DISTRIBUCIÓN GEOGRÁFICA, PREDICCIÓN ESPACIAL Y DIVERSIDAD DE LOS HÁBITATS LITORALES EN LA COSTA CATALANA

Maria Elena Cefalì

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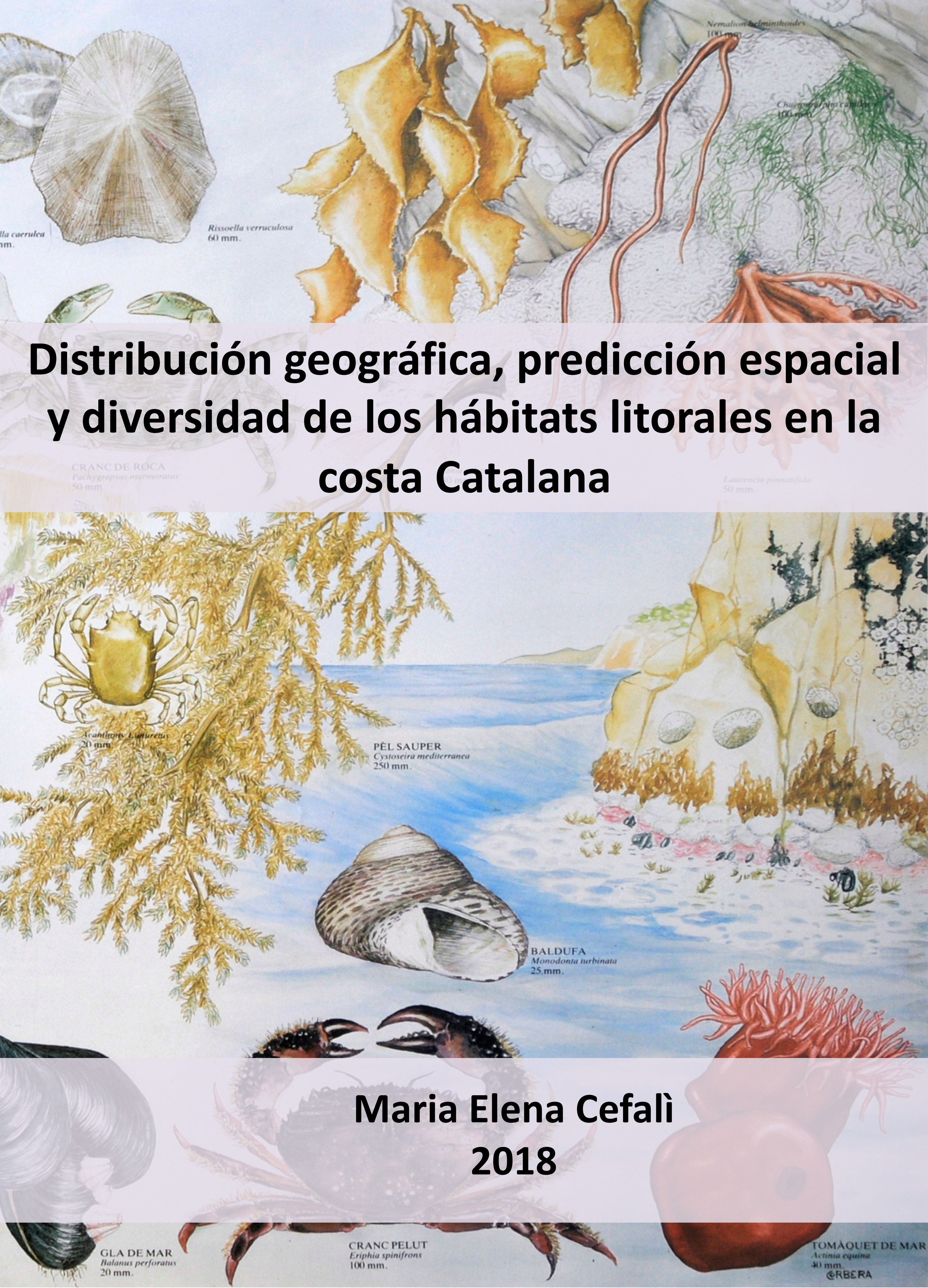

Distribución geográfica, predicción espacial y diversidad de los hábitats litorales en la costa Catalana

Maria Elena Cefalì

2018

Universitat de Girona

Tesis Doctoral

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Dirigida por:

Emma Cebrian Pujol
Enric Ballesteros Sagarra

Tutora:
Emma Cebrian Pujol

Memoria presentada para optar al título de doctora por la Universidad de Girona

Esta Tesis ha sido preparada como compendio de artículos en acuerdo con el reglamento de la Universidad de Girona. Incluye tres artículos, dos de los cuales han sido publicados en revistas científicas y uno ha sido enviado y está en fase de revisión.

A continuación se presentan las referencias originales de cada artículo presente en esta Tesis y en el apartado Apéndice, una copia del formato publicado por las respectivas revistas.

1. Cefalì, M.E., Cebrian, E., Chappuis, E., Terradas, M., Mariani, S., Ballesteros, E. Community-dependent variability in species composition and richness at a regional scale. Under review in *Estuarine, Coastal and Shelf Science. Sent on the 28th of September 2018.*
   IF$_{2017}$ = 2,413; 1st Quartile in category Marine & Freshwater Biology (23/64) and Oceanography (14/64)

2. Cefalì, M. E., Cebrian, E., Chappuis, E., Pinedo, S., Terradas, M., Mariani, S., Ballesteros, E. (2016). Life on the boundary: environmental factors as drivers of habitat distribution in the littoral zone. *Estuarine, Coastal and Shelf Science*, 172, 81-92
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   IF$_{2017}$ = 2,413; 1st Quartile in category Marine & Freshwater Biology (23/64) and Oceanography (14/64)

3. Cefalì, M. E., Ballesteros, E., Riera, J. L., Chappuis, E., Terradas, M., Mariani, S., Cebrian, E. (2018). The optimal sampling design for littoral habitats modelling: A case study from the north-western Mediterranean. *PloS One*, 13(5), e0197234.
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   IF$_{2016}$ = 2,806; 1st Quartile in Multidisciplinary Science (15/64)

A ti por la vida misma…

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Contenidos

Abreviaciones

A: *Artificial*

AIC: *Akaike Information Criterion*

Arti: *Artificialization*

AUC: *Area Under the Curve*

Ban fus: *Bangia atropurpurea*

CARLIT: *Cartografía litoral*

CATLIT: *Cartografía litoral de catenas*

Cer cil: *Ceramium ciliatum*

Cer Osm: *Ceramium spp./ Osmundea spp.*

Cht spp: *Chthamalus spp.*

Cor elo: *Corallina elongata*

Cor elo: *Corallina elongata*

Cor elo: *Corallina elongata*

CSIC: *Consejo Superior de Investigación Científica*

Cys cae: *Cystoseira caespitosa*

Cys med: *Cystoseira mediterranea*

Cys med: *Cystoseira mediterranea*

D: *Deviance*

DEM: *Digital Elevation Model*

Den pet: *Dendropoma petraeum*

DOW: Downscaled Ocean Waves

E: *East*

EC: *European Commission*

e.g.: *exempli gratia*

ESRI: *Environmental System Research Institute*

EUNIS: *European Nature Information System*

F: *Frequency*

Gel cri: *Gelidium crinale*

Gel pus: *Gelidium pusilum*

Geo: *Geology*

GIS: *Geographical Information Systems*

GLM: *Generalized linear modelos*

H: *Horizonte*

HDF: *Hierarchical Data Format*

HDM: *Habitats Distribution Models*

Hil : *Hildenbrandia rubra and*

Hydro: *Hydrodynamism*

i.e.: *id est*

ICC: *Institut Cartogràfic de Catalunya*

IGCC: *Institut Geològic i Cartogràfic de Catalunya*

IL: *Infralitoral*

IQR: *Latitudinal Interquartile Ranges*

Lit vic: *Lithophyllum cf.vickersiae*

Km: *Kilometros*

Lit bys: *Lithophyllum byssoides*

Lit inc: *Lithophyllum incrustans*

Lit inc: *Infralittoral Lithophyllum incrustans*

LPRE : *Lista Patrón de Habitats Españoles*

MDS: *Multi Dimensional Scaling*

ML : *Mediolitoral*

Myt gal: *Mytilus galloprovincialis*

N: *Natural*

N: *North*

N: *Number points*

NASA: *National Aeronautics and Space Administration*

NE: *NorthEast*

Nem tin: *Nemoderma tingitanum*

Neo bra: *Neogoniolithon brassica-florida*

nMDS: *non-metric Multi-Dimensional Scaling*

NW: *NorthWest*

OBIS: *Ocean Biogeographic Information System*

Ori: *Orientation*

PA: *Photophilic algae*

PCA: *Principal Component Analysis*

PCO: *Principal Coordinates Analysis*

Phy: *Phymatolithon lenormandii*

Pol ser: *Polysiphonia sertularioides*

Pte cap: *Pterocladiella capillacea*

Pyr elo: *Pyropia elongata*

Ral ver: *Ralfsia verrucosa*

Ris ver: *Rissoella verruculosa*

ROC: *Receiver Operating Characteristic*

S: *South*

SA: *Sciaphilic algae*

Sab alv: *Sabellaria alveolata*

SDM: *Species Distribution Models*

se: *Sensitivity*

SE: *SouthEast*

SIL: *Infralittoral sciaphilic*

spe: *Specificity*

SST: *Sea Surface Temperature*

Subs: *Substrate*

SW: *SouthWest*

Ulv :*Ulvales*

UTM: Universal Transverse Mercator

Ver Eur: Verrucaria amphibia y Euraphia depressa

W: West

WH: Wave Height

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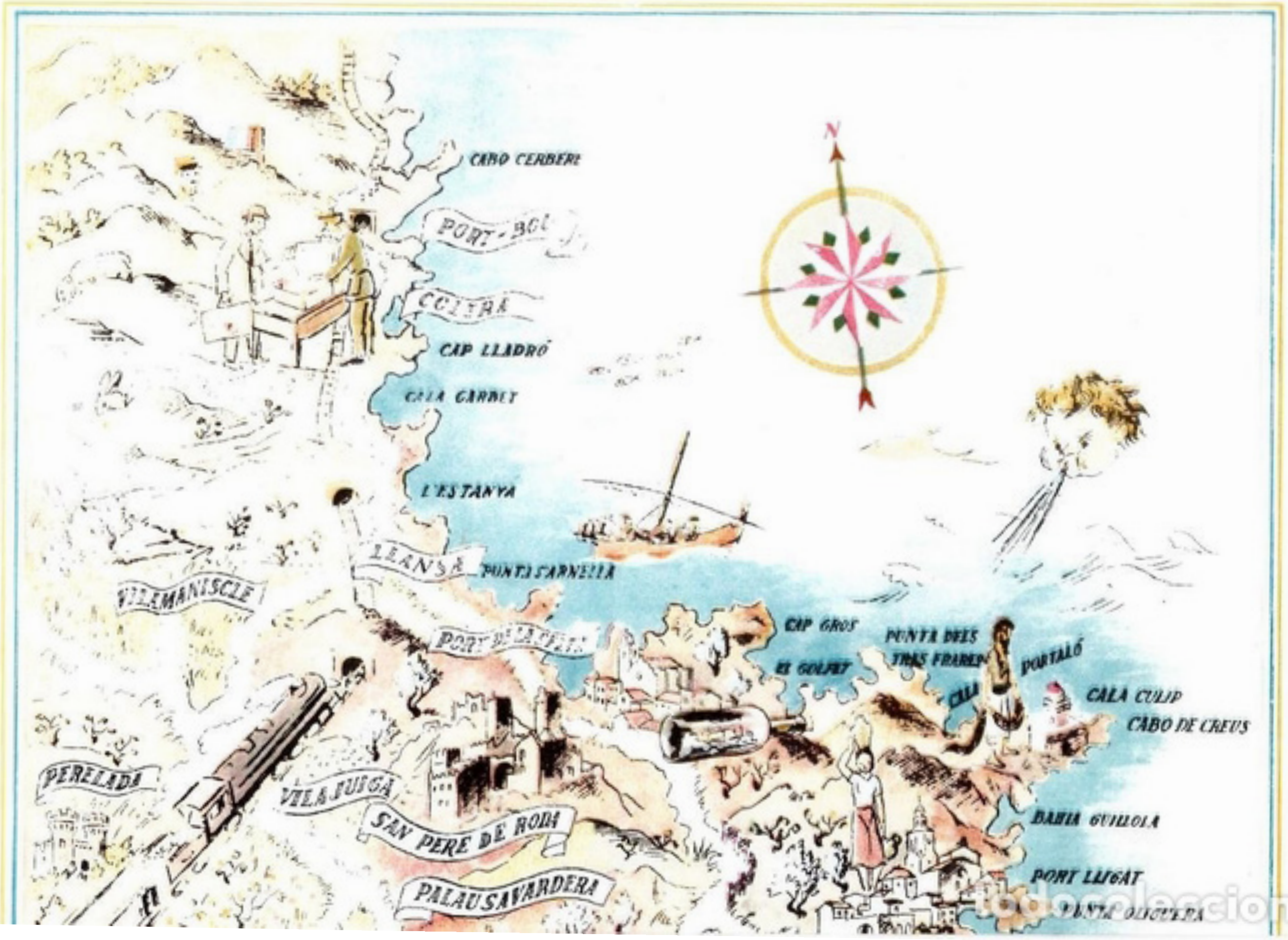
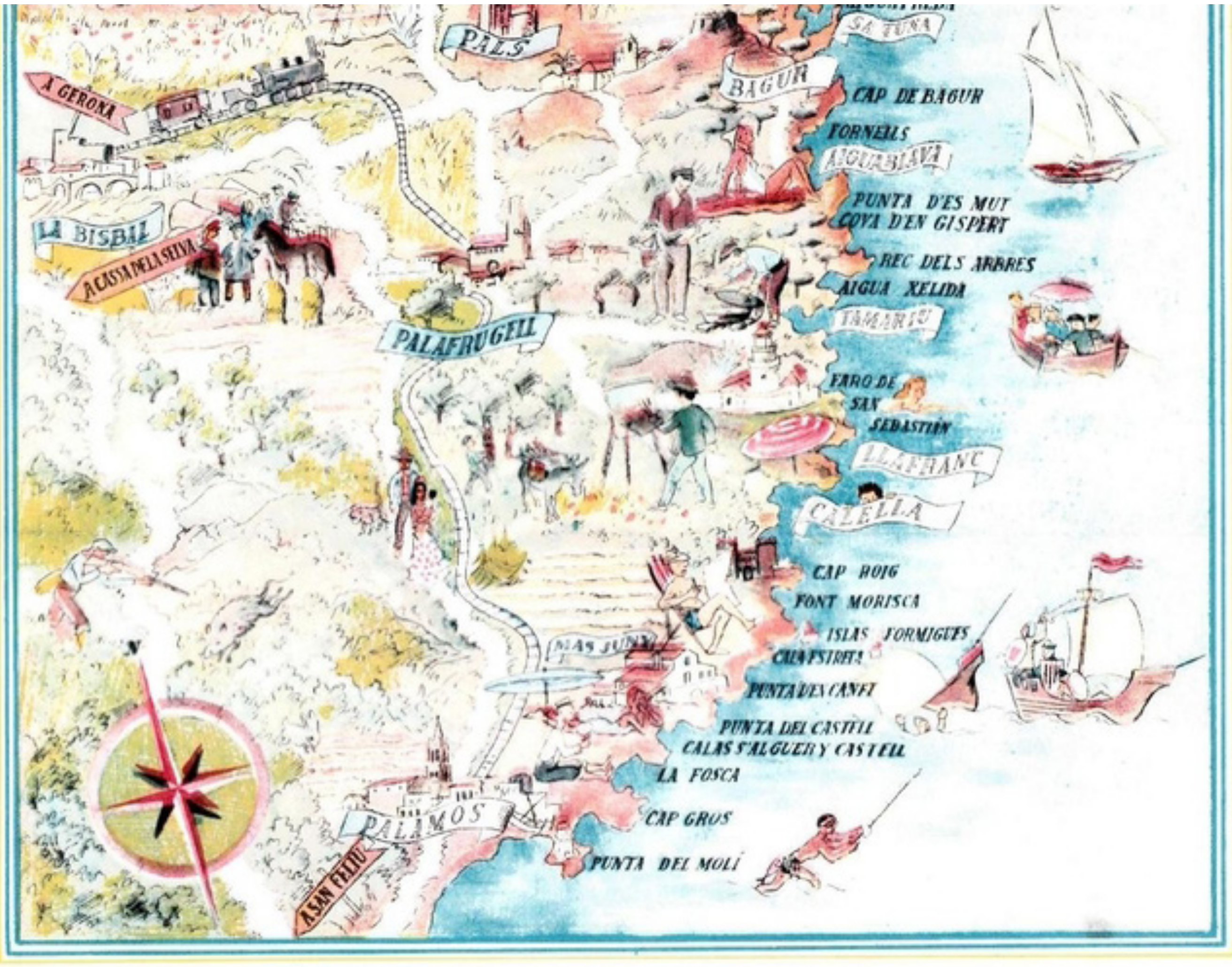


N
CABO CERBERE
PORT-BOU
COLERA
CAP LLADRÓ
CALA GARBET
L'ESTANYA
LLANSÁ
PUNTA S'ARNELLA
VILAMANISCLE
PORT DE LA SELVA
CAP GROS
EL GOLFET
PUNTA DELS TRES FRARES
CALA
PORTALÓ
CALA CULIP
CABO DE CREUS
PERELADA
VILAJUIGA
SAN PERE DE RODA
PALAU SAVARDERA
BAHIA GUILLOLA
PORT LLIGAT
PUNTA OLIGUERA



SA TUNA
PALS
BAGUR
CAP DE BAGUR
A GERONA
FORNELLS
AIGUABLAVA
PUNTA D'ES MUT
COVA D'EN GISPERT
LA BISBAL
A CASSA DE LA SELVA
REC DELS ARBRES
AIGUA XELIDA
TAMARIU
PALAFRUGELL
FARO DE SAN SEBASTIÁN
LLAFRANC
CALELLA
CAP ROIG
FONT MORISCA
ISLAS FORMIGUES
MAS JUNY
CALA ESTRETA
PUNTA D'EN CANFI
PUNTA DEL CASTELL
CALAS S'ALGUER Y CASTELL
LA FOSCA
CAP GROS
PALAMÓS
PUNTA DEL MOLÍ
A SAN FELIU

Abstract

According to the Habitats Directive (92/43/ECC) a habitat is defined as “the terrestrial or aquatic area, whether entirely natural or semi-natural, differentiated by its geographical, biotic and abiotic characteristics, in which the species live in any state of their life cycle”. Moreover, according to the Marine Strategy Framework Directive (2008/56/EC), each member state has to characterize the diversity of its natural marine spaces by means of the habitats cartography, represented by their biotic characteristics and using appropriate classifications systems. In Catalonia, to fulfill these needs, an exhaustive cartography of the littoral habitats was carried out, characterizing and identifying them according to Corine Biotopes, EUNIS (European Nature Information System) classification and LPRE (Lista Patrón de los Hábitats Españoles) whether they grow over rocks, sand, gravel, pebbles or mud.

The littoral zone can be divided into three levels: supralittoral (rarely submerged and usually affected by splash), mediolittoral (emerged and usually swept by the waves) and infralittoral (usually submerged). Organisms are distributed vertically following the humidity gradient and generating a gradual and continuous succession of different communities/habitats from the supralittoral level to the upper infralittoral level. Data derived from the characterization, identification and accurate cartography of coastal marine habitats on rocky shores along the Catalan coast, has allowed the development of this Doctoral Thesis that is divided into three main chapters, two of which have already been published in Scientific Journals.

The first objective of the thesis (Chapter 2.1) is to find out if a habitat can be differentiated at the level of species composition and species richness due to its geographical position, i.e. along the latitudinal gradient from northern to southern Catalonia. To accomplish this, the most frequent habitats of the mediolitoral and upper infralittoral levels have been chosen and their internal variability has been analyzed along their full distribution range. The results have proven that the horizontal variation determining the structure and species composition results to be community dependent and that a general pattern at a regional scale is lacking. Habitats with a wide geographic distribution usually present some variation, which is related to changes in the environmental factors across the geographical gradient.

In the Chapter 2.2 we explore the relative importance of environmental factors such as littoral’s geomorphological features, wave exposure, water temperature and orientation in determining the presence of littoral habitats along Catalonia’s shoreline by using Geographical Information Systems and Generalized Linear Models. Regional differences in the presence/absence of mediolittoral habitats are apparently driven by seawater temperature and substrate type. Wave exposure, coastal slope and geological features are only relevant to those habitats with specific environmental needs. In contrast, infralittoral habitats do not show any regional distribution pattern and selected factors only play a moderate role in habitat distribution at the local scale. This chapter provides the basis for the development of models oriented at predicting the distribution of littoral marine habitats, which is the aim of chapter 2.3.

Species distribution models are used in the chapter 2.3 to predict potential distributions of habitats and to model the effects of environmental changes. By using a huge database of 16,098 points over 563 km of coastline, logistic predictive models according to different sampling strategies are assessed and validated. A regularly interspaced strategy with a sample of 20% of the coastline provides the best compromise between sampling cost, effort and accuracy. Model performance is strongly dependent upon habitat characteristics.

This is the first study that, using a huge regional data set, identifies the variability of littoral habitats across hundreds of kilometers, relates environmental factors to littoral habitats distribution, and tries to model their distribution according to the most relevant environmental factors. This knowledge can be used to develop conservation actions and environmental management plans of a littoral zone heavily impacted by human activities.

Resum

Segons la Directiva Hàbitats (92/43/ECC) un hàbitat es defineix com “una àrea aquàtica o terrestre, tant natural com seminatural, diferenciada per les seves característiques geogràfiques, biòtiques i abiòtiques, on les espècies hi viuen en qualsevol etapa del seu cicle de vida”. A més, d’acord amb la Directiva Marc d’Estratègia Marina (2008/56/EC), cada estat membre té l’obligació de caracteritzar la diversitat dels seus espais naturals marins mitjançant una cartografia dels hàbitats, representats per les seves característiques biòtiques i utilitzant sistemes de classificació apropiats. A Catalunya, per complir amb aquests requeriments, es va realitzar una cartografia exhaustiva dels hàbitats litorals, caracteritzant-los i identificant-los segons els sistemes de classificació CORINE Biotopes, EUNIS (European Nature Information System) i LPRE (Lista Patrón de los Hábitats Españoles), tant si es presentaven sobre roca, sorra, graves, còdols o fangs.

La zona litoral pot ser dividida en tres estatges: supralitoral (rarament submergit i afectat regularment pels esquitxos), mediolitoral (emergit i constantment remullat per les onades), i infralitoral (habitualment submergit). Els organismes es distribueixen verticalment seguint el gradient d’humitat, tot generant una successió contínua de diferents comunitats/hàbitats des de l’estatge supralitoral fins a la part superior de l’estatge infralitoral. Les dades provinents de la caracterització, identificació i cartografia acurada dels hàbitats marins costaners rocosos al llarg de la costa catalana, han permès la realització d’aquesta tesi doctoral, la qual es divideix en tres capítols principals, dos dels quals ja han estat publicats en revistes científiques.

El primer objectiu de la tesi (Capítol 2.1) és esbrinar si un hàbitat es pot diferenciar per la seva composició i la seva riquesa específica independentment de la seva situació geogràfica, és a dir, al llarg del gradient latitudinal de la costa catalana. Per a comprovar-ho, es van escollir els hàbitats més freqüents de l’estatge mediolitoral i de la part superior de l’estatge infralitoral i es va analitzar la seva variabilitat interna en tot el seu rang de distribució a Catalunya. Els resultats mostren que la variació horitzontal que determina l’estructura i la composició específica depèn de cada comunitat i que no hi ha cap patró a escala regional. Els hàbitats amb una distribució geogràfica més àmplia mostren sovint una certa variabilitat que es relaciona amb canvis en els factors ambientals associats al gradient geogràfic.

En el capítol 2.2 s’explora la importància relativa de factors ambientals tals com les característiques geomorfològiques del litoral, l’exposició a les onades, la temperatura de l’aigua i l’orientació de la costa en determinar la presència dels hàbitats litorals al llarg de la costa catalana, mitjançant la utilització de Sistemes d’Informació Geogràfica (SIG) i Models Linears Generalitzats (GLM). Les diferències regionals en la presència o absència dels hàbitats mediolitorals semblen explicar-se per la temperatura de l’aigua i pel tipus de substrat. L’exposició a les onades, la inclinació de la costa i les característiques geològiques només són rellevants per aquells hàbitats amb requeriments

ambientals específics. En canvi, els hàbitats infralitorals no mostren cap patró de distribució regional i els factors ambientals seleccionats només juguen un paper moderat en explicar la seva distribució a nivell local. Aquest capítol proporciona la base per al desenvolupament de models orientats a predir la distribució dels hàbitats marins litorals, que és el tercer objectiu de esta Tesis (Capítol 2.3).

En el capítol 2.3 s'utilitzen models de distribució d'espècies per predir les distribucions potencials dels hàbitats i modelar els efectes dels canvis ambientals. Utilitzant una gran base de dades constituïda per 16.098 punts distribuïts al llarg de 563 km de costa es van estimar i validar diferents estratègies de mostreig mitjançant models de predicció logístics. Una estratègia basada en el mostreig discontinu del 20% de la línia de costa maximitza el compromís entre cost de mostreig, esforç i precisió en la predicció. Tot i així, la robustesa del model és fortament depenent de les característiques dels hàbitats.

Aquest és el primer estudi que, utilitzant una extensa base de dades regional, identifica la variabilitat dels hàbitats litorals al llarg de centenars de kilòmetres, relaciona els factors ambientals amb la distribució dels hàbitats litorals, i intenta modelar la seva distribució utilitzant els factors ambientals més rellevants. Els coneixements assolits poden fer-se servir per desenvolupar accions de conservació i plans de gestió ambiental en una zona litoral fortament impactada per les activitats humanes.

Resumen

Según la Directiva Hábitats (92/43/ECC) un hábitat se define como “una área acuática o terrestre, tanto natural como semi-natural, diferenciada por sus características geográficas, bióticas y abióticas, donde las especies viven en cualquier etapa de su ciclo de vida”. Además, de acuerdo con la Directiva Marco de Estrategia Marina (2008/56/EC), cada estado miembro tiene la obligación de caracterizar la diversidad de sus espacios naturales marinos mediante una cartografía de hábitats, representados por sus características bióticas y utilizando los sistemas de clasificación apropiados. En Cataluña, para cumplir con estos requerimientos, se realizó una cartografía exhaustiva de los hábitats litorales, caracterizándolos e identificándolos según los sistemas de clasificación CORINE Biotopes, EUNIS (European Nature Information System) y LPRE (Lista Patrón de los Hábitats Españoles), tanto si se presentaban sobre roca, arena, grava, cantos rodados o fangos.

La zona litoral se puede dividir en tres pisos: supralitoral (raramente sumergido y afectado regularmente por las salpicaduras), mediolitoral (emergido y constantemente remojado por las olas) e infralitoral (habitualmente sumergido). Los organismos se distribuyen verticalmente siguiendo el gradiente de humedad, generándose una sucesión continua de diferentes comunidades/hábitats desde el piso supralitoral hasta la parte superior del piso infralitoral. Los datos provenientes de la caracterización, identificación y cartografía precisa de los hábitats marinos costeros rocosos de la costa catalana han permitido realizar esta tesis doctoral, dividida en tres capítulos principales, dos de los cuales ya han sido publicados en sendas revistas científicas.

El primer objetivo de la tesis (Capítulo 2.1) consiste en averiguar si un hábitat se puede diferenciar por su composición y riqueza específica independientemente de su situación geográfica, es decir, al largo del gradiente latitudinal de la costa catalana. Para comprobarlo, se escogieron los hábitats más frecuentes del piso mediolitoral y de la parte superior del piso infralitoral, analizándose su variabilidad interna en todo el rango de distribución de Cataluña. Los resultados muestran que la variación horizontal que determina su estructura y composición específica depende de cada comunidad y que no hay ningún patrón a escala regional. Los hábitats con una distribución geográfica más amplia muestran una cierta variabilidad que se relaciona con cambios en los factores ambientales asociados al gradiente geográfico.

En el Capítulo 2.2 se explora la importancia relativa de factores ambientales tales como las características geomorfológicas del litoral, la exposición al oleaje, la temperatura del agua y la orientación de la costa en la presencia o ausencia de los hábitats litorales en la costa catalana, mediante la utilización de Sistemas de Información Geográfica (SIG) y Modelos Lineares Generalizados (GLM). Las diferencias regionales en la presencia o ausencia de los hábitats mediolitorales parecen explicarse por la temperatura del agua y el tipo de sustrato. La exposición

al oleaje, la inclinación de la costa y las características geológicas solamente son relevantes para aquellos hábitats con requerimientos ambientales específicos. En cambio, los hábitats infralitorales no muestran ningún tipo de distribución regional y los factores ambientales seleccionados solo juegan un papel moderado en explicar su distribución a nivel local. Este capítulo proporciona las bases para el desarrollo de modelos orientados a predecir la distribución de los hábitats marinos litorales, tercer objetivo de esta Tesis (Capítulo 2.3).

En el Capítulo 2.3 se utilizan modelos de distribución de especies para predecir las distribuciones potenciales de los hábitats y modelar los efectos de los cambios ambientales. Utilizando una extensa base de datos con 16.098 puntos distribuidos a lo largo de 563 km de costa se estimaron y validaron diferentes estrategias de muestreo mediante modelos de predicción logísticos. Una estrategia basada en el muestreo discontinuo del 20% de la línea de costa maximiza el compromiso entre coste de muestreo, esfuerzo y precisión en la predicción. Sin embargo, la robustez del modelo depende fuertemente de las características de los hábitats.

Este es el primer estudio que, utilizando una extensa base de datos regional, identifica la variabilidad de los hábitats litorales a lo largo de centenares de kilómetros, relaciona los factores ambientales con la distribución de los hábitats litorales e intenta modelar su distribución utilizando los factores ambientales más relevantes. Los conocimientos adquiridos pueden utilizarse para desarrollar acciones de conservación y planes de gestión ambiental en una zona litoral fuertemente impactada por las actividades humanas.

Introducción

Un hábitat puede definirse como “el área terrestre o acuática diferenciada por sus características geográficas, bióticas y abióticas, ya sean enteramente naturales o seminaturales, en las cuales viven las especies en cualquier estado de su ciclo de vida” (Directiva Hábitats 92/43/ECC). En este contexto, un hábitat representa una unidad operativa útil para caracterizar, organizar y clasificar las agrupaciones de los diferentes organismos con el objetivo de describir la biodiversidad y la distribución de las especies a lo largo de diferentes escalas espaciales.

La necesidad de describir el entorno natural ha llevado a la descripción de los hábitats desde antiguo, lo cual fue de alguna manera sistematizado a principios y mediados del siglo XX mediante aproximaciones diversas como la fitosociología o la bionomía marina (Feldmann 1937; Braun-Blanquet 1964; Boudouresque 1971; Ballesteros 1992). Estos esfuerzos se basaban en describir unidades de vegetación (asociaciones) definidas por unas especies “fieles” a dichas unidades (las especies “características”) que se ordenaban en una clasificación jerárquica de distintos niveles (alianzas, órdenes, clases). Aunque este sistema de describir y clasificar las unidades de vegetación fue ampliamente aceptada en los países mediterráneos, en el mundo anglosajón se optaba por una descripción de las comunidades naturales definidas por las especies dominantes.

A principios de los años 90 la comunidad europea adopta un sistema propio de clasificación de las comunidades naturales, el CORINE Biotopes Manual of the European Community (CBM) (Devillers et al. 1991), el cual clasifica jerárquicamente todos los hábitats, también los semi-naturales y los artificiales, y los identifica mediante un código que aporta información sobre los grupos y subgrupos en los que el hábitat está incluido y que permite averiguar la similitud entre los hábitats. Dicho sistema CORINE tiene como misión principal ayudar a representar los hábitats para definir los usos del suelo y, por lo tanto, no posee una misión de conservación de la biodiversidad. Al mismo tiempo se creaba EUNIS (European Nature Information System) como parte del BDC (Biodiversity Data Center) de la UE cuya misión principal era aportar información sobre el medio ambiente (especies, hábitats y lugares) que asistiera a la implementación de estrategias de conservación de la biodiversidad a nivel europeo. EUNIS desarrolló una propuesta de clasificación de hábitats paralela a CORINE (Davies et al. 2004; Galparsoro et al. 2012). Al igual que CORINE esta clasificación es jerárquica pero solamente hasta cierto nivel (habitualmente 3) y a partir de este nivel las unidades se obtienen de otros sistemas de clasificación, a menudo elaborados por organizaciones estatales o supranacionales (caso del Convenio de Barcelona). EUNIS también engloba todo tipo de hábitats (incluidos los artificiales), los identifica mediante códigos jerarquizados y los define como “una área donde las plantas y los animales viven, y que se caracteriza primariamente por sus características físicas (topografía, fisionomía vegetal o animal, características del suelo, clima, calidad del agua, etc.) y secundariamente por las especies animales o vegetales que la habitan" (Davies et al. 2004).

Sea como fuese, CORINE y EUNIS son solamente sistemas de clasificación de hábitats y ello no debe confundirnos a la hora de caracterizarlos ya que los hábitats los moldea la naturaleza y estas plataformas solo los clasifican para remarcar sus similitudes y diferencias y ayudar en los mecanismos de protección y gestión.

Casi paralelamente a la creación de CORINE y EUNIS la misma comunidad europea propuso la Directiva Hábitats (92/43/EEC), cuya finalidad es la de garantizar la conservación de una serie de especies y hábitats considerados vulnerables y para los que los países miembros debían proponer unas medidas específicas de conservación y el establecimiento de unas áreas de protección (Red Natura 2000). La nomenclatura y clasificación de dichos hábitats no coincidía sin embargo e inexplicablemente con las propuestas de CORINE biotopes ni de EUNIS por lo que fue necesario crear una serie de correspondencias entre unos y otros hábitats, a menudo inexacta y no recíproca.

Muy posteriormente a la Directiva Hábitats apareció la Directiva Europea de Estrategia Marina (2008/56/EEC) cuya función es velar por alcanzar o mantener un buen estado ecológico del medio marino y perseverar en su protección y conservación. Para ello, según el Anexo II de esta Directiva, los estados miembros debían definir y cartografiar los tipos de hábitats y sus componentes biológicos dentro de los límites de sus aguas territoriales. Para poder cumplir este reto, las políticas de gestión y conservación, necesitan clasificaciones de hábitats para ampliar los conocimientos sobre la diversidad biológica y su distribución espacial, para desarrollar acciones más efectivas en la preservación y conservación de la naturaleza. Esta necesidad hace imprescindible que las clasificaciones sean lo más consensuadas posibles tanto a nivel descriptivo como metodológico.

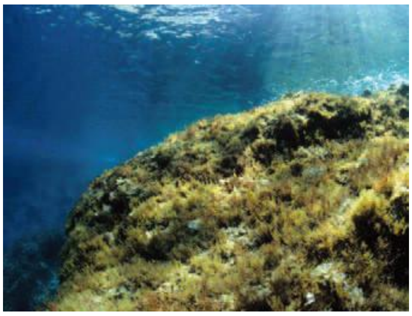
Habida cuenta de la existencia de EUNIS y CORINE y del hecho que dentro de EUNIS a partir de cierto nivel jerárquico se adoptan otras clasificaciones de hábitats dificulta el establecimiento de una clasificación de hábitats aceptada y compartida en toda Europa, con una terminología común y consensuada (Costello 2009). En España y en relación al medio marino, la comunidad científica ha obviado esta carencia creando un inventario con el mismo sistema jerárquico que EUNIS y que incluye todos los hábitats atlánticos, macaronésicos y mediterráneos conocidos en el territorio español (Lista Patrón de los Hábitats Españoles, LPRE, Templado et al. 2012). El criterio de clasificación utilizado por EUNIS y por LPRE permite considerar los hábitats a los distintos niveles de clasificación en su estructura jerárquica. Por ejemplo podemos hablar de los hábitats a nivel 3 y nos estaremos refiriendo básica y mayoritariamente a las características del medio físico mientras que si lo hacemos a nivel 4 o 5 nos estaremos refiriendo a un hábitat más preciso donde se tienen en cuenta sus particularidades florísticas/faunísticas (ver Tabla1.1 y Figura 1.1).

Tabla 1.1. Hábitats LPRE. Clasificación según LPRE de los hábitats mediolitorales de costa rocosa en Catalunya.

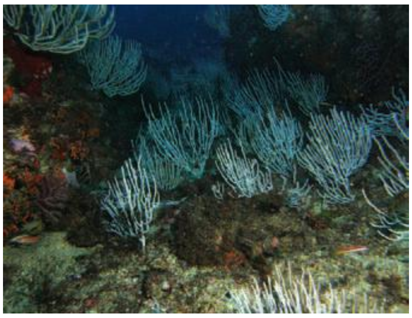
Código	**Nivel**	**Hábitat**
02	1	Piso mediolitoral
0201	2	Piso mediolitoral rocoso y otras sustratos duros
020101	3	Roca mediolitoral expuesta
02010115	4	Cornisa de *Lithophyllum byssoides* sobre roca mediolitoral expuesta
020102	3	Roca mediolitoral moderadamente expuesta
02010214	4	Horizonte de *Chthamalus* spp. sobre roca mediolitoral moderadamente expuesta
02010215	4	Horizonte de *Rissoella verruculosa* sobre roca mediolitoral moderadamente expuesta
02010216	4	Horizonte de *Ralfsia verrucosa* sobre roca mediolitoral moderadamente expuesta
02010218	4	Roca mediolitoral moderadamente expuesta con *Pyropia elongata*
02010219	4	Roca mediolitoral moderadamente expuesta con *Polysiphonia sertularioides*
02010220	4	Roca mediolitoral moderadamente expuesta con *Bangia fuscopurpurea*
02010225	4	Horizonte de *Lithophyllum byssoides* sobre roca mediolitoral moderadamente expuesta
02010224	4	Roca mediolitoral moderadamente expuesta con *Mytilus galloprovincialis*
02010226	4	Horizonte de *Neogoniolithon brassica-florida* y/o *Dendropoma petraeum* sobre roca mediolitoral moderadamente expuesta
02010227	4	Horizonte de *Corallina elongata* sobre roca mediolitoral moderadamente expuesta
02010229	4	Horizonte de *Lithophyllum* cf. *vickersiae* sobre roca mediolitoral moderadamente expuesta
02010231	4	Roca mediolitoral moderadamente expuesta con *Ulva compressa*
02010234	4	Roca mediolitoral moderadamente expuesta con *Gelidium pusillum*/*Gelidium crinale*
0201011202	4	Roca mediolitoral expuesta con ceramieales
020103	3	Roca mediolitoral protegida
02010308	4	Horizonte de *Nemoderma tingitanum* sobre roca mediolitoral protegida
02010309	4	Horizonte de *Lithophyllum* spp. sobre roca mediolitoral protegida
02010310	4	Roca mediolitoral protegida con *Ceramium ciliatum*
020104	3	Hábitats singulares de roca mediolitoral
02010401	4	Charcos mediolitorales, permanentemente salinos

02010101- Roca mediolitoral muy expuesta o expuesta con *Chthamalus spp.* . San Vicente, A Coruña . Juan Junoy

02010215- Horizonte de *Rissoella verruculosa sobre Roca* mediolitoral moderadamente expuesta.
Ses Illetes, Tossa de Mar, Girona. Enric Ballesteros



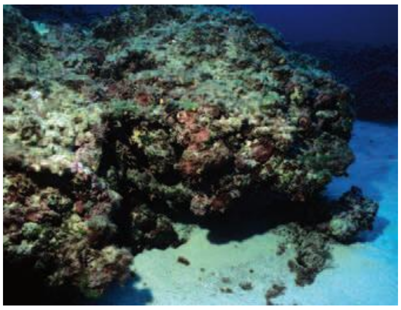
0301030504- Roca infralitoral de modo calmo, bien iluminada, com *Cystoseira brachycarpa v. balearica.*
Cap de Llebeig, Cabrera. Enric Ballesteros



0301041407- Roca infralitoral medianamente iluminada, sin fucalescon *Eunicella singularis.* Mar de Alborán, Ceuta. Óscar Ocaña

0201040110- Charcos mediolitorales con anémonas (*Anemonia-Aiptasia*). San Vicente, A Coruña . Juan Junoy

02010223- Arrecife biógeno de *Dendropoma petraeum sobre roca* moderadamente expuesta.
Cabo Roig, Alicante. José Templado



03020104- Coralígeno con dominancia de algas, sin fucales ni laminariales. Cap Cavalleria, Menorca. Enric Ballesteros

Figura 1.1. Habitats marinos de sustrato rocoso. Algunos ejemplos de hábitats marinos identificados por sus características biológicas y clasificados según la Lista Patrón de Hábitats Marinos Españoles (LPRE; Fuente: Templado et al. 2012).

La gran variabilidad de hábitats es debida a su distribución espacial siguiendo los gradientes ambientales, donde cada especie está adaptada a determinadas condiciones ambientales. La variabilidad ambiental dibuja así el paisaje con su diversidad biológica, tanto a gran como a pequeña escala. Ello es especialmente relevante en las zonas cercanas a la interface agua/aire, donde la disponibilidad de agua es el factor más crítico para la supervivencia de la mayoría de especies. Esta disponibilidad produce un gradiente de humedad muy intenso, presente desde los sistemas acuáticos continentales hasta el litoral marino. Este gradiente determina la distribución contigua de los hábitats según su tolerancia al estrés hídrico (Hutchinson 1975), creando patrones de distribución vertical a lo largo del gradiente, la zonación. En los márgenes de ríos, lagos y humedales, la fluctuación del nivel del agua determina la distribución vertical de las especies vegetales (Turner and Begg 1981; Spence 1982; Day, et al. 1988; Hellsten and Riihimäki 1996; Porporato et al. 2001; Riis and Hawes 2002; Leyer 2005; Wilcox and Nichols 2008; Bornette and Puijalon 2011) y es el factor más importante en mantener la diversidad de especies dentro de cada comunidad de plantas (Keddy 1984; Pollock et al. 1998; Silvertown et al. 1999; Lenssen et al. 2004). Estos patrones de distribución son posibles gracias a las diferentes respuestas fisiológicas de cada especie en cada punto del gradiente hídrico, cosa que permite una baja competencia entre especies y, en consecuencia, la coexistencia de diferentes comunidades a lo largo de grandes escalas espaciales (Keddy 1984; Silvertown et al. 1999; 2001; Lenssen et al. 2004). Los sistemas vegetales de ribera o de los márgenes de lagos, son ecológicamente tan importantes y característicos que sus parámetros han sido incluidos en planes de gestión, conservación y restauración llevando a la necesidad de desarrollar técnicas de cartografía y clasificación de estos sistemas (Keddy 1983; Smith and Huston 1989; Muller 1997). Los mismos patrones de zonación se manifiestan en el litoral marino donde el gradiente de humedad que se genera desde los lugares raramente sumergidos hasta los habitualmente sumergidos da lugar a lo que habitualmente se conoce como zona intermareal. Sobre substrato rocoso, los organismos (mayoritariamente macroalgas y algunos animales sésiles) se distribuyen verticalmente, de arriba abajo, siguiendo este gradiente de humedad (Figura 1.2). Múltiples evidencias científicas han demostrado que las especies ocupan su lugar a lo largo del gradiente vertical según sus adaptaciones y tolerancia a la falta periódica del agua formando una secuencia espacial especifica que da lugar a la zonación litoral (Wahlenberg 1812; Baker 1909; Zaneveld 1937; Stephenson and Stephenson 1949; Mokyevsky 1960; Ballesteros and Romero 1988; Barnes and Hughes 1999; Chappuis et al. 2014). En el Mediterráneo Occidental, la ausencia de mareas hace imposible la distinción de una zona intermareal y la división de la zona litoral se hace en tres niveles: el piso supralitoral (raramente sumergido y afectado habitualmente por las salpicaduras), el piso mediolitoral (emergido per habitualmente barrido por las olas) y el piso infralitoral (comúnmente sumergido). Lejos de ser

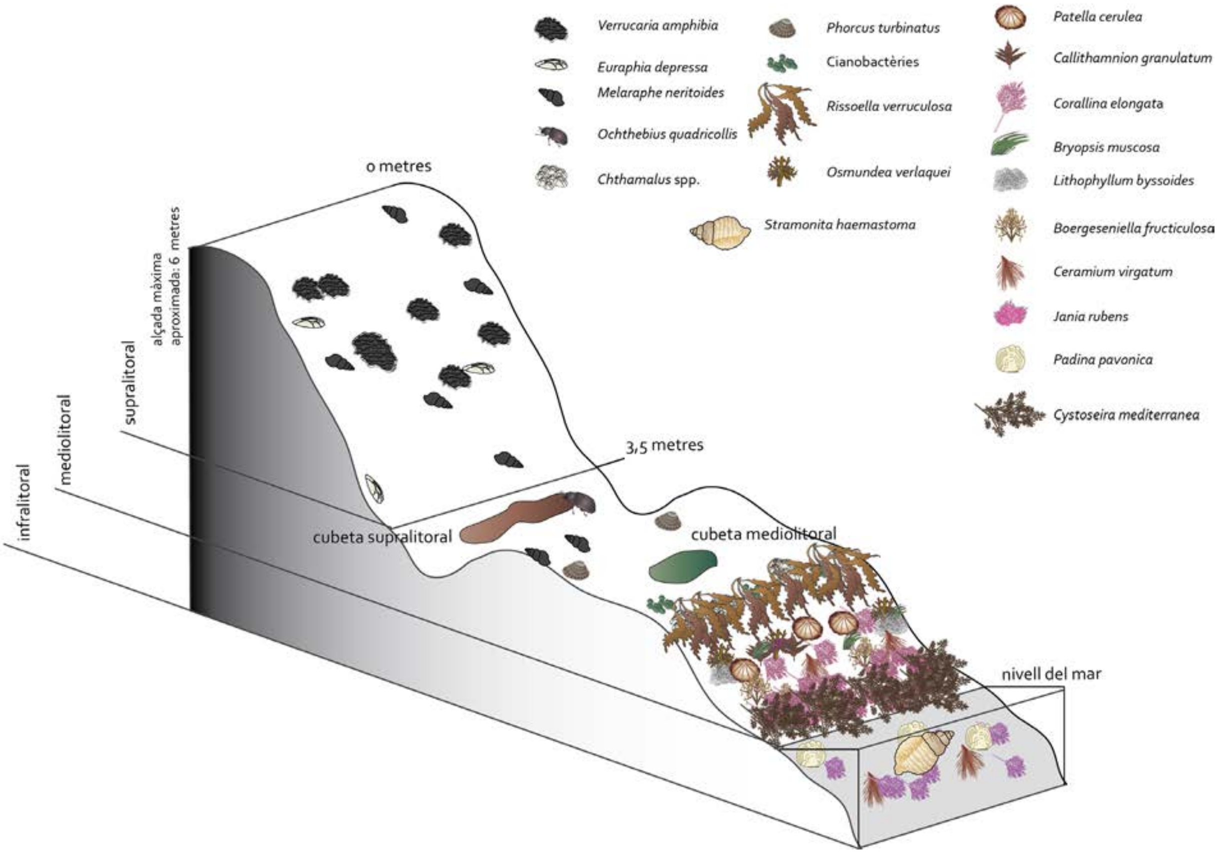


Figura 1.2. Zonación litoral. Distribución vertical de los organismos desde el piso supralitoral hasta el piso infralitoral superior (-1m; Esquema: Simone Mariani).

sencilla, la estructuración de las especies y las comunidades a lo largo de esta zona litoral muestra una gran complejidad pese a su estrecha dimensión que a menudo no supera los pocos metros de ancho. La zonación vertical de hábitats que se establece es consistente a escala regional y dentro de la misma área geográfica (Chappuis et al. 2014). Cada comunidad (en el sentido fitosociológico) o hábitat (a escala 4-5 de EUNIS) tiende a ocupar una posición determinada a lo largo del gradiente (Figura 1.3) generando así una sucesión gradual y continua de comunidades/hábitats diferentes desde el piso supralitoral hasta el piso infralitoral (Boudouresque 1971; Ballesteros and Romero 1988; Chappuis et al. 2014).

La diversidad de hábitats, sobre todo en los pisos mediolitoral e infralitoral, es elevada (Chappuis et al. 2014). En el piso supralitoral pocas especies pueden soportar situaciones tan extremas de frecuente emersión, así que hay básicamente una comunidad presente, poblada por unas pocas especies (e.g. *Euraphia depressa, Melarhaphe neritoides, Echinolittorina punctata, Verrucaria amphibia*) mientras que las comunidades se diversifican en los otros dos pisos. En los

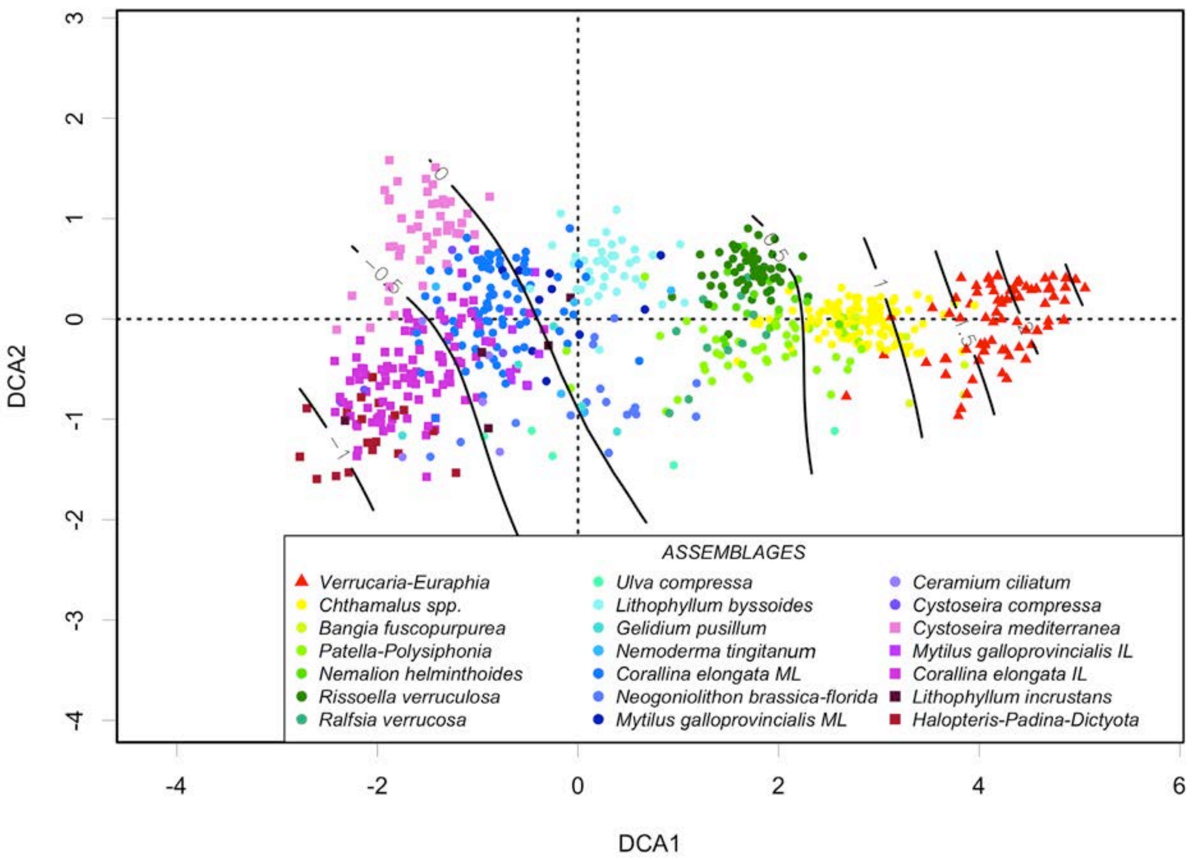


Figura 1.3. Distribución vertical de las comunidades. Distribución vertical de las comunidades del litoral rocoso en los diferentes niveles supralitoral, mediolitoral (ML) e infralitoral (IL). Fuente Chappuis et al. 2014.

pisos supralitoral y mediolitoral superior las especies se distribuyen posiblemente siguiendo el gradiente de humedad, mientras que en los pisos mediolitoral inferior e infralitoral la distribución de las especies es más confundida, segregándose en función de características ambientales que predisponen a la dominancia de diferentes estrategias de vida (especies oportunistas, resistentes al stress y competidoras) (Figura 1.4) (Chappuis et al. 2014).

1.1 Cartografía de los hábitats litorales de Catalunya.

La Generalitat de Catalunya ejerciendo el traspaso de poderes en Medio Ambiente propiciado por el Estado Español, y para cumplir con el Anexo II de la Directiva de Estrategia Marina, encargó al Centre d'Estudis Avançats de Blanes (CSIC) un proyecto para caracterizar, identificar y cartografiar los hábitats presentes en la franja litoral de la costa catalana. La cartografía de la franja litoral comprendía los pisos supralitoral, mediolitoral e infralitoral superior, tanto sobre sustrato rocoso como de arena, grava, guijarros o fango y tenía dos objetivos principales: realizar una cartografía

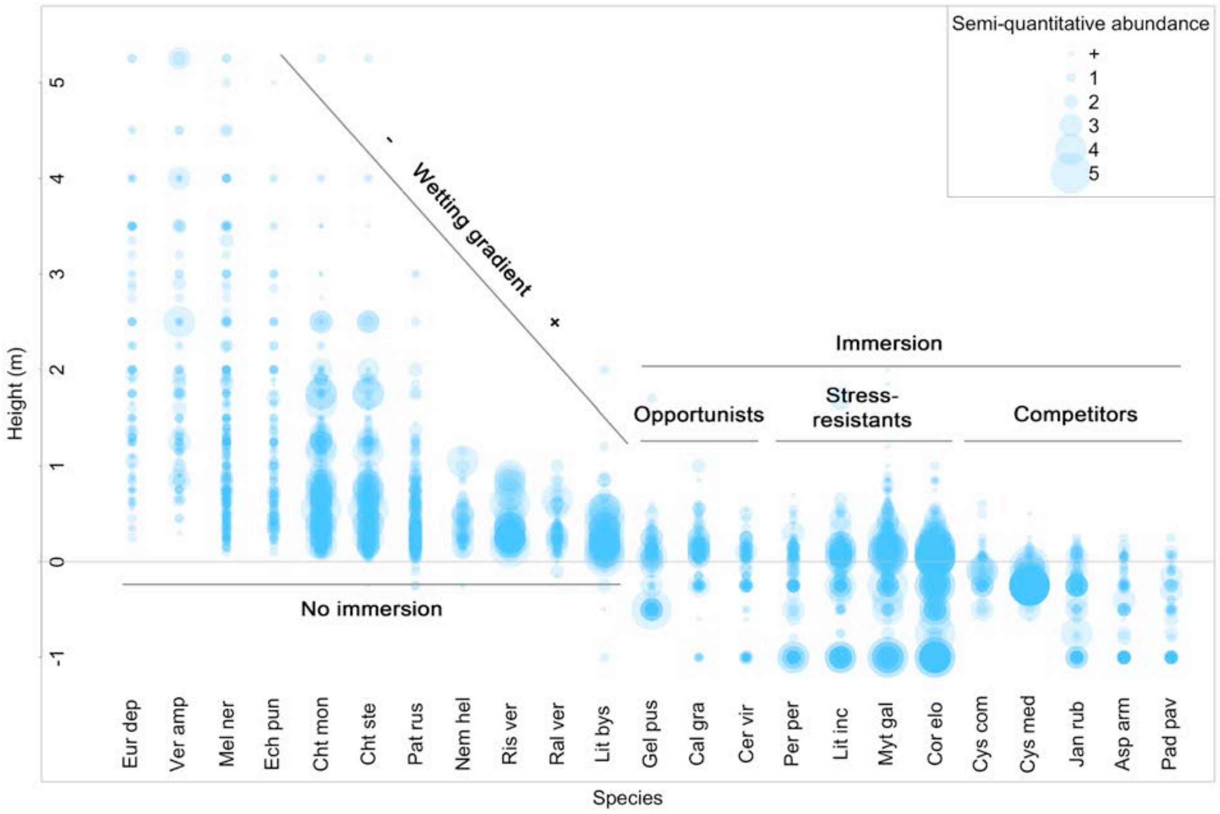


Figura 1.4. Distribución vertical de las especies. Distribución vertical de las especies a lo largo del gradiente hidrico con indicación de las estrategias de vida para las especies situadas en la parte inferior del litoral. Fuente: Chappuis et al. 2014.

digital y proporcionar un manual para todos los hábitats identificados. Aquí nos centraremos exclusivamente en los hábitats de substrato rocoso.

Los avances informáticos de los últimos años han facilitado la realización de la cartografía de los hábitats en formato digital. Estas mejoras permiten hoy en día registrar y evaluar los cambios que afectan los sistemas naturales a lo largo del tiempo. Tales metodologías son indispensables para cartografiar y localizar los hábitats con gran precisión y permiten la elaboración de unos planes de gestión y conservación a diversas escalas territoriales.

Primero, la identificación de los hábitats se corresponde con las franjas de organismos que se establecen a lo largo del gradiente vertical y a las que clásicamente se les denominaba horizontes (Feldmann 1937; Ballesteros 1992; Giaccone 1997; Boudouresque 2004). En cualquier punto del litoral se observa un número variable de horizontes dispuestos desde el piso supralitoral hasta la parte superior del piso infralitoral (Figura 1.5). En nuestro caso un hábitat está constituido por una especie principal (la más abundante y de la cual coge el nombre) y que tenga una distribución definida a lo largo del eje de variación vertical constituido por el gradiente de humedad.

Generalmente estas especies coinciden con especies estructurales de desarrollo estacional y están acompañadas por otras especies que pueden ser exclusivas o no de cada hábitat.

El obstáculo principal relativo a la cartografía de los hábitats a lo largo de amplias superficies o líneas de costa, está representado por la necesidad de compatibilizar el detalle en la descripción durante el trabajo de campo, con la introducción de la información capturada en las bases de datos y los programas de cartografía digital. Para poder realizar una cartografía exhaustiva, en continuo, de todos los hábitats litorales se ideó una metodología denominada CATLIT (Mariani et al. 2014).

En este sentido se optó por utilizar un sistema que permite simplificar tanto la anotación en el campo de los diferentes hábitats como la entrada de datos en un Sistema de Información Geográfica (GIS). Como resulta extremadamente laboriosa la tarea de anotar todos los horizontes en cada punto, para simplificar esta operación se aplicó un sistema heredado de los estudios geológicos y frecuentemente utilizado en la descripción de las comunidades vegetales que aparecen a lo largo de un gradiente ambiental: la "catena" (Rivas-Martínez 1976; Rivas-Martínez 2005).

Figura 1.5. Horizontes de hábitats. Zonación y distribución longitudinal, formando horizontes, de los hábitats litorales en diferentes ambientes rocosos de la costa catalana.

Por definición, una "catena" se entiende como la secuencia contigua de comunidades de plantas a lo largo de cambios en los factores ambientales (temperatura, humedad, topografía, ect..), (Rivas-Martínez 2005). Aquí se identificó como una combinación única de horizontes (Figura 1.6). Esto permitió crear una cartografía linear y en continuo, recorriendo toda la costa y registrando la longitud ocupada por cada hábitat desde el piso supralitoral hasta el piso infralitoral superior, y desde el norte hasta el sur de Catalunya (Figura 1.7). Los hábitats se clasificaron siguiendo CORINE biotopes, con su correspondencia en la Lista Patrón Referencia Estatal (LPRE) y, cuando presente, EUNIS y Directiva Hábitats (Ballesteros et al. 2014). La cartografía digital realizada en un soporte GIS, se representó por una línea de costa, donde a cada porción de costa le correspondía un código de catena con toda la información de los hábitats asociados y a la longitud ocupada (Figura 1.7).

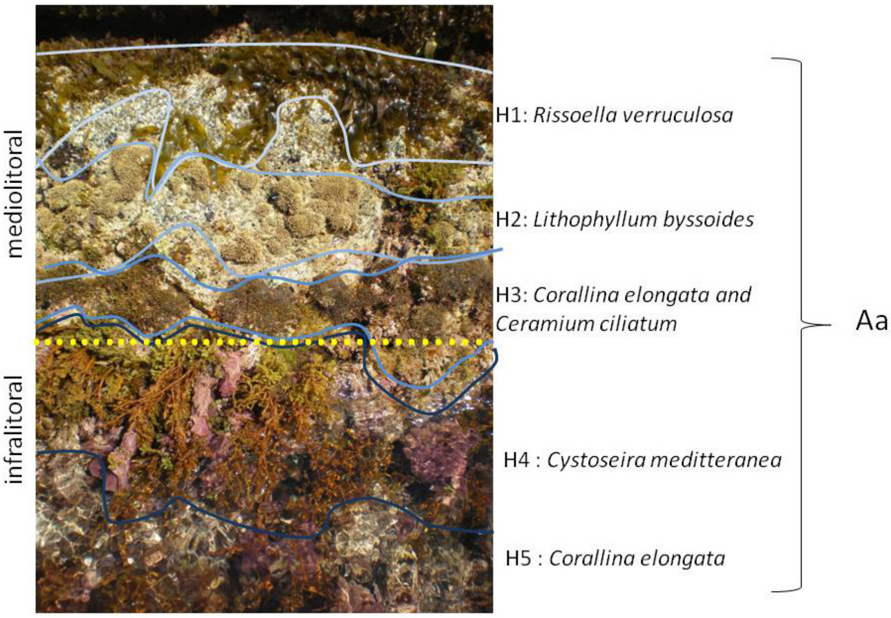


Figura 1.6. Catena de hábitats. Aspecto de la secuencia contigua de las comunidades/hábitats formando una específica “catena” (Aa), en esta representación queda excluido el piso supralitoral. H: horizonte (formado por cada hábitat).

Figura 1.7. Cartografía en continuo. Cartografía linear*:* representación cartográfica de las diferentes catenas y los hábitats que simbolizan a lo largo de un tramo de costa. Las imágenes muestran el aspecto de los hábitats en el litoral, donde muchos de ellos se reconocen navegando como bandas separadas. Fuente: Mariani et al. 2014.

A parte la identificación y cartografía, otro objetivo importante del proyecto fue la caracterización de los hábitats, o sea su descripción, aspecto, abundancia y composición específica. Para ello, se realizó un muestreo puntual, con 153 transectos a lo largo de la costa escogidos de tal forma que englobaban la máxima variabilidad morfológica de la costa y el número de hábitats. En cada transecto se recolectó la información sobre la posición, recubrimiento y abundancia de todas las especies componentes cada hábitat. Esta información permitió realizar un manual descriptivo de todos los hábitats litorales de Catalunya. Para cada hábitat se ofrecía una descripción de la ecología, las especies componentes y sus relativas dominancias y abundancias, a parte de su posición geográfica y grado de distribución (Ballesteros et al. 2014). En el substrato rocoso de origen natural, se identificaron un total de 12 hábitats en el piso infralitoral superior, 19 en el piso mediolitoral y solo 1 en el piso supralitoral (Ballesteros et al. 2014). Globalmente, los hábitats más abundantes y más característicos de la diversidad biológica de la franja litoral en Catalunya son solo 10 (Mariani et al. 2014): un único hábitat en el piso supralitoral, seis hábitats en el piso mediolitoral, y dos en el piso infralitoral superior (Figuras 1.8 y 1.9).

El resultado conjunto de la cartografía digital y el Manual de hábitats, fue un estudio único y pionero en el Mediterráneo, demostrando la posibilidad de realizar cartografías con elevada resolución sobre una extensa superficie linear (1100 km) y a la vez proporcionar una valiosa información sobre las características ecológicas de cada hábitat presente a nivel regional.

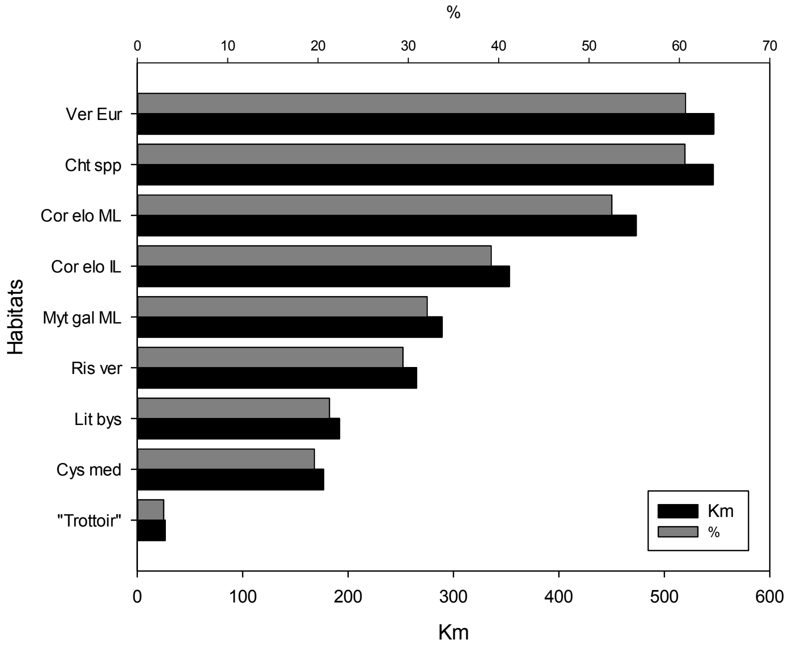


Figura 1.8. Hábitats litorales más frecuentes. Frecuencia y extensión de los hábitats rocosos más comunes a lo largo de la costa rocosa en Catalunya, más el "Trottoir". Abreviaciones: Ver Eur *(Verrucaria amphibia y Euraphia depressa),* Cht spp *(Chthamalus spp.),* Cor elo ML *(Corallina elongata mediolitoral),* Cor elo IL *(C. elongata infralitoral),* Myt gal ML *(Mytilus galloprovincialis mediolitoral),* Ris ver *(Rissoella verruculosa),* Lit bys *(Lithophyllum byssoides),* Cys med *(Cystoseira mediterranea).*

18.16 Penya-segats i roques de la franja supralitoral, ocupats sobretot per líquens (*Verrucaria*)
Foto: Grup Cartografia - CEAB (CSIC)

18.1311+ Penya-segats i roques de la part superior de l'estatge mediolitoral amb *Chthamalus stellatus -Chthamalus montagui*
Foto: S. Mariani

18.1313+Penya-segats i roques de la part superior de l'estatge mediolitoral amb *Rissoella verruculosa*
Foto: Grup Cartografia - CEAB (CSIC)

SUPRALITORAL

MEDIOLITORAL

18.121+ Penya-segats i roques de la part inferior de l'estatge mediolitoral amb *Lithophyllum byssoides*
Foto: Grup Cartografia - CEAB (CSIC)

18.113+ Penya-segats i roques del límit inferior de l'estatge mediolitoral amb Mytilus galloprovincialis
Foto: S. Mariani

18.132 Tenasses *de Lithophyllum byssoides* de l'estatge mediolitoral de la Mediterrània
Foto: Grup Cartografia - CEAB (CSIC)

18.111+ Penya-segats i roques del límit inferior de l'estatge mediolitoral amb Corallina elongata
Foto: S. Pinedo

11.24121+Fons infralitorals rocosos, batuts per l'onatge i ben il·luminats, amb *Corallina elongata*
Foto: S. Pinedo

11.2411+ Fons infralitorals rocosos, batuts per l'onatge, amb *Cystoseira mediterranea*
Foto: Grup Cartografia CEAB - CSIC

INFRALITORAL SUPERIOR

Figura 1.9. Hábitats del litoral rocosos en Cataluña. Los hábitats más extensos y frecuentes del litoral rocoso a Catalunya, clasificados mediante el código Corine Biotopes Fuente: Ballesteros et al. 2014.

1.2 Objetivos

Si un hábitat puede ser considerado como unidad de trabajo para cartografiar e identificar la diversidad biológica, se espera que la estructura y diversidad de especies de las comunidades formadoras del hábitat sea lo más estable posible a escalas espaciales regionales, que son los puntos de partida del análisis paisajístico de un territorio. Si las comunidades son redundantes en términos de composición y riqueza de especies a escalas regional podremos predecir mejor los efectos de perturbaciones o fluctuaciones inducidas por el hombre en el tiempo y el espacio. A pesar de que la disponibilidad hídrica es el factor más importante en determinar la zonación vertical de los hábitats litorales (Wahlenberg 1812; Baker 1909; Zaneveld 1937; Stephenson and Stephenson 1949; Mokyevsky 1960; Ballesteros and Romero 1988; Barnes and Hughes 1999; Chappuis et al. 2014), su distribución depende también de otros factores abióticos como la temperatura (van den Hoek 1982; Breeman 1988), exposición al oleaje (Levin y Paine 1974), la pendiente (Whorff et al. 1995; Benedetti-Cecchi et al. 2000), la salinidad (Wallentinus 1991) y litología. Los factores bióticos tales como la competencia (Bulleri et al. 2002; Mangialajo et al. 2012), el herbivorismo (Underwood y Jernakoff 1981; Thomas 1994), la depredación (Underwood y Jernakoff, 1981), la facilitación (Erlandsson et al. 2011), la dispersión (Burrows et al. 2009) y la interacción entre los factores bióticos y abióticos (Underwood y Jernakoff 1981) también juegan un papel importante en la determinación de la presencia de un hábitat y sus características.

En las últimas décadas, la disponibilidad de datos ambientales adquiridos mediante nuevos sistemas tecnológicos unido al uso de nuevas metodologías estadísticas, han permitido cuantificar de forma más exhaustiva y realista estas relaciones, ampliando tanto el conocimiento ecológico como el rango geográfico de la distribución de las especies. Concretamente, los Modelos de Distribución de Especie (SDMs) están siendo utilizados con el objetivo de estudiar y predecir la distribución geográfica de las especies, sobretodo vegetales (Robinson et al. 2011), para entender la ecología, conservación y gestión de los sistemas naturales. Cuando los hábitats presentan una relación significativa con el ambiente a nivel regional, es posible predecir la presencia de cada hábitat a partir de variables abióticas. En consecuencia, cada vez más se utilizan modelos explicativos, para calcular la probabilidad de encontrar los distintos hábitats en zonas no exploradas, utilizando solo variables medio-ambientales. Sin embargo los resultados de estos modelos dependen en gran medida de la estrategia de muestreo y fiabilidad de los datos de base.

Todos estos presupuestos se han desarrollado y averiguados en los tres artículos, en cierta medida complementarios, que componen la parte central de esta Tesis.

El primer objetivo (Capítulo 2.1) ha sido averiguar la importancia de la variabilidad geográfica en determinar la composición específica y la riqueza de los hábitats. En otras palabras, bloqueando el eje vertical en la variabilidad ambiental de la zona litoral y considerando cada hábitat por separado hemos averiguado si la variación horizontal, entendida como la posición geográfica de cada comunidad a lo largo del gradiente latitudinal, pueda tener un papel relevante en aportar variación dentro de las comunidades, en su estructura o en su riqueza específica.

Aprovechando la base cartográfica a escala regional y con elevada resolución espacial (unidad mínima de muestreo 10 m) obtenida en el proyecto "Cartografía de los hábitats litorales de Catalunya", el segundo objetivo (Capítulo 2.2) ha sido estudiar la relación entre los factores ambientales y la distribución geográfica de los hábitats litorales. Estos, posicionados en distintos niveles de la zonación litoral, presentan diferentes patrones de distribución geográfica, donde la variabilidad ambiental, tanto morfológica de la costa como físico-química del agua, tiene un papel importante en determinar la presencia, abundancia y desarrollo de cada hábitat a escala local o regional. A partir de de Modelos de Distribución de Especie (SDMs), y relacionando la base de datos cartográficos con datos ambientales de procedencias diversas, hemos estudiado la distribución geográfica de los hábitats litorales pudiendo detectar el nivel de importancia de las variables abióticas en determinar su distribución en el litoral rocoso a nivel regional en Catalunya.

Valiéndonos de las observaciones reales sobre la presencia o ausencia de cada hábitat y de la relación entre hábitat y factores ambientales, el tercer objetivo (Capítulo 2.3) ha sido explorar que estrategias de muestreo proporcionarían los modelos predictivos más reales, ya que podemos validar la robustez y credibilidad de los resultados. En este capítulo, hemos averiguado la mejor metodología de muestreo y la mínima unidad muestreo para obtener predicciones realísticas, y que parámetros hay que considerar a la hora de modelar: estrategia o unidad de muestreo, frecuencia o características de los hábitats.

Entender cómo y porqué los hábitats o las especies se distribuyen a nivel geográfico es básico para poder predecir de un lado su presencia en zonas inexploradas, y del otro como respondería o cambiaría su distribución espacial a causa de perturbaciones climáticas o presiones entrópicas. Si la realización de cartografías de hábitats está en la base de las buenas políticas de gestión del medio y su conservación, la mayoría de las veces obtener cartografías extensas es un logro muy anhelado pero poco realizable sobre todo a nivel marino, por la dificultad logística y el gran esfuerzo económico que conlleva.

Al disponer de una enorme cantidad de datos este es, a nuestro conocimiento, el primer estudio de los hábitats litorales que analiza globalmente su distribución geográfica, su relación con las variables ambientales, se indaga sobre modelos predictivos de su distribución y se evalúa su homogeneidad/heterogeneidad a lo largo de gradientes geográficos a escala regional.

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Resultados

Capítulo 2.1

Community-dependent variability in species composition and richness at a regional scale

Maria Elena Cefalì[1,2*], Emma Cebrian[1,3], Eglantine Chappuis[1], Marc Terradas[4], Simone Mariani[1,5],Enric Ballesteros[1]

[1]Centre d'Estudis Avançats de Blanes-CSIC, Acc. Cala Sant Francesc 14, 17300 Blanes, Girona, Spain
[2]Instituto Español de Oceanografía (IEO), Estació d'Investigació Jaume Ferrer, PO Box 502, 07701 Maó, Spain
[3]Departament de Ciències Ambientals, Facultat de Ciències, Universitat de Girona, 17071 Girona, Spain
[3]Departament de Ciències del Mar i Biologia Aplicada, Universitat d'Alacant, Apartat de Correus 99, 03080 Alacant, Spain
[5]Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Universitat de Barcelona, Spain

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Abstract

Identifying scales at which most of the spatial heterogeneity occurs is important to understand how ecological communities are structured. Rocky shore communities are distributed vertically as a response to strong water availability gradients. There has been much debate about the relative importance of vertical and horizontal variation gradients in littoral community structure and richness. In this study we assessed if horizontal variability is responsible for changes in community structure at a regional scale (hundreds of Km) by restraining vertical variability. We studied ten different rocky shore communities from the upper mediolittoral to the upper infralittoral level with different geographical distribution patterns. We aimed at assessing if structure and species richness are affected by their geographical position of each community. The results proved that horizontal variation in species composition and richness was community dependent and there was no common pattern at a regional scale. Communities with a wide geographic distribution typically showed some variation, which was related to changes in the environmental factors across the geographical gradient. This study sheds light on the existence of latitudinal variability in species composition and richness at a regional scale in rocky shores. It also strongly supports the validity of littoral communities and habitats from conservation panels as consistent ecosystem subdivisions and reliable working units.

Keywords: littoral communities, rocky substrate, algae, Mediterranean Sea, horizontal variation, vertical variation.

2.1.1 Introduction

The different processes driving species or communities' distribution produce variability at different spatial scales (Levin 1992). A wide array of physical and biological factors, in fact, may determine scale-dependent patterns and processes in community species composition and richness (Dungan et al. 2002; Fraschetti et al. 2005). In littoral rocky shores, for instance, heterogeneous environments support and shape diverse communities of sessile and mobile organisms (Dungan et al. 2002). A prominent feature of these systems is that communities generally occur at a specific height on the shore as a result of the strong environmental gradient of water availability from high to low levels. This well-known pattern has been the focus of many studies in many places around the world and it is commonly known as vertical zonation (Stephenson and Stephenson 1949; Lewis 1964; Paine 1974; Ballesteros & Romero 1988; Ballesteros 1992; Benedetti-Cecchi 1999; Menconi et al. 1999; Underwood and Chapman 1998; Chappuis et al. 2014). This strong vertical gradient have inspired many studies accounting for predation (Paine 1974), competition (Connell 1961), grazing (Coleman et al. 2006), and relation with abiotic factors in structuring intertidal communities (Archambault and Bourget 1996; Valdiviaet al. 2011). Environmental factor variation and its effects on community heterogeneity has been assessed by different authors from patch scale (10s cm) to larger scales (10s, 100s m) (Fraschetti et al. 2005; Noda 2009; Gaspar et al. 2017). Besides, patterns of vertical zonation in community structure may vary horizontally particularly at a regional scale (Gaspar et al. 2017). Identifying the scales at which most spatial heterogeneity occurs, in fact, is important to understand how communities are distributed (Menconi et al. 1999).

In recent years, some attention has been paid to ascertain at which spatial scale vertical or horizontal gradients produce variability in intertidal and littoral communities (Benedetti-Cecchi 2001; Valdivia et al. 2011; Chappuis et al. 2014). Some authors have shown that littoral assemblages varied horizontally at scales that ranged from 10s to 100s metres (Benedetti-Cecchi 2001; Valdivia et al. 2011), while a vertical gradient of variation was detectable only at smaller spatial scales (10s cm). These results support a model of spatial distribution of intertidal communities in which horizontal and vertical variation have the same importance in rocky shore communities (Benedetti-Cecchi 2001).

Other authors acknowledged that vertical variation was the most important factor also at a regional scale. Chappuis et al. (2014) have shown that despite the physical heterogeneity of the shore, the variation across the vertical axis is overall larger than that found across the horizontal axis at a wide regional scale and within the same biogeographical area. Thus, vertical zonation can be considered the main source of variation of species distribution in North-Western Mediterranean rocky shores. However, these authors have also shown that factors associated with both latitudinal and longitudinal gradients may play an important role in shaping the littoral communities. In spite of its apparent relevance, however, these patterns have not received further attention.

The variability within a community can be measured as the changes occurring in the composition and abundance of species. Our main hypothesis here is that if the vertical gradient is restrained and we deal with only one community occupying the same level in the shore, horizontal variability is the main source of variation in the structure of each community at a regional scale. To test this hypothesis we have selected ten littoral communities from different levels on the shore, different environmental conditions and different regional distribution patterns an attempt to assess whether species composition and richness co-vary with community geographic position on the horizontal axis or, on the contrary, there are other more important factors shaping differences in community structure (e.g. Underwood 1978; Archambault and Bourget 1996; Menconi et al. 1999). Apart from the general ecological relevance of answering these questions, the eventual outcome of this approach is especially important when we want to ascertain the proportion of variability explained by horizontal environmental variability on littoral communities. If communities are redundant in terms of species composition and richness across regional scales we may better predict the effects of strong disturbances or man-induced fluctuations in time and space. This is particularly important when we try to implement management practices based on the monitoring of habitats.

2.1.2 Materials and Methods

2.1.2.1 Study site and sampling

Catalonia is situated in the north-western Mediterranean Sea and its 1100 km long coastline is formed by 39% of natural rocky shores, 30% of artificial hard-bottoms (breakwaters, sea walls, jetties, etc.) and 30% of beaches (Marianiet al. 2014). Tidal ranges are imperceptible, but wave splash and sea level variability associated with changes in atmospheric pressure allows the existence of clear zonation patterns (Ballesteros and Romero 1988; Ballesteros 1992; Chappuis et al. 2014). Moreover, coastline morphology seems to be driving the geographical distribution of littoral organisms from north to south (Cefalì et al. 2016). For this study, 143 rocky shore sites were sampled along the Catalan coast following a latitudinal gradient (Ballesteroset al. 2014; Chappuis et al. 2014) (Figure 2.1.1). Sites included both natural and artificial rocky shores and were selected to cover a wide range of environmental

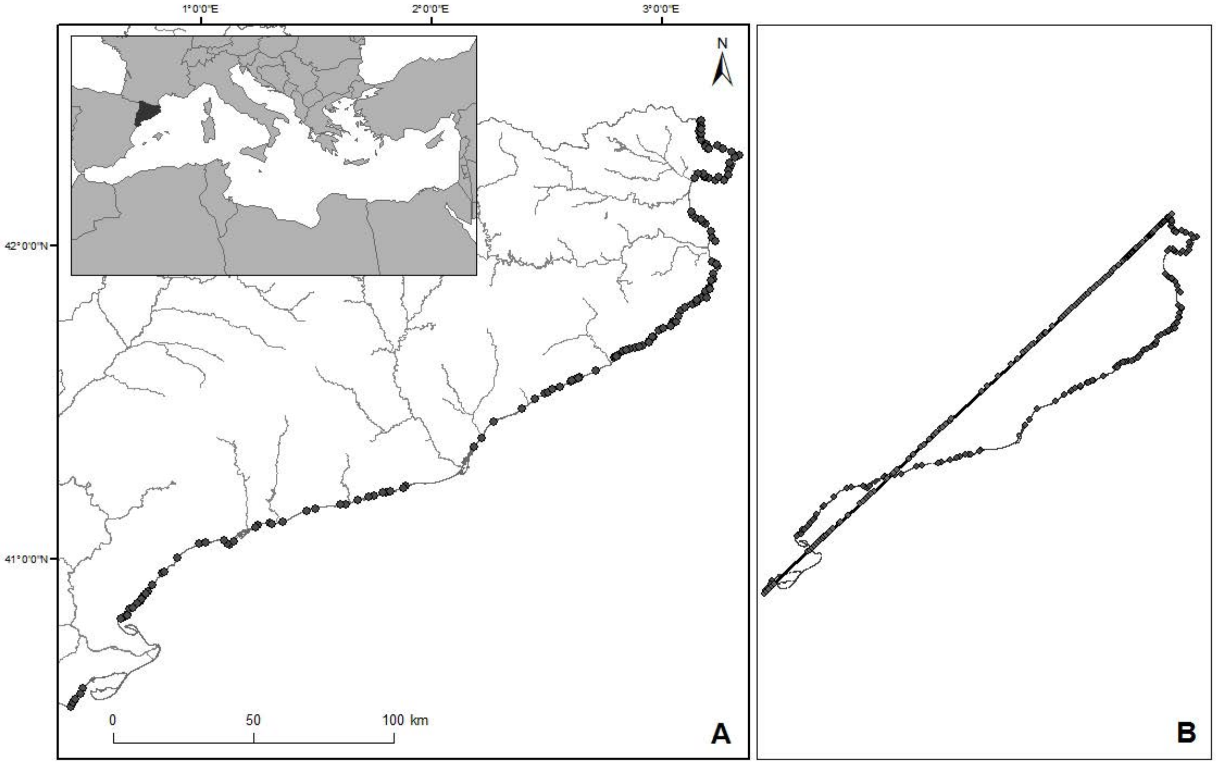


Figure 2.1.1. Map of the study site. In A the position of the 143 sampled localities is showed and in B the projection of these localities in a southwest-northeast axis.

conditions regarding sea surface temperature, hydrodynamics, substrate type, coastal geomorphology and geology.

The distance between sampling sites ranged from 3.5 km to 5 km. Sampling was performed from May to July, when algal development was at its maximum (Ballesteros 1988, 1991a, b, 1992). Zonation at each site was described by means of a vertical transect, which was geo-located using a GPS (European Datum 1950, UTM Zone 31N). The uppermost part of each transect was placed at the highest point reached by any marine organism (usually the lichen Verrucaria amphibia or the small periwinkle Melarhaphe neritoides) and the lowermost part was situated at -1 m a. m. s. l., covering the whole supralittoral and mediolittoral levels and the uppermost part of the infralittoral level. Transects were 2 m wide in order to include small-scale variation due to patchiness and microhabitats (e.g. Underwood and Chapman 1996; Valdivia et al. 2011).

Specific communities dominated by conspicuous species or species guilds were recognized along each transect by means of a bionomical approach (Abbiati et al. 1987; Morri et al. 2004) (Figure 2.1.2). Communities were identified, named after the dominant species (Ballesteros

1991a, 1992) and characterized through phytosociological plots. All visible flora and fauna (sessile and mobile) comprised within each plot was recorded using a Braun-Blanquet cover-abundance scale (Braun-Blanquet 1964). When necessary, specimens were removed and later identified in the laboratory to species level (only a few cryptic taxa were classified to higher taxonomic levels). For this study, only communities present at least in 10 different transects were selected (Table 2.1.1).

The Catalan coastline stretches diagonally from NE to SW, and consequently longitude and latitude coordinates are highly correlated (0.93 Pearson correlation, $p < 0.05$) providing similar information (Chappuis et al. 2014). In order to obtain a "linear distance" between transects a straight line was drawn from the point situated most in the southwest to the one located farther in the northeast, using ArcGis 10.1 (ESRI©). All 143 transects were projected over this line (Figure 2.1.1B). The south-western most transect was used as the start point (zero Km) and the linear distance of all transects to this point was calculated (Figure 2.1.1B).

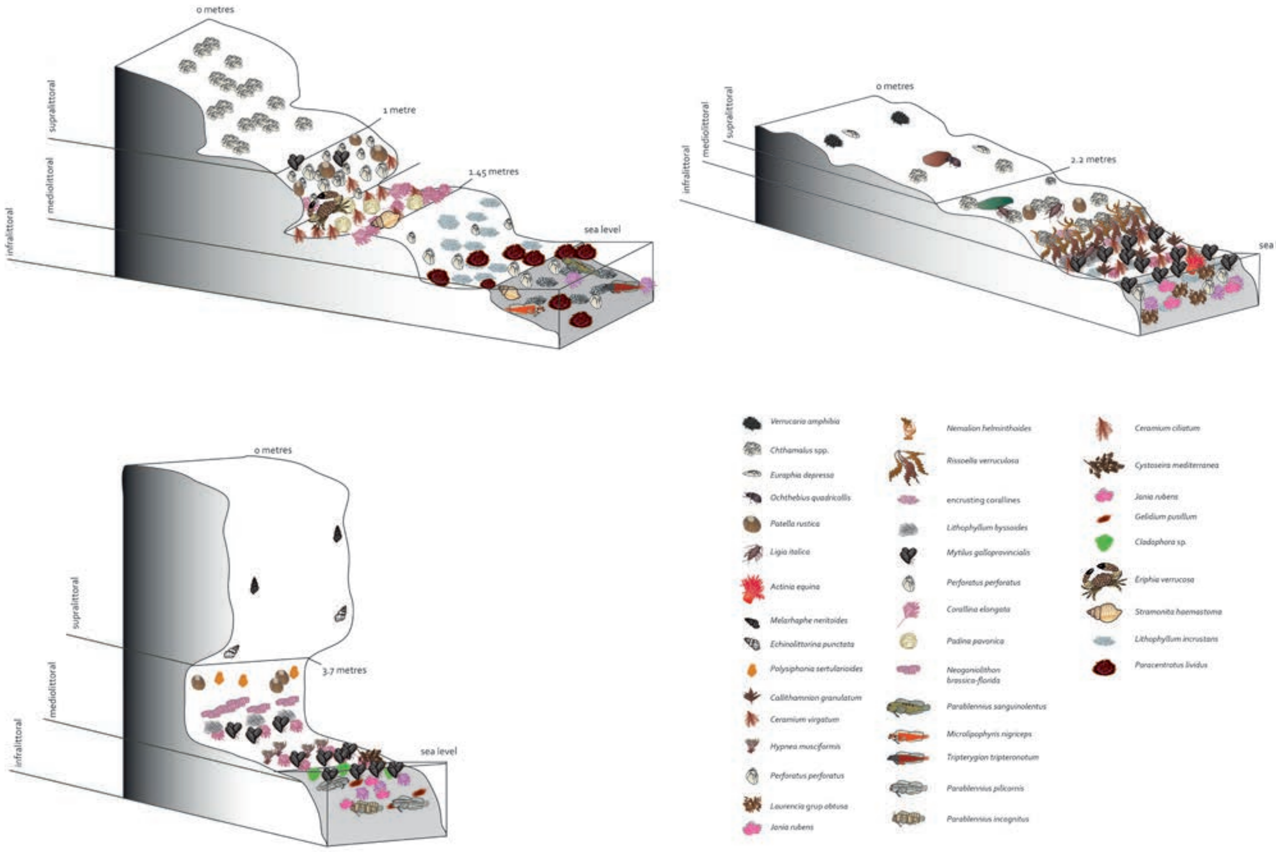


Figure 2.1.2. Schematic representation of transects from different sites.

Table 2.1.1. Communities studied. The communities are listed following their position in accordance with their vertical distribution, from the upper mediolittoral to the upper infralittoral levels. Total number of transects where each community was found and average species richness wit standard deviation (SD) are presented for each community.

	Community	**Code**	**Nº transects**	**Species Richness**	
				mean	SD
Mediolittoral	*Chthamalus* spp.	Cht spp	115	4.9	± 1.6
	Ralfsia verrucosa	Ral ver	11	5.5	± 2.6
	Rissoella verruculosa	Ris ver	53	8.2	± 2
	Lithophyllum byssoides	Lit bys	39	11.5	± 4
	Neogoniolithon brassica-florida	Neo bra	18	8.7	± 2.8
	Corallina elongata (mediolittoral)	Cor elo med	83	11.6	± 4.7
	Mytilus galloprovincialis mediolittoral	Myt gal med	11	8.5	± 2
Infralittoral	*Mytilus galloprovincialis* (infralittoral)	Myt gal infra	10	10.6	± 4.7
	Corallina elongata (infralittoral)	Cor elo infra	99	14.9	± 7
	Cystoseira mediterranea	Cys med	47	15.2	± 5

2.1.2.2 Statistical analysis

Cover-abundance data were transformed to a more symmetric and fully numerical scale according to van der Maarel (1979). The data were transformed [with log (X+1)] to reduce the contribution of the most abundant species for each community, and a matrix of Bray-Curtis similarity was built for each community separately. Then, a series of principal coordinates analysis (PCOs) were used to illustrate the community distribution patterns, and to identify gradients in species composition for each community. PCO is equivalent to principal component analyses (PCA), but with a higher flexibility of resemblance measures (Anderson and Willis 2003; Anderson 2008).

The linear distance (horizontal variability) was projected as a factor in the multivariate space for each community. Moreover, to quantify and to test the relationship between the linear distance and the variance explained in the multivariate space, a linear regression model was carried out between the linear distance and the variance explained from each PCOs axis (x,

y) for each community separately and for the species richness of each community. When models were significant, R^2 values were used for the interpretation of the relationships between variables.

Multivariate analysis was performed using Primer 6 (Clarke & Gorley 2006) with the Permanova+ add-on package (Anderson et al. 2008), while linear regression models were developed with R software (R Development Core Team 2011).

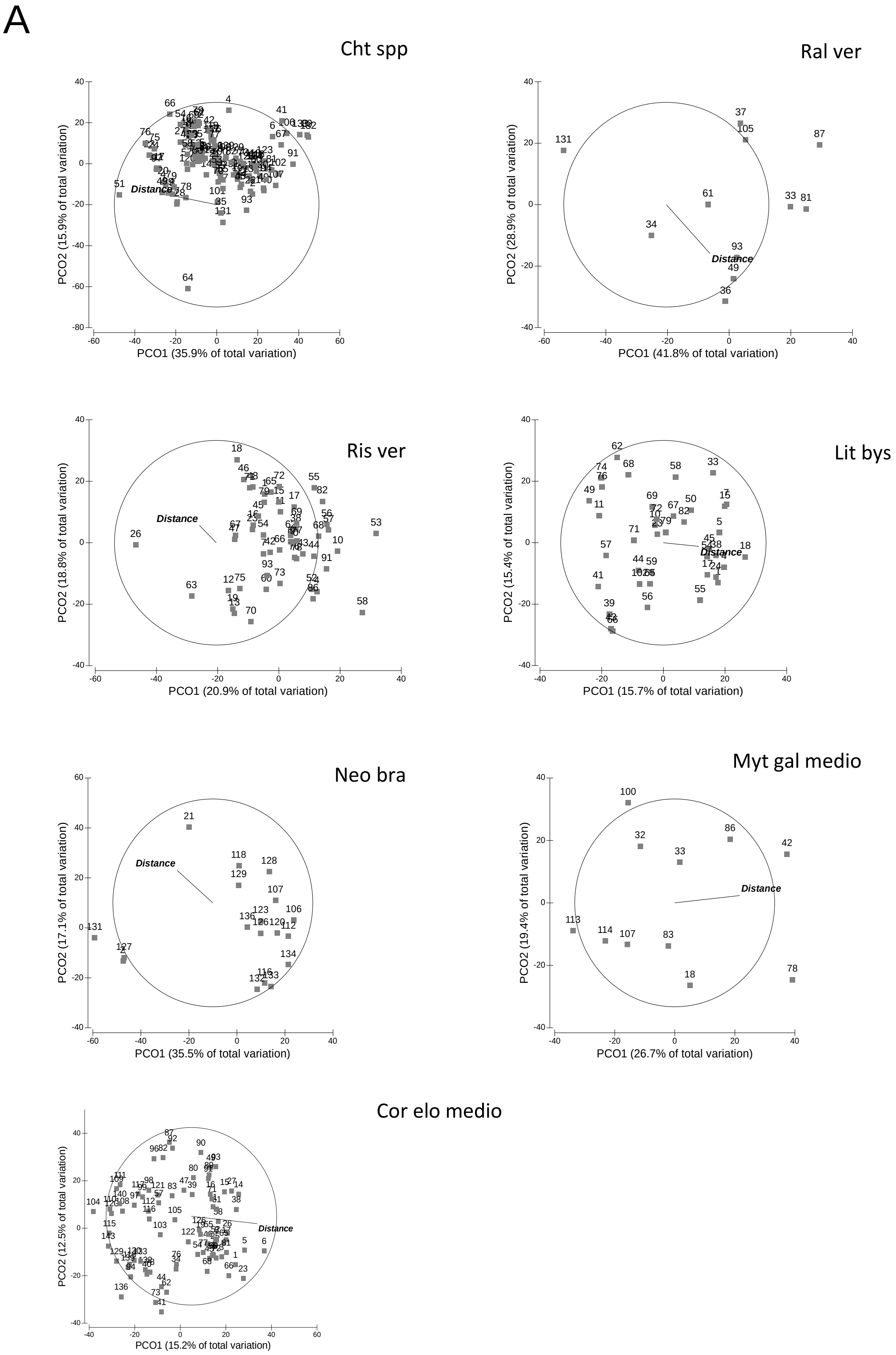
2.1.3 Results

Three community categories could be distinguished according to its presence along the coastline: i) frequent and widely distributed (*Chthamalus* spp. in the upper mediolittoral, *Corallina elongata* in the mediolittoral, *Corallina elongata* and *Cystoseira mediterranea* in the upper infralittoral), ii) frequent and locally distributed (*Rissoella verruculosa* and *Lithophyllum byssoides* in the mediolitoral) and iii) rare and irregularly distributed (*Ralfsia verrucosa*, *Neogoniolithon brassica-florida, Mytilus galloprovincialis* in the mediolittoral and *Mytilus galloprovincialis* in the upper infralittoral (see Table 2.1.1).

Both community structure and species richness strongly varied among the communities studied, with no specific patterns of abundance or distribution (Table 2.1.2). All frequent and widely distributed communities showed a significant relationship between linear distance and the variance explained by the first axis in the multivariate space (Table 2.1.2). Up to 35.9% of the variability in community composition for *Chthamalus* spp. was explained by the first axis in the PCO, which was also significantly correlated with linear distance (Figure 2.1.3, Table 2.1.2). However, species richness did not show any relationship with linear distance, although the points were distributed according to species richness along the y-axis (results not showed). For both mediolittoral and infralittoral *C. elongata* communities, linear distance was significantly related both to the principal axis X ($R^2 = 0.56$ and 0.10 respectively; Table 2.1.2) and species richness (Figure 2.1.3; Table 2.1.2). Linear distance was related to the second axis Y ($R^2 = 0.33$) and with species richness ($R^2 = 0.\ 10$) for the *Cystoseira mediterranea* community. The amount of variability explained by the first axis for the community of *L. byssoides* was low (15.7%) and related to linear distance ($R^2 = 0.12$); however, no relationship was found with species richness. The same pattern was found for the mediolittoral community of *M. galloprovincialis* (Table 2.1.2). The variability in the communities of *R. verruculosa, R.verrucosa, N. brassica-florida* and *M. galloprovincialis* infralittoral did not show any relationship with the linear distance or with species richness (Table 2.1.2).

Table 2.1.2. Results of linear regression. R2 values of the linear regressions between: the linear distance, the X and Y PCO axis, and the species richness for each community are showed. Significant correlations are in bold. p values are: p<0.01 (*), p<0.001 (**), p<0.0001.For species name codes see Table 2.1.1.

	Linear Distance		x-Axis PCO	y-Axis PCO	Species richness
Mediolittoral	**Cht spp**	R^2	**0.17*****	0.82	0.002
	Ral ver	R^2	0.18	0.22	0.001
	Ris ver	R^2	0.03	0.03	0.0007
	Lit bys	R^2	**0.12***	0.001	0.07
	Neo bra	R^2	0.013	0.09	0.008
	Cor elo med	R^2	**0.56*****	0.02	**0.11****
	Myt gal med	R^2	**0.42***	0.005	0.03
Infralittoral	**Myt gal infra**	R^2	0.01	0.28	0.02
	Cor elo infra	R^2	**0.10****	0.002	**0.08*****
	Cys med	R^2	2.6e-05	**0.33*****	**0.10***


A
Cht spp
PCO1 (35.9% of total variation)
PCO2 (15.9% of total variation)
Ral ver
PCO1 (41.8% of total variation)
PCO2 (28.9% of total variation)
Ris ver
PCO1 (20.9% of total variation)
PCO2 (18.8% of total variation)
Lit bys
PCO1 (15.7% of total variation)
PCO2 (15.4% of total variation)
Neo bra
PCO1 (35.5% of total variation)
PCO2 (17.1% of total variation)
Myt gal medio
PCO1 (26.7% of total variation)
PCO2 (19.4% of total variation)
Cor elo medio
PCO1 (15.2% of total variation)
PCO2 (12.5% of total variation)
Distance

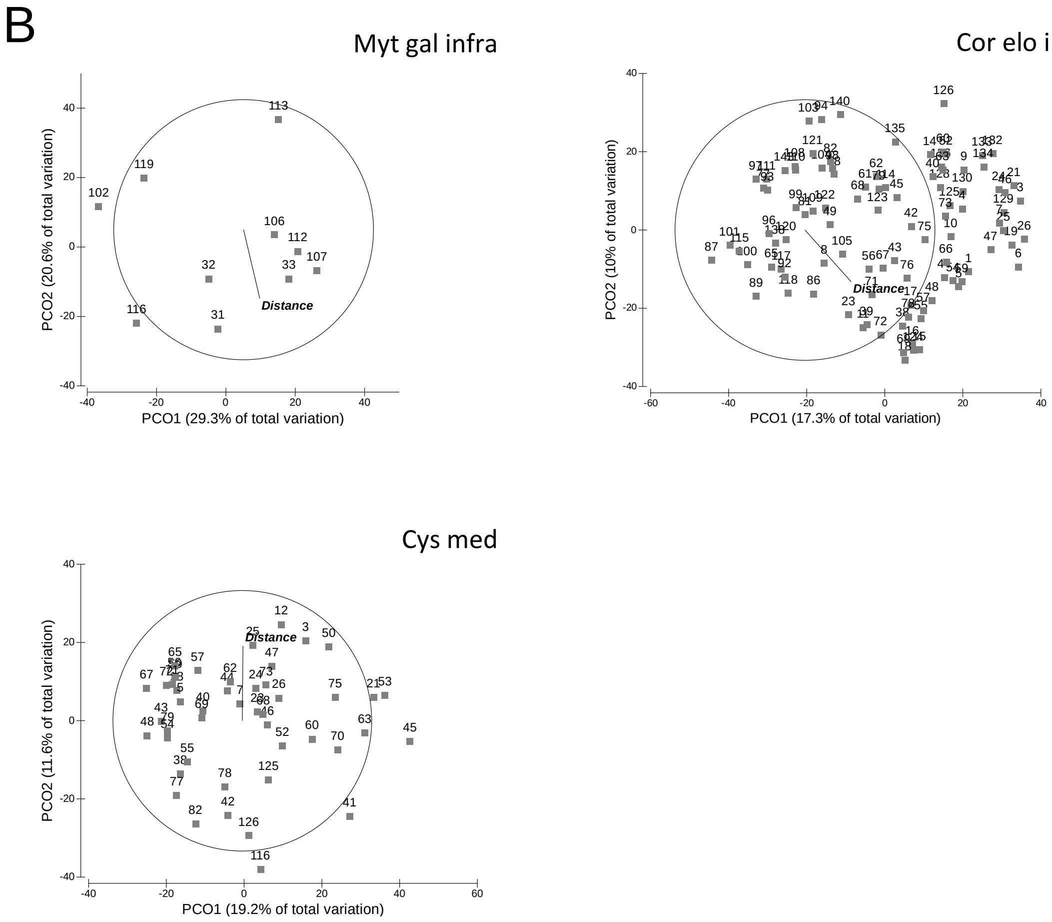


Figure 2.1.3. PCO plots for each community. PCO plots for each community from the mediolittoral (A) and the infralittoral (B) levels, with projection of the linear distance. Each PCO was performed on Bray-Curtis resemblance matrix, with data previously transformed with log (X+1). The codes of each community are explained in Table 2.1

2.1.4 Discussion

Patterns of horizontal variation in species composition and richness for the rocky-shore communities studied here were clearly community dependent. Except for the *Lithophyllum byssoides* community, all rare and geographically localized communities did not show any significant relationship between structure and horizontal variation. On the contrary, communities with a wide geographical distribution typically showed significant horizontal variability with the exception of the ubiquitous *Chthamalus* spp. community, which was had the lowest species richness (Table 2.1.1) and did not show any variability in species composition and richness along the horizontal gradient. Three frequent communities (*Corallina elongata* from the mediolittoral and the infralittoral levels and *Cystoseira mediterranea* from the infralittoral), showed high geographical variability. They were also the most complex and richest in species (Ballesteros and Romero 1988; Ballesteros 1988 a,b, 1992). However this geographical variation can be related to other environmental factors, associated with differences in coastal morphology or differences in land use from north to south. In fact, *Corallina elongata* is a stress-tolerant species that can grow either in polluted or unpolluted environments (Ballesteros et al. 1984). The existence of horizontal variability in this case could be related to environmental features like eutrophication, which is locally detectable along the Catalan coast (Ballesteros et al. 2007, Pinedo et al. 2007, 2013). In contrast, the *Cystoseira mediterranea* community only thrives in uncontaminated waters, although it is much more frequent in the northern coast (Figure 2.1.1; Table 2.1.2).

We show here that horizontal variation in species composition and richness is low for most of the studied communities (meaning that they are constant, redundant). Ranges of horizontal variation were far away from the 75% of the variance explained by the vertical variation (Chappuis et al. 2014). Thus, we may conclude that the variability associated with differences in community structure and richness at the regional scale considered is much lower than the variability associated with vertical zonation.

When biogeographical patterns of rocky intertidal communities have been examined at broad spatial scales, (i.e. latitudinal differences around 20º) the results have proved a consistent interaction between horizontal variation in community structure and geographical distances (Blanchette et al. 2008). This variation has been related to typical latitudinal gradients like sea surface temperature (SST) or the presence of up-welling zones and differential wave exposure and recruitment, all factors associated with the wide spatial scales considered (Blanchette et al. 2008; Tuya et al. 2012; Tuya and Haroun 2006; Valdivia et al. 2011). For example, in regions with large differences in SST a strong coupling between coastal oceanographic features and rocky-shore community structure has been found (Steneck and Dethier 1994; Bustamante et al. 1995; Menge et al. 1999; Broitman 2001; Schils and Coppejans 2003; Tuya et al. 2006). Differences in pattern of water circulation and resource availability have been often proposed to explain large-scale variability in macroalgae community structure (Santelices 1990; Menconi et al. 1999). Variation in community structure and species richness with latitude and the associated patterns of energy availability and climate factors, are common and thoroughly described for a broad range of marine and terrestrial taxa (Macpherson and Duarte 1994; Oshawa 1995; Gaston 2000; Gray 2001; Macpherson 2002; Hawkins et al. 2003; Rex et al. 2003; Sales et al. 2012; Chappuis et al. 2012; Alahuhta 2015).

In spite of all this evidence, however, some authors have shown that local environmental features like topography, geology, and wave exposure as well as species interactions, which are often unrelated to latitudinal gradient, may play important roles in structuring rocky

intertidal communities (Blanchette et al. 2008).
Similarly, in this study, local factors such as coastal morphology, coastal artificialization, eutrophication, wave exposure, and biological interactions (see Cefalì et al. 2016), which are probably masking the geographical variability associated to latitude, represent possible sources of variation (Fraschetti et al. 2005; Menconi et al. 1999; Noda 2009). Thus, the detailed pattern of change with latitude depends on scale, reflecting a pattern of spatial variation in species richness and community structure that is complex to explain. Considering factors related to latitudinal gradients as the only forces shaping littoral communities may produce misleading conclusions. In fact, latitude per se cannot be the only determining variation, but a correlate of several causal environmental factors (Gaston 2000).

In summary, thanks to our exhaustive high-resolution sampling, we demonstrate that geographical variation in species composition and richness at the scale of hundreds of Km, but with only 1 degree latitude, is weak or even undetectable. The low variance explained by the horizontal distance, thus, points out to other factors as possible drivers for community variability and our communities are consistently similar across a broad regional scale. All this is critical for implementing conservation panels like the Habitats Directive (92/43/EC) and the Marine Strategy Framework Directive (2008/56/E) for which littoral communities and habitats ought to be necessarily framed into consistent ecosystem subunits. This study strongly supports the validity of these communities/habitats as reliable working units.

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Capítulo 2.2

Life on the boundary: environmental factors as drivers of habitat distribution in the littoral zone

Maria Elena Cefalì[a*], Emma Cebrian[a,b], Eglantine Chappuis[a], Susana Pinedo[a], Marc Terradas[c], Simone Mariani[a,d], Enric Ballesteros[a]

[a] Centre d'Estudis Avançats de Blanes-CSIC, Acc. Cala Sant Francesc 14, 17300 Blanes, Girona, Spain
[b] Departament de Ciències Ambientals, Facultat de Ciències, Universitat de Girona, 17071 Girona, Spain
[c] Departament de Ciències del Mar i Biologia Aplicada, Universitat d'Alacant, Apartat de Correus 99, 03080 Alacant, Spain
[d] Departament d'Ecologia, Facultat de Biologia, Universitat de Barcelona, Avgda. Diagonal 643, 08028 Barcelona, Spain

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Abstract

The boundary between land and sea, i.e. the littoral zone, is home to a large number of habitats whose distribution is primarily driven by the distance to the sea level but also by other environmental factors such as littoral's geomorphological features, wave exposure, water temperature or orientation. Here we explore the relative importance of those major environmental factors that drive the presence of littoral rocky habitats along 1100 km of Catalonia's shoreline (Spain, NW Mediterranean) by using Geographic Information Systems and Generalized Linear Models. The distribution of mediolittoral and upper infralittoral habitats responded to different environmental factors. Mediolittoral habitats showed regional differences drawn by sea-water temperature and substrate type. Wave exposure (hydrodynamism), slope and geological features were only relevant to those mediolittoral habitats with specific environmental needs. We did not find any regional pattern of distribution in upper infralittoral habitats, and selected factors only played a moderate role in habitat distribution at the local scale. This study shows for the first time that environmental factors determining habitat distribution differ within the mediolittoral and the upper infralittoral zones and provides the basis for further development of models oriented at predicting the distribution of littoral marine habitats.

Keywords: mediolittoral, upper infralittoral, benthic assemblages, algae, seaweeds, regional scale.

2.2.1. Introduction

The littoral zone of seas and oceans is host to a rich array of biologically diverse and socio-economically important ecosystems (Martínez et al. 2007). Littoral species and habitats may show non-random distributions along the vertical axis perpendicular to the seashore. These distributions are mainly regulated by a strong gradient of environmental conditions, which results in a pattern known as zonation. Zonation is essentially driven by seawater availability (Stephenson and Stephenson 1949; Lewis 1964; Dayton 1971; Foster 1971; Ballesteros and Romero 1988; Chappuis et al. 2014). Nonetheless, at wide geographical scales, other distribution patterns arise as a result of the uneven distributions of environmental factors like seawater temperature (van den Hoek 1982; Breeman 1988), wave exposure (Levin and Paine 1974; Denny 1985), shore slope (Whorff et al. 1995; Benedetti-Cecchi et al. 2000), salinity (Wallentinus 1991), rock mineral composition (Bavestrello et al. 2000; Guidetti et al. 2004), nutrient availability (Arévalo et al. 2007), or biotic interactions among organisms (Dayton 1971; Connell 1972; Underwood and Jernakoff 1984; Hawkins and Hartnoll 1985; Janke 1990; Menconi et al. 1999; Benedetti-Cecchi 2000; HilleRisLambers et al. 2012). Additionally, species and habitats thriving on rocky shores regularly face anthropogenic pressures that lead to significant changes in their abundance and distribution patterns (e.g. Thompson et al. 2002; Thibaut et al. 2005; Smith et al. 2007; Airoldi & Beck 2007; Mangialajo et al. 2008; Pinedo et al. 2013; Campbell et al. 2014), especially in densely populated areas (e.g. Ballesteros et al. 2007; Pinedo et al. 2007).

Only few studies have dealt with the distributions of littoral species and habitats at regional scales, and the information available mostly arises from observations (e.g. Stephenson and Stephenson 1950, 1954; Underwood 1981; Ballesteros and Romero 1988; Blanchette et al. 2008; Ramos et al., 2014; Chappuis et al., 2014) and experiments (e.g. Lubchenco, 1980; Menge et al. 1999; Benedetti-Cecchi et al. 1999; Harley 2003) at local scales. Nevertheless, an increasing number of studies aim to identify (Harley et al. 2006; Martínez et al. 2012; Bermejo et al. 2015) or predict (Huang et al. 2011; Martin et al. 2014) species and habitats distribution patterns across wide geographical areas. In all cases, sampling resolution seems to represent the limiting factor for pattern detection (Archambault and Bourget 1996; Fraschetti et al. 2005; Tello and Stevens, 2010).

The Mediterranean is a tideless sea (Ballesteros and Romero 1988) whose littoral zone (i.e. the boundary between terrestrial and marine domains) here is split into two different zones: the mediolittoral and the upper infralittoral (Ros et al. 1985). The mediolittoral zone harbours species and habitats that require or tolerate immersion but cannot thrive in permanent or semi-permanent immersion. The upper infralittoral zone harbours species and habitats that require permanent immersion although they can occasionally survive for short periods of time in emerged conditions. Algae, barnacles and limpets are unevenly distributed across the mediolittoral and infralittoral zones, usually making evident belts or habitats (Chappuis et al. 2014).

The main goal of this study is to identify the environmental drivers of the distribution of mediolittoral and upper infralittoral habitats at a regional scale (> 1000 Km coastline). We rely on a high-resolution GIS-based cartographic database of all littoral habitats found along 1100 km of shoreline in Catalonia (Spain, NW Mediterranean) (Mariani et al. 2014) and physical variables (e.g., substrate type, temperature, hydrodynamism, etc.) as proxies to describe the range of abiotic conditions that define the subsequent distribution of littoral habitats at a regional scale.

Specifically, we aim to (1) identify the subset of environmental variables driving the distribution of littoral habitats at a regional scale; (2) explore the relative importance of each variable in determining the habitat presence both in the mediolittoral zone and in the upper infralittoral zone, and (3) determine the relative importance of local factors (i.e. slope, orientation, geology, substrate type, wave exposure), regional factors (i.e. seawater temperature), and anthropogenic pressures (i.e. coastal artificialization) in shaping the distribution of littoral and upper infralittoral habitats**.**

2.2.2. Materials and Methods

2.2.2.1 Study area

The coastline of Catalonia (Spain, NW Mediterranean Sea) stretches along 1100 km and is constituted of 39% natural rocky shores, 30% artificial hard-bottom shores (breakwaters, sea walls, jetties, etc.), and 30% beaches (see Mariani et al. 2014). Data on littoral habitat distribution and environmental variables were collected along the entire coast, concretely between 3º10’28.072”E, 42º26’17.619”N and 0º30’57.001”E, 40º31’26.302”N. In this study, only hard-substrate habitats (both natural and artificial) were considered. The Catalan littoral zone (from the supralittoral down to the upper infralittoral zone at -1 m, as defined by Chappuis et al. (2014) encompasses most of the Mediterranean littoral habitat diversity (Ballesteros et al. 2007; Mariani et al. 2014), thus providing an excellent opportunity to explore the relationships between habitat and the distributions of environmental variables (see Figure 2.2.1).

2.2.2.2 Input data

2.2.2.2.1 Habitats

A habitat is here considered following the definition of the European Habitats Directive (92/43/EEC, see Mariani et al. 2014). The habitats were recognised in the field from their macroscopic biological features (i.e. the presence of dominant species; see Mariani et al. 2014), and corresponded to littoral habitats recognised by at least one of the three main classification

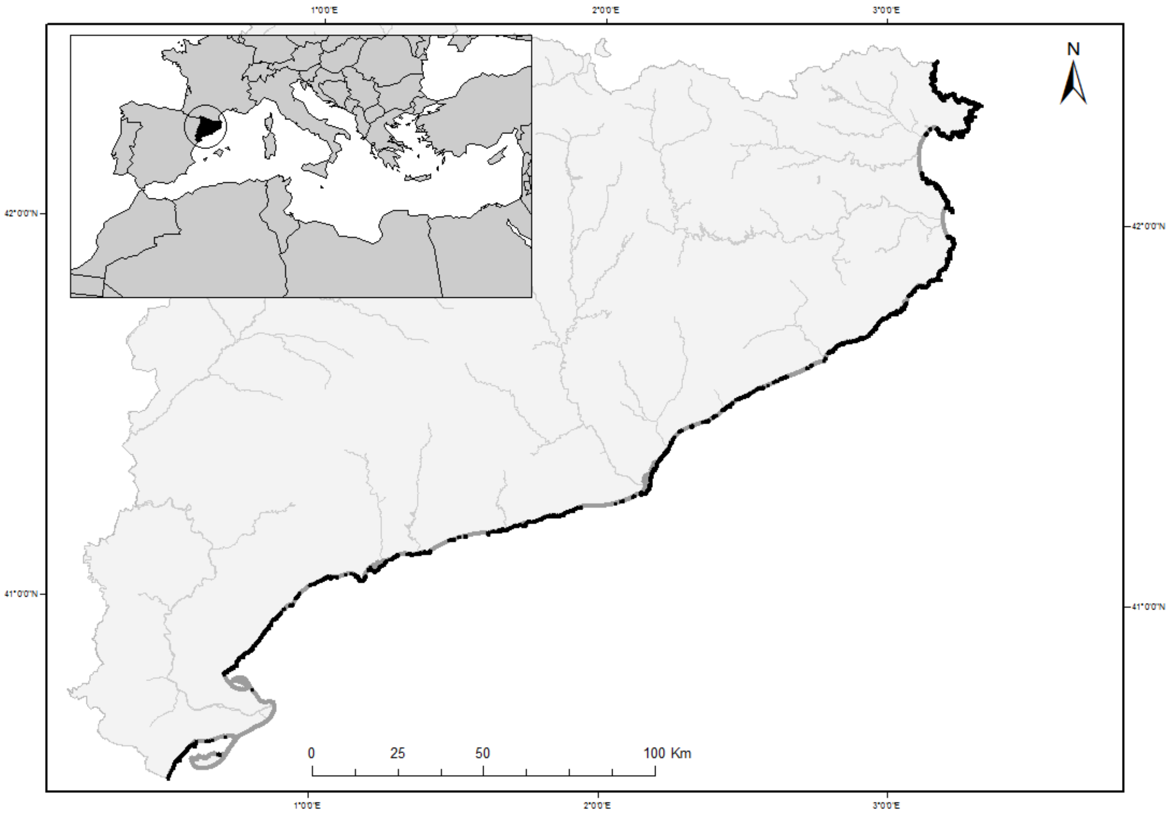

Figure 2.2.1. Coastline of Catalonia. Rocky and other hard-bottom shores are colored in black.

schemes used in the Mediterranean Sea (CORINE Biotopes, EUNIS, and LPRE lists; see Ballesteros et al. 2014).

All littoral habitats distributed from the supralittoral to the upper infralittoral (0-1 m depth) zones were digitally mapped along Catalonia using the Cat-LIT methodology (Mariani et al. 2014), at 1:1500 scale. The minimal sampling unit was 10 m (Ballesteros et al. 2014; Mariani et al. 2014), thus the rocky coast was split into 15,934 segments. The coastline polyline layer contained all data about the habitat composition for each segment. Among all identified habitats, those that were widespread [e.g. habitats from the supralittoral zone and the upper mediolittoral zone dominated by lichens (*Verrucaria amphibia*), periwinkles (*Melarhaphe neritoides*, *Echinolittorina punctata*) and barnacles (*Euraphia depressa*, *Chthamalus* spp.) and those that were present in coast segments measuring less than 10 m (see exceptions in Mariani et al. 2014) were eliminated from the data set to prevent confounding statistical results. The final dataset included data on the distribution of 29 littoral habitats, 19 in the mediolittoral zone and 10 in the upper infralittoral zone (Table 2.2.1).

2.2.2.2.2 Environmental variables

Data on environmental parameters relative to substrate features (slope, orientation, and

Table 2.2.1. List of the habitats studied. Each habitat is named after the principal species that characterizes it. Different frequencies of habitats occurrence for data sets of 16.098 points and 1000 points are presented.

Mediolittoral Habitats	**Code**	**% (16098 points)**	**% (1000 points)**
Mediolittoral *Corallina elongata*	Cor elo ML	84.3	82
Mediolittoral *Mytilus galloprovincialis*	Myt gal ML	50.9	47.3
Rissoella verruculosa	Ris ver	47.9	41.3
Lithophyllum byssoides	Lit bys	34.9	30.5
Gelidium pusilum/Gelidium crinale	Gel pus/Gel cri	12.9	14.1
Ulvales	Ulv	8.0	10.2
Ralfsia verrucosa	Ral ver	7.7	9.1
"Trottoir" (*Lithophyllum byssoides* rim)	Trottoir	7.2	6.4
Polysiphonia sertularioides	Pol ser	6.4	7.3
Ceramium spp./ *Osmundea* spp.	Cer Osm	4.5	6.2
Ceramium ciliatum	Cer cil	4.2	4.2
Lithophyllum cf.*vickersiae*	Lit vic	3.9	3.6
Nemoderma tingitanum	Nem tin	2.8	2.7
Neogoniolithon brassica-florida	Neo bra	2.8	3.4
Bangia atropurpurea	Ban fus	0.8	1
Hildenbrandia rubra and *Phymatolithon lenormandii*	Hil Phy	0.7	0.8
Dendropoma petraeum	Den pet	0.5	0.5
Mediolittoral *Lithophyllum incrustans*	Lit inc ML	0.4	0.4
Pyropia elongata	Pyr elo	0.3	0.3

Infralittoral Habitats	**Code**	**% (16098 points)**	**% (1000 points)**
Infralittoral *Corallina elongata*	Cor elo IL	64.9	62.4
Cystoseira mediterranea	Cys med	28.4	23.5
Photophilic algae	PA	24.1	26.1
Infralittoral sciaphilic *Corallina elongata*	Cor elo SIL	4.6	4.7
Infralittoral *Lithophyllum incrustans*	Lit inc IL	2.6	2.7
Sciaphilic algae	SA	1.2	1
Infralittoral *Mytilus galloprovincialis*	Myt gal IL	1.0	1.2
Cystoseira caespitosa	Cys cae	1.0	1
Pterocladiella capillacea	Pte cap	0.2	-
Sabellaria alveolata	Sab alv	0.1	-

geology), substrate type, coastal artificialization, wave exposure (hydrodynamism), and seawater temperature were obtained from different sources (Table 2.2.2).

Slope and orientation (relative to the cardinal points) of the coast were obtained from a Digital Elevation Model (DEM) created with a LiDAR detection method by the Institut Cartogràfic de Catalunya (ICC). The DEM was in raster format with pixel resolution of 2×2 meters. Slope and

Table 2.2.2. List and description of the environmental variables studied. A detailed explanation on the variable source and the calculation method are provided in the text.

Variables	Levels	Layer geometry	ID	Units	Source
Temperature	Average Sea Surface Temperature	Points	SST mean	ºC	MODIS
	P90 Sea Surface Temperature	Points	SST P90	ºC	MODIS
	P10 Sea Surface Temperature	Points	SST P10	ºC	MODIS
Hydrodynamism			Hydro	meters	DOW
	Average wave height	Points	hmean	meters	DOW
	Minimum wave height	Points	hmin	meters	DOW
	Maximum wave height	Points	hmax	meters	DOW
Orientation			Ori	qualitative	DEM
	North	Raster	N	qualitative	DEM
	NorthEast	Raster	NE	qualitative	DEM
	East	Raster	E	qualitative	DEM
	SouthEast	Raster	SE	qualitative	DEM
	South	Raster	S	qualitative	DEM
	SouthWest	Raster	SW	qualitative	DEM
	West	Raster	W	qualitative	DEM
	NorthWest	Raster	NW	qualitative	DEM
Slope			Slope	degrees	DEM
	0º - 10.8º	Raster	1	degrees	DEM
	10.8º - 22.8º	Raster	2	degrees	DEM
	22.8º - 45.1º	Raster	3	degrees	DEM
	45.1º - 68.2º	Raster	4	degrees	DEM
	68.16º - 87.8º	Raster	5	degrees	DEM
Geology			Geo	qualitative	IGCC
	Metamorphic	Polygons		qualitative	IGCC
	Mineral	Polygons		qualitative	IGCC
	Plutonic	Polygons		qualitative	IGCC
	Sedimentary	Polygons		qualitative	IGCC
	Artificial	Polygons		qualitative	IGCC
Artificialization			Arti	qualitative	CARLIT
	Natural	Polyline	N	qualitative	CARLIT
	Artificial	Polyline	A	qualitative	CARLIT
Substrate type		Polyline	Subs	qualitative	CAT-LIT
	Rock	Polyline	2	qualitative	CAT-LIT
	Rock without supralittoral	Polyline	3	qualitative	CAT-LIT
	Natural rocky boulders	Polyline	4	qualitative	CAT-LIT
	Harbour docks	Polyline	5	qualitative	CAT-LIT
	Breakwaters	Polyline	6	qualitative	CAT-LIT
	Caves	Polyline	8	qualitative	CAT-LIT
	Concrete walls	Polyline	9	qualitative	CAT-LIT
	Underwater rocks	Polyline	10	qualitative	CAT-LIT

orientation were calculated with a surface spatial analysis tools in ArcGis. Slope was classified into five categories and orientation into eight levels (Table 2.2.2). The geological features of the rocky shore (i.e. the mineral composition) were provided by the Institut Geològic i Cartogràfic de Catalunya (IGCC, www.igc.cat) at 1:50.000 scale. Five different categories were considered: sedimentary (calcareous, lutite, graywake), plutonic (mostly granitic), metamorphic (schists), mineral (quartz and barite), and artificial.

Eight substrate types were recognized in situ for each coastal segment: continuous rock, partially emerged rock (without supralittoral zone), submerged rock (lacking supralittoral and mediolittoral zones), natural boulders, artificial boulders (breakwaters), concrete walls, and caves. Information on coastal artificialization [i.e. whether a substrate was natural or artificial (man-made)] was obtained from the CARLIT data set (see Ballesteros et al. 2007) at a scale of 1:1000 (Table 2.2.2).

Data on wave exposure were estimated using the Downscaled Ocean Waves model (DOW) (Camus et al. 2013), with a resolution of 0.01 degrees latitude and 0.008 degrees longitude, along the shore. The mean, maximum, and minimum wave height values were calculated for a dataset of 3091 points along the coat and corresponding to a time frame of ten years (1998 to 2008) (Table 2.2.2).

Daily mean Sea Surface Temperature (SST) from January 2003 to December 2010 was obtained from satellite measurements performed by the MODIS (aqua) sensor system (http://oceancolor.gsfc.nasa.gov/), available as “Ocean Level-2” HDF data by NASA’s Goddard Space Flight Center. We considered only high-quality temperature readings (flag values of 0 or 1), and we discarded less reliable readings (flag values of 2 or 3) (see Serrano et al. 2013). Over the SST study period, the mean annual temperature and mean annual 90th and 10th percentiles were determined for 200 points along the Catalan coastline.

2.2.2.3 Spatial data processing

The coastline layer, which included data on habitat distributions and substrate type, was converted into a point layer dataset with an ArcGis data management tool, where points were spaced 10 m from each other, to match the habitat data resolution.

In order to perform the statistical analysis, all the layers carrying environmental variables were overlapped and joined into the habitat layer in ArcGis. Different spatial tools were applied to combine all layers, depending on whether the layer was a vector or a raster. Within the vector layers, a closest spatial joint analysis was performed between the habitat dataset and all the other vector layers (exposure, geology, SST, and artificialization). An extraction spatial analysis with a bilinear interpolation was performed for the slope and orientation rasters. Nevertheless, deviations of overlapping values of all environmental variables were revised and corrected when necessary. This layer-by-layer procedure and particularly the continuous validation from expert knowledge used to generate the final database allowed minimising possible generation and propagation of errors deriving from uncertainty problems (e.g. different sensors, extrapolation from unknown parameters, different interpolations etc. see Leung, 2010). Finally, a layer of 16.098 points with biological and environmental information was obtained. Data processing for all environmental variables is summarized in Figure 2.2.2. The projection system European Datum 1950 UTM Zone 31N was used. All spatial analysis and spatial data processing were performed in ArcGIS 10.1 (©ESRI).

2.2.2.4 Statistical analysis

The four quantitative variables were tested for multi-collinearity based on Pearson's rank correlations (r>0.7). This resulted in a subset of three uncorrelated variables: mean and minimum wave heights and mean SST. The uncorrelated quantitative variables and all the qualitative variables were included in the analysis.

The availability of seawater and environmental variables tested (e.g. wave exposure, seawater temperature, slope) may have differential effects among the habitats of the mediolittoral and the upper infralittoral zones. Consequently, they were analysed separately.

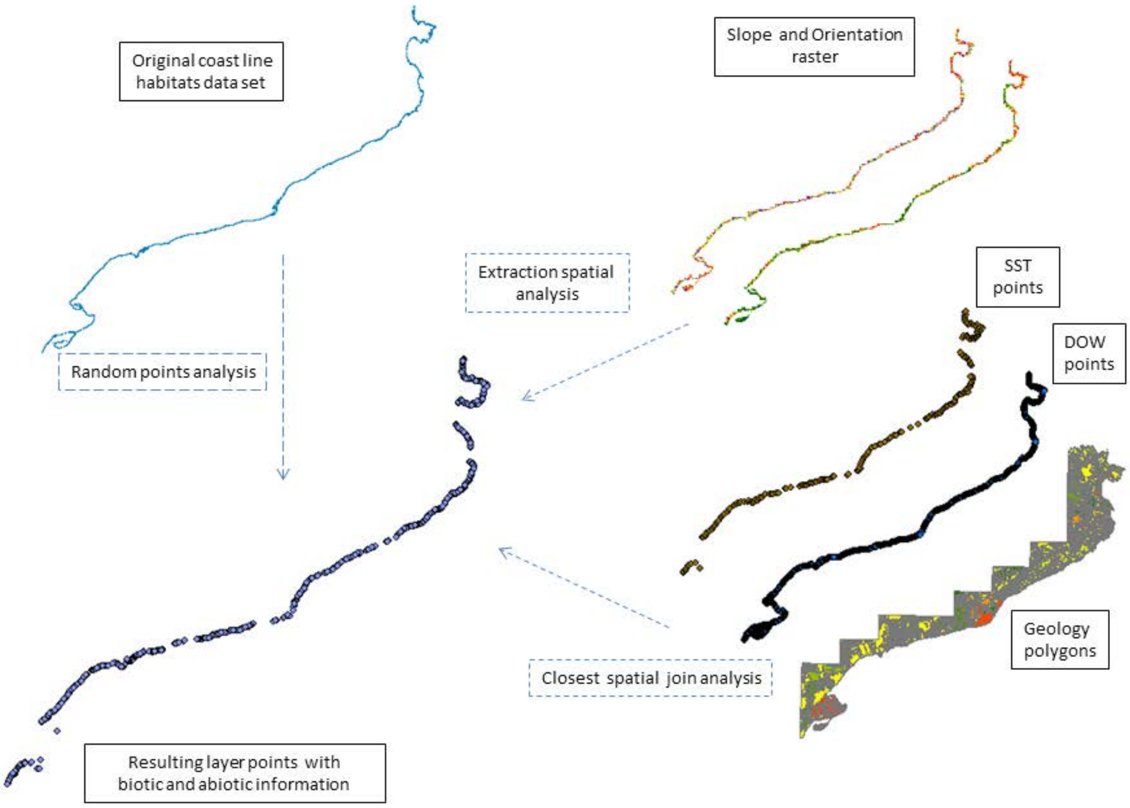

Figure 2.2.2.Spatial data processing diagram. Rectangles of solid line correspond to layer name and geometry, rectangles with dashed line correspond to spatial processing. See the text for details.

Generalized Linear Models (GLM, McCullagh and Nelder 1989) were developed to describe the relationship between the distribution of habitats and environmental variables using the entire dataset (16.098 points). Specifically, we performed logistic regression models assuming a binomial distribution with a logistic link function. The best model for each habitat, among the candidate models, was selected with the *glmulti* function (in the glmulti R package; Calcagno 2013), and based on AIC values. Selected models were further analysed and the significance of the variables included was tested with Likelihood Ratio Test. The significant z values of the models were used for the interpretation of the relationships between variables (habitat vs. environmental variables). The fit of the model (D^2) was calculated as the proportion (%) of explained deviance:

$$D^2 = (\text{null deviance - residual deviance}) / \text{null deviance} * 100$$

To show the relative importance of each variable in the models, the mean and the dispersion of the significant z values (percentile 5% and 95%), both for the mediolittoral and upper infralittoral zones, were plotted in a boxplot diagram.

Presence/absence habitat data were analysed by a non-metric multi-dimensional scaling (nMDS) based on the Bray-Curtis similarity index to visualize spatial patterns. To simplify the computing effort and only for the multivariate analyses, the dataset was reduced to a lower resolution. For this aim, the layer was resampled in ArcGIS obtaining a matrix of 1000 points (one point every 120 m) along the coast. The subset was considered representative of the database, as the habitat occurrence frequencies matched between datasets (see Table 2.2.1). A bioenv analysis (in the vegan R package; Okasen et al. 2013) was performed to investigate the relationship between habitats and environmental variables, and to identify the subset of variables showing the maximum correlation with habitats dissimilarity. Those variables with maximum correlation from the bioenv analysis were projected in the nMDS with *ordisurf* function (in the vegan R package; Okasen et al. 2013).

All statistical tests were performed with the R software (R Development Core Team 2011).

2.2.3. Results

The results of the logistic regression models are summarized in Tables 2.2.3 and 2.2.4. The variability explained by the environmental variable models for the mediolittoral habitats ranged between 5.2% and 72.6% (Table 2.2.3). The highest values were shown by the habitat of mediolittoral caves dominated by the encrusting red algae *Hildenbrandia rubra* and *Phymatolithon lenormandii* (72.6%), the habitat dominated by the encrusting red alga *Neogoniolithon brassica-florida* (50.0%), and the habitat dominated by the erect red alga *Rissoella verruculosa* (47.2%).

Table 2.2.3. Selected GLMs for mediolittoral habitats. D^2 is the explained deviance of the model considering all significant variables. The z value is the Wald statistic for testing the null hypothesis that the corresponding regression coefficient is zero. The z value sign shows the relation (positive or negative) between the variable and habitat presence. Only z values with significant p values (Pr(>|z|)) were considered and presented in the table.

Mediolittoral Habitats	**Models with z values**	**D^2**
H. rubra and *P. lenormandii*	-3.4 sedimentary, +2.6 SST average, +2.08 h average	72.6%
N. brssica-florida	+14.98 SST average, -8.05 h min, +2.21 h average, +2.2 slope3	50.0%
R. verruculosa	-29.68 SST average, +22.9 plutonic, -21.9 sedimentary, -4.5 slope5, +3.2 h average, -2.8 slope 4, +2.7 Arti N	47.2%
D. petraeum	+6.8 SST average, +5.2 h average, -4.7 h minimum, +2.3 slope3, +2.2 slope2	41.5%
P. sertularioides	+21.3 SST average, -7.5 h minimum, +6 h average, +5.8 slope3, +4.3 slope4, -3.8 Arti N, +2.3 O	39.2%
Ulvales	+11.7 SST average, +9.96 artificial, +7.3 Arti N,-5.8 h average, +5.4 plutonic, +5.9 sedimentary, -4.02 slope3, +3.4 NO, +2.1 O, -3.3 h minimum, +1.96 NE	23.2%
"Trottoir"	+22.2 sedimentary, +18.5 h average, +13.5 slope 4, +13.1 slope3, +11.4 slope5, -11.97 SST average, +10.6 h minimum, +5.5 slope2, -2.9 SE, -4.1 SO	35.3%
Gelidium spp.	+30.3 SST average, - 7.6 h minimum, +6.4 plutonic, -3.95 artificial, +2.9 h average	33.6%
C. ciliatum	+18.4 SST average, +7.3 h average, -5.5 h minimum,+ 2.8 O, +2 SO	29.6%
R. verrucosa	+14.2 h average, +12.9 h minimum, +11.2 sedimentary, +9.4 slope5, +8.7 artificial, +5.2 slope4, +5.05 slope3, +3.8 plutonic, -2 SST average	29.1%
L. byssoides	-25.1 SST average, +15.4 h average, +12.8 h minimum, -10.9 sedimentary, +9.9 plutonic, +2.9 mineral, 2.6 slope2, -2.3 slope5	25.0%
B. fuscopurpurea	+5.9 artificial, +4.05 h average, -3.2 slope3, +2.7plutonic, +2.3 sedimentary	24.5%
L. cf *vickaersiae*	-13.9 SST average, +6.8 sedimentary, -3.9 slope4, +2.8 Arti N, -2.7 slope5, -2.6 slope3	21.9%
P.elongata	+5.2 SST average	21.6%
Ceramium sp./*Osmundea* sp.	+16.7 SST average, +5.7 artificial, +3.2 plutonic, +2.9 sedimentary, -2.9 h minimum, -2.4 SE	20.4%
N.tingitanum	+9.8 plutonic, -9.6 SST average, +4.6 h minimum, -3.9 slope4, -3.8 slope3, -3.3 slope2, +3.2 artificial, +3.7 sedimentary, +2.5 Arti N	15.2%
L. incrustans ML	+5.4 slope5, +3.2 SST average, -2.04 slope2	14.4%
C. elongata ML	-19.9 SST average, -7.1 artificial, -6.9 Arti N, -3.6 sedimentary	11.5%
M. galloprovincialis ML	+9.4 h average, +7.8 SST average, +7.6 h minimum, +3.8 slope2, +2.4 slope3, +2.02 SE	5.2%

Table 2.2.4. Selected GLMs for infralittoral habitats. D^2 is the explained deviance of the models considering all significant variables. The z value is the Wald statistic for testing the null hypothesis that the corresponding regression coefficient is zero. The z value sign shows the relation (positive or negative) between the variable and habitat presence. Only z values with significant p values (Pr(>|z|)) were considered and presented in the table.

Infralittoral Habitats	Models with z values	D^2
S. alveolata	-4.7 h average, +3.3 SST average	70.2%
Sciaphilic *C. elongata*	+12.9 sedimentary, +11.2 slope5, +9.3 slope4, -9.6 SST average,+8.9 plutonic, +8.4 slope3, +7.5 h average, +3.03 h minimum, +2.3 slope2, +2.2 mineral	36.3%
P. capillacea	-2.9 SST average, +2 slope4, -2 plutonic	26.4%
C. mediterranea	+14.9 plutonic, +14.4 h average, -11.7 slope3, -11.6 SST average, -11.5 slope4, +9.6 h minimum, -7 slope5, -5.7 slope2, +4.05 Arti N, -4.2 NO, -2.8 artificial, +2.25 S, +2 mineral	22.6%
M. galloprovincialis	+7.4 SST average, +2.5 h average, -2.5 h minimum, -2.2 slope3, -2 slope 2, +2 O	21.9%
Sciaphilic Algae	+7.2 slope4, +6.8 sedimentary, +5.9 slope5, +5.3 slope3, +5mineral, +4.8 plutonic, +3.6 slope2, +3.6 h minimum	18.4%
L. incrustans	-11.4 SST average, -7 plutonic, -3.5 h average, -3.5 h minimum, +2.4 Arti N	16.7%
Photophilic Algae	-21.7 h average, -17.8 plutonic, -13.7 h minimum, -9.7 slope3, -8.5 slope4, -6.1slope5, +6 Arti N, -3.6 slope2, -3.5 artificial, -3.06 sub5, -2.24 sub6, -2.4 sub9	9.7%
C. elongata	+17.4 h average, +13.8 plutonic, -13.7 Arti N, +11.97 h minimum, -9.4 sedimentary, +6.04 slope3, -5.15 artificial, +3.6 slope2, +2.6 slope4, -2.1 NO	9.2%
C. casespitosa	-3.7 plutonic, -3.6 SST average, -2.6 slope4, -2.09 slope3	8.8%

The lowest values were shown by *Mytilus galloprovincialis* beds (5.2%), mediolittoral *Corallina elongata* turfs (11.5%), *Lithophyllum incrustans* barrens (14.6%), and *Nemoderma tingitanum* crusts (15.2%). D^2 overall ranged between 20 and 40% for the rest of habitats (Table 2.2.3).

The variability explained by the environmental variable models for the upper infralittoral habitats ranged between 8.8% and 70.2% (Table 2.2.4). The highest value was shown by the reefs of *Sabellaria alveolata* and the lowest by the algal beds of *Cystoseira caespitosa*. D^2 ranged between 9% and 36% for the other habitats (Table 2.2.4).

In the mediolittoral zone, "Trottoir" *(Lithophyllum byssoides* rim) and *Ralfsia verrucosa* crusts were found along steep shores with high wave exposures, and low water temperatures. While *Lithophyllum byssoides* rims were best associated with calcareous substrates, *Ralfsia verrucosa* crusts were found preferentially on both granitic and calcareous rocks, also on artificial substrates. The habitats of *Rissoella verruculosa* and *Lithophyllum byssoides* cushions were associated with low temperatures, moderate slopes on shores highly exposed to wave action, preferably over plutonic rocks. Furthermore, *Rissoella verruculosa* was negatively correlated with coastal artificialization. The habitats of *Nemoderma tingitanum* and *Lithophyllum* cf. *vickersiae* were also associated with low temperatures and moderate slopes on exposed shores. Moreover, *Nemoderma tingitanum* did not show any geological preference regarding the substrate. In contrast, the habitat dominated by *Lithophyllum* cf. *vickersiae* seemed to prefer natural, sedimentary substrates. The mediolittoral habitat of *Corallina elongata*, was associated with low temperatures, but did not show any relationship with other variables. The habitat characterized by *Polysiphonia sertularioides* was present on moderately exposed, artificial, steep shores with high water temperatures. The habitat characterized by *Neogonioliton brassica-florida* and *Dendropoma petraeum* was present on shores with moderate slopes and hydrodynamism, but high water temperature. These environmental conditions were associated also with the distribution of the mediolittoral mussel beds, although the total variance explained was very low. The habitats of *Hildenbrandia rubra* and *Phymatolithon lenormandii*, *Gelidium* spp., *Ceramium ciliatum*, and *Ceramium – Osmundea*, which showed strong association with moderately exposed shores and high water temperatures, had no relationship with slope. Coastal steepness and high seawater temperatures were strongly related to the presence of barrens of *Lithophyllum incrustans*. The habitat dominated by *Ulva* spp. and *Cladophora* spp. (as Ulvales in Table 2.2.3) showed no particular preference for any substrate, either artificial or natural, but preferred sites with high seawater temperatures with no preference for slope, wave exposure or geomorphology. The habitat dominated by *Bangia fuscopurpurea* was indifferent to steepness, and was associated with all types of exposed substrate, artificial and both plutonic and sedimentary. Finally, high water temperature was the only variable shown by the best model fit for the habitat dominated by the red alga *Pyropia elongata.* Only seven habitats showed a significant relationship (either positive or negative) with orientation. One exception was the *Lithophyllum byssoides* rim, which was negatively associated with south-east and south-west orientations.

In the upper infralittoral zone, all sciaphilic habitats, those dominated either by *Corallina elongata* or by *Plocamium cartilagineum* and *Schottera nicaensis* were mostly present on steep shores, with low seawater temperature, and strong hydrodynamism. Furthermore, these habitats appeared both on plutonic and sedimentary substrates. The upper infralittoral habitat dominated by *Corallina elongata*, seemed to prefer sites with moderate to high slopes and strong hydrodynamism, and its presence was abundant over granites. The habitat of *Pterocladiella capillacea* was present on steep slopes, and with low water temperatures. Low water temperatures were positively related to habitats dominated by *Cystoseira caespitosa* and *Cystoseira mediterranea,* regardless of any particular slope. In the case of the habitat of *Cystoseira mediterranea*, high wave exposure and natural granitic substrates were associated to its presence. Upper infralittoral barrens of *Lithophyllum incrustans* seemed to prefer sites with low water temperature and low wave exposure. In contrast, the only upper infralittoral habitats that preferred sites with high water temperatures were *Sabellaria alveolata* reefs and mussel beds. The first one appeared on sheltered shores, the second on exposed ones. The presence of photophilic algae seemed to be unrelated to any level of slope, but it was associated with low wave exposures. There was a weak association between the orientation and the distribution of upper infralittoral habitats. Nevertheless, the presence of *Cystoseira mediterranea* stands was positively associated with south-oriented shores.

Different combinations of environmental variables were selected in the models to explain each individual habitat occurrence. Water temperature, slope, wave exposure, and geological features were selected for most of the habitats and showed the highest contributions both for mediolittoral and upper infralittoral habitats. More specifically, water temperature showed the greatest contribution to mediolittoral habitats models, followed by hydrodynamism (wave exposure), geology, artificialization, and slope (Figure 2.2.3a). In the upper infralittoral habitats, hydrodynamism showed the greatest contribution, followed by water temperature, slope, geology and artificialization (Figure 2.2.3b).

The bioenv analysis showed that mean water temperature and substrate type were the variables explaining the highest dissimilarity between habitats, i.e. 30% for the mediolittoral zone and 25% for the upper infralittoral zone.

The results of the nMDSs revealed how mediolittoral habitats were differently distributed across the temperature gradient (Figure 2.2.4a). This pattern was not so evident for the upper infralittoral habitats (Figure 2.2.4b). Regarding substrate types, natural continuous rock was positively associated with several habitats (rims and cushions of *Lithophyllum byssoides*, *Rissoella verruculosa*, *Ralfsia verrucosa*, and *Cystoseira mediterranea*). Breakwaters were associated with mediolittoral and infralittoral habitats of *Corallina elongata*. Caves were always associated with habitats of *Hildenbrandia rubra* and *Phymatolithon lenormandii* in the mediolittoral zone and sciaphilic habitats in the upper infralittoral zone. The other habitats did not display any preference for a particular substrate type (Figure 2.2.4a,b).

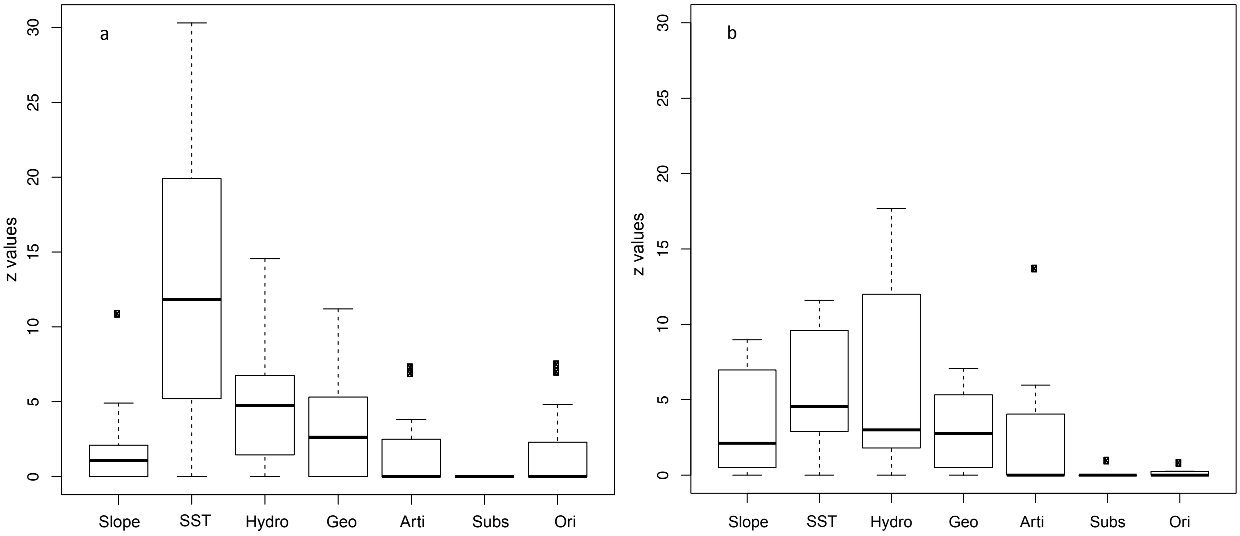

Figure 2.2.3. Boxplots of significant GLMs z values. Boxplots of significant GLMs z values for a) mediolittoral zone models, b) upper infralittoral zone models. The mean and the percentiles (5% and 95%) of z values are shown. See Table 2.2.2 for codes explanation.

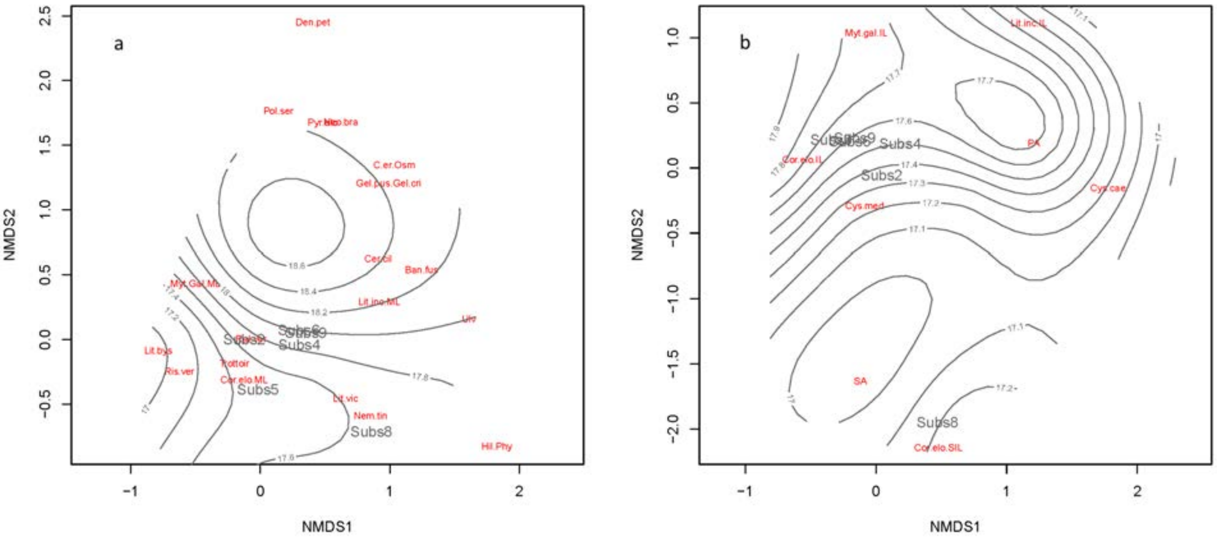

Figure 2.2.4. nMDS for mediolittoral and upper infrallittoral habitats. nMDS for mediolittoral and upper infrallittoral habitats a) nMDS of the mediolittoral habitats. b) nMDS of the upper infralittoral habitats. SST mean (isothermal lines) and substrate type are fitted in both plots. See table 2.2.1 and 2.2.2 for abbreviations. Each habitat is represented by its centroid. The analysis has been performed with a database of 1000 points (see text).

2.2.4 .Discussion

Our study provides a general perspective on the relationship between the presence of littoral habitats and environmental factors and sheds some light on the importance of these variables as possible drivers for the distributions of both mediolittoral and infralittoral Mediterranean habitats on rocky shores. The abiotic factors analysed here have been generally disregarded in previous studies. Specifically, most research has focussed on the distribution of a single or a few habitats locally (Martin et al. 2014; Martínez et al. 2012; Bermejo et al. 2015). Our study is the first one examining the relationships between factors such as shore slope, orientation, geology, substrate type, wave exposure, seawater temperature, and coastal artificialization in shaping the distribution of a large number of habitats (19 from the mediolittoral zone and 10 from the infralittoral zone), at a very high resolution and at a regional scale. We found that the relative importance of the considered environmental variables differs among mediolittoral and upper infralittoral habitats. Despite their proximity to infralittoral habitats, mediolitoral habitats show strong dependence on limited, unpredictable water availability. However, different mediolittoral habitats rarely coexist at the same height at a same place. Abiotic factors related to seawater features (i.e seawater temperature) and coastal morphology may play important roles in determining the success of a particular habitat in a particular place (Feldmann 1937; Ballesteros 1992; Giaccone et al. 1993). Heterogeneity of coastal morphology (e.g. rock geology, slope, and orientation) may regulate the presence of specific mediolittoral habitats (e.g. *Rissoella verruculosa* vs. *Ralfsia verrucosa* or *Polysiphonia sertularioides*; *Lithophyllum byssoides* vs. “Trottoir” or *Neogoniolithon brassica-florida*). Although very limited periods of aerial exposure under prevailing conditions of calm waters and high atmospheric pressures occur (Rodríguez-Prieto and Polo 1996), the upper infralittoral zone never faces the harsh conditions of the mediolittoral zone. It also shows lower habitat diversity in the first meter. In general, the main factors that affect the presence and distribution of uppermost infralittoral habitats (always or almost always submerged) are related to nutrient availability (Ballesteros 1992; Arevalo et al. 2007; Ballesteros et al. 2007; Pinedo et al. 2013, 2015) or light intensity (Ballesteros 1992; Rinné et al. 2011). Seawater temperature emerges as the main factor determining habitat distribution in the mediolittoral zone, followed by other factors such as hydrodynamism, geology and slope. On the contrary, the main factor driving habitat distribution in the upper infralittoral zone is hydrodynamism, followed by seawater temperature, slope and geology. Temperature has long been recognized as a key factor governing seaweed biogeography (e.g. Stephenson 1944; Lewis 1964; Lünning 1984; Pakker et al. 1995; Anderson et al. 2012; Wernberg et al. 2013) and reproduction (Lüning 1990; Ballesteros 1991) and since it varies with latitude (Mieszkowska et al. 2006; Martínez et al. 2012), it is often responsible for the distribution of northern/southern geographic boundaries of seaweeds (Breeman 1988). Some mediolittoral habitats show a strong relationship with the seawater mean temperature gradient (17º-18.6º) from northern to southern Catalan waters. In fact, some habitats, such as the "Trottoir", are circumscribed to the northernmost coast (i.e. coldest waters). Others are far more abundant in the north, such as the habitats dominated by *Rissoella verruculosa* or *Lithophyllum byssoides*. Other habitats, like the barrens of *Neogoniolithon brassica-florida*, are exclusively present in the south (i.e. warmer waters). Temperature variation in the study area is due to the effects of the warm-water Balearic current in the southern coast and the colder, deep-water generated current from the Lions Golf in the northern coast (Font et al. 1988). However, although quite reduced (less than two degrees ºC), temperature variation in the studied area is a relevant factor driving mediolittoral benthic habitat distributions. On the contrary, while water temperature plays an important role, upper infralittoral habitats do not show latitudinal differences in their distributions. For example, while *Sabellaria alveolata* reefs are only present in the southern coast, the rest of upper infralittoral habitats do not show any latitudinal difference at the geographical scale considered.

Hydrodynamism exerts direct and indirect effects on benthic organisms (Denny 2006) and it plays a central role in coastal environments (Nishihara and Terada 2010; Rattray et al. 2015). Hydrodynamism, namely wave exposure, is especially important in heterogeneous areas where it plays a key role in determining the distribution of macroalgae (Snikars et al. 2014). The role of wave exposure in shaping habitat distributions in the mediolittoral zone is crucial for reducing hydric stress due to prolonged emersion times (Chappuis et al. 2014). Increased water movement enhances nutrient availability to seaweeds (Ballesteros 1989). Many macroalgae-dominated habitats (i.e. "Trottoir", *Lithophyllum byssoides, Rissoella verruculosa*, *Ralfsia verrucosa*) are best developed in high exposed areas. Nevertheless, very strong hydrodynamism can generate a mechanical stress which only a few, morphologically-adapted species, can withstand, causing breakage or even death in adult macrophytes (Viejo et al. 1995; Diez et al. 2003). In areas with high levels of erosion by sand scour, habitats are usually dominated by turf algae (such as *Polysiphonia sertularioides*, *Gelidium* spp.), which are well-known to be adapted to sand scour (Airoldi 1998). Habitats dominated by Ulvales are mainly present in sheltered areas also subjected to sand scour. At the infralittoral zone, habitats dominated by either *Cystoseira mediterranea*, sciaphilic algae, *Corallina elongata* or *Mytilus galloprovincialis*, require high water renewal (Bellan-Santini 1965; Ballesteros 1992) and reach their optimum development on exposed coasts (although *Mytilus galloprovincialis* can also grow in sheltered areas like bays or lagoons where it is cultivated). Other habitats show an opposite trend; this is the case of photophilic algal assemblages, *Sabellaria alveolata* reefs and infralittoral *Lithophyllum incrustans* barrens, which are far more frequent in sheltered areas. Slope and orientation are local factors also associated with seaweed distribution on the shore (see Diez et al. 2003). However, we found only a minor effect of rocky slope on the distribution of habitats both in the mediolittoral and in the upper infralittoral zone. Two exceptions are the "Trottoir", often accompanied by the habitat dominated by *Ralfsia verrucosa*, which are very characteristic of steep cliffs with reduced light levels (Boudouresque 2004; Mannino 2003). Rock steepness also benefits the presence of habitats formed by sciaphilic algae in the upper infralittoral zone. Although orientation has been documented to have an influence on terrestrial and rocky shore habitats and species (Boyce et al. 2005; Harley 2008) we did not find any particular effect on the habitats studied here, both for the mediolittoral and the upper infralittoral zones. Another factor with a secondary but significant relation with habitat distribution in this study is geology, i.e. rock mineral content (Harris et al. 2013). Algae are unable to absorb nutrients or any other chemical component directly from the rocky substrate. However, Feldmann (1937) and Giaccone et al. (1993) have observed a close relationship between the presence of some seaweeds and rock types. For instance, "Trottoir" has already been reported to better develop over calcareous substrates (Mannino 2003) and *Rissoella verruculosa* over granites or schists (Feldmann 1937). Additionally, in the mediolittoral zone, we have observed widespread, massive presence of the habitat dominated by *Lithophyllum* cf. *vickersiae* on graywake rocks. Guidetti et al. (2004) report a preference of photophilic algae for granitic rocks and of sciaphilic algae for limestones, although we did not find this pattern in the upper infralittoral zone. Affinities between some habitats and the geology seem to be related with the texture and hardness of the different minerals, which has an effect on the recruitment and survival of certain algae (see Bourget et al. 1994). There is a clear difference between habitats usually growing over natural rock, and those present on man-made structures (e.g. harbour docks, breakwaters) (Connell & Glassby 1999; Smith and Rule 2002; Bulleri and Chapman 2004; Ballesteros et al. 2007). Man-made structures usually do not harbour habitats with highly specific environmental requirements (e.g. *Lithophyllum byssoides*, *Rissoella verruculosa*, "Trottoir", *Neogoniolithon brassica-florida*, *Cystoseira mediterranea*), and are usually colonized by pioneering (Ulvales, *Polysiphonia sertularioides*, *Gelidium* spp., *Mytilus galloprovincialis*) or stress-resistant species (*Corallina elongata*). Normally, artificial structures are abundant along coasts with high human pressures, where only tolerant habitats and species thrive (Ballesteros et al. 2007). Furthermore, pioneering species show a high propagule production and dispersal (Ceccherelli and Rossi 1984; Bacchiocchi and Airoldi 2003), thus allowing a more rapid colonization of new structures (Airoldi 2000). Studying species-environment relationships is crucial to elucidate habitat pattern distributions. Littoral zones are ecologically important areas for a variety of reasons and detailed scientific information is needed to develop and implement appropriate measures of habitat protection and conservation. Knowledge on the biophysical components of these systems is still poor (see Rattray et al. 2015) and this study represents an important contribution towards a better understanding of the habitat-environment relationships.

These relationships are at the core of predictive geographical modelling in ecology (Guisan and Zimmermann 2000) and predictive species distribution models currently represent an essential tool for biodiversity conservation and management (Côté and Reynolds 2002).

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Capítulo 2.3

The optimal sampling design for littoral habitats modelling: a case study from the north-western Mediterranean

Maria Elena Cefalì[1,2*], Enric Ballesteros[1], Joan Lluís Riera[3], Eglantine Chappuis[1], Marc Terradas[4], Simone Mariani[1,3], Emma Cebrian[1,5]

[1]Centre d'Estudis Avançats de Blanes-CSIC, Acc. Cala Sant Francesc 14, 17300 Blanes, Girona, Spain
[2]Estación de Investigación Jaume Ferrer, Instituto Español de Oceanografía (IEO), PO Box 502, 07701 Mahón, Spain
[3] Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Universitat de Barcelona, Gran Via de les Corts Catalanes 585, 08007 Barcelona, Spain
[4] Departament de Ciències del Mar i Biologia Aplicada, Universitat d'Alacant, Apartat de Correus 99, 03080 Alacant, Spain
[5] Institut d'Ecologia Aquàtica, Universitat de Girona, Plaça Sant Domènec 3, 17071 Girona, Spain

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Abstract

Species distribution models (SDMs) have been used to predict potential distributions of habitats and to model the effects of environmental changes. Despite their usefulness, currently there is no standardized sampling strategy that provides suitable and sufficiently representative predictive models for littoral marine benthic habitats. Here we aim to establish the best performing and most cost-effective sample design to predict the distribution of littoral habitats in unexplored areas. We also study how environmental variability, sample size, and habitat prevalence may influence the accuracy and performance of spatial predictions. For first time, a large database of littoral habitats (16,098 points over 562,895 km of coastline) is used to build up, evaluate, and validate logistic predictive models according to a variety of sampling strategies. A regularly interspaced strategy with a sample of 20% of the coastline provided the best compromise between usefulness (in terms of sampling cost and effort) and accuracy. However, model performance was strongly depen upon habitat characteristics. The proposed sampling strategy may help to predict the presence or absence of target species or habitats thus improving extensive cartographies, detect high biodiversity areas, and, lastly, develop (the best) environmental management plans, especially in littoral environments.

Keywords: seaweeds, species spatial distributions, species distribution models, SDM, predictive models, logistic regression.

2.3.1 Introduction

The prediction of species and habitat distributions through numerical models still represents one of the most challenging areas of work in ecology (Elith and Leathwick 2009), especially in light of the current scenario of a rapidly changing environment. Species distribution models (SDMs) and habitat distribution models (HDMs) find many applications in ecology (Guisan and Zimmermann 2000; Vaughan and Ormerod, 2005), including conservation and management (Lehmann et al. 2002), and, in conjunction with rich, high coverage data sets and simulation experiments, may help in designing efficient sampling strategies for habitat suitability modelling (Hirzel and Guisan 2002) for both terrestrial and marine areas.

SDMs and HDMs are statistical models of the relationship between species and habitat distributions, and those environmental variables that potentially drive such distributions (Guisan and Zimmermann 2000). Mechanistic, empirical (or correlative), and theoretical models can be used, depending on the research objectives and the variables available (Guisan and Zimmermann 2000). Empirical models are most frequently used, especially those coupling the distributions of species and environmental variables (Franklin 2010). Recent access to data from remote sensing techniques and geomorphological cartographies, as well as rapid advances in geographical information systems (GIS) have provided large sets of species and environmental data to build empirical models (Elith and Leathwick 2009). Empirical models relate known occurrences (presence and absence) of species or habitats to the environmental variables that best reflect the species' or habitats' environmental requirements. Once the empirical model is fitted, the output is used to predict the most suitable or unsuitable areas for species and habitats (Guisan et al. 2007).

The degree to which causal relationships between species/habitat distributions and the predictor variables are unveiled depends on the adequacy of the predictors used for model building and on the quality of species or habitats occurrence data (Araújo and Guisan 2006; Tessarolo et al. 2014). Sample size, sample design, species and habitat characteristics, environmental stratification, and species prevalence are also important for the success of predictive spatial distribution models (Fielding and Bell 1997; Guisan and Zimmermann 2000; Stockwell and Peterson 2002; Franklin 2010; Tessarolo et al. 2014). The paucity of fine environmental and species occurrence data for marine ecosystems may explain why sea-focused SDMs and HDMs are fewer compared to terrestrial ones (Robinson et al. 2011). However, many efforts have been made in recent years to collect data on environmental variables and species distributions (e.g. BIO-ORACLE (Tyberghein et al. 2012), OBIS, www.iobis.org), thus allowing the application of SDMs to marine systems. Most models aim to predict the potential distribution of one or a few benthic species or habitats of special conservation interest (Bekkby and Moy 2011; Reiss et al. 2011; Giusti et al. 2014; Martin et al. 2014; Reiss et al. 2014; Falace et al. 2015), endangered fish species that are commercially exploited (Giannoulaki et al. 2011; Tugores et al. 2011; La Mesa et al. 2015), or the effects of global change on a single species or habitat (Martínez et al. 2007; Hawkins et al. 2008; Helmuth et al. 2011; Gallon et al. 2014; Sarà et al. 2014). Nevertheless, most researchers have not yet analyzed the importance of sample size, sampling design, or species occurrences to build up accurate SDMs for marine environments. Those parameters are crucial for achieving the best accuracy (as measured by AUC, area under the receiver operating characteristic [ROC] curve) and performance (measured as sensitivity and specificity) in predictive SDMs (Hirzel and Guisan 2002).

The littoral zone harbors a rich array of habitats (Burrows et al. 2009; Cruz-Motta et al. 2010; Chappuis et al. 2014) with specific environmental requirements. Habitat cartographies require much detail to cope with the small-scale variability of littoral habitats and species distributions. This variability requires big, often expensive sampling efforts. It is paramount then, to define valid, logistically easy-to-perform and competitive sampling strategies to achieve species distribution models for large spatial areas. Additionally, littoral habitats are often exposed to many environmental pressures and disturbances (Airoldi and Beck 2007). Monitoring possible changes in habitat distribution patterns, especially in relation to anthropogenic pressures may help improve both local and international management actions and build up new bioindicators to be used in Habitat Directives. In Europe, for instance, this is critical to conservation actions for the Habitats Directive (92/43/EC) and the Marine Strategy Framework Directive (2008/56/EC) and thus this study reinforces the validity of these habitats as working units. Hence, there is an increasing need to investigate the extent of the relationships between species, habitats, and environmental pressures to obtain models that predict with the maximum accuracy and performance littoral habitat shifts in response to environmental changes (Foley et al. 2010; Snickars et al. 2014).

Recently, Cefalì et al. (2016) analyzed the relationship between littoral habitats and environmental factors from a large, high-resolution dataset (16.098 data points), identifying the environmental variables associated with the spatial distributions from a total of 29 littoral habitats. In this paper, we use this dataset, which integrates the occurrence (presence and absence) of rocky littoral habitats and that of environmental variables such as shore slope, geology, wave exposure, seawater temperature, and substrate type, (Cefalì et al. 2016; Mariani et al. 2014) to build HDMs for a long (562, 895 km) stretch of rocky coastline. Specifically, in this study, we explored the relevance of sampling design and sample size to the accuracy and performance of predictive models. Our aim was to assess the best sampling strategy to predict the distribution of coastal habitats with a resolution of tens of meters. The specific objectives of this study are: 1) to identify the best (in terms of accuracy, performance, and cost-effectiveness) sampling strategy and sample size for building predictive models for six rocky littoral habitats and to produce predictive maps of potential habitat distribution at a regional scale; 2) to assess changes in model accuracy and performance for habitats with different distributional patterns (i.e. abundant and widely distributed, abundant and locally distributed, uncommon habitats); and 3) to examine how sample size, sample design, habitat characteristics, and habitat prevalence (occurrence, frequency) may influence model accuracy and performance.

2.3.2 Material and methods

2.3.2.1 Ethics statements

The permission for the field studies and especially for the MPAs (Illes Medes, Montgrí, and S'Encalladora Marine Reserve and the National Park of Cap de Creu) was provided by the Catalonia Government. This study bases on observational data and any animal or algae, endangered or protected species were collected.

2.3.2.2 Study site

Data on littoral habitat distribution and environmental variables were collected along the whole coast of Catalonia (North-Western Mediterranean between 3º 10' 28.072" E, 42º 26' 17.619" N and 0º 30' 57.001" E, 40º 31' 26.302" N) (Figure 2.3.1). This coast shows high geomorphological heterogeneity (Agencia Catalana de l'Aigua 2005: Ballesteros et al. 2007), a very complex tectonic setting (Santanach et al. 1986), and strong differences in the geometry of the coastline from north to south. The northern coast is in fact much more irregular than the central and southern ones. The studied coast encompasses most of the Mediterranean rocky littoral habitat diversity, including natural and artificial (man-made) hard-bottom environments (Mariani et al. 2014). Sampling was done by recording the presence of all habitats from the supralittoral to the upper infralittoral level (-1 m a.m.s.l.). More details about the sampling and dataset generation for this exhaustive habitat cartography are in Mariani et al. (2014) and Cefalì et al. (2016). The original database is a layer of 16,098 points with biological (habitat presence) and environmental information (Figure 2.3.1) and covers the complete rocky coastline (562,895 km) of Catalonia (10 m resolution). Habitats are defined following the definition of the European Habitats Directive (92/43/EEC) and named by the dominant species. This exhaustive cartography of the littoral habitats is available online for the entire Catalan coast from (http://mediambient.gencat.cat/es/05_ambits_dactuacio/patrimoni_natural/sistemes_dinformacio/habitats/habitats-litorals-/).

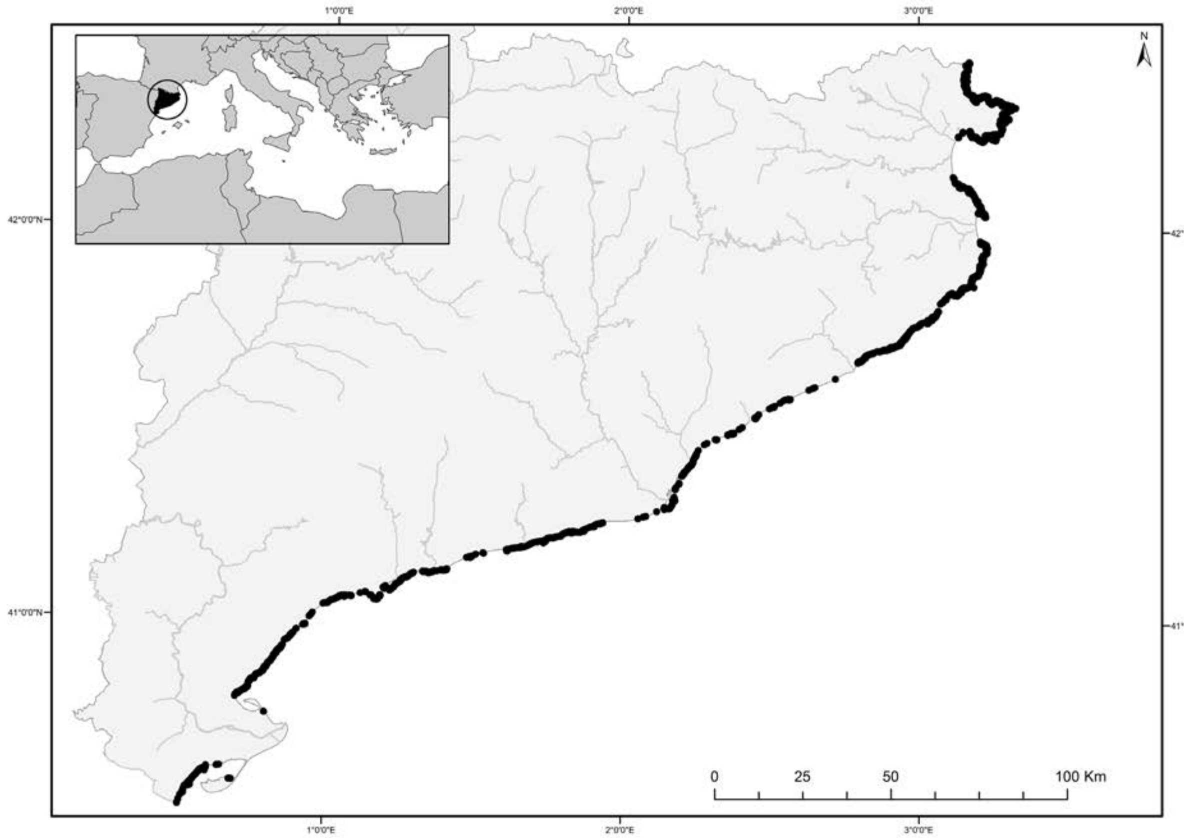

Figure 2.3.1. Map of the study site. The 16,098 points along the coast contain information on habitats presence/absence and values of environmental variables. The map was created with ArcGis 10.1 (ESRI).

2.3.2.3 Data collection

We have modeled the spatial distribution of six littoral habitats (Table 2.3.1), which were strongly and significantly influenced by environmental variables (Cefalì et al. 2016). These habitats showed different distributional patterns, although most of them had clear north distributions. The habitats of the red alga *Rissoella verruculosa* and the crusts (no rim-forming) of the coralline alga *Lithophyllum byssoides* were also abundant but nearly absent in the south (Ballesteros et al. 2014). The rim-forming *Lithophyllum byssoides* (so-called “Trottoir”, present in the northern coast) and the *Neogoniolithon brassica-florida* concretions (present in the south) were overall uncommon and localized (Ballesteros et al. 2014). Finally, the habitat of the cave-dwelling red algae *Hildenbrandia rubra* and *Phymatolithon lenormandii* showed a very scattered distribution along the coast (Ballesteros et al. 2014). The habitat dominated by the brown alga *Cystoseira mediterranea* (Ballesteros 1988; Feldmann 1937; Pinedo et al. 2013; Ballesteros et al. 2014) was overall abundant and widespread.

Table 2.3.1. List of the habitats studied. Number of occurrences and frequency (F) of selected habitats in the original database (16,098) are presented. Each habitat is named after the principal species that characterizes it. Habitat characteristics are from Ballesteros et al. (2014).

Habitat	N	F (%)	Habitat characteristics
Rissoella verruculosa	7710	47.9	Mediolittoral habitat from exposed littoral environments, preferably on plutonic rocks dominated by the red alga *R. verruculosa*.
Lithophyllum byssoides	5621	34.9	Mediolittoral habitat from environments with high desiccation levels and strong hydrodynamism dominated by the red coralline *L. byssoides*.
Lithophyllum byssoides rims ("Trottoir")	1154	7.2	Characteristic rims of the red coralline *L. byssoides* on very exposed, mediolittoral rock with low irradiance, preferably on calcareous or metamorphic rock.
Neogoniolithon brassica-florida	528	2.8	Association with the red coralline *N. brassica-florida* and/or the mollusc *D. petraeum* on moderately-to-calm mediolittoral rocks.
Hildenbrandiarubra/ Phymatolithonlenormandii	119	0.7	Mediolittoral caves and overhangs.
Cystoseira mediterranea	4576	28.4	Shallow, exposed and well-lit infralittoral rock dominated by the brown alga *C. mediterranea.*

The distribution of all habitats (Table 2.3.1) was significantly influenced by environmental variables (Cefalì et al. 2016). The variables used as predictors were (Table 2.3.2): minimum and mean wave height (WH, data from 1998 to 2008), estimated using the Downscaled Ocean Waves model (DOW) (Camus et al. 2013); mean sea surface temperature (SST; data from 2003 to 2010), obtained from satellite measurements performed by the MODIS (aqua) sensor system (http://oceancolor.gsfc.nasa.gov/), available as "Ocean Level-2" HDF data by NASA's Goddard Space Flight Center; rock slope, obtained from a Digital Elevation Model (DEM) created with a LiDAR detection method by the Institut Geològic i Cartogràfic de Catalunya (IGCC); rock geology (plutonic, sedimentary,

Table 2.3.2. List and description of the environmental variables studied. A detailed explanation on the variable source and the calculation method are provided in the text.

Environmental predictors	**UnitsorCategories**	**Source**	**Year**
Average Sea Surface Temperature	16.8º – 18.7º ºC	MODIS	2003-2013
Average Wave Height	0.02 – 0.9 m	DOW	1998-2008
Minimum Wave Height	0.01 – 0.07m	DOW	1998-2008
Slope	0º – 10.8º	DEM	2014
	10.8º – 22.8º	DEM	2014
	22.8º – 45.1º	DEM	2014
	45.1º – 68.2º	DEM	2014
	68.2º – 87.8º	DEM	2014
Geology	Metamorphic	IGCC	2000
	Mineral	IGCC	2000
	Plutonic	IGCC	2000
	Sedimentary	IGCC	2000
	Artificial	IGCC	2000
Substrate type	Natural	CARLIT	2012
	Artificial	CARLIT	2012

metamorphic and mineral), provided by the Institut Geològicic i Cartogràfic de Catalunya (IGCC, www.igc.cat); finally, the substrate type (an index of two categories identifying whether the rocky substrate was natural or man-made), obtained from the CARLIT data set (Ballesteros et al. 2007). As detailed in Cefalì et al. (2016), spatial resolution grain sizes were: 0.01º latitude and 0.008º longitude for minimum and mean wave height; a data point every 10 km for mean sea surface temperature; a raster format with pixel resolution of 2 x 2m for rock slope; a 1:50.000 map scale for rock geology and a map scale of 1:1000 for substrate type.

2.3.2.4 Sampling scenarios

Two strategies for data sampling were compared to address the first objective of the study, aggregated and interspaced. For the aggregated sampling strategy, a unique stretch of arbitrarily chosen neighboring points was selected (Figure 2.3.2). For the interspaced sampling, we selected a minimum of 5 data units (stretches of continuous points) interspaced by equivalent numbers of unselected data points (Figure 2.3.2). To assess changes in model accuracy and performance for habitats with different distributional patterns (see above), different scenarios were performed for the aggregated samplings considering different spatial distributions from north to south (Figure 2.3.2). The interspaced sampling inherently gathered data from the whole coast.

To define the best cost effective sampling size, we tested 5 different sampling sizes from the original matrix (16.098 points; 562.895 km): 10% (1.610 points; 56.290 km), 20% (3.219 points; 112.579 km), 30% (4.829 points; 168.868 km), 40% (6.439 points; 225.158 km), and 50% (8.049 points; 281.447 km) and for both, the aggregated and interspaced sampling (Figure 2.3.2). We compared the models performed with both aggregated and interspaced scenarios and different sampling sizes. Additionally, null models were fitted to randomly selected points for each sampling size (from 10% to 50%). All scenarios were applied to each of the 6 selected habitats. All spatial selections were performed in ArcGIS 10.1 (ESRI), whereas the random sampling for null models was made in R (R Development Core Team 2011).

2.3.2.5 Habitat modelling

Since our habitat data were binary, to describe the relationship between the distribution of habitats and environmental variables (Table 2.3.2) we fitted generalized linear models with binomial error distribution and the logistic link function (GLM, (McCullagh and Nelder 1989)) using the entire dataset (16.098 points). The most parsimonious model for each habitat was obtained through variable selection using the “glmulti” function in the glmulti R package (Calcagno 2013) based on AIC values. The environmental variables selected for each of the habitats are listed in Table 2.3.3. Samples, selected as described in the previous section, were used as training datasets to build the models. The remaining data were used as test data for model validation. For example, in Figure 2.3.2, the 10% portion of the coast sampled was used as training dataset and the remaining 90% was used as test dataset. The same procedure was repeated to compare the performance of all models built for each of the sampling scenarios. Model fit was assessed as the proportion (%) of explained deviance (D^2):

$$D^2 = (\text{null deviance-residual deviance})/(\text{null deviance}) \times 100$$

Altogether, we fitted 19 models for each of the 6 selected habitats. The same procedure was conducted for the null models, where each random selection (10%, 20%, 30%, 40%, and 50%)

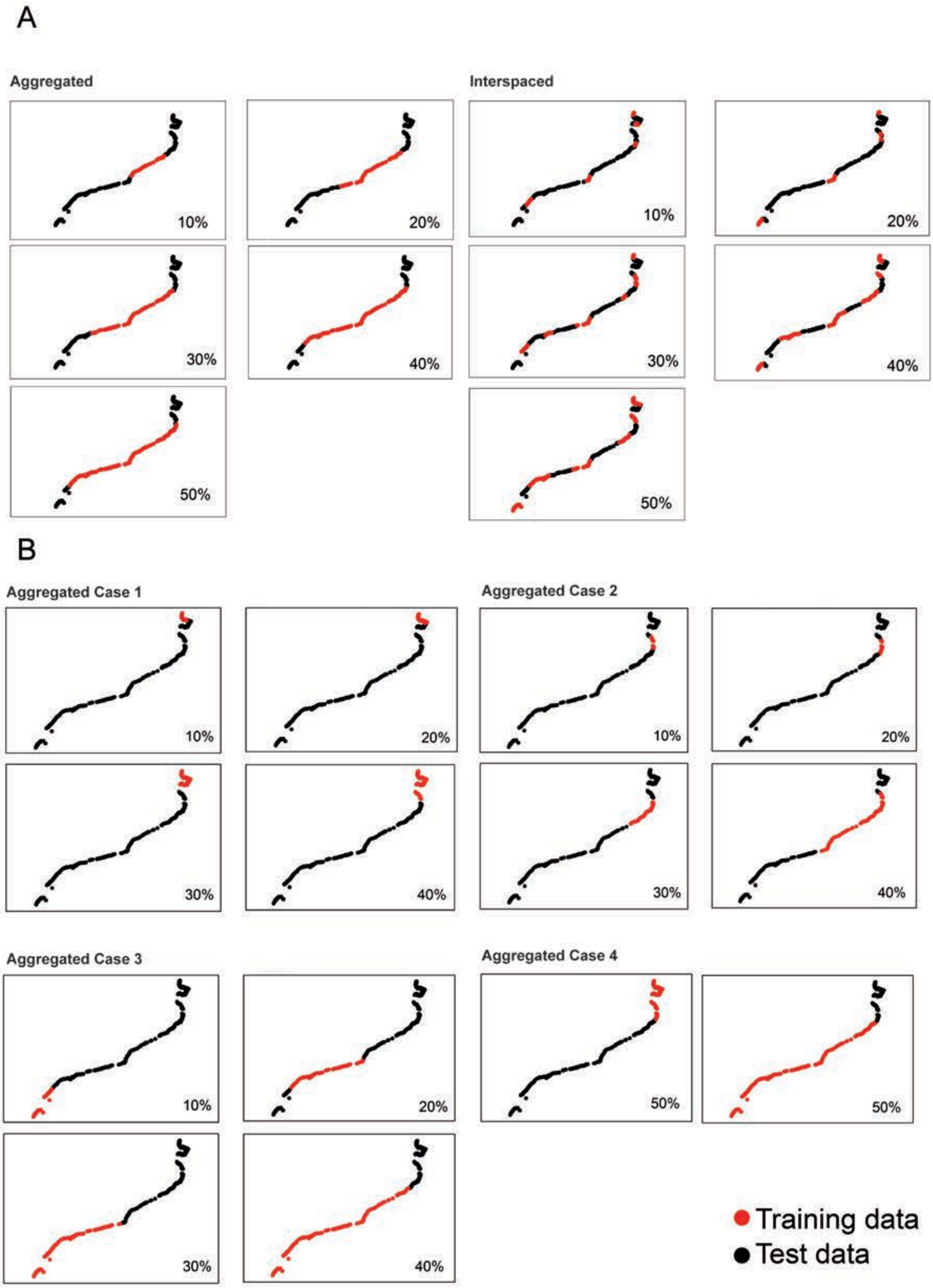

Figure 2.3.2. Sampling designs. Sampling scenarios considered in this study based on combinations of sampling size (20%, 30%, 40%, 50%) and sampling strategy: A) aggregated and interspaced; B) aggregated case 1, case 2, case 3 and case 4. Red dots represent data points selected for model training whereas black dots represent data points used for model validation. Random samples for null models are not depicted. Please notice that the percent sampling size (either red or black dots) may appear unrealistic at the scale of the figure. This is because of the extremely irregular shape of the northern portion of coast where much more data points exist.

Table 2.3.3. Principal results of models predictions. The most important environmental predictors, the best cost-effective models, the frequency (F %) of habitat in each sampling strategy and the model prediction results are shown. For more information about relationships between predictors and habitats, see Cefalì et al. 2016.

	Principal environmental predictors	**Best cost effective model strategies**	**Habitat F (%)**	**AUC**	**threshold**	**se**	**spe**
R. verruculosa	SST average WH average Slope Geology Sustratetype	20% interspaced	0.4936	0.87	0.57	0.90	0.74
L. byssoides	SST average WH average WH minimum Slope Geology	20% interspaced	0.3988	0.77	0.40	0.92	0.54
L. byssoides rims	SST average WH average WH minimum Slope Geology	10% interspaced	0.160	0.87	0.18	0.74	0.86
		20% interspaced	0.031	0.75	0.03	0.74	0.68
N. brassica-florida	SST average WH average WH minimum Slope	30% aggregated	0.01	0.90	0.21	0.94	0.87
		20% interspaced	0.399	0.77	0.4	0.92	0.54
Hildenbrandia / Phymatholiton	SST average WH average Geology	20% interspaced	0.0037	0.73	0.01	0.37	0.90
		30% interspaced	0.0033	0.81	0.01	0.65	0.79
		30% aggregated case 2	0.0161	0.82	0.02	0.74	0.81
C. mediterranea	SST average WH average WH minimum Slope Geology Substratetype	20% interspaced	0.295	0.77	0.37	0.84	0.61

was used as training data and tested on the remaining data, and repeated 10 times. For the null models, the D^2 value presented is the mean and standard deviation of the 10 fitted models. All statistical analyses were performed in R (R Development Core Team 2011).

2.3.2.6 Model validation

Model selection based on AIC identifies the “best” model among the set of candidate models, but it does not measure its performance in predicting independent data. To assess the predictive accuracy and performance of our models, we employed three statistics that compare the predictions to the observations in the test data: AUC (area under the receiver operating characteristic [ROC] curve), sensitivity (se), and specificity (spe). Because binomial GLM predictions are continuous probabilities between 0 and 1, we must specify a cut-off threshold to convert the continuous predictor to a discrete, binary predictor in order to calculate the percentage of correct classifications (Fielding and Bell 1997). AUC is a synthetic index of the model accuracy, and is independent of threshold choice, weighing omission, and commission errors equally (Fielding and Bell 1997; Pearce and Ferrier 2000; Lobo et al. 2008). We used the AUC, which ranges from 0 to 1, as first model selection, where values ≤ 0.5 indicating that the model had not predictive power and 1 meaning that we had a good model. Following Swets (1988), models providing values > 0.9 were considered “highly accurate”, those providing values in the range 0.7–0.9 were considered “useful”, and those with AUC below 0.7 are “poorly accurate”.

However, to select the best models and their discrimination power, it is necessary to calculate the percentage of predicted versus observed presences and absences. For this purpose, sensitivity and specificity were derived from a confusion matrix. Sensitivity (or true positive rate) is the portion of data points for which presence was correctly predicted, whereas specificity (true negative rate) is the portion of data points for which absence was correctly predicted (Fielding and Bell 1997). Because habitats differed in their prevalence, we decided to use habitat-specific classification thresholds that maximized the sum of sensitivity and specificity (Liu et al. 2005). Both sensitivity and specificity range from 0 when the model is completely inaccurate to 1 when either presences or absences are well predicted (Forbes 1995; Fawcett 2006). The mean AUC, sensitivity and specificity of the 10 null models were also calculated. Analysis of AUC, and sensitivity specificity were performed in R (R Development Core Team 2011), using the pROC (Robin et al. 2011) and SDMTools (Van Der Wal et al. 2014) packages respectively.

2.3.3 Results

2.3.3.1 Best model strategy

Model accuracy and performance in predicting the distribution of the six benthic littoral habitats were tested for sampling design, sample size, and habitat prevalence. Only models with high accuracy (AUC > 0.70) and performance (sensitivity and specificity > 0.60) were considered.

As expected, null models were the most accurate and had the highest performance values (high AUC, sensitivity and specificity values) (Figure 2.3.3), and provided performance standards against which to compare the other sampling strategies. Although model performance was habitat-dependent, in general it was strongly dependent on the sampling design, with the best strategy being the interspaced data collection. The prediction performed with the interspaced strategy

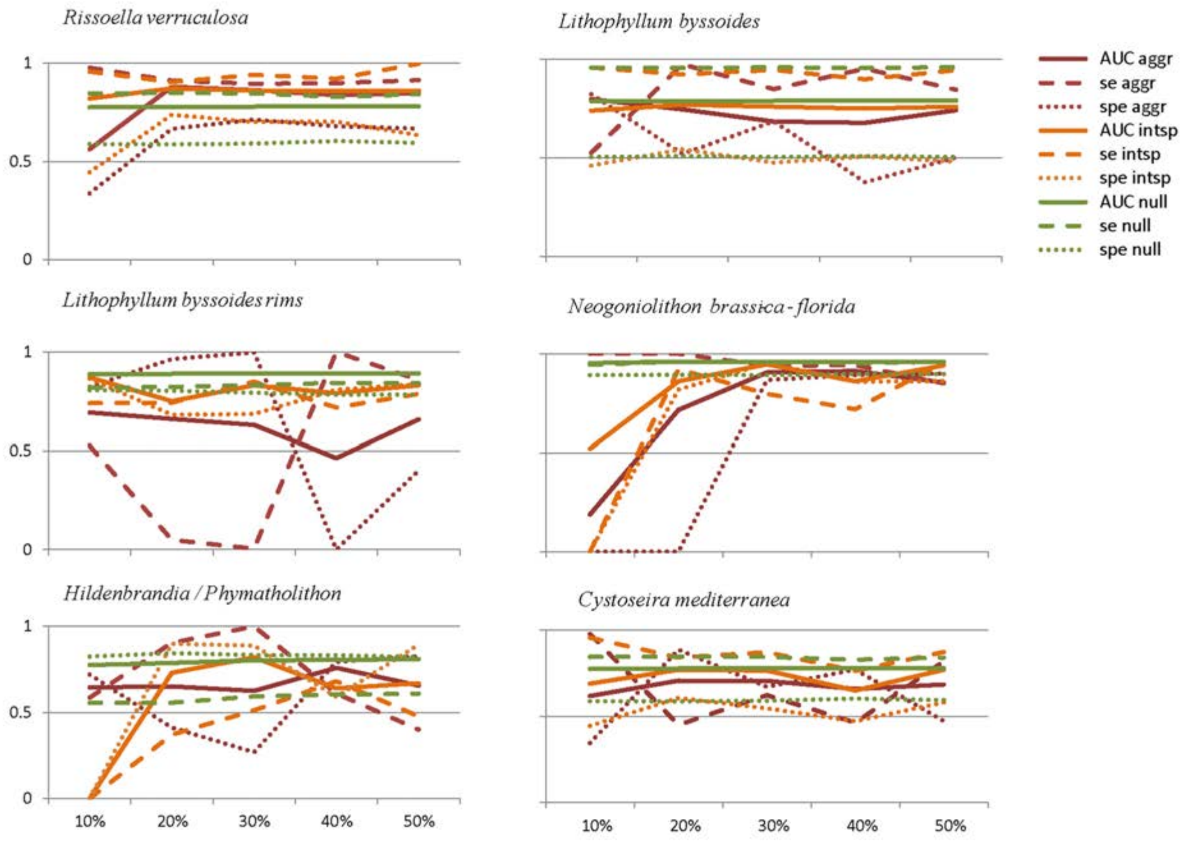

Figure 2.3.3.Statistical diagnostics of the predictive models. Statistical diagnostics of the predictive models for the aggregated strategy (aggr), the interspaced strategy (intsp) and the null (null) models. In each panel, the x-axis shows the sample size for the training data set (Figure 2.3.2). The y-axis, with values from 0 to 1, shows AUC, sensitivity (se), and specificity (spe) for each of the three sampling strategies.

obtained accuracy and performance values close to the null models for all habitats studied, regardless the habitat spatial distribution (Figure 2.3.3, Table 2.3.3, S1 File (Apéndice)).

In contrast, the results of aggregated sampling designs depended on the prevalence of the habitat considered. In fact, aggregated strategies performed well where habitat prevalence was high (i.e. *Rissoella verruculosa*, *Lithophyllum byssoides, Cystoseira mediterranea*) or with large sampling size (i.e. *Hildenbrandia/Phymatholiton* and *Neogoniolithon brassica-florida*). In contrast, habitat sample size and spatial distribution had lower effect on model accuracy and performance with the interspaced strategy. In fact, with the interspaced sampling and only 20% sampling size, we reached sufficient prevalence to obtain good model predictions for all the habitats considered. In general, with the interspaced design, increasing sample size did not substantially increase model accuracy and performance (Figure 2.3.3, Table 2.3.3, S1 File (Apéndice)). These results agreed with the null models, where increasing sample size did not always result in increased accuracy and performance prediction (Table 2.3.3, S1 File (Apéndice)).

2.3.3.2 Predictive Habitat models

Model performance was clearly habitat-dependent. Models for abundant but localized habitats (*Rissoella verruculosa* and *Lithophyllum byssoides*) were in general highly accurate and showed good performance (high specificity and sensitivity), with values comparable to those of null models (AUC > 0.80 for both habitats) (Table A and Table B in S1 File (Apéndice)). The interspaced design provided the best model predictions (Figure 2.3.4). With 20% sample size we obtained models with good accuracy and performance for *R. verruculosa* (AUC = 0.87, sensitivity = 0.90 and specificity = 0.73) and for *L. byssoides* (AUC = 0.77, sensitivity = 0.92 and specificity = 0.54). In the interspaced design, increasing habitat occurrence improved model accuracy and prediction performance independently of sample size. With the aggregated designs, accurate and good performance models were obtained only with large sample sizes, regardless of habitat occurrence (Figure 2.3.4, Table 2.3.3, Table A and Table B in S1 File (Apéndice)).

For uncommon and localized habitats (i.e. *Lithophyllum byssoides* rims and *Neogoniolithon brassica-florida* concretions), model predictions were accurate and performed well with both aggregated and interspaced strategies. However, using the aggregated strategy, a large sample size was necessary to obtain good predictions. In contrast, when the interspaced strategy was used, a sample size of only 20% was enough to get AUC values higher than 0.7 for both habitats, 0.74 sensitivity and 0.68 specificity for *L. byssoides* rims, and of 0.92 sensitivity and 0.81 specificity for *N. brassica-florida* (Figure 2.3.4, Table 2.3.3, Table C and Table D in S1 File (Apéndice)).

For the uncommon and scattered habitat of *Hildenbrandia/Phymatholiton*, few models yielded good accuracy and performance. In fact, with the interspaced design and 20% sample size, predictions were accurate (AUC of 0.73) and specific (specificity of 0.90), but the model was not sensitive enough (sensitivity of 0.37) (Table 2.3.3). Only the aggregated case 2, with 30% sample size, provided a prediction with good accuracy and performance, possibly as a result of the higher habitat frequency (Table 2.3.3 and Table E in S1 File (Apéndice)).

At the infralittoral level, for the widespread and abundant habitat of *Cystoseira mediterranea,* the 20% sample size interspaced model was again the most accurate, with AUC of 0.77 (Figure 2.3.4), but more sensitive (sensitivity of 0.84 and specificity of 0.61) (Table 2.3.3 and Table F in S1 File (Apéndice)). With the exceptions of the most widespread habitats, aggregated sampling designs led to low accuracy models, independently of sample size or habitat prevalence (aggregated case 2 with 40% sample size, aggregated with 50% and interspaced with 50% sample size), (Table F in S1 File (Apéndice)).

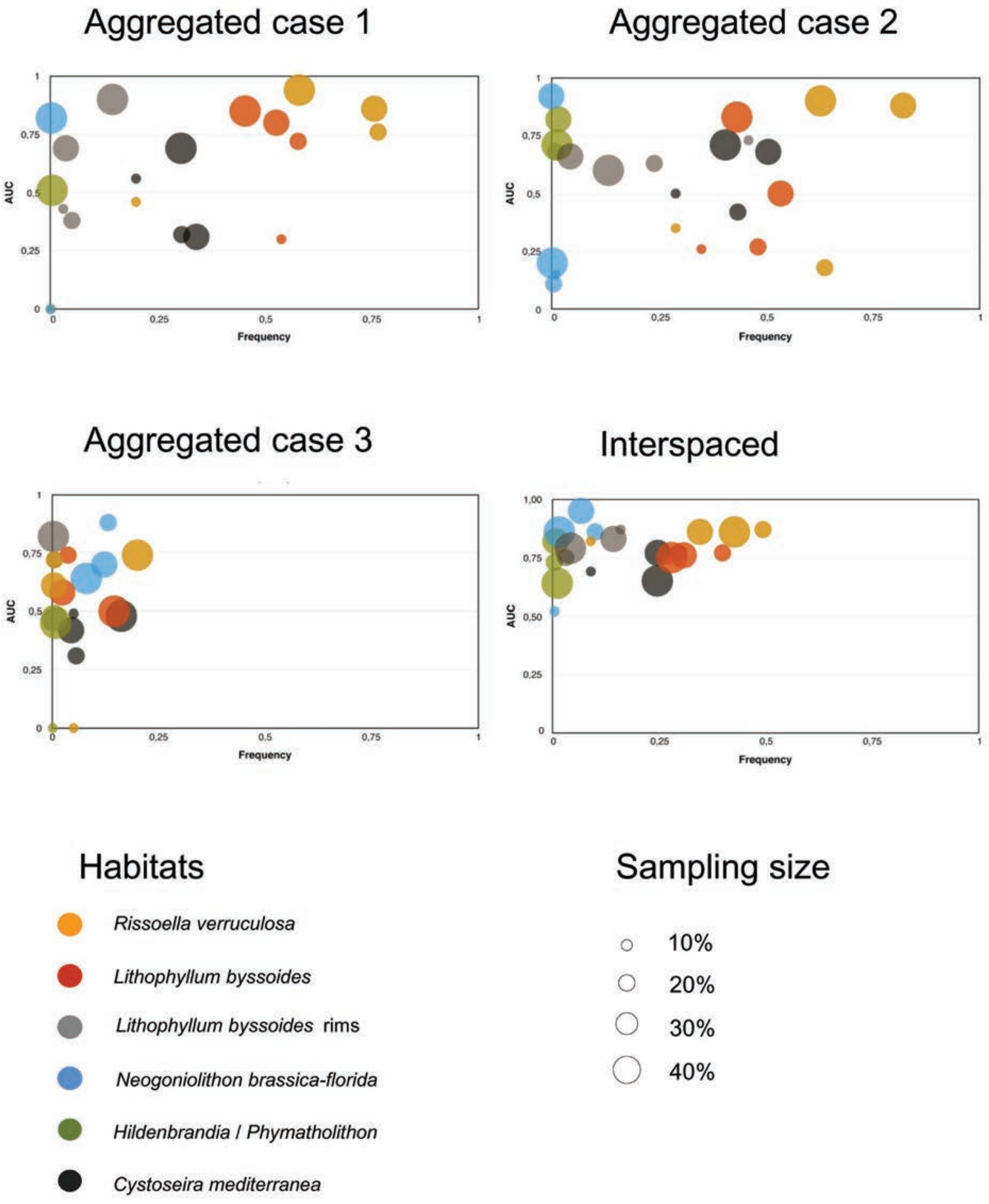

Figure 2.3.4. Habitat frequency and AUC values. Relation between habitat frequency (x-axis) and AUC values (y-axis), for sample sizes from 10 to 40% are presented.

2.3.4 Discussion

We found strong consistency (*sensu* Oreskes et al. 1994) between the distributions predicted by our models and those observed in the field for the six rocky littoral habitats studied, which ranged from uncommon to frequent and from localised to scattered along the whole coastline. Additionally, our models show that, in terms of minimum effort and highest accuracy, the interspaced is the best sampling strategy for accurate and well-performing predictions. Hirzel and Guisan (2002) established that, when habitats with different distributional patterns are considered, the regular and 'equally-stratified' sampling strategies may yield the most accurate and robust predictive models based on simulated data. Our results from field data clearly support this idea.

Technically speaking, the interspaced sampling design ensured that the training datasets adequately represented the distribution of the environmental conditions faced by the different habitats (S2 Table). Completeness, or the degree to which the habitat spatial range of environmental variables is covered by the sample, has been shown to positively affect SDMs, especially when the SDMs are used to infer distribution data from other locations (Franklin 2010; Kadmon, et al. 2016) . Here we show that the interspaced sampling strategy reduced the environmental divergence between the two data sets better than the aggregated strategy, thus improving the accuracy of predictive models.

Sampling size has also been suggested to have strong effects on SDM or HDM predictive accuracy (Hirzel and Guisan 2002; Stockwell and Peterson 2002; Reese et al. 2005; Lobo et al. 2008; Guisan et al. 2014). In our interspaced models, increasing sample size did not increase accuracy or model performance, because accuracy depends on the habitat prevalence. Thus, an interspaced sampling design also guarantees a representative coverage of habitats occurrences (prevalence) with a minimum number of observations (Araújo and Guisan 2006). In fact, with only 20% of the sample size (3.216 observations out of 16.098) we achieved accurate prediction models (high AUC) of the distribution of nearly all studied habitats for the rest of the coast (Figure 2.3.3). This means that by sampling a relatively small fraction of the littoral (20% of the coast), the ranges of environmental variables driving the presence or the absence of several habitats were well-covered. Our high-resolution sampling provided a large amount of high-quality observations. Thus, the split-sample approach with the interspaced design did not reduce the model capacity to fit the data (Guisan and Zimmermann 2000). However, when an aggregated strategy was used, both model accuracy and performance strongly depended on the habitat distribution. Either high sample size or high habitat prevalence in the training data set was needed to build accurate models (Figures 2.3.3 and 2.3.4). In fact, the aggregated strategy might prove useful when modelling focuses on a single habitat, but may require prior knowledge of where the habitat occurs.

In order to compare predicted vs. observed distributions with the interspaced strategy and a sample size of 20%, we transformed the probabilities into binary (presence/absence) maps (Figure 2.3.5). Although all the habitats considered here contain specialist species, which are strongly associated with the environmental variables considered, we obtained the best model predictions with both abundant and uncommon habitats. This supports results obtained in previous studies (Jiménez-Valverde et al. 2008; Franklin 2010). In fact, model effectiveness strongly depends on the relation between species and predictors (Jiménez-Valverde et al. 2008; Fourcade et al. 2018). The habitats of *Rissoella verruculosa* and *Lithophyllum byssoides* were more abundant in the northern coast (where they occur in 68% and 49% of sampling points, respectively, Figure 2.3.5), where environmental conditions are suitable for their optimum development (Cefalì et al. 2016). These habitats are spatially strongly associated with the explanatory variables used, so the accuracy of the resulting models was high. Performance was also high because the habitat prevalence in the training data reached nearly 50%, thus covering the suitable range and improving the capacity of the model to discern between presences and absences in the test data (Figure 2.3.4). Models tend to perform better when habitat prevalence is intermediate (McPherson et al. 2004). This effect is to be expected because logistic probabilities are computed on the values of the predictors as well as on the relative proportion of presence/absence data (Real et al. 2006; Lobo et al. 2008).

For rare habitats like the *Lithophyllum byssoides* “rims” and *Neogoniolithon brassica-florida* concretions, which are uncommon but locally aggregated (present in 7.2% and 3.3% of data points, respectively, with latitudinal interquartile ranges [IQR] of 6.3 and 6.6 km) we obtained useful predictions depending on their prevalence in training data. However, the presence of *N. brassica-florida* was over predicted (Figure 2.3.5) although the values of both sensitivity and specificity were high.

The cave habitat dominated by *Hildenbrandia* and *Phymatolithon,* was uncommon but scattered along the coast (Cefalì et al. 2016) (0.7% of data points but latitudinal IQR of 22 km). Although highly accurate (as measured by AUC), the model showed high specificity but low sensitivity, i.e. it was able to detect habitat absence but failed to detect habitat presence (low true positive rate, Figure 2.3.5). Habitats with low prevalence in the training data and absent from many coastline points may have led to misspecification of the response curve (Austin and Meyers 1996; Franklin, 2010). In fact, when one of the two events (presence or absence) is over represented with respect to the other, mean probabilities tend to be biased towards the most common event (Hosmer and Lemesbow 1980; Cramer 1999; Lobo et al. 2008; Sastre and Lobo, 2009). The model also failed to predict the presence of the habitat of *Cystoseira mediterranea* (Figure 2.3.5). Accuracy and specific performance were moderate, although the habitat was abundant along the coast. Therefore, while model outputs were useful (as measured by AUC) they only predicted well the habitat absence but they were not the best to predict its presence.

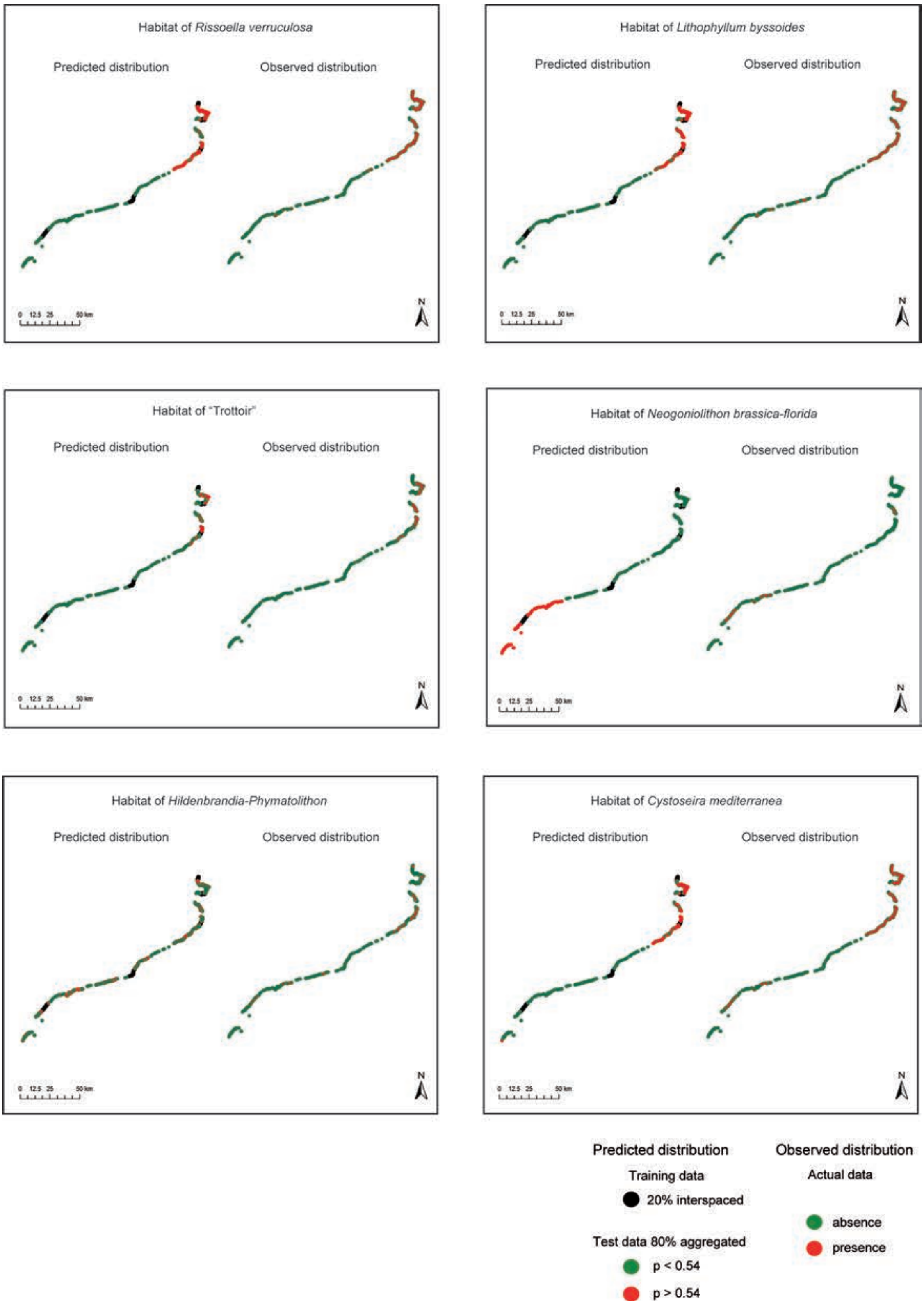

Figure 2.3.5.Predicted distribution vs. observed distribution. Predicted distribution vs. observed distribution along the Catalan coastline for the six habitats considered. The coastline on the left side of each panel represents the training data and the probability of habitat occurrence in the test data; the coastline in the right side represents the observed habitats as recorded in the Cartography of the Littoral Habitats (see Material and Methods section).

From our results, the most important factors in model prediction were the sampling strategy and the habitat prevalence. However, we observed that low environmental dispersion between training and test data is essential to improve the outputs models. Sample size influenced the models effectiveness mostly when the aggregated strategy was used.

Our data showed that using the right sample design (interspaced) we may obtain a fair representation of habitat prevalence following the environmental variability in both our training and test datasets. Spatially biased (i.e. aggregated) survey designs have been proven to cover inefficiently the real geographic pattern of species distribution within a region (Hosmer and Lemesbow 1980; Cramer 1999). Some authors have stressed that incrementing sample sizes may lead to higher model performance in predicting species distributions (Stockwell and Peterson 2002). In contrast, for uncommon habitats, either localized or scattered, increasing sample size may not necessarily increase the number of presences in the training dataset.

In brief, the interspaced sampling procedure allows reaching useful and accurate predictive models, whereas performance is dependent on the occurrence and distribution of each habitat. We also highlight that it is not only the accuracy of the model that should be considered, but performance is also crucial to get reliable ecological information on the distribution patterns. Sampling is often costly and time consuming, especially for marine environments. When the aim is to predict the geographical distributions of species and habitats, static, comparative, empirical models, rather than mechanistic models (Guisan et al., 2000; Guisan and Zimmermann 2000), may help reduce significantly the sampling effort by identifying the best sampling strategy in terms of cost and effort. This information is particularly relevant for littoral marine environments, for which SDMs have lacked so far a systematic and planned sampling strategy and model performance has never been considered. These cost effective sampling strategies can be applied to different habitats in different areas, especially those where field work and ground-truthing of habitat distributions have not been yet performed (i.e. in some unexplored areas of the southern and eastern Mediterranean Sea). Nevertheless, it is pivotal to be in possession of data about the best environmental variables to combine with habitat data, thus obtaining the best predictions across seascapes. Finally, the outcome of these models is essential to improve extensive habitat cartographies, to inform studies addressed at detecting high biodiversity areas, to identify and design protected areas and, in general, to implement management plans, especially in littoral environments.

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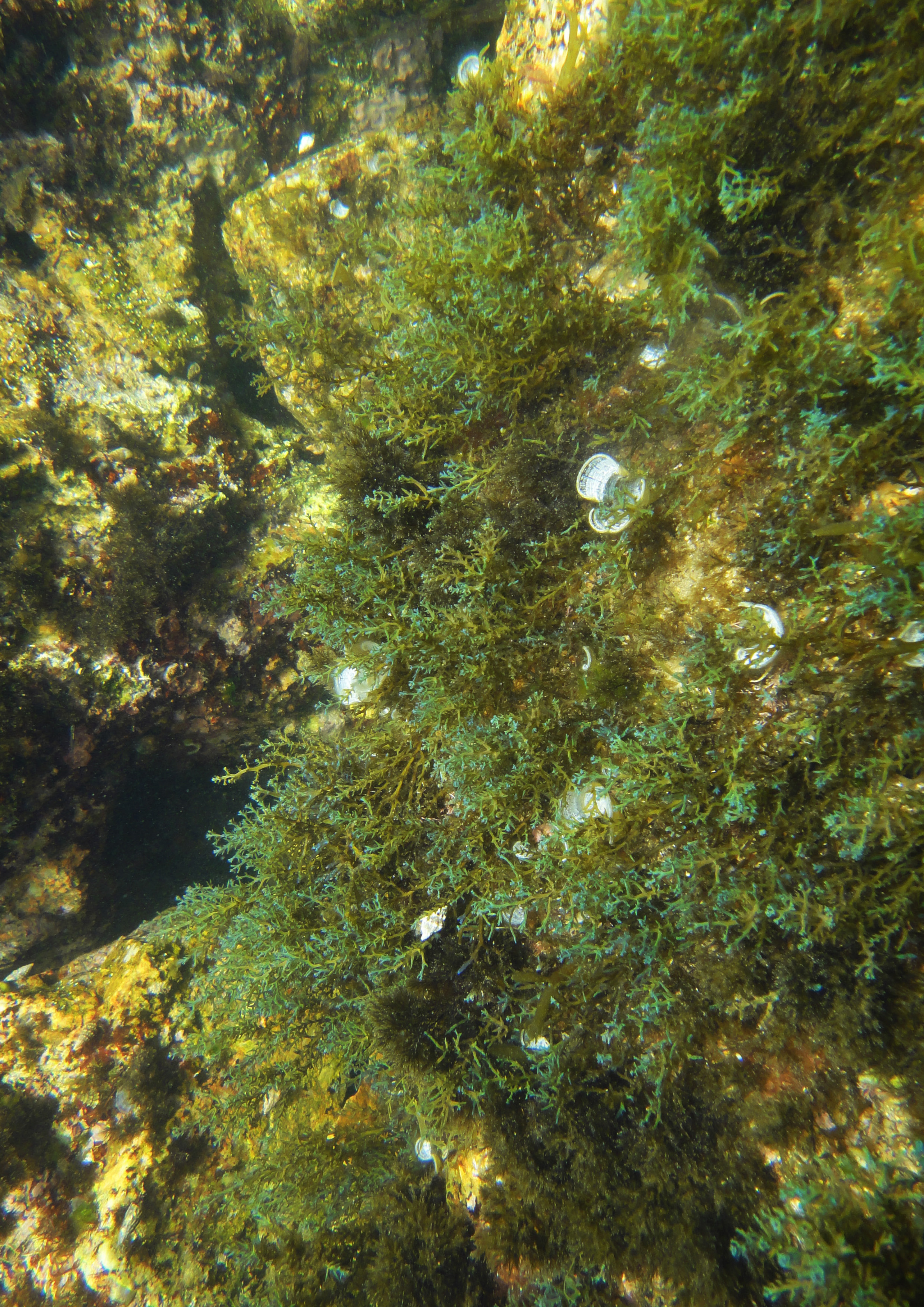

Discusión de los Resultados

Los distintos hábitats litorales se caracterizan por una composición y una riqueza de especies con una alta estabilidad espacio-temporal. Esto vale sobre todo para los hábitats más frecuentes de la costa catalana como *Chthamalus spp., Corallina elongata* mediolitoral*, C. elongata* infralitoral*, Mytilus galloprovincialis* mediolitoral*, Rissoella verruculosa, Lithophyllum byssoides, Cystoseira mediterranea* (Mariani et al. 2014).Por su redundancia, cada comunidad es homogénea a nivel regional y la variación horizontal, en este caso longitudinal, no dicta patrones de distribución y las comunidades no se diferencian, por su posición geográfica. Aunque en algunas de ellas sí que se observan ciertas diferencias internas en composición y riqueza de especies (como en los hàbitats de *Corallina elongata* mediolitoral e infralitoral y en el de *C. mediterranea*), pero estas pueden atribuirse a efectos antrópicos (Arévalo et al. 2007; Pinedo et al. 2007). Los pequeños cambios que se observan en las comunidades son el reflejo de las condiciones particulares en las cuales viven. Así pues, los hábitats litorales pueden considerarse como entidades bien definidas y utilizarse para manejo y conservación, al ser característicos de la diversidad biológica de la costa rocosa a nivel regional (Muller 1997).

De todas formas, los hábitats litorales no están distribuidos homogéneamente a nivel geográfico y presentan patrones de distribución espacial que no son aleatorios si no que están determinados por las condiciones morfológicas de la costa y los parámetros fisicoquímicos de las masas de agua. Sin embargo, el piso mediolitoral, con gran diversidad de hábitats, está muy influenciado por las variables ambientales, más incluso que la parte superior del piso infralitoral.

En el piso mediolitoral la temperatura del agua y el oleaje son las variables más influyentes en determinar el patrón regional y geográfico de la distribución de los hábitats y por lo tanto determinan en gran medida las diferencias latitudinales a nivel biológico. No sorprende que en un sistema regido en la capacidad de resistencia de las especies al estrés hídrico, la fuerza del oleaje sea un factor muy importante. Sin embargo, estas variables no son suficientes por si solas para explicar la variabilidad latitudinal sino que esta resulta de la interacción de diversos factores: la naturaleza de la roca y su pendiente, la temperatura del agua y la altura de las olas. Estos factores determinan mayoritariamente la presencia de los hábitats a nivel geográfico, su composición, su diversidad y la extensión que recubren. De hecho, si consideramos dos tramos de costa rocosa situados uno al norte y el otro al sur, estos pueden estar expuestos a la misma fuerza de oleaje, pero los hábitats que encontramos pueden ser distintos. En el norte el substrato granítico o carbonatado con elevada pendiente y agua relativamente fría favorece determinados hábitats (*Rissoella verruculosa*, *Lithophyllum byssoides*, "Trottoir"), mientras que en el sur el agua más caliente y las pendientes más suaves favorecen la presencia de otros tipos hábitats (*Neogoniolithon brassica-florida,* Gelidiales). Además, en el sur de Catalunya, la morfología de la costa está caracterizada por fondos muy pocos profundos y arenosos, y como consecuencia la erosión aumenta con el oleaje debido al levantamiento de arena, dejando espacio al desarrollo de hábitats formados por comunidades más oportunistas y con ciclos de vida muy rápidos como las algas filamentosas. Al contrario, los hábitats del piso infralitoral están influenciados mayoritariamente por el hidrodinamismo, y no presentaron un patrón regional de distribución. Los hábitats del piso infralitoral objeto de este estudio (i.e. *Cystoseira* spp., *C. elongata*, *L. incrustans,* algas fotófilas o esciófilas), se diferencian por elegir zonas con diferentes grados de exposición al oleaje, zonas calmadas o zonas expuestas, y esto no genera patrones de distribución geográfica. Sin embargo, la morfología de la costa o su naturaleza no son determinantes en las comunidades del piso infralitoral, donde los nutrientes y la exposición solar, juntos al oleaje, serían mejores descriptores.

Aun así, para algunos hábitats, las relaciones entre su presencia y las variables ambientales han resultado tan significativas que nos han permitido encontrar mucha consistencia entre la distribución espacial predicha y las observaciones realizadas en el campo. Hemos testado la rigurosidad de los modelos predictivos de distribución de hábitats en el sistema litoral a escalas espaciales grandes, con diferentes distribuciones geográficas y adaptaciones ambientales. El principal resultado ha sido resaltar la importancia de cómo y dónde muestrear para predecir la distribución de los hábitats. Si la metodología escogida es la correcta, el área de muestreo (% del área total) para obtener estimas fiables de la distribución de diversos hábitats litorales en zonas inexploradas puede llegar a ser baja. Hemos demostrado que un muestreo discontinuo a lo largo del área de estudio es el más adecuado para predecir la presencia/ausencia de diferentes hábitats puesto que se aumenta la probabilidad de capturar la máxima heterogeneidad ambiental y también la presencia y ausencia de los hábitats. De hecho las características de los hábitats y su relación con las variables utilizadas son factores imprescindibles a la hora de crear modelos de distribución. Hábitats raros o muy localizados son, en general, muy especializados (relaciones con el ambiente circundante muy significativas) y en consecuencia son los más apropiados para obtener modelos de predicción robustos y con alta verosimilitud. Al contrario, para hábitats con una distribución más amplia, y sobre todo del piso infralitoral, son más difíciles de modelar con las variables disponibles en este estudio.

Los resultados obtenidos en el segundo artículo se han reflejado en el tercero. Los hábitats que presentaron claros patrones de distribución espacial, son los que mejor resultado dan en la modelización predictiva. Las zonas elegidas necesitan englobar la máxima heterogeneidad ambiental y la relación entre los factores ambientales y el hábitat tiene que ser fuerte y determinante. Los modelos de distribución de especies (por lo menos con datos binomiales) necesitan identificar las variables que se relacionan con los distintos hábitats y las que no, para poder así calcular la probabilidad de su presencia y ausencia lo más acertado posible. Aunque estos conceptos surgieron y se discutieron anteriormente, (Guisan et al. 2007; Guisan and Zimmermann, 2000; Hirzel and Guisan 2002; Jiménez-Valverde et al. 2008; Sastre and Lobo 2009), esta es la primera vez que se han podido validar con datos reales, a gran escala espacial y considerando diferentes hábitats simultáneamente.

Por esta razón, los modelos de distribución se ajustan independientemente de si un hábitat es raro o abundante, y su bondad depende de la solidez de las relaciones entre este hábitat y las variables explicativas utilizadas como predictivas. De hecho, los hábitats del piso mediolitoral han dado respuestas más explicativas porque las variables ambientales seleccionadas, en su mayoría indirectas, estaban más relacionadas con la variabilidad del piso mediolitoral (oleaje, naturaleza de la roca, temperatura, pendiente). Al pasar del piso mediolitoral al infralitoral, y a pesar de su estrecha cercanía, las características ambientales cambian completamente y también lo hacen las variables ambientales determinantes del desarrollo de los hábitats. La luz, los nutrientes, las corrientes además de las interacciones biológicas, como pueden ser la herbivoría y la competitividad por el espacio, modulan la diversidad de hábitats. Las interacciones bilógicas son importantes también en el piso mediolitoral (Dayton 1971; Connell 1972; Underwood and Jernakoff 1984; Hawkins and Hartnoll 1985; Menconi et al. 1999; HilleRisLambers et al. 2012), pero los organismos que se distribuyen a lo largo del gradiente vertical, lo hacen no por ser mejores competidores, si no porque están representados por especies cuya fisiología les permite tolerar tales condiciones extremas (Wilson and Keddy, 1985). Al contrario, hábitats del piso infralitoral como el de *C. mediterranea*, a pesar de su elevada especificidad y vulnerabilidad (Ballesteros et al. 2007), no ofreció la respuesta esperada. A pesar de haber obtenido informaciones útiles con variables indirectamente relacionadas a su crecimiento, como la pendiente de la roca y la fuerza del oleaje, seguramente si se hubiesen utilizado variables ambientales más directamente relacionadas con su *optimum*, como por ejemplo la concentración de nutrientes o la irradiación solar, se hubieran obtenido resultados más robustos y patrones más regionales.

Bajo estos supuestos, la misma técnica puede ser utilizada para cualquier tipo de hábitat y a cualquier escala, siempre y cuando las variables bióticas y abióticas que se pretenden relacionar tengan una resolución espacial comparable. Esto hace que los modelos de distribución de hábitats sean herramientas poderosas para diseñar proyectos de gestión y conservación porque permiten detectar espacialmente zonas de elevada diversidad biológicas y temporalmente, los probables cambios en el paisaje debidos a perturbaciones naturales o antrópicas.

Sin embargo, es imprescindible un conocimiento previo tanto de la zona que se pretende identificar y caracterizar, como de los aspectos ecológicos y biológicos de los hábitats que se quieren modelar y predecir. Cuando esto no se cumpla, es muy difícil interpretar los resultados y detectar situaciones de subestimación o sobreestimación de un modelo sobre la probabilidad de incidencia de un hábitat.

Gracias a los trabajos desarrollados en esta tesis, hemos adquirido conocimientos sobre las características y singularidades de algunos de los hábitats litorales Mediterráneos, a nivel regional, y hemos podido modelar su distribución mediante técnicas utilizadas en la ecología del paisaje y la gestión ambiental. Trabajar en el sistema litoral tiene pocos impedimentos logísticos y costes bajos, mientras que las respuestas que se obtienen a nivel de diversidad, especificidad y calidad ambiental son elevadas y ventajosas. Hemos comprobado como complejidad ambiental y complejidad biológica van intrínsecamente unidas. La composición de los hábitats, en los ambientes menos antropizados y con óptimas condiciones ambientales (fuerte pendiente, roca rugosa, elevado hidrodinamismo) puede llegar a ser muy rica. Algunos de estos hábitats están formados por especies estructurales, longevas y vulnerables, lo que los hace muy sensibles a los cambios y perturbaciones ambientales.

Uno de los objetivos de realizar cartografías de hábitats, es obtener una fotografía instantánea de la diversidad de paisaje de un territorio. Esto se abordó con éxito ya hace tiempo en ambientes terrestres, pero diversas limitaciones logísticas dificultaban abarcar grandes escalas espaciales y elevadas resoluciones en el ambiente marino. En este trabajo y mediante una cartografía del sistema litoral, se determinan las relaciones biofísicas entre los componentes de este ecosistema. Se demuestra como un pequeño porcentaje de área muestreada pero correctamente distribuida es útil para predecir la distribución de los hábitats a partir de variables ambientales. Los hábitats que mejor se ajustan a estos modelos son los que más caracterizan la diversidad biológica de una costa, por sus específicas necesidades ambientales y, por la fidelidad en la distribución geográfica. Conocimientos como los obtenidos en este trabajo son indispensables para dar soporte a otros estudios que intenten establecer las áreas con elevada biodiversidad, identificar zonas sensibles de conservación y mejorar así los planes de gestión.

En nuestra opinión, nuestra contribución es pionera en el sentido que pone en relación una gran cantidad de datos biológicos con una elevada resolución de factores ambientales para abarcar una escala espacial que englobe la diversidad biológica regional. Esto ha sido posible gracias a la posibilidad de utilizar nuevas técnicas de análisis datos y modelización acoplados a conocimientos clásicos de la ecología. La posibilidad de alcanzar nuevas fuentes de datos derivadas de las nuevas tecnología (modelos ambientales, 3D, robótica submarina) junto a los conocimientos clásicos de la ecología y a muestreos reales (donde sea posible) puede abrir más posibilidades para la exploración y caracterización de nuevos espacios marinos con la finalidad de aumentar los conocimientos sobre la diversidad a grandes escalas espaciales y con el objetivo aplicado de mejorar la explotación de los recursos e implementar planes de conservación y gestión más acordes con las necesidades humanas y las características de los sistemas naturales.

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Conclusiones

- La variación horizontal (y latitudinal) no presenta patrones comunes de variación en la composición y riqueza de especies en los hábitats litorales. Esta variación depende de cada hábitat y está asociada a factores antrópicos y a su situación geográfica.

- Por su estabilidad, los hábitats litorales aquí definidos son subdivisiones consistentes en el medio litoral y unidades de trabajo útiles para su manejo en planes de gestión y conservación.

- La distribución geográfica de los hábitats no es aleatoria, sino que puede explicarse en función de diversos factores ambientales.

- Los hábitats mediolitorales muestran diferencias regionales según la temperatura del agua de mar y el tipo de sustrato. La exposición a las olas (hidrodinamismo), la pendiente y las características geológicas solo fueron relevantes para aquellos hábitats mediolitorales con necesidades ambientales específicas y no encontramos ningún patrón regional de distribución en los hábitats del piso infralitoral superior donde los factores seleccionados solo desempeñaron un papel moderado en la distribución a escala local.

- Una estrategia de muestreo intermitente o discontinua de forma regular muestreando el 20% de toda la línea de costa proporciona el mejor compromiso entre la utilidad (en términos de coste y esfuerzo de muestreo) y la precisión de los modelos predictivos.

- El rendimiento de un modelo de predicción espacial depende en gran medida de las características del hábitat y de su relación con las variables ambientales seleccionadas.

- En el sistema litoral, los modelos de distribución de hábitats han demostrado su eficacia, pero debe remarcarse que, sin un conocimiento previo sobre la ecología de cada hábitat, la interpretación de los resultados puede llevar a errores de sobre o subestimación sobre la predicción espacial.

Apéndices

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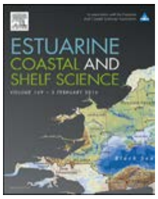

Life on the boundary: Environmental factors as drivers of habitat distribution in the littoral zone

Maria Elena Cefalì [a, *], Emma Cebrian [a, b], Eglantine Chappuis [a], Susana Pinedo [a], Marc Terradas [c], Simone Mariani [a, d], Enric Ballesteros [a]

[a] *Centre d'Estudis Avançats de Blanes-CSIC, Acc. Cala Sant Francesc 14, 17300, Blanes, Girona, Spain*
[b] *Departament de Ciències Ambientals, Facultat de Ciències, Universitat de Girona, 17071, Girona, Spain*
[c] *Departament de Ciències del Mar i Biologia Aplicada, Universitat d'Alacant, Apartat de Correus 99, 03080, Alacant, Spain*
[d] *Departament d'Ecologia, Facultat de Biologia, Universitat de Barcelona, Avgda. Diagonal 643, 08028, Barcelona, Spain*

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ABSTRACT

The boundary between land and sea, i.e. the littoral zone, is home to a large number of habitats whose distribution is primarily driven by the distance to the sea level but also by other environmental factors such as littoral's geomorphological features, wave exposure, water temperature or orientation. Here we explore the relative importance of those major environmental factors that drive the presence of littoral rocky habitats along 1100 Km of Catalonia's shoreline (Spain, NW Mediterranean) by using Geographic Information Systems and Generalized Linear Models. The distribution of mediolittoral and upper infralittoral habitats responded to different environmental factors. Mediolittoral habitats showed regional differences drawn by sea-water temperature and substrate type. Wave exposure (hydrodynamism), slope and geological features were only relevant to those mediolittoral habitats with specific environmental needs. We did not find any regional pattern of distribution in upper infralittoral habitats, and selected factors only played a moderate role in habitat distribution at the local scale. This study shows for the first time that environmental factors determining habitat distribution differ within the mediolittoral and the upper infralittoral zones and provides the basis for further development of models oriented at predicting the distribution of littoral marine habitats.

1. Introduction

The littoral zone of seas and oceans is host to a rich array of biologically diverse and socio-economically important ecosystems (Martínez et al., 2007). Littoral species and habitats may show non-random distributions along the vertical axis perpendicular to the seashore. These distributions are mainly regulated by a strong gradient of environmental conditions, which results in a pattern known as zonation. Zonation is essentially driven by seawater availability (Stephenson and Stephenson, 1949; Lewis, 1964; Dayton, 1971; Foster, 1971; Ballesteros and Romero, 1988; Chappuis et al., 2014). Nonetheless, at wide geographical scales, other distribution patterns arise as a result of the uneven distributions of environmental factors like seawater temperature (van den Hoek, 1982; Breeman, 1988), wave exposure (Levin and Paine, 1974; Denny, 1985), shore slope (Whorff et al., 1995; Benedetti-Cecchi et al., 2000), salinity (Wallentinus, 1991), rock mineral composition (Bavestrello et al., 2000; Guidetti et al., 2004), nutrient availability (Arévalo et al., 2007), or biotic interactions among organisms (Dayton, 1971; Connell, 1972; Underwood and Jernakoff, 1984; Hawkins and Hartnoll, 1985; Janke, 1990; Menconi et al., 1999; Benedetti-Cecchi, 2000; HilleRisLambers et al., 2012). Additionally, species and habitats thriving on rocky shores regularly face anthropogenic pressures that lead to significant changes in their abundance and distribution patterns (e.g. Thompson et al., 2002; Thibaut et al., 2005; Smith et al., 2007; Airoldi and Beck, 2007; Mangialajo et al., 2008; Pinedo et al., 2013; Campbell et al., 2014), especially in densely populated areas (e.g. Ballesteros et al., 2007; Pinedo et al., 2007).

Only few studies have dealt with the distributions of littoral species and habitats at regional scales, and the information available mostly arises from observations (e.g. Stephenson and Stephenson, 1950, 1954; Underwood, 1981; Ballesteros and

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* Corresponding author.
E-mail address: mcefali@ceab.csic.es (M.E. Cefalì).

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Romero, 1988; Blanchette et al., 2008; Ramos et al., 2014; Chappuis et al., 2014) and experiments (e.g. Lubchenco, 1980; Menge et al., 1999; Benedetti-Cecchi et al., 1999; Harley, 2003) at local scales. Nevertheless, an increasing number of studies aim to identify (Harley et al., 2006; Martínez et al., 2012; Bermejo et al., 2015) or predict (Huang et al., 2011; Martin et al., 2014) species and habitats distribution patterns across wide geographical areas. In all cases, sampling resolution seems to represent the limiting factor for pattern detection (Archambault and Bourget, 1996; Fraschetti et al., 2005; Tello and Stevens, 2010).

The Mediterranean is a tideless sea (Ballesteros and Romero, 1988) whose littoral zone (i.e. the boundary between terrestrial and marine domains) here is split into two different zones: the mediolittoral and the upper infralittoral (Ros et al., 1985). The mediolittoral zone harbours species and habitats that require or tolerate immersion but cannot thrive in permanent or semi-permanent immersion. The upper infralittoral zone harbours species and habitats that require permanent immersion although they can occasionally survive for short periods of time in emerged conditions. Algae, barnacles, and limpets are unevenly distributed across the mediolittoral and infralittoral zones, usually making evident belts or habitats (Chappuis et al., 2014).

The main goal of this study is to identify the environmental drivers of the distribution of mediolittoral and upper infralittoral habitats at a regional scale (>1000 Km coastline). We rely on a high-resolution GIS-based cartographic database of all littoral habitats found along 1100 Km of shoreline in Catalonia (Spain, NW Mediterranean) (Mariani et al., 2014) and physical variables (e.g., substrate type, temperature, hydrodynamism, etc.) as proxies to describe the range of abiotic conditions that define the subsequent distribution of littoral habitats at a regional scale.

Specifically, we aim to (1) identify the subset of environmental variables driving the distribution of littoral habitats at a regional scale; (2) explore the relative importance of each variable in determining the habitat presence both in the mediolittoral zone and in the upper infralittoral zone, and (3) determine the relative importance of local factors (i.e. slope, orientation, geology, substrate type, wave exposure), regional factors (i.e. seawater temperature), and anthropogenic pressures (i.e. coastal artificialization) in shaping the distribution of mediolittoral and upper infralittoral habitats.

2. Materials and methods

2.1. Study area

The coastline of Catalonia (Spain, NW Mediterranean Sea) stretches along 1100 Km and is constituted of 39% natural rocky shores, 30% artificial hard-bottom shores (breakwaters, sea walls, jetties, etc.), and 30% beaches (see Mariani et al., 2014). Data on littoral habitat distribution and environmental variables were collected along the entire coast, concretely between 3º10′28.072″E, 42º26′17.619″N and 0º30′57.001″E, 40º31′26.302″N. In this study, only hard-substrate habitats (both natural and artificial) were considered. The Catalan littoral zone (from the supralittoral down to the upper infralittoral zone at −1 m, as defined by Chappuis et al., 2014) encompasses most of the Mediterranean littoral habitat diversity (Ballesteros et al., 2007; Mariani et al., 2014), thus providing an excellent opportunity to explore the relationships between habitat and the distributions of environmental variables (see Fig. 1).

2.2. Input data

2.2.1. Habitats

A habitat is here considered following the definition of the European Habitats Directive (92/43/EEC, see Mariani et al., 2014). The habitats were recognised in the field from their macroscopic biological features (i.e. the presence of dominant species; see Mariani et al., 2014), and corresponded to littoral habitats recognised by at least one of the three main classification schemes used in the Mediterranean Sea (CORINE Biotopes, EUNIS, and LPRE lists; see Ballesteros et al., 2014).

All littoral habitats distributed from the supralittoral to the upper infralittoral (0–1 m depth) zones were digitally mapped along Catalonia using the Cat-LIT methodology (Mariani et al., 2014), at 1:1500 scale. The minimal sampling unit was 10 m (Ballesteros et al., 2014; Mariani et al., 2014), thus the rocky coast was split into 15,934 segments. The coastline polyline layer contained all data about the habitat composition for each segment. Among all identified habitats, those that were widespread [e.g. habitats from the supralittoral zone and the upper mediolittoral zone dominated by lichens (*Verrucaria amphibia*), periwinkles (*Melarhaphe neritoides*, *Echinolittorina punctata*) and barnacles (*Euraphia depressa*, *Chthamalus* spp.) and those that were present in coast segments measuring less than 10 m (see exceptions in Mariani et al., 2014) were eliminated from the data set to prevent confounding statistical results. The final dataset included data on the distribution of 29 littoral habitats, 19 in the mediolittoral zone and 10 in the upper infralittoral zone (Table 1).

2.2.2. Environmental variables

Data on environmental parameters relative to substrate features (slope, orientation, and geology), substrate type, coastal artificialization, wave exposure (hydrodynamism), and seawater temperature were obtained from different sources (Table 2).

Slope and orientation (relative to the cardinal points) of the coast were obtained from a Digital Elevation Model (DEM) created with a LiDAR detection method by the Institut Cartogràfic de Catalunya (ICC). The DEM was in raster format with pixel resolution of 2 × 2 m. Slope and orientation were calculated with a surface spatial analysis tools in ArcGis. Slope was classified into five categories and orientation into eight levels (Table 2).

The geological features of the rocky shore (i.e. the mineral composition) were provided by the Institut Geològic i Cartogràfic de Catalunya (IGCC, www.igc.cat) at 1:50.000 scale. Five different categories were considered: sedimentary (calcareous, lutite, graywake), plutonic (mostly granitic), metamorphic (schists), mineral (quartz and barite), and artificial.

Eight substrate types were recognized in situ for each coastal segment: continuous rock, partially emerged rock (without supralittoral zone), submerged rock (lacking supralittoral and mediolittoral zones), natural boulders, artificial boulders (breakwaters), concrete walls, and caves.

Information on coastal artificialization [i.e. whether a substrate was natural or artificial (man-made)] was obtained from the CARLIT data set (see Ballesteros et al., 2007) at a scale of 1:1000 (Table 2).

Data on wave exposure (hydrodynamism) were estimated using the Downscaled Ocean Waves model (DOW) (Camus et al., 2013), with a resolution of 0.01° latitude and 0.008° longitude, along the shore. The average, maximum, and minimum wave height values were calculated for a dataset of 3091 points along the coat and corresponding to a time frame of ten years (1998–2008) (Table 2).

Daily mean Sea Surface Temperature (SST) from January 2003 to December 2010 was obtained from satellite measurements performed by the MODIS (aqua) sensor system (http://oceancolor.gsfc.nasa.gov/), available as “Ocean Level-2” HDF data by NASA's Goddard Space Flight Center. We considered only high-quality temperature readings (flag values of 0 or 1), and we discarded less reliable readings (flag values of 2 or 3) (see Serrano et al., 2013).

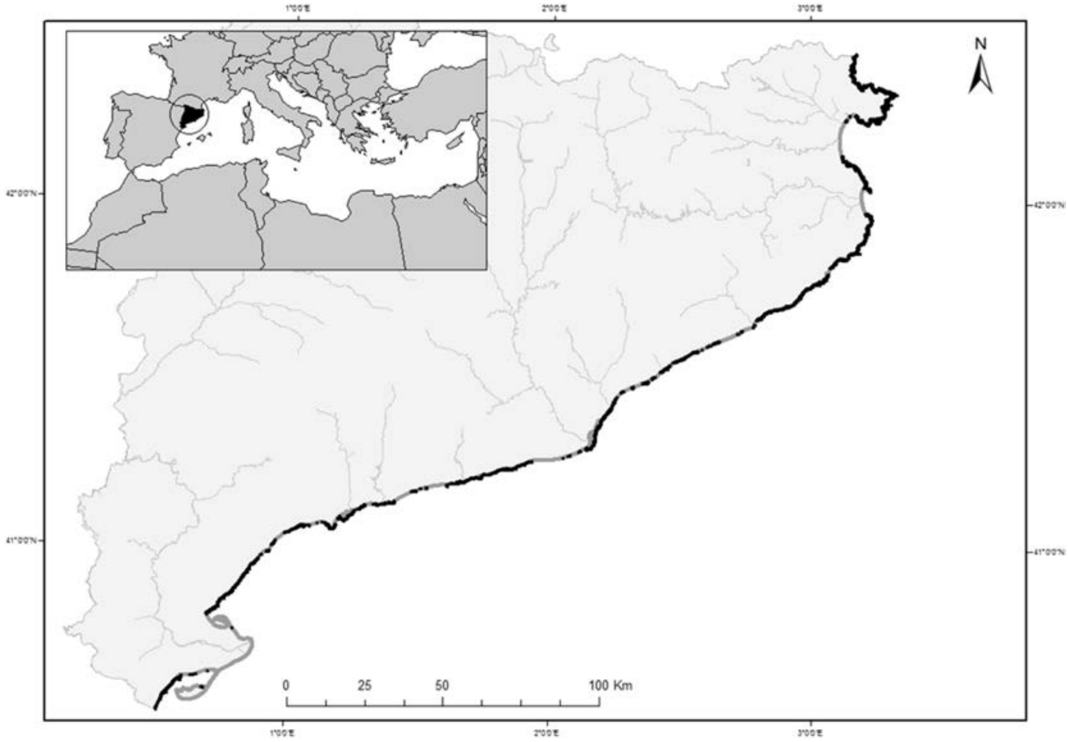

Fig. 1. Coastline of Catalonia. Rocky and other hard-bottom shores are coloured in black.

Table 1
List of the habitats studied. Each habitat is named after the principal species that characterizes it. Different frequencies of habitats occurrence for data sets of 16,098 points and 1000 points are presented.

Habitats	Code	% (16,098 points)	% (1000 points)
Mediolittoral			
Mediolittoral *Corallina elongata*	Cor elo ML	84.3	82
Mediolittoral *Mytilus galloprovincialis*	Myt gal ML	50.9	47.3
Rissoella verruculosa	Ris ver	47.9	41.3
Lithophyllum byssoides	Lit bys	34.9	30.5
Gelidium pusilum/Gelidium crinale	Gel pus/Gel cri	12.9	14.1
Ulvales	Ulv	8.0	10.2
Ralfsia verrucosa	Ral ver	7.7	9.1
"Trottoir" (*Lithophyllum byssoides* rim)	Trottoir	7.2	6.4
Polysiphonia sertularioides	Pol ser	6.4	7.3
Ceramium spp./*Osmundea* spp.	Cer Osm	4.5	6.2
Ceramium ciliatum	Cer cil	4.2	4.2
Lithophyllum cf. *vickersiae*	Lit vic	3.9	3.6
Nemoderma tingitanum	Nem tin	2.8	2.7
Neogoniolithon brassica-florida	Neo bra	2.8	3.4
Bangia atropurpurea	Ban fus	0.8	1
Hildenbrandia rubra and *Phymatolithon lenormandii*	Hil Phy	0.7	0.8
Dendropoma petraeum	Den pet	0.5	0.5
Mediolittoral *Lithophyllum incrustans*	Lit inc ML	0.4	0.4
Pyropia elongata	Pyr elo	0.3	0.3
Upper Infralittoral			
Infralittoral *Corallina elongata*	Cor elo IL	64.9	62.4
Cystoseira mediterranea	Cys med	28.4	23.5
Photophilic algae	PA	24.1	26.1
Infralittoral sciaphilic *Corallina elongata*	Cor elo SIL	4.6	4.7
Infralittoral *Lithophyllum incrustans*	Lit inc IL	2.6	2.7
Sciaphilic algae	SA	1.2	1
Infralittoral *Mytilus galloprovincialis*	Myt gal IL	1.0	1.2
Cystoseira caespitosa	Cys cae	1.0	1
Pterocladiella capillacea	Pte cap	0.2	–
Sabellaria alveolata	Sab alv	0.1	–

Over the SST study period, the average annual temperature and average annual 90th and 10th percentiles were determined for 200 points along the Catalan coastline.

2.3. Spatial data processing

The coastline layer, which included data on habitat distributions

Table 2
List and description of the environmental variables studied. A detailed explanation on the variable source and the calculation method are provided in the text.

Variables	Levels	Layer geometry	ID	Units	Source
Temperature			SST		
	Average Sea Surface Temperature	Points	SST average	ºC	MODIS
	P90 Sea Surface Temperature	Points	SST P90	ºC	MODIS
	P10 Sea Surface Temperature	Points	SST P10	ºC	MODIS
Hydrodynamism			Hydro		
	Average wave height	Points	h average	meters	DOW
	Minimum wave height	Points	h minimum	meters	DOW
	Maximum wave height	Points	h maximum	meters	DOW
Orientation			Ori		
	North	Raster	N	qualitative	DEM
	NorthEast	Raster	NE	qualitative	DEM
	East	Raster	E	qualitative	DEM
	SouthEast	Raster	SE	qualitative	DEM
	South	Raster	S	qualitative	DEM
	SouthWest	Raster	SW	qualitative	DEM
	West	Raster	W	qualitative	DEM
	NorthWest	Raster	NW	qualitative	DEM
Slope			Slope		
	0° − 10.8°	Raster	1	degrees	DEM
	10.8° − 22.8°	Raster	2	degrees	DEM
	22.8° − 45.1°	Raster	3	degrees	DEM
	45.1° − 68.2°	Raster	4	degrees	DEM
	68.16° − 87.8°	Raster	5	degrees	DEM
Geology			Geo		
	Metamorphic	Polygons		qualitative	IGCC
	Mineral	Polygons		qualitative	IGCC
	Plutonic	Polygons		qualitative	IGCC
	Sedimentary	Polygons		qualitative	IGCC
	Artificial	Polygons		qualitative	IGCC
Artificialization			Arti		
	Natural	Polyline	N	qualitative	CARLIT
	Artificial	Polyline	A	qualitative	CARLIT
Substrate type			Subs		
	Rock	Polyline	2	qualitative	CAT-LIT
	Rock without supralittoral	Polyline	3	qualitative	CAT-LIT
	Natural rocky boulders	Polyline	4	qualitative	CAT-LIT
	Harbour docks	Polyline	5	qualitative	CAT-LIT
	Breakwaters	Polyline	6	qualitative	CAT-LIT
	Caves	Polyline	8	qualitative	CAT-LIT
	Concrete walls	Polyline	9	qualitative	CAT-LIT
	Underwater rocks	Polyline	10	qualitative	CAT-LIT

and substrate type, was converted into a point layer dataset with an ArcGis data management tool, where points were spaced 10 m from each other, to match the habitat data resolution.

In order to perform the statistical analysis, all the layers carrying environmental variables were overlapped and joined into the habitat layer in ArcGis. Different spatial tools were applied to combine all layers, depending on whether the layer was a vector or a raster. Within the vector layers, a closest spatial joint analysis was performed between the habitat dataset and all the other vector layers (exposure, geology, SST, and artificialization). An extraction spatial analysis with a bilinear interpolation was performed for the slope and orientation rasters. Nevertheless, deviations of overlapping values of all environmental variables were revised and corrected when necessary. This layer-by-layer procedure and particularly the continuous validation from expert knowledge used to generate the final database allowed minimising possible generation and propagation of errors deriving from uncertainty problems (e.g. different sensors, extrapolation from unknown parameters, different interpolations etc. see Leung, 2010). Finally, a layer of 16,098 points with biological and environmental information was obtained. Data processing for all environmental variables is summarized in Fig. 2. The projection system European Datum 1950 UTM Zone 31N was used. All spatial analysis and spatial data processing were performed in ArcGIS 10.1 (©ESRI).

2.4. *Statistical analysis*

The two quantitative variables were tested for multi-collinearity based on Pearson's rank correlations ($r > 0.7$). This resulted in a subset of three uncorrelated variables: mean and minimum wave heights and mean SST. The uncorrelated quantitative variables and all the qualitative variables were included in the analysis.

The availability of seawater and environmental variables tested (e.g. wave exposure, seawater temperature, slope) may have differential effects among the habitats of the mediolittoral and the upper infralittoral zones. Consequently, they were analysed separately.

Generalized Linear Models (GLM, McCullagh and Nelder, 1989) were developed to describe the relationship between the distribution of habitats and environmental variables using the entire dataset (16,098 points). Specifically, we performed logistic regression models assuming a binomial distribution with a logistic link function. The best model for each habitat, among the candidate models, was selected with the *glmulti* function (in the glmulti R package; Calcagno, 2013), and based on AIC values. Selected models were further analysed and the significance of the variables included was tested with Likelihood Ratio Test. The significant z values of the models were used for the interpretation of the relationships between variables (habitat vs. environmental variables). The fit of the model (D^2) was calculated as the proportion (%) of explained deviance:

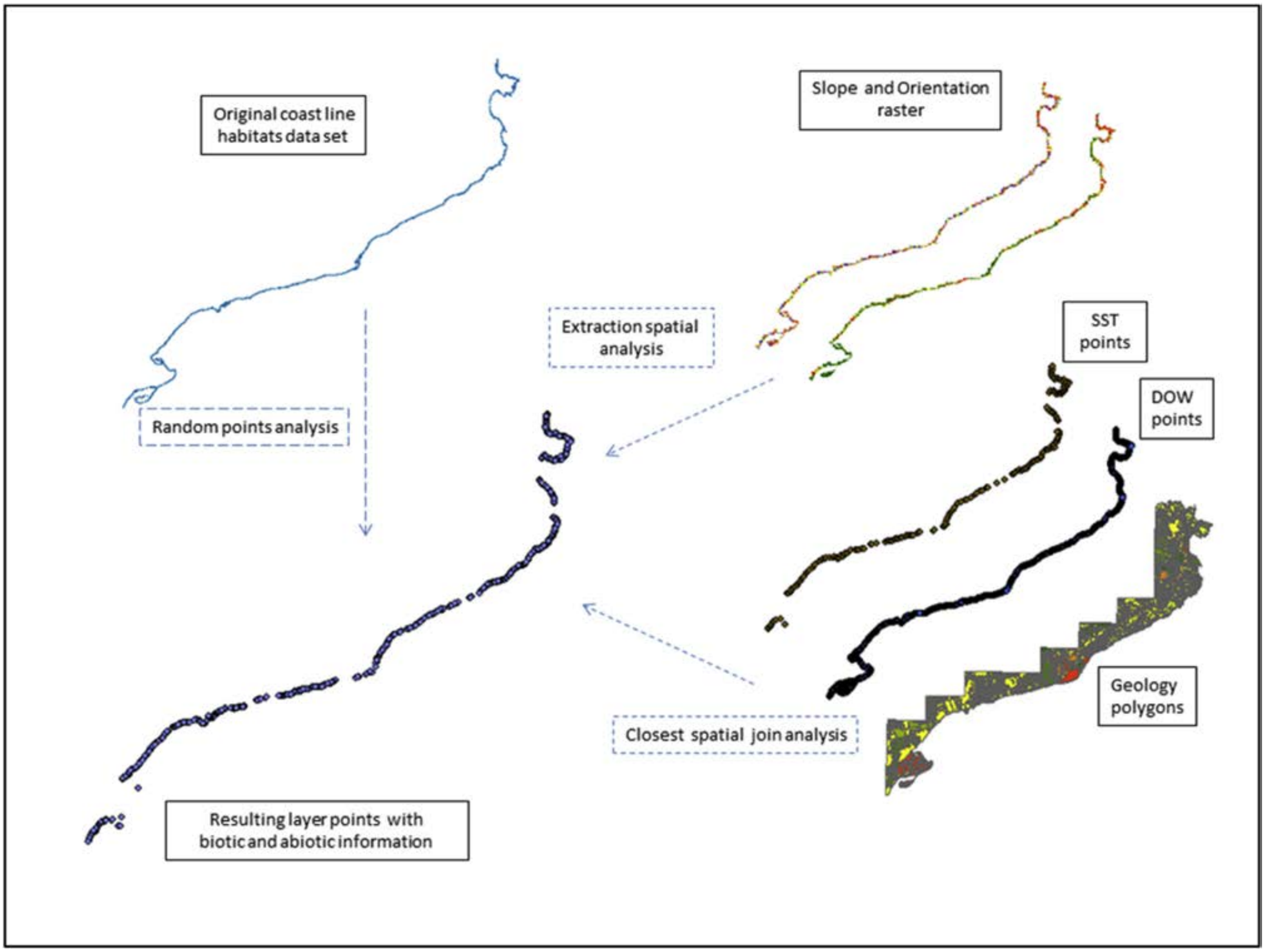

Fig. 2. Spatial data processing diagram. Rectangles of solid line correspond to layer name and geometry, rectangles with dashed line correspond to spatial processing. See the text for details.

$$D^2 = (\text{null deviance} - \text{residual deviance})/\text{null deviance}*100$$

To show the relative importance of each variable in the models, the mean and the dispersion of the significant z values (percentile 5% and 95%), both for the mediolittoral and upper infralittoral zones, were plotted in a boxplot diagram.

Presence/absence habitat data were analysed by a non-metric multi-dimensional scaling (nMDS) based on the Bray–Curtis similarity index to visualize spatial patterns. To simplify the computing effort and only for the multivariate analyses, the dataset was reduced to a lower resolution. For this aim, the layer was resampled in ArcGIS obtaining a matrix of 1000 points (one point every 120 m) along the coast. The subset was considered representative of the database, as the habitat occurrence frequencies matched between datasets (see Table 1). A bioenv analysis (in the vegan R package; Oksanen et al., 2013) was performed to investigate the relationship between habitats and environmental variables, and to identify the subset of variables showing the maximum correlation with habitats dissimilarity. Those variables with maximum correlation from the bioenv analysis were projected in the nMDS with *ordisurf* function (in the vegan R package; Oksanen et al., 2013).

All statistical tests were performed with the R software (R Development Core Team, 2011).

3. Results

The results of the logistic regression models are summarized in Tables 3 and 4. The variability explained by the environmental variable models for the mediolittoral habitats ranged between 5.2% and 72.6% (Table 3). The highest values were shown by the habitat of mediolittoral caves dominated by the encrusting red algae *Hildenbrandia rubra* and *Phymatolithon lenormandii* (72.6%), the habitat dominated by the encrusting red alga *Neogoniolithon brassica-florida* (50.0%), and the habitat dominated by the erect red alga *Rissoella verruculosa* (47.2%). The lowest values were shown by *Mytilus galloprovincialis* beds (5.2%), mediolittoral *Corallina elongata* turfs (11.5%), *Lithophyllum incrustans* barrens (14.6%), and *Nemoderma tingitanum* crusts (15.2%). D^2 overall ranged between 20 and 40% for the rest of habitats (Table 3).

The variability explained by the environmental variable models for the upper infralittoral habitats ranged between 8.8% and 70.2% (Table 4). The highest value was shown by the reefs of *Sabellaria alveolata* and the lowest by the algal beds of *Cystoseira caespitosa*. D^2 ranged between 9% and 36% for the other habitats (Table 4).

In the mediolittoral zone, "Trottoir" (*Lithophyllum byssoides* rim) and *Ralfsia verrucosa* crusts were found along steep shores with high wave exposures, and low water temperatures. While *L. byssoides* rims were best associated with calcareous substrates, *R. verrucosa* crusts were found preferentially on both granitic and

Table 3
Selected GLMs for mediolittoral habitats. D^2 is the explained deviance of the model considering all significant variables. The z value is the Wald statistic for testing the null hypothesis that the corresponding regression coefficient is zero. The z value sign shows the relation (positive or negative) between the variable and habitat presence. Only z values with significant p values (Pr(>|z|)) were considered and presented in the table.

Mediolittoral habitats	Models with z values	D^2
H. rubra and *P. lenormandii*	−3.4 sedimentary, +2.6 SST average, +2.08 h average	72.6%
N. brassica-florida	+14.98 SST average, −8.05 h minimum, +2.21 h average, +2.2 slope3	50.0%
R. verruculosa	−29.68 SST average, +22.9 plutonic, −21.9 sedimentary, −4.5 slope5, +3.2 h average, −2.8 slope 4, +2.7 Arti N	47.2%
D. petraeum	+6.8 SST average, +5.2 h average, −4.7 h minimum, +2.3 slope3, +2.2 slope2	41.5%
P. sertularioides	+21.3 SST average, −7.5 h minimum, +6 h average, +5.8 slope3, +4.3 slope4, −3.8 Arti N, +2.3 W	39.2%
Ulvales	+11.7 SST average, +9.96 Arti A, +7.3 Arti N,−5.8 h average, +5.4 plutonic, +5.9 sedimentary, −4.02 slope3, +3.4 NW, +2.1 W, −3.3 h minimum, +1.96 NE	23.2%
"Trottoir"	+22.2 sedimentary, +18.5 h average, +13.5 slope 4, +13.1 slope3, +11.4 slope5, −11.97 SST average, +10.6 h minimum, +5.5 slope2, −2.9 SE, −4.1 SW	35.3%
Gelidium spp.	+30.3 SST average, - 7.6 h minimum, +6.4 plutonic, −3.95 Arti A, +2.9 h average	33.6%
C. ciliatum	+18.4 SST average, +7.3 h average, −5.5 h minimum,+ 2.8 W, +2 SW	29.6%
R. verrucosa	+14.2 h average, +12.9 h minimum, +11.2 sedimentary, +9.4 slope5, +8.7 Arti A, +5.2 slope4, +5.05 slope3, +3.8 plutonic, −2 SST average	29.1%
L. byssoides	−25.1 SST average, +15.4 h average, +12.8 h minimum, −10.9 sedimentary, +9.9 plutonic, +2.9 mineral, 2.6 slope2, −2.3 slope5	25.0%
B. fuscopurpurea	+5.9 Arti A, +4.05 h average, −3.2 slope3, +2.7plutonic, +2.3 sedimentary	24.5%
L. cf *vickersiae*	−13.9 SST average, +6.8 sedimentary, −3.9 slope4, +2.8 Arti N, −2.7 slope5, −2.6 slope3	21.9%
P. elongata	+5.2 SST average	21.6%
Ceramium sp./*Osmundea* sp.	+16.7 SST average, +5.7 Arti A, +3.2 plutonic, +2.9 sedimentary, −2.9 h minimum, −2.4 SE	20.4%
N. tingitanum	+9.8 plutonic, −9.6 SST average, +4.6 h minimum, −3.9 slope4, −3.8 slope3, −3.3 slope2, +3.2 Arti A, +3.7 sedimentary, +2.5 Arti N	15.2%
L. incrustans ML	+5.4 slope5, +3.2 SST average, −2.04 slope2	14.4%
C. elongata ML	−19.9 SST average, −7.1 Arti A, −6.9 Arti N, −3.6 sedimentary	11.5%
M. galloprovincialis ML	+9.4 h average, +7.8 SST average, +7.6 h minimum, +3.8 slope2, +2.4 slope3, +2.02 SE	5.2%

Table 4
Selected GLMs for infralittoral habitats. D^2 is the explained deviance of the models considering all significant variables. The z value is the Wald statistic for testing the null hypothesis that the corresponding regression coefficient is zero. The z value sign shows the relation (positive or negative) between the variable and habitat presence. Only z values with significant p values (Pr(>|z|)) were considered and presented in the table.

Infralittoral habitats	Models with z values	D^2
S. alveolata	−4.7 h average, +3.3 SST average	70.2%
Sciaphilic *C. elongata*	+12.9 sedimentary, +11.2 slope5, +9.3 slope4, −9.6 SST average,+8.9 plutonic, +8.4 slope3, +7.5 h average, +3.03 h minimum, +2.3 slope2, +2.2 mineral	36.3%
P. capillacea	−2.9 SST average, +2 slope4, −2 plutonic	26.4%
C. mediterranea	+14.9 plutonic, +14.4 h average, −11.7 slope3, −11.6 SST average, −11.5 slope4, +9.6 h minimum, −7 slope5, −5.7 slope2, +4.05 Arti N, −4.2 NW, −2.8 Arti A, +2.25 S, +2 mineral	22.6%
M. galloprovincialis	+7.4 SST average, +2.5 h average, −2.5 h minimum, −2.2 slope3, −2 slope 2, +2 W	21.9%
Sciaphilic Algae	+7.2 slope4, +6.8 sedimentary, +5.9 slope5, +5.3 slope3, +5mineral, +4.8 plutonic, +3.6 slope2, +3.6 h minimum	18.4%
L. incrustans	−11.4 SST average, −7 plutonic, −3.5 h average, −3.5 h minimum, +2.4 Arti N	16.7%
Photophilic Algae	−21.7 h average, −17.8 plutonic, −13.7 h minimum, −9.7 slope3, −8.5 slope4, −6.1 slope5, +6 Arti N, −3.6 slope2, −3.5 Arti A, −3.06 sub5, −2.24 sub6, −2.4 sub9	9.7%
C. elongata	+17.4 h average, +13.8 plutonic, −13.7 Arti N, +11.97 h minimum, −9.4 sedimentary, +6.04 slope3, −5.15 Arti A, +3.6 slope2, +2.6 slope4, −2.1 NW	9.2%
C. caespitosa	−3.7 plutonic, −3.6 SST average, −2.6 slope4, −2.09 slope3	8.8%

calcareous rocks, also on artificial substrates. The habitats of *R. verruculosa* and *L. byssoides* cushions were associated with low temperatures, moderate slopes on shores highly exposed to wave action, preferably over plutonic rocks. Furthermore, *R. verruculosa* was negatively correlated with coastal artificialization. The habitats of *N. tingitanum* and *Lithophyllum* cf. *vickersiae* were also associated with low temperatures and moderate slopes on exposed shores. Moreover, *N. tingitanum* did not show any geological preference regarding the substrate. In contrast, the habitat dominated by *L.* cf. *vickersiae* seemed to prefer natural, sedimentary substrates. The mediolittoral habitat of *C. elongata*, was associated with low temperatures, but did not show any relationship with other variables. The habitat characterized by *Polysiphonia sertularioides* was present on moderately exposed, artificial, steep shores with high water temperatures. The habitat characterized by *N. brassica-florida* and *Dendropoma petraeum* was present on shores with moderate slopes and hydrodynamism, but high water temperature. These environmental conditions were associated also with the distribution of the mediolittoral mussel beds, although the total variance explained was very low. The habitats of *H. rubra* and *P. lenormandii*, *Gelidium* spp., *Ceramium ciliatum*, and *Ceramium*/*Osmundea*, which showed strong association with moderately exposed shores and high water temperatures, had no relationship with slope. Coastal steepness and high seawater temperatures were strongly related to the presence of barrens of *L. incrustans*. The habitat dominated by *Ulva* spp. and *Cladophora* spp. (as Ulvales in Table 3) showed no particular preference for any substrate, either artificial or natural, but preferred sites with high seawater temperatures with no preference for slope, wave exposure or geomorphology. The habitat dominated by *Bangia fuscopurpurea* was indifferent to steepness, and was associated with all types of exposed substrate, artificial and both plutonic and sedimentary. Finally, high water temperature was the only variable shown by the best model fit for the habitat dominated by the red alga *Pyropia elongata*. Only seven habitats showed a significant relationship (either positive or negative) with orientation. One exception was the *L. byssoides* rim, which was negatively associated with south-east and south-west orientations.

In the upper infralittoral zone, all sciaphilic habitats, those dominated either by *C. elongata* or by *Plocamium cartilagineum* and *Schottera nicaensis* (SA, see Table 1) ere mostly present on steep shores, with low seawater temperature, and strong hydrodynamism. Furthermore, these habitats appeared both on plutonic and sedimentary substrates. The upper infralittoral habitat dominated by *C. elongata*, seemed to prefer sites with moderate to high slopes and strong hydrodynamism, and its presence was abundant over granites. The habitat of *Pterocladiella capillacea* was present on steep slopes, and with low water temperatures. Low water temperatures were positively related to habitats dominated by *C. caespitosa* and *Cystoseira mediterranea*, regardless of any particular slope. In the case of the habitat of *C. mediterranea*, high wave exposure and natural granitic substrates were associated with its presence. Upper infralittoral barrens of *L. incrustans* seemed to prefer sites with low water temperature and low wave exposure. In contrast, the only upper infralittoral habitats that preferred sites with high water temperatures were *S. alveolata* reefs and mussel beds. The first one appeared on sheltered shores, the second on exposed ones. The presence of photophilic algae seemed to be unrelated to any level of slope, but it was associated with low wave exposures. There was a weak association between the orientation and the distribution of upper infralittoral habitats. Nevertheless, the presence of *C. mediterranea* stands was positively associated with south-oriented shores.

Different combinations of environmental variables were selected in the models to explain each individual habitat occurrence. Water temperature, slope, wave exposure, and geological features were selected for most of the habitats and showed the highest contributions both for mediolittoral and upper infralittoral habitats. More specifically, water temperature showed the greatest contribution to mediolittoral habitats models, followed by hydrodynamism (wave exposure), geology, slope, and artificialization (Fig. 3a). In the upper infralittoral habitats, hydrodynamism showed the greatest contribution, followed by water temperature, slope, geology and artificialization (Fig. 3b).

The bioenv analysis showed that mean water temperature and substrate type were the variables explaining the highest dissimilarity between habitats, i.e. 30% for the mediolittoral zone and 25% for the upper infralittoral zone.

The results of the nMDSs revealed how mediolittoral habitats were differently distributed across the temperature gradient (Fig. 4a). This pattern was not so evident for the upper infralittoral habitats (Fig. 4b). Regarding substrate types, natural continuous rock was positively associated with several habitats (rims and cushions of *L. byssoides*, *R. verruculosa*, *R. verrucosa*, and *C. mediterranea*). Breakwaters were associated with mediolittoral and infralittoral habitats of *C. elongata*. Caves were always associated with habitats of *H. rubra* and *P. lenormandii* in the mediolittoral zone and sciaphilic habitats in the upper infralittoral zone. The other habitats did not display any preference for a particular substrate type (Fig. 4a,b).

4. Discussion

Our study provides a general perspective on the relationship between the presence of littoral habitats and environmental factors and sheds some light on the importance of these variables as possible drivers for the distributions of both mediolittoral and infralittoral Mediterranean habitats on rocky shores. The abiotic factors analysed here have been generally disregarded in previous studies. Specifically, most research has focussed on the distribution of a single or a few habitats locally (Martin et al., 2014; Martínez et al., 2012; Bermejo et al., 2015). Our study is the first one examining the relationships between factors such as shore slope, orientation, geology, substrate type, wave exposure, seawater temperature, and coastal artificialization in shaping the distribution of a large number of habitats (19 from the mediolittoral zone and 10 from the infralittoral zone), at a very high resolution and at a regional scale. We found that the relative importance of the considered environmental variables differs among mediolittoral and upper infralittoral habitats. Despite their proximity to infralittoral habitats, mediolitoral habitats show strong dependence on limited, unpredictable water availability. However, different mediolittoral habitats rarely coexist at the same height at a same place. Abiotic factors related to seawater features (i.e seawater temperature) and coastal morphology may play important roles in determining the success of a particular habitat in a particular place (Feldmann, 1937; Ballesteros, 1992; Giaccone et al., 1993). Heterogeneity of coastal morphology (e.g. rock geology, slope, and orientation) may regulate the presence of specific mediolittoral habitats (e.g. *R. verruculosa* vs. *R. verrucosa* or *P. sertularioides*; *L. byssoides* vs. “Trottoir” or *N. brassica-florida*). Although very limited periods of aerial exposure under prevailing conditions of calm waters and high atmospheric pressures occur (Rodríguez-Prieto and Polo, 1996), the upper infralittoral zone never faces the harsh conditions of the mediolittoral zone. It also shows lower habitat diversity in the first meter. In general, the main factors that affect the presence and distribution of uppermost infralittoral habitats (always or almost always submerged) are related to nutrient availability (Ballesteros, 1992; Arevalo et al., 2007; Ballesteros et al., 2007; Pinedo et al., 2013, 2015) or light intensity (Ballesteros, 1992; Rinne et al., 2011). Seawater temperature emerges as the main factor determining habitat distribution in the mediolittoral zone, followed by other factors such as hydrodynamism, geology and slope. On the contrary, the main factor driving habitat distribution in the upper infralittoral zone is hydrodynamism, followed by seawater temperature, slope and geology. Temperature has long been recognized as a key factor governing seaweed biogeography (e.g. Stephenson, 1944; Lewis, 1964; Lüning, 1984; Pakker et al., 1995; Anderson et al., 2012; Wernberg et al., 2013) and reproduction (Lüning, 1990; Ballesteros, 1991) and since it varies with latitude (Mieszkowska et al., 2006; Martínez et al., 2012), it is often responsible for the distribution of northern/southern geographic boundaries of seaweeds (Breeman, 1988). Some mediolittoral habitats show a strong relationship with the seawater mean temperature gradient (17°–18.6°) from northern to southern Catalan waters. In fact, some habitats, such as the “Trottoir”, are circumscribed to the northernmost coast (i.e. coldest waters). Others are far more abundant in the north, such as the habitats dominated by *R. verruculosa* or *L. byssoides*. Other habitats, like the barrens of *N. brassica-florida*, are exclusively present in the south (i.e. warmer waters). Temperature variation in the study area is due to the effects of the warm-water Balearic current in the southern coast and the colder, deep-water generated current from the Lions Golf in the northern coast (Font et al., 1988). However, although quite reduced (less than two degrees °C), temperature variation in the studied area is a relevant factor driving mediolittoral benthic habitat distributions. On the contrary, while water temperature plays an important role, upper infralittoral habitats do not show latitudinal differences in their distributions. For example, while *S. alveolata* reefs are only present in the southern coast, the rest of upper

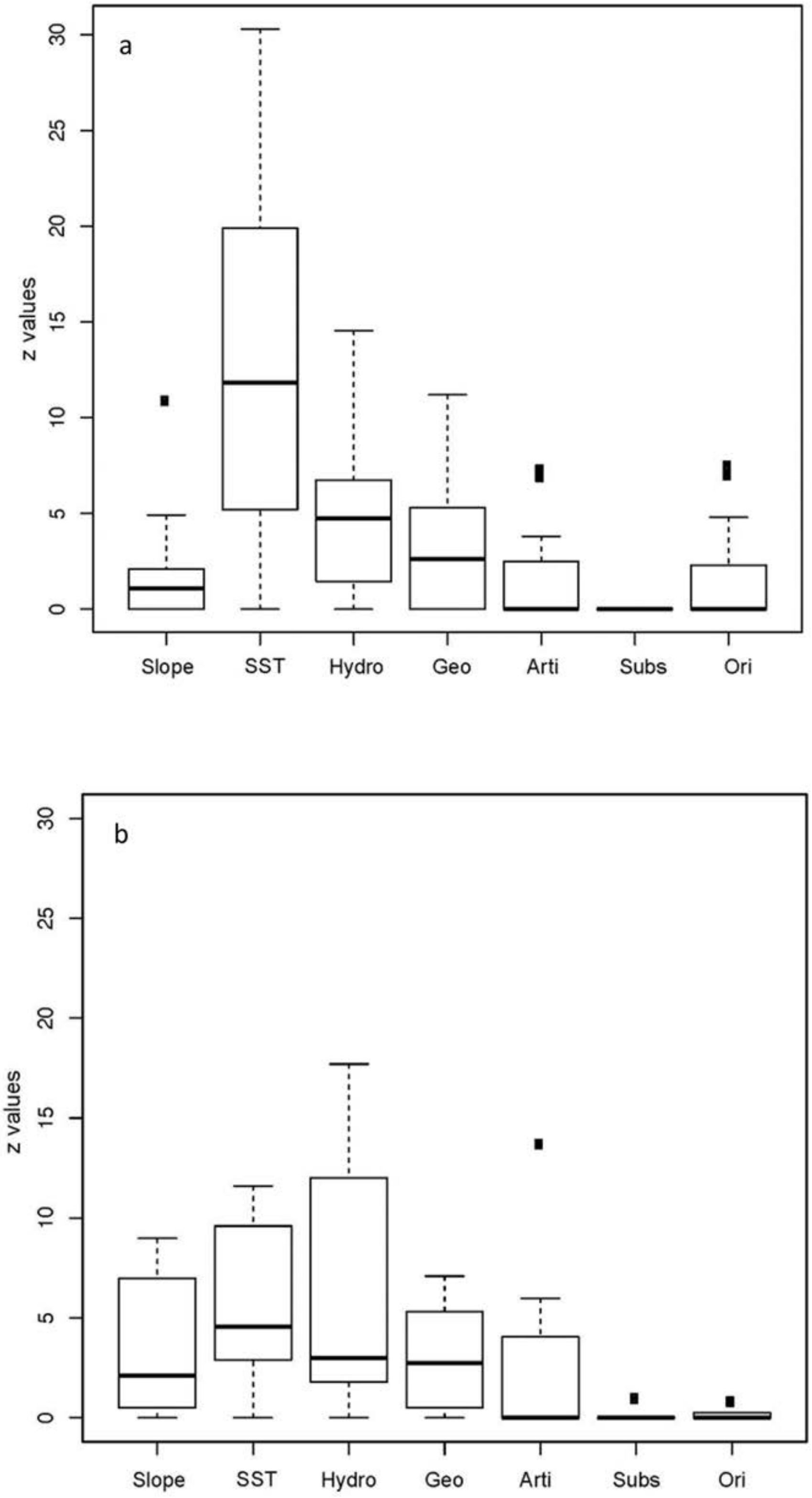

Fig. 3. Boxplots of significant GLMs z values for a) mediolittoral zone models, b) upper infralittoral zone models. The mean, the percentiles (5% and 95%) and the outliers of z values are shown. See Table 2 for codes explanation.

infralittoral habitats do not show any latitudinal difference at the geographical scale considered.

Hydrodynamism exerts direct and indirect effects on benthic organisms (Denny, 2006) and it plays a central role in coastal environments (Nishihara and Terada, 2010; Rattray et al., 2015). Hydrodynamism, namely wave exposure, is especially important in heterogeneous areas where it plays a key role in determining the distribution of macroalgae (Snickars et al., 2014). The role of wave

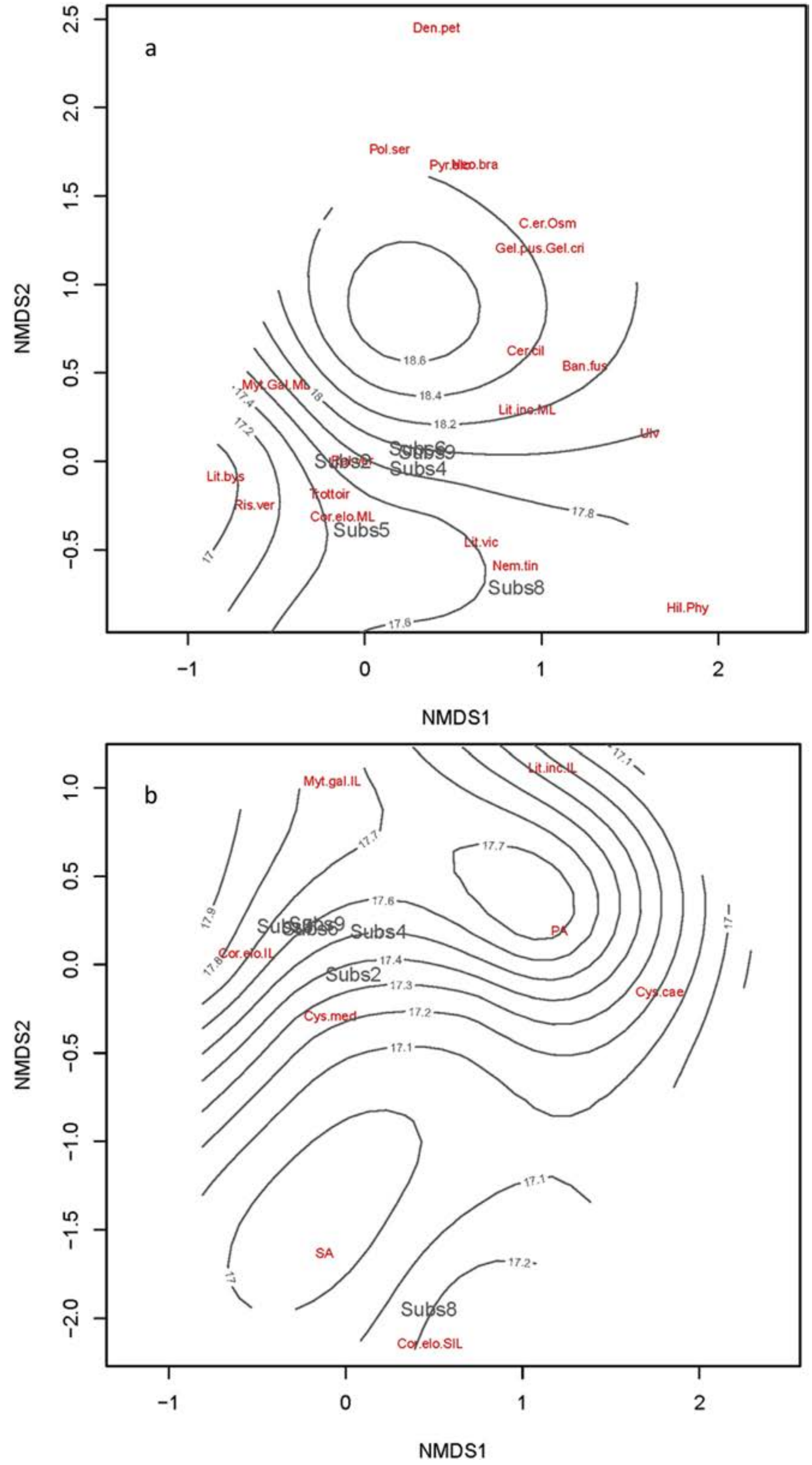

Fig. 4. a) nMDS of the mediolittoral habitats. b) nMDS of the upper infralittoral habitats. SST mean (isothermal lines) and substrate type are fitted in both plots. See Tables 1 and 2 for abbreviations. Each habitat is represented by its centroid. The analysis has been performed with a database of 1000 points (see text).

exposure in shaping habitat distributions in the mediolittoral zone is crucial for reducing hydric stress due to prolonged emersion times (Chappuis et al., 2014). Increased water movement enhances nutrient availability to seaweeds (Ballesteros, 1989). Many macroalgae-dominated habitats (i.e. “Trottoir”, *L. byssoides*, *R. verruculosa*, *R. verrucosa*) develop better in high exposed areas. Nevertheless, very strong hydrodynamism can generate a mechanical stress which only a few, morphologically-adapted species, can withstand, causing breakage or even death in adult macrophytes (Viejo et al., 1995; Diez et al., 2003). In areas with high levels of erosion by sand scour, habitats are usually dominated by turf algae (such as *P. sertularioides*, *Gelidium* spp.), which are well-known to be adapted to sand scour (Airoldi, 1998). Habitats dominated by Ulvales are mainly present in sheltered areas also subjected to sand scour. At the infralittoral zone, habitats dominated by either *C. mediterranea*, sciaphilic algae, *C. elongata* or *M. galloprovincialis*, require high water renewal (Bellan-Santini, 1965; Ballesteros, 1992) and reach their optimum development on exposed coasts (although *M. galloprovincialis* can also grow in sheltered areas like bays or lagoons where it is cultivated). Other habitats show an opposite trend; this is the case of photophilic algal assemblages, *S. alveolata* reefs and infralittoral *L. incrustans* barrens, which are far more frequent in sheltered areas. Slope and orientation are local factors also associated with seaweed distribution on the shore (see Diez et al., 2003). However, we found only a minor effect of rocky slope on the distribution of habitats both in the mediolittoral and in the upper infralittoral zone. Two exceptions are the "Trottoir", often accompanied by the habitat dominated by *R. verrucosa*, which are very characteristic of steep cliffs with reduced light levels (Mannino, 2003; Boudouresque, 2004). Rock steepness also benefits the presence of habitats formed by sciaphilic algae in the upper infralittoral zone. Although orientation has been documented to have an influence on terrestrial and rocky shore habitats and species (Boyce et al., 2005; Harley, 2008) we did not find any particular effect on the habitats studied here, both for the mediolittoral and the upper infralittoral zones. Another factor with a secondary but significant relation with habitat distribution in this study is geology, i.e. rock mineral content (Harris et al., 2013). Algae are unable to absorb nutrients or any other chemical component directly from the rocky substrate. However, Feldmann (1937) and Giaccone et al. (1993) have observed a close relationship between the presence of some seaweeds and rock types. For instance, "Trottoir" has already been reported to better develop over calcareous substrates (Mannino, 2003) and *R. verruculosa* over granites or schists (Feldmann, 1937). Additionally, in the mediolittoral zone, we have observed widespread, massive presence of the habitat dominated by *L.* cf. *vickersiae* on graywake rocks. Guidetti et al. (2004) report a preference of photophilic algae for granitic rocks and of sciaphilic algae for limestones, although we did not find this pattern in the upper infralittoral zone. Affinities between some habitats and the geology seem to be related to the texture and hardness of the different minerals, which has an effect on the recruitment and survival of certain algae (see Bourget et al., 1994). There is a clear difference between habitats usually growing over natural rock, and those present on man-made structures (e.g. harbour docks, breakwaters) (Connell and Glassby, 1999; Smith and Rule, 2002; Bulleri and Chapman, 2004; Ballesteros et al., 2007). Man-made structures usually do not harbour habitats with highly specific environmental requirements (e.g. *L. byssoides*, *R. verruculosa*, "Trottoir", *N. brassica-florida*, *C. mediterranea*), and are usually colonized by pioneering (Ulvales, *P. sertularioides*, *Gelidium* spp., *M. galloprovincialis*) or stress-resistant species (*C. elongata*). Normally, artificial structures are abundant along coasts with high human pressures, where only tolerant habitats and species thrive (Ballesteros et al., 2007). Furthermore, pioneering species show a high propagule production and dispersal (Ceccherelli and Rossi, 1984; Bacchiocchi and Airoldi, 2003), thus allowing a more rapid colonization of new structures (Airoldi, 2000). Studying species-environment relationships is crucial to elucidate habitat pattern distributions. Littoral zones are ecologically important areas for a variety of reasons and detailed scientific information is needed to develop and implement appropriate measures of habitat protection and conservation. Knowledge on the biophysical components of these systems is still poor (see Rattray et al., 2015) and this study represents an important contribution towards a better understanding of the habitat-environment relationships. These relationships are at the core of predictive geographical modelling in ecology (Guisan and Zimmermann, 2000) and predictive species distribution models currently represent an essential tool for biodiversity conservation and management (Côté and Reynolds, 2002).

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RESEARCH ARTICLE

The optimal sampling design for littoral habitats modelling: A case study from the north-western Mediterranean

Maria Elena Cefalì[1,2]*, Enric Ballesteros[1], Joan Lluís Riera[3], Eglantine Chappuis[1], Marc Terradas[4], Simone Mariani[1,3], Emma Cebrian[1,5]

1 Centre d'Estudis Avançats de Blanes-CSIC, Acc. Cala Sant Francesc, Girona, Spain, **2** Estación de Investigación Jaume Ferrer, Instituto Español de Oceanografía (IEO), Mahón, Spain, **3** Departament de Biologia Evolutiva, Ecologia i CiènciesAmbientals, Facultat de Biologia, Universitat de Barcelona, Gran Via de les Corts Catalanes, Spain, **4** Departament de Ciències del Mar i Biologia Aplicada, Universitat d'Alacant, Apartat de Correus, Spain, **5** Institut d'Ecologia Aquàtica, Universitat de Girona, Plaça Sant Domènec, Spain

* malen.cefali@ieo.es

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Data Availability Statement: The data collected for this study is freely available from the Catalonia Government website at: http://mediambient.gencat.cat/es/05_ambits_dactuacio/patrimoni_natural/sistemes_dinformacio/habitats/habitats-litorals-/. Additionally, the environmental data collected for the present study is available within the Supporting Information files.

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Abstract

Species distribution models (SDMs) have been used to predict potential distributions of habitats and to model the effects of environmental changes. Despite their usefulness, currently there is no standardized sampling strategy that provides suitable and sufficiently representative predictive models for littoral marine benthic habitats. Here we aim to establish the best performing and most cost-effective sample design to predict the distribution of littoral habitats in unexplored areas. We also study how environmental variability, sample size, and habitat prevalence may influence the accuracy and performance of spatial predictions. For first time, a large database of littoral habitats (16,098 points over 562,895 km of coastline) is used to build up, evaluate, and validate logistic predictive models according to a variety of sampling strategies. A regularly interspaced strategy with a sample of 20% of the coastline provided the best compromise between usefulness (in terms of sampling cost and effort) and accuracy. However, model performance was strongly depen upon habitat characteristics. The proposed sampling strategy may help to predict the presence or absence of target species or habitats thus improving extensive cartographies, detect high biodiversity areas, and, lastly, develop (the best) environmental management plans, especially in littoral environments.

Introduction

The prediction of species and habitat distributions through numerical models still represents one of the most challenging areas of work in ecology [1], especially in light of the current scenario of a rapidly changing environment. Species distribution models (SDMs) and habitat distribution models (HDMs) find many applications in ecology [2, 3], including conservation and management [4], and, in conjunction with rich, high coverage data sets and simulation experiments, may help in designing efficient sampling strategies for habitat suitability modelling [5] for both terrestrial and marine areas.

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SDMs and HDMs are statistical models of the relationship between species and habitat distributions, and those environmental variables that potentially drive such distributions [2]. Mechanistic, empirical (or correlative), and theoretical models can be used, depending on the research objectives and the variables available [2]. Empirical models are most frequently used, especially those coupling the distributions of species and environmental variables [6]. Recent access to data from remote sensing techniques and geomorphological cartographies, as well as rapid advances in geographical information systems (GIS) have provided large sets of species and environmental data to build empirical models [1]. Empirical models relate known occurrences (presence and absence) of species or habitats to the environmental variables that best reflect the species' or habitats' environmental requirements. Once the empirical model is fitted, the output is used to predict the most suitable or unsuitable areas for species and habitats [7].

The degree to which causal relationships between species/habitat distributions and the predictor variables are unveiled depends on the adequacy of the predictors used for model building and on the quality of species or habitats occurrence data [8, 9]. Sample size, sample design, species and habitat characteristics, environmental stratification, and species prevalence are also important for the success of predictive spatial distribution models [2, 6, 8, 10, 11]. The paucity of fine environmental and species occurrence data for marine ecosystems may explain why sea-focused SDMs and HDMs are fewer compared to terrestrial ones [12]. However, many efforts have been made in recent years to collect data on environmental variables and species distributions (e.g. BIO-ORACLE [13], OBIS, www.iobis.org), thus allowing the application of SDMs to marine systems. Most models aim to predict the potential distribution of one or a few benthic species or habitats of special conservation interest [14–19], endangered fish species that are commercially exploited [20–22], or the effects of global change on a single species or habitat [23–27]. Nevertheless, most researchers have not yet analyzed the importance of sample size, sampling design, or species occurrences to build up accurate SDMs for marine environments. Those parameters are crucial for achieving the best accuracy (as measured by AUC, area under the receiver operating characteristic [ROC] curve) and performance (measured as sensitivity and specificity) in predictive SDMs [5].

The littoral zone harbors a rich array of habitats [28–30] with specific environmental requirements. Habitat cartographies require much detail to cope with the small-scale variability of littoral habitats and species distributions. This variability requires big, often expensive sampling efforts. It is paramount then, to define valid, logistically easy-to-perform and competitive sampling strategies to achieve species distribution models for large spatial areas. Additionally, littoral habitats are often exposed to many environmental pressures and disturbances [31]. Monitoring possible changes in habitat distribution patterns, especially in relation to anthropogenic pressures may help improve both local and international management actions and build up new bioindicators to be used in Habitat Directives. In Europe, for instance, this is critical to conservation actions for the Habitats Directive (92/43/EC) and the Marine Strategy Framework Directive (2008/56/EC) and thus this study reinforces the validity of these habitats as working units. Hence, there is an increasing need to investigate the extent of the relationships between species, habitats, and environmental pressures to obtain models that predict with the maximum accuracy and performance littoral habitat shifts in response to environmental changes [32, 33].

Recently, Cefalì et al. [34] analyzed the relationship between littoral habitats and environmental factors from a large, high-resolution dataset (16,098 data points), identifying the environmental variables associated with the spatial distributions from a total of 29 littoral habitats. In this paper, we use this dataset, which integrates the occurrence (presence and absence) of rocky littoral habitats and that of environmental variables such as shore slope, geology, wave exposure, seawater temperature, and substrate type, [34, 35] to build HDMs for a long

(562,895 km) stretch of rocky coastline. Specifically, in this study, we explored the relevance of sampling design and sample size to the accuracy and performance of predictive models. Our aim was to assess the best sampling strategy to predict the distribution of coastal habitats with a resolution of tens of meters. The specific objectives of this study are: 1) to identify the best (in terms of accuracy, performance, and cost-effectiveness) sampling strategy and sample size for building predictive models for six rocky littoral habitats and to produce predictive maps of potential habitat distribution at a regional scale; 2) to assess changes in model accuracy and performance for habitats with different distributional patterns (i.e. abundant and widely distributed, abundant and locally distributed, uncommon habitats); and 3) to examine how sample size, sample design, habitat characteristics, and habitat prevalence (occurrence, frequency) may influence model accuracy and performance.

Material and methods

Ethics statements

The permission for the field studies and especially for the MPAs (Illes Medes, Montgrí, and S'Encalladora Marine Reserve and the National Park of Cap de Creu) was provided by the Catalonia Government. This study is based on observational data and no animal or algae, endangered or protected species were collected.

Study site

Data on littoral habitat distribution and environmental variables were collected along the whole coast of Catalonia (North-Western Mediterranean between 3º 10' 28.072" E, 42º 26' 17.619" N and 0º 30' 57.001" E, 40º 31' 26.302" N) (Fig 1). This coast shows high geomorphological heterogeneity [36, 37], a very complex tectonic setting [38], and strong differences in the geometry of the coastline from north to south. The northern coast is in fact much more irregular than the central and southern ones. The studied coast encompasses most of the Mediterranean rocky littoral habitat diversity, including natural and artificial (man-made) hard-bottom environments [35]. Sampling was done by recording the presence of all habitats from the supralittoral to the upper infralittoral level (-1 m a.m.s.l.). More details about the sampling and dataset generation for this exhaustive habitat cartography are in Mariani et al. [35] and Cefalì et al. [34]. The original database is a layer of 16,098 points with biological (habitat presence) and environmental information (Fig 1) and covers the complete rocky coastline (562,895 km) of Catalonia (10 m resolution). Habitats are defined following the definition of the European Habitats Directive (92/43/EEC) and named by the dominant species. This exhaustive cartography of the littoral habitats is available online for the entire Catalan coast from (http://mediambient.gencat.cat/es/05_ambits_dactuacio/patrimoni_natural/sistemes_dinformacio/habitats/habitats-litorals-/).

Data collection

We have modeled the spatial distribution of six littoral habitats (Table 1), which were strongly and significantly influenced by environmental variables [34]. These habitats showed different distributional patterns, although most of them had clear north distributions. The habitats of the red alga *Rissoella verruculosa* and the crusts (no rim-forming) of the coralline alga *Lithophyllum byssoides* were also abundant but nearly absent in the south [39]. The rim-forming *Lithophyllum byssoides* (so-called "Trottoir", present in the northern coast) and the *Neogoniolithon brassica-florida* concretions (present in the south) were overall uncommon and localized [39]. Finally, the habitat of the cave-dwelling red algae *Hildenbrandia rubra* and *Phymatolithon*

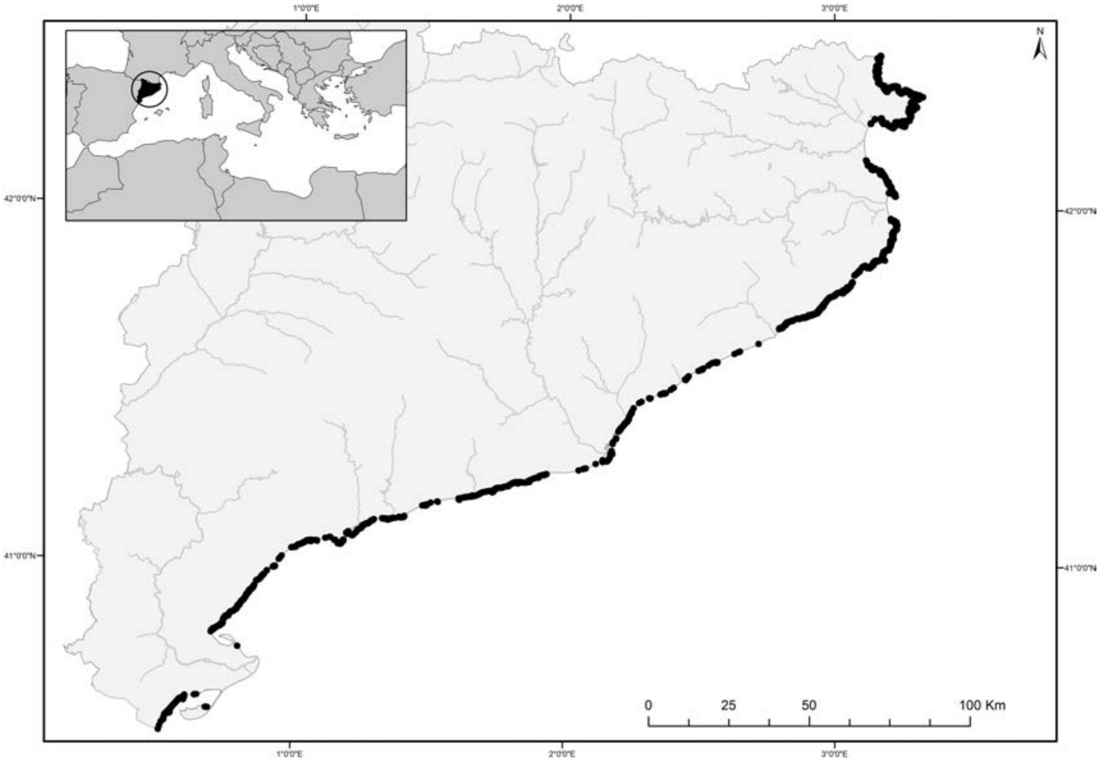

Fig 1. Map of the study site. The 16,098 points along the coast contain information on habitats presence/absence and values of environmental variables. The map was created with ArcGis 10.1 (ESRI).

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lenormandii showed a very scattered distribution along the coast [39]. The habitat dominated by the brown alga *Cystoseira mediterranea* [39–42] was overall abundant and widespread.

The distribution of all habitats (Table 1) was significantly influenced by environmental variables [34]. The variables used as predictors were (Table 2): minimum and mean wave height (WH, data from 1998 to 2008), estimated using the Downscaled Ocean Waves model (DOW) [43]; mean sea surface temperature (SST; data from 2003 to 2010), obtained from satellite measurements performed by the MODIS (aqua) sensor system (http://oceancolor.gsfc.nasa.gov/), available as "Ocean Level-2" HDF data by NASA's Goddard Space Flight Center; rock slope,

Table 1. List of the habitats studied. Number of occurrences and frequency (F) of selected habitats in the original database (16,098) are presented. Each habitat is named after the principal species that characterizes it. Habitat characteristics are from Ballesteros et al. [39].

Habitat	N	F (%)	Habitat characteristics
Rissoella verruculosa	7710	47.9	Mediolittoral habitat from exposed littoral environments, preferably on plutonic rocks dominated by the red alga *R. verruculosa*.
Lithophyllum byssoides	5621	34.9	Mediolittoral habitat from environments with high desiccation levels and strong hydrodynamism dominated by the red coralline *L. byssoides*.
Lithophyllum byssoides rims ("Trottoir")	1154	7.2	Characteristic rims of the red coralline *L. byssoides* on very exposed, mediolittoral rock with low irradiance, preferably on calcareous or metamorphic rock.
Neogoniolithon brassica-florida	528	2.8	Association with the red coralline *N. brassica-florida* and/or the mollusc *D. petraeum* on moderately-to-calm mediolittoral rocks.
Hildenbrandia rubra/ Phymatolithon lenormandii	119	0.7	Mediolittoral caves and overhangs.
Cystoseira mediterranea	4576	28.4	Shallow, exposed and well-lit infralittoral rock dominated by the brown alga *C. mediterranea*.

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Table 2. List and description of the environmental variables studied. A detailed explanation on the variable source and the calculation method are provided in the text.

Environmental predictors	Units or Categories	Source	Year
Average Sea Surface Temperature	16.8° – 18.7° °C	MODIS	2003–2013
Average Wave Height	0.02–0.9 m	DOW	1998–2008
Minimum Wave Height	0.01–0.07 m	DOW	1998–2008
Slope	0° – 10.8°	DEM	2014
	10.8° – 22.8°	DEM	2014
	22.8° – 45.1°	DEM	2014
	45.1° – 68.2°	DEM	2014
	68.2° – 87.8°	DEM	2014
Geology	Metamorphic	IGCC	2000
	Mineral	IGCC	2000
	Plutonic	IGCC	2000
	Sedimentary	IGCC	2000
	Artificial	IGCC	2000
Substrate type	Natural	CARLIT	2012
	Artificial	CARLIT	2012

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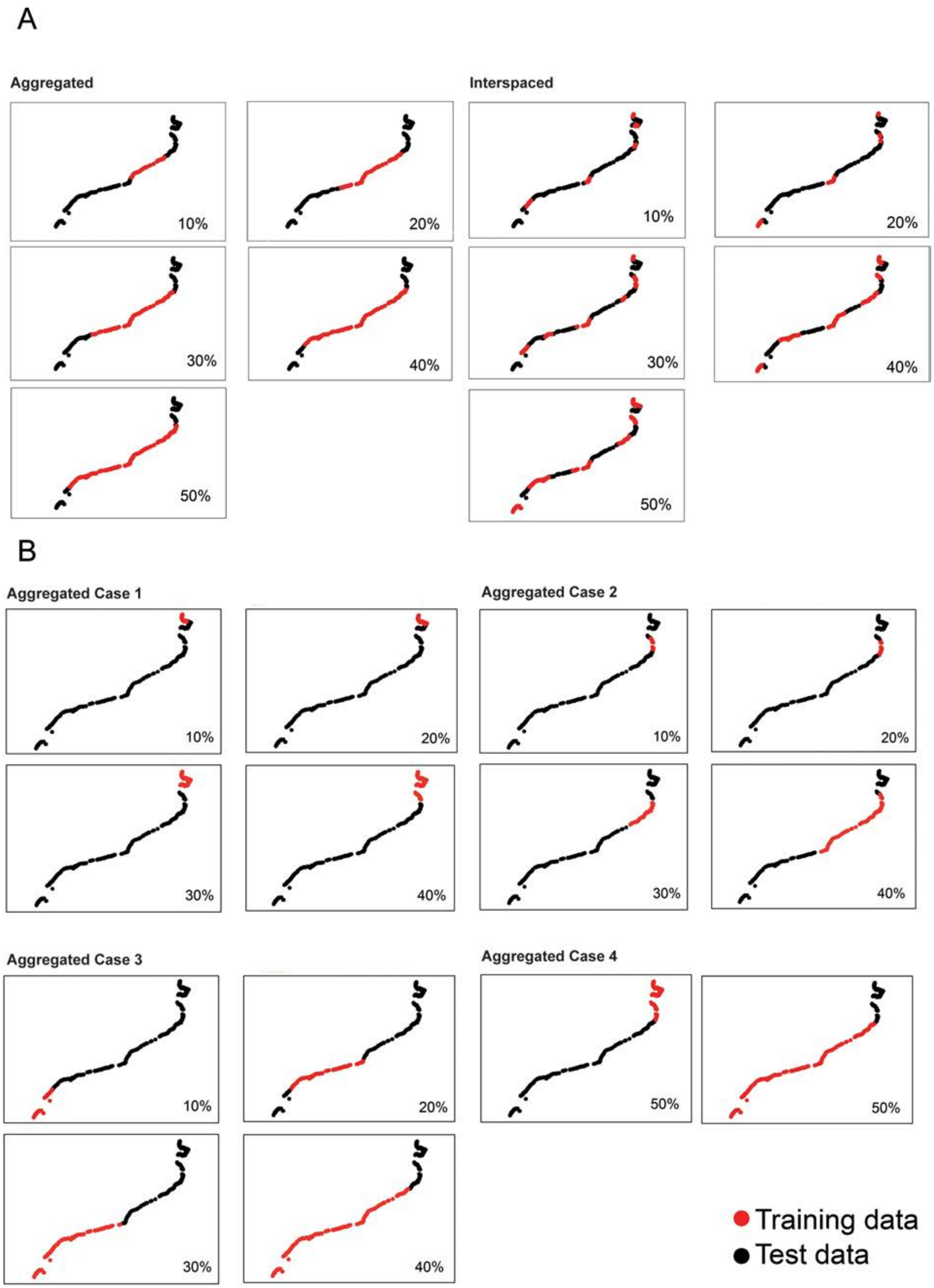
obtained from a Digital Elevation Model (DEM) created with a LiDAR detection method by the Institut Geològic i Cartogràfic de Catalunya (IGCC); rock geology (plutonic, sedimentary, metamorphic and mineral), provided by the Institut Geològicic i Cartogràfic de Catalunya (IGCC, www.igc.cat); finally, the substrate type (an index of two categories identifying whether the rocky substrate was natural or man-made), obtained from the CARLIT data set [37]. As detailed in Cefalì et al. [34], spatial resolution grain sizes were: 0.01° latitude and 0.008° longitude for minimum and mean wave height; a data point every 10 km for mean sea surface temperature; a raster format with pixel resolution of 2 x 2m for rock slope; a 1:50.000 map scale for rock geology and a map scale of 1:1000 for substrate type.

Sampling scenarios

Two strategies for data sampling were compared to address the first objective of the study, aggregated and interspaced. For the aggregated sampling strategy, a unique stretch of arbitrarily chosen neighboring points was selected (Fig 2). For the interspaced sampling, we selected a minimum of 5 data units (stretches of continuous points) interspaced by equivalent numbers of unselected data points (Fig 2). To assess changes in model accuracy and performance for habitats with different distributional patterns (see above), different scenarios were performed for the aggregated samplings considering different spatial distributions from north to south (Fig 2). The interspaced sampling inherently gathered data from the whole coast.

To define the best cost effective sampling size, we tested 5 different sampling sizes from the original matrix (16,098 points; 562,895 km): 10% (1,610 points; 56,290 km), 20% (3,219 points; 112,579 km), 30% (4,829 points; 168,868 km), 40% (6,439 points; 225,158 km), and 50% (8,049 points; 281,447 km) and for both, the aggregated and interspaced sampling (Fig 2). We compared the models performed with both aggregated and interspaced scenarios and different sampling sizes. Additionally, null models were fitted to randomly selected points for each sampling size (from 10% to 50%). All scenarios were applied to each of the 6 selected habitats. All spatial selections were performed in ArcGIS 10.1 (ESRI), whereas the random sampling for null models was made in R (R Development Core Team 2011).


A
Aggregated
10%
20%
30%
40%
50%
Interspaced
10%
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B
Aggregated Case 1
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20%
30%
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Aggregated Case 3
10%
20%
30%
40%
Aggregated Case 4
50%
50%
● Training data
● Test data

Fig 2. Sampling designs. Sampling scenarios considered in this study based on combinations of sampling size (20%, 30%, 40%, 50%) and sampling strategy: A) aggregated and interspaced; B) aggregated case 1, case 2, case 3 and case 4. Red dots represent data points selected for model training whereas black dots represent data points used for model validation. Random samples for null models are not depicted. Please notice that the percent sampling size (either red or black dots) may appear unrealistic at the scale of the figure. This is because of the extremely irregular shape of the northern portion of coast where much more data points exist.

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Habitat modelling

Since our habitat data were binary, to describe the relationship between the distribution of habitats and environmental variables (Table 2) we fitted generalized linear models with binomial error distribution and the logistic link function (GLM, [44]) using the entire dataset (16,098 points). The most parsimonious model for each habitat was obtained through variable selection using the "glmulti" function in the glmulti R package [45] based on AIC values. The environmental variables selected for each of the habitats are listed in Table 3. Samples, selected as described in the previous section, were used as training datasets to build the models. The remaining data were used as test data for model validation. For example, in Fig 2, the 10% portion of the coast sampled was used as training dataset and the remaining 90% was used as test dataset. The same procedure was repeated to compare the performance of all models built for each of the sampling scenarios. Model fit was assessed as the proportion (%) of explained

Table 3. Principal results. The most important environmental predictors, the best cost-effective models, the frequency (F %) of habitat in each sampling strategy and the model prediction results are shown. For more information about relationships between predictors and habitats, see Cefalì et al. [34].

	Principal environmental predictors	Best cost effective model strategies	Habitat F (%)	AUC	threshold	se	spe
R. verruculosa	SST average WH average Slope Geology Substrate type	20% interspaced	0,4936	0,87	0,57	0,90	0,74
L. byssoides	SST average WH average WH minimum Slope Geology	20% interspaced	0,3988	0,77	0,40	0,92	0,54
L. byssoides rims	SST average WH average WH minimum Slope Geology	10% interspaced	0,160	0,87	0,18	0,74	0,86
		20% interspaced	0,031	0,75	0,03	0,74	0,68
N. brassica-florida	SST average WH average WH minimum Slope	30% aggregated	0,01	0,90	0,21	0,94	0,87
		20% interspaced	0,399	0,77	0,4	0,92	0,54
Hildenbrandia / Phymatholiton	SST average WH average Geology	20% interspaced	0,0037	0,73	0,01	0,37	0,90
		30% interspaced	0,0033	0,81	0,01	0,65	0,79
		30% aggregated case 2	0,0161	0,82	0,02	0,74	0,81
C. mediterranea	SST average WH average WH minimum Slope Geology Substrate type	20% interspaced	0,295	0,77	0,37	0,84	0,61

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deviance (D^2):

$$D^2 = \frac{(null\ deviance - residual\ deviance)}{null\ deviance} \times\ 100$$

Altogether, we fitted 19 models for each of the 6 selected habitats. The same procedure was conducted for the null models, where each random selection (10%, 20%, 30%, 40%, and 50%) was used as training data and tested on the remaining data, and repeated 10 times. For the null models, the D^2 value presented is the mean and standard deviation of the 10 fitted models. All statistical analyses were performed in R (R Development Core Team 2011).

Model validation

Model selection based on AIC identifies the "best" model among the set of candidate models, but it does not measure its performance in predicting independent data. To assess the predictive accuracy and performance of our models, we employed three statistics that compare the predictions to the observations in the test data: AUC (area under the receiver operating characteristic [ROC] curve), sensitivity (se), and specificity (spe). Because binomial GLM predictions are continuous probabilities between 0 and 1, we must specify a cut-off threshold to convert the continuous predictor to a discrete, binary predictor in order to calculate the percentage of correct classifications [10]. AUC is a synthetic index of the model accuracy, and is independent of threshold choice, weighing omission, and commission errors equally [10, 46, 47]. We used the AUC, which ranges from 0 to 1, as first model selection, where values ≤ 0.5 indicating that the model had not predictive power and 1 meaning that we had a good model. Following Swets [48], models providing values > 0.9 were considered "highly accurate", those providing values in the range 0.7–0.9 were considered "useful", and those with AUC below 0.7 are "poorly accurate".

However, to select the best models and their discrimination power, it is necessary to calculate the percentage of predicted versus observed presences and absences. For this purpose, sensitivity and specificity were derived from a confusion matrix. Sensitivity (or true positive rate) is the portion of data points for which presence was correctly predicted, whereas specificity (true negative rate) is the portion of data points for which absence was correctly predicted [10]. Because habitats differed in their prevalence, we decided to use habitat-specific classification thresholds that maximized the sum of sensitivity and specificity [49]. Both sensitivity and specificity range from 0 when the model is completely inaccurate to 1 when either presences or absences are well predicted [50, 51]. The mean AUC, sensitivity and specificity of the 10 null models were also calculated. Analysis of AUC, and sensitivity specificity were performed in R (R Development Core Team 2011), using the pROC [52] and SDMTools [53] packages respectively.

Results

Best model strategy

Model accuracy and performance in predicting the distribution of the six benthic littoral habitats were tested for sampling design, sample size, and habitat prevalence. Only models with high accuracy (AUC > 0.70) and performance (sensitivity and specificity > 0.60) were considered.

As expected, null models were the most accurate and had the highest performance values (high AUC, sensitivity and specificity values) (Fig 3), and provided performance standards against which to compare the other sampling strategies. Although model performance was

Fig 3. Statistical diagnostics of the predictive models for the aggregated strategy (aggr), the interspaced strategy (intsp) and the null (null) models. In each panel, the x-axis shows the sample size for the training data set (Fig 2). The y-axis, with values from 0 to 1, shows AUC, sensitivity (se), and specificity (spe) for each of the three sampling strategies.

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habitat-dependent, in general it was strongly dependent on the sampling design, with the best strategy being the interspaced data collection. The prediction performed with the interspaced strategy obtained accuracy and performance values close to the null models for all habitats studied, regardless the habitat spatial distribution (Fig 3, Table 3, S1 File).

In contrast, the results of aggregated sampling designs depended on the prevalence of the habitat considered. In fact, aggregated strategies performed well where habitat prevalence was high (i.e. *Rissoella verruculosa*, *Lithophyllum byssoides*, *Cystoseira mediterranea*) or with large sampling size (i.e. *Hildenbrandia/Phyma tholiton* and *Neogoniolithon brassica-florida*). In contrast, habitat sample size and spatial distribution had lower effect on model accuracy and performance with the interspaced strategy. In fact, with the interspaced sampling and only 20% sampling size, we reached sufficient prevalence to obtain good model predictions for all the habitats considered. In general, with the interspaced design, increasing sample size did not substantially increase model accuracy and performance (Fig 3, Table 3, Tables A-F in S1 File). These results agreed with the null models, where increasing sample size did not always result in increased accuracy and performance prediction (Table 3, Tables A-F in S1 File).

Predictive habitat models

Model performance was clearly habitat-dependent. Models for abundant but localized habitats (*Rissoella verruculosa* and *Lithophyllum byssoides*) were in general highly accurate and showed good performance (high specificity and sensitivity), with values comparable to those of null models (AUC $>$ 0.80 for both habitats) (Table A and Table B in S1 File). The interspaced design provided the best model predictions (Fig 4). With 20% sample size we obtained models with good accuracy and performance for *R. verruculosa* (AUC = 0.87, sensitivity = 0.90 and specificity = 0.73) and for *L. byssoides* (AUC = 0.77, sensitivity = 0.92 and specificity = 0.54). In the interspaced design, increasing habitat occurrence improved model accuracy and prediction performance independently of sample size. With the aggregated designs, accurate and good performance models were obtained only with large sample sizes, regardless of habitat occurrence (Fig 4, Table 3, Table A and Table B in S1 File).

For uncommon and localized habitats (i.e. *Lithophyllum byssoides* rims and *Neogoniolithon brassica-florida* concretions), model predictions were accurate and performed well with both aggregated and interspaced strategies. However, using the aggregated strategy, a large sample size was necessary to obtain good predictions. In contrast, when the interspaced strategy was used, a sample size of only 20% was enough to get AUC values higher than 0.7 for both habitats, 0.74 sensitivity and 0.68 specificity for *L. byssoides* rims, and of 0.92 sensitivity and 0.81 specificity for *N. brassica-florida* (Fig 4, Table 3, Table C and Table D in S1 File).

For the uncommon and scattered habitat of *Hildenbrandia/Phymatholiton*, few models yielded good accuracy and performance. In fact, with the interspaced design and 20% sample size, predictions were accurate (AUC of 0.73) and specific (specificity of 0.90), but the model was not sensitive enough (sensitivity of 0.37) (Table 3). Only the aggregated case 2, with 30% sample size, provided a prediction with good accuracy and performance, possibly as a result of the higher habitat frequency (Table 3 and Table E in S1 File).

At the infralittoral level, for the widespread and abundant habitat of *Cystoseira mediterranea*, the 20% sample size interspaced model was again the most accurate, with AUC of 0.77 (Fig 4), but more sensitive (sensitivity of 0.84 and specificity of 0.61) (Table 3 and Table F in S1 File). With the exceptions of the most widespread habitats, aggregated sampling designs led to low accuracy models, independently of sample size or habitat prevalence (aggregated case 2 with 40% sample size, aggregated with 50% and interspaced with 50% sample size), (Table F in S1 File).

Discussion

We found strong consistency (*sensu* Oreskes et al. [54]) between the distributions predicted by our models and those observed in the field for the six rocky littoral habitats studied, which ranged from uncommon to frequent and from localised to scattered along the whole coastline. Additionally, our models show that, in terms of minimum effort and highest accuracy, the interspaced is the best sampling strategy for accurate and well-performing predictions. Hirzel and Guisan [5] established that, when habitats with different distributional patterns are considered, the regular and 'equally-stratified' sampling strategies may yield the most accurate and robust predictive models based on simulated data. Our results from field data clearly support this idea.

Technically speaking, the interspaced sampling design ensured that the training datasets adequately represented the distribution of the environmental conditions faced by the different habitats (S1 Table). Completeness, or the degree to which the habitat spatial range of environmental variables is covered by the sample, has been shown to positively affect SDMs, especially when the SDMs are used to infer distribution data from other locations [6, 55]. Here we show

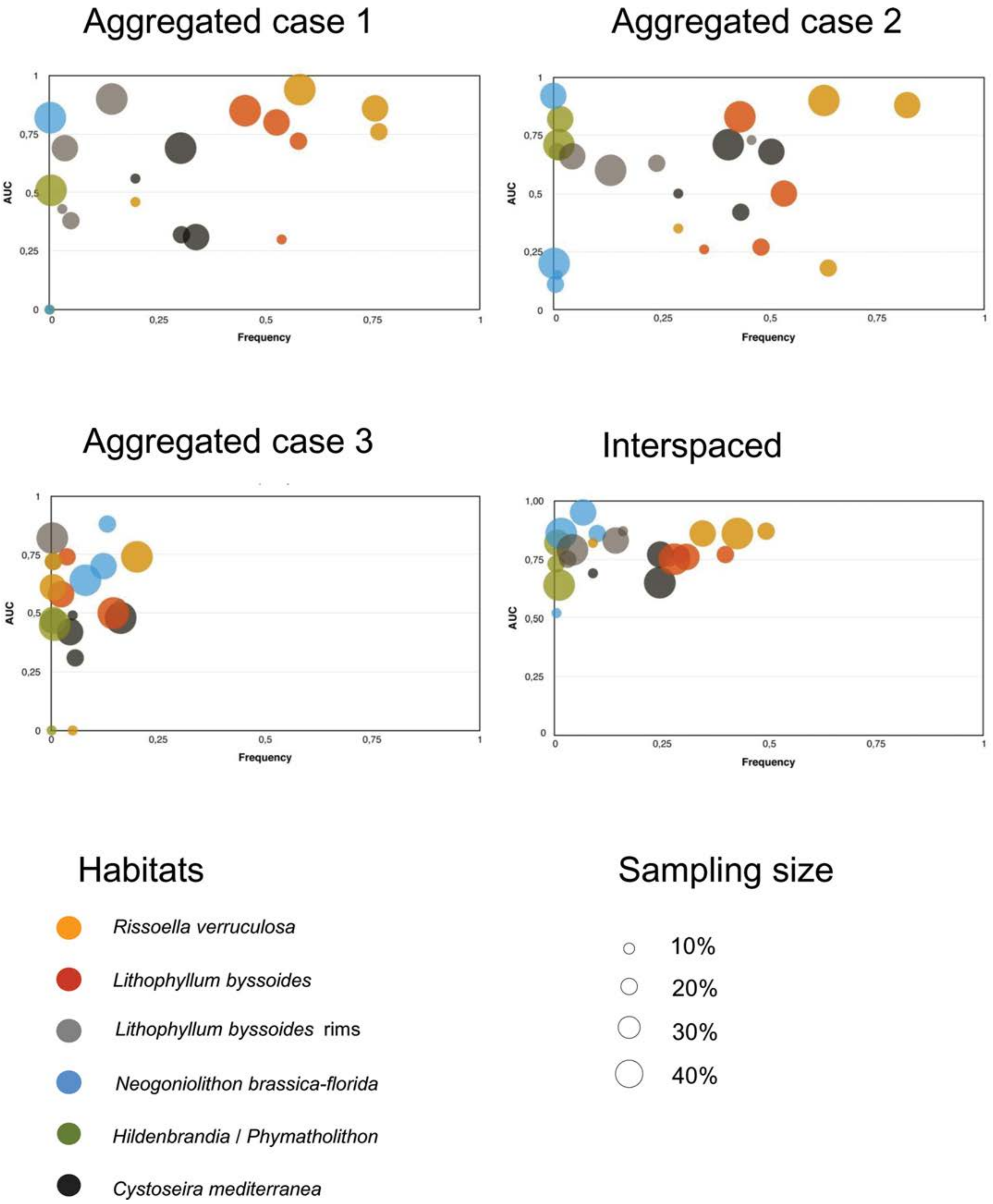

Fig 4. Habitat frequency and AUC values. Relation between habitat frequency (x-axis) and AUC values (y-axis), for sample sizes from 10% to 40% are presented.

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that the interspaced sampling strategy reduced the environmental divergence between the two data sets better than the aggregated strategy, thus improving the accuracy of predictive models.

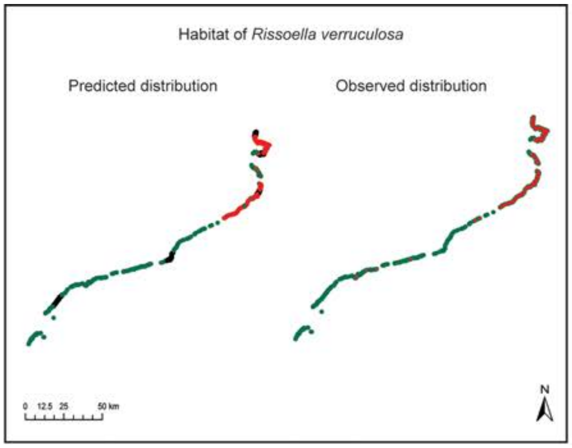
Sampling size has also been suggested to have strong effects on SDM or HDM predictive accuracy [5, 11, 47, 56, 57]. In our interspaced models, increasing sample size did not increase accuracy or model performance, because accuracy depends on the habitat prevalence. Thus, an interspaced sampling design also guarantees a representative coverage of habitats occurrences (prevalence) with a minimum number of observations [8]. In fact, with only 20% of the sample size (3,216 observations out of 16,098) we achieved accurate prediction models (high AUC) of the distribution of nearly all studied habitats for the rest of the coast (Fig 3). This means that by sampling a relatively small fraction of the littoral (20% of the coast), the ranges of environmental variables driving the presence or the absence of several habitats were well-covered. Our high-resolution sampling provided a large amount of high-quality observations. Thus, the split-sample approach with the interspaced design did not reduce the model capacity to fit the data [2]. However, when an aggregated strategy was used, both model accuracy and performance strongly depended on the habitat distribution. Either high sample size or high habitat prevalence in the training data set was needed to build accurate models (Figs 3 and 4). In fact, the aggregated strategy might prove useful when modelling focuses on a single habitat, but may require prior knowledge of where the habitat occurs.

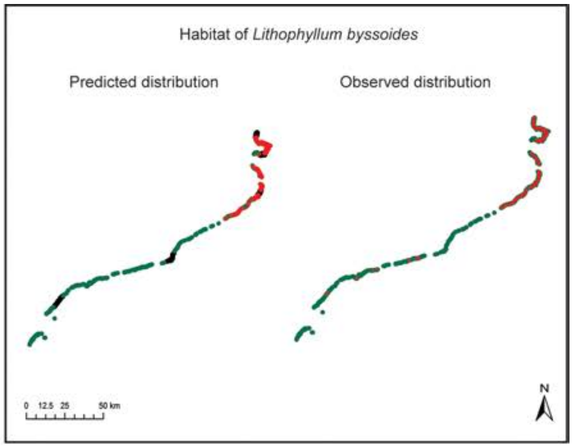
In order to compare predicted vs. observed distributions with the interspaced strategy and a sample size of 20%, we transformed the probabilities into binary (presence/absence) maps (Fig 5). Although all the habitats considered here contain specialist species, which are strongly associated with the environmental variables considered, we obtained the best model predictions with both abundant and uncommon habitats. This supports results obtained in previous studies [6, 58]. In fact, model effectiveness strongly depends on the relation between species and predictors [58, 59].

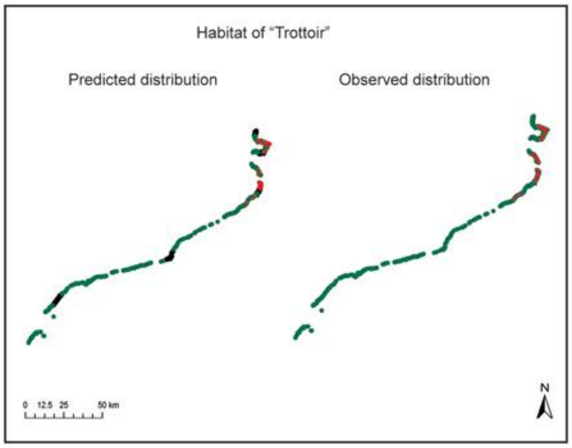
The habitats of *Rissoella verruculosa* and *Lithophyllum byssoides* were more abundant in the northern coast (where they occur in 68% and 49% of sampling points, respectively, Fig 5), where environmental conditions are suitable for their optimum development [34]. These habitats are spatially strongly associated with the explanatory variables used, so the accuracy of the resulting models was high. Performance was also high because the habitat prevalence in the training data reached nearly 50%, thus covering the suitable range and improving the capacity of the model to discern between presences and absences in the test data (Fig 4). Models tend to perform better when habitat prevalence is intermediate [60]. This effect is to be expected because logistic probabilities are computed on the values of the predictors as well as on the relative proportion of presence/absence data [47, 61].

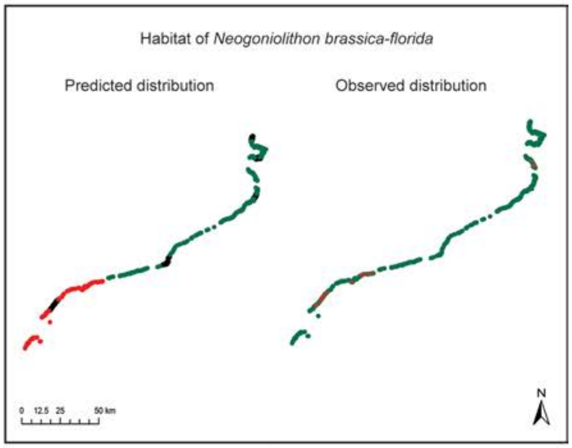
For rare habitats like the *Lithophyllum byssoides* "rims" and *Neogoniolithon brassica-florida* concretions, which are uncommon but locally aggregated (present in 7.2% and 3.3% of data points, respectively, with latitudinal interquartile ranges [IQR] of 6.3 and 6.6 km) we obtained useful predictions depending on their prevalence in training data. However, the presence of *N. brassica-florida* was over predicted (Fig 5) although the values of both sensitivity and specificity were high.

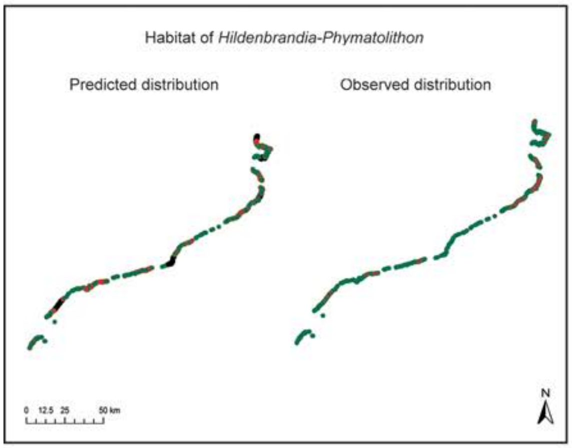
The cave habitat dominated by *Hildenbrandia and Phymatolithon*, was uncommon but scattered along the coast [34] (0.7% of data points but latitudinal IQR of 22 km). Although highly accurate (as measured by AUC), the model showed high specificity but low sensitivity, i.e. it was able to detect habitat absence but failed to detect habitat presence (low true positive rate, Fig 5). Habitats with low prevalence in the training data and absent from many coastline points may have led to misspecification of the response curve [6, 62]. In fact, when one of the two events (presence or absence) is over represented with respect to the other, mean probabilities tend to be biased towards the most common event [47, 63–65]. The model also failed to predict

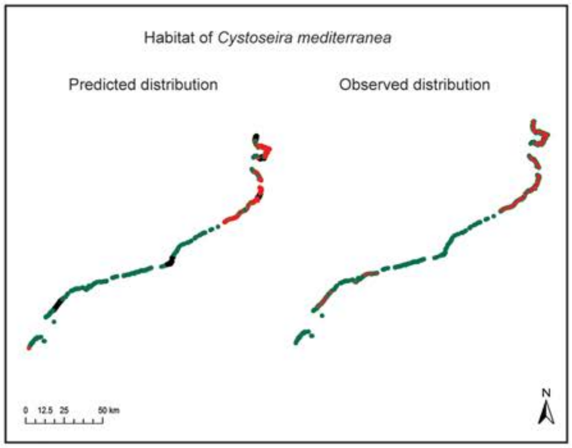












Predicted distribution

Training data

● 20% interspaced

Test data 80% aggregated

🟢 $p < 0.54$

🔴 $p > 0.54$

Observed distribution

Actual data

🟢 absence

🔴 presence

Fig 5. Predicted distribution vs. observed distribution along the Catalan coastline for the six habitats considered. The coastline on the left side of each panel represents the training data and the probability of habitat occurrence in the test data; the coastline in the right side represents the observed habitats as recorded in the Cartography of the Littoral Habitats (see Material and Methods section).

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the presence of the habitat of *Cystoseira mediterranea* (Fig 5). Accuracy and specific performance were moderate, although the habitat was abundant along the coast. Therefore, while model outputs were useful (as measured by AUC) they only predicted well the habitat absence but they were not the best to predict its presence.

From our results, the most important factors in model prediction were the sampling strategy and the habitat prevalence. However, we observed that low environmental dispersion between training and test data is essential to improve the outputs models. Sample size influenced the models effectiveness mostly when the aggregated strategy was used.

Our data showed that using the right sample design (interspaced) we may obtain a fair representation of habitat prevalence following the environmental variability in both our training and test datasets. Spatially biased (i.e. aggregated) survey designs have been proven to cover inefficiently the real geographic pattern of species distribution within a region [63, 64]. Some authors have stressed that incrementing sample sizes may lead to higher model performance in predicting species distributions [11]. In contrast, for uncommon habitats, either localized or scattered, increasing sample size may not necessarily increase the number of presences in the training dataset.

In brief, the interspaced sampling procedure allows reaching useful and accurate predictive models, whereas performance is dependent on the occurrence and distribution of each habitat. We also highlight that it is not only the accuracy of the model that should be considered, but performance is also crucial to get reliable ecological information on the distribution patterns. Sampling is often costly and time consuming, especially for marine environments. When the aim is to predict the geographical distributions of species and habitats, static, comparative, empirical models, rather than mechanistic models [2], may help reduce significantly the sampling effort by identifying the best sampling strategy in terms of cost and effort. This information is particularly relevant for littoral marine environments, for which SDMs have lacked so far a systematic and planned sampling strategy and model performance has never been considered. These cost effective sampling strategies can be applied to different habitats in different areas, especially those where field work and ground-truthing of habitat distributions have not been yet performed (i.e. in some unexplored areas of the southern and eastern Mediterranean Sea). Nevertheless, it is pivotal to be in possession of data about the best environmental variables to combine with habitat data, thus obtaining the best predictions across seascapes. Finally, the outcome of these models is essential to improve extensive habitat cartographies, to inform studies addressed at detecting high biodiversity areas, to identify and design protected areas and, in general, to implement management plans, especially in littoral environments.

Supporting information

S1 File. Tables A-F. Results of logistic regression models. Results of logistic regression models for all sampling strategy designs are presented for each habitat and for all sample sizes. For training data, the number (N) and frequency (F) of the habitat occurrence are presented. Results of null models are shown with the mead and standard deviation of the 10 models calculated. The D^2 is the Deviance of the model in the training data; AUC is the area under the receiver operating characteristic (ROC) curve, se and spe are the sensitivity and specificity respectively, for the predictive model in the test data.
(PDF)

S1 Table. Full data base. Projected coordinates, environmental variables and the presence/absence (1/0) of each habitat are presented for each point. Slope code: 1 = 0º-10.8º; 2 = 10.8º-22.8º; 3 = 22.8º-45.1º; 4 = 45.1º-68.2º; 5 = 68.2º-87.8º. Habitats code: Riv = *Rissoella verruculosa*; Lby = *Lithophyllum byssoides*; Tro = *Lithophyllum byssoides* rims ("Trottoir"); Neo = *Neogoniolithon brassica-florida*; Hph = *Hildenbrandia rubra/ Phymatolithon lenormandi*.
(XLSX)

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Author Contributions

Conceptualization: Maria Elena Cefalì, Enric Ballesteros, Eglantine Chappuis, Simone Mariani, Emma Cebrian.

Data curation: Maria Elena Cefalì, Simone Mariani.

Formal analysis: Maria Elena Cefalì, Joan Lluís Riera.

Funding acquisition: Enric Ballesteros, Emma Cebrian.

Investigation: Maria Elena Cefalì, Enric Ballesteros, Eglantine Chappuis, Marc Terradas, Simone Mariani, Emma Cebrian.

Methodology: Maria Elena Cefalì, Joan Lluís Riera, Simone Mariani, Emma Cebrian.

Project administration: Enric Ballesteros.

Resources: Enric Ballesteros, Emma Cebrian.

Software: Maria Elena Cefalì, Joan Lluís Riera.

Supervision: Enric Ballesteros, Joan Lluís Riera, Eglantine Chappuis, Marc Terradas, Simone Mariani, Emma Cebrian.

Validation: Enric Ballesteros, Joan Lluís Riera, Eglantine Chappuis, Simone Mariani, Emma Cebrian.

Writing – original draft: Maria Elena Cefalì, Enric Ballesteros, Joan Lluís Riera, Eglantine Chappuis, Marc Terradas, Simone Mariani, Emma Cebrian.

Writing – review & editing: Maria Elena Cefalì, Enric Ballesteros, Joan Lluís Riera, Simone Mariani, Emma Cebrian.

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S1 File

Table A-F. Results of logistic regression models

Results of logistic regression models for all sampling strategy designs are presented for each habitat and for all sample sizes. For training data, the number (N) and frequency (F) of the habitat occurrence are presented. Results of null models are shown with the mead and standard deviation of the 10 models calculated. The D^2 is the Deviance of the model in the training data; AUC is the area under the receiver operating characteristic (ROC) curve, se and spe are the sensitivity and specificity respectively, for the predictive model in the test data.

Table A. Habitat of *Rissoella verruculosa*

Models strategy	**training data**	**N**	**F**	**D2**	**test data**	**AUC**	**threshold**	**se**	**spe**
Aggregated									
	10%	686	0,4261	34,98	90%	0,62	0,55	0,98	0,35
	20%	1039	0,3226	53,70	80%	0,71	0,28	0,45	0,89
	30%	1308	0,2935	19,39	70%	0,71	0,20	0,62	0,67
	40%	1803	0,2780	19,39	60%	0,66	0,43	0,46	0,77
	50%	2509	0,3123	62,20	50%	0,68	0,48	0,82	0,47
Interspaced									
	10%	146	0,0900	58	90%	0,82	0,02	0,96	0,44
	20%	1614	0,4936	49	80%	0,87	0,57	0,90	0,74
	30%	1545	0,3219	56,30	70%	0,86	0,71	0,81	0,76
	40%	2751	0,4273	51	60%	0,86	0,37	0,92	0,70
	50%	3610	0,4500	51,90	50%	0,86	0,02	1,00	0,63
Aggregated case 1									
	10%	319	0,2000	14	90%	0,46	0,67	0,00	1,00
	20%	2467	0,7659	9,15	80%	0,76	0,07	0,23	0,90
	30%	3857	0,7569	8,90	70%	0,86	0,12	0,97	0,74
	40%	3774	0,5821	24	60%	0,94	0,01	0,72	0,91
Aggregated case 2									
	10%	466	0,2900	36,00	90%	0,35	0,01	0,92	0,18
	20%	2084	0,6375	42,00	80%	0,18	0	1	0
	30%	3915	0,8206	6,20	70%	0,88	0,69	0,98	0,69
	40%	4043	0,6283	33,40	60%	0,90	0,17	0,98	0,74
Aggregated case 3									
	10%	75	0,0500	NA	90%	NA	NA	NA	NA
	20%	15	0,0047	6	80%	0,72	0,05	0,80	0,59
	30%	15	0,0036	10,40	70%	0,61	0,99	0,88	0,28
	40%	1283	0,1998	73	60%	0,74	0,53	0,61	0,86
Aggregated case 4									
	50%_a	5125	0,6368	16,60	50%_b	0,94	0,44	0,96	0,91
	50%_b	2584	0,3210	67,10	50%_a	0,73	0,88	0,71	0,71
Null models									
mean	10%	761	0,4726	45,84	90%	0,89	0,45	0,89	0,77
sd		18	0,011	2,22		0,00	0,04	0,03	0,02
mean	20%	1532	0,4762	45,00	80%	0,89	0,45	0,90	0,77
sd		32	0,010	0,79		0,00	0,02	0,02	0,01
mean	30%	2306	0,4779	44,65	70%	0,89	0,45	0,90	0,77
sd		34	0,007	1,42		0,00	0,01	0,01	0,01
mean	40%	3056	0,4751	44,35	60%	0,89	0,45	0,91	0,77
sd		45	0,007	0,85		0,00	0,02	0,01	0,01
mean	50%	3839	0,4774	44,66	50%	0,89	0,46	0,90	0,78
sd		32	0,004	0,62		0,00	0,01	0,01	0,00

Table B. Habitat of *Lithophyllum byssoides*

Models strategy

Aggregated	**training data**	**N**	**F**	**D2**	**test data**	**AUC**	**threshold**	**se**	**spe**
	10%	658	0,4087	29,55	90%	0,80	0,05	0,53	0,82
	20%	1123	0,3486	53,70	80%	0,75	0,43	0,97	0,52
	30%	1343	0,3014	27,84	70%	0,68	0,29	0,97	0,43
	40%	1828	0,2818	19,39	60%	0,68	0,58	0,95	0,38
	50%	2505	0,3118	62,20	50%	0,74	0,59	0,85	0,50
Interspaced									
	10%	443	0,2700	39	90%	0,74	0,02	0,96	0,46
	20%	1304	0,3988	25,70	80%	0,77	0,40	0,92	0,54
	30%	1016	0,2421	27,60	70%	0,75	0,24	0,96	0,42
	40%	1800	0,2796	29,50	60%	0,75	0,30	0,90	0,51
	50%	2844	0,3500	25,60	50%	0,76	0,19	0,94	0,48
Aggregated case 1									
	10%	867	0,5400	5	90%	0,30	0,47	0,99	0,017
	20%	1865	0,5790	4,40	80%	0,72	0,09	0,25	0,89
	30%	2691	0,5281	5,30	70%	0,80	0,12	0,93	0,62
	40%	2951	0,4552	8,80	60%	0,85	0,01	0,81	0,77
Aggregated case 2									
	10%	571	0,3500	16	90%	0,26	0	1	0
	20%	1575	0,4818	7,80	80%	0,27	0,09	0,98	0,03
	30%	2551	0,5347	3,30	70%	0,50	0,36	0,90	0,62
	40%	2784	0,4326	13	60%	0,83	0,13	0,95	0,62
Aggregated case 3									
	10%	18	0,0100	NA	90%	NA	NA	NA	NA
	20%	119	0,0370	16,20	80%	0,74	0,93	0,96	0,45
	30%	109	0,0227	23,50	70%	0,58	0,97	0,91	0,19
	40%	932	0,1451	7,30	60%	0,50	0,53	0,97	0,08
Aggregated case 4									
	50%_a	3917	0,4867	5,70	50%_b	0,87	0,33	0,89	0,77
	50%_b	1703	0,2116	36	50%_a	0,53	0,62	0,63	0,45
Null models									
mean	10%	554	0,3439	24,31	90%	0,79	0,23	0,96	0,50
sd		16	0,0102	1,61		0,002	0,03	0,005	0,005
mean	20%	1111	0,3453	23,70	80%	0,79	0,25	0,96	0,51
sd		37	0,0114	1,02		0,001	0,08	0,302	0,161
mean	30%	1689	0,3499	23,67	70%	0,79	0,24	0,96	0,50
sd		29	0,0060	0,61		0,002	0,02	0,002	0,003
mean	40%	2221	0,3453	23,33	60%	0,79	0,24	0,96	0,51
sd		42	0,0065	0,71		0,004	0,05	0,016	0,019
mean	50%	2796	0,3476	23,45	50%	0,79	0,24	0,96	0,50
sd		25	0,0031	0,30		0,002	0,08	0,304	0,160

Table C. Habitat of *Lithophyllum byssoides* rim ("Trottoir")

Models strategy	training data	N	F	D2	test data	AUC	threshold	se	spe
Aggregated									
	10%	15	0,01	34,98	90%	0,69	0,90	0,53	0,82
	20%	17	0,01	53,70	80%	0,66	0,04	0,05	0,96
	30%	17	0,00	29,03	70%	0,63	0,03	0,00	1,00
	40%	51	0,01	19,39	60%	0,46	0,00	1	0
	50%	175	0,02	62,20	50%	0,66	0,15	0,86	0,40
Interspaced									
	10%	267	0,160	35	90%	0,87	0,18	0,74	0,86
	20%	102	0,031	27	80%	0,75	0,03	0,74	0,68
	30%	282	0,059	27	70%	0,81	0,07	0,82	0,68
	40%	268	0,042	33	60%	0,79	0,05	0,72	0,81
	50%	931	0,116	37	50%	0,83	0,04	0,79	0,84
Aggregated case 1									
	10%	52	0,030	66	90%	0,43	0,01	0,02	0,98
	20%	160	0,050	23	80%	0,38	1	0	1
	30%	183	0,036	17	70%	0,69	0,01	0,74	0,61
	40%	942	0,145	41	60%	0,90	0,04	0,88	0,79
Aggregated case 2									
	10%	749	0,460	28	90%	0,73	0,02	0,94	0,58
	20%	786	0,240	37	80%	0,63	0,49	0,95	0,48
	30%	212	0,044	20	70%	0,66	0,001	1	0,31
	40%	859	0,133	46	60%	0,60	0,01	1	0,32
Aggregated case 3									
	10%	0	0,000	NA	90%	NA	NA	NA	NA
	20%	0	0,000	NA	80%	NA	NA	NA	NA
	30%	0	0,000	NA	70%	NA	NA	NA	NA
	40%	16	0,002	22	60%	0,82	0,18	0,68	0,86
Aggregated case 4									
	50%_a	1133	0,141	22	50%_b	0,37	0,28	0,71	0,38
	50%_b	23	0,003	22	50%_a	0,82	0,18	0,75	0,79
Null models									
mean	10%	112,4	0,0698	32,74	90%	0,89	0,08	0,82	0,81
sd		7,7	0,0048	2,87		0,002	0,02	0,037	0,040
mean	20%	228,6	0,0711	32,60	80%	0,89	0,08	0,82	0,80
sd		10,7	0,0033	2,06		0,003	0,02	0,041	0,038
mean	30%	344,7	0,0714	31,70	70%	0,89	0,07	0,83	0,79
sd		18,2	0,0038	1,79		0,005	0,02	0,038	0,035
mean	40%	460,2	0,0715	31,68	60%	0,89	0,07	0,84	0,78
sd		11,3	0,0018	1,59		0,006	0,03	0,042	0,044
mean	50%	577,4	0,0718	31,82	50%	0,89	0,07	0,84	0,78
sd		21,1	0,0026	0,76		0,004	0,02	0,040	0,040

Table D. Habitat of *Neogoniolithon brassica-florida*

Models strategy

	training data	N	F	D2	test data	AUC	threshold	se	spe
Aggregated									
	10%	0	0	34,98	90%	0,19	0	1	0
	20%	0	0	53,70	80%	0,72	0	1	0
	30%	24	0,01	29,03	70%	0,90	0,21	0,94	0,87
	40%	157	0,02	19,39	60%	0,91	0,21	0,94	0,89
	50%	422	0,05	62,20	50%	0,85	0,31	0,85	0,90
Interspaced									
	10%	443	0,270	39	90%	0,74	0,02	0,96	0,46
	20%	1304	0,399	25,70	80%	0,77	0,4	0,92	0,54
	30%	1016	0,242	27,60	70%	0,75	0,24	0,96	0,42
	40%	1800	0,280	29,50	60%	0,75	0,3	0,90	0,51
	50%	2844	0,350	25,60	50%	0,76	0,19	0,94	0,48
Aggregated case 1									
	10%	867	0,540	5	90%	0,3	0,47	0,99	0,017
	20%	1865	0,579	4,40	80%	0,72	0,09	0,25	0,89
	30%	2691	0,528	5,30	70%	0,80	0,12	0,93	0,62
	40%	2951	0,455	8,80	60%	0,85	0,01	0,81	0,77
Aggregated case 2									
	10%	571	0,350	16	90%	0,26	0	1	0
	20%	1575	0,482	7,80	80%	0,27	0,09	0,98	0,03
	30%	2551	0,535	3,30	70%	0,50	0,36	0,90	0,62
	40%	2784	0,433	13	60%	0,83	0,13	0,95	0,62
Aggregated case 3									
	10%	18	0,010	NA	90%	NA	NA	NA	NA
	20%	119	0,037	16,20	80%	0,74	0,93	0,96	0,45
	30%	109	0,023	23,50	70%	0,58	0,97	0,91	0,19
	40%	932	0,145	7,30	60%	0,50	0,53	0,97	0,08
Aggregated case 4									
	50%_a	3917	0,487	5,70	50%_b	0,87	0,33	0,89427	0,77401
	50%_b	1703	0,212	36,20	50%_a	0,53	0,62	0,63441	0,44783
Null models									
mean	10%	553,7	0,344	24,31	90%	0,79	0,23	0,96	0,50
sd		16,4	0,010	1,61		0,002	0,03	0,005	0,005
mean	20%	1110,9	0,345	23,70	80%	0,79	0,25	0,96	0,51
sd		36,6	0,011	1,02		0,001	0,08	0,302	0,161
mean	30%	1688,5	0,350	23,67	70%	0,79	0,24	0,96	0,50
sd		28,8	0,006	0,61		0,002	0,02	0,002	0,003
mean	40%	2221,2	0,345	23,33	60%	0,79	0,24	0,96	0,51
sd		41,6	0,006	0,71		0,004	0,05	0,016	0,019
mean	50%	2795,5	0,348	23,45	50%	0,79	0,24	0,96	0,50
sd		24,7	0,003	0,30		0,002	0,08	0,304	0,160

Table E. Habitat of *Hildenbrandia - Phymatholiton*

Models strategy	training data	N	F	D2	test data	AUC	threshold	se	spe
Aggregated									
	10%	20	0,012	34,98	90%	0,64	0,01	0,59	0,72
	20%	52	0,016	53,70	80%	0,65	0,01	0,90	0,41
	30%	63	0,014	19,39	70%	0,63	0,01	1	0,27
	40%	76	0,012	19,39	60%	0,76	0,02	0,61	0,79
	50%	92	0,011	62,20	50%	0,66	0,01	0,4	0,83
Interspaced									
	10%	5	0,0030	NA	90%	NA	NA	NA	NA
	20%	12	0,0037	20,40	80%	0,73	0,01	0,37	0,90
	30%	16	0,0033	13,40	70%	0,81	0,01	0,65	0,79
	40%	72	0,0112	12	60%	0,64	0,01	0,68	0,59
	50%	75	0,0093	8	50%	0,67	0,03	0,48	0,89
Aggregated case 1									
	10%	2	0,0010	NA	90%	NA	NA	NA	NA
	20%	6	0,0019	NA	80%	NA	NA	NA	NA
	30%	10	0,0020	NA	70%	NA	NA	NA	NA
	40%	25	0,0039	9,80	60%	0,51	0,84	0,12	0,95
Aggregated case 2									
	10%	9	0,0050	NA	90%	NA	NA	NA	NA
	20%	31	0,0095	8,70	80%	0,68	0,01	0,73	0,56
	30%	77	0,0161	12,20	70%	0,82	0,02	0,74	0,81
	40%	84	0,0131	9,20	60%	0,71	0,03	0,46	0,92
Aggregated case 3									
	10%	2	0,0010	NA	90%	NA	NA	NA	NA
	20%	17	0,0053	8,70	80%	0,72	0,01	0,67	0,67
	30%	17	0,0041	26	70%	0,47	0,99	0,53	0,52
	40%	49	0,0076	12,20	60%	0,45	0,06	0,87	0,22
Aggregated case 4									
	50%_a	41	0,0093	8,90	50%_b	0,50	0,02	0,80	0,34
	50%_b	78	0,0055	14,10	50%_a	0,64	0,12	0,63	0,70
Null models									
mean	10%	11,1	0,0069	23,24	90%	0,78	0,01	0,56	0,82
sd		2,0	0,0013	8,97		0,029	0,004	0,12	0,06
mean	20%	21,6	0,0067	18,37	80%	0,79	0,01	0,56	0,84
sd		2,1	0,0006	3,17		0,031	0,004	0,06	0,03
mean	30%	33,8	0,0070	16,60	70%	0,80	0,01	0,59	0,83
sd		3,4	0,0007	2,72		0,029	0,004	0,09	0,04
mean	40%	43,8	0,0068	16,19	60%	0,80	0,01	0,60	0,83
sd		5,4	0,0008	1,56		0,022	0,000	0,05	0,03
mean	50%	59,3	0,0074	15,76	50%	0,81	0,01	0,61	0,82
sd		6,6	0,0008	2,60		0,026	0,003	0,07	0,04

Table F. Habitat of *Cystoseira mediterranea*

Models strategy

Aggregated	**training data**	**N**	**F**	**D2**	**test data**	**AUC**	**threshold**	**se**	**spe**
	10%	686	0,426	34,98	90%	0,62	0,55	0,98	0,35
	20%	1039	0,323	53,70	80%	0,71	0,28	0,45	0,89
	30%	1308	0,294	19,39	70%	0,71	0,20	0,62	0,67
	40%	1803	0,278	19,39	60%	0,66	0,43	0,46	0,77
	50%	2509	0,312	62,20	50%	0,68	0,48	0,82	0,47
Interspaced									
	10%	149	0,090	20	90%	0,69	0,02	0,96	0,44
	20%	966	0,295	16	80%	0,77	0,37	0,84	0,61
	30%	899	0,187	27,50	70%	0,50	0,01	0,89	0,15
	40%	1585	0,246	16,40	60%	0,65	0,24	0,76	0,47
	50%	1869	0,230	20	50%	0,77	0,19	0,87	0,58
Aggregated case 1									
	10%	319	0,200	16	90%	0,56	0,67	0,00	1,00
	20%	990	0,307	5,30	80%	0,32	0,19	0,99	0,01
	30%	1736	0,341	8,90	70%	0,31	0,91	0,92	0,14
	40%	1976	0,305	5,90	60%	0,69	0,10	1,00	0,45
Aggregated case 2									
	10%	466	0,290	14	90%	0,50	0,01	0,92	0,18
	20%	1421	0,435	9,70	80%	0,42	0,07	0,77	0,28
	30%	2414	0,506	8,60	70%	0,68	0,19	0,98	0,37
	40%	2615	0,406	9,40	60%	0,71	0,31	0,67	0,65
Aggregated case 3									
	10%	75	0,05	33	90%	0,49	0,00	1,00	0,00
	20%	179	0,06	17,30	80%	0,31	0,00	1,00	0,00
	30%	186	0,04	15,40	70%	0,42	0,00	1,00	0,00
	40%	1037	0,16	31,30	60%	0,48	0,49	0,98	0,05
Aggregated case 4									
	50%_a	2778	0,35	6,30	50%_b	0,60	0,43	1,00	0,44
	50%_b	1797	0,22	38	50%_a	0,62	0,38	0,56	0,60
Null models									
mean	10%	459,3	0,2853	21,67	90%	0,78	0,29	0,84	0,59
sd		18,4	0,0114	1,15		0,003	0,016	0,025	0,025
mean	20%	919,3	0,2858	21,49	80%	0,78	0,28	0,85	0,59
sd		29,5	0,0092	0,80		0,002	0,024	0,016	0,017
mean	30%	1363,7	0,2826	21,07	70%	0,78	0,28	0,85	0,59
sd		25,0	0,0052	0,70		0,002	0,015	0,016	0,017
mean	40%	1826,5	0,2839	21,04	60%	0,78	0,29	0,83	0,60
sd		34,7	0,0054	0,50		0,003	0,024	0,030	0,029
mean	50%	2277,4	0,2832	20,89	50%	0,78	0,28	0,84	0,59
sd		26,8	0,0033	0,37		0,003	0,032	0,037	0,037

Table A. Habitat of *Rissoella verruculosa*

Models strategy

	training data	N	F	D2	test data	AUC	threshold	se	spe
Aggregated									
	10%	686	0,4261	34,98	90%	0,62	0,55	0,98	0,35
	20%	1039	0,3226	53,70	80%	0,71	0,28	0,45	0,89
	30%	1308	0,2935	19,39	70%	0,71	0,20	0,62	0,67
	40%	1803	0,2780	19,39	60%	0,66	0,43	0,46	0,77
	50%	2509	0,3123	62,20	50%	0,68	0,48	0,82	0,47
Interspaced									
	10%	146	0,0900	58	90%	0,82	0,02	0,96	0,44
	20%	1614	0,4936	49	80%	0,87	0,57	0,90	0,74
	30%	1545	0,3219	56,30	70%	0,86	0,71	0,81	0,76
	40%	2751	0,4273	51	60%	0,86	0,37	0,92	0,70
	50%	3610	0,4500	51,90	50%	0,86	0,02	1,00	0,63
Aggregated case 1									
	10%	319	0,2000	14	90%	0,46	0,67	0,00	1,00
	20%	2467	0,7659	9,15	80%	0,76	0,07	0,23	0,90
	30%	3857	0,7569	8,90	70%	0,86	0,12	0,97	0,74
	40%	3774	0,5821	24	60%	0,94	0,01	0,72	0,91
Aggregated case 2									
	10%	466	0,2900	36,00	90%	0,35	0,01	0,92	0,18
	20%	2084	0,6375	42,00	80%	0,18	0	1	0
	30%	3915	0,8206	6,20	70%	0,88	0,69	0,98	0,69
	40%	4043	0,6283	33,40	60%	0,90	0,17	0,98	0,74
Aggregated case 3									
	10%	75	0,0500	NA	90%	NA	NA	NA	NA
	20%	15	0,0047	6	80%	0,72	0,05	0,80	0,59
	30%	15	0,0036	10,40	70%	0,61	0,99	0,88	0,28
	40%	1283	0,1998	73	60%	0,74	0,53	0,61	0,86
Aggregated case 4									
	50%_a	5125	0,6368	16,60	50%_b	0,94	0,44	0,96	0,91
	50%_b	2584	0,3210	67,10	50%_a	0,73	0,88	0,71	0,71
Null models									
mean	10%	761	0,4726	45,84	90%	0,89	0,45	0,89	0,77
sd		18	0,011	2,22		0,00	0,04	0,03	0,02
mean	20%	1532	0,4762	45,00	80%	0,89	0,45	0,90	0,77
sd		32	0,010	0,79		0,00	0,02	0,02	0,01
mean	30%	2306	0,4779	44,65	70%	0,89	0,45	0,90	0,77
sd		34	0,007	1,42		0,00	0,01	0,01	0,01
mean	40%	3056	0,4751	44,35	60%	0,89	0,45	0,91	0,77
sd		45	0,007	0,85		0,00	0,02	0,01	0,01
mean	50%	3839	0,4774	44,66	50%	0,89	0,46	0,90	0,78
sd		32	0,004	0,62		0,00	0,01	0,01	0,00

Table B. Habitat of *Lithophyllum byssoides*

Models strategy

Aggregated

	training data	N	F	D2	test data	AUC	threshold	se	spe
	10%	658	0,4087	29,55	90%	0,80	0,05	0,53	0,82
	20%	1123	0,3486	53,70	80%	0,75	0,43	0,97	0,52
	30%	1343	0,3014	27,84	70%	0,68	0,29	0,97	0,43
	40%	1828	0,2818	19,39	60%	0,68	0,58	0,95	0,38
	50%	2505	0,3118	62,20	50%	0,74	0,59	0,85	0,50
Interspaced									
	10%	443	0,2700	39	90%	0,74	0,02	0,96	0,46
	20%	1304	0,3988	25,70	80%	0,77	0,40	0,92	0,54
	30%	1016	0,2421	27,60	70%	0,75	0,24	0,96	0,42
	40%	1800	0,2796	29,50	60%	0,75	0,30	0,90	0,51
	50%	2844	0,3500	25,60	50%	0,76	0,19	0,94	0,48
Aggregated case 1									
	10%	867	0,5400	5	90%	0,30	0,47	0,99	0,017
	20%	1865	0,5790	4,40	80%	0,72	0,09	0,25	0,89
	30%	2691	0,5281	5,30	70%	0,80	0,12	0,93	0,62
	40%	2951	0,4552	8,80	60%	0,85	0,01	0,81	0,77
Aggregated case 2									
	10%	571	0,3500	16	90%	0,26	0	1	0
	20%	1575	0,4818	7,80	80%	0,27	0,09	0,98	0,03
	30%	2551	0,5347	3,30	70%	0,50	0,36	0,90	0,62
	40%	2784	0,4326	13	60%	0,83	0,13	0,95	0,62
Aggregated case 3									
	10%	18	0,0100	NA	90%	NA	NA	NA	NA
	20%	119	0,0370	16,20	80%	0,74	0,93	0,96	0,45
	30%	109	0,0227	23,50	70%	0,58	0,97	0,91	0,19
	40%	932	0,1451	7,30	60%	0,50	0,53	0,97	0,08
Aggregated case 4									
	50%_a	3917	0,4867	5,70	50%_b	0,87	0,33	0,89	0,77
	50%_b	1703	0,2116	36	50%_a	0,53	0,62	0,63	0,45
Null models									
mean	10%	554	0,3439	24,31	90%	0,79	0,23	0,96	0,50
sd		16	0,0102	1,61		0,002	0,03	0,005	0,005
mean	20%	1111	0,3453	23,70	80%	0,79	0,25	0,96	0,51
sd		37	0,0114	1,02		0,001	0,08	0,302	0,161
mean	30%	1689	0,3499	23,67	70%	0,79	0,24	0,96	0,50
sd		29	0,0060	0,61		0,002	0,02	0,002	0,003
mean	40%	2221	0,3453	23,33	60%	0,79	0,24	0,96	0,51
sd		42	0,0065	0,71		0,004	0,05	0,016	0,019
mean	50%	2796	0,3476	23,45	50%	0,79	0,24	0,96	0,50
sd		25	0,0031	0,30		0,002	0,08	0,304	0,160

Table C. Habitat of *Lithophyllum byssoides* rim ("Trottoir")

Models strategy

	training data	N	F	D2	test data	AUC	threshold	se	spe
Aggregated									
	10%	15	0,01	34,98	90%	0,69	0,90	0,53	0,82
	20%	17	0,01	53,70	80%	0,66	0,04	0,05	0,96
	30%	17	0,00	29,03	70%	0,63	0,03	0,00	1,00
	40%	51	0,01	19,39	60%	0,46	0,00	1	0
	50%	175	0,02	62,20	50%	0,66	0,15	0,86	0,40
Interspaced									
	10%	267	0,160	35	90%	0,87	0,18	0,74	0,86
	20%	102	0,031	27	80%	0,75	0,03	0,74	0,68
	30%	282	0,059	27	70%	0,81	0,07	0,82	0,68
	40%	268	0,042	33	60%	0,79	0,05	0,72	0,81
	50%	931	0,116	37	50%	0,83	0,04	0,79	0,84
Aggregated case 1									
	10%	52	0,030	66	90%	0,43	0,01	0,02	0,98
	20%	160	0,050	23	80%	0,38	1	0	1
	30%	183	0,036	17	70%	0,69	0,01	0,74	0,61
	40%	942	0,145	41	60%	0,90	0,04	0,88	0,79
Aggregated case 2									
	10%	749	0,460	28	90%	0,73	0,02	0,94	0,58
	20%	786	0,240	37	80%	0,63	0,49	0,95	0,48
	30%	212	0,044	20	70%	0,66	0,001	1	0,31
	40%	859	0,133	46	60%	0,60	0,01	1	0,32
Aggregated case 3									
	10%	0	0,000	NA	90%	NA	NA	NA	NA
	20%	0	0,000	NA	80%	NA	NA	NA	NA
	30%	0	0,000	NA	70%	NA	NA	NA	NA
	40%	16	0,002	22	60%	0,82	0,18	0,68	0,86
Aggregated case 4									
	50%_a	1133	0,141	22	50%_b	0,37	0,28	0,71	0,38
	50%_b	23	0,003	22	50%_a	0,82	0,18	0,75	0,79
Null models									
mean	10%	112,4	0,0698	32,74	90%	0,89	0,08	0,82	0,81
sd		7,7	0,0048	2,87		0,002	0,02	0,037	0,040
mean	20%	228,6	0,0711	32,60	80%	0,89	0,08	0,82	0,80
sd		10,7	0,0033	2,06		0,003	0,02	0,041	0,038
mean	30%	344,7	0,0714	31,70	70%	0,89	0,07	0,83	0,79
sd		18,2	0,0038	1,79		0,005	0,02	0,038	0,035
mean	40%	460,2	0,0715	31,68	60%	0,89	0,07	0,84	0,78
sd		11,3	0,0018	1,59		0,006	0,03	0,042	0,044
mean	50%	577,4	0,0718	31,82	50%	0,89	0,07	0,84	0,78
sd		21,1	0,0026	0,76		0,004	0,02	0,040	0,040

Table D. Habitat of *Neogoniolithon brassica-florida*

Models strategy	**training data**	**N**	**F**	**D2**	**test data**	**AUC**	**threshold**	**se**	**spe**
Aggregated									
	10%	0	0	34,98	90%	0,19	0	1	0
	20%	0	0	53,70	80%	0,72	0	1	0
	30%	24	0,01	29,03	70%	0,90	0,21	0,94	0,87
	40%	157	0,02	19,39	60%	0,91	0,21	0,94	0,89
	50%	422	0,05	62,20	50%	0,85	0,31	0,85	0,90
Interspaced									
	10%	443	0,270	39	90%	0,74	0,02	0,96	0,46
	20%	1304	0,399	25,70	80%	0,77	0,4	0,92	0,54
	30%	1016	0,242	27,60	70%	0,75	0,24	0,96	0,42
	40%	1800	0,280	29,50	60%	0,75	0,3	0,90	0,51
	50%	2844	0,350	25,60	50%	0,76	0,19	0,94	0,48
Aggregated case 1									
	10%	867	0,540	5	90%	0,3	0,47	0,99	0,017
	20%	1865	0,579	4,40	80%	0,72	0,09	0,25	0,89
	30%	2691	0,528	5,30	70%	0,80	0,12	0,93	0,62
	40%	2951	0,455	8,80	60%	0,85	0,01	0,81	0,77
Aggregated case 2									
	10%	571	0,350	16	90%	0,26	0	1	0
	20%	1575	0,482	7,80	80%	0,27	0,09	0,98	0,03
	30%	2551	0,535	3,30	70%	0,50	0,36	0,90	0,62
	40%	2784	0,433	13	60%	0,83	0,13	0,95	0,62
Aggregated case 3									
	10%	18	0,010	NA	90%	NA	NA	NA	NA
	20%	119	0,037	16,20	80%	0,74	0,93	0,96	0,45
	30%	109	0,023	23,50	70%	0,58	0,97	0,91	0,19
	40%	932	0,145	7,30	60%	0,50	0,53	0,97	0,08
Aggregated case 4									
	50%_a	3917	0,487	5,70	50%_b	0,87	0,33	0,89427	0,77401
	50%_b	1703	0,212	36,20	50%_a	0,53	0,62	0,63441	0,44783
Null models									
mean	10%	553,7	0,344	24,31	90%	0,79	0,23	0,96	0,50
sd		16,4	0,010	1,61		0,002	0,03	0,005	0,005
mean	20%	1110,9	0,345	23,70	80%	0,79	0,25	0,96	0,51
sd		36,6	0,011	1,02		0,001	0,08	0,302	0,161
mean	30%	1688,5	0,350	23,67	70%	0,79	0,24	0,96	0,50
sd		28,8	0,006	0,61		0,002	0,02	0,002	0,003
mean	40%	2221,2	0,345	23,33	60%	0,79	0,24	0,96	0,51
sd		41,6	0,006	0,71		0,004	0,05	0,016	0,019
mean	50%	2795,5	0,348	23,45	50%	0,79	0,24	0,96	0,50
sd		24,7	0,003	0,30		0,002	0,08	0,304	0,160

Table E. Habitat of *Hildenbrandia - Phymatholiton*

Models strategy	**training data**	**N**	**F**	**D2**	**test data**	**AUC**	**threshold**	**se**	**spe**
Aggregated									
	10%	20	0,012	34,98	90%	0,64	0,01	0,59	0,72
	20%	52	0,016	53,70	80%	0,65	0,01	0,90	0,41
	30%	63	0,014	19,39	70%	0,63	0,01	1	0,27
	40%	76	0,012	19,39	60%	0,76	0,02	0,61	0,79
	50%	92	0,011	62,20	50%	0,66	0,01	0,4	0,83
Interspaced									
	10%	5	0,0030	NA	90%	NA	NA	NA	NA
	20%	12	0,0037	20,40	80%	0,73	0,01	0,37	0,90
	30%	16	0,0033	13,40	70%	0,81	0,01	0,65	0,79
	40%	72	0,0112	12	60%	0,64	0,01	0,68	0,59
	50%	75	0,0093	8	50%	0,67	0,03	0,48	0,89
Aggregated case 1									
	10%	2	0,0010	NA	90%	NA	NA	NA	NA
	20%	6	0,0019	NA	80%	NA	NA	NA	NA
	30%	10	0,0020	NA	70%	NA	NA	NA	NA
	40%	25	0,0039	9,80	60%	0,51	0,84	0,12	0,95
Aggregated case 2									
	10%	9	0,0050	NA	90%	NA	NA	NA	NA
	20%	31	0,0095	8,70	80%	0,68	0,01	0,73	0,56
	30%	77	0,0161	12,20	70%	0,82	0,02	0,74	0,81
	40%	84	0,0131	9,20	60%	0,71	0,03	0,46	0,92
Aggregated case 3									
	10%	2	0,0010	NA	90%	NA	NA	NA	NA
	20%	17	0,0053	8,70	80%	0,72	0,01	0,67	0,67
	30%	17	0,0041	26	70%	0,47	0,99	0,53	0,52
	40%	49	0,0076	12,20	60%	0,45	0,06	0,87	0,22
Aggregated case 4									
	50%_a	41	0,0093	8,90	50%_b	0,50	0,02	0,80	0,34
	50%_b	78	0,0055	14,10	50%_a	0,64	0,12	0,63	0,70
Null models									
mean	10%	11,1	0,0069	23,24	90%	0,78	0,01	0,56	0,82
sd		2,0	0,0013	8,97		0,029	0,004	0,12	0,06
mean	20%	21,6	0,0067	18,37	80%	0,79	0,01	0,56	0,84
sd		2,1	0,0006	3,17		0,031	0,004	0,06	0,03
mean	30%	33,8	0,0070	16,60	70%	0,80	0,01	0,59	0,83
sd		3,4	0,0007	2,72		0,029	0,004	0,09	0,04
mean	40%	43,8	0,0068	16,19	60%	0,80	0,01	0,60	0,83
sd		5,4	0,0008	1,56		0,022	0,000	0,05	0,03
mean	50%	59,3	0,0074	15,76	50%	0,81	0,01	0,61	0,82
sd		6,6	0,0008	2,60		0,026	0,003	0,07	0,04

Table F. Habitat of *Cystoseira mediterranea*

Models strategy

	training data	N	F	D2	test data	AUC	threshold	se	spe
Aggregated									
	10%	686	0,426	34,98	90%	0,62	0,55	0,98	0,35
	20%	1039	0,323	53,70	80%	0,71	0,28	0,45	0,89
	30%	1308	0,294	19,39	70%	0,71	0,20	0,62	0,67
	40%	1803	0,278	19,39	60%	0,66	0,43	0,46	0,77
	50%	2509	0,312	62,20	50%	0,68	0,48	0,82	0,47
Interspaced									
	10%	149	0,090	20	90%	0,69	0,02	0,96	0,44
	20%	966	0,295	16	80%	0,77	0,37	0,84	0,61
	30%	899	0,187	27,50	70%	0,50	0,01	0,89	0,15
	40%	1585	0,246	16,40	60%	0,65	0,24	0,76	0,47
	50%	1869	0,230	20	50%	0,77	0,19	0,87	0,58
Aggregated case 1									
	10%	319	0,200	16	90%	0,56	0,67	0,00	1,00
	20%	990	0,307	5,30	80%	0,32	0,19	0,99	0,01
	30%	1736	0,341	8,90	70%	0,31	0,91	0,92	0,14
	40%	1976	0,305	5,90	60%	0,69	0,10	1,00	0,45
Aggregated case 2									
	10%	466	0,290	14	90%	0,50	0,01	0,92	0,18
	20%	1421	0,435	9,70	80%	0,42	0,07	0,77	0,28
	30%	2414	0,506	8,60	70%	0,68	0,19	0,98	0,37
	40%	2615	0,406	9,40	60%	0,71	0,31	0,67	0,65
Aggregated case 3									
	10%	75	0,05	33	90%	0,49	0,00	1,00	0,00
	20%	179	0,06	17,30	80%	0,31	0,00	1,00	0,00
	30%	186	0,04	15,40	70%	0,42	0,00	1,00	0,00
	40%	1037	0,16	31,30	60%	0,48	0,49	0,98	0,05
Aggregated case 4									
	50%_a	2778	0,35	6,30	50%_b	0,60	0,43	1,00	0,44
	50%_b	1797	0,22	38	50%_a	0,62	0,38	0,56	0,60
Null models									
mean	10%	459,3	0,2853	21,67	90%	0,78	0,29	0,84	0,59
sd		18,4	0,0114	1,15		0,003	0,016	0,025	0,025
mean	20%	919,3	0,2858	21,49	80%	0,78	0,28	0,85	0,59
sd		29,5	0,0092	0,80		0,002	0,024	0,016	0,017
mean	30%	1363,7	0,2826	21,07	70%	0,78	0,28	0,85	0,59
sd		25,0	0,0052	0,70		0,002	0,015	0,016	0,017
mean	40%	1826,5	0,2839	21,04	60%	0,78	0,29	0,83	0,60
sd		34,7	0,0054	0,50		0,003	0,024	0,030	0,029
mean	50%	2277,4	0,2832	20,89	50%	0,78	0,28	0,84	0,59
sd		26,8	0,0033	0,37		0,003	0,032	0,037	0,037

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