographical distance (*i.e.* Isolation By Distance or IBD) and the oceanographic connections by comparing the ratio $F_{ST}/(1-F_{ST})$ with the logarithm of spatial distance or the oceanographic time (Rousset, 1997). Spatial distance was computed as the shortest way by sea connecting two stations. This distance varied between 2 and 36 km. Distance means the shortest distance by sea, not the shortest distance as the crow flies. Oceanographic times were measured as a proxy of oceanographic connections.

We then tested the correlation between genetic distance and hydrodynamic connectivity by comparing $F_{ST}/(1-F_{ST})$ with the lack of connection (*i.e.* 1 - proportion of connection) between sites according to the wind periods (see below for the wind regimes). In both cases, the correlations between matrices were tested with a Mantel test implemented in the IBD Web Service v.3.23 (Jensen *et al.,* 2005) with 1 000 permutations.

Modelling

Concerning the hydrodynamics, we experimented with a preliminary modelling study of the hydrodynamics in the Bay of Marseille, using the 3D-model POM (Princeton Ocean Model) on a 250 × 350 horizontal grid with a fine horizontal resolution of 100 m and 11 vertical sigma levels. The Bay of Marseille (the central bay in and around Marseille) exhibits spatial heterogeneity of the wind-induced hydrodynamic structures, and high variability at short scales according to the local wind direction (Pradal & Millet, 2006, 2013).

Then, taking into account more realistic forcing (physical process influencing the simulation), a version of the MARS3D model (3D hydrodynamic Model for Applications at Regional Scale, version V8; Lazure & Dumas, 2008), called RHOMA (for Rhône-Marseille Area), was implemented over a more extensive domain, extending from the Rhône River to Cap Sicié (near Toulon, eastern Provence), with a horizontal resolution of 200 m (Pairaud *et al.,* 2011).

Local wind regime

We considered the wind statistics computed over the inter-annual 30-year period 1971-2000 at the Météo France meteorological station at Marignane, located 20 km northwest of the central bay. The corresponding wind rose (Fig. 2) highlights two prevailing NW 320°-340° and SE 100°-160° wind sectors, regardless of the

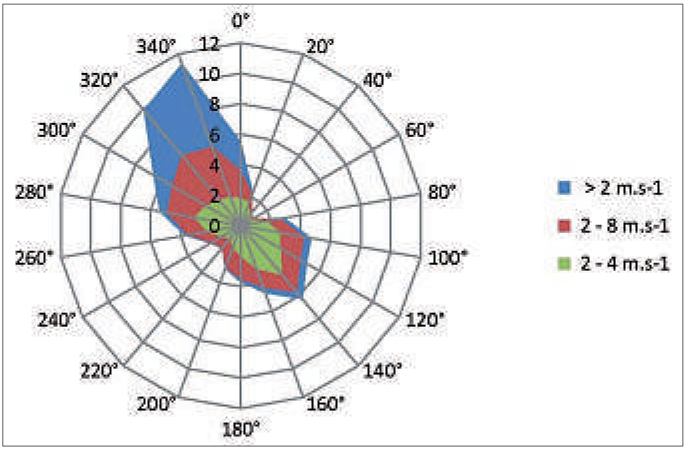

Fig. 2. Wind rose measured at the Météo France station at Marignane, over the 1971-2000 period ; colours refer to the three cumulative classes of wind intensity : 2-4, 2-8 and > 2 m·s^{-1} and the corresponding frequencies of occurrence (0% through 12%) are reported within the diagram.

three classes of wind intensity considered: between 2 and 4 m·s^{-1}, 2 and 8 m·s^{-1}, and all intensities > 2 m·s^{-1} combined. The frequencies of occurrence in time over the 1971-2000 period, for wind events greater than 2 m·s^{-1}, are 21.1% and 16.2%, for the NW 320°-340° and SE 100°-160° sectors, respectively.

Marine current fields

Current and salinity fields were computed at a fine resolution by a 3D numerical model simultaneously forced (i.e. model simultaneously utilizing different outputs or parameters influencing the studied model) by the atmosphere, in particular local winds, the Rhone River inputs and offshore circulation. Therefore, currents, temperature and salinity fields have been computed by using the RHOMA version of the MARS3D model on a 503 × 240 horizontal grid extending from the Rhône River to Cap Sicié (near Toulon, eastern Provence), with a fine horizontal resolution of 200 m, 30 vertical sigma layers and a time step fixed at 60 s. This model, described in detail in Pairaud *et al.* (2011), takes into account the forcing by the north-western Mediterranean general circulation, by means of a nesting strategy with the large scale MARS3D-MENOR configuration (1.2 km resolution). The model is forced every 3 h at its upper boundary by atmospheric fluxes (modelled wind field, rain and heat fluxes) from the MM5 meteorological model (3 km resolution). In addition, the model is forced by the average daily inputs from the Rhône River, measured at the Beaucaire station and provided by the Compagnie Nationale du Rhône. The model results were validated both statistically and on selected processes for the two years, 2007 and 2008, by comparisons with *in situ* measurements of temperature, salinity, currents and satellite images.

We considered the set of results computed by the model RHOMA during the seasonal 4-month period from May to August 2008, which was considered as the season of sexual reproduction for *C. amentacea*. Then, we selected within this 4-month period two sets of current, temperature and salinity fields liable to be considered as representative of both typical prevailing NW and SE wind situations (Fig. 2). A first 30-hour period from 6 June (00:00, Local Time LT) to 7 June (6:00, LT) 2008 was chosen as characterized by intense and well-established current structures induced by a strong NW-330° wind, reaching a maximum speed of 11 m·s^{-1}. A second 30-hour period from 26 May (12:00, LT) to 27 May (18:00, LT) 2008 was chosen as characterized by intense and well-established current structures induced by a strong SE 130°-140° wind, reaching a maximum speed of 12 $m{\cdot}s^{-1}$.

Lagrangian transport

The Lagrangian trajectories of the propagules (zygotes or rafts) of *C. amentacea* through the Bay of Marseille were computed with the ICHTHYOP software (Lett *et al*., 2008). In our study, the ICHTHYOP model was run taking into account the 3-hour resolution fields of current, temperature and salinity previously computed by the RHOMA model for both selected NW and SE wind periods. Each computation took into account the same initial condition for its source point: a patch of 500 particles featuring a diameter of 200 m and a subsurface thickness of 20 cm. In addition, we considered, in each ICHTHYOP computation, passive particles (zygotes or rafts) without any biological behaviour, an extremely low density of 1 $kg.m^{-3}$ and no sinking velocity.

Fifty-four source points have been considered in the ICHTHYOP computations, which were located around the bay on the basis of the relevance of their respective situations (Fig. 1). We checked with ICHTHYOP the computations of both direct and inverse trajectories of surface passive particles issued from (for direct trajectories) or targeting (for inverse trajectories) each of the 54 source points (Fig. 1) considered and successively taking into account SE 130°-140° and NW 330° strong wind forcing situations.

Past distribution of *C. amentacea*

We rebuilt the past shorelines suitable for *C. amentacea* from 20 000 years BP to before the industrial age (200 years ago), using a 3D-spatial analysis of the depth contours (every 2 m) (data from the Service Hydrographique et Océanographique de la Marine). We calculated the slope of beaches along the current shoreline (~1-2%), we calculated the slope along the past shorelines (– 120 m and – 50 m, corresponding to 20 000 and 11 000 years BP, respectively), and considered the probable location of river mouths at that time, in order to infer the putative presence of beaches (unsuitable substrate for *C. amentacea*) or of rocky substrates. For the modern period before the industrial age, we used the shoreline used in Thibaut *et al.* (2014). Maps of the possible suitable habitat for *C. amentacea* were made with ®ArcGIS 10.3.

RESULTS

Population genetic structure and diversity

The parameters describing the levels of genetic diversity within populations are given in Table 1. The mean number of alleles per locus varied between 2.7 and 4.2 (total mean = 3.5, SD = 0.6). High and significant multilocus F_{IS} values were obtained at all the sites (Table 1).

Table 1. List of the samples used for genetic analyses. *n*: number of individuals; *Na*: mean number of alleles per locus, H_{obs}: observed heterozygosity, H_{exp}: expected heterozygosity, F_{IS}: fixation index with its significance on the basis of an exact test. *** indicates a p-value < 0.001. The indicated values are based on a mean over the six loci

Name	*Latitude*	*Longitude*	*n*	*Na*	H_{obs}	H_{exp}	F_{IS}
West Limit	43°20’32.69N	5°1’8.04E	30	2.8	0.35	0.43	0.21***
Carro	43°19’39.15N	5°2’30.67E	28	2.7	0.31	0.41	0.25***
Niolon	43°20’21.83N	5°15’35.42E	34	3.5	0.34	0.41	0.18***
Planier	43°11’51.29N	5°13’46.76E	31	4.2	0.38	0.48	0.20***
Tiboulen	43°12’36.39N	5°20’4.38E	30	4.0	0.34	0.41	0.16***
Riou	43°10’32.61N	5°23’13.13E	30	4.0	0.35	0.45	0.22***

The pairwise F_{ST} varied between 0.09 (for the comparison between Carro and Planier) and 0.34 (comparison between Carro and Tiboulen), and all the comparisons were significant (Table 2).

Table 2. Matrix of genetic differentiation and connectivity of *C. amentacea* within the Bay of Marseille: genetic differentiation (F_{ST}) and frequencies of occurrence of hydrodynamic connections between the 6 populations. Wind statistics are provided by the Météo France station at Marignane over the 1971-2000 period (see text for details)

Pairs of sampling sites	*Distance (km)*	*Genetic differentiation* F_{ST}	*Connection frequencies (%)*	*Wind statistics at Marignane station*
Carro – West Limit	2.6	0.15	0.162	SE 100°-160°
Niolon – West Limit	20.5	0.30	0	–
Planier – West Limit	23.0	0.12	0.162	SE 100°-160°
Tiboulen – West Limit	29.3	0.24	0	–
Riou – West Limit	35.5	0.28	0	–
Niolon – Carro	17.6	0.26	0	–
Planier – Carro	21.2	0.09	0.162	SE 100°-160°
Tiboulen – Carro	26.4	0.34	0	–
Riou – Carro	32.9	0.24	0	–
Planier-Niolon	15.5	0.13	0.212	NW 320°-340°
Tiboulen – Niolon	15.1	0.32	0	–
Riou – Niolon	22.3	0.21	0	–
Tiboulen – Planier	7.7	0.21	0	–
Riou – Planier	12.8	0.15	0.162	SE 100°-160°
Riou – Tiboulen	6.6	0.28	0	–

All pairwise differentiation tests were significant. Three genetic clusters were identified with the STRUCTURE software according to the delta K (Fig. S1, see doi/107872/crya/v.37.iss4.2016.S1). The populations of *C. amentacea* can be grouped in a red cluster with the two most western populations located at West-Limit and Carro, a blue cluster grouping the populations at Niolon and Riou and a

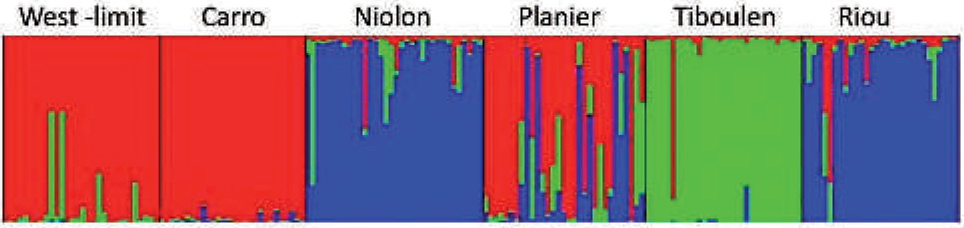

Fig. 3. Genetic structure of the six populations of *C. amentacea* collected around and near the Bay of Marseille, obtained with STRUCTURE.

green cluster with one population located at Tiboulen. The population of *C. amentacea* located at Planier Island cannot be attributed to one of these three clusters but is mainly shared between the red and blue clusters (Fig. 3).

Concerning the INSTRUCT analysis, the Gelman-Rubin statistics for the convergence of log-likelihood was 1.074 for the model of population structure only and 1.159 for the model with population inbreeding coefficients, which indicated a good convergence in both cases. The optimal K inferred by INSTRUCT was K = 7 for the first model and K = 8 for the second. Nevertheless, these K values correspond to a high individual admixture level (Fig. S2 for the model with inference of population inbreeding coefficients). We therefore analysed the INSTRUCT results at K = 3, the value retained with STRUCTURE. At K = 3 and for both models INSTRUCT gave results very similar to those obtained with STRUCTURE (Fig. S2, see doi/10.7872/crya/v.37.iss4.2016.S2).

Computed trajectories

The time needed to travel from a site colonised by *C. amentacea* to another suitable site can be very short. For example, on May 27, under SE 130-140° strong wind (12 $m \cdot s^{-1}$) conditions, a particle originating at the neighbouring of Planier Island takes 12 h to reach Carro or West-Limit. It can also take 12 h between Planier Island and East-Sausset. Under the same wind conditions, the travel time required can be e.g. 4 h between Riou and Planier, 4 h between Tiboulen and West Pomègues, 6 h between Tiboulen and South-If, and 18 h between Planier Island and Niolon (Fig. 4).

Connectivity

The studied populations of *C. amentacea* are more connected by the water currents induced by the SE wind than currents induced by the NW wind (Fig. 4, Table 2).

Hydrodynamic connections are represented by the frequencies of occurrence for the corresponding wind situations. Therefore, we took into account only the connections linking together the two western stations, West-Limit and Carro, and those linking Planier Island to the other parts of the bay, except the Tiboulen station which connected with no other site. Zero frequency was applied to the other pairs of stations, since no connection clearly appeared between them from our computations (Table 2).

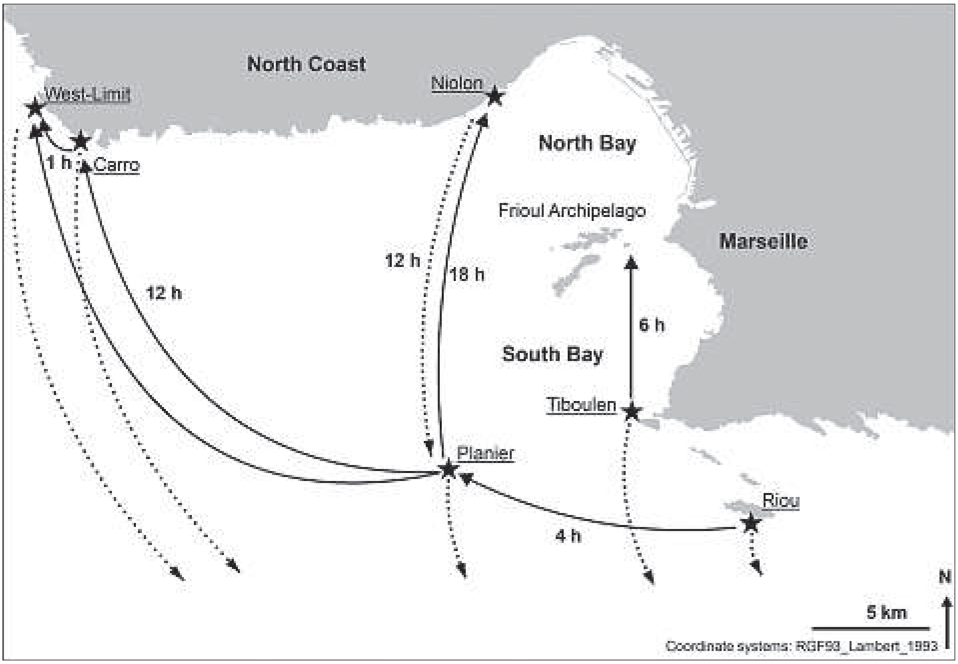

Fig. 4. Schematic map of strong wind-induced connections within the Bay of Marseille between the 6 studied sites, for surface passive particles, computed from MARS3D-RHOMA model and ICHTHYOP tool, over 30-hour periods and under both wind regimes: SE 130°-140° (maximum 12 $m \cdot s^{-1}$) in solid lines and NW 330° (maximum 11 $m \cdot s^{-1}$) in dotted lines. Adjacent to the arrows, the connection time computed on May and June 2008 under strong wind conditions (see Material and Methods). Stars refer to the six sampling sites for genetic analyses of *C. amentacea*.

Populations of *C. amentacea* at Planier are directly linked to the populations of the red cluster (West-Limit and Carro) under a SE wind regime and connected to the blue Cluster (Niolon) by water currents under a NW wind regime. The population located at Tiboulen is not directly connected by water currents to any of the other five populations, regardless the wind direction considered. The population located at Riou is only connected by a water current under the SE regime to Planier and subsequently to Carro and West-Limit (Fig. 4). Niolon is connected to Planier under the NW wind regime. Finally, the western part of the bay is not directly linked to the inner part of the bay, regardless the wind regime considered (Fig. 4).

While the Mantel test of correlation between genetic and geographical distances was not significant (p = 0.16), the correlation between the genetic and oceanographic connections was significant (p = 0.006). The relationship between F_{ST} and hydrodynamic patterns was non-linear but comprised two clearly distinct groups of comparison. Thus, the lowest F_{ST} (ranging from 0.09 to 0.15) were associated with the highest frequency of connection induced by the water currents, whereas the other site pairs with higher F_{ST} values (from 0.21 to 0.34) were not considered as connected on the basis of our simulations (Table 2). This corresponded well with the clusters obtained in Figure 3: Carro and West-Limit grouped together and Planier appearing as admixed between different clusters. The populations sampled at Riou and Niolon (blue cluster in Figure 3) were not directly linked by water current and exhibited a high F_{ST} value (0.21) (Table 2).

DISCUSSION

Short-distance dispersal

The life cycle of *C. amentacea* contains only one diploid vegetative phase, often interpreted as a sporophyte. The reduction of the chromosomes number takes place during the formation of the gametes in the hermaphrodite conceptacles grouped within terminal receptacles. Reproduction occurs in late spring and early summer. Fertilization is oogamous, with thousands of bi-flagellate male gametes meeting female gametes in the vicinity of conceptacles; the zygotes (= eggs) are then dispersed (Hoek, *et al.,* 1995; Susini, 2006). The zygote diameter is ca. 100 µm, which is relatively large, so that the dispersal range is low (a few dozen centimetres), under calm conditions; the formation of the fertilisation membrane, which allows their fixation to the substrate, occurs after 12 h, the first rhizoids appear after 48 h, and the embryo begins to increase in size after 7 days (Susini, 2006; Mangialajo *et al.,* 2012). The generation time is unknown. No vegetative multiplication was ever observed.

In the study area, *C. amentacea* displayed a strong genetic structure as observed for other Fucales (e.g. Tatarenkov *et al.,* 2007; Neiva *et al.,* 2014). Most connections were limited, which is consistent with the significant and high differentiation observed between all populations and with dissemination occurring mainly over short distances, step-by-step, due to the very low dispersal range of the zygotes (Mangialajo *et al.,* 2012).

Long-distance dispersal

The relationship between F_{ST} and the oceanographic connection rate, even if very low, suggests that water currents can play a significant role by connecting distant populations. This can maintain an evolutionary connection between populations (i.e. belonging to the same genetic cluster), but probably with independent demography. The colonisation of man-made structures by *C. amentacea* has been observed up to 3.3 km from the nearest natural population, which confirms the possibility of dispersal at this distance (Thibaut *et al.,* 2014). Our results confirm the connections between sites as much as 23 km apart (Table 2). The distribution of dispersal distances of *C. amentacea* is therefore probably leptokurtic, with a low mean dispersal distance, and the possibility of rare dispersal events at higher distances.

Long-distance dispersal of fertilized zygotes probably occurs under strong hydrodynamic conditions. However, due to the time of formation of the fertilisation membrane, allowing their fixation to the substrate, and the beginning of the zygote development (Susini, 2006), the successful fixation window ranges between 12 and 48 h after fertilisation. Consequently, the connectivity between distant sites involves a transport time falling within this time interval, which is consistent with our results. During storms, the buoyancy of fertilised zygotes is highly probable. Deciduous branches of *C. amentacea* are negatively buoyant, so that they cannot be dispersed under calm conditions. However, rafts of Ectocarpales (Phaeophyceae) mucilage, species with aerocysts such as *Cystoseira compressa* or *Sargassum vulgare* (the other aerocyst-bearing species such as *C. barbata*, *S. acinarium* and *S. hornschuchii* are extinct in Western Provence, Thibaut *et al.,* 2015b), or recently shed *Posidonia oceanica* leaves (the aerarium of which is a network of lacunae filled with gas; Boudouresque *et al.* 2012) can include *C. amentacea* detached branchlets harbouring hundreds of fertile conceptacles, and putatively allow their long-distance dispersal. Both *C. compressa* and *P. oceanica* are common in the Bay of Marseille. Lastly, the dispersal of *C. amentacea* branches by animals (gulls) was also reported (Bartoli *et al.*, 1997).

Genetic structure: the lack of IBD and the presence of distinct clusters

The genetic structure of *C. amentacea* in the Bay of Marseille was not correlated with the geographical proximity of the analysed populations. The lack of IBD in our data could be explained by four non-mutually exclusive hypotheses:

(i) the reduced dispersal of this species could induce a spatial genetic structure at shorter distances than considered here,

(ii) the presence of distinct genetic clusters can break the IBD pattern. It would therefore be interesting to test for spatial genetic structure in *C. amentacea* at short distances by considering spatially localized individuals in order to obtain better estimates of dispersal abilities (e.g. Ledoux et al. 2010a; Aurelle & Ledoux, 2013),

(iii) the current genetic structure could reflect ancient genetic structures, at a time when the sea level was far below the current level and the shape of the coastline and of geographical barriers was different from the current one (see below),

(iv) the genetic structure could correspond to chaotic genetic patchiness (e.g. Broquet *et al.,* 2013), thus reflecting the random arrival of differentiated cohorts, with a “priority effect” (see below), for individuals replenishing the population on a previously free substrate. This can induce a Wahlund effect which could partly explain the observed F_{IS} (Arnaud-Haond *et al.,* 2008).

Our results indicate that hydrodynamics is a better predictor of genetic differentiation than IBD. Our modelling of connectivity shows that the surface circulation induced by the two prevailing NW and SE wind regimes can explain, at least partly, the main patterns of genetic differentiation between the populations of *C. amentacea* in the Bay of Marseille. The correlation between hydrodynamics and genetic structuring has been observed in other studies on metazoans (Foster *et al.,* 2012) and a correlation between larval dispersal and gene flow can be observed at coarse scales (see discussion in Hellberg, 2009). In Southern France, a survey of red coral (*Corallium rubrum*) populations indicated a significant correlation between genetic distance and both geographical distance and distances based on the major currents (Ledoux *et al.,* 2010a,b). Nevertheless, this correlation is not always observed (e.g. Berry *et al.,* 2012) which could point to an inappropriate study scale, as in IBD analyses. It may also be necessary to refine biological parameters in modelling. In the case of *C. amentacea*, we did not include the possibility of dispersal via gulls (Bartoli *et al.,* 1997; Thibaut et *al*., 2014), which would have required a specific modelling approach. The significant correlation observed between hydrodynamics connectivity, based on zygotes and rafts only, and genetic connectivity, indicates that actual bird mediated dispersal could be rare enough not to invalidate this correlation or that it occurs at different spatial scales.

The high differentiation observed in the Bay of Marseille for *C. amentacea* is quite unusual at that scale for a marine species with a free dispersal stage. But it has been observed in some algal species, for even smaller scales, with a genetic differentiation driven by tidal dynamics (Engel *et al.,* 2004; Krueger-Hadfield *et al.,* 2013). Hereafter, we compare our results with other population genetics studies in the study area, despite differences in the depth ranges and the biology of the considered species. Significant genetic structure has been demonstrated, on the basis of mitochondrial DNA, for the cave mysid *Hemimysis margalefi* (crustaceans), with a genetic break between the north and south part of the Bay of Marseille (Lejeusne & Chevaldonné, 2006). The potential link between the western limit of the north coast and the southern islands observed in this study was not observed for *H. margalefi*. For the sea urchin *Paracentrotus lividus*, differentiation between the north coast and the Marseille areas was found, but as only two sites were sampled, the comparison is difficult (Penant *et al.,* 2013). Conversely, for the teleost *Apogon imberbis,* weak and mostly non-significant differentiation was observed in the Bay of Marseille, through eight microsatellite loci (Muths *et al.,* 2015): this could be linked to the duration of the larval phase of this species (18-24 days), which might hinder genetic differentiation at that scale. The studies most similar to the present one in terms of sampling sites, markers and differentiation patterns, dealt with the octocorals *Corallium rubrum* and *Paramuricea clavata* (Ledoux *et al.,* 2010b; Mokhtar-Jamaï *et al.,* 2011). In these two species, significant differences were observed for most pairwise comparisons. Nevertheless, even for these low dispersal species, the observed F_{ST} were lower than for *C. amentacea*. For *C. rubrum*, three clusters were observed in the Bay of Marseille (Ledoux *et al.,* 2010b): one corresponded to the western part of the north coast and to the area of Riou Island: this agrees with the connection evidenced here between Riou and West-Limit. A second cluster for *C. rubrum* grouped the other populations from the southern coast, and the third comprised only a population from the northern part of the Bay, close to Niolon. The isolation of the latter population is not in agreement with what was observed for *C. amentacea*. For *P. clavata,* the only locality from the northern coast appeared admixed between localities from the southern part of the Marseille area and a cluster with more distant samples from the Ligurian Sea (Mokhtar-Jamaï *et al.,* 2011).

Genetic structure: the possible role of the priority effect and historical events

It is worth noting that the possible arrival of a zygote does not imply a successful recruitment. Firstly, local populations produce millions of zygotes, and the vast majority of them will be unsuccessful in producing a new individual. Secondly, in suitable habitats, a very narrow and shallow fringe, the substrate is already occupied by a high density of individuals, with a continuous canopy (~100% percent cover). There is probably neither enough room nor enough light for recruits. The development of young individuals on old individuals (as epiphytes) is unknown in *C. amentacea,* but probable on the basal part, while recruitment coincides with the seasonal falling of the secondary axes. As a result, the current genetic pattern could reflect the "priority effect" i.e. the importance of the timing of arrival of the propagules.

When the habitat became suitable for *C. amentacea*, several thousand years ago, at the end of the Ice Age (Last Glacial Maximum), or more recently, after episodes of massive mortality such as long-lasting low sea level due to exceptionally high atmospheric pressure episodes, after exceptionally cold winters during the Little Ice Age, during the maximum level of pollution of the Bay of Marseille (from the late 19th to the late 20th century), etc., recolonization of the free areas was achieved by the first arriving zygotes. Subsequently, further arriving zygotes found the substrate occupied, so that their success was unlikely. The priority effect is thought to play a major role in the observed patterns of distribution of species and populations (see e.g. Lawler & Morin, 1993; Louette & Meester 2007; Geange & Stier 2009 and references therein).

Another explanation, which could be combined with the priority effect, would be that of chaotic genetic patchiness: in that case, the observed structure could be the consequence of random recruitment from differentiated propagule groups (e.g. through variance in reproductive success or collective dispersal; Broquet et al., 2013). One consequence of chaotic genetic patchiness is the observation of genetic structure at distances below the dispersal capability, which could be what we observed here. Nevertheless, the observation of a correlation between hydrodynamics and genetic differentiation does not point to a completely random process.

Twenty thousand years ago, at Last Glacial Maximum (LGM), the sea level was 120-130 m below the current sea level, and the shape of the coastline was very different (Fig. 5). Subsequently, the sea level rose from 120-130 m to 0.5 m below the current sea-level, 2 000 years ago (Mohrange, 2003). Hard substrates suitable for *C. amentacea* were probably present, separated by unsuitable areas (beaches?), with a pattern different from the present one. The possible past distribution of *C. amentacea* indicates that the populations were probably already fragmented, which could have induced the formation of different genetic clusters which could still persist. Nevertheless this interpretation depends on the occurrence of *C. amentacea* in this area, 20 000 years ago.

Did the distribution of *C. amentacea* follow the sea level rise, and genetic patterns therefore reflect ancient distribution patterns based on the ancient coastline shape? In fact, the sea level rise has been relatively rapid, with increases of up to 3.7 and 2.5 m per century, 14 000 and 12 000-11 000 years ago, respectively (Collina-Girard, 2003). Whether or not the *C. amentacea* belt, if present, was capable of shifting upwards is questionable. In addition, the mean annual Sea-Surface Temperature (SST) was ~8 °C lower during the LGM than today, in the study area (Kuhlemann *et al.,* 2008). Although the lethal low temperature level of *C. amentacea* is unknown, its absence from such cold waters may be expected. In contrast, fucoids currently restricted to the North Atlantic Ocean, e.g. *Fucus vesiculosus*, probably occurred in the NW Mediterranean Sea, not only during the LGM, but also up to 6 000 years ago (Assis *et al.*, 2014). There is no direct competition between *Fucus* species and *Cystoseira* species, as the former thrive in the midlittoral zone and the latter in the infralittoral fringe. The co-occurrence in the same area of *F. vesiculosus* and of *C. tamariscifolia,* a species close to *C. amentacea,* has been documented in the northern Atlantic. In any case, the occurrence of *C. amentacea* in the study area is probably relatively recent, at the Holocene timescale; the colonization therefore proceeded from one or several distant, possibly southern and eastern Mediterranean refugia, potentially corresponding to distinct genetic clusters. In any case, the current persistence of previously differentiated clusters requires that current gene flow is restricted enough not to erase this differentiation.

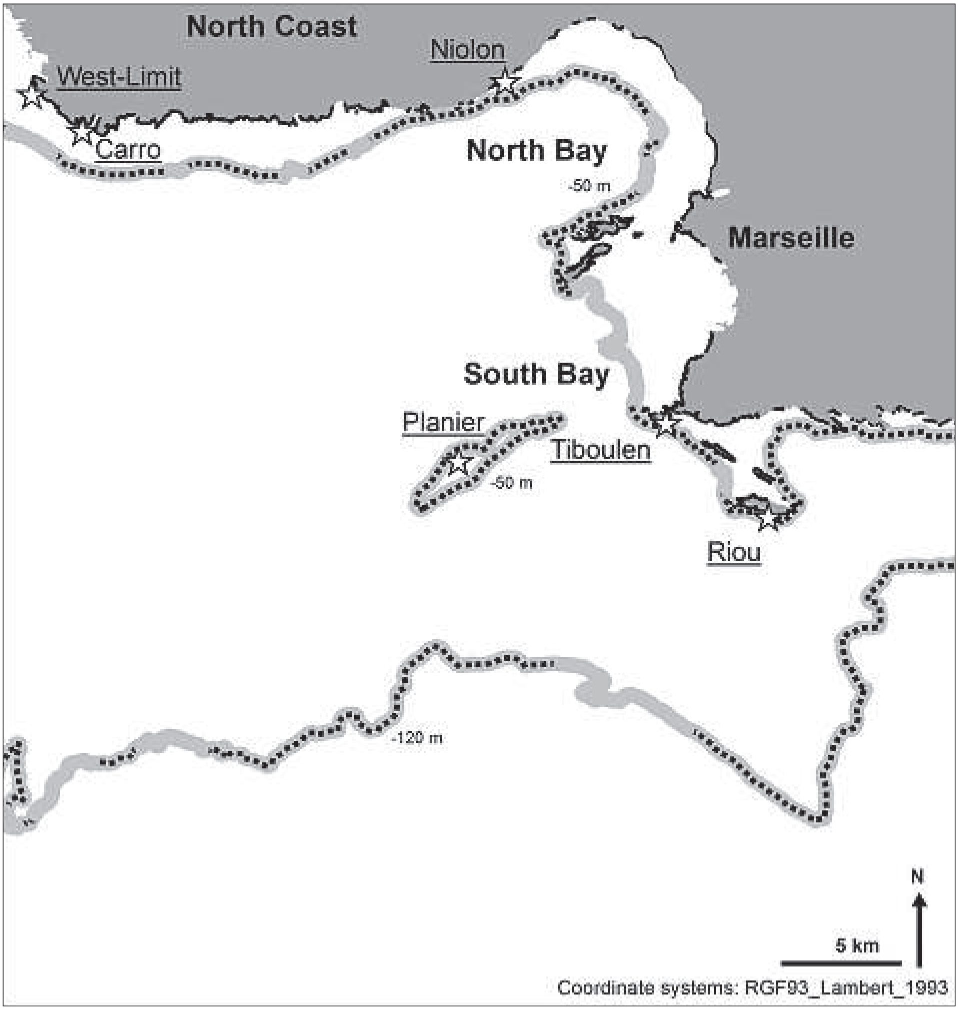

Fig. 5. Current shoreline of the study area (above); blackline: suitable habitats for *C. amentacea* before the industrial age (two centuries ago). The contour of the shoreline when the sea-level was 50 m and 120 m below the current sea-level, ~11 000 and ~20 000 years BP, respectively (below). Dotted line: putative rocky shore (according to the current slope), suitable for macroalgae. Stars refer to the six sampling sites for genetic analyses of *C. amentacea*.

Do the observed genetic clusters correspond to past allopatric divergence or do they correspond to a more recent differentiation in the Marseille area? The aforementioned biological characteristics of *C. amentacea* could be favorable to the persistence of differentiated clusters. More detailed, multigenic approaches would be useful to obtain a better estimate of the level and time of divergence between clusters and the impact of past divergence on the current structure.

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