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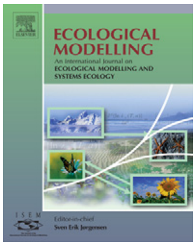

Predicting suitable habitat for the European lobster (*Homarus gammarus*), on the Basque continental shelf (Bay of Biscay), using Ecological-Niche Factor Analysis

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ABSTRACT

Predicting species distribution and habitat suitability (HS) modelling, across broad spatial scales, is now a major challenge in marine ecology. The resulting knowledge is of considerable use in supporting the implementation of environmental legislation, integrated coastal zone management and ecosystem-based fisheries management. This contribution considers the identification of seafloor morphological characteristics, together with wave energy conditions, that determine the presence of European lobster (*Homarus gammarus*); and it predicts suitable habitats over the Basque continental shelf (Bay of Biscay), in summer. The results obtained, by applying Ecological-Niche Factor Analysis (ENFA), indicate that lobster habitat differs considerably from the mean environmental condition over the study area; likewise, that it is restrictive in terms of the range of conditions in which they dwell. The best of the environmental predictors found to be: distance to the rock substrate; Benthic Position Index; wave flux over the seafloor; and the underlying bathymetry. A habitat suitability map was produced, with a high model quality (Boyce index: 0.98 ± 0.06). The most suitable habitat for European lobster are locations at the boundary between sedimentary- and rocky-bottoms, coincident with seafloor depressions with a steep slope, with medium to high wave energy conditions, and located within a range of water depths of 35–40 m. This approach demonstrates the applicability of the method in case studies where only presence data are available, together with the inclusion of environmental variables obtained from different sources.

1. Introduction

Natural resource management requirements (e.g., ecosystem-based approaches, marine protected areas, fishing, habitat identification), have led to the increasing use of species habitat modelling. Different statistical and mathematical techniques have been applied to develop predictive habitat distribution models (Guisan and Zimmermann, 2000). Amongst these, envelope-based approaches, such as Ecological-Niche Factor Analysis (ENFA), are considered particularly advantageous; this is because, with respect to more standard techniques, it does not require absence data. In ENFA, presence data is used instead, to compare with environmental conditions (Hirzel et al., 2002; Braunisch et al., 2008). ENFA has been applied more frequently to terrestrial habitat modelling (Estrada-Pena and Venzal, 2007; Vina et al., 2008), however, recently, it has been used also in the marine environment (Oviedo, 2007; Praca and Gannier, 2008; Skov et al., 2008).

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Habitat distribution models statistically link field observations, to a set of environmental variables or spatial predictors, reflecting some key characteristics of the niche (Guisan and Zimmermann, 2000; Hirzel and Guisan, 2002). Specifically, habitat suitability (HS) modelling has been used successfully in understanding species niche requirements and predicting potential species distribution, e.g., it has been applied to the spiny lobster (*Panulirus argus*), using satellite data in shallow water (Bello et al., 2005), to gorgonian corals in deep-water (Bryan and Metaxas, 2007), to squat lobster distribution in deep-water (Wilson et al., 2007), mapping macrobenthic communities (Degraer et al., 2008), and predictive mapping of fish species richness (Pittman et al., 2007). The application of such methods to marine species, linked closely to the benthic environment, requires reliable information on seabed characteristics. Multibeam echosounders (MBES) are becoming a standard tool for seafloor mapping, due to their ability to provide high-resolution data sets and extensive coverage; they are especially valuable for benthic habitat mapping and shellfish resource studies (Edwards et al., 2003; Kostylev et al., 2003; Orpin and Kostylev, 2006; Ryan et al., 2007).

In the particular case of shellfish, the American lobster (*Homarus americanus*) fishery is well known, on the basis of several studies (Incze et al., 2000; Rowe, 2002; Smith and Tremblay, 2003; Wahle, 2003). Conversely, for the European lobster (*Homarus gammarus*), most of the present knowledge has been derived from aquaculture studies (Van der Meeren, 2005). Fishery studies have been undertaken only in northern countries, such as the United Kingdom (Bannister and Howard, 1991; Smith et al., 2001; Lizarraga-Cubedo et al., 2003), Ireland (Browne et al., 2001; Tully et al., 2001) or Norway (Tveite, 1979; Agnalt et al., 2007).

In the Basque Country, a marine habitat mapping programme started in 2004 (Galparsoro et al., 2008), where one of the objectives was to determine habitat suitability for some key species, including the economically important *H. gammarus*. Although along the Basque coast this fishery is limited, in terms of number of fishing vessels or catches, its socio-economic importance in some ports is very high (Arregi et al., 2004). However, there is a lack of information on the *H. gammarus* fishery and on the official registration of catches (Borja, 1987), leading to an underestimate of the population size (Puente, 2002). This lack of information makes it difficult to understand the stock and its management to maintain a sustainable fishery.

The objectives of the present contribution are (i) to define the main seafloor features and wave energy conditions that determine the presence of *H. gammarus* and (ii) to predict habitat suitability for the lobster, using ENFA.

2. Materials and methods

2.1. Study area and lobster sampling

The study area is located in the inner continental shelf of the Basque Country, in the southeastern part of the Bay of Biscay (Fig. 1). The main lobster fishing ports within the area are those of San Sebastian and Pasaia.

H. gammarus is distributed along the eastern Atlantic, from Lofoten Islands (Norway) in the North Atlantic, to Morocco and the Black Sea in the Mediterranean (Holthuis, 1991). The lobster is territorial, with nocturnal activity (Smith et al., 1998); it feeds on a range of benthic invertebrates (Smith et al., 2001), mainly crustaceans and bivalve molluscs. The lobster appears usually in the infralittoral and the circalittoral (20–60 m water depth), over seabeds incorporating rock blocks and sandy galleries (Templado et al., 2004). Cooper and Uzmann (1980) have described how lobsters tend to excavate holes or tunnels with one or more exits below rocks, with there being a relationship between hole size and the size of the individual. Moreover, Howard (1980) has established a significant relationship between the size of individuals and substrate type.

Lobster sampling surveys were undertaken between 7 June and 10 August 2007, with a professional lobster fishing boat. The survey was carried out during the permitted period for fishing, in summer. A total of 17 lobster pot lines were laid, near the ports of San Sebastian and Pasaia (Fig. 1). Each line was 650 m long, including 60 pots. The initial, middle (or bearing change) and final positions of the lines were recorded, using GPS. In all cases, the pots were located at the limit between a rock bed and the presence of sand patches, based upon the experience of the fishermen. Pots were deployed in the afternoon and recovered in the morning, taking advantage of the night activity of the lobsters. For each line, the number of lobsters, their sex and morphometric measurements (carapace length and width) were recorded (Bald et al., 2008).

2.2. Multibeam echosounder data

Ship-borne MBES data were acquired, as part of the continental shelf characterisation and habitat mapping programme survey, between 2005 and 2006. Bathymetric and seafloor backscatter information were acquired, using high-resolution SeaBat 7125 and SeaBat 8125 MBES. Both sets of equipment had similar characteristics (RESON, 2002, 2006).

Most of the work was carried out using the SeaBat 7125 model; its operational frequency is 400 kHz, producing 256 beams in a 128° angle swath and using up to 50 swaths per second. The beam width is 0.5° along-track and 1° across-track, producing very small footprints; these, in turn, result in high horizontal resolution digital elevation models (DEM). The MBES was coupled with an Agp132 (TRIMBLE) global position system, receiving differential corrections. An OCTANS III (IXSEA) gyrocompass and motion sensor was utilised, to compensate for the movement of the vessel. Furthermore, a portable SVP 15 (RESON) was used, to measure sound velocity profiles throughout the entire water column (Ernstsen et al., 2006). The software package PDS2000 was used to integrate the MBES data, with the information from all the auxiliary sensors during the surveys—data acquisition and synchronization. This software was used in real-time, as well as in the post-processing of the integrated data. Tidal correction was applied using the nearest tide gauge and 1 m resolution seafloor DEM was produced in projected coordinate UTM, Zone 30 N (WGS84). The DEM was generalised into a 5 m grid, in order to increase the speed of computational processing; finally, it was exported into ESRI grid format and integrated into a Geographic Information System (ArcGIS; ESRI). The

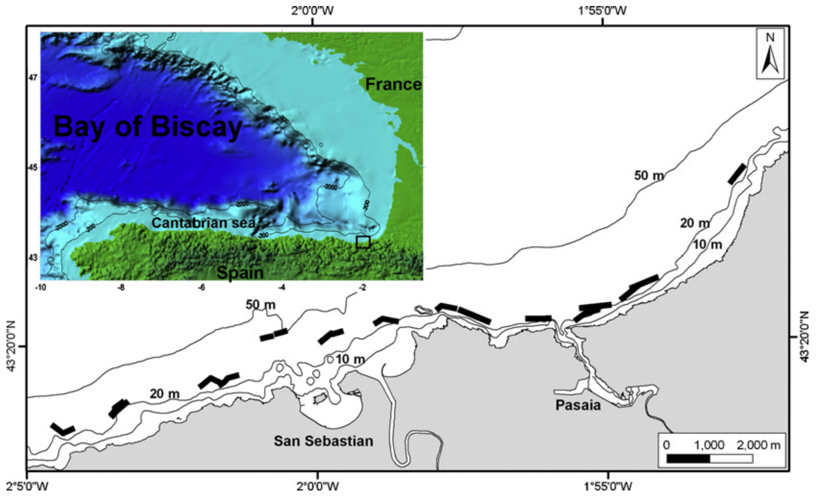

Fig. 1 – Location of the study area, within the southeastern part of the Bay of Biscay, with thick black lines representing the sampling positions.

methodology described has been used elsewhere, for other parts of the Basque continental shelf, for mapping (Galparsoro et al., 2008) and characterisation of blast furnace slag disposal areas (Borja et al., 2008).

2.3. *Seafloor morphological feature extraction*

The quantitative topographic descriptors of the seabed were obtained from the DEM. Backscatter information was analysed for seafloor classification, but was not incorporated into the ENFA because the data were not calibrated and the study was oriented towards seafloor morphology analysis. Ten seafloor morphological features were extracted, using the spatial algorithms implemented in an ArcGIS 8.1 3D Analyst extension and LandSerf 2.3 software (Wood, 2007). Multiscale analysis was performed with 3 × 3, 9 × 9 and 27 × 27 cell windows (except for the Benthic Position Index; BPI); this provided an analysis distance of 15 m × 15 m, 45 m × 45 m and 135 m × 135 m, respectively. Slope was calculated as the maximum rate of change, in degrees, between each cell and its neighbours. Orientation (i.e. aspect) distribution within the study area was calculated as the direction of the cell's slope faces; it was measured in a clockwise sense, relative to North. This parameter is useful in determining the exposure of the seafloor to wave flux. Curvature was calculated as a second derivative of the surface. Planimetric curvature was calculated as the curvature of the surface, perpendicular to the slope direction. Profile curvature was calculated as the rate of change of slope, for each of the cells. Benthic Position Index (BPI) was calculated using ArcGIS extension Benthic Terrain Modeler (BTM), Version 1.0 (Wright et al., 2005). The BPI value provides an indication of whether any particular pixel forms part of a positive (e.g., crest) or negative (e.g., trough) feature, of the surrounding terrain (Wilson et al., 2007). Two different calculations were undertaken: (i) Broad-Scale BPI, with scale factors of 15, 45, 135 and 500 m; and (ii) Fine-Scale BPI, with an scale factor of 15 m. Rugosity was calculated also with the BTM extension, cited above. The rugosity was calculated as a measure of terrain complexity. The BTM measure of rugosity is based upon the Surface Areas and Elevation Grids ArcView extension, available from Jenness Enterprises (Jenness, 2006). Seafloor types were classified into rocky seafloor and soft seafloor, on the basis of the interpretation of the MBES information. Finally, Euclidean distance from rocky seafloor was calculated for the entire study area, using an Euclidean distance algorithm in ArcGIS.

2.4. *Wave flux over the seafloor*

The distribution of wave energy over the continental shelf was calculated using a coastal hydrodynamic numerical modelling software (SMC) (González et al., 2007). SMC consists of a series of numerical programs developed specifically for the application of the methodology proposed in the Spanish Beach Nourishment and Protection Manual. The MOPLA module (GIOC, 2003) is a morphological evolution model for coastal areas, integrated into the SMC software, from which it receives the necessary input data (e.g., bathymetry, wave data, sea-level). Wave data were obtained from the Comprehensive Ocean Atmospheric Data Set (COADS), supplied through the US National Centre for Atmospheric Research (NCAR) and the National Oceanic and Atmospheric Administration (NOAA) (Table 1). This database is used also by the SMC software.

Most representative cases were simulated, and waves were propagated up to the coast. The results were processed to obtain the average wave flux, in Watts per metre of wave front width, using linear wave theory:

$$F = \frac{\rho g H^2}{8} Cg$$

$$L = \frac{gT^2}{2\pi} \tanh\left(\frac{2\pi h}{L}\right)$$

$$Cg = \frac{L}{2T}\left(1 + \frac{2kh}{\sinh(2kh)}\right)$$

$$k = \frac{2\pi}{L}$$

Table 1 – Mean annual wave distribution offshore, along the Basque coast. Data extracted from the SMC software database (for details, see text).

	Swell	Sea	Calm
Significant height (m)	3	2.1	Sum of all directions that are not capable of wave propagation, up to the coast
Peak period (s)	13	8	
Peak direction (°)	297	318	
Percentage of occurrence	22	56.6	21.4

where $\rho = 1025\,\mathrm{kg\,m^{-3}}$, $g = 9.81\,\mathrm{m\,s^{-2}}$, H = wave height (in m), Cg = group celerity (in $\mathrm{m\,s^{-1}}$), L = wavelength (in m), T = wave period (in s) and h = water depth (in m).

The vertical distribution of the flux of the energy (using the linear theory of waves) has a distribution which is proportional to

$$\frac{\cosh^2[k(h+z)]}{\cosh(kh)\sinh(kh)}$$

where z is the vertical position related to the mean level, with positive values lying upwards.

Thereafter, the average wave energy flux in the first metre over the seafloor is given by

$$F = \frac{1}{100}\left(\frac{F_{\mathrm{swell}}}{\mathrm{Tp}_{\mathrm{swell}}}P_{\mathrm{swell}} + \frac{F_{\mathrm{sea}}}{\mathrm{Tp}_{\mathrm{sea}}}P_{\mathrm{sea}} + P_{\mathrm{calm}}\right)$$

where F_{swell} is the energy flux at the sea bed, for a certain geographical location and for an average swell wave, F_{sea} is the energy flux at the sea bed, for a certain geographical location and for an average sea wave, $\mathrm{Tp}_{\mathrm{swell}}$ is the peak period of a swell wave, $\mathrm{Tp}_{\mathrm{sea}}$ is the peak period of a sea wave, P_{swell} is the percentage occurrence of swell, P_{sea} is the percentage occurrence of sea waves, and finally P_{calm} is the percentage of calms.

Mean wave flux, per metre of fetch over the first metre above the seafloor was calculated, for all of the continental shelf, using a 20 m grid cell size. Finally, the grid was resampled to the same resolution as the remainder of the grids, i.e. 5 m. This procedure does not increase the resolution of the data; besides, it was undertaken to homogenise and to operate between different layers in the software. Similar tools have been used previously in investigating the influence of wave energy, on other benthic species such as in *Pollicipes pollicipes* (Borja et al., 2006).

2.5. *Ecological-Niche Factor Analysis and habitat suitability map production*

The ENFA approach, developed by Hirzel et al. (2002) computes suitability functions by comparing the species distribution in the eco-geographical variables (EGVs) space, with that of the whole set of cells. For this, independent EGVs describe, quantitatively, some characteristics for each of the cells. The EGV may represent topographical features (e.g., altitude, slope), ecological data (e.g., seagrass cover, nitrate concentration), or human structures, e.g., distance to the nearest coastline, road density. With respect to more standard techniques, a particular advantage in the use of ENFA is that it does not require 'absence data'. The factor analysis method is applied, to transform several correlated variables into the same number of uncorrelated factors. As these factors explain the same amount of the total variance, subsequent analyses may be restricted to the few important factors, e.g., those explaining the largest part of the variance, without losing significant information. Prior to applying the ENFA a covariance matrix and a correlation tree were computed, in order to identify the highly correlated variables, as such to remove them from later analysis, as they are considered redundant. Following ENFA, the criterion adopted for the selection of the number of factors was carried out using the 'broken-stick distribution' (Hirzel et al., 2002). The factor analysis may permit the extraction of linear combinations of the original variables, on which the focal species shows most of its Marginality (M) and Specialization (S). M represents the ecological distance between the species optimum and the mean habitat within the reference area (Hirzel et al., 2002). It is defined as the absolute difference between global mean (m_{G}) and species mean (m_{S}), divided by 1.96 standard deviations (δ_{G}) of the global distribution:

$$M = \frac{\langle m_{\mathrm{G}} - m_{\mathrm{S}}\rangle}{1.96\delta_{\mathrm{G}}}$$

M will lie mostly between zero and one. A large value (close to one) means that the species lives in a very particular habitat, relative to the reference set. The equation is used mainly to explain the principle of the method. The operational definition of Marginality, implemented in the Biomapper 3.2 software, is provided by an equation which is a multivariate extension of the above equation. Similarly, S is defined as the ratio of the standard deviation of the global distribution (∂_{G}), to that of the focal species (∂_{S}):

$$S = \frac{\partial_{\mathrm{G}}}{\partial_{\mathrm{S}}}$$

A randomly selected set of cells may be anticipated to have a Specialization of one; any value exceeding unity indicates some form of Specialization. In order to establish which spatial scale was performing best, the ENFA was applied independently to each analysis scale. After selecting the best analysis scale, in relation to the resulting Marginality and Specialization, a HS map was produced. The resulting HS map is defined as a composition of cells, or pixels, whose quantitative values range from 0 to 1 (Hirzel et al., 2006). These values indicate how close the local environment is to the species' optimal conditions; as such, higher values are associated with more suitable areas.

The HS was calculated using the Medians Algorithm. As no independent data were available, the predictive accuracy of the suitability maps was evaluated by a Jack-knife Area-Adjusted Frequency Cross-Validation procedure; it was applied with 10 partitions, together with a random seed, following the method described by Boyce et al. (2002). This approach produces a confidence interval (of between 0 and 1), around the predicted accuracy of the habitat model (Skov et

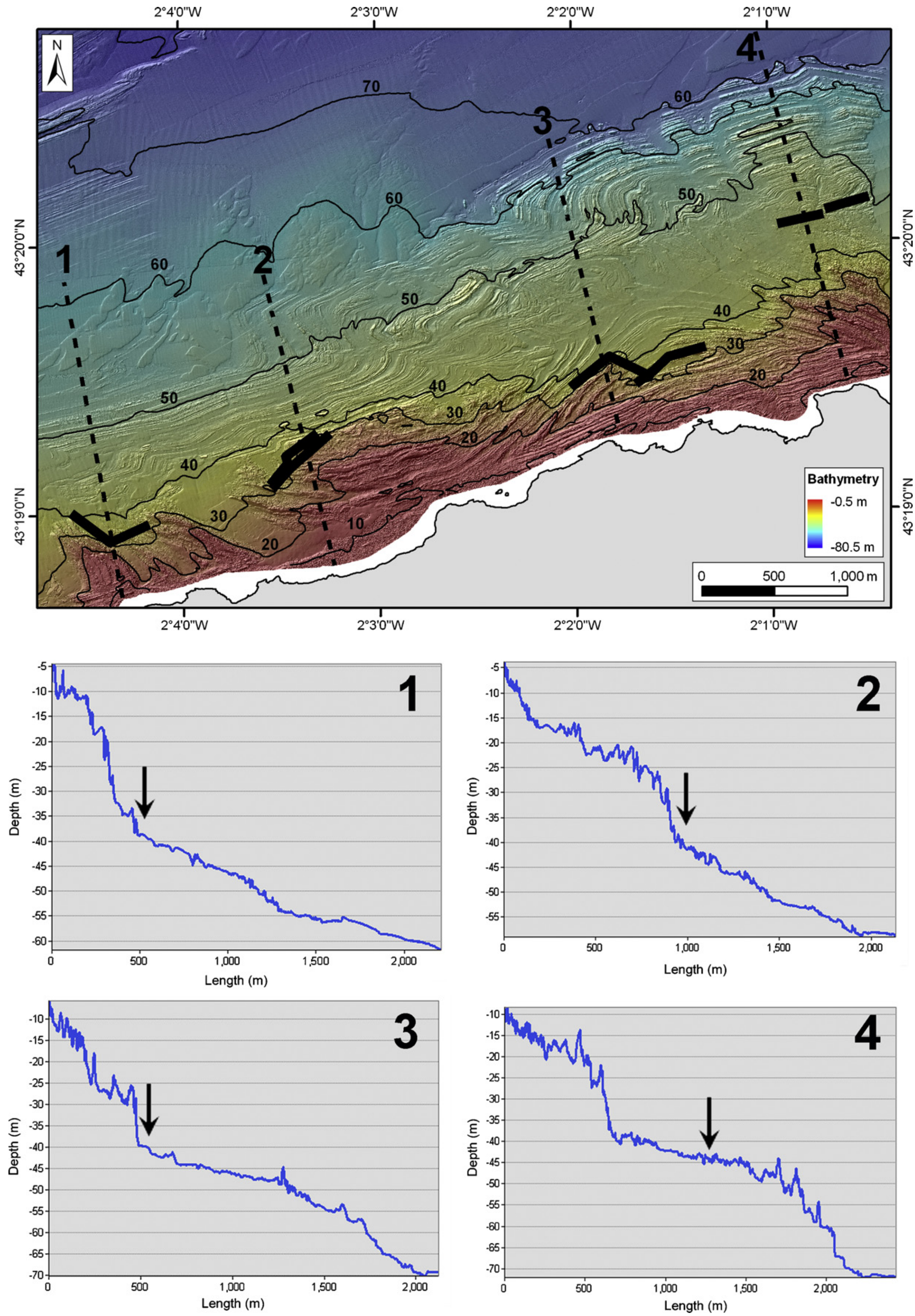

Fig. 2 – (a) Shaded relief of the digital elevation model derived from the multibeam survey (black solid lines indicate sampling pot line locations, whilst the dashed lines indicate the location of the bathymetric profiles, shown in (b)). (b) Bathymetric profiles with the arrow indicating the location of the pot deployments (see text for details).

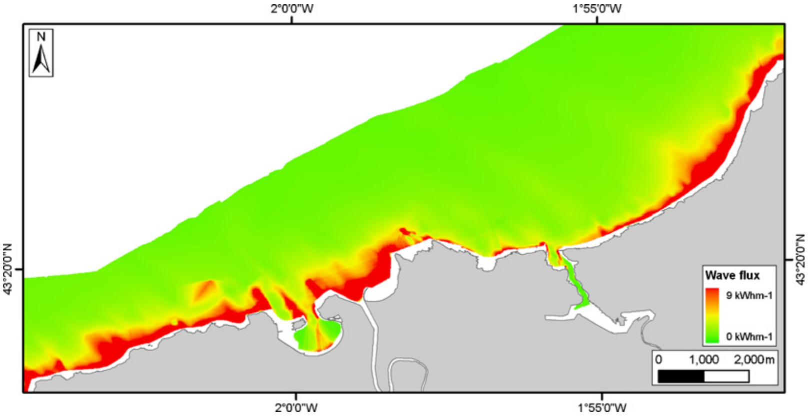

Fig. 3 – Wave flux distribution in the first metre of the water column above the seabed.

al., 2008). Values lying close to 0 indicate low confidence of the model, whereas 1 indicates the best confidence. The Boyce index provides a predicted-to-expected ratio curve, which offers further insights into the model quality: robustness, HS resolution, and deviation from randomness. Such information assists in reclassifying predicted maps, into meaningful HS classes. Thus, the continuous Boyce index is a reliable measure of 'presence-only' based predictions (Hirzel et al., 2006).

3. Results

3.1. *Seafloor morphology*

The total area of the seabed characterized was 84.9 km^2, with 3,358,221 cells. In terms of seafloor morphology, eustatic sea-level changes are highly relevant in controlling the present geomorphology of the area. The water depth range over the study area lay between 0.5 and 89.3 m, with slope values ranging from 0°, for a sedimentary seabed, up to a steep slope of 65.5°, for certain rocky beds. A shallow and high roughness bedrock belt, associated with coastal topography, is dominant; it has a slope of approximately 10%, following an inflexion point at around 32–40 m water depth (Fig. 2). Thereafter, the platform extends offshore, with a milder slope (ranging between 1.5% and 2%). Over this area, the seafloor roughness is lower and sand patches occur commonly between the exposed rock strata. In very shallow waters, blocks originating from coastal cliff erosion processes appear.

The seafloor slopes in all directions, but the westerly component (226°) dominates in response to the reshaping action of waves, over the sedimentary bottom. In terms of seafloor types, 16.2 km^2 were classified as being rocky (18.1%, of the total surface), with 67.7 km^2 as a sedimentary bottom (75.8%, of the total surface). The maximum Euclidean distance to rock, for the entire study area, was 1400 m.

The wave flux over the first metre from the seafloor varied from 0 kW h m^{-1} (i.e. areas without wave influence) to 9 kW h m^{-1} (Fig. 3). The most energetic areas were (i) those oriented towards the NW (main wave front orientation) and (ii) locations where the water depth decreased dramatically

Table 2 – Lobster sampling data obtained in June–August 2007, including the initial and final position of each pot line, the number of lobsters fished and the water depth.

Date	Hour	Initial latitude (north)	Initial longitude (west)	Final latitude (north)	Final longitude (west)	Number of lobsters	Depth (m)
2007/06/07	8:33	43.31685	−2.07619	43.31608	−2.06955	3	−40.9
2007/06/07	9:13	43.32161	−2.05412	43.31820	−2.05909	2	−39.7
2007/06/07	9:34	43.32430	−2.03369	43.32486	−2.02661	11	−39.7
2007/06/08	7:56	43.32679	−2.02217	43.32533	−2.02655	4	−35.5
2007/06/08	9:59	43.32165	−2.05518	43.31844	−2.05928	8	−40.0
2007/06/12	7:50	43.33712	−1.98339	43.33756	−1.97621	6	−34.8
2007/06/12	9:40	43.34056	−1.91513	43.33994	−1.92449	14	−38.6
2007/06/13	8:26	43.34001	−1.95912	43.33714	−1.94993	5	−30.6
2007/06/13	10:41	43.34154	−1.91262	43.34479	−1.90688	3	−38.0
2007/06/14	6:51	43.34009	−1.95943	43.33987	−1.96548	5	−35.4
2007/06/14	8:24	43.33575	−1.99212	43.33325	−1.99912	9	−33.7
2007/06/20	11:12	43.33787	−1.93242	43.33787	−1.94000	12	−36.5
2007/06/20	12:48	43.34633	−1.90155	43.34393	−1.90983	3	−31.8
2007/06/29	7:23	43.36947	−1.87644	43.36556	−1.88077	1	−34.2
2007/06/29	8:39	43.33963	−1.91857	43.33725	−1.92585	0	−34.2
2007/08/10	7:51	43.33598	−2.00817	43.33522	−2.01197	4	−49.5
2007/08/10	8:45	43.33493	−2.01207	43.33432	−2.01600	2	−44.6

Table 3 – Marginality and Specialization results, after ENFA, for different scales and multi-scale analysis.

Scale	Marginality	Specialization
3 × 3	0.983	2.418
9 × 9	1.196	2.138
27 × 27	1.514	2.261
Multi-scale	1.861	1.618

towards the coast, resulting in the concentration of wave energy.

3.2. *Lobster presence*

Information on the seafloor, together with data on the presence of lobster were integrated into a GIS (Fig. 2). Across each pot line, bathymetric profiles were extracted and the locations of the lines were plotted, together with their associated bathymetric profiles. The pots were located always on the lowest part of a steep slope, at the boundary with the sandy bottom (revealing a mild slope). The mean water depth of the lobster catches was 37.5 m. In total, 92 lobsters were caught in 17 pot line deployments. The average number of lobsters caught along each line was 5.3. Only along one of the pot lines lobsters were not caught, indicating the high selectivity of the locations where the pots were deployed (Table 2).

3.3. *ENFA*

The Box-Cox algorithm was applied to normalise the 11 eco-geographic variables. Since 10 of them were derived from multibeam bathymetric information, a covariance matrix was calculated for all of the eco-geographical variables in order to determine which of them were correlated. Variables which were highly correlated are redundant; as such, not providing additional information for the habitat prediction model. Profile curvature and plan curvature were removed on the basis of their high correlation with curvature ($r = 0.9$ and 0.7, respectively). Fine-Scale BPI was also removed, due to its correlation with curvature ($r = 0.7$). Seafloor type was removed from the analysis, due to its correlation with slope ($r = 0.7$). Although Euclidean distance to rock was correlated with slope, it was retained for subsequent analyses; this was because of its significance in the presence of lobster. After removing the correlated variables, 7 eco-geographical variables were incorporated into the ENFA: aspect, curvature, bathymetry, Broad-Scale BPI, curvature, Euclidean distance to rocky seafloor, and wave flux over the seafloor. ENFA was applied, individually, for each spatial scale of analysis and for the multi-scale analysis. The best results were obtained at a 3 × 3 scale analysis and, hence, for the maximum resolution analysis (Table 3). The overall Marginality was 0.983, whilst the overall Specialization was 2.418, with a tolerance of 0.414. These results indicate that lobster habitat differs considerably from the mean environmental conditions over the study area; likewise, that it is restrictive in the range of conditions in which it dwells.

Three factors were retained on the basis of comparison with the 'broken-stick distribution' (Hirzel et al., 2002), accounting for 96% of the information explained. Marginality

Table 4 – Variance explained by all of the ecological factors. Eigen values (in brackets) are sorted out by decreasing absolute value of coefficients on the marginality factor. *Abbreviations*: Spec., Specialization; Euclidean dist., Euclidean distance; BS BPI, Broad-Scale Benthic Position Index; Wave flux, Wave flux in the first meter over seafloor.

Marginality (65%)	Spec. 1 (22%)	Spec. 2 (7%)	Spec. 3 (2%)	Spec. 4 (2%)	Spec. 5 (1%)	Spec. 6 (1%)	Spec. 7 (1%)
Euclidean dist. (−0.55)	Bathymetry (−0.86)	Wave flux (−0.78)	Orientation (−0.97)	Euclidean dist. (0.63)		Curvature (0.98)	Slope (−0.78)
BS BPI (−0.49)	Euclidean dist. (−0.50)	Bathymetry (0.62)		Wave flux (0.48)	Slope (−0.36)	Slope (−0.15)	Wave flux (0.39)
Slope (0.45)	Wave flux (0.10)	BS BPI (−0.11)	Euclidean dist. (0.09)	Bathymetry (−0.39)	Wave flux (0.19)	Euclidean dist. (−0.09)	Euclidean dist. (−0.32)
Wave flux (0.35)	Slope (−0.05)		Slope (−0.07)	BS BPI (−0.34)	Bathymetry (−0.12)	Wave flux (0.05)	BS BPI (−0.24)
Bathymetry (0.34)	Orientation (−0.02)	Orientation (0.02)	BS BPI (0.03)	Slope (0.32)	Euclidean dist. (−0.06)	Bathymetry (−0.02)	
	Curvature (0.01)	Slope (0.01)	Bathymetry (−0.01)	Curvature (0.07)	Orientation (−0.05)	Orientation (0.02)	Bathymetry (−0.15)
Orientation (−0.08)		Curvature (0.01)	Wave flux (0.01)	Orientation (−0.02)	Curvature (−0.05)		Orientation (0.05)
Curvature (0.01)	BS BPI (0.00)	Euclidean dist. (0.01)	Curvature (0.00)		BS BPI (0.03)	BS BPI (0.01)	Curvature (−0.05)

Table 5 – Distribution of values of the five eco-geographical variables, as identified by ENFA, to be the most significant for lobster presence. For each variable, maximum, minimum, mean values and standard deviations were calculated, for the lobster overall and the presence areas.

	Overall area				Presence areas			
	Maximum	Minimum	Mean	S.D.	Maximum	Minimum	Mean	S.D.
Euclidean distance to rock (m)	3950	0	597	243	158	0	30	44
Broad-scale Benthic Position Index	28	−17	0.5	2.71	9	−7	−1.1	2.9
Slope (°)	65	0	3	3.94	44	0	6	6
Wave flux (kW h m^{-1})	12	0	0.2	0.37	0.63	0.09	0.3	0.09
Bathymetry (m, below chart datum)	−88	−1	−47	19.6	−47	−30	−37	4.14

alone accounted for 64% of the total Specialization. The environmental variables that most determined the presence of lobsters, in order of importance, were distance to rock, Broad-Scale Benthic Position Index, wave flux over the seafloor, and bathymetry (Table 4). The distribution of the most significant variables, in the overall area and in those with a lobster presence, were compared.

The inverse relationship between lobster presence and distance to rock indicates a lobster preference for locations near to rock.

The results obtained indicate that lobster capture sites were located at a mean distance, from rock, of 30 m (±44) (Table 5). On the other hand, lobster capture areas were associated with a negative BPI (−1.2 ± 2.9), indicating its preference for seafloor depressions and regions that are topographically lower than the surrounding area of the seabed. The mean slope value over the lobster presence area was 6° (±6), which is higher than within the overall area. In terms of wave energy, the mean wave flux value associated with lobster presence was 0.3 kW h m^{-1} (±0.09), indicating areas with higher values than the overall mean. Moreover, the standard deviation of this parameter is very low, indicating a very narrow range of values associated with the locations where lobsters were observed. Finally, the mean water depth of lobster catchment areas was 37 m (±4).

The cross-validation of the model quality, for the overall curve, resulted in a Boyce index of 0.98 ± 0.06; this is indicative of the predictive power of the model, with 'best-fit' being obtained for 4 equal-area bins. The HS map was reclassified, resulting in a map incorporating a range of values lying between 12 and 88. The HS value of 12–25 accounted for 2,467,396 cells, 25–50 for 531,077 cells, 50–75 for 320,299 cells,

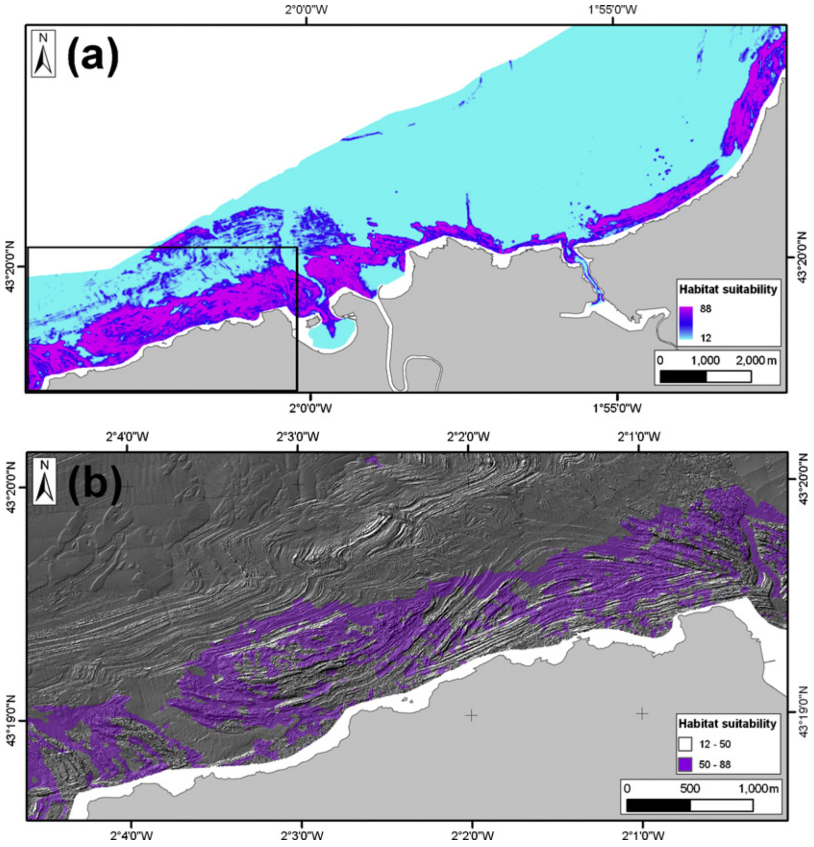

Fig. 4 – (a) Habitat suitability map for lobster over the whole of the study area. (b) Detail of a certain area where a semi-transparent habitat suitability map is overlain on the shaded relief of the digital elevation model.

and 75–88 for 17,795,658 cells. This pattern corresponds to 73.9%, 15.9%, 9.6% and 0.6% of the total surface of the study area, respectively (Fig. 4).

4. Discussion

The most suitable habitat for the European lobster, within the Basque coast, are locations lying at the boundary between sedimentary and rocky bottoms. Such areas are coincident with seafloor depressions with a steep slope, located in water depths ranging between 35 and 40 m, subjected to medium to high wave energy. These results are comparable to those obtained by Wilson et al. (2007) for the squat lobster *Munida* sp. in terms of the seafloor morphological characteristics that best explain the presence of the lobster. The most suitable habitat was found to be on mound summits, covered with coral rubble. The BPI, together with the mean curvature, were the main eco-geographic factors contributing to the Marginality of the species. The eco-geographical variables multi-scale ENFA approach was identified as providing better results than the one-scale analysis. In contrast, for the present study, the maximum resolution scale has been identified as resulting in the best results. This could be explained by the fact that the study area is very irregular, especially for the rocky seafloor; thus, increasing the analysis window appears to homogenise the seafloor features that are representative of the habitat of the lobster.

The results indicate that the distribution of the European lobster is limited to depressions within the seabed, near to rocky outcrops. This limitation appears to operate because lobsters need to avoid currents, created by tidal and wave action (Howard and Nunny, 1983). European lobsters are distributed in shallower water depths than the squat lobster. In fact, the food-gathering activity of lobsters is limited to currents of $<25\,\mathrm{cm\,s^{-1}}$, although they occur commonly in areas where near-bed currents reach, at least, twice this particular value (Shelton et al., 1981). This observation suggests that bottom topography is important, not only in providing shelter from predators, thereby reducing natural mortality, but also increasing the availability of food and the potential for growth and reproduction (Shelton et al., 1981). This latter author states that Scottish fishermen found that their pots fished best on the sides of what they identified as peaks on the echosounder; this is because lobsters feed most actively on the lee side of the ridges. Such an observation is consistent with the findings of the present investigation.

Karnofsky et al. (1989) have described, for the American lobster, that rocky areas (incorporating creeks and crevices) appear to be adequate for refuge-finding. Lobster is a shelter-dwelling animal, which spends more than 95% of the time in shelter, whenever possible, this expresses significant fidelity to one particular shelter (Paille et al., 2002). Hence, the physical structure of the habitat is a key factor in determining both the size and number of its inhabitants (Linnane et al., 2000). Similarly, spiny lobster density has been found elsewhere to be highest in channels, followed by hard bottom and patch reefs (Eggleston and Dahlgren, 2001). This association is because they provide abundant refuges, together with a likely corridor for migrating juveniles. The presence of sand on the surrounding seabed can facilitate shelter-digging under rocks, also for the active hunting of buried prey (Karnofsky et al., 1989).

The most significant eco-geographical variables are indicative of other ecological variables, which induce the presence of the lobster. For example, Lawton and Lavalli (1995) concluded that seagrass is a highly complex habitat, providing refuge from predators and supporting the high abundances of many organisms, which may serve as food for lobsters. Bello et al. (2005) found that coral-dominated seabed contained the largest proportion of the preferential habitat, as well as the highest lobster densities in summer. However, in winter, fishing effort extended to deeper areas of the reef, due to the diminution of the resource in shallow located areas; this indicates migratory movements of this specie. In turn, European lobster exhibits low migratory patterns, as demonstrated in an experiment undertaken by Smith et al. (2001). These investigations found that 95% of the recaptured lobsters moved less than 3.8 km, from their original release positions, over periods of up to 862 days. The directional distribution of the movements appeared to be related to the spatial configuration of the local lobster habitat, with a marked tendency for offshore movement (Smith et al., 2001).

For the present study, the quality of the derived model could be considered as being good according to the accepted statistical test (e.g., Boyce index (Boyce et al., 2002)). Nonetheless, special care should be taken in the representativeness of the lobster sampling. The presence of lobster is based upon the location of the lobster fishing areas; thus, in turn, was undertaken because it was not possible to fish out of the allocated period. The bias in sampling (i.e. using fishery-dependent data, from pots located in similar environments) could influence the resulting predictive map. In future, a random deployment of pots would permit patterns to be established across a broader range of seascape types; as such, any absence data would have been reliable and useful to enhance the model calibration (Brotons et al., 2004).

The ENFA was created to predict faunal distributions susceptible to erroneous or ‘false’ absences, due to an animal’s ability to disperse or hide during field surveys (Hirzel et al., 2002); in study, this situation could be comparable to the ‘catchability’ of the lobster. Hence, the ENFA is an alternative approach to modelling species potential distributions, when there is no reliable absence data (Zaniewski et al., 2002). Differences in the lobster captures can be related to three factors: (i) the availability of the resource, (ii) empirical knowledge of fishermen, about lobster habitat, and (iii) the effort needed to catch the lobsters (Bello et al., 2005). In our case, the experience of fishermen has demonstrated good knowledge of the preferred lobster habitats. The presence of lobster is restricted to certain areas, with particular environmental characteristics that have been delimited and described, on the basis of ENFA.

Some authors have determined habitat suitability for fish and invertebrate species, including American lobster in terms of surface area, based upon GIS approaches (Brown et al., 2000). Nonetheless, the use of approaches such as ENFA permits the inclusion of other environmental variables, making the analysis more powerful; the abundance and population structure of lobsters appeared, elsewhere, to be determined largely by environmental conditions and HS (Pulfrich et al., 2003).

Future studies include random sampling for model quality estimation and the application of other statistical techniques for the comparison of results. The inclusion of new environmental variables should be considered, such as, calibrated backscatter information and other oceanographic variables (water currents, temperature or wind).

Habitat models are important tools for understanding the ecological niche of a particular species. However, these must be considered carefully if they are intended to represent reality, providing information on the need for improved resource management and habitat conservation (Etnoyer and Morgan, 2007). As highlighted by Butler (2005), fishery and environmental managers are faced with multiple, often conflicting, demands of resource users, politicians and scientists, when considering strategies for resource management. Hence, the use of 'envelope-based' approaches, such as the ENFA, permits the integration of environmental and biological data, to better understand benthic resource distribution and habitat suitability.

5. Conclusions

The Marginality and Specialization values obtained from the ENFA indicate that the presence of the European lobster (*H. gammarus*) is determined by a range of environmental parameters; which differ from the mean conditions over the study area. The preferred habitat lies adjacent to the rocky seafloor with depressions, characterized by steeply sloping seabed in shallow waters and subjected to medium–high wave energy.

To the knowledge of the authors, this is the first occasion that habitat modelling has been carried out for the European lobster. Likewise, that shallow water high-resolution seabed topographic information has been used, in combination with wave flux over the seafloor, for lobster habitat modelling. Future work will focus upon the realisation of specific surveys, with random sampling, in order to quantify statistically the reliability of the lobster distribution model.

The increase in the availability of high-resolution and full coverage seabed information, together with an improved knowledge of the species biology and behavioural knowledge, demonstrate that multiparametric analysis is a valuable method for the discrimination of specific areas. These areas fulfil certain combinations of characteristics, which increase the probability of the presence of the lobster. Such information is essential for integrated coastal zone management and for decision-makers, as well as for the basic knowledge for the adoption of ecosystem-based resource management actions.

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