Universitat de Girona

CYSTOSEIRA-DOMINATED ASSEMBLAGES FROM SHELTERED AREAS IN THE MEDITERRANEAN SEA : DIVERSITY, DISTRIBUTION AND EFFECTS OF POLLUTION

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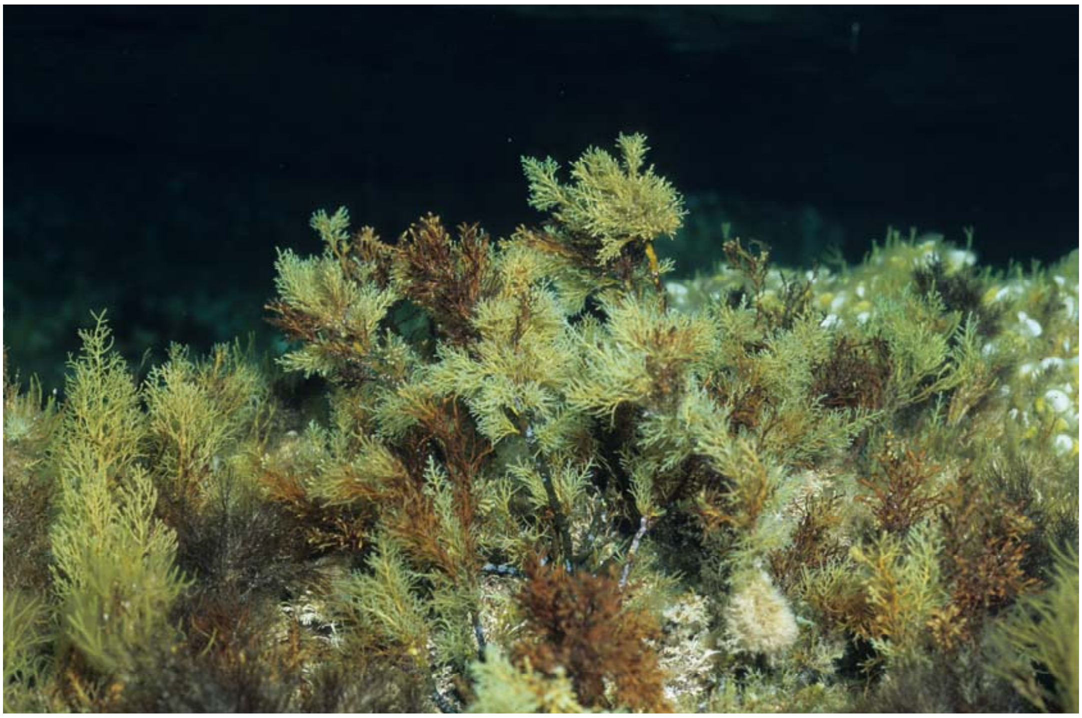
Cystoseira-dominated assemblages from sheltered areas in the Mediterranean Sea:

Diversity, distribution and effects of pollution

Ph.D. Thesis



Marta Sales Villalonga

2010

Universitat de Girona

CENTRE D'ESTUDIS AVANÇATS DE BLANES

Tesi doctoral

Cystoseira-dominated assemblages from sheltered areas in the Mediterranean Sea: Diversity, distribution and effects of pollution

Memòria presentada per optar al títol de doctora per la Universitat de Girona

Marta Sales Villalonga

Blanes, abril 2010

Programa de doctorat: Ecologia fonamental i aplicada. Sistemes marins

El director de la Tesi	El tutor de la Tesi
Dr. Enric Ballesteros	**Dr. Sergi Sabater**
Investigador científic	Professor titular
Centre d'Estudis Avançats de Blanes (CSIC)	Facultat de Ciències (UdG)

Universitat de Girona

CENTRE D'ESTUDIS AVANÇATS DE BLANES

El Dr. Enric Ballesteros Sagarra, investigador científic del Centre d'Estudis Avançats de Blanes (CSIC), i el Dr. Sergi Sabater, professor titular de la Facultat de Ciències (UdG)

CERTIFIQUEN:

Que aquest treball, titulat "*Cystoseira*-dominated assemblages from sheltered areas in the Mediterranean Sea: diversity, distribution and effects of pollution", que presenta Marta Sales Villalonga per a l'obtenció del títol de doctora, ha estat realitzat sota la direcció i la tutoria de

Enric Ballesteros	Sergi Sabater
Director de la Tesi	Tutor de la Tesi

Girona, 13 d'abril de 2010

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Un passeig per Menorca i altres platges mediterrànies

Com s’ha fet aquesta tesi

És possible que tot vagi començar l’estiu del 2003 a la badia de Fornells, quan estava treballant al Diving Fornells ja que, després d’uns anys de participar en diversos projectes, m’havia quedat sense feina de biòloga. En Kike i l’Emma van venir a fer una de les seves campanyes a la Reserva Marina i en Juli, qui portava el Diving Fornells en aquell moment, em va dir: has d’anar a treballar amb en Kike. Jo me’l vaig mirar amb cara de moniato i li vaig dir: no sé, no sé. Uns dies més tard, aprofitant una lumbàlgia de l’Emma, vaig anar a substituir-la comptant feixos de *Cymodocea* i *Zostera* a 4 metres de fondària durant més de dues hores i durant dos dies. No m’estranya que alguns de nosaltres acabem amb lumbàlgia: amb aquell botilot que no sé el què deu pesar i un raig de ploms a la cintura. Al final li vaig acabar demanant a en Kike si hi havia alguna possibilitat de treballar amb ell. Em va dir que la cosa estava complicada, però que li donés un currículum. I al cap de 9 mesos estava fent les maletes per anar a viure a Blanes, d’entrada només per 7 mesos. M’ho vaig prendre com una prova, ja que no em veia ni treballant a un centre de recerca ni vivint a Blanes.

Si no em veia treballant a un centre de recerca, encara menys em veia fent la tesi. Però allò de la feina i el centre de recerca em va començar a agradar més del que em pensava. I només al cap de tres mesos de ser-hi ja estava demanant una beca per poder-m’hi quedar un any més (què em va agafar?). Jo sempre havia pensat que la feina, quanta menys en pogués fer millor, i la resta del temps a gaudir de la vida. I em veia ficant-me en el món de la recerca, un món que des de fora veia, i segueixo veient, com de gran sacrifici i dedicació. Però no és més sacrifici complir rutinàriament un horari per a fer una feina que ens satisfà només a mitges? Bé, sigui com sigui, vaig demanar aquella beca per un any amb la idea de fer el

DEA i després ja veuria si feia o no la tesi. Em vaig passar una primavera passejant per les cales de Menorca i anotant les abundàncies de les diferents espècies de *Cystoseira* que hi trobava. Aquell any, el 2005, vaig passar l'hivern a Blanes i l'estiu a Menorca, va ser un any fantàstic! I quan ja estava a punt d'acabar-se, jo ja em veia acabant el meu període de recerca i entrant a fer feina com a tècnica a l'equip del Kike. En Kike tenia fama de no voler dirigir tesis, i jo ja feia alguns anys que havia acabat la carrera i no tenia gaires possibilitats de tenir una beca. I com qui no vol la cosa, el setembre en Kike em va dir: l'any que ve, ja saps, si aconsegueixes diners decideixes el que fas; si no, jo mano. En aquell moment vaig veure claríssim que preferia la primera opció, així que vaig començar a navegar per Internet a la recerca d'una beca que al menys pogués demanar. I en vaig trobar una, em costava de creure. Em vaig assegurar que fos cert el que em semblava haver entès i vaig començar a preparar els papers, i vaig tenir la sort que me la van donar. Així, a partir d'aquest moment ja estava "oficialment" fent la tesi. Això era l'abril de 2006.

A partir d'aleshores vaig començar a fer feina de camp gairebé a totes hores. A Cala Pregonda m'hi dec haver passat més hores que ningú, a totes les hores del dia i en les diferents èpoques de l'any. Sense vent, amb sol o pluja, comptant i mesurant *Cystoseiras* com una boja. Allà vaig fer el meu rècord d'hores seguides a l'aigua: 6 hores, sense sortir, de veritat. Tenia una certa rutina: gairebé cada dia que no feia vent anava a Cala Pregonda, i un cop al mes anava a Cala Barril i al Macar de Tirant. M'encantava: estar en contacte amb la natura a llocs bonics, tota sola. Quan arribava l'estiu i s'omplien les cales de gent em posava de mal humor, havien envaït el meu espai. Després de dos anys de feina de camp en solitari, amb algunes excepcions de visites i feina conjunta amb en Kike, en Boris i na Maria, va ser enviat el comando Fiona i Emma. Gairebé em maten. Jo estava acostumada al meu ritme menorquí. Vam fer en quatre dies el que jo creia que es podia fer fent molta feina durant una setmana. Com ho vam fer? Fent feina de sol a sol, o més, i anat a un ritme frenètic. Em costava assimilar el que fèiem durant el dia, que bàsicament es tractava de trasplantar *Cystoseiras* de Fornells a Maó per veure com reaccionaven a la contaminació. Al cap de 10 o 15 dies van venir en Bernat i en Xavi. Jo tenia por de trobar-me un desastre: els trasplantaments desenganxats, perduts o fets malbé. I com que els dos s'havien ofert a venir algun dia a ajudar-me els vaig dir que aquell era el moment. Per sort, tot estava bastant bé i no els vaig donar molta feina.

Vaig interrompre aquesta rutina en diverses ocasions per anar a fer campanyes o estades a altres llocs del Mediterrani i completar així els meus inventaris a una escala espacial més gran. Vaig fer una campanya a Còrsega i Sardenya en la qual em va acompanyar primer en Kike i al final, n'Eva. Va durar un mes i ens vam passejar per les cales de Còrsega i Sardenya mostrejant comunitats de *Cystoseira crinita*. La major part dels dies vam dormir a terra: a càmpings, platges o a la casa dels guardes de Scandola. Fèiem moltes hores de feina i molts kilòmetres. Després vaig fer una estada a Croàcia i una a Bulgària, on també em vaig passejar per les cales buscant *Cystoseira crinita*. A Istria, al nord de Croàcia, n'hi havia molta, i na Ljiljana em va acompanyar en les sortides de camp. A Bulgària hi havia dues espècies de *Cystoseira*: una era *C. barbata* i l'altra encara no ho sabem. En Mitko em va acompanyar en les sortides de camp que vaig fer allà.

Durant aquests anys de feina de camp vivia a Menorca i passava algun temps a Blanes, tal com segueixo fent. Les visites a Blanes les aprofitava bàsicament per repassar i acabar d'identificar les alguetes amb en Kike (les difícils i les no tant difícils), per escriure, fer paperassa, etc.

El treball de laboratori de la tesi no ha requerit la utilització de gaires aparells complexos. La major part de la feina ha consistit a separar mostres amb pinces i safates de laboratori i identificar espècies amb lupa i microscopi. Només a l'última part vaig haver de fer immersió en el laboratori de perillosos per preparar mostres per fer anàlisis de metalls pesants. Sort que l'Emma em va ajudar i vam anar molt més ràpid. També vaig passar algunes hores al "zulo" de la microbalança, que està en una micro-habitació.

Una vegada acabada la feina de camp i de laboratori, va venir la part d'escriure. A jo m'agrada escriure, quan era petita somniava que un dia seria escriptora, però aquí em teniu.. Ha estat quasi un any d'analitzar dades, llegir molt, i escriure. D'aquest any, tres mesos els he passat a Auckland, Nova Zelanda, treballant amb la Marti Anderson i el seu equip, el que m'ha permès millorar els meus coneixements d'estadística i el meu anglès.

Finalment, els agraïments. Vull agrair a en Kike que m'hagi dirigit la tesi i m'hagi ensenyat a observar i interpretar la natura. A l'Emma que hagi col·laborat en aquesta tesi, que m'hagi transmès entusiasme, que m'hagi acollit a casa seva, i tantes coses més. A la Fiona també per haver participat en la part final de la tesi. Ha estat un plaer treballar amb vosaltres dues. A la Marti Anderson i a la Ljiljana Ivesa, que em van acollir respectivament a Nova Zelanda i a Croàcia. Gràcies per tot el que m'heu ensenyat i pel que heu compartit amb jo.

Del CEAB, on s'ha desenvolupat aquesta tesi, un agraïment general pel bon ambient i el companyerisme i el cop de mà aquell que cal aquí o allà alguna vegada. De manera especial, a la gent de l'equip del Kike: Susana, gràcies per ensenyar-me estadística; Xavi, gràcies per ajudar-me amb coses diverses, des de senzills problemes informàtics a recollir aigua a les cales de Menorca; Boris, gràcies per venir a recollir aigua amb mi per tota Menorca i pels comptatges de *Cystoseira*; això també va per la Maria; Raquel, gràcies per ensenyar-me a separar mostres; la Paula i la Neus també em van acompanyar a buscar mostres d'aigua; Paoletta, gràcies per preparar algunes de les mostres de metalls; Emma, gràcies per ensenyar-me GIS, la preparació de les mostres de metalls i no sé quantes coses més; Toni, gràcies per acollir-me al teu despatx al principi. També gràcies a molta altra gent: Enric Sala: per portar-me mostres de Grècia i Turquia i per convidar-me a fer una campanya amb tu a Menorca; Rafel Coma: pels comentaris sobre la demografia i per ensenyar-me com va això de la massilla; Sònia, per ser-hi i ser una bona companyia en tot moment i pel bon rotllo mentre vam compartir casa; Cristina, per animar-me en moments clau i per compartir el despatx amb mi encara que per poc temps; Simone i Miquel, per compartir el pis amb mi al final de la tesi, les xerradetes i els sopars; i a tots els companys de feina amb els que he compartit xerrades, dinars i estones: Andrea, Laura, Òscar, Tina, Mireia, Guillermo, Eduard, Joao, Dani, Xabi, Raffaele, Marc, Maria Elena, Adriana, Roser, Arianna, Santi, etc. Ramon, gràcies per "curar" l'ordinador quan està "malalt", i Roser, Marta, Susanna, Gemma i Carmela, gràcies per aclarir papers, comandes, i per ser tan simpàtiques.

Altres persones de fora del CEAB han col·laborat a aquesta tesi bé aportant-hi directament alguna cosa, o bé influint en el meu aprenentatge i llavors col·laborant-hi igualment, encara que indirectament. En Francesc Oliva i en Miquel de Cáceres, professors del curs de doctorat d'Anàlisi Multivariant van mostrar interès per la meva feina i em van ajudar amb l'anàlisi del tercer capítol: no sé si hauria descobert mai la transformació de Van der Maarel o l'estadístic de la silueta sense vosaltres. En Jordi Camp i l'Eva Flo, del CMIMA, també van mostrar interès i em van fer

comentaris molt interessants sobre el tercer capítol de la tesi. A Menorca, el personal del Parc Natural Albufera des Grau (Miquel, Òscar, Biel, Cuca) m'han permès utilitzar el laboratori i també m'han acompanyat i ajudat en algunes sortides de camp. També gràcies al personal de la Direcció General de Pesca (Pep, Oliver) per concedir-me els permisos per treballar a la Reserva Marina del Nord, i també als vigilants (David i Fabi) per acompanyar-me en alguna sortida de camp. Gràcies també a l'OBSAM per concedir suport en diferents formes: finançament, facilitar-me cartografia, ajuda amb el GIS, ajuda al camp, etc. També han ajudat en la logística del treball de camp diversos amics que m'han acompanyat i ajudat en el mostreig i que, fins i tot, han anat a cercar-me mostres quan jo no hi era (Eva, Ricard, Mercè, Agnès, Melisa, Txus, David, Aina, Sílvia, Joan). Ricard, gràcies per transformar-me aquelles coordenades que estaven en un sistema que no "tocava". Miquel, gràcies per ajudar-me a discernir entre els torrents permanents, estacionals i ocasionals i per altres discussions teòriques com les variacions del nivell del mar durant el Quaternari. Amb en Lluis Cardona, professor de la Universitat Pompeu Fabra, he col·laborat en diversos estudis abans de començar la tesi i també durant el desenvolupament de la mateixa, el que ha contribuït a la meva formació com a científica. La Conxi Rodríguez i el seu equip de la Universitat de Girona s'han encarregat de l'herborització d'alguns dels espècimens més destacats trobats durant el mostreig de la tesi.

L'autora de la tesi ha rebut finançament mitjançant una Beca I3P de postgrau del CSIC i una beca del programa FI de la Generalitat de Catalunya, ambdues cofinançades pel Fons Social Europeu. A més, la doctoranda ha rebut finançament de la Generalitat de Catalunya i del CSIC per realitzar estades en centres estrangers. El finançament de les campanyes de mostreig i les analítiques ha anat a càrrec de diversos projectes pertanyents al Centre d'Estudis Avançats de Blanes amb fons de l'Agència Catalana de l'Aigua, l'Agència Balear de l'Aigua i de la Qualitat Ambiental, i el Plan Nacional (Projecte GRACCIE, CSD2007-00067). També s'han rebut subvencions provinents de l’Institut Menorquí d’Estudis i del Consell Insular de Menorca.

Gràcies a tots els amics pel suport moral al llarg d’aquesta tesi o en diferents moments del seu desenvolupament. Als de Catalunya: Emma, Xavi, Sònia, Cristina, Roser, Oriol, Eva, Neus, Dani, als del Hockei-sub, ... i als de Menorca: Eva, Ricard, David, Agnès, Txus, Joan, Gemma, Carles, Fel, Ferran, Geni, Bep, Iolanda...

Finalment, gràcies als meus pares i al meu germà pel suport incondicional en tot moment.

Es Mercadal, Menorca, 10 de març de 2010

Marta Sales

Resum

Resum

Les macroalgues dels ordres Laminarials i Fucals (Feofícies, Heterocontòfits) són algues grans i morfològicament complexes. Canvien les condicions ambientals del seu entorn proper, creant ombra i refugi; i també serveixen com a substrat per a nombroses algues i invertebrats. En ambients marins, aquestes macroalgues juguen un paper semblant al que juguen els arbres en boscos terrestres. Mentre als fons rocosos infralitorals de la majoria d'oceans temperats hi dominen algues de l'ordre Laminarials (coneguts amb el nom anglès de "kelps"), al Mar Mediterrani són espècies del gènere *Cystoseira* (Fucals) les que dominen aquest tipus de fons.

En el marc d'aquesta tesi, s'han estudiat les comunitats dominades per espècies del gènere *Cystoseira* que viuen en àrees someres i calmades del Mar Mediterrani. Per una banda, s'han descrit les comunitats dominades per *Cystoseira crinita*, tant a nivell local com a nivell regional. D'altra banda, s'han identificat els factors ambientals que més influeixen en la distribució de les espècies de *Cystoseira* de zones calmades a Menorca (Illes Balears). Finalment, s'han estudiat els efectes de la contaminació en tres espècies del gènere *Cystoseira*.

S'han portat a terme mostrejos a badies i cales de diferents regions del Mediterrani per tal d'obtenir inventaris de la composició específica i de l'estructura de les comunitats dominades per *C. crinita*. Les dades referents a factors ambientals han estat obtingudes durant el treball de camp o utilitzant cartografia i Sistemes d'Informació Geogràfica (GIS). A més, també s'han realitzat anàlisis de concentració de nutrients i de

metalls pesants en aigua de mar, sediments i teixits de les algues al laboratori.

La identitat, qüestionada per altres ficòlegs, de *Cystoseira crinita* com a espècie dominant de les comunitats del Cap Cors (Còrsega) estudiades i descrites per Molinier fa cinquanta anys ha estat confirmada. No s'han detectat canvis substancials a llarg termini en la composició i estructura de les comunitats dominades per *C. crinita* del Cap Cors, en concordança amb la bona qualitat ambiental de la zona. Les comunitats dominades per *C. crinita* s'han descrit tenint en compte gran part de la seva àrea de distribució (el Mar Mediterrani). Les característiques principals que semblen definir les comunitats dominades per *C. crinita* a nivell Mediterrani són: una cobertura total de les espècies i una cobertura de *C. crinita* similars, juntament amb una elevada abundància de l'epífit *Haliptilon virgatum*.

La variació biogeogràfica de les comunitats dominades per *C. crinita* es caracteritza, principalment, per canvis en l'abundància de les espècies entre les diverses regions estudiades. Aquesta variació ha permès identificar diferents regions que coincideixen, parcialment, amb les regions biogeogràfiques prèviament descrites al Mar Mediterrani. Les principals diferències trobades en el nostre estudi respecte la biogeografia clàssica del Mediterrani, que proposa una divisió principal a l'est de Sicília, dividint el Mar Mediterrani en dues conques (est i oest) han estat dues. La primera és una gran diferència entre les comunitats de Menorca (nord de les Illes Balears) i Formentera (sud de les Illes Balears), mostrant les comunitats de Formentera una major afinitat amb algunes de les comunitats del Mar Egeu (concretament les de les illes del Dodecanès, a Grècia). La segona és una major semblança de les comunitats del nord de l'Adriàtic amb les del nord-oest del Mediterrani, que no pas amb les de l'est del Mediterrani. A més, no s'ha trobat correlació entre la longitud geogràfica i la riquesa en espècies, el que contradiu la visió clàssica que suggereix que al Mediterrani es dóna un gradient d'empobriment de oest a est, o sigui, en el sentit de colonització d'espècies des de l'Atlàntic. En canvi, el que sí s'ha trobat ha estat una correlació positiva entre la riquesa específica i la latitud.

Les principals espècies de *Cystoseira* que viuen a les cales i badies de Menorca són *C. crinita, C. spinosa* v. *tenuior, C. barbata, C. foeniculacea* v. *tenuiramosa* i *C. compressa* v. *pustulata*. *C. crinita* i *C. spinosa* v. *tenuior* dominen comunitats complexes amb una elevada densitat d'individus de *Cystoseira* a la majoria de cales de la costa nord, on el grau d'exposició és intermedi. *C. barbata, C. foeniculacea* v. *tenuiramosa* i *C. compressa* v. *pustulata* apareixen esparses entre herbeis de la fanerògama *Cymodocea nodosa* a badies extremadament calmades, com les badies de Fornells i Addaia. Els principals factors que influeixen en la distribució d'aquestes espècies són: alçada de la costa, concentració de nitrats i nitrits a l'aigua, inclinació de la costa al primer metre de fondària, naturalesa del fons de la cala i distància a la urbanització més propera. Les cales amb costa baixa, inclinació horitzontal i fons de roca coberts per algues o fanerògames presenten un elevat nombre d'espècies de *Cystoseira,* constituint comunitats molt estructurades. A les cales amb costa elevada, inclinació vertical i/o concentració elevada de nitrats, el nombre i abundància d'espècies de *Cystoseira* és reduït. A les cales situades a la proximitat de ports importants (Maó i Ciutadella) les algues del gènere *Cystoseira* hi són totalment absents. A més, la desaparició de les espècies *C. crinita* i *C. barbata* del port de Maó ha pogut ser documentada gràcies a l'existència de dades històriques proporcionades pel reconegut botànic i algòleg Joan Joaquim Rodríguez-Femenías.

A l'experiment portat a terme per estudiar els efectes de la contaminació en les espècies *C. crinita*, *C. barbata* i *C. spinosa* v. *tenuior*, es van trasplantar individus de *Cystoseira* d'una badia natural (Fornells) a dues àrees del port de Maó amb diferents nivells de contaminació (Cala Llonga: lloc molt contaminat; Cala Teulera: lloc lleugerament contaminat). Els individus de *Cystoseira* trasplantats al lloc molt contaminat, on es van detectar elevades concentracions de metalls pesants, van mostrar efectes negatius en la supervivència i el creixement. Amb aquest resultat s'ha aportat la primera evidència experimental de la desaparició de *Cystoseira* relacionada amb la contaminació. A Cala Teulera, la zona lleugerament contaminada, les concentracions de metalls pesants, tot i ser més elevades que les concentracions detectades al lloc control (Fornells), no excedien diversos valors de referència proposats per diferents autors com a valors a partir dels quals hi pot haver efectes negatius en la biota. En aquest lloc, els espècimens de *Cystoseira* no van mostrar disminució en la seva supervivència ni en el seu creixement, indicant doncs, que les espècies desaparegudes a Cala Teulera hi poden viure actualment. La causa més probable és una millora de la qualitat de l'aigua relacionada amb la construcció d'infraestructures per a la conducció i el tractament de les aigües residuals. La recuperació natural de les poblacions de *Cystoseira* és nul·la, o molt lenta, a causa de la baixa dispersió que presenten els zigots de les espècies de *Cystoseira*. Per tant, doncs, se suggereix el trasplantament d'espècimens adults de *Cystoseira* com a tècnica per restaurar poblacions extingides.

Resumen

Resumen

Las macroalgas de los órdenes Laminariales y Fucales (Feofíceas, Heterocontófitos) son algas grandes y morfológicamente complejas. Alteran las condiciones ambientales de su entorno, creando sombra y refugio; y también sirven de sustrato para numerosas algas e invertebrados. En ambientes marinos, estas macroalgas juegan un papel ecológico parecido al que juegan los árboles en los bosques terrestres. Las algas del orden Laminariales (conocidas con el nombre inglés de "kelps") ocupan gran parte de los fondos rocosos infralitorales en la mayoría de océanos templados, mientras que en el Mar Mediterráneo las algas que habitan este tipo de fondos son especies del género *Cystoseira* (Fucales).

En el marco de esta tesis, se han estudiado comunidades dominadas por especies del género *Cystoseira* que viven en áreas someras y calmadas del Mar Mediterráneo. Por un lado, se han descrito las comunidades dominadas por *Cystoseira crinita*, tanto a nivel local como a nivel regional. Por otro lado, se han identificado los factores ambientales que más influyen en la distribución de las especies de *Cystoseira* en las zonas calmadas de Menorca (Islas Baleares). Finalmente, se han estudiado los efectos de la contaminación en tres especies del género *Cystoseira*.

Se han llevado a cabo muestreos en bahías y calas de diferentes regiones del Mediterráneo para obtener inventarios de la composición específica y de la estructura de las comunidades dominadas por *C. crinita*. Los datos referentes a factores ambientales se han obtenido durante las visitas de campo o utilizando cartografía y Sistemas de Información Geográfica (GIS). También se han realizado análisis de concentración de nutrientes y de metales pesados en agua de mar, sedimentos y tejidos de las algas en el laboratorio.

La identidad, cuestionada por algunos ficólogos, de *Cystoseira crinita* como especie dominante de las comunidades del Cap Corse (Córcega) estudiadas y descritas por Molinier hace cincuenta años ha sido confirmada. No se han detectado cambios substanciales a largo término en la composición y estructura de las comunidades dominadas por *C. crinita* del Cap Corse, en concordancia con la buena calidad ambiental de la zona. Las comunidades dominadas por *C. crinita* se han descrito teniendo en cuenta gran parte de su área de distribución (el Mar Mediterráneo). Las características principales que parecen definir las comunidades dominadas por *C. crinita* a nivel Mediterráneo son: una cobertura total de las especies y una cobertura de *C. crinita* parecidas, junto con una elevada abundancia del alga epífita *Haliptilon virgatum*.

La variación biogeográfica de las comunidades dominadas por *C. crinita* se caracteriza, principalmente, por cambios en la abundancia de las especies entre las diferentes regiones estudiadas. Esta variación ha permitido identificar diferentes regiones que coinciden, parcialmente, con las regiones biogeográficas previamente descritas en el Mar Mediterráneo. Las principales diferencias encontradas en nuestro estudio respecto a la biogeografía clásica del Mediterráneo, que propone una división principal al este de Sicilia, dividiendo el Mar Mediterráneo en dos cuencas (este y oeste), han sido dos. La primera es una gran diferencia entre las comunidades de Menorca (norte de las Islas Baleares) y Formentera (sur de las Islas Baleares), mostrando las comunidades de Formentera una mayor afinidad con algunas de las comunidades del Mar Egeo (concretamente las de las islas del Dodecaneso, en Grecia). La segunda es un mayor parecido entre las comunidades del Adriático norte y las del Mediterráneo noroeste, que entre las del Adriático y las del Mediterráneo este. Por otro lado, el gradiente de empobrecimiento en especies en dirección este, sugerido por diversos estudiosos de la biodiversidad Mediterránea, se contradice con nuestros resultados en base a los cuales no se ha detectado correlación alguna entre la longitud geográfica y la riqueza en especies.

Las principales especies de *Cystoseira* que viven en las calas y bahías de Menorca son *C. crinita*, *C. spinosa* v. *tenuior*, *C. barbata*, *C. foeniculacea* v. *tenuiramosa* y *C. compressa* v. *pustulata*. *C. crinita* y *C. spinosa* v. *tenuior* dominan comunidades complejas con una elevada densidad de individuos de *Cystoseira* en la mayoría de las calas de la costa norte, donde el grado de exposición es intermedio. *C. barbata*, *C. foeniculacea* v. *tenuiramosa* y *C. compressa* v. *pustulata* aparecen dispersas entre praderas de la fanerógama *Cymodocea nodosa* en bahías extremadamente calmadas, como las bahías de Fornells y Addaia. Los principales factores que influyen en la distribución de estas especies son: altitud de la costa, concentración de nitratos y nitritos en el agua, inclinación de la costa en el primer metro de profundidad, naturaleza del fondo de la cala y distancia a la urbanización más próxima. Las calas con costa baja, inclinación horizontal y fondo de roca cubierto por algas o fanerógamas presentan un elevado número de especies de *Cystoseira*, constituyendo comunidades muy estructuradas. En las calas con costa alta, inclinación vertical y/o concentración alta de nitratos, el número y abundancia de especies de *Cystoseira* es reducido. En las calas situadas en la proximidad de puertos importantes (Maó y Ciutadella) las algas del género *Cystoseira* están totalmente ausentes. Además, la desaparición de las especies *C. crinita* y *C. barbata* del puerto de Maó ha podido ser documentada gracias a la existencia de datos históricos obtenidos por el reconocido botánico y algólogo Joan Joaquim Rodríguez-Femenías.

En el experimento llevado a cabo para estudiar el efecto de la contaminación en las especies *C. crinita*, *C. barbata* y *C. spinosa* v. *tenuior*, se trasplantaron individuos de *Cystoseira* de una bahía natural (Fornells) a dos áreas del puerto de Maó con diferentes niveles de contaminación (Cala Llonga: muy contaminado; Cala Teulera: ligeramente contaminado). Los individuos de *Cystoseira* trasplantados al lugar muy contaminado, donde se detectaron elevadas concentraciones de metales pesados, mostraron efectos negativos en la supervivencia y el crecimiento. Con este resultado se ha aportado la primera evidencia experimental de la desaparición de *Cystoseira* relacionada con la contaminación. En Cala Teulera, zona ligeramente contaminada, las concentraciones de metales pesados, aunque eran más elevadas que las concentraciones detectadas en la zona control (Fornells), no excedían diversos valores de referencia propuestos por varios autores como valores a partir de los cuales se pueden dar efectos negativos en la biota. En esta zona, los especímenes de *Cystoseira* no mostraron disminución en la supervivencia ni en el crecimiento, sugiriendo que las especies desaparecidas de Cala Teulera pueden vivir actualmente en este lugar. La causa más probable de este resultado es una mejora de la calidad del agua relacionada con la construcción de infraestructuras para la conducción y el tratamiento de las aguas residuales. La recuperación natural de las poblaciones de *Cystoseira* es nula, o muy lenta, debido a la baja capacidad de dispersión de los zigotos de las algas del género *Cystoseira*. Por lo tanto, se sugiere el trasplante de especímenes adultos de *Cystoseira* como técnica para restaurar poblaciones extinguidas.

Summary

Summary

Macroalgae of the orders Laminariales and Fucales (Phaeophyceae, Heterokontophyta) are big and morphologically complex algae. They change environmental conditions around them, creating shadow and shelter and also, serve as substrate to other algae and invertebrates. In short, in the marine environment these brown seaweeds play the same role that trees do in terrestrial forests. While shallow waters of most temperate oceans are dominated by algae of the order Laminariales (known as kelps) in the Mediterranean Sea species of the genus *Cystoseira* (Fucales) are the dominant species in shallow rocky bottoms.

In this thesis, the assemblages dominated by species of the genus *Cystoseira* that thrive in shallow sheltered areas of the Mediterranean have been studied. First, we have addressed the description of the assemblages dominated by *Cystoseira crinita* both at local and regional level. Second, we have identified the main factors driving the distribution of *Cystoseira* species in sheltered areas from Minorca (Balearic Islands). Finally, we have studied the effects of pollution in three *Cystoseira* species.

Surveys have been carried out in bays and coves from different regions of the Mediterranean Sea in order to obtain inventories of the species composition and structure of the assemblages. Data on environmental factors has been obtained during the field surveys, and also using Geographical Information System (GIS) tools. Laboratory work has been required for analysing nutrient concentration in seawater and algal tissues, and for analysing heavy metal concentration in sediments and algal tissues.

Cystoseira crinita has been identified as the dominant species in the same sites that were surveyed by Molinier fifty years ago, thus confirming the identity of this species, and noticing that no substantial long-term changes have occurred in these assemblages from Cap Corse (northern Corsica). The assemblages dominated by *C. crinita* have been described taking into account the regional context (the Mediterranean Sea), which coincides with the distributional range of *C. crinita*. Similar total cover and similar cover of the dominant species, together with high abundance of the epiphyte *Haliptilon virgatum* have been identified as the main features characterizing *C. crinita*-dominated assemblages at Mediterranean scale.

Assemblages dominated by *C. crinita* show shifts in species abundances among regions, partly coinciding with previously described biogeographical sectors. Two departures of the classical biogeographical view of the Mediterranean, which places the main division close to Sicily, have been found. The first is a strong shift between the assemblages from Minorca (northern Balearic Islands) and Formentera (southern Balearic Islands), the latter showing higher affinity with Dodecanese Islands (Aegean Sea, Greece). The second is a higher similarity of the assemblages from northern Adriatic to those from north-western Mediterranean than to those from eastern Mediterranean. Moreover, it has not been found any correlation between longitude and species richness, in contrast with a classical view that invokes a biodiversity impoverishment gradient from western to eastern Mediterranean. However, a significant positive correlation has been found between latitude and species richness.

The main *Cystoseira* species inhabiting shallow sheltered areas in Minorca were *C. crinita*, *C. spinosa* v. *tenuior*, *C. barbata*, *C. foeniculacea* v.

tenuiramosa and *C. compressa* v. *pustulata*. *C. crinita* and *C. spinosa* v. *tenuior* dominate dense settlements in most of the northern coves of the island, with an intermediate exposure degree. *C. barbata*, *C. foeniculacea* v. *tenuiramosa* and *C. compressa* v. *pustulata* appear sparse within *Cymodocea nodosa* meadows in extremely sheltered areas. The main factors identified to influence *Cystoseira* species distribution in sheltered areas are: coast height, nitrate and nitrite concentration in seawater, coast slope at 0-1 m depth, nature of the bottom and urbanisation distance. Coves with low coast, horizontal slope and rocky bottoms, covered by seaweeds or seagrasses present a high number of *Cystoseira* species forming dense settlements. Features like high coast, vertical slope, and elevated nitrate concentration prevent the presence of *Cystoseira* species. Coves situated at the vicinity of important harbours were completely devoid of *Cystoseira* specimens, and the disappearance of some *Cystoseira* species could be documented for Maó harbour due to the existence of historical data.

In a field experiment conducted to examine pollution effects on *Cystoseira crinita*, *C. barbata* and *C. spinosa* v. *tenuior*, *Cystoseira* specimens were transplanted from a non-impacted sheltered bay to two areas of Maó harbour displaying different levels of pollution. The results of the experiment evidenced a relationship between high concentrations of heavy metals and reduced survival and growth of *Cystoseira* specimens transplanted to the highly polluted area. *Cystoseira* specimens transplanted to the slightly polluted area did not show negative responses to pollution. These results demonstrate that *Cystoseira* specimens can live in this area with the current environmental conditions, which probably have improved due to the building of new infrastructures for waste water management. The natural recovery of *Cystoseira* populations is nil or very slow due to the low dispersion range of the zygotes of *Cystoseira* species. Therefore, transplantation is suggested as a tool for restoring extinct populations.

Introduction

Introduction

Macroalgae, why macroalgae?

The term macroalgae refers to a group of photosynthetic organisms, phylogenetically diverse, which includes multicellular red, green and brown algae (Lobban & Harrison 1994). Marine macroalgae (known as seaweeds), together with marine flowering plants (known as seagrasses), are the main benthic primary producers of the marine realm (Mann 1973). The sublittoral zone on most temperate rocky shores is dominated by brown algae of the orders Laminariales (known as kelps) and Fucales (Ribera et al. 1992, Steneck et al. 2002). These big perennial macroalgae are considered engineering or foundation species, since display a three-dimensional structure that provides habitat for a high number of algae and invertebrates (Mann 1973, Dayton 1985, Graham 2004). Assemblages dominated by Fucales and Laminariales present important parallels with terrestrial forests, with different vegetation layers occupied by morphologically different algae (Ros et al. 1985, Dayton 1994). Nowadays, because of widespread human impacts, long-lived species such as perennial macroalgae are declining in many areas across the earth (Airoldi & Beck 2007, Coleman et al. 2008, Connell et al. 2008) in favour of more opportunistic species.

The Mediterranean "kelps"

The Mediterranean is an enclosed sea which lies among Europe, Asia and Africa, with a coastline of 46.000 km (Boudouresque 2004). The Mediterranean is a warm-temperate sea, but its superficial waters present very particular characteristics which contrast with temperate open oceans: extreme reduction of tides, oligotrophic waters, relatively high salinity and high mean water temperature (Ros et al. 1985). These oceanographic conditions, and mainly the low dissolved nutrient concentrations in seawater, prevent the growth of kelp beds (only present close to the entrance of the Atlantic and in some deep areas of the western Mediterranean) and of several temperate members of the Fucales. In contrast, these conditions seem to be quite favourable for species of the genus *Cystoseira* (Fucales, Heterokontophyta), which has experienced an outstanding diversification in the last five million years (Roberts 1978). *Cystoseira* species are widespread in the Mediterranean infralittoral and upper circalittoral zones, where they play the same role as kelps do in the sublittoral zone from temperate oceans. *Cystoseira* C. Agardh was thought to be a genus of worldwide distribution, with about 80% of the species occurring in the Mediterranean and adjoining Atlantic coasts (Roberts 1978), but recent molecular evidence has shown that it is restricted to the northern Atlantic Ocean and the Mediterranean Sea (Draisma et al. in press).

The recent geological history of the Mediterranean is a key-factor for understanding its present biodiversity features. The Mediterranean basin became dessicated around six million years ago, during the Messinian salinity crisis, and refilled 5.3 million years ago, with the re-opening of the Straits of Gibraltar (Hsu et al. 1973, Krijgsman et al. 1999, Garcia-Castellanos et al. 2009). Therefore most of the biota present in the Mediterranean, including *Cystoseira* species, comes from the Atlantic. A few *Cystoseira* species entered the Mediterranean from the Atlantic and started a speciation process that is still active (Ercegovic 1952). This fact, together with a high morphological variability within *Cystoseira* species has created confusion in the identity of *Cystoseira* species and has created controversy among taxonomists (Roberts 1978, Verlaque 1987, Verlaque et al. 1999).

Species of the genus *Cystoseira* dominate several assemblages in infralittoral and circalittoral rocky bottoms, which have been described by Feldmann (1937), Molinier (1960), Giaccone (1973) Verlaque (1987) and Ballesteros (1988, 1990a,b). Floristic composition and structure of these assemblages have been studied by Boudouresque (1969, 1971, 1985), Giaccone (1973), Ballesteros (1992) and Giaccone et al. (1994). Seasonality and productivity have been studied by Ballesteros (Ballesteros 1988, 1990a,b) and Pizzuto (1999). These studies have originated considerable knowledge of many ecological aspects of *Cystoseira*-dominated assemblages. However, all of them have been performed at local scale although some *Cystoseira* species are distributed throughout the Mediterranean. The Mediterranean Sea is quite heterogeneous, and 13 different biogeographic sectors have been recognized (Pérès & Picard 1964, Bianchi & Morri 2000, Bianchi 2007). Differences in species composition among these sectors, as well as a gradient of species richness impoverishment from west to east have been suggested as the main biological features characterising Mediterranean biogeography (Boudouresque 2004, Coll et al. in press). Therefore, some biogeographical variation is expected within the assemblages dominated by the same species at a regional level.

Species of the genus *Cystoseira* are experiencing substantial decline in many areas of the Mediterranean (Cormaci & Furnari 1999, Thibaut et al. 2005, Serio et al. 2006). Eutrophication and pollution have been blamed as the main causes of this decline (Bellan-Santini 1968, Golubic 1970, Munda 1974, Munda 1982, Munda 1993, Arévalo et al. 2007), although other factors like overgrazing and climate change have also been suggested as possible causes (Thibaut et al. 2005, Serio et al. 2006). All *Cystoseira* species but *Cystoseira compressa* are included in the recent (2010) revision of the Annex II of the Barcelona Convention. Because of their sensitiveness to anthropogenic impacts, *Cystoseira* species are being used as indicators of good water quality in the implementation of the EU Water-Framework Directive (2000/60/EC) (Orfanidis et al. 2003, Ballesteros et al. 2007, Pinedo et al. 2007, Orlando-Bonaca et al. 2008, Asnaghi et al. 2009, Ivesa et al. 2009).

There are several *Cystoseira* species inhabiting shallow sheltered areas in the Mediterranean (Table 1). In these environments, impacts such as pollution and increase in sedimentation rates are magnified by the low water circulation. Moreover, these areas have been a target for human settlements, making *Cystoseira* species thriving in shallow sheltered areas an especially interesting subject of study.

Despite the high diversity of *Cystoseira* species that thrive in sheltered areas, only four different phytosociological associations have been described: *Cystoseiretum crinitae* Molinier 1960, *Cystoseiretum barbatae* Pignatti 1962, *Cystoseiretum caespitosae* Ballesteros 1990 and *Cystoseiretum balearicae* Verlaque 1987 (Verlaque 1987, Giaccone et al. 1994). The *Cystoseiretum barbatae* has been described from the northern Adriatic in sheltered estuarine environments. The *Cystoseiretum caespitosae* is restricted to a reduced area from the western Gulf of Lions. The *Cystoseiretum crinitae* and the *Cystoseiretum balearicae* are more widespread, and they are present at least in the whole western Mediterranean but some doubts exist in the delimitation of the first association as it was considered to gather very different facies or sub-associations (Molinier 1960, Giaccone et al. 1994).

*_Cystoseira algeriensis_ J. Feldmann
Cystoseira amentacea (C. Agardh) Bory
Cystoseira amentacea var. _spicata_ (Ercegovic) Giaccone (=_Cystoseira spicata_ Ercegovic)
Cystoseira amentacea var. _stricta_ Montagne [=_Cystoseira stricta_ (Montagne) Sauvageau]
*_Cystoseira balearica_ Sauvageau [=_Cystoseira brachycarpa_ J. Agardh var. _balearica_ (Sauvageau) Giaccone]
*_Cystoseira barbata_ (Stackhouse) C. Agardh
*_Cystoseira barbata_ f. _repens_ Zinova & Kalugina
*_Cystoseira barbata_ f. _insularum_ Ercegovic
*_Cystoseira barbata_ var. _tophuloidea_ (Ercegovic) Giaccone
*_Cystoseira barbatula_ Kützing (=_Cystoseira graeca_ Schiffner ex Gerloff & Nizamuddin)
*_Cystoseira brachycarpa_ J. Agardh
*_Cystoseira caespitosa_ Sauvageau
Cystoseira compressa (Esper) Gerloff & Nizamuddin
Cystoseira compressa f. _plana_ (Ercegovic) Cormaci, Furnari, Scammacca & Serio
*_Cystoseira compressa_ var. _pustulata_ Ercegovic
*_Cystoseira corniculata_ (Turner) Zanardini
*_Cystoseira crinita_ Duby
*_Cystoseira crinitophylla_ Ercegovic
*_Cystoseira elegans_ Sauvageau
*_Cystoseira foeniculacea_ (Linnaeus) Greville [=_Cystoseira discors_ (Linnaeus) C. Agardh]
*_Cystoseira foeniculacea_ f. _tenuiramosa_ (Ercegovic) Gómez-Garreta, Barceló, Ribera & Rull
*_Cystoseira foeniculacea_ f. _schiffneri_ (Hamel) Gómez-Garreta, Barceló, Ribera & Rull
*_Cystoseira humilis_ Schousboe ex Kützing
*_Cystoseira humilis_ var. _myriophylloides_ (Sauvageau) Price & John
Cystoseira hyblaea Giaccone
Cystoseira jabukae Ercegovic
Cystoseira jabukae f. _tenuissima_ (Ercegovic) Cormaci, Furnari, Giaccone, Scammacca & Serio
Cystoseira mediterranea Sauvageau
*_Cystoseira rayssiae_ Ramon
Cystoseira sauvageauana Hamel
Cystoseira sedoides (Desfontaines) C. Agardh
Cystoseira spinosa Sauvageau (=_Cystoseira adriatica_ Sauvageau)
*_Cystoseira spinosa_ var. _tenuior_ (Ercegovic) Cormaci, Furnari, Giaccone, Scammacca & Serio
*_Cystoseira squarrosa_ De Notaris
*_Cystoseira susanensis_ Nizamuddin
Cystoseira tamariscifolia (Hudson) Papenfuss

Table 1. Mediterranean species of _Cystoseira_ thriving in shallow waters. Those thriving mainly in sheltered environments are preceded by * (data compiled from different authors).

Objectives

Objectives and structure of the thesis

The main objectives of the thesis have been:

(1) To study the species composition and structure of the assemblages dominated by *C. crinita*.

(2) To study the main factors influencing *Cystoseira* species distribution in sheltered areas.

(3) To study experimentally the effects of pollution in different *Cystoseira* species thriving in sheltered areas.

To show how these objectives have been adressed, the results of the thesis have been structured in four chapters:

Chapter 1 is focused on the study of *Cystoseira crinita*-dominated assemblages from Cap Corse, where this assemblage was originally described by Molinier (1960). The motivation for this study was first, that there was controversy on the identity of the dominant species of the assemblages described by Molinier (Verlaque 1987); and second, the study of these *C. crinita*-dominated assemblages offered the opportunity to compare our data to historical data collected by Roger Molinier in 1958.

After having confirmed the presence of conspicuous *C. crinita*-dominated assemblages in the same sites where the assemblage was originally described, we re-describe the assemblage at a regional (=Mediterranean) level in **chapter 2**. This offers the opportunity to study the biogeographical variation of *C. crinita*-dominated assemblages across the Mediterranean.

In **chapter 3**, the distribution of the different *Cystoseira* species present in sheltered areas in Minorca (Balearic Islands) and its relationship with numerous geomorphological factors and anthropogenic pressures is studied. Although anthropogenic pressures seem to be the main cause of the decline that *Cystoseira* species are experiencing in the Mediterranean, this study tries to find out which natural environmental factors are also important drivers of *Cystoseira* species distribution.

After having confirmed that urban development and eutrophication are among the most important factors influencing the distribution of *Cystoseira* species in Minorca (chapter 3), an experimental study on the pollution effects on *Cystoseira* is conducted in **chapter 4**. *Cystoseira* specimens are transplanted from a non-polluted area to two areas displaying different levels of pollution. The principal aim in this chapter is to provide the first experimental evidence of pollution effects on *Cystoseira* species. As a secondary aim, the experiment tests the possibility of recovery of *Cystoseira* populations following water quality improvement.

Methodology

Methodology

Study area

Different study areas, including the whole Mediterranean or just a part of it, have been used for the studies presented in the different chapters (Fig. 1.).

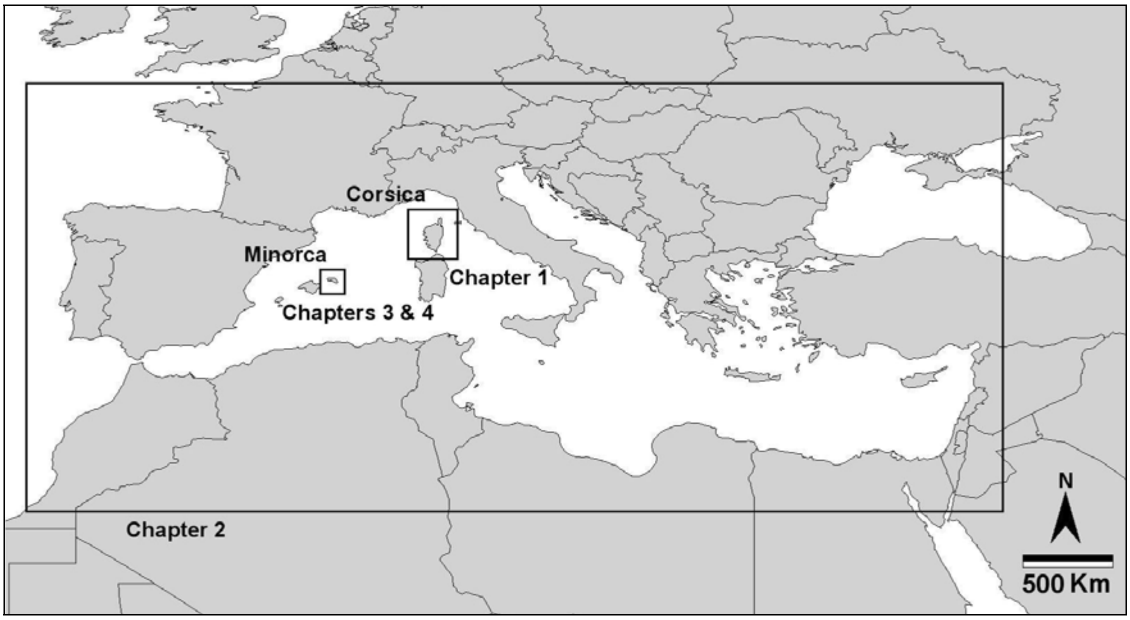


Fig. 1. Map of the study area.

The Mediterranean Sea is the biggest enclosed sea of the world, with a coastline of 46.000 km and a surface of 2.5 million km^2 (Boudouresque 2004). The Mediterranean communicates with the Atlantic Ocean in the west, with the Marmara and the Black Sea in the north-east, and also with the Red Sea through the Suez Canal in the south-east. The Mediterranean is a concentration basin, with higher rates of evaporation than inflow from rivers and rain. Without the water flowing in from the Black Sea and, especially from the Atlantic, the Mediterranean would dry up.

Despite being a temperate sea, the Mediterranean presents many particularities in comparison to open temperate oceans: extreme reduction of tides, oligotrophy, and relatively high temperature and salinity (the former especially in summer) (Ros et al. 1985).

Historically, the Mediterranean is a remnant of the ancient Tethys Ocean, which was an eastward open water body during the Triassic (220 my ago). In the Cretaceous (120 my ago), the Tethys ocean connected with the Atlantic creating a big continuous tropical ocean. During the Oligocene (30 my ago) a shrinkage of the Tethys took place, and culminated in the Miocene (10 my ago) with the formation of the Suez Isthmus separating the Mediterranean from the Indopacific. In the late Miocene (6 my ago) the communication with the Atlantic closed, and the Mediterranean became almost completely desiccated. In the Pliocene (5 my ago), the Mediterranean re-established communication with the Atlantic and was repopulated by species of Atlantic origin. Various glaciations, with warm inter-glacial periods, succeeded during the Quaternary, producing alternative boreal and subtropical immigration waves.

The Mediterranean is geographically and oceanographically very heterogeneous (Béthoux 1979, Bosc et al. 2004); as a consequence, up to 13 different biogeographic sections have been recognised (Pérès & Picard 1964, Bianchi & Morri 2000, Bianchi 2007). The Mediterranean is considered a hotspot of species diversity, holding more than 17,000 species (Coll et al. in press), and with a macroalgal flora which is placed amongst the world's richests (Bolton 1994).

Collection of data

The studies on the species composition and structure of *Cystoseira crinita*-dominated assemblages (chapters 1 and 2) were based on inventories of species abundances carried out with non-destructive (chapter 1) and destructive (chapter 2) sampling. The sample size was 625 cm^2, which is a greater area than the minimum sampling area for Mediterranean infralittoral assemblages (Coppejans 1980). Visual estimation of species cover in Braun-Blanquet scale (1951) was used in chapter 1, and horizontal cover in cm^2 measured on specimens horizontally placed over a laboratory tray (Ballesteros 1986) was used in chapter 2.

In chapter 3, visual estimations of species cover in Braun-Blanquet (1951) scale was also used. Moreover, various environmental parameters were measured during the field work or over maps using a Geographic Information System (GIS). Water samples were also collected for inorganic nutrient concentration analyses.

Finally, in chapter 4, a transplantation experiment was conducted. The data collected came from field observation (survival and growth of plants), or from laboratory analyses (heavy metal and nutrient content in sediments, seawater and algal tissues).

Laboratory analysis

In chapters 1, 2 and 3 species which could not be identified in the field were preserved in 4% formalin:seawater and identified in the laboratory. In chapters 3 and 4, nutrient concentrations in seawater and algal tissues, and heavy metal concentrations in sediment and algal tissues were analysed in the laboratory following the methods of Grashoff et al. (1983) and Cebrian et al. (2007).

Data analysis

In chapters 1, 2 and 3, multivariate techniques available in PRIMER v.6. + PERMANOVA (Clarke & Gorley 2006, Anderson et al. 2008) were the main statistical tools used. For ordination of biological data, Multidimensional Scaling (MDS; Kruskal & Wish 1978) was used. The group average agglomerative clustering technique was used for classification purposes. SIMPER analysis was used for comparisons of species abundances between different groups of samples. Analysis of Similarities (ANOSIM; Clarke 1993) and PERMANOVA (Anderson 2001) were also used for comparisons of groups of samples. Distance-based linear model routine (DistiLM; Legendre & Anderson 1999) and distance-based redundancy analysis (dbRDA; McArdle & Anderson 2001) were used to examine the relationships between biological data and environmental factors.

In chapter 4, univariate analyses, mainly Analysis of Variance (ANOVA), were used to test for differences in various parameters among experimental treatments.

Results

Chapter 1

Long-term comparison of assemblages dominated by *Cystoseira crinita* (Fucales, Heterokontophyta) from Cap Corse (Corsica, north-western Mediterranean)

Introduction

Brown algae of the orders Laminariales and Fucales are the main ecosystem engineer species dominating rocky shallow areas in temperate seas all around the world (Ribera et al. 1992, Steneck et al. 2002). Seaweed beds dominated by these macroalgae are very productive and their three-dimensional structure supplies habitat and shelter for a large number of species (Feldmann 1937, Giaccone 1973, Mann 1973, Dayton 1985a, Graham 2004). Over the last few decades, assemblages dominated by kelps and fucoids have experienced a general decline related to urbanisation (Airoldi & Beck 2007, Connell et al. 2008) and overfishing, through the effect of trophic cascades (Estes & Duggins 1995, Steneck 1998) leading to habitat and ecosystem services loss (Dobson et al. 2006).

Cystoseira (Fucales) is the main genus of erect macroalgae functioning as ecosystem engineers in the Mediterranean Sea (Giaccone 1973, Ballesteros 1992). *Cystoseira* spp. assemblages harbour a large number of algal and invertebrate species (e.g. Ballesteros 1990a, b, Ballesteros et al. 2009) and they dominate algal assemblages in most of the infralittoral and upper-circalittoral rocky bottoms in unimpacted areas (Giaccone 1973). The genus *Cystoseira* is believed to have speciated in the ancient Tethys Sea and to have recolonized the Mediterranean after the Messinian crisis about 6 million years ago (Roberts 1978, Amico et al. 1985). Currently, it is especially abundant and diversified in the Mediterranean Sea and on the adjacent Atlantic coasts (Roberts 1978).

Floristic composition and structure of the assemblages dominated by *Cystoseira* species are fairly well known (e.g. Boudouresque 1969, 1971, 1985, Giaccone 1973, Ballesteros 1992, Giaccone et al. 1994). Spatial trends of these assemblages have been studied at local (Feldmann 1937, Ercegovic 1952, Giaccone & Bruni 1973) and regional scales (Báez et al. 2005). Temporal trends have been reported at a seasonal scale (Ballesteros 1988, 1990a, b, Rodríguez-Prieto & Polo 1998, Pizzuto 1999). In addition, long-term studies have mainly reported disappearances (Munda 1982, 1993, Cormaci & Furnari 1999, Thibaut et al. 2005, Serio et al. 2006) but also recovery of *Cystoseira* species (Zavodnik et al. 2002) at a local scale. The loss of *Cystoseira* populations has often been attributed to eutrophication (Munda 1974, 1993, Soltan et al. 2001, Arévalo et al. 2007, Mangialajo et al. 2008) but other possible causes include overgrazing, climate change and invasive species (Arenas et al. 1995, Rico & Fernández 1997, Thibaut et al. 2005, Serio et al. 2006). A very slow recovery of *Cystoseira* assemblages has been observed, probably due to its low dispersion ability (Díez et al. 2009). However, Zavodnik et al. (2002) and Hanel (2002) reported recolonisation by many Fucalean species in the Northern Adriatic, which was attributed to a decreased herbivory pressure.

Cystoseira crinita has been reported from most of the Mediterranean countries (Ribera et al. 1992). Assemblages dominated by this species appear generally in the upper infralittoral zone of semi-exposed areas (Gómez-Garreta et al. 2000). *Cystoseira crinita*-dominated assemblages were originally described as an algal association (*Cystoseiretum crinitae*) by Molinier (1960) in Cap Corse (northern Corsica). He considered them as the most complex photophilic Mediterranean seaweed assemblage developing in shallow rocky areas. However, most Mediterranean shallow water assemblages dominated by *Cystoseira* are devoid of *C. crinita* but support a similar species, *Cystoseira brachycarpa* var. *balearica* (e.g. Verlaque 1987, Giaccone et al. 1994). Thus, concern about the identification of *C. crinita* by Molinier (1960) arose (Verlaque 1987).

The present work is aimed at determining possible changes in species composition and relative abundances of *C. crinita* assemblages from Cap Corse by a comparison of Molinier's data (obtained in 1958) and data obtained by the authors in 2007. The specific objectives are:

(1) To check the presence and possible disappearances of *C. crinita* assemblages in Cap Corse and to obtain information about the distribution and state of assemblages for the entire island of Corsica.

(2) To describe possible alterations in the species composition of the assemblages from Cap Corse.

Materials and Methods

Study area

Corsica (France) is the fourth largest island in the Mediterranean Sea, situated in the NW Mediterranean close to the north of Italy and the south-east of France (Fig. 1). The island has 1000 km of coastline. Its northern and western coasts have extensive rocky shores with several coves, while on the eastern coast there are long sandy beaches and estuaries. Cap Corse, a prominent peninsula in the north of the island, has several coves and small bays suitable for the development of shallow water algal assemblages. Human influence is generally low in Cap Corse since only a few small villages and towns exist. Moreover, there is no industrial development and, although livestock is present, the topography of the zone does not allow extensive cultivation of land.

Sampling

Molinier's descriptions of site locations were carefully reviewed before our sampling was carried out. The 15 sites reported by Molinier (1960) as

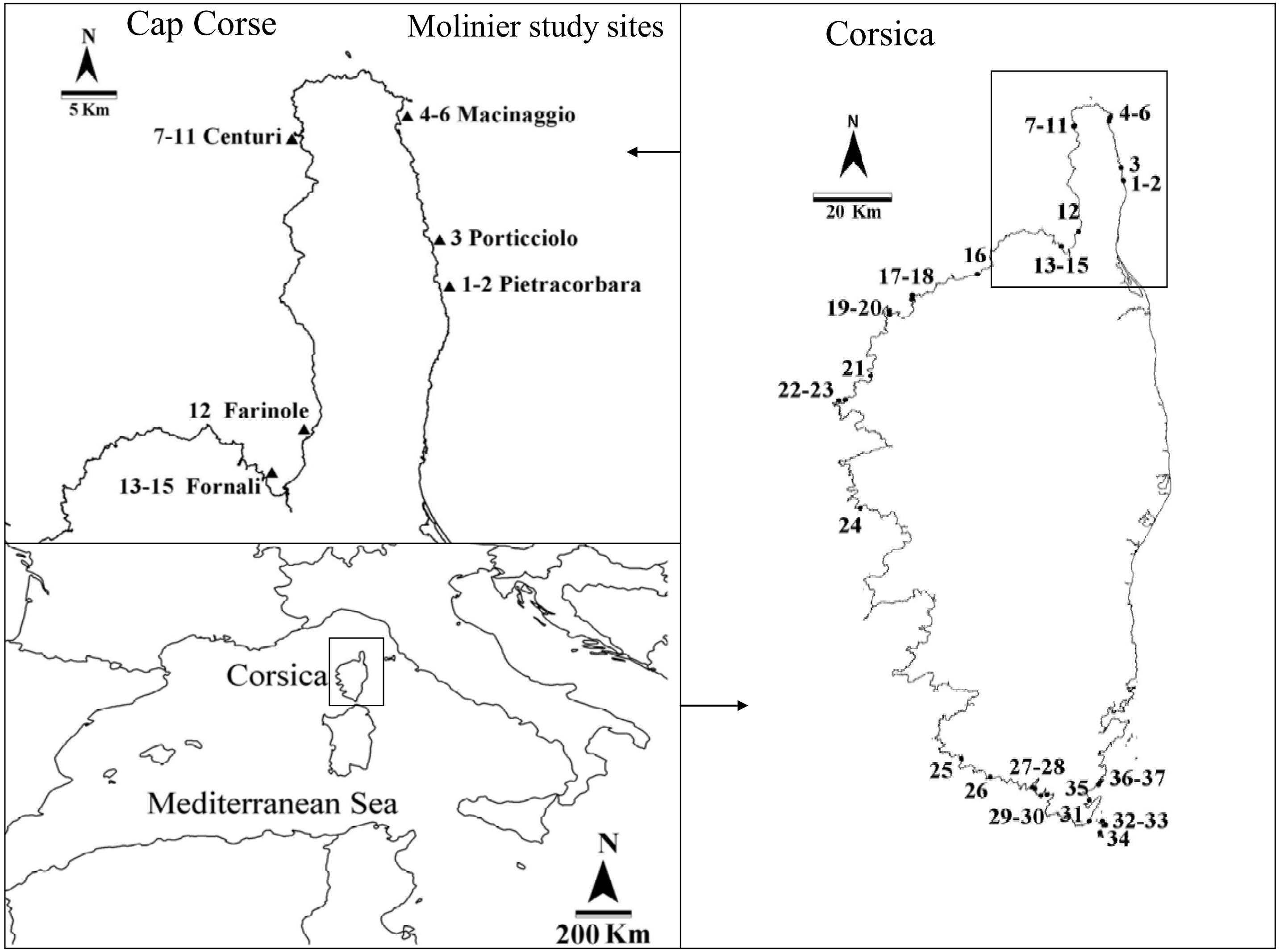


Fig. 1. Location of the study sites.

having dense populations of *C. crinita* (assemblages attributed to the sub-association *Cystoseiretum crinitae typicum*) were revisited. No date of collection is reported in Molinier study; therefore, we decided to carry out our sampling in spring (June 2007), which coincides with the moment of maximum development of littoral communities. Moreover, 22 new study sites already known for harbouring *C. crinita* assemblages were visited around Corsica Island. At each site, the presence of such assemblages was checked for and, whenever they were present, were sampled using the same procedure used by Molinier (1960). A frame of 25 x 25 cm – which is greater than the minimal sampling area and is largely representative both of the species composition and the relative species abundances (Coppejans 1980, Ballesteros 1992) - was haphazardly placed within a dense *C. crinita* stand at each site, and a species list was created estimating algal species cover as follows: + (< 1%), 1 (1-5%), 2 (5-25%), 3 (25-50%), 4 (50-75%), 5 (>75%) (Braun-Blanquet 1951). Species that could not be identified in the field were collected, fixed in 4% formalin:seawater and subsequently identified in the laboratory.

Data analysis

A matrix of algal species abundances (data both from Molinier's samples and from 2007 samples) was constructed for each site. Scientific names of species listed by Molinier were updated according to Algaebase (Guiry & Guiry 2008) and, as taxonomic resolution was higher in our lists, some species in some genera were merged (Table 1). Species from our lists with a total abundance lower than 1% and not recorded by Molinier were not considered for the analysis to avoid the presence of rare species whose abundance would not be properly quantified by the used sampling areas.

The combined transformation of Van der Maarel (1979) was applied to the dataset in order to convert Braun-Blanquet indices to numerical data. Next, a distance-matrix was created using Bray-Curtis distance (Bray & Curtis 1957). Finally, a MDS ordination (Kruskal & Wish 1978) was performed on the whole dataset and in a subset of the data from Cap Corse (using old and new data) to visualize multivariate patterns of distribution of the samples. Species which showed a Spearman correlation with the ordination of > 0.55 were represented as overlaid vectors in the second MDS (data only from Cap Corse).

The sites from Cap Corse were grouped into five locations, as some of them were very close one to another (10s to 100 m). Three or four sites were present within each location, except at Farinole, where there was only one sampled site. A PERMANOVA (Anderson 2001) with the factors time (1958, 2007) and location (Pietracorbara, Macinaggio, Centuri and Fornali; Farinole was excluded from the analysis) was applied to the data in order to test for differences in species composition and abundances between sampling times and among locations. Pairwise PERMANOVA tests were done for the factor time in each level of the factor location, as a significant interaction between the two tested factors was found. Monte Carlo *P*-values were calculated as the number of replicates per locality was small (3 or 4). In addition, SIMPER analysis was carried out in order to identify the species which contributed most to the differences between the samples from the two studies. All the multivariate analyses were performed with PRIMER v.6 (Clarke & Gorley 2006).

Results

Seaweed assemblages dominated by *Cystoseira crinita* were found at all the sites previously sampled by Molinier, except at Centuri harbour (Site

7, "Centuri: interieur du grand jetée"). Moreover, the presence of assemblages dominated by *C. crinita* was confirmed from 22 more sites around Corsica Island (see location of the sites in Fig. 1).

A complete species list with abundances per site generated for the 15 sites from Cap Corse is presented in Table 2. A reduced list (the one used for the statistical analyses), with the species merged as mentioned in the previous section and showing the species average abundance per sampling time (1958 and 2007), is presented in Table 1. The cover of *C. crinita* was high in the current samples (78% in average, Table 1) and this species was sometimes mixed with other *Cystoseira* species like *C. barbata, C. compressa* and *C. spinosa v. tenuior* (see Table 2). Although the average cover of *C. crinita* was generally higher in our samples than in Molinier's (78.6% vs. 67.9%, Table 1), a similar structure with different layers (encrusting, turf, erect and epiphytes) appeared in both groups of samples. The encrusting layer was characterized by the coralline *Neogoniolithon brassica-florida* and the brown alga *Pseudolithoderma adriaticum*. The most common species of turf-forming algae in both groups of samples were the green alga *Dasycladus vermicularis*, the red algae *Laurencia* spp., and the brown algae *Halopteris scoparia* and *Padina pavonica*, as well as other species belonging to the Dictyotaceae. Finally, the epiphyte layer was characterized by the articulated coralline *Haliptilon virgatum* and *Jania rubens*, and the brown alga *Sphacelaria cirrosa* (Tables 1 and 2).

Several species recorded in 2007 and not in 1958 included members of the genus *Ceramium, Acrothamnion preissii, Hypnea musciformis, Rytiphlaea*

Table 1. Reduced list of species used for the comparison between data from 1958 and 2007. The acronyms shown are used to represent the species which are more correlated with the ordination in Fig. 3. Results of SIMPER analysis are shown as cumulative % contribution to dissimilarity between 1958 and 2007.

Species	Acronym	1958(a)	2007(b)	% Con.(c)
Neogoniolithon brassica-florida	Neobra	15.50	51.43	14.96
Haliptilon virgatum and *Jania rubens*	Halvir	51.96	28.43	29.66
Sphacelaria cirrosa	Sphcir	14.89	26.57	39.28
Pseudolithoderma adriaticum	Pseadr	5.79	19.00	47.43
Cystoseira crinita	Cyscri	67.86	78.57	53.86
Dictyota spp. *(D. dichotoma, D. dichotoma* v. *intricata, D. fasciola, Dictyotaceae* unidentified*)*	Dicspp	5.18	13.57	58.80
Epiphytic Melobesiae	EpiMel	3.46	11.50	63.04
Cladophora spp. *(C. laetevirens, C. lehmaniana, C. coelothrix, C. nigrescens, C. pellucida, C. prolifera)*	Claspp	0.50	11.00	67.25
Laurencia spp. *(L. obtusa, L. microcladia)*	Lausp	6.39	2.64	70.06
Cystoseira spp. *(C. balearica, C. barbata, C. compressa* v. *compressa, C. compressa* v. *pustulata, C. foeniculacea* v. *tenuiramosa, C. spinosa* v. *tenuior, C. stricta)*	Cysspp	0.14	6.68	72.56
Dictyopteris polypodioides	Dicpol	0.14	6.39	74.98
Halopteris scoparia	Halsco	4.71	2.89	77.37
Dasycladus vermicularis	Dasver	5.71	1.64	79.33
Peyssonnelia spp. *(P. dubyi, P. harveyana, P. squamaria, P. rubra)*	Peyspp	0.14	4.82	81.23
Flabellia petiolata	Flapet	0.29	4.29	83.06
Rytiphlaea tinctoria	Ryttin	0.00	5.18	84.87
Padina pavonica	Padpav	4.50	1.07	86.50
Hypnea musciformis	Hypmus	0.00	4.36	88.07
Herposiphonia secunda	Hersec	3.54	0.14	89.46
Valonia utricularis	Valutr	0.50	3.04	90.77
Feldmannia caespitula v. *lebelii*	Felcae	1.61	1.25	91.83
Lophosiphonia spp. *(L. cristata, L. obscura)*	Lopspp	0.36	2.68	92.88
Cladostephus spongiosus	Claver	0.43	1.68	93.70

Species	Acronym	1958[(a)]	2007[(b)]	% Con.[(c)]
Rhodymenia ardissonei	Rhoard	0.00	1.61	94.36
Polystrata fosliei	Polfos	0.00	1.61	95.00
Amphiroa spp. *(A. rigida, A. cryptarthrodia)*	Amprig	0.07	1.54	95.63
Corallina elongata	Corelo	0.14	1.46	96.22
Ceramium spp. *(C. codii, G. flaccida)*	Cerspp	0.00	1.46	96.82
Gelidium latifolium	Gellat	0.00	1.25	97.30
Alsidium spp. *(A. corallinum, A. helminthocorton)*	Alssp	0.07	1.25	97.75
Parviphycus tenuissimus	Gelpan	0.00	0.64	98.00
Halopythis incurva	Halinc	0.36	0.36	98.24
Anadyomene stellata	Anaste	0.43	0.21	98.47
Acrothamnion preissii	Acrpre	0.00	0.50	98.66
Acetabularia acetabulum	Aceace	0.29	0.43	98.85
Wrangelia penicillata	Wrapen	0.43	0.00	99.02
Chondrachantus acicularis	Choaci	0.00	0.43	99.18
Pseudochlorodesmis furcellata	Psefur	0.00	0.36	99.33
Halimeda tuna	Haltun	0.07	0.36	99.47
Grateloupia dichotoma	Gradic	0.00	0.36	99.61
Taonia atomaria	Taoato	0.00	0.29	99.72
Dasya spp. *(D. corymbifera, D. rigidula)*	Dasspp	0.00	0.21	99.80
Erythrocystis montagnei	Erymon	0.21	0.00	99.89
Liagora viscida	Liavis	0.21	0.00	99.97
Jania longifurca	Janlon	0.00	0.07	100.00

(a,b) : average % cover of species for old and new data.
(c): percentage cumulative contribution to dissimilarity.

tinctoria, Chondracanthus acicularis, Parviphycus tenuissimus and *Pseudochlorodesmis furcellata*. A few species, like *Erythrocystis montagnei, Liagora viscida* and *Wrangelia penicillata*, were found only in 1958 (Tables 1 and 2).

In Figure 2, a picture of the typical *Cystoseira crinita*-dominated assemblage is shown.

Table 2. Complete species-list of the sites from Cap Corse. Abundances of the species are shown in Braun-Blanquet scale(a).

	1	2	3	4	5	6	8	9	10	11	12	13	14	15
Acetabularia acetabulum	+	+	+					+			+	+		
Acrothamnion preissii		+	+				+	+	+	+	+			
Alsidium corallinum									2					
Alsidium helminthocorton									2					
Amphiroa cryptarthrodia					+									
Amphiroa rigida		+					+					2	+	
Anadyomene stellata	+												+	+
Boergeseniella fruticulosa							+							
Ceramiaceae (unidentified)														+
Ceramium codii					2									
Chaetomorpha aerea					+									
Chondracanthus acicularis									+	1				
Chondria dasyphylla									+					
Chondria sp.									+					
Cladophora coelothrix		+	+			+		3	+				+	2
Cladophora laetevirens	1	2	+		+	+	+			+				
Cladophora lehmanniana										+				
Cladophora nigrescens						+								
Cladophora pellucida					+									
Cladophora prolifera	3	+	1		+				1					2

	1	2	3	4	5	6	8	9	10	11	12	13	14	15
Cladophora sp.										2				
Cladostephus spongiosus	1	2							+					
Codium bursa													+	
Corallina elongata	+		2									+	+	
Cystoseira brachycarpa v. balearica													1	
Cystoseira barbata								1						3
Cystoseira compressa var. pustulata													2	
Cystoseira crinita	5	5	5	5	5	5	5	4	5	5	4	4	4	4
Cystoseira foeniculacea var. tenuiramosa													1	
Cystoseira spinosa var. tenuior								1	+					
Dasya corymbifera							+				+			
Dasya rigidula		+												
Dasycladus vermicularis			1	+		+		1			1		1	+
Delesseriaceae (unidentified)		+								1				
Dictyopteris polypodioides	1	+	+				2		1	1		2	3	
Dictyota dichotoma v. *intricata*	1		+		1		2	+	1	+		+	+	+
Dictyota fasciola	2	+	+			+	1	+	+		+	+	+	
Dictyotaceae (unidentified)				+		+	+	2		1		2	3	4
Falkenbergia sp.						+								
Feldmannia caespitula											2			
Feldmannia irregularis							+							

	1	2	3	4	5	6	8	9	10	11	12	13	14	15
Flabellia petiolata		+	+		+	2		+			+			3
Gayliella flaccida		+									+			
Gelidium crinale									+					
Gelidium latifolium			2											
Grateloupia dichotoma										1				
Halimeda tuna									1					
Haliptilon virgatum	2	4	2	3	3	3	1	1	+	+	1	5	3	+
Halopithys incurva									1					
Halopteris scoparia	+	+	1			+	1	1	1	2				
Herposiphonia secunda							+				+			
Hydrolithon farinosum				2	1	2	2	1	1		2	+	3	3
Hypnea musciformis							3	+	2	1				
Jania longifurca											+			
Jania rubens		1	2						+		+			
Laurencia microcladia	+							+	+	+				
Laurencia obtusa									2	2				
Liebmannia leveillei										+				
Lophosiphonia cristata								+						
Neogoniolithon brassica-florida	4	2	3	2	4	2	4	5	5	5	2	4	4	3

	1	2	3	4	5	6	8	9	10	11	12	13	14	15
Padina pavonica	+	+							+	+	1	+	1	
Palisada papillosa									+					
Parviphycus tenuissimus					1			+	+		+		+	
Peyssonnelia dubyi		2			1							1		
Peyssonnelia harveyana									2					
Peyssonnelia squamaria	2	+								1				
Phyllophora crispa										+				
Plocamium cartilagineum										+				
Polysiphonia sp.								+						
Polystrata fosliei								1			2			
Porphyra sp.		+												
Pseudochlorodesmis furcellata				+	+	+							+	+
Pseudolithoderma adriaticum		2	3	4	2	1	2	1		2	4	2	+	1
Rhodymenia ardissonei	2		1											
Rytiphlaea tinctoria								3	2	2				
Siphonocladus pusillus						+								
Sphacelaria cirrosa	1	2	3		+		4	3	5	3	4	+	1	2
Taonia atomaria	+	+	+					+						
Ulva sp.										+				
Valonia utricularis			+		3		+	+		+			+	

[a] +: < 1% cover, 1: 1-5% cover, 2: 5-25% cover, 3: 25-50% cover, 4: 50-75% cover, 5: >75% cover.

Fig. 2. Typical *Cystoseira crinita*-dominated assemblage.

PERMANOVA showed a significant interaction between the factors time and location. Pair-wise tests for the factor time in each location showed significant differences between old and current assemblages only in Centuri, although the *P*-value for Pietracorbara was quite close to 0.05 (Table 3).

Table 3. PERMANOVA results on species composition and abundances of *C. crinita* assemblages for the factor time and location.

Source	df	Main effects			Location	Pair-wise tests 1958, 2007	
		SS	F	P		t	P (MC[c])
Time[a]	1	5382.8	7.4348	**0.0001**	Pietracorbara	1.7517	0.0565
Location[b]	3	5120.7	2.3576	**0.0003**	Macinaggio	1.5366	0.128
Time x Loc	3	4310.0	1.9844	**0.0026**	Centuri	2.5208	**0.0041**
Residual	18	13032.0			Fornali	1.5494	0.1056
Total	25	28206.0					

(a,b): Factors time and location are treated as fixed.

(c): Monte Carlo P-values.

Patterns observed in both MDS ordinations segregated old and new data according to the species composition and abundances (Figs. 3 and 4). According to the species overlain in the MDS on the Cap Corse data (Fig. 4) and the SIMPER analysis (Table 1) there were several species which differed in average abundance between historical and present samples. The encrusting algae *Pseudolithoderma adriaticum* and *Neogoniolithon brassica-florida* were much more abundant in 2007 than in 1958 (Table 1). Some photophilic algae, like *Haliptilon virgatum, Padina pavonica, Laurencia* spp. and *Dasycladus vermicularis* appeared to be more abundant in 1958 than in 2007 (Table 1). The opposite pattern was observed for *Cladophora* spp. and for some sciaphilic species such as *Valonia utricularis, Flabellia petiolata, Peyssonnelia* spp. and *Dictyopteris polypodioides* (Table 1).

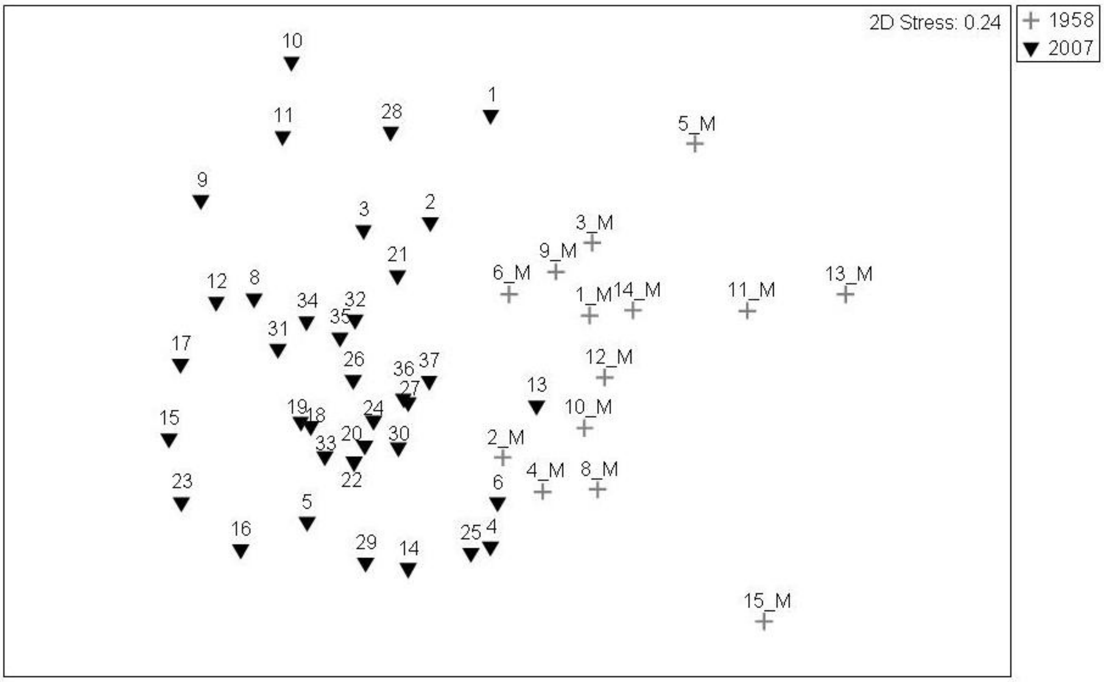


Fig. 3. MDS ordination all the sampling sites based on species composition and abundances of *C. crinita* assemblages.

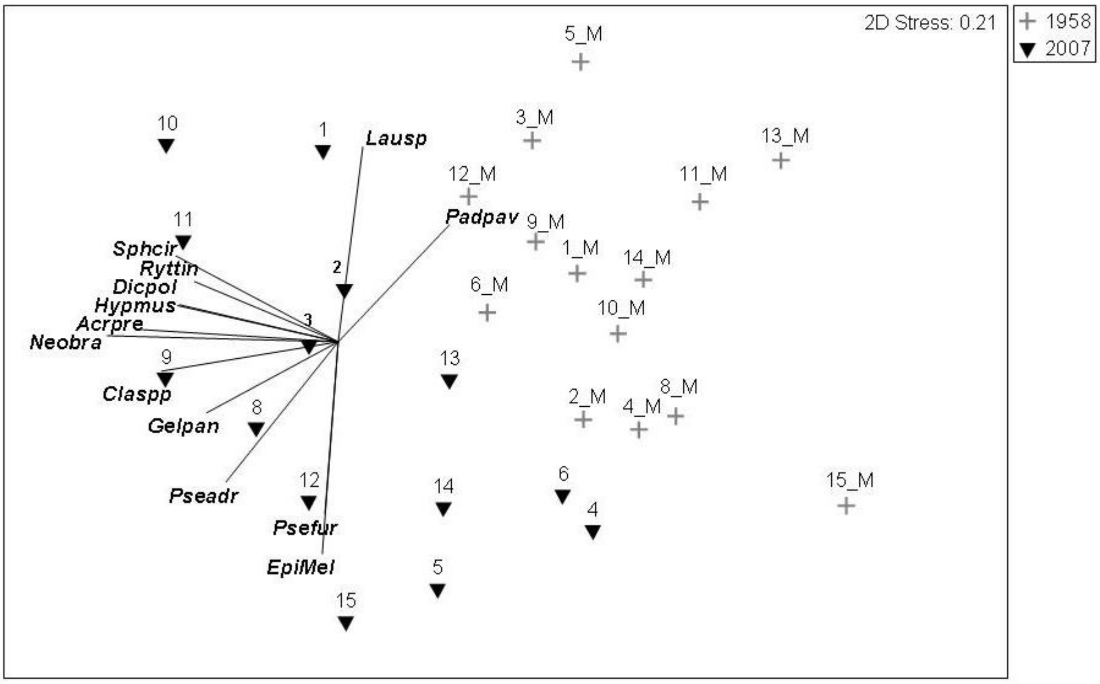


Fig. 4. MDS ordination of the sites from Cap Corse based on species composition and abundances of *C. crinita* assemblages. The represented species are those that show a Spearman correlation with the ordination > 0.55.

Discussion

The finding of *Cystoseira crinita* at the majority of the study sites as the most abundant *Cystoseira* species suggests that the identification of the species by Molinier (1960) was correct. *C. crinita* distribution in the North Western Mediterranean is restricted to shallow and relatively sheltered areas (Ballesteros 1992, Sales & Ballesteros 2009). This is also true for Corsica, as we always found *C. crinita* in this kind of environment and we also observed that *Cystoseira brachycarpa* var. *balearica* replaced *C. crinita* in deeper waters. Thus, although we confirm the presence of *C. crinita* in the localities studied by Molinier, its presence was restricted to shallow (< 1 m) sheltered areas and with a reduced surface coverage. In contrast, Molinier (1960) suggested that *C. crinita*-dominated assemblages were representative of shallow rocky shores in the entire Mediterranean.

C. crinita-dominated assemblages were present at 14 of the 15 places that Molinier sampled in 1958 (with *C. crinita* cover > 60%), as well as at 22 other sites around Corsica. The only study site where *C. crinita* had disappeared was Centuri harbour and, therefore, the decline of *C. crinita* in Cap Corse seems to be restricted to places where the natural habitat has been profoundly altered. These findings are in contrast with the decline of the species of the genus *Cystoseira* observed in other areas where anthropogenic disturbances are considered to be small (Cormaci & Furnari 1999, Thibaut et al. 2005, Serio et al. 2006).

Slight changes in the species composition and abundances between the assemblages sampled in 1958 and in 2007 were detected by PERMANOVA. The only location where the differences were significant was Centuri, and a near-significant *P*-value was found for Pietracorbara. Although *C. crinita*-dominated assemblages had disappeared from the harbour of Centuri, outside the harbour the changes detected in the assemblages do not seem to correspond to human pressure as we did not find any species indicating pollution or stress.

Despite the small differences evidenced by PERMANOVA, several species differed in average abundance between the samples from 1958 and 2007, as shown by SIMPER analysis. Several explanations can be suggested for these differences. The first is the possible difference between observers in sorting accuracy, taxonomic competence or quantification estimates by visual cover. For example, there is no apparent reason for the higher values of cover by encrusting species in 2007 samples. The subjectivity in the estimation of visual percent cover is high, as different observers can provide different values. However, comparisons between this methodology and other more accurate methodologies, like random-point quadrats, have demonstrated that visual estimation is a legitimate technique for estimating benthic organism cover, even by different observers (Meese & Tomich 1992, Dethier et al. 1993). Differences in taxonomic competence between observers, as pointed out by Rindi & Guiry (2004), could have resulted in some records of species only found in one of the studies. The causes could be misidentifications or different ability of observers to detect small species like *Ceramium* spp. (only found in 2007) or *Erythrocystis montagnei* (only found in 1958).

Secondly, seasonality could also explain divergences between 1958 and 2007, as it is very important in Mediterranean shallow benthic communities (Ballesteros 1991, 1992). For example, the photophilic species *Haliptilon virgatum, Padina pavonica* and *Laurencia* spp., more abundant in 1958 than in 2007, usually have their highest abundance at the end of the summer. An opposite pattern is seen in several sciaphilic species, more abundant in 2007 than in 1958, which generally show maximum abundance in spring (Ballesteros 1992, Pizzuto 1999). Late spring was chosen for sampling in the present study, because it coincides with the maximum development of littoral communities (Ballesteros 1992). No information on date of collection is provided by Molinier (1960), but he could have carried out his surveys during summer and not in late spring. In that case, some of the observed differences could be due to seasonal changes.

Finally, the observed differences could also be related to long-term changes in community composition caused by natural disturbances, such as increased herbivory or storms. These disturbances can cause cyclic or occasional fluctuations, leading to states in which canopy algae completely dominate the seascape and to other states in which these algae partially or completely disappear. Such natural fluctuations have been described for kelp-dominated assemblages (Dayton 1985a, b, Estes & Duggins 1995) and may explain long-term changes in the presence and abundance of Fucales in western Ireland (Rindi & Guiry 2004).

An unequivocal change between 1958 and 2007 is the appearance of the introduced filamentous red alga *Acrothamnion preissii*, which was reported for the first time in the Mediterranean by Cinelli & Sartoni (1969). This alga is highly invasive on rhizomes of *Posidonia oceanica* (Linné) Delile associated with a decrease in biodiversity of flora and fauna inhabiting these biogenic structures as epiphytes (Piazzi & Cinelli 2000, Piazzi et al. 2002). However, although the species was found at seven out of the 14 locations surveyed, it was always very low in abundance.

In conclusion, *C. crinita* assemblages still remain in most of the places where they were present 50 years ago. This pattern is probably general for the whole island of Corsica, as we have observed similar habitats and assemblages in several sites around the island. In fact, some areas of Corsica are considered to be reference situations for the implementation of the European Water Framework Directive when using macroalgae as biological elements (Pinedo et al. 2007, Ballesteros et al. 2007), which is in agreement with the small changes in algal assemblages detected between 1958 and 2007.

Chapter 2

Biogeographical patterns of algal communities from the Mediterranean Sea: *Cystoseira crinita*–dominated assemblages as a case study

Introduction

Biogeography is the study of distributional patterns in biodiversity, and examines affinities and/or differences in the biota present in different regions (Bianchi & Morri 2000). Although in the marine environment connectivity among different regions is usually greater than in its terrestrial counterpart (Carr et al. 2003), marine biogeographical regions have been described at a variety of spatial scales (Golikov et al. 1990, Longhurst 1998, Shears et al. 2008). Among the factors underlying biogeographical patterns in the marine realm, temperature seems to be pivotal (Breeman 1988, Cambridge et al. 1990, Adey & Steneck 2001, Blanchette et al. 2008) but other factors such as salinity, currents and tides might also play a role in determining patterns of diversity at regional scales (Adey & Steneck 2001, Phillips 2001). Finally, history has been invoked as a key factor in the distribution of diversity at large scales (Barber et al. 2000, Phillips 2001, Kerswell 2006).

Most of the biota present in the Mediterranean Sea stems from geologically recent times as the Mediterranean basin became desiccated around six million years ago, during the Messinian salinity crisis, and refilled 5.3 million years ago (Hsu et al. 1973, Krijgsman et al. 1999, Garcia-Castellanos et al. 2009). Despite of its relatively youthness, the Mediterranean is considered a hotspot of species diversity, holding more than 17,000 species (Coll et al., in press), and with a macroalgal flora which is placed amongst the world's richests (Bolton 1994). The Mediterranean is divided into several sub-basins (Coll et al., in press) which, coupled with basin-scale water circulation and other oceanographic factors (Béthoux 1979, Hopkins 1985, Malanotte-Rizzoli & Hecht 1988, Bosc et al. 2004), have led to the recognition of different biogeographic areas (Pérès & Picard 1964, Giaccone 1971a, Bianchi &

Morri 2000, Bianchi 2007). Presence/absence of species in different areas has been considered the key factor for defining Mediterranean biogeographical regions, together with a pattern of decrease in biodiversity from north-west to south-east (e.g. Boudouresque 2004, Bianchi 2007, Coll et al., in press). Recent efforts have been directed to summarize the knowledge on Mediterranean biodiversity including both species occurrence and spatial patterns of species diversity by Coll et al. (in press). Also, the MacroBen database, coordinated by Somerfield et al. (2009), which joins data on biodiversity of invertebrates from soft bottoms from different regions in Europe, allow the examination of general biodiversity patterns across marine environments at regional scales. However, we know of no studies that address Mediterranean biodiversity patterns at the level of whole assemblages dominated by macroalgae.

Macroalgae of the genus *Cystoseira* are the primary structural species in Mediterranean sublittoral rocky bottoms (Feldmann 1937, Giaccone 1973, Ballesteros 1988, 1990a, b, 1992, Ballesteros et al. 1998). This contrasts with the majority of other temperate marine systems, where kelps play this role (Steneck et al. 2002). Assemblages dominated by *Cystoseira* species rank amongst the most productive in the Mediterranean (Ballesteros 1989a) and provide habitat for a considerable number of other algae and invertebrate species (Molinier 1960, Boudouresque 1972, Ballesteros 1992). Although some *Cystoseira* species are very restricted in their spatial distribution, others are distributed throughout the entire Mediterranean (Cormaci et al. 1992, Ribera et al. 1992), thus providing a good basis for examining patterns in biogeography across the Mediterranean at the assemblage/community level.

Cystoseira crinita is a Mediterranean endemic species which forms dense stands in shallow, rather sheltered, and well illuminated areas (Feldmann

1937, Molinier 1960, Ribera et al. 1992, Pizzuto 1997, Sales & Ballesteros 2009). Assemblages dominated by *C. crinita* were described by Molinier (1960) as characteristic of shallow rocky habitats in Corsica (NW Mediterranean) and assumed by Giaccone (1968, 1971b) and Giaccone et al. (1994) to be representative of shallow rocky habitats for the entire Mediterranean. Ballesteros (1992) and Pizzuto (1999) studied seasonal variation in composition and structure of *C. crinita*-dominated assemblages from Catalonia and Sicily. All of these previous studies were done at local scales. Given the key role that *C. crinita* plays in structuring assemblages, it is of special interest to describe the species composition of the assemblages dominated by this species across the Mediterranean.

The aims of the present study are two-fold:

(1) To describe the specific composition of the assemblages occurring in *C. crinita* –dominated habitats at a regional (Mediterranean) scale.

(2) To provide quantitative data on the similarity of communities in these habitats from a variety of localities across the Mediterranean and to compare these patterns with previously defined biogeographical regions and biodiversity gradients.

Materials and Methods

Study area

The Mediterranean Sea is the biggest enclosed sea of the world, with a coastline of 46.000 km and a surface of 2.5 million km^2 (Boudouresque 2004). It is a warm-temperate sea (Zabala & Ballesteros 1989); however, it presents many particularities in comparison to open temperate oceans:

extreme reduction of tides, oligotrophy, and relatively high temperature and salinity (the former especially in summer) (Ros et al. 1985). The Mediterranean is geographically and oceanographically very heterogeneous (Béthoux 1979, Bosc et al. 2004); as a consequence, up to 13 different biogeographic sections have been recognised (Pérès & Picard 1964, Bianchi & Morri 2000, Bianchi 2007).

Sampling

Cystoseira crinita-dominated assemblages were surveyed at 101 sites from 9 different regions across the Mediterranean Sea (Fig. 1). The longitudes sampled spanned from Spain (1º25′ E) to Turkey (30º26′ E). The surveyed regions were Catalonia (n=1), Minorca (n=14) and Formentera (n=3) (Spain), Corsica (n=36) (France), Sardinia (n=14) (Italy), Istria (n=26) (Croatia), Dodecanese (n=2) and Cyclades islands (n=2) (Greece) and Lycia (n=3) (Turkey). These regions corresponded to four previously defined biogeographical sectors according to Bianchi (2007) (see Fig. 2).

To avoid potential seasonal differences, all samples were collected during late spring of 2007 or 2008. All the samples were collected from coves, bays or shallow areas with a low to medium degree of exposure, and little or no obvious human-derived impacts. The depth at which the samples were obtained ranged from 0.2 to 1 meters. At each site, a sample measuring 25 x 25 cm (625 cm^2) was collected, removing the whole community with a hammer and chisel (Boudouresque 1971a). This sampling area is greater than the minimum sampling area for the Mediterranean infralittoral assemblages (Coppejans 1980, Ballesteros 1992). After collecting the samples, algae and sessile invertebrates were

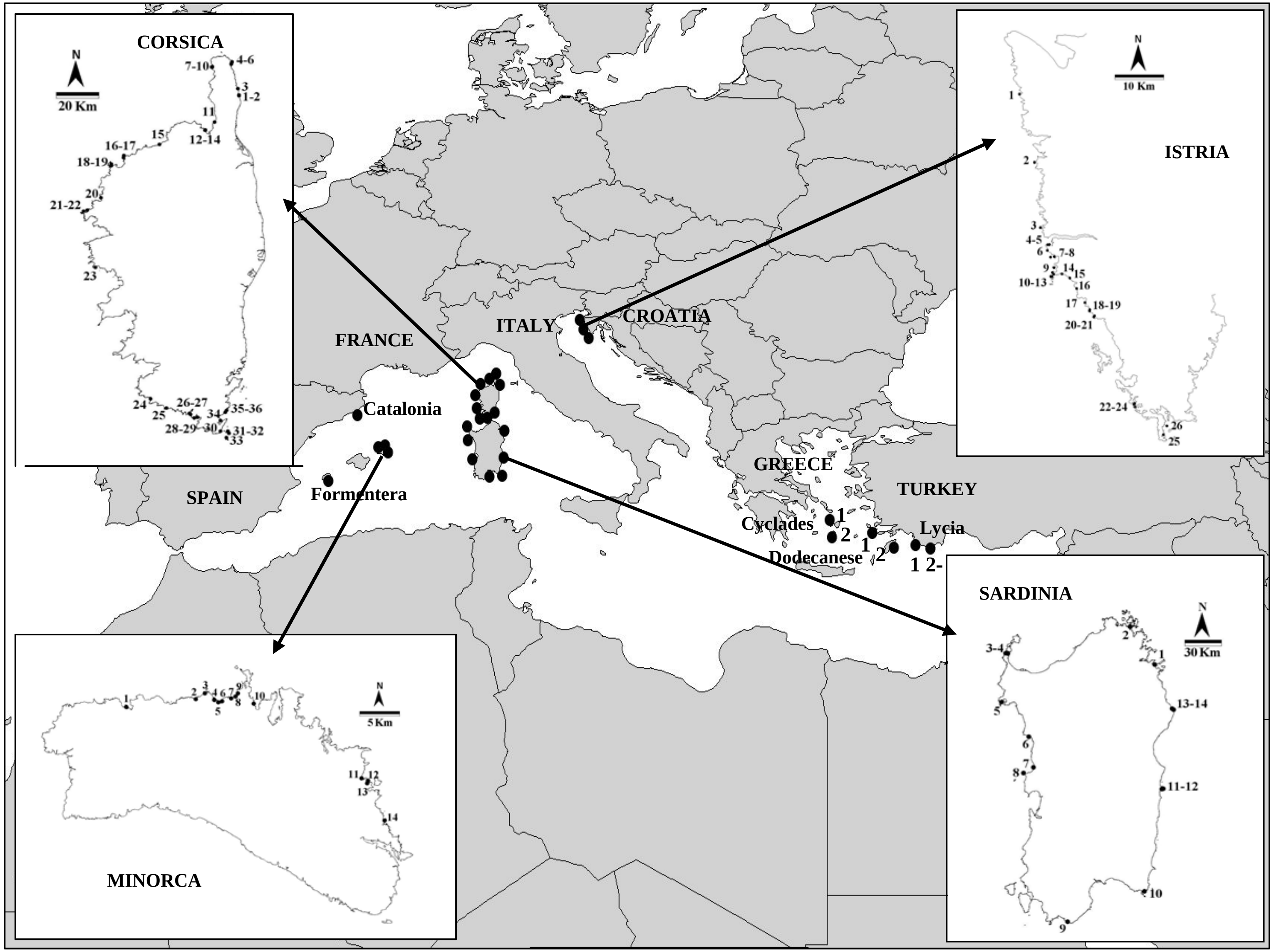


Fig. 1. Map of the study area.

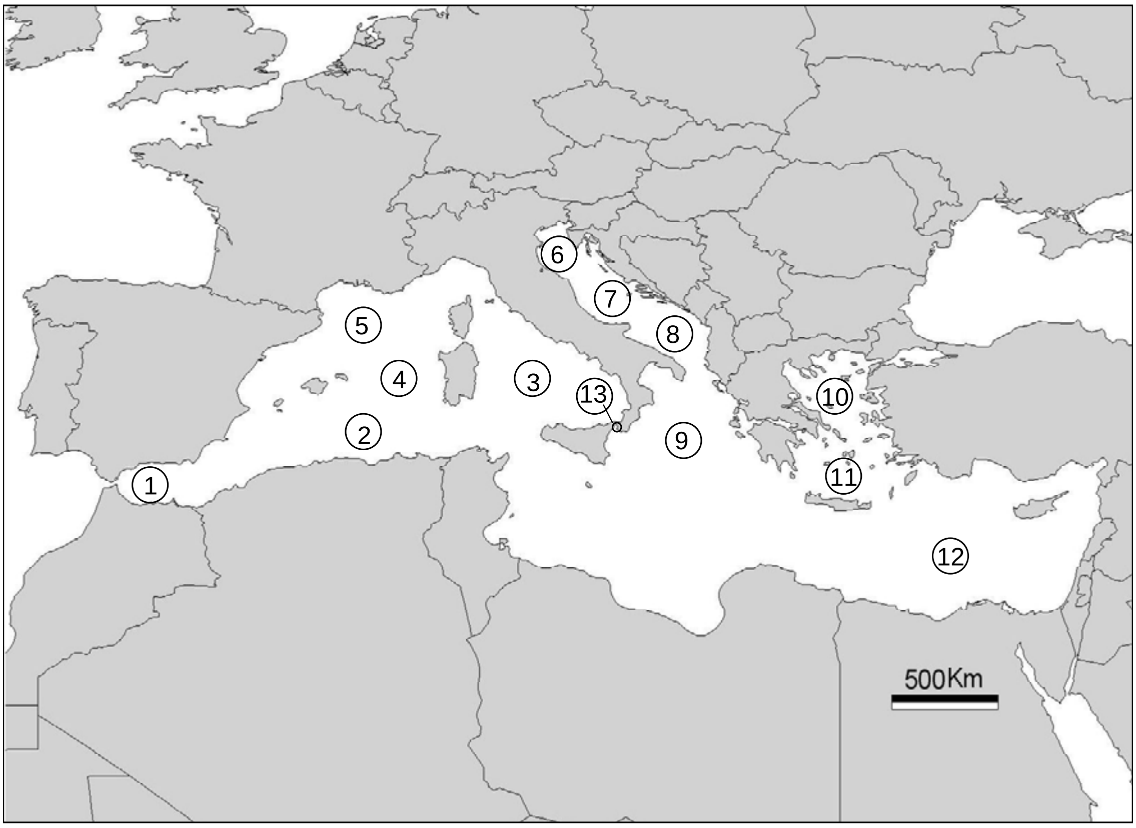


Fig.2. Major biogeographic sectors within the Mediterranean Sea (Bianchi 2007): (1) Alboran Sea; (2) Algeria and north Tunisia coasts; (3) southern Tirrenian Sea; (4) Balearic Sea to Sardinia Sea; (5) Gulf of Lions and Ligurian Sea; (6) northern Adriatic Sea; (7) central Adriatic Sea; (8) southern Adriatic Sea; (9) Ionian Sea; (10) northern Aegean Sea; (11) southern Aegean Sea; (12) Levant Sea; (13) Straits of Messina.

identified. Relative abundances of species were measured as horizontal coverage in cm^2 by spreading specimens/individuals over a laboratory tray to form a thin layer (Ballesteros 1986). Therefore, species cover was not measured as a percentage of substrate occupied by each species but as the area covered by each species when it was placed horizontally. From here on, we will use the word "cover" to refer to horizontal cover in cm^2. Species which could not be identified in the field were preserved in 4% formalin in seawater and identified later in the laboratory.

Data analysis

Different multivariate analytical procedures were used to investigate possible patterns of variation in the composition of the assemblages among samples and regions. First of all, the data matrix of species coverages was fourth-root transformed. A reasonably severe transformation was appropriate in order to reduce the contribution of the most abundant species, especially the dominant alga *C. crinita*. Next, a Bray-Curtis similarity (Bray & Curtis 1957) matrix was constructed on the full set of data (all samples) and also on the basis of the average coverages of species per region. Non-metric multidimensional scaling (MDS) ordination (Kruskal & Wish 1978) was done to visualise patterns of community similarities. A hierarchical group-average agglomerative clustering method accompanied by SIMPROF tests (Clarke et al. 2008) (9999 permutations, 0.1% significance level; Potter et al. 2001) was used to explore potential grouping structures among the samples. The previously articulated hypothesis of decreasing richness from west to east and from north to south was tested by linear regressions of species richness (number of species per sample) *vs* longitude and also *vs* latitude.

After these analyses using the whole data set, a subset of the data from the regions most intensively sampled [Balearic Islands (merging Minorca and Formentera), Corsica, Sardinia, Istria and the Southern Aegean Sea (merging Cyclades, Dodecanese and Lycia)] were examined in greater detail. Analysis of Similarities (ANOSIM; Clarke 1993) was used to test the null hypothesis of no differences among the communities obtained from the five different regions. Univariate analyses (one-way ANOVA) were used to compare regions for some specific aspects of the community. The individual variables tested were: total cover, cover of *C. crinita*, cover of Chlorophyta (green algae), and cover of sessile invertebrates. One-way ANOVA tests (comparing regions) were also done on the number of species per sample (species richness, S) and Simpson's evenness (1 - λ'; Simpson 1949). Finally, the relative coverages of the ten most abundant species of each region were represented graphically to help describe similarities and/or differences in community structure among the regions.

The statistical package Primer v.6 (Clarke & Gorley 2006) was used for the multivariate analyses, and Statistica v.6 was used for the univariate analyses.

Results

A total of 234 species were identified from the samples, consisting of 5 cyanobacteria, 194 macroalgae and 35 sessile invertebrates. A common structure was present across the entire study area, with the species divided into four different layers: canopy, turf-forming, encrusting and epiphyte. The canopy layer was always dominated by *Cystoseira crinita*, although other species of the genus *Cystoseira* were also occasionally abundant. The encrusting layer consisted mainly of the coralline alga *Neogoniolithon brassica-florida*, except in Catalonia (northern Spain), where the encrusting layer was represented mainly by *Litophyllum incrustans*, another coralline alga. The brown alga *Pseudolithoderma adriaticum* was an important component of the encrusting layer in Corsica, Sardinia and Minorca. A turf-forming layer of primarily the red algae *Corallina elongata* and *Laurencia* spp. appeared frequently in almost all the regions. The brown alga *Stypocaulon scoparium* and various species from the family Dictyotaceae were other important components of the turf-forming stratum. Finally, the green algae *Dasycladus vermicularis, Flabellia petiolata, Valonia utricularis* and various species of the genus *Cladophora* appeared frequently in the understory turf community of the samples. *Cystoseira* plants were usually covered by epiphytes, with *Haliptilon virgatum* and *Sphacelaria cirrosa* being the most common and abundant. Despite being low in cover, some species of the genus *Dasya* and *Ceramium* were also found as epiphytes on *Cystoseira* (Table 1).

Three introduced species were identified in the samples: the filamentous red algae *Acrothamnion preissii* and *Womersleyella setacea* and the green alga *Caulerpa racemosa* v. *cylindracea*. *A. preissii* appeared frequently in the samples from Minorca, Corsica and Sardinia, although low in cover. *W. setacea* and *C. racemosa* v. *cylindracea* appeared only in one of the samples from Kimolos (Cyclades Islands, Greece) (Table 1).

Sessile invertebrates generally represented less than 1 % of the total coverage of the assemblages. The most common species were the hydrozoan *Aglaophenia kirchenpaueri*, the bryozoans *Amathia lendigera*, *Turbicellepora magnicostata* and *Scrupocellaria* sp., the ascidians *Cystodites dellechiajei* and various species from the family Didemnidae, and the sponges *Ircinia fasciculata* and *Ircinia variabilis* (Table 1).

In the Appendix, at the end of the thesis, complete species lists of all study sites in this chapter are presented.

Table 1. Average species abundances per region (in cm^2 horizontal cover).

	Catalonia	Corsica	Sardinia	Minorca	Formentera	Istria	Cyclades	Dodecanese	Lycia
Cyanobacteriae									
Calothrix confervicola				5.99	39.73	6.5			
Lyngbya semiplena			0.01						
Lyngbya sp.									
Phormidium sp.				0.01					
Symploca hydnoides			0.59	0.94					
Macroalgae									
Acetabularia acetabulum		0.22	0.09			1.37	0.4		
Acrothamnion preissii		0.66	0.27	0.69	0.17	0.06			
Aglaothamnion scopulorum			0.01			7.98			
Aglaozonia parvula (stadium)						0.31			
Alsidium corallinum		1.17	20.89			1.01			
Alsidium helminthochorton		1.83	1.31		0.43	0.52			
Amphiroa cryptarthrodia		0.02							
Amphiroa rigida		3.42	1			0.44	0.4	2.05	
Anadyomene stellata		0.06	1.02				0.4		
Anotrichium barbatum									
Boergeseniella fruticulosa		5.22	64.43	35.85		45.42	0.4		0.53
Botryocladia botryoides									20.83
Botryocladia sp.						0.49			
Bryopsis duplex									

	Catalonia	Corsica	Sardinia	Minorca	Formentera	Istria	Cyclades	Dodecanese	Lycia
Bryopsis sp.									
Callithamnion corymbosum			0.01		0.07				
Caulerpa racemosa v. *cylindracea*							5.45		
Ceramiaceae unidentified		1.47							
Ceramium ciliatum	0.2				0.67	0.81			
Ceramium circinatum			0.36						
Ceramium codii		1.11							
Ceramium deslongchampsii						0.02			
Ceramium diaphanum		0.01	0.09	0.01	1.57	2.15			0.53
Ceramium siliquosum v. *zostericola*	1.3								
Ceramium sp.			0.01			0.01			
Ceramium tenerrimum						0.11			
Chaetomorpha linum	0.5	0.23	0.03	0.29	0.17	0.43			
Champia parvula	0.2					0.26			
Chondracanthus acicularis	5.9	0.75				0.9			
Chondria capillaris	0.3		0.14		0.07	0.02			
Chondria dasyphylla		0.01	0.14		0.37				
Chondria sp.		0.06		0.01					
Choreonema thuretii			0.01	0.01			0.1		0.53
Chrysonephos lewisii		0.42							
Chylocladia verticillata						1.73			
Cladophora albida			0.43			0.12			

	Catalonia	Corsica	Sardinia	Minorca	Formentera	Istria	Cyclades	Dodecanese	Lycia
Cladophora cf. *sericea*						1.58			
Cladophora coelothrix		6.63	0.52	0.29		0.47			
Cladophora dalmatica			0.06			0.44	0.8		
Cladophora hutchinsiae						1.52			
Cladophora laetevirens	198.3	19.19	2.79	7.16	2.3		0.8		
Cladophora lehmanniana		2.13	0.45	0.21					
Cladophora nigrescens		4.65				0.03			
Cladophora pellucida		1.04					14.05		
Cladophora prolifera	3.3	47.26	14.83	14.21		7.57	1.55		
Cladophora rupestris			0.02						
Cladophora socialis		0.69							
Cladophora sp. 1		1.39		0.88		10.21			
Cladophora sp. 2		0.33							
Cladophora vagabunda	5.6	0.29	1.14	4.91	0.6	0.77			
Cladophoropsis membranacea			2.29						
Cladosiphon sp.			0.01						
Cladostephus spongiosus		1.85				0.33			
Codium bursa		0.01							
Contarinia peyssonneliaeformis				0.14					
Corallina elongata	1.6	20.41	5.23	41.08		70.51	6.25	5.85	4.7
Corallinaceae encrusting								1.55	31.27
Corallophila cinnabarina									

	Catalonia	Corsica	Sardinia	Minorca	Formentera	Istria	Cyclades	Dodecanese	Lycia
Crouania attenuata						0.11			
Cryptonemia lomation						0.04			15.63
Cystoseira balearica		1.17	2.36						
Cystoseira barbata		26.03	28.64			62.94			
Cystoseira compressa v. *compressa*		3.33	7.86			23.98	40.65		1.2
Cystoseira compressa v. *pustulata*		1.81	0.79			7.94			
Cystoseira corniculata						0.06			
Cystoseira crinita	2633	2069.28	1878.07	2380.64	3275.53	1950.21	1868.5	1445	1796.67
Cystoseira foeniculacea v. *tenuiramosa*		0.58							
Cystoseira jabukae		0.14							
Cystoseira spinosa v. *tenuior*		0.72	0.86	81.86					
Dasya corymbifera	2	0.19	0.04			6.45	0.8	54.5	97.93
Dasya rigidula		0.12	0.22	0.01		0.04			1.57
Dasycladus vermicularis		8.32	7.74	9.43	17.93	0.40		127.45	
Delesseriaceae unidentified 1		0.07							
Delesseriaceae unidentified 2		0.01							
Dictyopteris polypodioides		13.4	1.5	0.01		21.81			60.97
Dictyota dichotoma						14.67			1.03
Dictyota dichotoma v. *intricata*		5.7	0.45			1.87			
Dictyota fasciola		2.37	0.46			1.25			6.77
Dictyota spiralis						0.18			
Dictyotaceae unidentified		33.15	109.68	4.48	3.77	0.26			

	Catalonia	Corsica	Sardinia	Minorca	Formentera	Istria	Cyclades	Dodecanese	Lycia
Digenea simplex			0.07						
Dipterosiphonia rigens		0.01	1.98	0.97	1.47				
Discosporangium mesarthrocarpum				0.07					
Erythrocystis montagnei			0.01						
Falkenbergia cf. *hillebrandii*-stadium		0.02	0.11						
Falkenbergia rufolanosa-stadium	5.2								
Feldmannia cf. *irregularis*	0.2	0.01							
Feldmannia lebelii	41.6	10.58	0.01	32.36		1.43			
Feldmannia sp.		15.28	1.43						
Flabellia petiolata		7.26	0.1	5.15	2.23	25.62	17.95		7.8
Gastroclonium clavatum						0.25			
Gayliella flaccida	0.2	0.01	0.02			0.44	1.55		1.03
Gelidiella sp.				0.01					
Gelidium crinale		0.11	0.09			7.25			
Gelidium latifolium		1.81							
Gelidium pusillum	0.9	0.06				7.89			
Gelidium spathulatum				1.57					
Grateloupia dichotoma		0.61							
Halimeda tuna		0.89	0.04	0.16	2.6	69.01	3.9		
Haliptilon virgatum	1.6	246.01	329.59	311.39	735.17	178	359.5	506.5	589.23
Halopithys incurva		0.22		11.11					
Halopteris filicina	0.2		0.07	0.36					

	Catalonia	Corsica	Sardinia	Minorca	Formentera	Istria	Cyclades	Dodecanese	Lycia
Halurus flosculosus		0.03	0.01						
Herposiphonia secunda	5.5	0.17	0.94	1.55	1.97	0.55	11.7	6.25	169.3
Heterosiphonia crispella					0.1				
Hildenbrandia crouaniorum		1.03	0.36						
Hydrolithon farinosum		79.17	91.93	128.69		46.24			
Hypnea musciformis	0.3	5.19							
Hypnea sp.						0.01			
Hypoglossum hypoglossoides						0.01			20.83
Janczewskia verrucaeformis								0.8	
Jania adhaerens			0.18	0.01					
Jania longifurca	191.1	0.19				0.15			
Jania rubens	23.1	13.48	5.73	85.89		22.15	3.9		2.6
Jania rubens v. *corniculata*									187.5
Jania sp.						0.1			
Laurencia cf. *obtusa*	11.4	4.54	0.11		7.03	3.04			
Laurencia chondrioides		0.07							
Laurencia microcladia		0.21	12.21						
Laurencia sp. 1							1.55		2.6
Laurencia sp. 2								3.9	
Laurencia sp. 3			0.19	0.15		8.09			
Laurencia sp. 4						1.39			
Lejolisia mediterranea		0.01							

	Catalonia	Corsica	Sardinia	Minorca	Formentera	Istria	Cyclades	Dodecanese	Lycia
Leptofauchea coralligena		1.81				0.77			
Liebmannia leveillei		0.06							
Lithophyllum incrustans	586								13.03
Lithophyllum pustulatum	89.4								
Lithophyllum sp.		0.17							
Lobophora variegata							10.95		4.48
Lophosiphonia cristata		0.1	0.29			0.01			
Lophosiphonia obscura					3.13	0.02			
Lophosiphonia reptabunda	0.5								
Lophosiphonia sp.		13.89							
Melobesiae unidentified						0.23			
Mesophyllum alternans		1.17							
Mesophyllum sp.							39.05		
Myriactula rivulariae	196.1			3.25		0.16			
Myriogramme sp.						0.01			
Neogoniolithon brassica-florida		388.22	305.54	170.13		178.83	93.75	226.5	140.63
Nitophyllum micropunctatum		0.04				4.04			
Osmundea truncata			0.04			0.72			
Padina pavonica	1.9	1.58	7.61	0.19	3.9	4.09	9.4		
Palisada papillosa		0.11	0.29			0.23			
Palisada patentirramea							3.9	15.65	
Palisada tenerrima			0.07		2.07				

	Catalonia	Corsica	Sardinia	Minorca	Formentera	Istria	Cyclades	Dodecanese	Lycia
Parviphycus tenuissimus		1.42	0.21	0.01		3.24			
Pedobesia lamourouxii							5.85		
Peyssonnelia cf. armorica				1.07					
Peyssonnelia dubyi		1.78			2.1				
Peyssonnelia harveyana		1.11		0.11		0.15		3.3	
Peyssonnelia rosa-marina		9.44	2.5			3.58		3.9	28.63
Peyssonnelia sp.		1.67				30.68			
Peyssonnelia squamaria		1.75				4.73			
Phyllophora crispa		0.06							
Plocamium cartilagineum	0.2	0.03							
Polysiphonia flocculosa					9.63				
Polysiphonia opaca		0.04	0.64		0.27				
Polysiphonia scopulorum	0.2								
Polysiphonia setigera	0.3								
Polysiphonia sp. 1	0.5		0.01						
Polysiphonia sp. 2			0.29						
Polysiphonia sp. 3		0.14							
Polysiphonia sp. 4							0.25		
Polystrata fosliei		1.11							
Porphyra sp.		0.03							
Pseudochlorodesmis furcellata		0.24							
Pseudolithoderma adriaticum		61.83	60.32	255.61					

	Catalonia	Corsica	Sardinia	Minorca	Formentera	Istria	Cyclades	Dodecanese	Lycia
Pterocladiella melanoidea		0.21							
Rhodophyllis divaricata		0.04							
Rhodophyllis strafforelloi				0.11		1.53			
Rytiphlaea tinctoria		27.89	94.5	46.07		1.54		99	
Sargassum vulgare						1.54	11.7		6.23
Siphonocladus pusillus		0.01					1.55		
Spermothamnion irregulare	0.3								
Spermothamnion repens			0.29		6.5	0.01	0.3		
Spermothamnion sp.						0.02			
Sphacelaria cirrosa	88.4	413.64	129.26	269.39	0.53	476.78	35.15	11.75	
Sphacelaria rigidula		0.01							
Spyridia filamentosa			1.59						
Stypocaulon scoparium	280.3	2.83	3.83	0.43	4.73	4.98			
Taonia atomaria		0.33				0.31			24.47
Titanoderma trochanter									1.03
Ulva multiramosa									
Ulva pseudolinza	2.8								
Ulva ramulosa	1116.6								
Ulva rigida	74.5					7.68			
Ulva sp.		0.14				0.01			
Valonia aegagropila		0.44	4.93			29.85			
Valonia utricularis		6.69	29.89	1.83		18.97			

	Catalonia	Corsica	Sardinia	Minorca	Formentera	Istria	Cyclades	Dodecanese	Lycia
Vickersia baccata						0.01			
Womersleyella setacea							3.15		
Wrangelia penicillata			0.01						
Wurdermannia miniata		0.01							
Sessile macroinvertebrates									
Actiniaria (unidentified)									1.03
Aetea anguina			0.36						
Aglaophenia kirchenpaueri			0.11				21.9		24.5
Aiptasia diaphana		0.04	0.07						
Amathia lendigera		0.39	0.14	1.29					
Amathia sp.						13.37			
Anemonia sulcata				2.14					
Arca noae		0.78		0.82					
Balanophyllia europaea		0.03	0.29						
Campanulariidae (unidentified)			0.21						
Chiton sp.			0.11						
Chlidonia pyriformis									15.63
Clavularia crassa							12.5		12.5
Crisia sp.						0.15	16.45		17.69
Cystodites dellechiajei						13.85			31.27
Didemnidae unidentified 1		0.06	0.03						
Didemnidae unidentified 2		0.33							

	Catalonia	Corsica	Sardinia	Minorca	Formentera	Istria	Cyclades	Dodecanese	Lycia
Didemnidae unidentified 3		0.06							
Didemnidae unidentified 4			0.21						
Didemnum granulosum							26.55		
Didemnum maculosum		0.11							
Encrusting bryozoan (unidentified)									11.98
Filicrisia geniculata						0.14			
Guanchia sp.							0.8		
Haliclona sp.		0.22							
Hymedesmia versicolor		0.56							
Ircinia fasciculata		0.25	0.29						
Ircinia variabilis		0.39		0.36		2.46	15.45		
Ostraea edulis						0.38			
Pherusella tubulosa						2			
Porifera unidentified		0.83							
Sarcotragus spinosula							3.5		
Scrupocellaria sp.						24.37			
Spondylus spinosus									7.8
Turbicellepora magnicostata		15.48	0.36	0.57				0.8	13.02

The MDS on averaged species data showed patterns of resemblances in community structure among the regions that reflected their relative geographical positions (Fig. 3). The maximum distance represented in the MDS was between Catalonia (Spain) and Lycia (Turkey). The three different regions from Spain were quite well-separated, with the island of Minorca appearing more similar to Corsica (France) and Sardinia (Italy) than to Formentera or Catalonia. The cluster analysis indicated 11 groups of samples, based on SIMPROF tests: (1) Catalonia, (2) Lycia (Turkey) plus one sample from Cyclades (Greece), (3) Formentera plus a sample from Dodecanese (Greece) (G-3), (4) a sample from Dodecanese (Greece) together with an atypical sample from Minorca, (5) the other sample from Dodecanese (Greece) , (6) the peninsula of Istria (Croatia), and (7, 8, 9, 10 and 11) Minorca, Corsica and Sardinia appeared to be more mixed, being mainly together in a group with a few outlying samples forming small groups of just one or two isolated sample units (Fig. 4). Although the stress in the two-dimensional image of the second MDS (Fig. 4) is quite high, the image observed in the three-dimensional image (not shown), with a stress of 0.17, shows similar patterns as those shown in Fig. 4. The correlation between longitude and species richness was very low and not significant. There was, however, a positive and significant correlation between latitude and species richness (Fig. 5).

ANOSIM indicated statistically significant differences between all the pairs of regions, except for Corsica and Sardinia (Table 1). The univariate (one-way ANOVA) analyses of the total cover and of the cover of *C. crinita* showed no significant differences among regions (Balearic Islands, Corsica, Sardinia, Istria and the Southern Aegean). However, there was significantly higher cover of green algae in Istria than in the Balearics and significantly higher cover of sessile invertebrates in Istria and in the Southern Aegean than in the other regions (Table 2, Fig. 6). The number

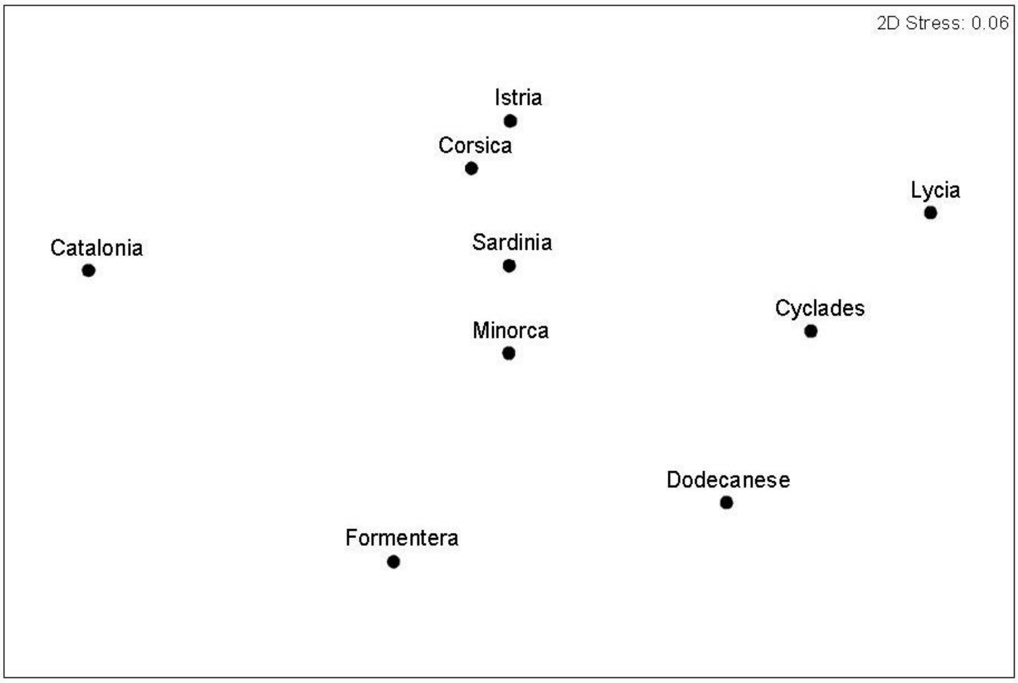


Fig. 3. MDS ordination on the averaged species abundances per region.

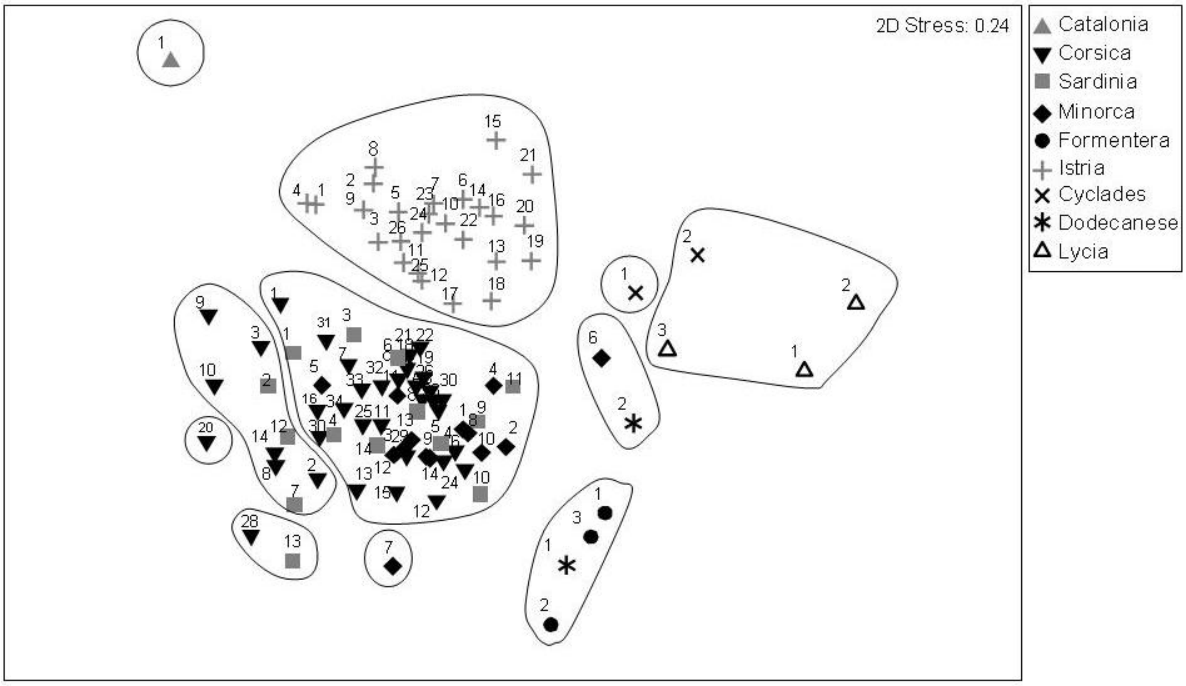


Fig. 4. MDS ordination on species abundances for the full data-set, showing results of the group average clustering analysis.

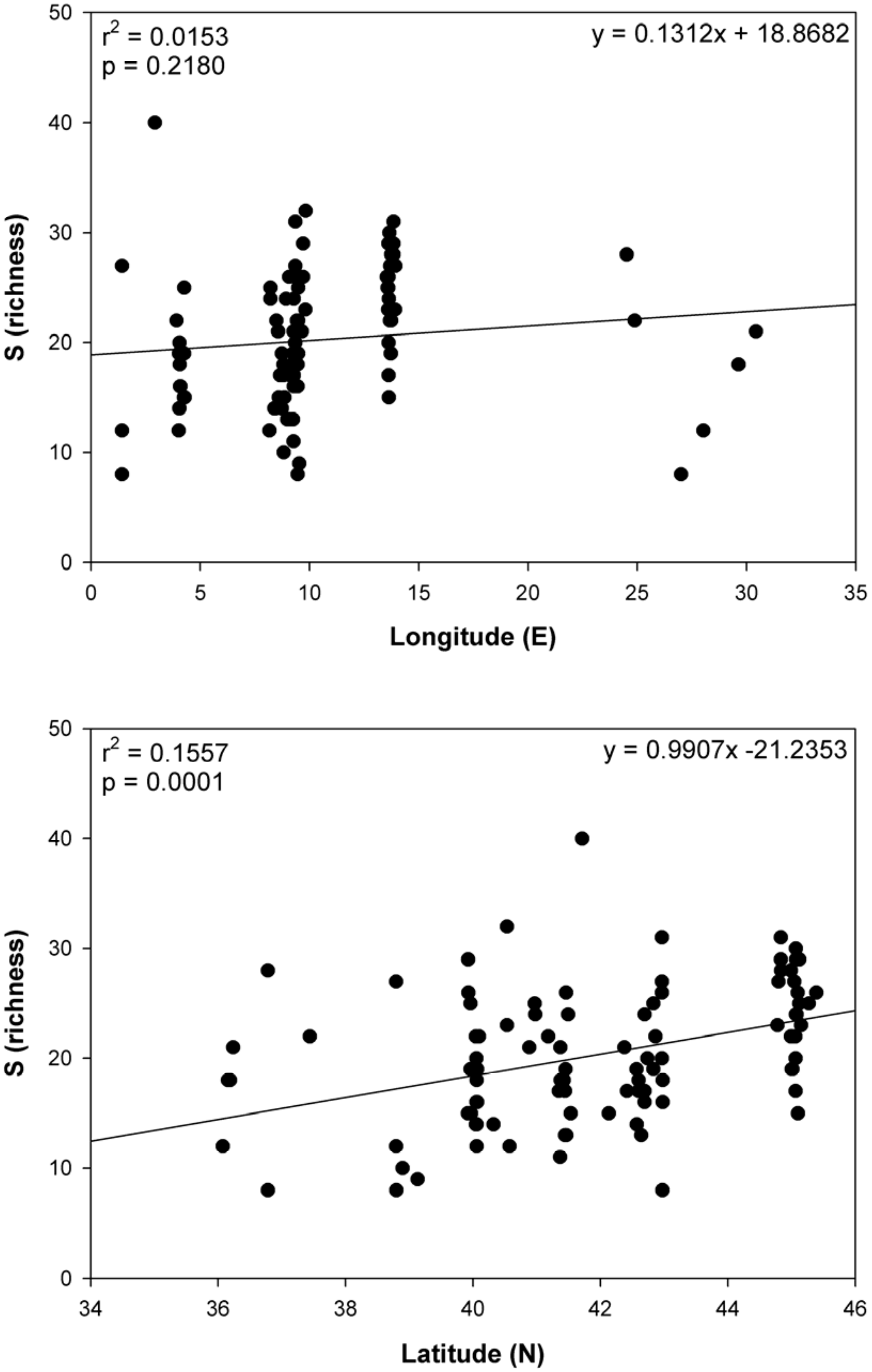


Fig. 5. Richness gradients across longitude and latitude, showing regression analyses results.

Table 2. Results of ANOSIM test on species abundances from the different studied regions.

	R	p
Global Test	0.531	**0.0001**
Pairwise Tests:		
Balearics, Corsica	0.217	**0.0020**
Balearics, Sardinia	0.183	**0.0010**
Balearics, Istria	0.772	**0.0001**
Balearics, S.Aegean	0.755	**0.0001**
Corsica, Sardinia	0.09	0.1050
Corsica, Istria	0.696	**0.0001**
Corsica, S.Aegean	0.893	**0.0001**
Sardinia, Istria	0.722	**0.0001**
Sardinia, S.Aegean	0.811	**0.0001**
Istria, S.Aegean	0.934	**0.0001**

Table 3. Results of one-way ANOVA tests on some specific components of the assemblage and on two diversity indices.

Variable	Transf.	ANOVA F	ANOVA p
Total cover	log	1.323	0.267
C. crinita cover	sqrt	1.987	0.103
Chlorophyta cover	sqrt	3.670	**0.008**
Invertebrates cover	4th root	7.474	**0.0001**
Species number	4th root	6.583	**0.0001**
Simpson's evenness	none	1.122	0.351

of species per sample was significantly higher in Istria than in the Balearic Islands, Corsica and the Southern Aegean regions. There were no significant differences, however, in the evenness of assemblages among regions (Table 2, Fig. 7).

The plots of the ten most abundant species per region evidenced that the most different region was the Southern Aegean, which, apart from *Cystoseira crinita*, only shared two species with the other regions (Fig. 8). These were the epiphyte *Haliptilon virgatum* and the encrusting coralline alga *Neogoniolithon brassica-florida*. The average cover of *H. virgatum* apparently increased from northern to southern regions (I < C < S < B < SA). *N. brassica-florida* was more abundant in Corsica and Sardinia than in Balearic Islands, Istria and the Southern Aegean. Moreover, the Southern Aegean region was the only one in which an invertebrate (the hydrozoan *Aglaophenia kirchenpaueri*) appeared among the ten most abundant species. Apart from *H. virgatum*, two other epiphytes appeared as important components of *C. crinita*-dominated assemblages from the Balearic Islands, Corsica, Sardinia and Istria: the brown alga *Sphacelaria cirrosa* and the encrusting coralline *Hydrolithon farinosum*. The epiphyte *S. cirrosa* apparently decreased from northern to southern areas (I > C > B > S), while *H. farinosum* showed the opposite pattern (I < C < B ~ S). In the Southern Aegean, the red filamentous algae *Herposiphonia secunda* and *Dasya corymbifera* were among the most important epiphytes of the assemblage. No turf-forming alga occurred in any of the regional lists of the 10 most abundant species. The articulated coralline alga *C. elongata* appeared in Minorca, Corsica and Istria; *Rityphlaea tinctoria* appeared in Minorca, Corsica, Sardinia and the Southern Aegean; and *Dictyota* spp. appeared only in Corsica and Sardinia. Finally, in the canopy layer, *C. barbata* co-occurred with the dominant species *C. crinita* in Corsica, Sardinia and Istria.

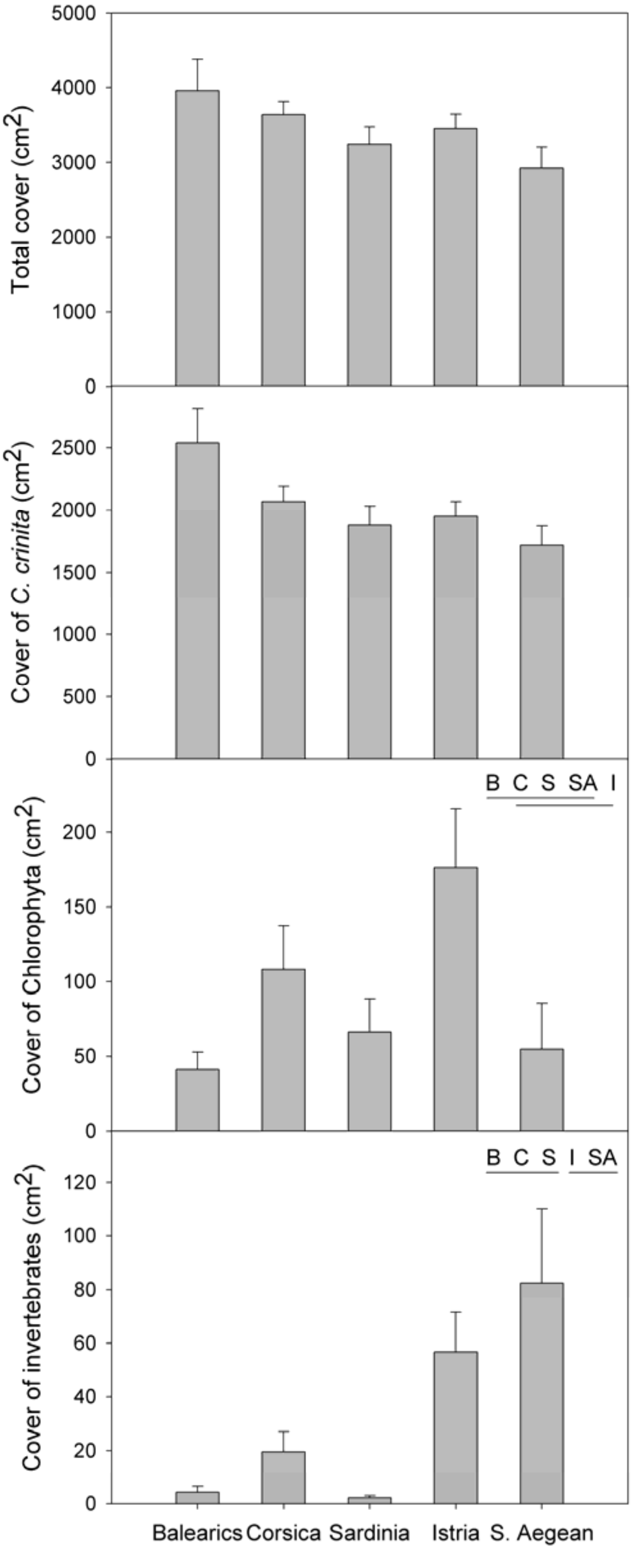


Fig. 6. Mean cover (+ 1SE) of different components of the studied assemblages for each region. ANOVA results are indicated in the upper-right corner (B: Balearic Islands, C: Corsica, S: Sardinia, I: Istria, SA: southern Aegean).

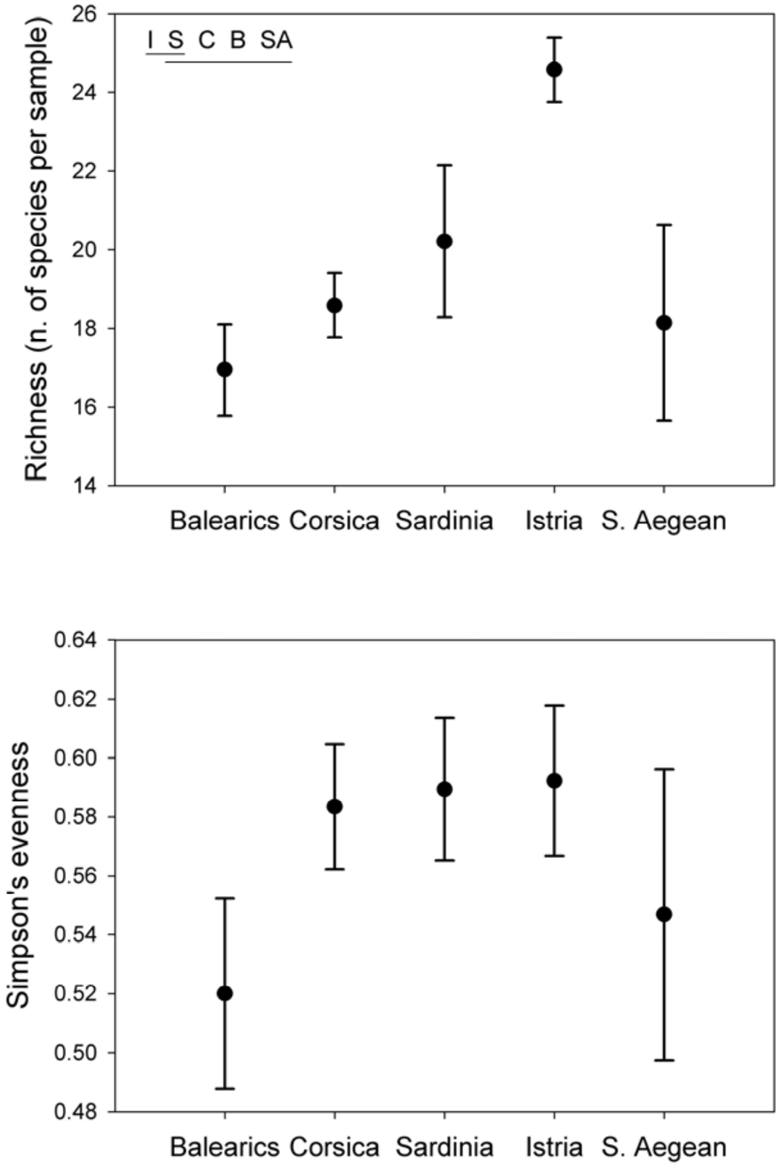


Fig. 7. Mean Richness and Simpson's evenness (± 1SE) calculated for each region.

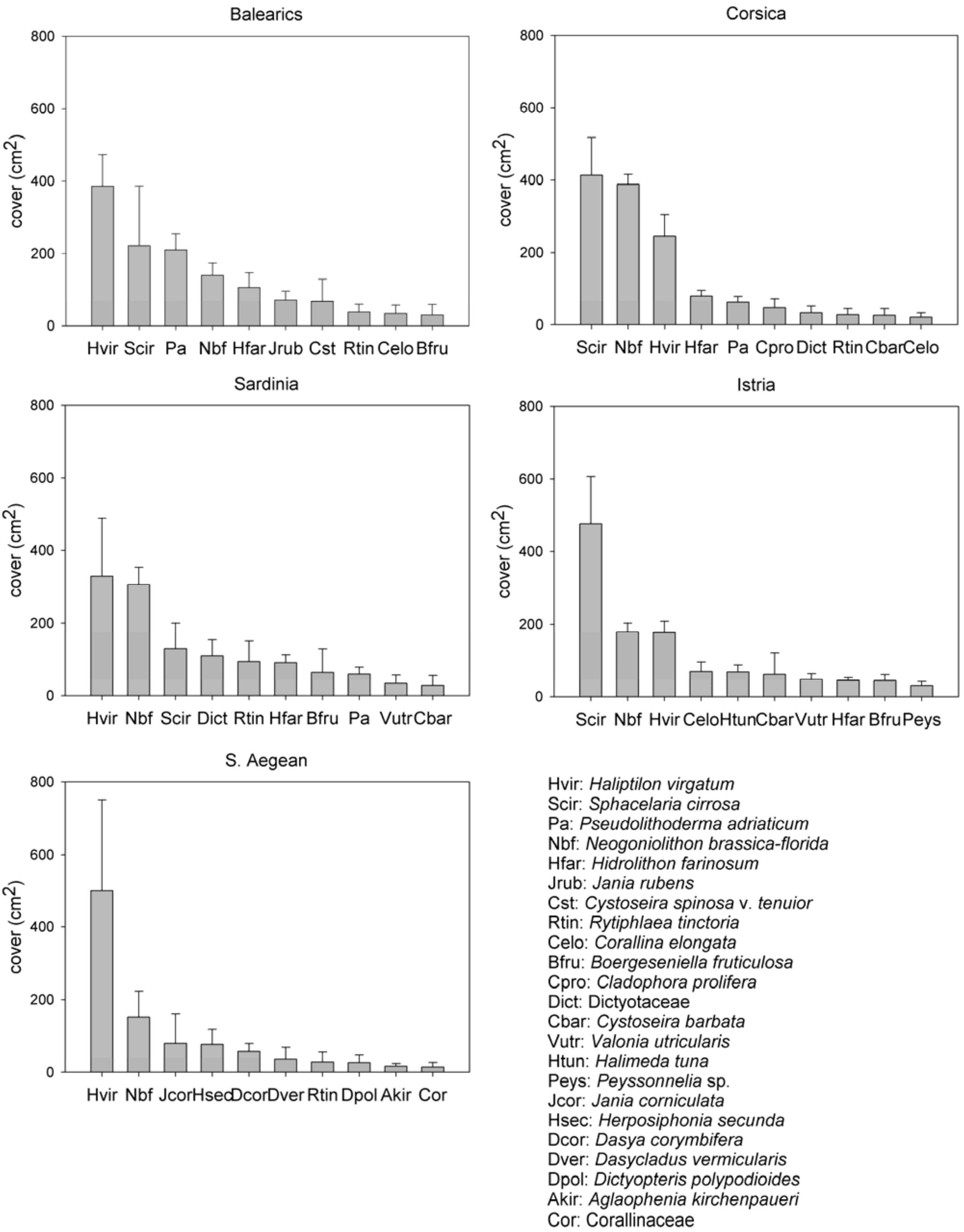


Fig. 8. Mean cover (+1 SE) of the ten most abundant species (excluding *Cystoseira crinita*) for each region.

Discussion

Seaweeds are the primary species of *C. crinita*-dominated assemblages, while invertebrates usually display low coverage in these shallow Mediterranean habitats (Zabala & Ballesteros 1989). The similarity in total cover and *Cystoseira crinita* cover in the assemblages from the different regions, and also the presence of the epiphyte *Haliptilon virgatum* are the defining characteristics of these assemblages across the Mediterranean as a whole. Other epiphytic species which were present in all or almost all of the studied regions were the red filamentous algae *Herposiphonia secunda* and *Dasya* spp. The turf-forming *Corallina elongata* and *Rytiphlaea tinctoria*, and the encrusting *Negoniolithon brassica-florida* were also present and abundant across almost all of these regions.

Despite these general features, marked shifts in relative coverages of species have been detected among the studied regions, in agreement with previously proposed biogeographic divisions of the Mediterranean Sea (Pérès & Picard 1964, Bianchi & Morri 2000, Bianchi 2007). This result accords with Adey and Steneck's idea (2001) that biogeographic regions should be determined by the relative coverages of species in assemblages.

Three introduced algal species have been found in the samples, but none of them seem to be causing any obvious impacts on *C. crinita*-dominated assemblages. Considering the habitat preference of these introduced species, only *C. racemosa* v. *cylindracea* could pose a potential threat to shallow algal assemblages, as it has been found in a wide range of depths and environments (Piazzi et al. 2005).

The grouping of samples, suggested by the combined results of the MDS and the cluster analysis, generally coincided with previously described biogeographic regions (Pérès & Picard 1964, Bianchi 2007). The only exception was Formentera (southern Balearic Islands), which was separated from Minorca (northern Balearic Islands) and placed relatively close to the samples from Dodecanese (Greece). A similar temperature and trophic regime between the south-western Mediterranean and the eastern Mediterranean (Bosc et al. 2004) could explain this pattern. Of our sampling sites, the only ones which were located south of the 14ºC February isotherm (Brasseur et al. 1996) were those from Formentera, Cyclades, Dodecanese and Lycia. Bianchi (2007) observed that the 15ºC February isotherm followed quite closely the biogeographic boundary between the western and eastern Mediterranean and also that the 14ºC isotherm could have some biogeographic relevance. Invertebrate assemblages from the south-western Mediterranean have also been found to be more similar to those from the eastern Mediterranean than to those from the north-western Mediterranean (Bianchi 2007). Despite this divergence between northern and southern Balearic Islands, the distances among samples shown by the MDS did tend to mirror the geographical positions of the regions. Similar findings, showing a high degree of spatial structure of intertidal and sublittoral assemblages at a regional level, have been reported for the whole Europe (Arvanitidis et al. 2009), for the western coast of the USA (Blanchette et al. 2008) and for the southern coast of Australia (Connell & Irving 2008).

The relative positions of the regions in the MDS plot suggest that longitude and latitude are more important than geographical distances. For example, Istria (northern Adriatic) appears quite close to Corsica and Sardinia, although the geographical distance by sea is fairly high. Based on the results of the MDS and the ANOSIM, *C. crinita*-dominated assemblages from Istria have more biological affinity with assemblages from the western Mediterranean than with assemblages from the eastern Mediterranean. This contrasts with the classical biogeographical divisions (Perès & Picard 1964, Bianchi & Morri 2000), which indicate a main biogeographical division close to the straits of Sicily, leaving the Adriatic in the eastern basin. The latitudinal range of the Adriatic Sea is more similar to the latitudinal range of the western Mediterranean, however, than to that of the eastern Mediterranean. Temperature is highly related to latitude, and it has been shown to be an important factor limiting the spatial distributions of seaweeds (Breeman 1988, Cambridge et al. 1990).

It is generally believed that there is a gradient of species richness which decreases from west to east in the Mediterranean Sea (Boudouresque 2004), an idea that is reinforced by results presented by different authors on different groups of animals (Arvanitidis et al. 2002, Coll et al. in press). To the contrary, we did not find any significant correlation between longitude and species richness in our study. Instead, a slight increase of species richness with latitude was found in our study, reinforcing the idea that temperature is a key factor determining macroalgal diversity patterns. Similarly, Renaud et al. (2009) found a slight increase in richness in invertebrates' assemblages with latitude in coastal European environments (including study sites in the Mediterranean Sea). At a global scale, macroalgal richness peaks at temperate latitudes (Kerswell 2006). It is possible that the climatic and oceanographic conditions of the northern Mediterranean, with lower temperatures and higher runoff of nutrients from rivers, are similar to those of temperate oceans where peaks in macroalgal richness are found. Other explanations, such as higher geomorphological complexity, are unlikely, as the southern-most regions sampled in this study included several morphologically complex islands.

The cover of green algae, which indicates relatively high nutrient levels (Ballesteros et al. 2007), was significantly higher in Istria than in other regions. In the northern Adriatic, runoff from rivers is relatively high, mainly due to the river Po, and water circulation is low due to the narrowness and the shallowness of this area, making it one of the most eutrophic of the Mediterranean (Bosc et al. 2004). There is no obvious explanation, however, for the relatively high cover of invertebrates found in the southern Aegean, but our results agree with those found by Kokatas (1976) in *C. crinita*-dominated assemblages from Izmir Gulf (Aegean Sea, Turkey).

Although this study embraced a much wider area than previous localised studies on macroalgal assemblages (e.g. Molinier 1960, Boudouresque 1972, Ballesteros 1992, Pizzuto 1999), it was still far from including all of the potential biogeographical variation occurring in the Mediterranean Sea. Moreover and unfortunately, the regions of Catalonia, Formentera, Cyclades, Dodecanese and Lycia were less intensively sampled than the other regions. The particular environments sheltering *Cystoseira crinita* assemblages (i.e., rocky platforms situated slightly below mean sea-level in places of medium exposure and high sediment loads; Ballesteros 1992) together with the high vulnerability of *C. crinita* to a variety of human-induced disturbances (Thibaut et al. 2005) were fairly rare in these areas, thus reducing the potential for more intensive sampling.

In conclusion, the variability in species composition and relative coverages of species within *Cystoseira crinita* -dominated assemblages show clear geographical patterns of relationships. However, we found some exceptions to the classical biogeographical view of the Mediterranean, which identifies a main division located near Sicily to delineate a western and an eastern basin. First, assemblages from the northern Adriatic showed higher affinity with those from the north-western Mediterranean than with those from the eastern Mediterranean. Second, a strong shift was detected between the northern and southern Balearic Islands. Moreover, species diversity did not decrease from west to east but, rather, from north to south. This challenges the notion that relatively low diversity is found in the eastern Mediterranean Sea.

Chapter 3

Shallow *Cystoseira* (Fucales, Heterokontophyta) assemblages thriving in sheltered areas from Minorca (NW Mediterranean): relationships with environmental factors and anthropogenic pressures

Introduction

Humans are largely disturbing natural ecosystems leading not only to a loss of biodiversity but also to a change in the landscape, due mainly to the regression of large and long-lived species (Steneck and Carlton 2001). Such changes have been observed in littoral habitats when affected by environmental degradation, involving the disappearance of engineering species such as kelps or seaweeds of the order Fucales (Munda 1993, Benedetti-Cecchi et al. 2001, Steneck et al. 2002, Thibaut et al. 2005, Airoldi and Beck 2007). Species of the genus *Cystoseira* (Fucales, Heterokontophyta), important engineering species in the Mediterranean phytal zone (Feldmann 1937, Giaccone 1973), have been affected by the environmental degradation of several areas and are currently suffering a general Mediterranean decline (Hoffmann et al. 1988, Chryssovergis & Panayotidis 1995, Rodríguez-Prieto & Polo 1996, Soltan et al. 2001, Thibaut et al. 2005, Serio et al. 2006). Eutrophication has been the main cause to blame for the rarefaction of *Cystoseira* species (Munda 1974, 1982, Hoffmann et al. 1988, Arévalo et al. 2007), although other factors like inorganic chemical pollution, increased turbidity levels, overgrazing and climate change have been suggested as possible causes (Cormaci & Furnari 1999, Thibaut et al. 2005, Serio et al. 2006). *Cystoseira* spp. assemblages dominate the seascape of most Mediterranean reference sites; they are well structured, complex, very productive and they hold high biodiversity (Boudouresque 1971b, 1972, Ballesteros 1988, 1990a,b, Ballesteros et al. 1998, 2009). All species of the genus *Cystoseira* but *C. compressa* are included in the Annex II of the Barcelona Convention and, thus, they deserve some protection at Mediterranean scale. However, despite the role of *Cystoseira* assemblages in the conservation of the Mediterranean seascape and biodiversity, its importance has not been recognized by the current European legislation in environmental conservation (e.g. Habitats Directive 1992/43/EC).

Several species of *Cystoseira* preferentially thrive in shallow waters of sheltered coves and bays. These habitats have been a target for human development along most of the Mediterranean coastal areas, in such a way that some of the species developing in these shallow and sheltered environments may be in serious regression along most of its previous distribution range (Thibaut et al. 2005). Although there is basic knowledge on the habitat preferences of each species of *Cystoseira* (e.g. Giaccone and Bruni 1973, Gómez-Garreta el al. 2000) there are no studies which try to disentangle the environmental factors affecting its distribution in the Mediterranean. The island of Minorca (Balearic Islands, Northwestern Mediterranean) presents abundant rocky shores with high geomorphological heterogeneity. Some impacted areas co-exist with several almost pristine small coves and bays. This charachteristics offer a unique system in which to study the relationship between shallow water *Cystoseira* species distribution and the environmental and anthropogenic factors affecting them.

The degree of development of *Cystoseira* littoral belts in exposed coasts (e.g. *Cystoseira mediterranea*, *Cystoseira amentacea* v. *stricta*, *Cystoseira compressa*) have been used to assess the ecological quality of the coastal water bodies regarding the European Water Framework Directive (2000/60/EC) (Ballesteros et al. 2007, Pinedo et al. 2007, Mangialajo et al. 2008). However, the possible utility of *Cystoseira* species from sheltered environments as indicators has not been addressed, although current existing information (Cormaci & Furnari 1999, Thibaut et al. 2005) suggest that they are extremely sensitive to water quality.

The aim in this chapter is to test which are the main environmental factors driving the present distribution of *Cystoseira* sheltered species in the island of Minorca, in order to obtain the necessary knowledge to use them as bioindicators.

Materials and methods

Study area

The island of Minorca is located in a very central position in the north-western Mediterranean (Fig. 1). It extends about 50 km from west to east and about 20 km from north to south; its coastline measures 441 km. The island is divided into two different geomorphological regions: north and south (Llompart et al. 1979). The Northern part is constituted by a variety of very ancient materials mainly non-carbonated; coastline is very irregular with very pronounced cliffs, small coves and big sheltered bays. The Southern part is formed by a carbonated block from the Miocene; coastline is very straight with rocky cliffs and narrow coves (Rosell & Llompart 2002). Minorca's coast is relatively well preserved; large areas are protected from urban expansion and many beaches and coves are totally wild and natural. Nevertheless, the island is not safe from touristic and industrial expansion and some focus of pollution and anthropogenic disturbances exist along the coast (Comas 2004, www.obsam.cat).

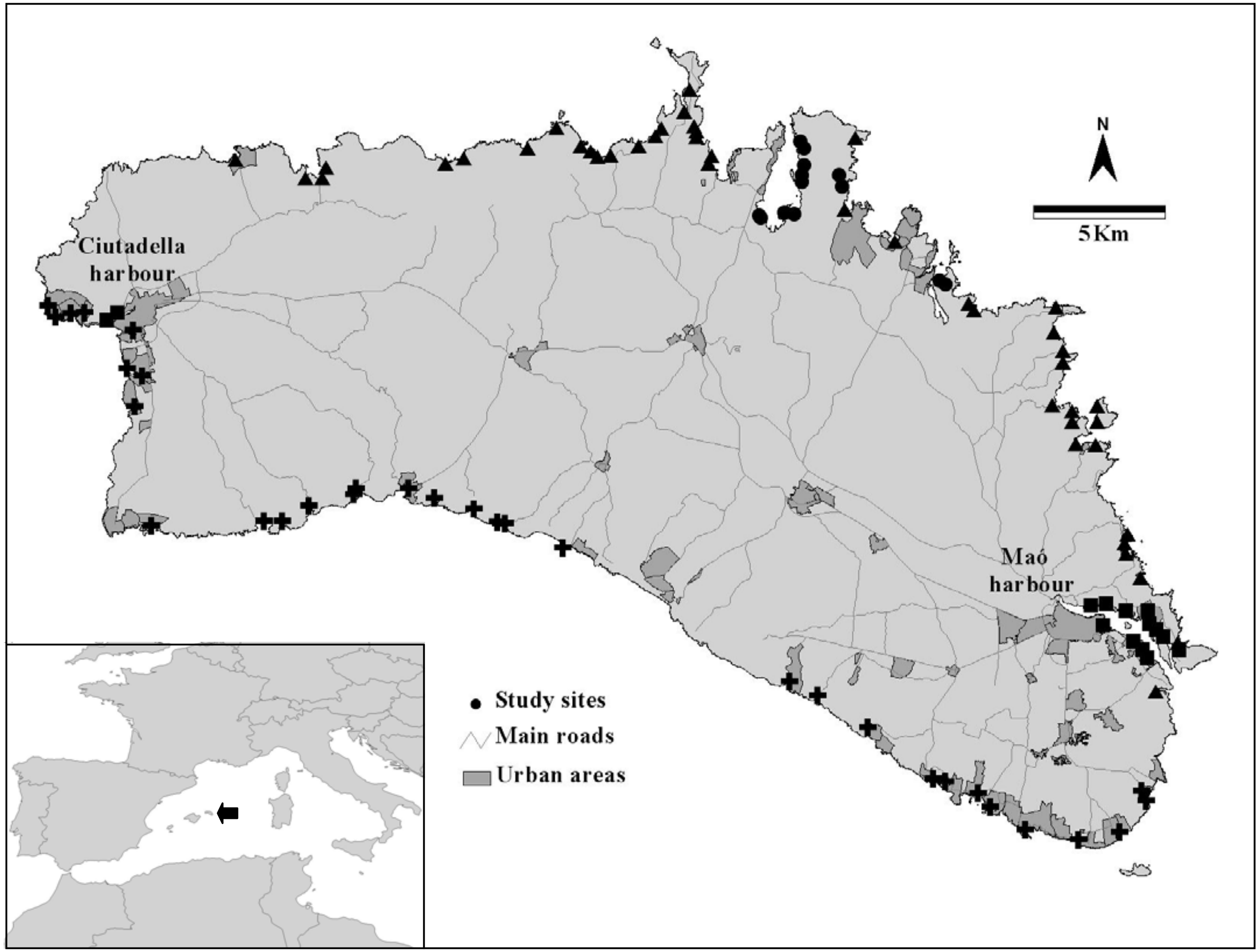


Fig. 1. Map of the study area (triangles: typical northern coves, rounds: very sheltered coves, cross: typical southern coves, squares: coves situated in the proximity of harbours).

Collection of data

Field work was carried out during May and June 2005, when populations of *Cystoseira spp.* are well developed and are easy to observe and identify (Ballesteros et al. 2007). The coastline of a total of 103 coves was surveyed by snorkeling and abundances of the different species of *Cystoseira* were recorded. These abundances were visually estimated and expressed in a semi-quantitative scale (**+**: < 5% coverage, **1**: 5-10% coverage, **2**: 11-25% coverage, **3**: 26-50% coverage, **4**: 51-75% coverage, **5**: > 75% coverage) (Braun-Blanquet 1951). *Cystoseira* specimens were usually identified in the field. Doubtful specimens were collected and identified in the laboratory using appropiate bibliography (Sauvageau 1912, Ercegovic 1952, Amico et al. 1985, Gómez-Garreta et al. 2000). Vouchers are kept in the University of Girona (UdG) herbarium (HGI-A 6998, 6999, 7000, 7003, 7004, 7005, 7006, 7009, 7010, 7017, 7019 and 7022).

Values of 14 environmental parameters (related to the morphology of the coastline, the wind and wave exposure, the characteristics of the bottom and anthropogenic pressures) were obtained for each sampled cove (Table 1). Some of the parameters such as coast height (divided into four different categories: high, medium and low cliff and flat rocky coast) or slope (divided into four categories: overhanging, vertical, subvertical and horizontal) were measured *in situ* during the field work. The values of other parameters, like exposure and urbanisation distance, were calculated over aerial photographs using GIS. Three water samples from each site (replicates) were collected at three dates during the study period (winter, spring and end of summer) in order to cover the seasonal variation of nutrients concentrations. Collected samples were conserved frozen at -20ºC and stored in darkness until the moment of analysis. Nitrate, nitrite, ammonium, phosphate and silicate concentration was determined according to Grasshoff et al. (1983) methods using an *Alliance Evolution II Autoanalyzer*.

Table 1. List and brief description of the studied parameters specifying the calculation method.

Parameter	Description	Calculation method
Slope[(a)]	Inclination of the substrate	field
Exposure[(b)]	Angle formed by two lines from the innermost central part of the cove to the the two outer edges (in degrees)	GIS
Morphological factor 1	% of rocky littoral	GIS
Morphological factor 2[(c)]	Littoral height	field
Morphological factor 3	% of coastline constituted by blocks	field
Bottom factor 1	% of vegetated bottom	GIS
Bottom factor 2	% of bottom covered by seagrass	GIS
Bottom factor 3	% of rocky bottom	GIS
Urbanisation distance[(d)]	Straight distance to the nearest town or urbanisation (in meters)	GIS
Nutrients concentrations	Phosphate, nitrite, nitrate, ammonium and silicate concentrations (in µM)	field + lab work

[(a)] Average degree of inclination of the substrate at the first meter of depth calculated from sectors to which we attributed the degree of inclination in categories (Overhanging: 105°; Vertical: 75°; Subvertical: 45° and Horizontal: 15°).

[(b)] When the coves where situated inside big bays the exposure was always considered 1.

[(c)] Average height of the littoral calculated from sectors of the cove to which we attributed height in categories corresponding to numerical values (Low: 1; Medium: 2; High: 3).

[(d)] It has been considered urbanisation any village or agglomeration of buildings.

Statistical analysis

The combined transformation of van der Maarel (1979) with an exponent of w=0.5 was applied to biological data (*Cystoseira* species abundances per site) to make possible arithmetic operations. A *Bray-Curtis* distance matrix (Bray & Curtis 1957) with a *dummy-variable* was, then, constructed.

A draftsman plot (Clarke & Gorley 2006) was performed with the environmental variables matrix in order to detect possible skewness of the variables and/or strong correlation among pairs of variables. As high correlation was found between nitrate and silicate concentration (r=0.96; p=0.00001), silicate concentration was eliminated from the environmental matrix. Furthermore, phosphate and nitrate concentrations where right-skewed, and therefore log(x+1)-transformed. Despite not being strongly skewed, nitrite and ammonium concentration were also log(x+1)-transformed in order to apply the same treatment to the same type of data (nutrient concentration).

Finally, distance-based linear model routine (DistlM) (Legendre & Anderson, 1999) was applied in order to analyse and model the relationship between biological data (*Cystoseira* spp. populations) and environmental factors. The selection criterion and selection procedure used were *step-wise* and *adjusted* R^2. The environmental definite matrix (without SiO_4 and with log transformed nutrient concentrations) was used as the predictor variable worksheet. dbRDA (distance-based redundancy analysis, McArdle & Anderson 2001) plot was made to allow the visualization of the sites ordination according to the multivariate regression model previously generated by applying DistlM. Given the strong differences on *Cystoseira* species composition observed between typical north coves, very sheltered north coves, south coves, and coves located in harbour areas, they were represented with different symbols in the plots and submitted to ANOSIM analysis (Clarke 1993).

Results

Eleven taxa belonging to the genus *Cystoseira* were found during the surveys (Table 2). As *C. spinosa* v. *spinosa and C.* cf. *mediterranea* appear at just two study sites, they have been excluded from the following descriptions and analysis. *C. amentacea var. stricta, C. compressa var. compressa* and *C. brachycarpa var. balearica* are distributed all around Minorca. These species thrive only in the outer parts of the coves being more typical from exposed areas, where they form extensive assemblages. The other species only appear in really shallow sheltered areas and are restricted or almost restricted to the north coast. *C. crinita, C. spinosa var. tenuior, C. algeriensis* and *C. compressa var. pustulata* are widespread along the entire north coast forming dense settlements at the inner parts of many coves. *C. crinita* and *C. spinosa var. tenuior* are the dominant taxa of well structured and rich assemblages at sheltered and semiexposed coves, which can be both monospecific or mixed. *C. foeniculacea var. tenuiramosa* and *C. barbata* are restricted to extremely sheltered environments with soft bottoms covered by seagrasses. In these conditions *Cystoseira* species can just grow attached to pebbles or even to seagrass rhizomes and, therefore, they almost never form dense settlements. Finally, up to 13 coves are completely devoid of any specimen of *Cystoseira* spp., most of them situated close or adjacent to harbours. Abundances of different species per site are presented in Figure 2 and in Table 3.

Table 2. Species found along the study area and their abundances (VA: very abundant, A: abundant, C: common, R: rare, VR: very rare).

Species	Abundance
C. stricta (Montagne) Sauvageau (=*C. amentacea var. stricta*)	VA
C. cf. mediterranea Sauvageau	VR
C. balearica Sauvageau (=*C. brachycarpa var. balearica*)	A
C. compressa (Esper) Gerloff & Nizamuddin *var. compressa*	VA
C. compressa (Esper) Gerloff & Nizamuddin *var. pustulata* Ercegovic (=*C. humilis* ?)	C
C. crinita (Desfontaines) Bory	C
C. spinosa Sauvageau *var. tenuior* (Ercegovic) Cormaci et al.	C
C. spinosa Sauvageau *var. spinosa*	VR
C. algeriensis Feldmann	R
C. foeniculacea (Linné) Greville *var. tenuiramosa* (Ercegovic) Gómez Garreta et al.	R
C. barbata C. Agardh	R

DistlM analysis shows a significant relationship between biological and environmental data when considering predictor variables individually. All the studied parameters except ammonium show significant relationship to the species data (Table 4A). Coast height and nitrate concentration are the factors explaining the highest percentage of variation in *Cystoseira* species composition and abundance (21 and 19 % respectively); the factors nitrite concentration, slope, % of rocky bottom, % of vegetated bottom and urbanisation distance explain also a considerable amount of variation in the biological data matrix (values between 14 and 17 %).

Table 3. Abundances of different *Cystoseira* species at the study sites expressed in *Braun-Blanquet* semi-quantitative scale (C.str: *C. amentacea var. stricta*; C.com: *C. compressa var. compressa*; C.pus: *C. compressa var. pustulata*; C. cri: *C. crinita*; C.bal: *C. brachycarpa var. balearica*; C.spit: *C. spinosa var. tenuior*; C.alg: *C. algeriensis*; C.foe: *C. foeniculacea var. tenuiramosa*; C.bar: *C. barbata*).

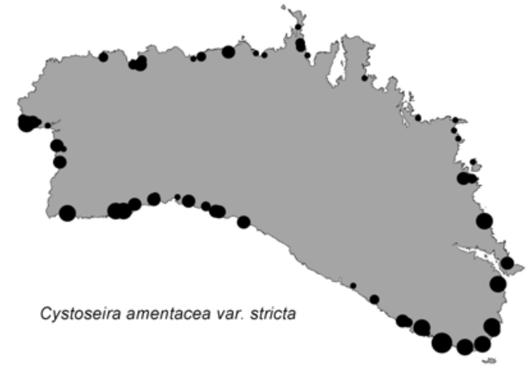
	Site	C.str	C.com	C.pus	C.cri	C.bal	C.spit	C.alg	C.foe	C.bar
1	Es Freus	2		+		+				
2	Es Murtar		1	4	2	2		1		
3	Sa Mesquida 1	+	1	4	2	3				
4	Sa Mesquida 2	3	2	3	3					
5	Raconada M		+	3	2	3		+		
6	Cala Avellana	1	1	1	+	2	1			
7	Es Grau	2	1	+	1	2		+		
8	Pl. Tamarells			1	1 _ 2		1 _ 2			
9	Ar. d'en Moro	+	+	1	2	3	3			
10	Tamarells S		1 _2	2	3 _ 4		4	+	1	
11	Tamarells N		2	2	3		3	1	2	
12	Sa Torreta		+	2	3			3	1	
13	Cavaller		2 _ 3	1	1	+	1	2		
14	Morella Nou	+	2	+	2 _ 3	2		2		
15	Tortuga	+	2	+	2	+		1		
16	S'Escala	+	2	+	4	1 _ 2	1	+		
17	S'Enclusa		2	+	3	1	1			
18	Mongofre	+	3	+	3 _ 4	+	1	1		
19	S'Estany		+	1	+		2	+	1	
20	Cala Rotja 1			2			2		2	
21	Arenal		+		+	1				
22	Son Parc	+	+		+	1				
23	Pudent 1		1	1	2	2	2	1		
24	Pudent 2		+	1	+		+			
25	Tosqueta		1	2	2	1	1		+	
26	S'Arenalet			1	+		1	2		+
27	Cabra Salada		+	+			+		+	1
28	S'Albufereta		+	1 _ 2	+			2	+	+
29	Es Pi			1				+	+	2

	Site	C.str	C.com	C.pus	C.cri	C.bal	C.spit	C.alg	C.foe	C.bar
30	En Pavada			+					+	+
31	S'Era			+			2		+	2
32	Cala Rotja 2						+		+	1
33	Miami 1			+					1	+
34	Miami 2			+					+	+
35	Talaieta		1 _2		3 _ 4	2	4			
36	Illots Tirant	+	2	1	4	3	4		1	
37	Binidonaire	1	2		3	3	3			
38	Sa Mitjera		2		1	3	2			
39	En Saler	1	2	+	1	3	1			
40	Cala Viola	+	2	1	1	2	1	+	+	
41	Sa Nitja		2	1	2	2	2	1	2	
42	Cala Rotja 3		2	1	3	1	3			
43	Cavalleria		3	+	3	+	2			
44	Mica		1	+	2	+	3			
45	Binimel ·à	+	1		3	3	+	+		
46	Morts		1	1	3	1	3	1	1	
47	Embarcador	+	+	1	4	+	2			
48	Pregonda		+	1	3	1	1		+	
49	Barril		1	+	3 _4		3	+		
50	Calderer	1 _ 2	1		3	2	+			
51	Alocs	1	2	+	2	2	1			
52	Pilar	+	1		2	1	+			
53	Vall 1	1	+		+	+				
54	Vall 2	2	1		2	+				
55	Fontanelles	1	1	2	3	2	1	1		
56	Morell	1	2			+		+		
57	Piques	1	+							
58	Forcat	3	+							
59	Brut	2	1			+				
60	Blanes	+	+							
61	Frares	+								
62	Busquets									
63	Platja Gran	+								

	Site	C.str	C.com	C.pus	C.cri	C.bal	C.spit	C.alg	C.foe	C.bar
64	Sa Caleta	1 _2	+							
65	Santandria	+								
66	Blanca	2	+							
67	Xoriguer	3	3			4				
68	Son Saura	3	2	3		2				
69	Talaier	3	+							
70	Turqueta	2	+			1				
71	Macarelleta	2	+			2				
72	Macarella	1	1							
73	Galdana	+								
74	Mitjana	2	1							
75	Trebalúger	1	+							
76	Fustam	2	1			+				
77	Escorxada	2	1							
78	Binigaus	2	+							
79	Cala'n Porter									
80	Cales Coves	+				+				
81	Canutells	1	+							
82	Binidalí	2	+							
83	Biniparratx	1	+							
84	Binisafulla	3	+							
85	Sa Barca	+	2_3			3		2		
86	Binibeca	4	2							
87	Biniancolla	3	+			+				
88	Pta Prima	3	+							
89	Caló Roig	2								
90	Alcaufar	2 _ 3								
91	St Esteve	3	1			+				
92	Pedrera									
93	Fonts									
94	Corb									
95	Figuera									
96	Nou Pinya									
97	Cala Rata									

	Site	C.str	C.com	C.pus	C.cri	C.bal	C.spit	C.alg	C.foe	C.bar
98	Apartió									
99	Llonga									
100	Cavallo									
101	Lladró									
102	St Jordi									
103	Teulera		1							

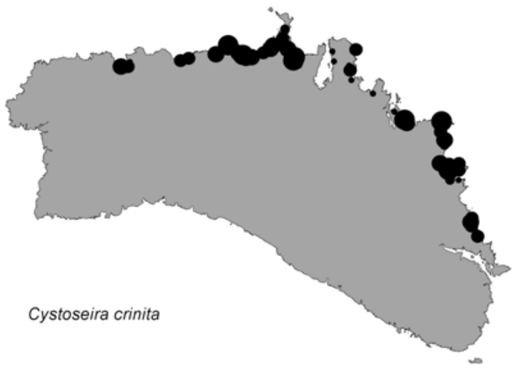
When considering the environmental factors toghether, that is, when adding sequentially these variables in a model in order to predict *Cystoseira* populations composition, the first chosen factor is coast height, followed by % of rocky bottom, nitrate concentration and so on (see Table 4B). The total variation in the composition and abundance of *Cystoseira* assemblages explained by all 13 environmental variables is 62.7%. However, after having added the 9th variable (phosphate concentration in sea water), the P-value is no longer statistically significant and therefore, it could be considered constructing and using a model with these 9 variables (explaining 60% of the species data variation).



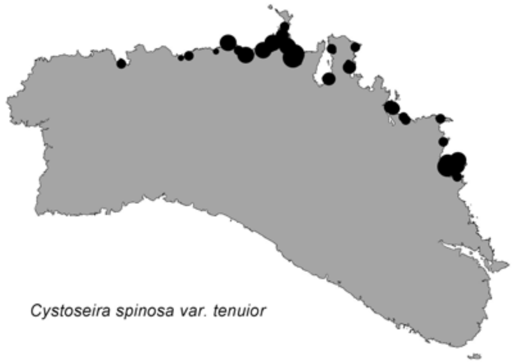
Cystoseira amentacea var. stricta

Cystoseira compressa var. compressa

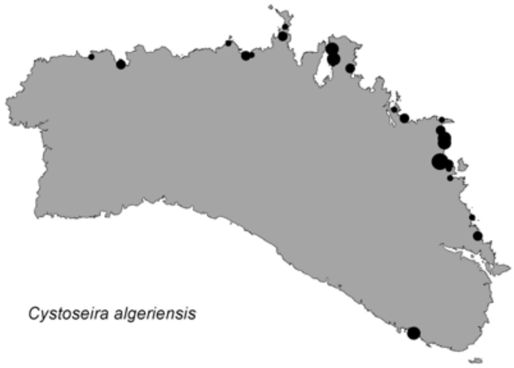
Cystoseira brachycarpa var. balearica



Cystoseira crinita



Cystoseira spinosa var. tenuior



Cystoseira algeriensis

Cystoseira compressa var. pustulata

Cystoseira foeniculacea var. tenuiramosa

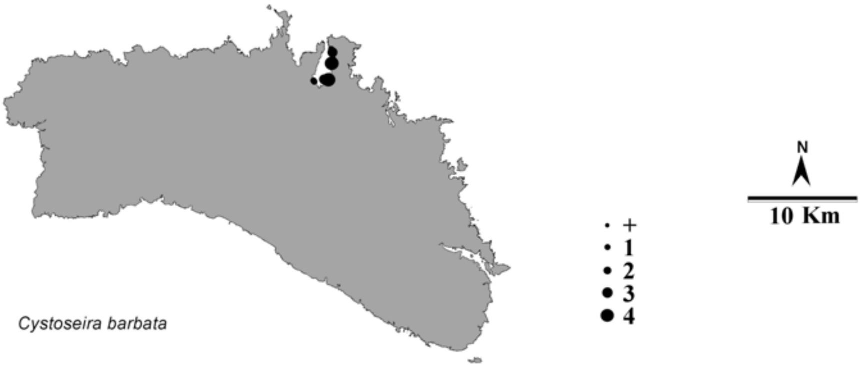


Fig. 2. Distribution and abundances of different *Cystoseira* species in the different sampled coves from Minorca (Balearic Islands) represented in Braun-Blanquet scale (+: very rare; 1: rare; 2: common; 3: abundant; 4: very abundant).

Table 4. (A) Tests for relationships between individual environmental variables and biological data. (B) Tests for relationships between envitonmental and biological data considering all environmental variables integrated in a multiple regression model.

(A) Marginal tests

Variable	Pseudo-F	P	% var.
exposure	9.021	**0.001**	8.20
MF1 (% rocky coast)	7.586	**0.001**	6.99
MF2 (coast height)	26.866	**0.001**	21.01
MF3 (% blocks)	10.849	**0.001**	9.70
slope	19.346	**0.001**	16.08
urb. distance	16.548	**0.001**	14.08
BF1 (% vegetated bottom)	17.010	**0.001**	14.41
BF2 (% seagrass)	6.231	**0.002**	5.81
BF3 (% rocky bottom)	19.211	**0.001**	15.98
Log([PO4]+1)	10.422	**0.001**	9.35
Log([NH4]+1)	0.455	0.689	0.45
Log([NO2]+1)	20.586	**0.001**	16.93
Log([NO3]+1)	23.475	**0.001**	18.86

(B) Sequential tests

Variable	Pseudo-F	P	% var.	cum.%var.
MF2 (coast height)	26.866	**0.001**	21.01	21.01
BF3 (% rocky bottom)	18.284	**0.001**	12.21	33.22
Log([NO3]+1)	11.458	**0.001**	6.93	40.15
BF2 (% seagrass)	7.207	**0.001**	4.10	44.25
BF1 (% vegetated bottom)	11.932	**0.001**	6.11	50.36
MF3 (% blocks)	6.565	**0.001**	3.18	53.53
exposure	4.905	**0.002**	2.28	55.81
Log([NH4]+1)	4.964	**0.003**	2.22	58.03
Log([PO4]+1)	4.608	**0.003**	1.98	60.01
urb. distance	2.142	0.098	0.91	60.92
MF1 (% rocky coast)	1.361	0.243	0.58	61.50
Log([NO2]+1)	1.419	0.244	0.60	62.10
slope	1.364	0.276	0.57	62.67

dbRDA plots allow the visualization of the relationship between biological and environmental variables. Environmental variables (Fig. 3) and *Cystoseira* species (Fig. 4) are represented in the plots as overlayed vectors using *multiple correlation type* (see Anderson et al. 2008 for further details). Only the factors presenting significant individual correlation with biological data are shown (Table 4A).

Values of the environmental parameters used for DistlM and dbRDA analyses are presented in Appendix 2.

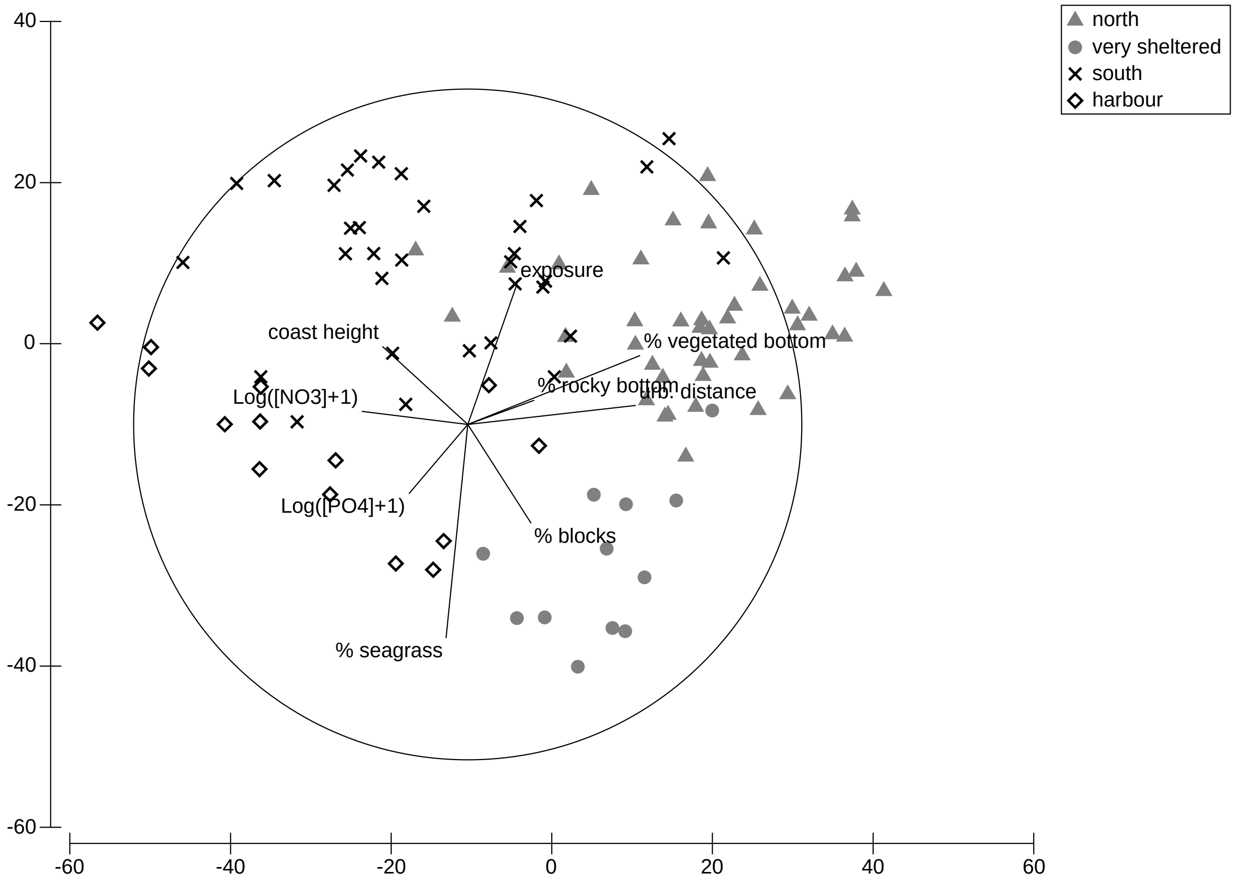


Fig. 3. Distance-based redundancy analysis showing relationships between the ordination of the sites based on *Cystoseira* communities and the environmental factors. Axis I explains 63.9% variation out of the fitted model and 38.4% of the total variation, while axis II explains respectively 26.9% and 16.2% of the variation.

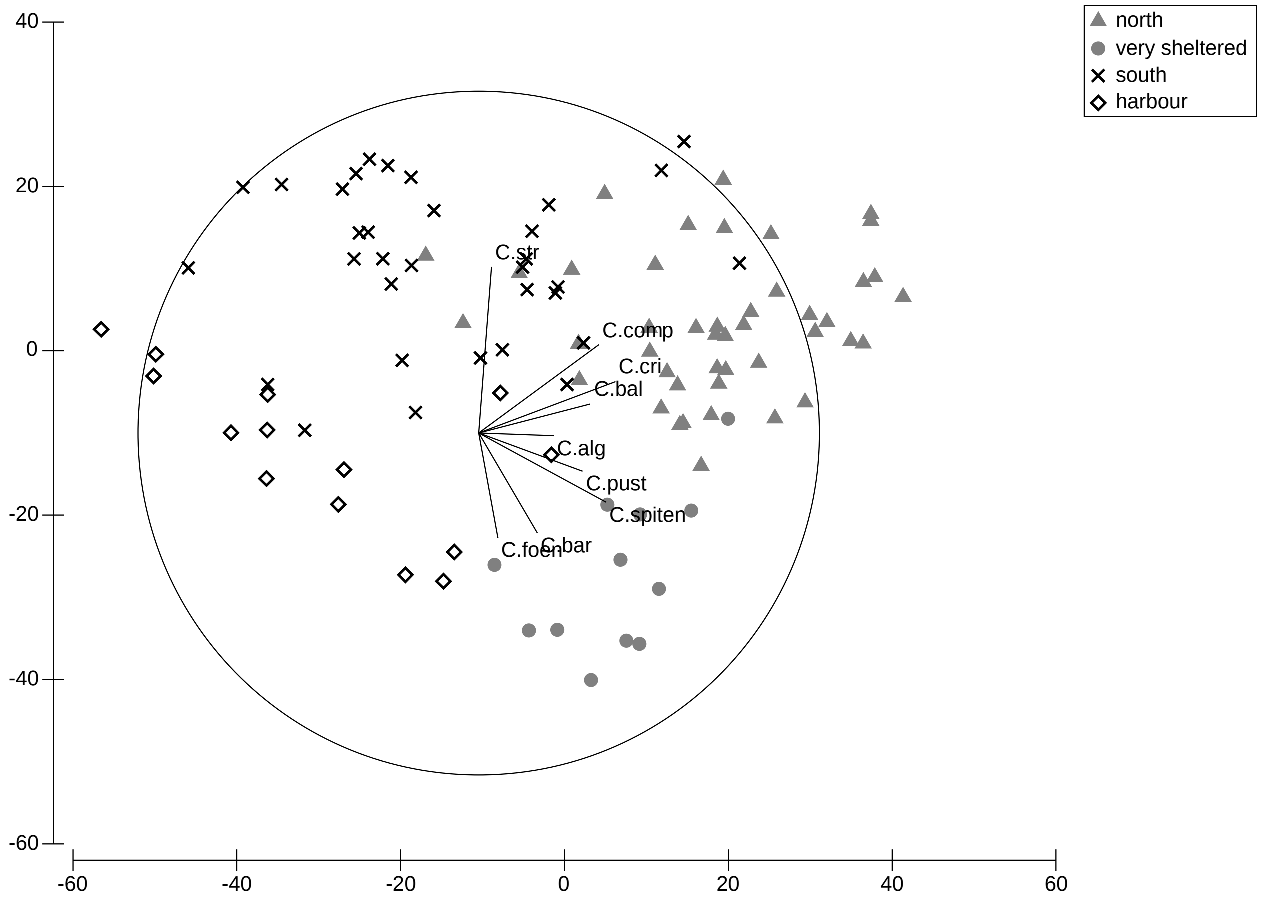


Fig. 4. Distance-based redundancy analysis showing direction of increasing abundances of different species along the study sites. C.str: *Cystoseira amentacea var. stricta*, C.comp: *C. compressa v. compressa*, C.cri: *C. crinita*, C.bal: *C. brachycarpa var. balearica*, C.alg: *C. algeriensis*, C.pust: *C. compressa v. pustulata*, C.spiten: *C. spinosa v. tenuior*, C.bar: *C. barbata*, C.foen: *C. foeniculacea v. tenuiramosa.* Axis I explains 63.9% variation out of the fitted model and 38.4% of the total variation, while axis II explains respectively 26.9% and 16.2% of the variation.

The variables that are more strongly related to the first dbRDA axis are urbanisation distance and % of vegetated bottom (positively related) and coast height, nitrate and phosphate concentration (negatively related). Therefore, coves are ordered from high to low urban pressure along the first axis. Nevertheless, this is not completely independent from some geomorphological factors, as coast height has a considerable negative correlation with the first axis. On the other hand, the variables more related to the second dbRDA axis are exposure and coast height (positively related) and % of seagrass bottom and % of blocks (negatively related). Concerning the different types of coves (ANOSIM: R = 0.821; p = 0.0001), most of the northern ones have a positive relationship to urbanisation distance and to % of vegetated bottom, and a negative relationship to nutrient concentration, while most of southern coves appear to be positively related to coast height and nitrate concentration. The coves from very sheltered places are positively related with the factors % of seagrass bottom and % of blocks, and negatively related to exposition and coast height. Finally, the coves situated nearby harbour areas, generally devoid of *Cystoseira*, show a positive relationship with nitrate and phosphate concentrations and a negative relationship with urbanisation distance.

When looking at the plot displaying the different *Cystoseira* species (Fig. 4), it can be appreciated that all of them have positive values in the first axis. Therefore, they seem to have some positive relationship with urbanisation distance and % of vegetated bottom yet *C. amentacea var. stricta*, *C. foeniculacea* and *C. barbata* show a stronger relationship with the second axis, and consequently with the factor exposure (positive for *C. amentacea var. stricta* and negative for the others).

Discussion

The genus *Cystoseira* is well represented in the rocky shallow sublittoral zones from sheltered areas in Minorca. The number of species found is high if compared to the current existing number in the continental coasts of Spain and France (e.g. Thibaut et al. 2009), but similar to that reported for the northern coast of Spain and southern coast of France at the beginning of the XXth century (Sauvageau 1912, Feldmann 1937, Thibaut et al. 2005). Species such as *Cystoseira crinita*, *Cystoseira foeniculacea* var. *tenuiramosa* and *Cystoseira barbata* that are still common in Minorca and that were common in the Alberes coast (southern France) one hundred years ago (Sauvageau 1912), have currently disappeared from the Alberes coast and other continental localities (Munda 1993, Chryssovergis & Panayotidis 1995, Thibaut et al. 2005), indicating the important habitat loss that has affected some European continental coasts, and which seems to be driven by a degradation in water quality and coastal modification.

Significant relationships have been detected between most of the studied factors and *Cystoseira spp.* composition and abundance at the coves. Our results show a high predictability of *Cystoseira* populations distribution starting from environmental variables, as 62,7% of the variation was explained when considering all the factors together in a model. Similar results have been found for other regions, where factors like pollution, wave exposure, slope or physiognomy of the bottom seem to be important in explaining the differences in shallow benthic vegetation patterns (Díez et al. 2003, Eriksson & Bergström 2005).

The distribution of the different species is not uniform along the coast of the island. The number of *Cystoseira* species and their abundances are much higher in the northern side than in the southern side. Human pressure is stronger in southern coves which are more urbanised and show higher levels of nitrate concentration. Likewise, there are important geomorphological differences between these two regions, being morphological features from southern coves less favourable for *Cystoseira* establishment. As historical data is not available for these coves, it is not possible to unequivocally report a regression of *Cystoseira*. However, the fact that the percentage of vegetated bottom at the coves is positively related with urbanisation distance reinforces the idea that coves devoid of *Cystoseira* have suffered from habitat degradation. In bioindicator studies it is a common problem that natural and human-induced processes are intrincately mixed, and ultimate interpretation is difficult and often requires long-term research (Levine 1984).

The absence of *Cystoseira*, in coincidence with high levels of nutrients concentrations at Maó harbour (where the disappearance of some *Cystoseira* species is confirmed by historical data; Rodríguez-Femenías 1889), supports the idea that most *Cystoseira* species are very sensitive and suitable for being used as bioindicators. In addition, seagrass meadows occupied a much more extensive area in the past than currently do in this area (www.obsam.cat). Although eutrophication is a major factor explaining the disappearance of *Cystoseira* spp. (Soltan et al. 2001, Arévalo et al. 2007, Pinedo et al. 2007), other pollutants such as heavy metals, herbicides, insecticides, halogens or polychlorinated biphenyls (PCBs) coming from agriculture and industrial activities (Boyle 1984) could also play a pivotal role in the structure of shallow rocky coastal assemblages. Industry is not highly developed in Minorca, but waste waters originated by this activity do not receive always the correct treatment. Moreover, costume jewellery was an important activity in Minorca in the past (López 1991), when waste waters were directly dumped into Maó harbour, and high levels of heavy metal concentrations have been reported for this area (García-Orellana, pers. comm.). On the other hand, agriculture is also an important activity in the island, which seems to be one of the main factors explaining the high levels of nitrates in subterranean waters, favoured by the calcareous nature of the substrate and the presence of karstic runoff from cultivated lands (www.obsam.cat). Generally, high nitrate concentrations are considered to be indicators of agricultural development (Camp, pers. comm., Scavia & Bricker 2006).

To summarize, for some coves from Maó harbour area the disappearance of some *Cystoseira* species, confirmed by historical data (Rodríguez-Femenías 1889), seems to be related to increased pollution levels. Yet, in some southern coves like Santandria, Cala'n Porter or Cala Galdana, strongly urbanised and showing high level of nitrate concentration, but with not favourable geomorphological features, it is difficult to assess the level of degradation because of the lack of historical data. Thus, if *Cystoseira spp.* have to be used as bioindicators from sheltered environments in the implementation of the European Water Framework Directive, this study shows the necessity of chosing adequate reference sites, as mentioned by Mangialajo et al. (2007).

We have identified the factors that determine the distribution of *Cystoseira* species thriving in sheltered localities from the coast of Minorca. The next step (i.e. to determine the utility of these species as bioindicators or to find the causes of their disappearance) needs a combination of long-term studies and experimental work as well as including other contaminants in the investigations. Although nutrient and heavy metal effects on *Cystoseira* or other long-lived species of the order Fucales or Laminariales are already known (Hopkin & Kain 1978, Munda & Veber 1996, Kut et al. 2000, Caliceti et al. 2002), few studies include other chemical contaminants, which should be much more dangerous for marine species (Boyle 1984, Levine 1984 and references therein). Future efforts should pay attention to the effects of all these contaminants. Our study also detects the value of the existence of previous studies in a region to be able to determine if degradation has occurred in a certain area or if natural variability and pressures account for the absence of *Cystoseira* assemblages. Thus, studying relationships between ecological factors and biological descriptors are of critical importance for obtaining data on the current ecological status and understand future changes that may undergo these assemblages.

In conclusion, the distribution of shallow *Cystoseira* species thriving in sheltered areas from Minorca (NW Mediterranean) depends on a high number of factors including geomorphological features, wave exposure and anthropogenic pressures. Although anthropogenic pressures are not the only factors determining the absence of *Cystoseira*, our data shows a positive relationship of rich and well developed *Cystoseira* assemblages to urbanisation distance and low levels of nutrient concentration. Moreover, the disappearance of some *Cystoseira* populations from the most impacted areas, which has been confirmed by historical data, points to a high sensitivity level of the studied *Cystoseira* species to pollution and their usefulness to be used as bioindicators.

Chapter 4

Pollution impacts and recovery potential in three species of the genus *Cystoseira* (Fucales, Heterokontophyta)

Introduction

Pollution is currently one of the main threats to marine biodiversity worldwide (Lotze et al. 2006). The number and variety of pollutants present in the sea is high, and excessive inorganic nutrients, heavy metals, detergents, herbicides and pesticides are common in coastal waters (Osterberg & Keckes 1977, Köck et al. 2010). Inorganic nutrients are present in natural environments, but their concentrations near urban areas are usually enhanced (Nixon 1995, Scavia & Bricker 2006). Overload of inorganic nutrients (or eutrophication) stimulates phytoplankton production and increases turbidity leading to changes in the species composition and the structure of littoral communities (McGlathery et al. 2007). Moreover, increased nutrient concentrations in seawater favour opportunistic species, while long-lived species such as seagrasses and perennial macroalgae gradually decline (Munda 1982, Schramm 1999).

Industrial activities introduce large amounts of heavy metals and other harmful substances to the environment (Nriagu & Pacina 1988). The threats of these substances to marine biota have been largely addressed by scientific work (Wundram et al. 1996, Macfarlane & Burchett 2001, Pospelova et al. 2002). Reduced survival, growth and photosynthetic activity have been detected in algae as a consequence of heavy metal pollution (Hopkin & Kain 1978, Chung & Brinkhuis 1986, Gledhill et al. 1997, Baumann et al. 2009). Moreover, algae can accumulate heavy metals and pass them on to organisms of other trophic levels such as molluscs, crustaceans, fishes and, ultimately, to humans (Pinto et al. 2003).

The most toxic pollutants, such as some heavy metals, can have lethal effects on sensitive species at relatively low concentrations (Phillips 1995). Disappearances of populations are of particular concern when the species involved are long-lived and/or habitat engineers. This is the case of the algae of the orders Fucales and Laminariales whose losses cause strong shifts in abundance and diversity of associated flora and fauna (Graham 2004). Indeed, the disappearance of numerous habitat-forming macroalgae has been attributed to pollution associated to urban development (Arnoux & Bellan-Santini 1972, Belsher 1977, Chryssovergis & Panayotidis 1995, Coleman et al. 2008, Connell et al. 2008, Mangialajo et al. 2008). Furthermore, these habitat-forming algae take a long time to recover when water quality improves (Soltan et al. 2001, Coleman et al. 2008, Díez et al. 2009).

Algae of the genus *Cystoseira* (Fucales, Heterokontophyta) are amongst the most important habitat-forming species in Mediterranean shallow waters (Feldmann 1937, Giaccone 1973), with around 30 species dominating very productive, complex and diverse assemblages at different depths (Boudouresque 1971c, 1972, Ballesteros 1988, 1990a, b, Ballesteros et al. 1998, 2009, Hereu et al. 2008). *Cystoseira* spp. are currently experiencing severe decline in many Mediterranean regions (Cormaci & Furnari 1999, Thibaut et al. 2005, Serio et al. 2006). Observational studies have generally suggested pollution as the main factor influencing the disappearance of *Cystoseira* spp. (Bellan-Santini 1968, Golubic 1970, Munda 1974, 1982, 1993, Chryssovergis & Panayotidis 1995, Arévalo et al. 2007). Experimental evidence for many Atlantic kelps and species of the order Fucales indicates strong negative impacts of heavy metal and other harmful substances on survival, growth, reproduction and settlement (Strömgren 1979, 1980, Chung & Brinkhuis 1986, Marsden et al. 2003). However, there are no studies providing experimental evidence for the disappearance of *Cystoseira* species related to pollution. Moreover, although in the EU great efforts are directed to improve water quality through the implementation of the Water

Framework Directive (WFD 2000/60/EC), and *Cystoseira* species are used as indicators of good water quality (Ballesteros et al. 2007), no recovery of *Cystoseira* populations after improvement of water quality has been detected (Soltan et al. 2001, Díez et al. 2009). Therefore, management measures addressed to facilitate the recovery of these populations in areas where water quality has improved may favour the re-establishment of *Cystoseira* populations.

The island of Minorca (Balearic Islands, NW Mediterranean) is a relatively well preserved area (Ballesteros 1989b) where dense *Cystoseira* spp. stands are still present in littoral environments (Sales & Ballesteros 2009). However, Maó harbour, a very enclosed bay, has suffered the impact of a very developed industry during the second half of the XIXth century and most of the XXth century (López 1991). For many years, sewage was continuously discharged via inshore outfalls into shallow waters of Maó harbour. In 1980, a deep-water ocean outfall was built (Hoyo 1981) and inshore discharge ceased, which likely resulted in some degree of water quality improvement in the area. Although *Cystoseira* spp. are currently almost extinct at Maó harbour (Sales & Ballesteros 2009), the presence of *Cystoseira* species was documented more than one century ago (Rodríguez-Femenías 1889). This suggests that Maó harbour shelters suitable habitats for those algae and that their extinction was probably due to increased pollution. Therefore, we hypothesized that *Cystoseira* species disappeared from Maó harbour due to the increased pollution related to urban and industrial activities during the XXth century.

The aim of this study was (1) to provide the first experimental evidence on the effect of pollution on *Cystoseira* spp. survival and fitness in Mediterranean coastal waters, and (2) to test if *Cystoseira* populations were able to recover in areas where management actions addressed to ameliorate seawater quality had been established. To achieve these objectives, we transplanted individuals of the species *C. crinita*, *C. barbata* and *C. spinosa v. tenuior* from a non-polluted area (Fornells Bay) to two places at Maó harbour displaying two different levels of pollution: a highly polluted area, to assess the effects of pollution on *Cystoseira* populations, and a slightly polluted area, to assess if *Cystoseira* was able to recover following water quality improvement.

Materials and methods

Study area

Minorca is the northern-most island of the Balearic Archipelago (NW Mediterranean) (Fig. 1), measuring about 50 km in length and 20 km in width. The number of *Cystoseira* species and the extension they cover in the rocky shores of the island is high in comparison to adjacent areas in the mainland (Sales & Ballesteros 2009) which is in agreement with its good water quality. However, some focuses of pollution exist around the two main towns: Maó and Ciutadella. Maó harbour is the most problematic area in Minorca due to the urban and industrial activities concentrated around it and to the fact that it is a very enclosed bay with low water exchange (Hoyo 1981). Besides shipping, several industrial activities have been and are being carried out in Maó, such as custom jewellery manufacture, production of electricity from fuel, aquaculture and discharge of gasoline transported to the island (López 1991, www.obsam.cat). Maó, the main town of the island, with 30.000 inhabitants, Es Castell, a smaller town with 8.000 inhabitants, and several small urbanisations are located at the shoreline of Maó harbour. The

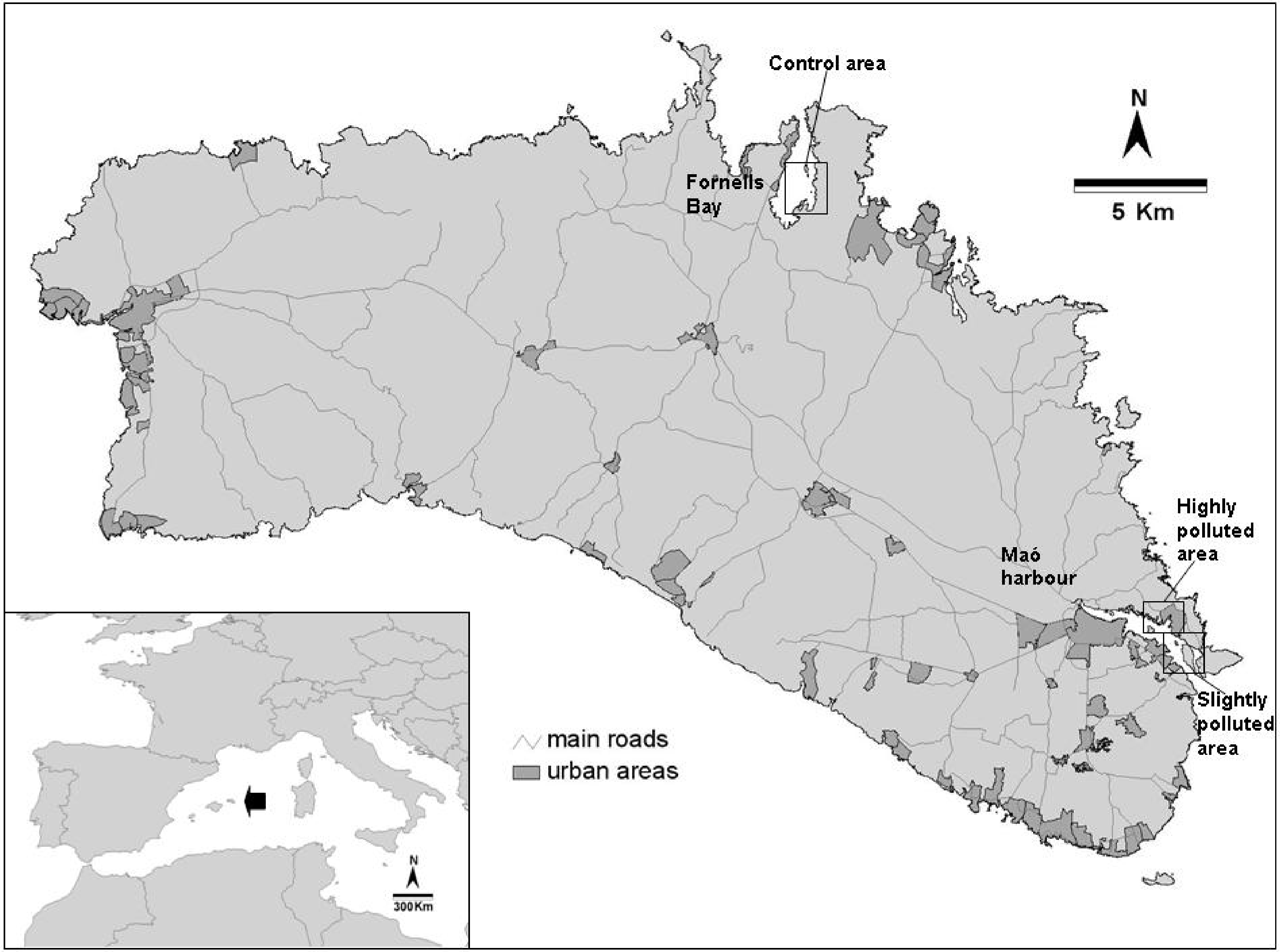


Fig. 1. Map of the study area.

waste waters from all these towns and urbanisations were directly dumped into the harbour until 1980, when a sewage outfall which diverted these waste waters to the open sea was built (Hoyo 1981). In contrast, Fornells Bay is a bay with a similar morphology to Maó with low human influence that still harbours extensive seagrass meadows (*Posidonia oceanica, Cymodocea nodosa, Zostera noltii*) (Delgado et al. 1997) and healthy *Cystoseira* spp. stands (Sales & Ballesteros 2009).

Transplants

Three different environmental situations were selected (Fig. 1). Fornells Bay was chosen as the control area. Cala Teulera (chosen as slightly polluted area) is a natural cove situated at the entrance of Maó harbour, which shelters a reduced meadow of the seagrass *Cymodocea nodosa* and some stands of *Cystoseira compressa* and *C. foeniculacea v. tenuiramosa*. Cala Llonga (chosen as a heavily polluted area) is an urbanised cove with a marina situated inside the Maó harbour, without seagrass meadows and no *Cystoseira* stands. The rocky shore is covered by a photophilic algal community dominated by members of the order Dictyotales like *Padina pavonica* and *Dictyota dichotoma*, less sensitive to pollution stress than *Cystoseira* spp. (Ballesteros et al. 2007). The bays chosen as control and polluted area have different orientations (north and east respectively), but there were no other bays with similar characteristics in the study area. In our experiment we chose three common *Cystoseira* species thriving in the upper sublittoral zone from sheltered areas: *C. barbata*, *C. crinita* and *C. spinosa v. tenuior*. None of these species are currently present at Maó harbour, although the presence of *C. barbata* and *C. crinita* was documented in the past by Rodríguez-Femenías (1889). We do not know whether *C. spinosa v. tenuior* has ever been present at Maó harbour, but this species is quite abundant in sheltered areas from the north coast of

Minorca (Sales & Ballesteros 2009) and thus likely to have been present in Maó.

The experiment was started in January 2008 and lasted 9 months. The experimental design consisted of four treatments: control (C), transplant control (TC), slightly polluted (SP) and highly polluted (HP). Between 16 and 20 *Cystoseira* specimens (replicates) of similar shape and length were used for each species and treatment. The control treatment (C) consisted of untouched specimens that were tagged at the beginning of the experiment and monitored throughout the experimental period. Other treatments consisted of *Cystoseira* specimens that were transplanted to the control area (TC), the slightly polluted area (SP) and the highly polluted area (HP). *Cystoseira* specimens were collected from the control area at random using a hammer and chisel together with a piece of substrate to avoid damage to the algal tissue. Specimens were transported to the SP and HP areas in tanks with aerated seawater by boat and van and then attached to the rocky substrate at the destination locations using Ivegor ® epoxy glue. The specimens transplanted to the control sites were submitted to the same procedure than the specimens transplanted to the polluted sites. All the transplanted specimens were tagged and the length of the main primary axis was measured (Ballesteros et al. 1998).

Throughout the experiment three water samples (replicates) were collected monthly from each location (Fornells Bay: C and TC treatments; Cala Teulera: SP treatment; Cala Llonga: HP treatment) in order to analyze dissolved nutrient concentrations. Sediment samples were also collected from the different locations at the beginning and at the end of the experimental period and analyzed for environmental heavy metal concentrations. All these samples were frozen at -20°C until analysis.

Survival of the *Cystoseira* specimens was checked during the visits to collect water samples, and presence of recruits was recorded for each species at each site. The experiment was finished after 9 months, when the number of survivors of some of the species and treatments was critical concerning the optimum number of necessary replicates for adequate sample and data analysis. At the end of the experiment, all living specimens were collected and transported to the laboratory, where the length of the main axis of each specimen was measured. *Cystoseira* epiphytes were removed as well as the sediment and any other foreign material, and specimens were subsequently rinsed in abundant seawater. Pieces of differently aged parts of each specimen (holdfast, stipe and branches) were cut and placed in small labelled plastic tubes, since differently-aged parts of some algae exhibit distinct accumulation of substances such as nutrients and heavy metals (Forsberg et al. 1988, Delgado et al. 1994, Burger et al. 2007). Samples were frozen at -20ºC.

Heavy metal and nutrient content

Concentration of inorganic dissolved nutrients (phosphates, nitrates, nitrites, ammonia and silicates) was measured in water samples according to Grasshoff et al. (1983) methods using an Alliance Evolution II Autoanalyzer. In addition, we determined total carbon, total nitrogen and total phosphorus contents for algal tissues. Tissue samples were freeze-dried and ground to a homogeneous powder in a glass mortar. Total C and total N in algal tissues were determined using a Carlo Erba CHN elemental analyzer. For P analyses, samples of 0.1 g were weighed and submitted to acid attack. After that, P content was determined using an inductively coupled plasma optical emission spectrometer (Thermo Jarrell Ash, ICAP 61E).

Concentrations of Cd, Pb, Cu, Cr, Zn, Mn, V, As and Hg were measured in algal tissue and sediment samples, which were freeze-dried and ground to a homogeneous powder in a glass mortar. Approximately 0.1 g of sample was subjected to digestion in Teflon reactors to which 3 ml of Merck Suprapur 65% nitric acid and 1 ml of H_2O_2 were added. The reactors were then placed in an oven at 95ºC during 24 h for digestion. After that, 6 ml of Milli Q water were added to each reactor and the final content of the reactors was transferred to vials. The solutions in the vials were then diluted 1 to 20 with 1% HNO_3 and 10 ppb of Rh was added as an internal standard. 71 blanks were prepared (reactors in which only the 3 ml of nitric acid and 1 ml of H_2O_2 were introduced, with no sample) and analyzed to be used as controls for possible contamination during the preparation of the digestions in the laboratory. Heavy metal content in tissue and sediment samples was analyzed using an inductively coupled plasma mass spectrometer (Perkin Elmer Elan 6000). The concentration of Cr, Cu and Mn exceeded sometimes the optimum range of concentration for ICP-MS, and an inductively coupled plasma optical emission spectrometer was then used (Thermo Jarrell Ash, ICAP 61E).

Data analysis

Two-way analysis of variance (ANOVA) was used to test for differences in dissolved nutrient concentrations in seawater among study locations and dates. The ANOVA design was crossed; study location was a fixed factor, while date was a random factor. As heavy metal concentrations in sediment samples from the beginning and the end of the experiment did not differ significantly (ANOVA; $p > 0.05$), all samples were considered as replicates. A one-way ANOVA was used to test for differences in heavy metal concentrations in sediments among study locations. Tukey post-hoc tests were applied to identify which locations differed from others.

Differences in nutrient and heavy metal content in algal tissues were analyzed with multivariate analysis of variance (MANOVA), with three fixed and crossed factors: species (with three levels: *C. barbata*, *C. crinita* and *C. spinosa*), part of the alga (with three levels: holdfast, stipe and branches), and treatment (with four levels: C, TC, SP and HP). MANOVA revealed a significant interaction species x tissue x treatment in nutrient and heavy metal content of algal tissue samples (Table 1). Therefore, and to simplify results, we decided to work separately for each *Cystoseira* species and to use only the nutrient and heavy metal concentrations from the stipes of the algae. We discarded holdfasts because they are in continuous contact with rock and sediment, which could cause interference in the analysis due to contamination with fine particles (Bryan & Hummerstone 1973). In addition, we decided not to use branches either, because of their temporary nature, especially in *C. spinosa*. In order to abridge the information, only Pb, Cu, Zn and As concentrations in algal tissues were examined by ANOVA to test for differences among experimental treatments. These heavy metals were chosen because they are amongst the most toxic trace metals (Macfarlane & Burchett 2001) and because most of the other metals were present in algal tissues at very low concentrations, often under the detection limits of the spectrometers.

Differences in C, N and P content in stipe tissue among experimental treatments were tested separately for each *Cystoseira* species using one-way ANOVAs. Post-hoc Tukey tests were applied to check which pairs of treatments differed. The same procedure was followed for the heavy metals Pb, Cu, Zn and As. In addition, the concentrations of these four heavy metals in algal tissues were divided by the heavy metal concentration in the sediments of the control sites (Bioaccumulation Factors: BF) in order to assess the amount of heavy metals in algae respect to the amount of heavy metals in the environment; Cebrian et al. 2007).

A chi-square test was used to test for differences in survival of individuals at the end of the experiment among treatments for each *Cystoseira* species. Finally, a one-way ANOVA was applied to test for differences in final growth (length increase) of the specimens among experimental treatments for each *Cystoseira* species.

Source	Wilks value	F	p
Species	0.177	91.69	**0.0001**
Part	0.667	9.87	**0.0001**
Treatment	0.157	30.07	**0.0001**
Species X Part	0.329	8.94	**0.0001**
Part X Treatment	0.471	3.26	**0.0001**
Species X Treatment	0.326	5.06	**0.0001**
Species X Part X Treatment	0.331	2.17	**0.0001**

Table 1. Results of the three-way MANOVA applied to nutrient and heavy metal concentration in algal tissues. The tested factors are *Cystoseira* species (fixed), part of the alga (fixed) and treatment (fixed). The factors are crossed.

Results

Dissolved nutrient concentrations in seawater and heavy metal concentrations in sediments

Inorganic nutrient concentrations in surface seawater were low at all localities and dates (Fig. 2). Minimum and maximum mean values were: phosphates (0.04-0.21 μM), nitrates (0.01-2.28 μM), nitrites (0.01-0.35 μM), ammonia (0.01-1.74 μM) and silicates (0.53-3.24 μM). Temporal variations with punctual concentration peaks were observed in dissolved nutrient concentrations among sites, as illustrated by the significant interaction term (treatment x date) for phosphates, nitrates, nitrites and ammonia (Table 2). Silicate concentrations differed among sites, with control sites showing the highest values.

Concentrations of most of the analyzed heavy metals were higher in sediments from polluted areas than in sediments from control area. This trend was true for lead, copper, chromium, zinc, manganese, vanadium and arsenic, for which significant differences among localities were detected (Fig. 3). The concentrations of these heavy metals at the slightly polluted area were 2 to 5-fold the concentrations at the control area. At the heavily polluted area, the concentrations were approximately 2-fold the concentrations at the slightly polluted area. Cadmium displayed an opposite trend, with higher concentrations at control areas than at polluted areas, while there were no significant differences among locations in mercury concentration.

Table 2. Results of the two-way ANOVAs applied to nutrient concentrations in seawater. The tested factors are locality (fixed) and date (random), and the factors are crossed.

Source	d.f.	F	p
PO_4			
Locality	2	2.009	0.163
Date	9	3.119	**0.018**
Locality X Date	18	7.836	**0.0001**
NO_3			
Locality	2	4.342	**0.029**
Date	9	1.583	0.19
Locality X Date	18	3.245	**0.0001**
NO_2			
Locality	2	2.129	0.148
Date	9	2.371	0.055
Locality X Date	18	8.456	**0.0001**
NH_4			
Locality	2	0.508	0.61
Date	9	2.719	**0.033**
Locality X Date	18	8.365	**0.0001**
SiO_4			
Locality	2	5.07	**0.018**
Date	9	1.41	0.247
Locality X Date	18	1.581	0.072

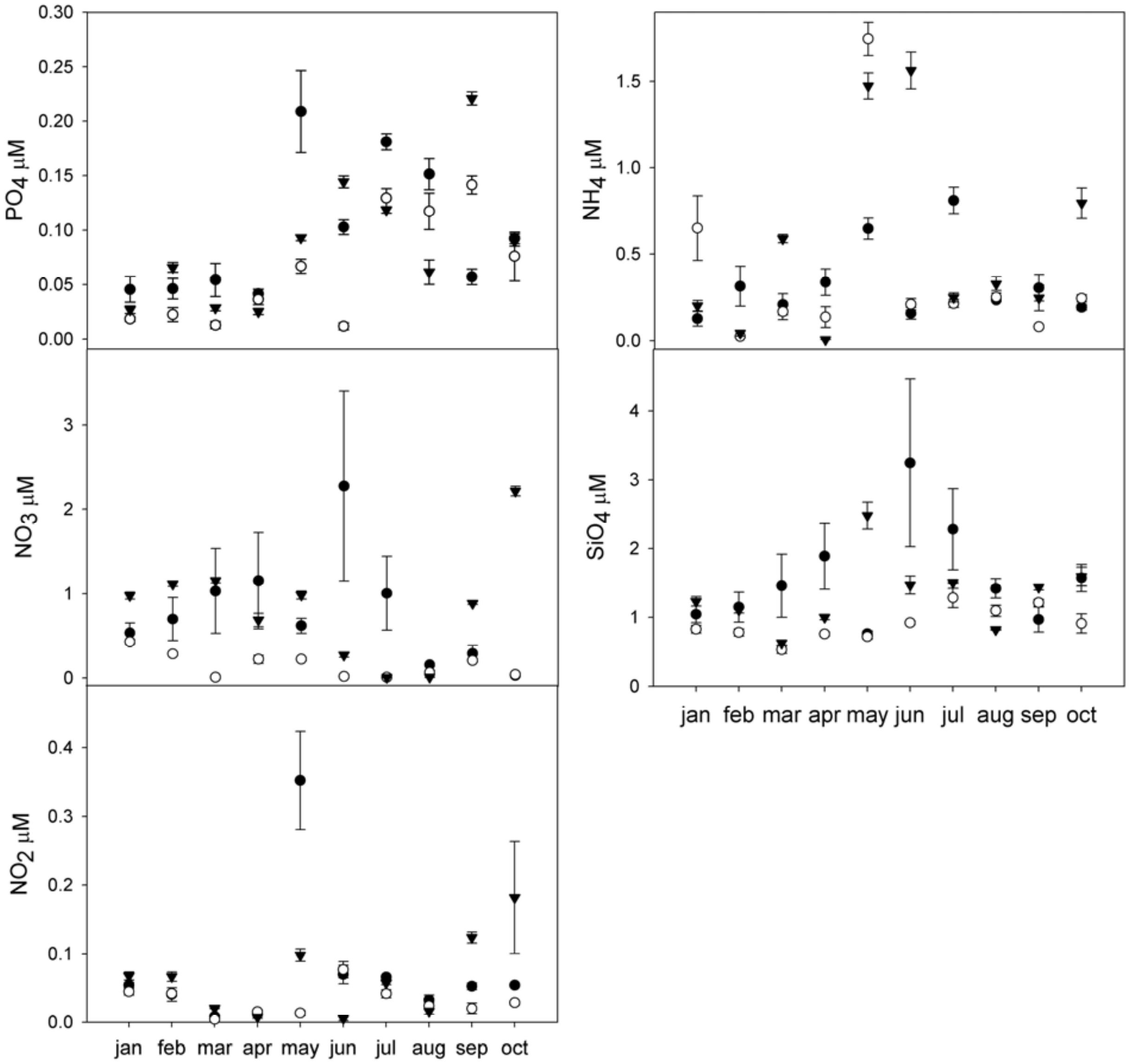


Fig. 2. Mean inorganic nutrient concentrations in seawater (± 1SE) from the different localities and dates. Full rounds: control area, empty rounds: slightly polluted area, triangles: heavily polluted area.

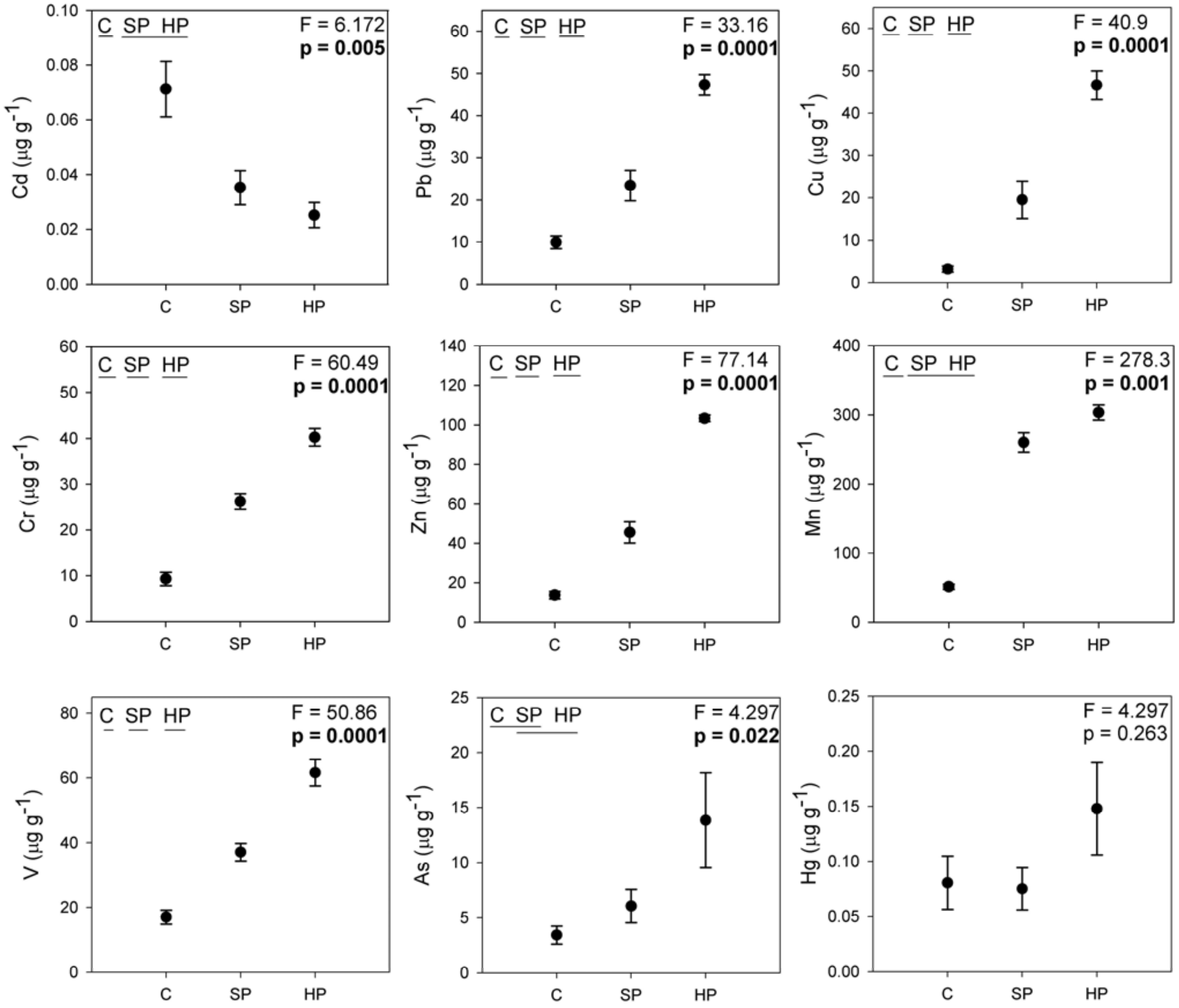


Fig. 3. Mean heavy metal concentrations in sediments (± 1SE) from the different localities. Results of the one-way ANOVAs among localities are shown in the upper-right corner of every graph.

Algal tissue nutrient and heavy metal content

Mean C percentage per species and treatment ranged from 29.66 to 34.40, being significantly higher in the slightly polluted area for *C. barbata* (Fig. 4a) and significantly lower in the highly polluted area for *C. crinita* and *C. spinosa* (Fig. 4b and 4c). Mean N percentage in *Cystoseira* stipes ranged from 0.74 to 1.46. For *C. barbata* specimens, N content was significantly higher in SP and HP treatments than in the TC treatment (Fig. 4d). In *C. crinita*, N content was significantly higher in SP and HP treatments than in control specimens (both C and TC treatments) (Fig. 4e). In *C. spinosa*, N percentage was significantly lower for SP treatment than for the rest of treatments (Fig. 4f). Taking into account all species and treatments, mean P concentration ranged from 34.23 to 82.82 ppm. Although ANOVA indicated significant differences in P content of *C. barbata* tissues among treatments, Tukey test did not detect any differences between pairs of treatments (Fig. 4g). P content was significantly higher in specimens from HP treatment than in specimens from SP treatment for *C. crinita* (Fig. 4h) and significantly higher in HP treatment than in TC treatment for *C. spinosa* (Fig. 4i).

Lead, copper and zinc concentrations increased in *Cystoseira* specimens transplanted to Maó harbour during the experiment (Fig. 5). Except for Pb in *C. barbata* (Fig. 5a), there were significant differences in these heavy metal concentrations among experimental treatments. Concentrations between C and TC treatments did not differ, while specimens submitted to HP and, sometimes to SP treatments, showed significantly higher heavy metal concentrations than control specimens (Fig. 5b to 5i). Cu concentration in *C. spinosa* showed a different trend with significantly higher concentration in specimens submitted to SP treatment compared to all other treatments (Fig. 5f). In contrast, arsenic concentration in

Cystoseira specimens showed a completely different pattern than the rest of analysed metals, with higher values in control specimens than in specimens transplanted to the polluted areas. In *C. barbata* specimens, As concentration was significantly higher for C treatment than for the rest of treatments (Fig. 5j). For *C. crinita*, specimens submitted to C and TC treatments showed significantly higher As concentration than specimens submitted to SP and HP treatments (Fig. 5k). Finally, for *C. spinosa*, although a slight decrease in As concentration was observed in the specimens submitted to SP and HP treatments compared to specimens submitted to control treatments, no significant differences were detected by ANOVA (Fig. 5l).

All species showed mean bioaccumulation factors (BF=metal concentration in algae/metal concentration in sediments of control sites) of < 1 for Pb, Cu and Zn. Meanwhile, the bioaccumulation factor for As was > 1, which means that this is the only of those heavy metals which is accumulated in a greater manner in algae than in sediments. (Table 3).

Table 3. Pb, Cu, Zn and As bioaccumulation factors (mean ± standard error) for the different *Cystoseira* species. The BF have been calculated for the stems of *Cystoseira* plants submitted to the control treatment.

	Bioaccumulation Factor			
	Pb	Cu	Zn	As
C. barbata	0.53 ± 0.21	0.33 ± 0.04	0.23 ± 0.02	5.81 ± 0.57
C. crinita	0.02 ± 0.001	0.29 ± 0.01	0.36 ± 0.01	1.40 ± 0.07
C. spinosa	0.03 ± 0.01	0.14 ± 0.01	0.09 ± 0.01	1.13 ± 0.08

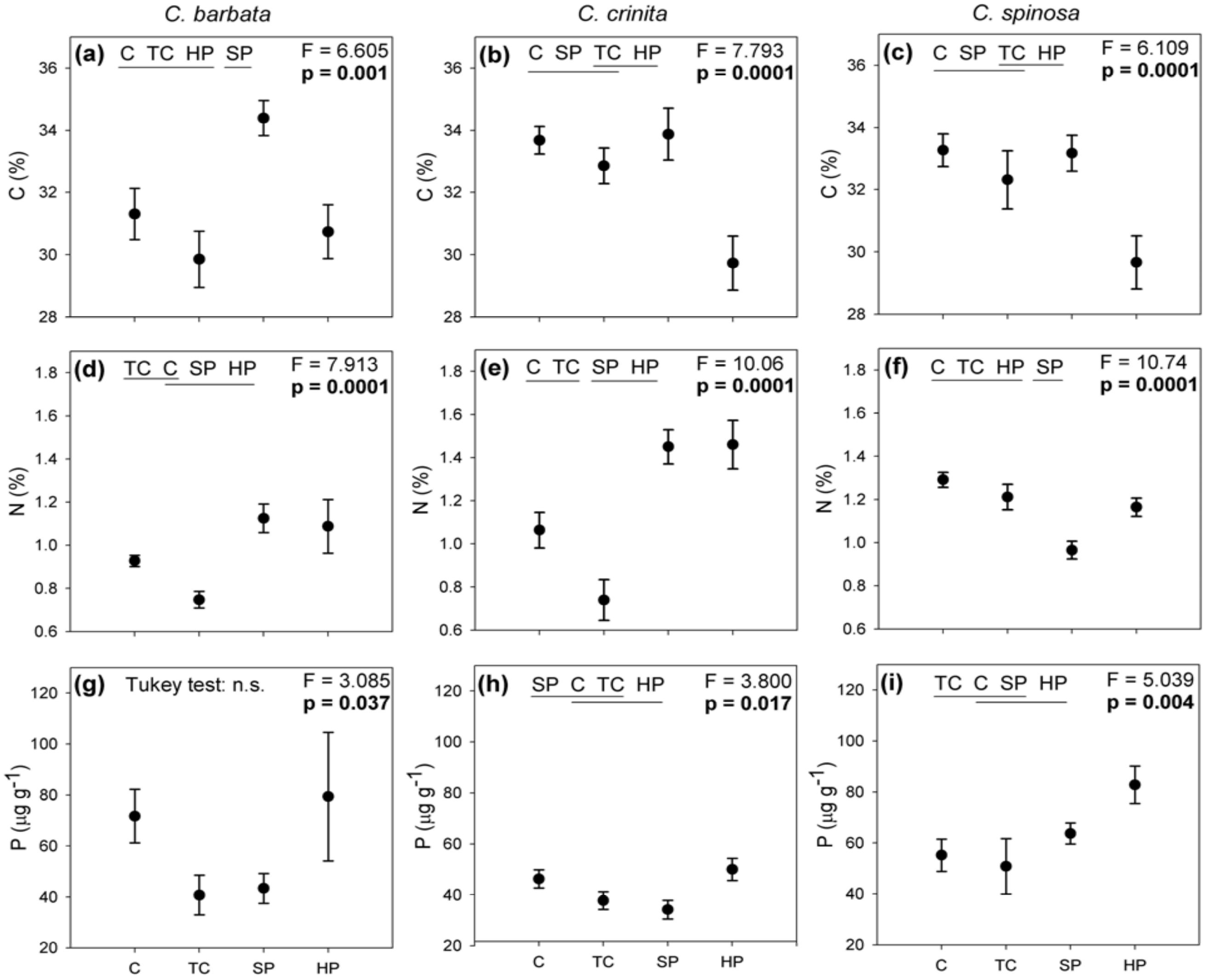


Fig. 4. Mean nutrient concentrations in algal tissue (±1 SE) for the different *Cystoseira* species and treatments. Results of the one-way ANOVAs among treatments are shown in the upper-right corner of every graph.

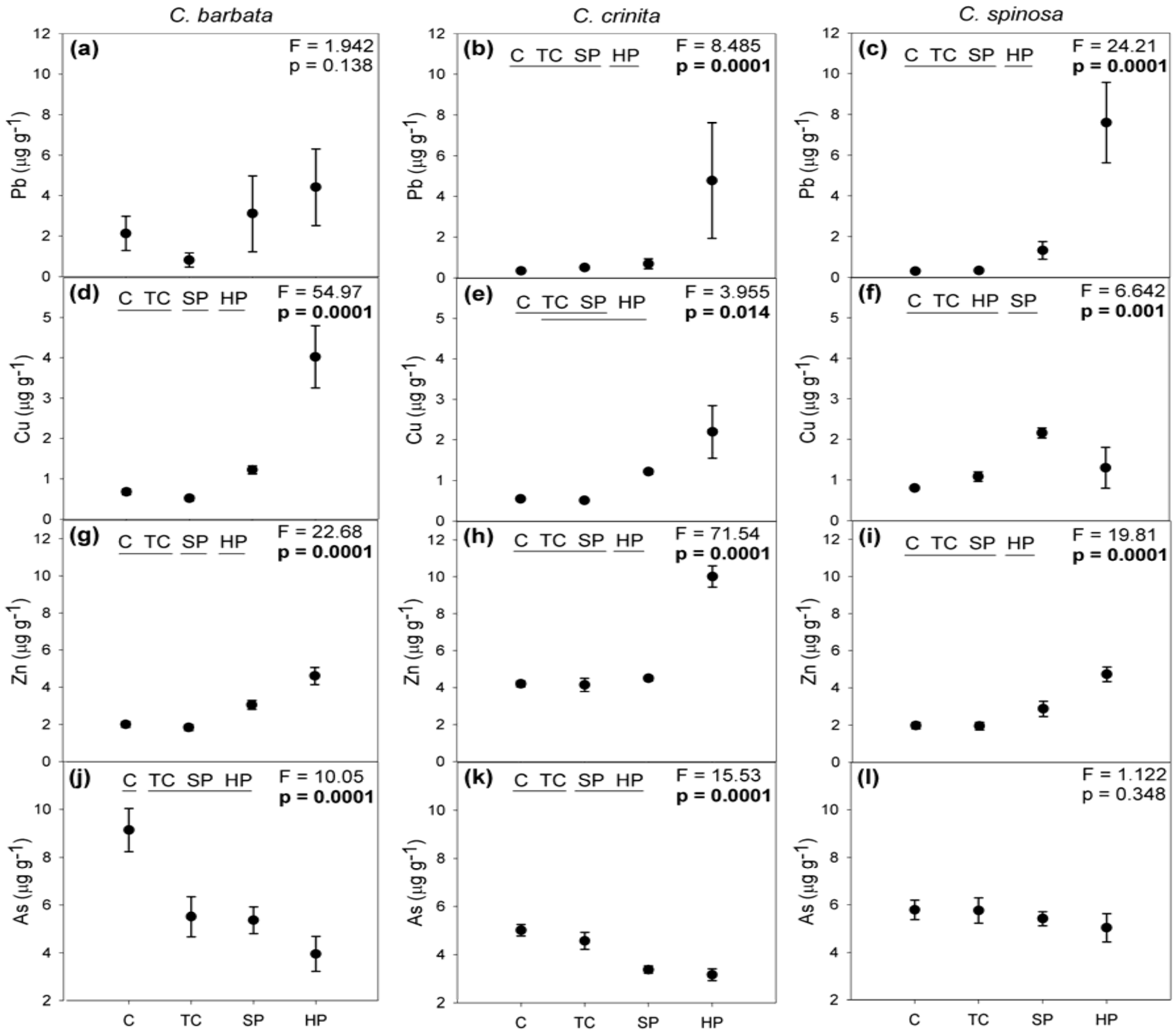
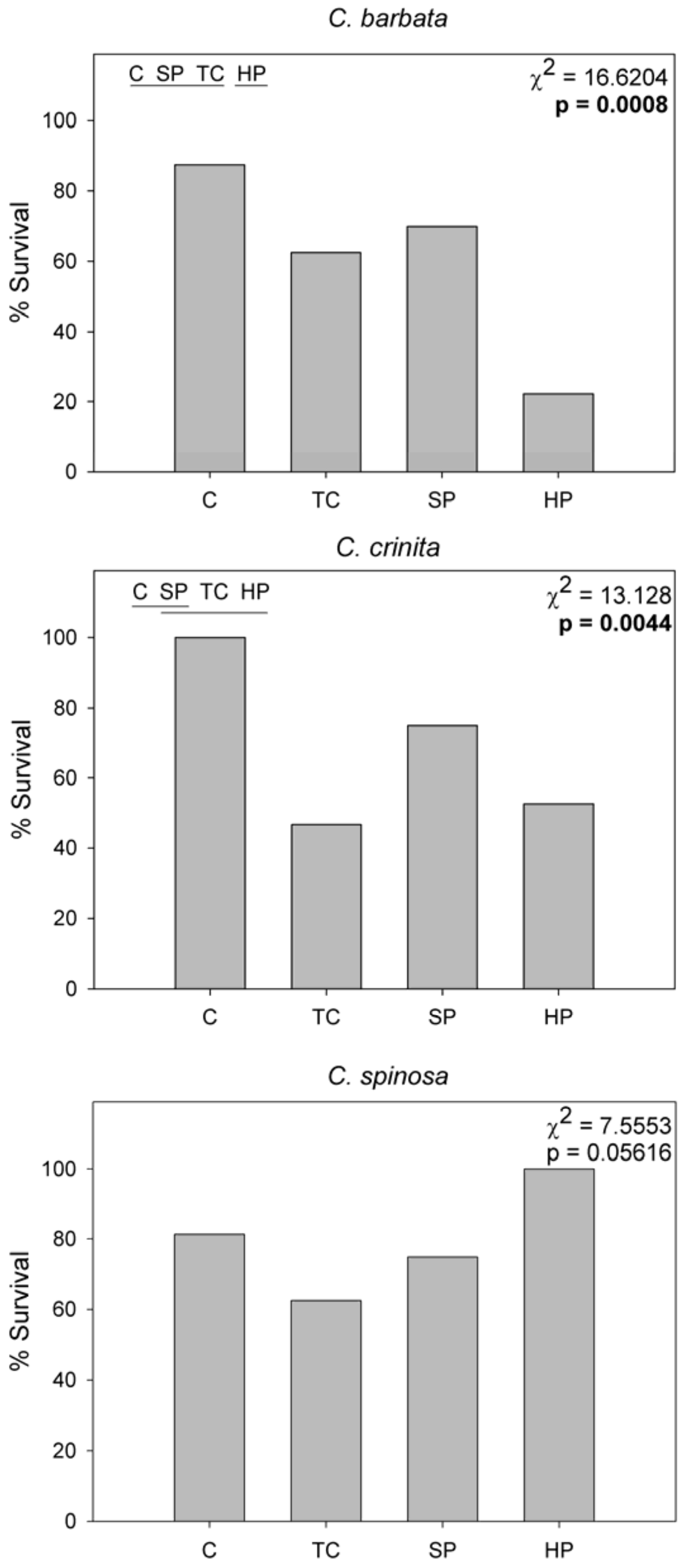


Fig. 5. Mean Pb, Cu, Zn and As concentrations in algal tissue (± 1 SE) for the different *Cystoseira* species and treatments. Results of the one-way ANOVAs among treatments are shown in the upper-right corner of every graph.

Survival and growth of algal specimens

Final survival was significantly lower for *C. barbata* specimens transplanted to the heavily polluted area than for specimens submitted to the rest of treatments. Chi-square test indicated that survival of *C. crinita* specimens transplanted to the HP area was significantly lower than survival of C specimens but not than TC specimens. Survival of *C. crinita* transplanted to the SP area did not differ from survival of specimens submitted to any other treatment. Finally, there were no differences in percent survival of *C. spinosa* specimens among treatments (Fig. 6).

C. barbata specimens transplanted to the slightly polluted area exhibited a significant increase in their length at the end of the experiment, while specimens from the other treatments exhibited a negative growth. *C. crinita* growth was very low in specimens from C, TC and SP treatments but very negative and significantly lower for specimens transplanted to the HP area. Growth of *C. spinosa* was almost nil in C, TC and SP treatments, and negative and significantly lower in specimens transplanted to HP area (Fig. 7). Recruits of the three *Cystoseira* species were found at the control area during all the experimental period, as well as at SP and HP areas seven months after transplantation where they survived and grew during the following two months.



C. barbata

C. crinita

C. spinosa

Fig. 6. Percent survival at the end of the experiment of the different *Cystoseira* species for the different experimental treatments. Chi-square test resutls are shown in the upper-right corner of every graph.

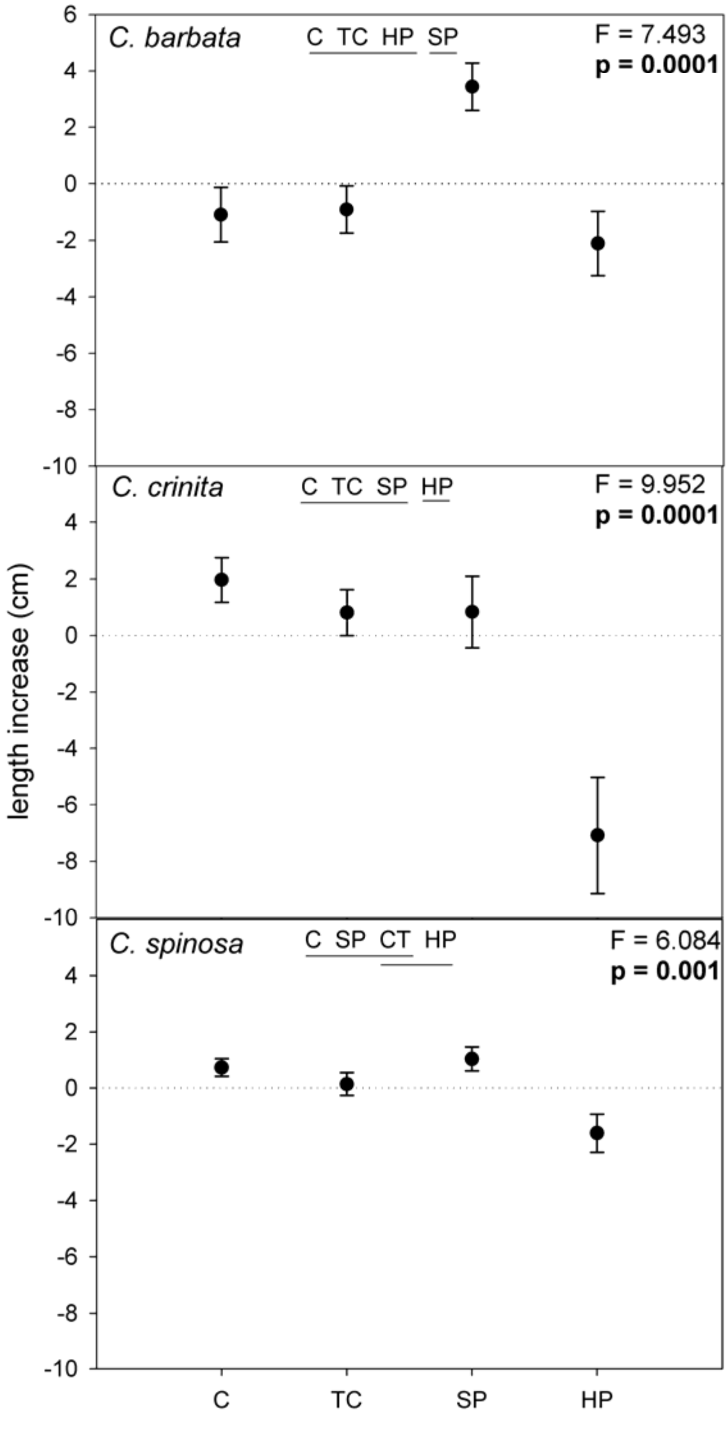


Fig. 7. Mean length increase (± 1SE) at the end of the experiment of the different *Cystoseira* species for the different experimental treatments. Results of the ANOVAs among treatments are shown in the upper-right corner.

Discussion

Heavy metal contamination at Maó harbour was confirmed by the high heavy metal concentration values found in the sediment, being in some cases around 10-fold the values detected in control areas. However, nutrient levels were very low and similar to the control area suggesting that the current urban waste water management is effective and that eutrophication is almost inexistent.

In fact, dissolved inorganic nutrient concentrations from Maó harbour detected in this study do not differ from characteristic values of unpolluted Mediterranean surface waters (Margalef 1974, Ballesteros 1989a, Ballesteros & Zabala 1993, Ramírez et al. 2005). In the 1970s, very low transparency of the water and phytoplankton blooms were frequent in Maó harbour (Hoyo 1981), which was probably due to high nutrient concentrations. With the construction of an outfall in 1980 water quality has likely improved. However, heavy metals are much more persistent than nutrients, and they can even remain in the environment for 10^8 years (Rainbow 1995). This, together with the fact that industry had a great importance in Maó during the second half of the XIXth century and most of the XXth century (López 1991), probably explains the high concentration of heavy metals found in the sediments of Maó harbour. Cu and Pb values from Cala Llonga exceeded the reference values considered by Long et al. (1995) as critical for possible adverse effects in the environment. Pb concentrations are especially high when compared with values from other harbours from the mainland in NW Mediterranean (Cebrian et al. 2003, 2007) and As concentrations are higher than the values given by Kut et al. (2000) for the Bosphorus, an area considered highly polluted. In Cala Teulera, although heavy metals concentrations were higher than in the control area, they were always much lower than those from the HP area and never exceeded the reference values of Long et al. (1995).

Heavy metal content increased consistently in specimens transplanted to Maó harbour. This was accompanied by reduced survival in *C. barbata* and reduced growth in *C. crinita* at the highly polluted area. *C. spinosa* survival was unaffected and, although the length of the main axis slightly decreased in specimens transplanted to HP, this did not differ significantly from TC specimens. This suggests that heavy metal pollution could be negatively affecting survival and growth of *Cystoseira* species with species-specific responses. Many authors have found that heavy metals block carbon uptake and photosynthesis, reducing growth and survival of different algal species. Hopkin & Kain (1978) found reduced survival and growth of *Laminaria hyperborea* exposed to different concentrations of mercury, copper, zinc and cadmium. Strömgren (1979, 1980) found that high concentrations of copper reduced the growth of *Ascophyllum nodosum*, *Pelvetia canaliculata*, *Fucus spiralis*, *Fucus vesiculosus* and *Fucus serratus*. Marsden et al. (2003) found reduced survival and growth rate in *Fucus gardneri* specimens transplanted near to an abandoned mine where acid mine drainage was present. There are also other pollutants such as polychlorinated biphenyls (PCBs), detergents and herbicides (Boyle 1984, Levine 1984, Phillips 1995) which are often present in waste waters and reduce survival and growth of some algal species (Hopkin & Kain 1978). Therefore, it is possible that these other pollutants also contributed to reduced survival and growth of *Cystoseira* species. Contaminated areas are often polluted by many substances (Windom 1992) and it is very difficult, if not impossible, to measure all of them.

No significant decrease in survival and growth was detected in specimens transplanted to the slightly polluted area; *C. barbata* specimens even increased their length and carbon content. *C. barbata* is generally considered a resistant species, as it is quite common in slightly polluted areas from the Adriatic and the Black Sea (Ghirardelli et al. 1973, Munda 1982, Kut et al. 2000). *C. barbata* could be favoured by moderate concentrations of some essential elements, like Cu and Zn or by other environmental variable not measured. In an experiment performed by Strömgren (1979), the growth rate of *Ascophyllum nodosum* increased with a moderate addition of copper. The good health shown by *Cystoseira* specimens after 9 months of transplant to Cala Teulera suggests that these species might be able to survive, and even recruit, in this area with the current conditions. These results suggest that an improvement in water quality at Maó harbour may have led to an amelioration of marine benthic communities. However, to ensure the maintenance of a population it is necessary not only that adults are able to survive, grow and recruit, but also that the number of recruits and their growth allow a sufficient population growth rate over time. Therefore, although our results point in a good direction, further investigation is needed in order to confirm the ability of *Cystoseira* populations to survive and maintain in these ameliorated area. On the other hand, even after the improvement of water quality inside the Maó harbour, probably dating from almost thirty years ago, there has not been a natural recovery of *Cystoseira* spp. stands. This should be related to the high size of the zygotes of the species of the genus *Cystoseira* and other members of the order Fucales (Guern 1962, Clayton 1992) which implies low dispersal ability (Chapman 1995, Kendrick & Walker 1991, 1995, Johnson & Brawley 1998, Dudgeon et al. 2001). Thus, transplant of *Cystoseira* specimens is suggested as a tool to be explored in order to restore extinct populations. Other authors have successfully used similar transplantation methodologies to examine the possibility of using them for environmental mitigation (Falace et al. 2006, Susini et al. 2007).

The species-specific responses to the different levels of pollution could be apparently contradictory. *C. barbata*, which is considered a relatively resistant species, was the only one which showed a significant decrease in survival in the HP area. *C. barbata* is a fast-growing species compared to other *Cystoseira* species (author non-published data). Species which present slow growth are often more resilient to changes; however, they have a lower recovery capacity.

Although *Cystoseira* spp. are sensitive to high nutrient levels in sea water (Rodríguez-Prieto & Polo 1996, Arévalo et al. 2007), eutrophication is not currently affecting *Cystoseira* species in Maó harbour as both N and P concentrations in seawater and in algal tissue were very low. A decrease in carbon content in *C. crinita* and *C. spinosa* specimens transplanted to the polluted areas and a carbon increase in *C. barbata* transplanted to the slightly polluted area was the only relevant pattern detected. Higher levels of carbon (~34%) coincided with *Cystoseira* specimens which were displaying positive growth, while lower levels of carbon (~29%) coincided with specimens which were showing negative growth, thus suggesting that carbon content could be an indicator of specimen's health. Similarly, loss of carbohydrates reserves has been described for *Posidonia oceanica* meadows affected by nutrient enriched loadings from a fish farm in Murcia (south-eastern Spain) (Ruiz et al. 2001).

For most metals, bioaccumulation factor values in biota of less than 1 are usually expected (Falusi & Olanipekun 2007). The bioaccumulation factors found in this study were all < 1, except for the trace element As. Other authors have described high accumulation of arsenic by brown algae (Morita & Shibata 1990, Kut et al. 2000, Tukai et al. 2002). Arsenic is accumulated by aquatic plants as arseno-sugars, a form of minor toxic impact (Phillips 1995). Sanders (1979) suggested that the high accumulation of arsenic in brown algae was related to a higher amount of phosphates in these algae. Moreover, the inverse absorption pattern found for As in comparison to other metals in *Cystoseira* submitted to the different treatments, suggests that *Cystoseira* normally accumulate As and this process is altered when specimens are stressed. However, the reason why macroalgae and, especially brown algae, accumulate arsenic remains unknown (Tukai et al. 2002).

To summarize, individuals of three *Cystoseira* species (*C. barbata*, *C. crinita* and *C. spinosa*) were transplanted from non-polluted to slightly-polluted (SP) and heavily-polluted (HP) areas, in places known to harbour *Cystoseira* spp. populations before pollution increased one century ago. *Cystoseira* specimens transplanted to the polluted areas absorbed heavy metals and increased their concentration in algal tissues. Negative effects in survival of *C. barbata* and growth of *C. crinita* were detected on specimens transplanted to the HP area. These results suggest that pollution could have been the cause that drove the disappearance of *Cystoseira* species at Maó harbour in the past. However, nor survival neither growth of any of the *Cystoseira* species was affected at the SP area. Probably due to an improvement in water quality related to the construction of a waste water outfall in 1980, nowadays *Cystoseira* specimens seem to be able to live in the less impacted areas of the harbour. Because of the low dispersal range of the zygotes of *Cystoseira* and the difficulty of natural recolonisation, transplantation is suggested as a tool to be explored for restoring extinct populations.

Discussion

Discussion

This thesis has focused on the study of Mediterranean macroalgae of the genus *Cystoseira* (Fucales, Heterokontophyta) thriving in shallow sheltered environments. The two first chapters deal with the assemblages dominated by *Cystoseira crinita*, one of the most widespread *Cystoseira*-dominated assemblages in the Mediterranean. Chapters three and four deal with the factors influencing the distribution of *Cystoseira* species thriving in sheltered environments and how pollution affects some of these species. Next, the most important results obtained are discussed.

Molinier's identification of *Cystoseira crinita* as the dominant species of assemblages thriving in shallow rocky bottoms in Cap Corse (1960) was questioned by other phycologists, as most Mediterranean shallow water assemblages are devoid of *C. crinita* but dominated by another similar species, *Cystoseira brachycarpa* v. *balearica* (e.g. Verlaque 1987, Giaccone et al. 1994). However, we confirmed that the identity of the dominant species of the assemblages surveyed by Molinier was *Cystoseira crinita*. Moreover, *Cystoseira crinita* was still present in 14 of the 15 sites where Molinier (1960) performed the "relevés" suggesting that, at least in Cap Corse (Corsica), *Cystoseira crinita* assemblages are not suffering a severe decline as it has been shown to be happening in other places (e.g. Thibaut et al. 2005). The assemblages from Cap Corse are representative of the assemblages present in the rest of Corsica and, thus, the association *Cystoseiretum crinitae* is correct and was unequivocally described. Detected differences of species composition and abundances between the "relevés" made by Molinier (1960) and ours are probably related to the different taxonomic expertise and/or to the different seasons when the sampling was performed.

The *Cystoseiretum crinitae*, as originally described by Molinier (1960), has been considered (e.g. Giaccone 1968, 1971a, Giaccone et al. 1994) the main photophilic Mediterranean seaweed association occurring in shallow and sheltered rocky areas. However, *Cystoseira crinita*-dominated assemblages have been found almost exclusively in particular environments subject to low to intermediate hydrodynamism in flat rocky bottoms between 0.2-0.8 m depth, preferentially situated close to beaches or inside littoral pools. As it is shown in chapter 3, different *Cystoseira* species dominate shallow rocky bottoms depending mainly on the exposure degree but also on other geomorphological features of the coast. Therefore, and without discussing whether the name *Cystoseiretum crinitae* should be given to those assemblages dominated by *Cystoseira crinita* or to most Mediterranean assemblages of photophilic algae thriving in sheltered places, *Cystoseira crinita* and its assemblages mainly thrive in areas with particular, very characteristic, environmental features.

The specific composition of the assemblages dominated by *Cystoseira crinita* are described at a regional level, taking into account the whole distribution area of the species, and also of the assemblage. This is the first time that an algal assemblage is studied at the scale of the whole Mediterranean. The biogeographical variation found at the assemblage level is characterized by shifts in species abundances among different regions, which partly coincide with the previously described biogeographical sectors (Pérès & Picard 1964, Bianchi & Morri 2000, Bianchi 2007). Latitude, and temperature, as an oceanographic factor closely related to latitude, is here suggested to be more important than geographic barriers such as the classical division of the Mediterranean in western and eastern basins (Pérès & Picard 1964). Moreover, the predicted diversity impoverishment from west to east is not found in our samples, contrasting with data reported on different groups of animals (Arvanitidis et al. 2002, Boudouresque 2004, Coll et al. in press).

However, we have detected a decrease in species diversity from north to south, in accordance with the general patterns described by Coll et al. (in press) across the Mediterranean. Criticisms of marine biogeography often centre on the failure of biogeographers to define provinces or regions objectively and to demonstrate that regional differences are not the result of differences between taxonomic groups or authors, or the intensity and distribution of collections (Adey & Steneck 2001). Thus, our conclusion is that more work is needed before general biodiversity patterns are invoked for the Mediterranean Sea.

The decline experienced by Mediterranean *Cystoseira* populations during the last decades has been mainly attributed to increased eutrophication and pollution (Bellan-Santini 1968, Golubic 1970, Munda 1982, Munda & Veber 1996, Arévalo et al. 2007). The low impacted areas surveyed for this thesis (Corsica and Minorca) presented high number of *Cystoseira* species thriving in sheltered areas, and conspicuous *Cystoseira crinita*-dominated assemblages. However, even in these low-impacted areas, *Cystoseira* species have disappeared where anthropogenic pressures are strong. This is the case of Centuri harbour in Corsica and Maó harbour in Minorca, where the existence of historical data (Rodríguez-Femenías 1889, Molinier 1960) provides a very valuable tool to notice the disappearance of *Cystoseira* populations.

Transplantation of *Cystoseira* specimens to two sites with different pollution levels in Maó harbour has detected a relationship between high levels of heavy metals, especially lead and copper, and reduced growth and survival of *Cystoseira* specimens. Arévalo et al. (2007) also demonstrated a tight relationship between dissolved nutrient concentration in seawater and disappearance of *Cystoseira*. However, and although it is fairly clear that pollution can be a cause of decline and even die off of entire *Cystoseira* populations, outstanding reductions of

Cystoseira populations have been documented in areas where pollution does not seem a major threat (Thibaut et al. 2005, Serio et al. 2006). In these cases, other causes like increased herbivory or climate change have been invoked. In our opinion, the causes driving the decline of *Cystoseira* populations in the Mediterranean are still not completely understood, although we suggest that the cumulative effects of eutrophication, heavy metal pollution and other (e.g. other pollutants, out-competition by other more tolerant species, habitat destruction) anthropogenic pressures are to be considered.

The establishment of monitoring programs (both including biological and environmental components of the ecosystems) would provide a good framework to improve our general understanding of population dynamics in *Cystoseira* (e.g. Ballesteros et al. 2009). Moreover, other aspects of the biology of *Cystoseira* species, like reproduction, recruitment, and growth are still poorly known, as noticed by Pardi et al. (2000). Comparisons of historical and present data are useful to explore long-term trends in ecology, otherwise impossible.

While many disappearances of *Cystoseira* populations have been documented, cases of recovery are rare and have only been documented for the north Adriatic (Hanel 2002, Zavodnik et al. 2002). Some authors have noticed that, even after water quality improvement, *Cystoseira* populations do not show signs of recovery, and that this is probably due to the low dispersal range of *Cystoseira* zygotes (Soltan et al. 2001, Díez et al. 2009). Our results agree with this low recovery potential. We have demonstrated that *Cystoseira* specimens transplanted to an area from where their disappearance has been documented (Rodríguez-Femenías 1889) show signs of good health, once the anthropogenic pressure has disappeared or has been reduced. However, even after the improvement of water quality and the demonstrated ability of *Cystoseira* specimens to survive with the current environmental conditions, *Cystoseira* populations have not been able to recover naturally. Transplantation is suggested as a tool to be explored in order to restore extinct populations once the main pressure that has driven the extinction has been eliminated and almost natural conditions have been restored. Of course, this should be always accompanied by a study of the impact of collection of specimens on the origin population.

To summarize, in this thesis it is confirmed that *Cystoseira crinita* is the dominant species of the assemblages described by Molinier about fifty years ago, and that these assemblages have not experienced substantial long-term changes in Cap Corse (Corsica). The assemblages dominated by *C. crinita* are described at regional scale, taking into account the biogeographical variation of the assemblage. The main factors (both natural and anthropogenic) driving the distribution of *Cystoseira* species in sheltered areas are identified. Finally, the first experimental evidence of disappearance of *Cystoseira* populations related to pollution is provided. Moreover, we show that the recovery of *Cystoseira* populations after improvement of water quality, although quite difficult due to the low dispersal range of zygotes, is possible by means of transplantation.

Conclusions

Conclusions

1. *Cystoseira crinita* is the dominant species of the assemblages surveyed and described by Molinier in Cap Corse (Corsica) fifty years ago, whose identity was questioned by other phycologists.

2. *Cystoseira crinita*-dominated assemblages from Cap Corse are not experiencing substantial decline, and also have not suffered important changes in species composition and structure since Molinier's description.

3. The defining characters of the assemblages dominated by *Cystoseira crinita* at a Mediterranean level are: similar total cover of species, similar total cover of *C. crinita* and high abundance of the epiphyte *Haliptilon virgatum*.

4. The biogeographical variation at the level of *Cystoseira crinita*-dominated assemblages across the Mediterranean Sea is characterised by shifts in species abundances among regions, and partially agree with previously defined biogeographical sectors.

5. In some cases, latitude and temperature (as a factor highly correlated with latitude) seem to be more important in defining the species composition of *C. crinita* assemblages than the main classical biogeographical division between the western and the eastern basin.

6. No correlation between longitude and species richness has been found in our samples, while a positive and significant correlation has been found between latitude and species richness.

7. The main factors influencing the distribution of *Cystoseira* species in sheltered areas from Minorca are: coastal height, nitrate and nitrite concentrations in seawater, coastal slope at the first meter of depth, nature of the cove or bay bottom and urbanisation distance.

8. The total absence of *Cystoseira* specimens at the vicinity of the main harbours in Minorca, and the proved disappearance of some *Cystoseira* species from Maó harbour, suggest pollution as the main driver of these extinctions.

9. Reduced survival and growth of *Cystoseira* specimens transplanted to a highly polluted area at Maó harbour reinforces the idea that pollution was the factor which drove the disappearance of *Cystoseira* populations in this the area.

10. The good health exhibited by *Cystoseira* specimens transplanted to a slightly polluted area of Maó harbour demonstrate that they can live in this area with the current environmental conditions, which are likely to have improved in recent years.

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Appendix 1

Species cover (in cm^2) at each of the sites sampled for Chapter 2

Sample size is 625 cm^2

	CAT-1	M-1	M-2	M-3	M-4	M-5	M-6	M-7	M-8	M-9	M-10	M-11	M-12	M-13	M-14	F-1	F-2	F-3
Cyanobacteriae																		
Calothrix confervicola		49.96		4.5				3		0.1	7.75		9.38	9.1		0.2	82.3	36.7
Lyngbya semiplena																		
Lyngbya sp.																		
Phormidium sp.								0.1										
Symploca hydnoides		9							1		3	0.1						
Actiniaria (unidentified)																		
Macroalgae																		
Acetabularia acetabulum																		
Acrothamnion preissii		0.7	1			0.5					1	2.5	2.5	0.5	1			0.5
Aglaothamnion scopulorum																		
Aglaozonia parvula (stadium)																		
Alsidium corallinum																		
Alsidium helminthochorton																	1.3	
Amphiroa cryptarthrodia																		
Amphiroa rigida																		
Anadyomene stellata																		
Anotrichium barbatum																		
Boergeseniella fruticulosa						501.9												
Botryocladia botryoides																		
Botryocladia sp.																		
Bryopsis duplex																		
Bryopsis sp.																		
Callithamnion corymbosum																	0.2	
Caulerpa racemosa v. *cylindracea*																		
Ceramiaceae unidentified																		
Ceramium ciliatum	0.2																2	
Ceramium circinatum																		
Ceramium codii																		
Ceramium deslongchampsii																		
Ceramium diaphanum		0.1				0.1											4.7	
Ceramium siliquosum v. *zostericola*	1.3																	

	CAT-1	M-1	M-2	M-3	M-4	M-5	M-6	M-7	M-8	M-9	M-10	M-11	M-12	M-13	M-14	F-1	F-2	F-3
Ceramium sp.																		
Ceramium tenerrimum																		
Chaetomorpha linum	0.5					2		2									0.5	
Champia parvula	0.2																	
Chondracanthus acicularis	5.9																	
Chondria capillaris	0.3																0.2	
Chondria dasyphylla																	1.1	
Chondria sp.											0.1							
Choreonema thuretii															0.1			
Chrisonephos lewisii																		
Chylocladia verticillata																		
Cladophora albida																		
Cladophora cf. *sericea*																		
Cladophora coelothrix				1.5			1						1.5					
Cladophora dalmatica																		
Cladophora hutchinsiae																		
Cladophora laetevirens	198.3	12			59.25	15				0.3		3.75	5	5			6.9	
Cladophora lehmanniana													3					
Cladophora nigrescens																		
Cladophora pellucida																		
Cladophora prolifera	3.3	2.4		10	59.25	126	0.2			0.5			0.5	0.1				
Cladophora rupestris																		
Cladophora socialis																		
Cladophora sp. 1		11.25								1								
Cladophora sp. 2																		
Cladophora vagabunda	5.6			4		28		32.75					2	2			1.6	0.2
Cladophoropsis membranacea																		
Cladosiphon sp.																		
Cladostephus spongiosus																		
Codium bursa																		
Contarinia peyssonneliaeformis			2															
Corallina elongata	1.6	3.85	403.5		5	0.5	52.5	2	40		67.5	0.2						
Corallophila cinnabarina																		

	CAT-1	M-1	M-2	M-3	M-4	M-5	M-6	M-7	M-8	M-9	M-10	M-11	M-12	M-13	M-14	F-1	F-2	F-3
Crouania attenuata																		
Cryptonemia lomation																		
Cystoseira balearica																		
Cystoseira barbata																		
Cystoseira compressa v. *compressa*																		
Cystoseira compressa v. *pustulata*																		
Cystoseira corniculata																		
Cystoseira crinita	2633	1249	1715	2375	3595	3346	1680	1335	1610	2275	1550	5560	1876	1813	3350	3298	2745	3784
Cystoseira foeniculacea v. *tenuiramosa*																		
Cystoseira jabukae																		
Cystoseira spinosa v. *tenuior*				4		52		1050					32.5	7.5				
Dasya corymbifera	2																	
Dasya rigidula								0.2										
Dasycladus vermicularis		4		23				13.5	2.25	59.25			30			6.3	46.9	0.6
Delesseriaceae unidentified 1																		
Delesseriaceae unidentified 2																		
Dictyopteris polypodioides									0.2									
Dictyota dichotoma																		
Dictyota dichotoma v.*intricata*																		
Dictyota fasciola																		
Dictyota spiralis																		
Dictyotaceae unidentified		3.75	0.2	6		2	0.8	1	4	11.25	10	0.2	14	7	2.5	2	9.3	
Digenea simplex																		
Dipterosiphonia rigens			0.5	5					5		1		2		0.1		0.8	3.6
Discosporangium mesarthrocarpum													1					
Encrusting Corallinaceae (unidentified)																		
Erythrocystis montagnei																		

	CAT-1	M-1	M-2	M-3	M-4	M-5	M-6	M-7	M-8	M-9	M-10	M-11	M-12	M-13	M-14	F-1	F-2	F-3
Falkenbergia cf. *hillebrandii*-stadium																		
Falkenbergia rufolanosa-stadium	5.2																	
Feldmannia cf. *irregularis*	0.2																	
Feldmannia lebelii	41.6				251.7			0.5	48.3		31		3	18.13	100.5			
Feldmannia sp.																		
Flabellia petiolata		1.5			0.1		69.5		0.5					0.5			6.7	
Gastroclonium clavatum																		
Gayliella flaccida	0.2																	
Gelidiella sp.													0.1					
Gelidium crinale																		
Gelidium latifolium																		
Gelidium pusillum	0.9																	
Gelidium spathulatum							22											
Grateloupia dichotoma																		
Halimeda tuna							2.25									7.8		
Haliptilon virgatum	1.6	966	96	150	91	30			300	1029	429	253.5	260	160	595	940.6	400.8	864.1
Halopithys incurva				71.5		84												
Halopteris filicina	0.2											2	3					
Halurus flosculosus																		
Herposiphonia secunda	5.5	0.5			0.5		20		0.1	0.1	0.5					0.9	3.1	1.9
Heterosiphonia crispella																		0.3
Hildenbrandia crouaniorum																		
Hydrolithon farinosum		124.9		237.5		16.73		5	32.2	568.8	62	444.8	131.3	145	33.5			
Hypnea musciformis	0.3																	
Hypnea sp.																		
Hypoglossum hypoglossoides																		
Janczewskia verrucaeformis																		
Jania adhaerens															0.1			
Jania longifurca	191.1																	
Jania rubens	23.1	108	4.5	4	208	5		25	14	220	341	13	20	40	200			
Jania rubens v. *corniculata*																		
Jania sp.																		

	CAT-1	M-1	M-2	M-3	M-4	M-5	M-6	M-7	M-8	M-9	M-10	M-11	M-12	M-13	M-14	F-1	F-2	F-3
Laurencia cf. *obtusa*	11.4																21.1	
Laurencia chondrioides																		
Laurencia microcladia																		
Laurencia sp. 1				2			0.1											
Laurencia sp. 2																		
Laurencia sp. 3																		
Laurencia sp. 4																		
Lejolisia mediterranea																		
Leptofauchea coralligena	0.6																	
Liebmannia leveillei																		
Lithophyllum incrustans	586																	
Lithophyllum pustulatum	89.4																	
Lithophyllum sp.																		
Lobophora variegata																		
Lophosiphonia cristata																		
Lophosiphonia obscura																	9.4	
Lophosiphonia reptabunda	0.5																	
Lophosiphonia sp.																		
Melobesiae unidentified																		
Mesophyllum alternans																		
Mesophyllum sp.																		
Miryactula rivulariae	196.1									45,5								
Myriogramme sp.																		
Neogoniolithon brassica-florida		125	31.25	375	476.3	187.5	143	194.5	31.25	312.5	62.5	218.8	66.5	95.25	62.5			
Nitophyllum micropunctatum																		
Osmundea truncata																		
Padina pavonica	1.9											0.2	2.5				11.7	
Palisada papillosa																		
Palisada patentirramea																		
Palisada tenerrima																	6.2	
Parviphycus tenuissimus														0.1				
Pedobesia lamourouxii																		
Peyssonnelia cf. *armorica*							15											

	CAT-1	M-1	M-2	M-3	M-4	M-5	M-6	M-7	M-8	M-9	M-10	M-11	M-12	M-13	M-14	F-1	F-2	F-3
Peyssonnelia dubyi	30														6.3			
Peyssonnelia harveyana						1.5												4
Peyssonnelia rosa-marina																		
Peyssonnelia sp.																		
Peyssonnelia squamaria																		
Phyllophora crispa																		
Plocamium cartilagineum	0.2																	
Polysiphonia flocculosa																	28.9	
Polysiphonia opaca																	0.8	
Polysiphonia scopulorum	0.2																	
Polysiphonia setigera	0.3																	
Polysiphonia sp. 1	0.5																	
Polysiphonia sp. 2																		
Polysiphonia sp. 3																		
Polysiphonia sp. 4																		
Polystrata fosliei																		
Porphyra sp.																		
Pseudochlorodesmis furcellata																		
Pseudolithoderma adriaticum		250	375	156.3		187.5	2	389	468.8	93.75	125	187.5	406.3	437.5	500			
Pterocladiella melanoidea																		
Rhodophyllis divaricata																		
Rhodophyllis strafforelloi			1.5															
Rytiphloea tinctoria				40		260		27		286					32			
Sargassum vulgare																		
Siphonocladus pusillus																		
Spermothamnion irregulare	0.3																	
Spermothamnion repens																4.1	6.6	8.8
Spermothamnion sp.																		
Sphacelaria cirrosa	88.4	0.3	1	0.3	15	1004			0.5	2		2689	10	16	33.5		1.1	0.5
Sphacelaria rigidula																		
Spyridia filamentosa																		
Stypocaulon scoparium	280.3					2						1	2	1			13.3	0.9
Taonia atomaria																		

	CAT-1	M-1	M-2	M-3	M-4	M-5	M-6	M-7	M-8	M-9	M-10	M-11	M-12	M-13	M-14	F-1	F-2	F-3
Titanoderma trochanter																		
Ulva multiramosa																		
Ulva pseudolinza	2.8																	
Ulva ramulosa	1117																	
Ulva rigida	74.5																	
Ulva sp.																		
Valonia aegagropila																		
Valonia utricularis		1.1		8			12	2					2.5					
Vickersia baccata																		
Womersleyella setacea																		
Wrangelia penicillata																		
Wurdermannia miniata																		
Sessile macroinvertebrates																		
Aetea anguina																		
Aglaophenia kirchenpaueri																		
Aiptasia diaphana																		
Amathia lendigera					6									12				
Amathia sp.																		
Anemonia sulcata		30																
Arca noae					2.5						4				5			
Balanophyllia europaea																		
Campanulariidae (unidentified)																		
Chiton sp.																		
Chlidonia pyriformis																		
Clavularia crassa																		
Crisia sp.																		
Cystodites dellechiajei																		
Didemnidae unidentified 1																		
Didemnidae unidentified 2																		
Didemnidae unidentified 3																		
Didemnidae unidentified 4																		
Didemnum granulosum																		

	CAT-1	M-1	M-2	M-3	M-4	M-5	M-6	M-7	M-8	M-9	M-10	M-11	M-12	M-13	M-14	F-1	F-2	F-3
Didemnum maculosum																		
Encrusting bryozoan (unidentified)																		
Filicrisia geniculata																		
Guanchia sp.																		
Haliclona sp.																		
Hymedesmia versicolor																		
Ircinia fasciculata																		
Ircinia variabilis		5																
Ostraea edulis																		
Pherusella tubulosa																		
Porifera unidentified																		
Sarcotragus spinosula																		
Scrupocellaria sp.																		
Spondylus spinosus																		
Turbicellepora magnicostata					8													

Appendix 1.1. Species horizontal cover (in cm^2) at the sites from Catalonia (CAT), Minorca (M) and Formentera (F).

	C-1	C-2	C-3	C-4	C-5	C-6	C-7	C-8	C-9	C-10	C-11	C-12	C-13	C-14	C-15	C-16	C-17	C-18
Cyanobacteriae																		
Calothrix confervicola																		
Lyngbya semiplena																		
Lyngbya sp.																		
Phormidium sp.																		
Symploca hydnoides																		
Actiniaria (unidentified)																		
Macroalgae																		
Acetabularia acetabulum	1	4	0.8					0.7			0.5	1						
Acrothamnion preissii		5.4	0.8				2	4	3	1	2				0.8	1.6	0.8	0.1
Aglaothamnion scopulorum																		
Aglaozonia parvula (stadium)																		
Alsidium corallinum									42									
Alsidium helminthochorton									50									
Amphiroa cryptarthrodia					0.8													
Amphiroa rigida		1					6					72	8		1	20	14	
Anadyomene stellata	1												0.5	0.4				
Anotrichium barbatum																		
Boergeseniella fruticulosa							2											
Botryocladia botryoides																		
Botryocladia sp.																		
Bryopsis duplex																		
Bryopsis sp.																		
Callithamnion corymbosum																		
Caulerpa racemosa v. *cylindracea*																		
Ceramiaceae unidentified														3				50
Ceramium ciliatum																		
Ceramium circinatum																		
Ceramium codii					40													
Ceramium deslongchampsii																		
Ceramium diaphanum																		
Ceramium siliquosum v. *zostericola*																		
Ceramium sp.																		

	C-1	C-2	C-3	C-4	C-5	C-6	C-7	C-8	C-9	C-10	C-11	C-12	C-13	C-14	C-15	C-16	C-17	C-18
Ceramium tenerrimum																		
Chaetomorpha linum					0,1											0.3	0.1	0.2
Champia parvula																		
Chondracanthus acicularis									2	25								
Chondria capillaris																		
Chondria dasyphylla									0.5									
Chondria sp.									2									
Choreonema thuretii																		
Chrisonephos lewisii																		
Chylocladia verticillata																		
Cladophora albida																		
Cladophora cf. *sericea*																		
Cladophora coelothrix		5	5			0,8		80	7				2	51		0.5	0.8	
Cladophora dalmatica																		
Cladophora hutchinsiae																		
Cladophora laetevirens	17	30	7		1	4	1			2							2	1
Cladophora lehmanniana										6							12	2
Cladophora nigrescens						0.5												
Cladophora pellucida					6													
Cladophora prolifera	200	5	20		2				6					36				2.5
Cladophora rupestris																		
Cladophora socialis																		
Cladophora sp. 1										50								
Cladophora sp. 2																		
Cladophora vagabunda																	8	
Cladophoropsis membranacea																		
Cladosiphon sp.																		
Cladostephus spongiosus	10	50							4									
Codium bursa													0.2					
Contarinia peyssonneliaeformis																		
Corallina elongata	2		80									7	5				59	123
Corallophila cinnabarina																		
Crouania attenuata																		

	C-1	C-2	C-3	C-4	C-5	C-6	C-7	C-8	C-9	C-10	C-11	C-12	C-13	C-14	C-15	C-16	C-17	C-18
Cryptonemia lomation																		
Cystoseira balearica													42					
Cystoseira barbata								15						596	326			
Cystoseira compressa v. *compressa*																		
Cystoseira compressa v. *pustulata*													65					
Cystoseira corniculata																		
Cystoseira crinita	1704	1910	1960	3100	2300	1680	1928	800	1770	1896	1434	520	1240	769	2292	1914	1610	3075
Cystoseira foeniculacea v. *tenuiramosa*													21					
Cystoseira jabukae																		
Cystoseira spinosa v. *tenuior*								20	6									
Dasya corymbifera							5				1.8							
Dasya rigidula		1														0.2		
Dasycladus vermicularis			17	1		3		12			20		15	2				
Delesseriaceae unidentified 1		0.4								1								
Delesseriaceae unidentified 2																		
Dictyopteris polypodioides	17	2	3				85		30	36		81	225				3.4	
Dictyota dichotoma																		
Dictyota dichotoma v.*intricata*	23		3		0.4		15	9	8	6		4	7	3	0.3			
Dictyota fasciola	40	3	6			2	16	2	2		8	1	5					
Dictyota spiralis																		
Dictyotaceae unidentified				3		15	2	30		12		20	250	605		27		
Digenea simplex																		
Dipterosiphonia rigens																		
Discosporangium mesarthrocarpum																		
Encrusting Corallinaceae (unidentified)																		
Erythrocystis montagnei																		
Falkenbergia cf. *hillebrandii*-stadium						0.8												
Falkenbergia rufolanosa-stadium																		
Feldmannia cf. *irregularis*							0.5											
Feldmannia lebelii											75							

	C-1	C-2	C-3	C-4	C-5	C-6	C-7	C-8	C-9	C-10	C-11	C-12	C-13	C-14	C-15	C-16	C-17	C-18
Feldmannia sp.															115			
Flabellia petiolata		0.5	3		1	36		0.5			7			200				
Gastroclonium clavatum																		
Gayliella flaccida		0.1									0.2							
Gelidiella sp.																		
Gelidium crinale									4									
Gelidium latifolium			65															
Gelidium pusillum																		
Gelidium spathulatum																		
Grateloupia dichotoma										22								
Halimeda tuna									28									
Haliptilon virgatum	160	380	120	445	234	196	20	15	8	4	30	1560	284	2.5	2.5	1.5	1150	590
Halopithys incurva									8									
Halopteris filicina																		
Halurus flosculosus																		
Herposiphonia secunda							1				0.2							
Heterosiphonia crispella																		
Hildenbrandia crouaniorum																		
Hydrolithon farinosum				80	40	20	40	20	15		30	5	200	400	350	200	80	8
Hypnea musciformis							120	4	45	18								
Hypnea sp.																		
Hypoglossum hypoglossoides																		
Janczewskia verrucaeformis																		
Jania adhaerens																		
Jania longifurca											7							
Jania rubens		30	65						0.2		2							39
Jania rubens v. *corniculata*																		
Jania sp.																		
Laurencia cf. *obtusa*									70	45								
Laurencia chondrioides															0.4	2		
Laurencia microcladia	3							0,5	2	1								
Laurencia sp. 1																		
Laurencia sp. 2																		

	C-1	C-2	C-3	C-4	C-5	C-6	C-7	C-8	C-9	C-10	C-11	C-12	C-13	C-14	C-15	C-16	C-17	C-18
Laurencia sp. 3																		
Laurencia sp. 4																		
Lejolisia mediterranea																		
Leptofauchea coralligena	40		25															
Liebmannia leveillei								2										
Lithophyllum incrustans																		
Lithophyllum pustulatum																		
Lithophyllum sp.																		
Lobophora variegata																		
Lophosiphonia cristata								3										
Lophosiphonia obscura																		
Lophosiphonia reptabunda																		
Lophosiphonia sp.																300		
Melobesiae unidentified																		
Mesophyllum alternans																		42
Mesophyllum sp.																		
Miryactula rivulariae																		
Myriogramme sp.																		
Neogoniolithon brassica-florida	550	50	160	75	350	150	500	525	520	550	50	400	400	350	190	426	480	700
Nitophyllum micropunctatum																		
Osmundea truncata																		
Padina pavonica	4	2							1	8	13	1	10					
Palisada papillosa									1.8									
Palisada patentirramea																		
Palisada tenerrima																		
Parviphycus tenuissimus					10			1	2		0.1		2			10		8
Pedobesia lamourouxii																		
Peyssonnelia cf. *armorica*																		
Peyssonnelia dubyi			19							15								
Peyssonnelia harveyana							40											
Peyssonnelia rosa-marina																		
Peyssonnelia sp.																		
Peyssonnelia squamaria	45	1								15							1	

	C-1	C-2	C-3	C-4	C-5	C-6	C-7	C-8	C-9	C-10	C-11	C-12	C-13	C-14	C-15	C-16	C-17	C-18
Phyllophora crispa										2								
Plocamium cartilagineum										1								
Polysiphonia flocculosa																		
Polysiphonia opaca																		
Polysiphonia scopulorum																		
Polysiphonia setigera																		
Polysiphonia sp. 1																		
Polysiphonia sp. 2																		
Polysiphonia sp. 3								5										
Polysiphonia sp. 4																		
Polystrata fosliei								15			25							
Porphyra sp.		1																
Pseudochlorodesmis furcellata				0.2	3	2							2	1				
Pseudolithoderma adriaticum		30	110	400	30	15	50	15		35	400	50	100	10	230	15	90	25
Pterocladiella melanoidea																5		1
Rhodophyllis divaricata																		
Rhodophyllis strafforelloi																		
Rytiphloea tinctoria								300	40	60								
Sargassum vulgare																		
Siphonocladus pusillus						0.2												
Spermothamnion irregulare																		
Spermothamnion repens																		
Spermothamnion sp.																		
Sphacelaria cirrosa	18	30	160		2		850	200	1200	450	750	3	10	180	3	950	1700	402
Sphacelaria rigidula																		
Spyridia filamentosa																		
Stypocaulon scoparium	5	3	22			0.7	10	9	18	19					0.1			
Taonia atomaria	4	2	3					3										
Titanoderma trochanter																		
Ulva multiramosa																		
Ulva pseudolinza																		
Ulva ramulosa																		
Ulva rigida																		

	C-1	C-2	C-3	C-4	C-5	C-6	C-7	C-8	C-9	C-10	C-11	C-12	C-13	C-14	C-15	C-16	C-17	C-18
Ulva sp.										5								
Valonia aegagropila																		
Valonia utricularis			5		165		4	1		2			0.4			30		
Vickersia baccata																		
Womersleyella setacea																		
Wrangelia penicillata																		
Wurdermannia miniata																		
Sessile macroinvertebrates																		
Aetea anguina																		
Aglaophenia kirchenpaueri																		
Aiptasia diaphana																		
Amathia lendigera																		
Amathia sp.																		
Anemonia sulcata																		
Arca noae																		
Balanophyllia europaea														1				
Campanulariidae (unidentified)																		
Chiton sp.																		
Chlidonia pyriformis																		
Clavularia crassa																		
Crisia sp.																		
Cystodites dellechiajei																		
Didemnidae unidentified 1																		
Didemnidae unidentified 2																		
Didemnidae unidentified 3																		
Didemnidae unidentified 4																		
Didemnum granulosum																		
Didemnum maculosum																		
Encrusting bryozoan (unidentified)																		
Filicrisia geniculata																		
Guanchia sp.																		
Haliclona sp.													3					

	C-1	C-2	C-3	C-4	C-5	C-6	C-7	C-8	C-9	C-10	C-11	C-12	C-13	C-14	C-15	C-16	C-17	C-18
Hymedesmia versicolor												20						
Ircinia fasciculata																		
Ircinia variabilis																		14
Ostraea edulis																		
Pherusella tubulosa																		
Porifera unidentified																		
Sarcotragus spinosula																		
Scrupocellaria sp.																		
Spondylus spinosus																		
Turbicellepora magnicostata																8	17	18

Appendix 1.2. Species horizontal cover (in cm^2) at the sites 1 to 18 from Corsica.

	C-19	C-20	C-21	C-22	C-23	C-24	C-25	C-26	C-27	C-28	C-29	C-30	C-31	C-32	C-33	C-34	C-35	C-36
Cyanobacteriae																		
Calothrix confervicola																		
Lyngbya semiplena																		
Lyngbya sp.				0.1														
Phormidium sp.																		
Symploca hydnoides																		
Actiniaria (unidentified)																		
Macroalgae																		
Acetabularia acetabulum																		
Acrothamnion preissii		0.1			0.5							1.7			0.1			
Aglaothamnion scopulorum																	0.1	
Aglaozonia parvula (stadium)																		
Alsidium corallinum																		
Alsidium helminthochorton							9		5	2								
Amphiroa cryptarthrodia																		
Amphiroa rigida															1.2			
Anadyomene stellata					0.2													
Anotrichium barbatum							0.1											
Boergeseniella fruticulosa									6				180					
Botryocladia botryoides																		
Botryocladia sp.																		
Bryopsis duplex																		
Bryopsis sp.																		
Callithamnion corymbosum							0.1											
Caulerpa racemosa v. *cylindracea*																		
Ceramiaceae unidentified																		
Ceramium ciliatum																		
Ceramium circinatum																		
Ceramium codii							0.1											
Ceramium deslongchampsii																		
Ceramium diaphanum		0.1			0.1													
Ceramium siliquosum v. *zostericola*																		
Ceramium sp.																		

	C-19	C-20	C-21	C-22	C-23	C-24	C-25	C-26	C-27	C-28	C-29	C-30	C-31	C-32	C-33	C-34	C-35	C-36
Ceramium tenerrimum																		
Chaetomorpha linum	0.2	0.1	0.1			1.4	0.1				5		0.1		0.1		0.1	0.2
Champia parvula																		
Chondracanthus acicularis																		
Chondria capillaris									0.1									
Chondria dasyphylla																		
Chondria sp.																		
Choreonema thuretii																		
Chrisonephos lewisii				15														
Chylocladia verticillata																		
Cladophora albida																		
Cladophora cf. *sericea*																		
Cladophora coelothrix		1.2		10					4			0.5				70	1	
Cladophora dalmatica																		
Cladophora hutchinsiae																		
Cladophora laetevirens		75		3		9		12			72	2				240	195	18
Cladophora lehmanniana	2		1.5	6			2		45									
Cladophora nigrescens											7					160		
Cladophora pellucida				30													1.5	
Cladophora prolifera		1.2	2.5	770		1	3	434	16		2		120			80		
Cladophora rupestris																		
Cladophora socialis				25														
Cladophora sp. 1	0.2																	
Cladophora sp. 2					12													
Cladophora vagabunda							1					1.5						
Cladophoropsis membranacea																		
Cladosiphon sp.																		
Cladostephus spongiosus			0.5															2
Codium bursa																		
Contarinia peyssonneliaeformis																		
Corallina elongata	440	0.3	6	0.4	2												10	
Corallophila cinnabarina																		
Crouania attenuata																		

	C-19	C-20	C-21	C-22	C-23	C-24	C-25	C-26	C-27	C-28	C-29	C-30	C-31	C-32	C-33	C-34	C-35	C-36
Cryptonemia lomation																		
Cystoseira balearica																		
Cystoseira barbata																		
Cystoseira compressa v. *compressa*			120															
Cystoseira compressa v. *pustulata*																		
Cystoseira corniculata																		
Cystoseira crinita	1720	2564	2332	1800	1890	1872	2050	1980	2134	2412	4150	3740	2960	3060	2400	1500	1970	2058
Cystoseira foeniculacea v. *tenuiramosa*																		
Cystoseira jabukae				5														
Cystoseira spinosa v. *tenuior*																		
Dasya corymbifera															0.1			0.1
Dasya rigidula						0.6	0.4	0.7			0.2	0.2				1		
Dasycladus vermicularis		1.2				106	0.8	1	4		1		2.5			1	18	94
Delesseriaceae unidentified 1			1															
Delesseriaceae unidentified 2															0.4			
Dictyopteris polypodioides																		
Dictyota dichotoma																		
Dictyota dichotoma v.*intricata*							0.4		18			108						
Dictyota fasciola	0.4																	
Dictyota spiralis																		
Dictyotaceae unidentified							0.5				7	100			122			
Digenea simplex																		
Dipterosiphonia rigens									0.2									
Discosporangium mesarthrocarpum																		
Encrusting Corallinaceae (unidentified)																		
Erythrocystis montagnei									0.1									
Falkenbergia cf. *hillebrandii*-stadium																		

	C-19	C-20	C-21	C-22	C-23	C-24	C-25	C-26	C-27	C-28	C-29	C-30	C-31	C-32	C-33	C-34	C-35	C-36
Falkenbergia rufolanosa-stadium																		
Feldmannia cf. *irregularis*																		
Feldmannia lebelii					50	10	51					65		130				
Feldmannia sp.				350				15	20	35							15	
Flabellia petiolata					0.1				2			8			3	0.1		
Gastroclonium clavatum																		
Gayliella flaccida																0.2		
Gelidiella sp.																		
Gelidium crinale																		
Gelidium latifolium																		
Gelidium pusillum			2															
Gelidium spathulatum																		
Grateloupia dichotoma																		
Halimeda tuna									4									
Haliptilon virgatum	800	158	237	2	450	158	6	800	1.3	252	85	0.4	30	5	1	24	182	462
Halopithys incurva																		
Halopteris filicina																		
Halurus flosculosus						1												
Herposiphonia secunda						0.8			3									1
Heterosiphonia crispella																		
Hildenbrandia crouaniorum			7														30	
Hydrolithon farinosum	200		100	2	30		20	80	120	110	120	40	120	70	25	85	60	180
Hypnea musciformis																		
Hypnea sp.																		
Hypoglossum hypoglossoides																		
Janczewskia verrucaeformis																		
Jania adhaerens																		
Jania longifurca																		
Jania rubens	6	32	6		33	2	15	5		19			120	56		43	12	
Jania rubens v. *corniculata*																		
Jania sp.																		
Laurencia cf. *obtusa*									48		0.3							
Laurencia chondrioides																		

	C-19	C-20	C-21	C-22	C-23	C-24	C-25	C-26	C-27	C-28	C-29	C-30	C-31	C-32	C-33	C-34	C-35	C-36
Laurencia microcladia											1							
Laurencia sp. 1																		
Laurencia sp. 2																		
Laurencia sp. 3																		
Laurencia sp. 4																		
Lejolisia mediterranea					0.3													
Leptofauchea coralligena																		
Liebmannia leveillei																		
Lithophyllum incrustans																		
Lithophyllum pustulatum																		
Lithophyllum sp.				6														
Lobophora variegata																		
Lophosiphonia cristata							0.7											
Lophosiphonia obscura																		
Lophosiphonia reptabunda																		
Lophosiphonia sp.				200														
Melobesiae unidentified																		
Mesophyllum alternans																		
Mesophyllum sp.																		
Miryactula rivulariae																		
Myriogramme sp.																		
Neogoniolithon brassica-florida	520	430	130	550	300	300	500	540	200	520	480	460	420	500	550	400	450	300
Nitophyllum micropunctatum															1.4			
Osmundea truncata																		
Padina pavonica						0.4			2				15		0.6			
Palisada papillosa									2									
Palisada patentirramea																		
Palisada tenerrima																		
Parviphycus tenuissimus				15									3					
Pedobesia lamourouxii																		
Peyssonnelia cf. *armorica*																		
Peyssonnelia dubyi																		
Peyssonnelia harveyana																		

	C-19	C-20	C-21	C-22	C-23	C-24	C-25	C-26	C-27	C-28	C-29	C-30	C-31	C-32	C-33	C-34	C-35	C-36
Peyssonnelia rosa-marina											60			40		240		
Peyssonnelia sp.		60																
Peyssonnelia squamaria													1					
Phyllophora crispa																		
Plocamium cartilagineum																		
Polysiphonia flocculosa																		
Polysiphonia opaca									1.5									
Polysiphonia scopulorum																		
Polysiphonia setigera																		
Polysiphonia sp. 1																		
Polysiphonia sp. 2																		
Polysiphonia sp. 3																		
Polysiphonia sp. 4																		
Polystrata fosliei																		
Porphyra sp.																		
Pseudochlorodesmis furcellata	0.5																	
Pseudolithoderma adriaticum	32		110	30	125	40	25			2	30	12	40	100	20	10	25	20
Pterocladiella melanoidea				1									0.5					
Rhodophyllis divaricata			1				0.5										0.1	
Rhodophyllis strafforelloi																		
Rytiphloea tinctoria									528	76								
Sargassum vulgare																		
Siphonocladus pusillus																		
Spermothamnion irregulare																		
Spermothamnion repens																		
Spermothamnion sp.																		
Sphacelaria cirrosa	250	1400	550	30	60		62	60	40	6	0.1	400	2400	2100	280	180	100	65
Sphacelaria rigidula			0.2															
Spyridia filamentosa																		
Stypocaulon scoparium		0.6	11				1.5					1				1		
Taonia atomaria																		
Titanoderma trochanter																		
Ulva multiramosa																		

	C-19	C-20	C-21	C-22	C-23	C-24	C-25	C-26	C-27	C-28	C-29	C-30	C-31	C-32	C-33	C-34	C-35	C-36
Ulva pseudolinza																		
Ulva ramulosa																		
Ulva rigida																		
Ulva sp.																		
Valonia aegagropila													5		11			
Valonia utricularis									4	18				10			1.5	
Vickersia baccata																		
Womersleyella setacea																		
Wrangelia penicillata																		
Wurdermannia miniata		0.5																
Sessile macroinvertebrates																		
Aetea anguina																		
Aglaophenia kirchenpaueri																		
Aiptasia diaphana															1.5			
Amathia lendigera		2	2				2.2	5			3							
Amathia sp.																		
Anemonia sulcata																		
Arca noae													28					
Balanophyllia europaea																		
Campanulariidae (unidentified)																		
Chiton sp.																		
Chlidonia pyriformis																		
Clavularia crassa																		
Crisia sp.																		
Cystodites dellechiajei																		
Didemnidae unidentified 1														2				
Didemnidae unidentified 2													12					
Didemnidae unidentified 3										2								
Didemnidae unidentified 4																		
Didemnum granulosum																		
Didemnum maculosum												4						

	C-19	C-20	C-21	C-22	C-23	C-24	C-25	C-26	C-27	C-28	C-29	C-30	C-31	C-32	C-33	C-34	C-35	C-36
Encrusting bryozoan (unidentified)																		
Filicrisia geniculata																		
Guanchia sp.																		
Haliclona sp.									2	3								
Hymedesmia versicolor																		
Ircinia fasciculata													9					
Ircinia variabilis																		
Ostraea edulis																		
Pherusella tubulosa																		
Porifera unidentified											30							
Sarcotragus spinosula																		
Scrupocellaria sp.																		
Spondylus spinosus																		
Turbicellepora magnicostata	13		55			1		27				200	130	6.2		65	17	

Appendix 1.3. Species horizontal cover (in cm^2) at the sites 19 to 36 from Corsica.

	S-1	S-2	S-3	S-4	S-5	S-6	S-7	S-8	S-9	S-10	S-11	S-12	S-13	S-14
Cyanobacteriae														
Calothrix confervicola														
Lyngbya semiplena						0.1								
Lyngbya sp.														
Phormidium sp.														
Symploca hydnoides	3								0.2		5			
Actiniaria (unidentified)														
Macroalgae														
Acetabularia acetabulum				0.2								1		
Acrothamnion preissii		0.1					3.7							
Aglaothamnion scopulorum		0.1												
Aglaozonia parvula (stadium)														
Alsidium corallinum							204					44..5	44	
Alsidium helminthochorton			15	0.3								3		
Amphiroa cryptarthrodia														
Amphiroa rigida			6	4	0.6	2.5						0.9		
Anadyomene stellata			0.3	2					2		1.5	1.5	7	
Anotrichium barbatum														
Boergeseniella fruticulosa						902								
Botryocladia botryoides														
Botryocladia sp.														
Bryopsis duplex														
Bryopsis sp.														
Callithamnion corymbosum												0.2		
Caulerpa racemosa v. *cylindracea*														
Ceramiaceae unidentified														
Ceramium ciliatum														
Ceramium circinatum	1	0.1										4		
Ceramium codii														
Ceramium deslongchampsii														
Ceramium diaphanum		0.2											0.1	1
Ceramium siliquosum v. *zostericola*														
Ceramium sp.								0.1						

	S-1	S-2	S-3	S-4	S-5	S-6	S-7	S-8	S-9	S-10	S-11	S-12	S-13	S-14
Ceramium tenerrimum														
Chaetomorpha linum		0.1				0.2							0.1	
Champia parvula														
Chondracanthus acicularis														
Chondria capillaris													2	
Chondria dasyphylla													2	
Chondria sp.														
Choreonema thuretii							0.1							
Chrisonephos lewisii														
Chylocladia verticillata														
Cladophora albida													1	5
Cladophora cf. *sericea*														
Cladophora coelothrix				0.3					1.5				5.5	
Cladophora dalmatica												0.8		
Cladophora hutchinsiae														
Cladophora laetevirens	21	15						2				1		
Cladophora lehmanniana	6		0.3											
Cladophora nigrescens														
Cladophora pellucida														
Cladophora prolifera	9	122					3.6	1				45		27
Cladophora rupestris										0.3				
Cladophora socialis														
Cladophora sp. 1														
Cladophora sp. 2														
Cladophora vagabunda		1											13	2
Cladophoropsis membranacea											32			
Cladosiphon sp.													0.1	
Cladostephus spongiosus														
Codium bursa														
Contarinia peyssonneliaeformis														
Corallina elongata	3		0.2								70			
Corallophila cinnabarina														
Crouania attenuata														

	S-1	S-2	S-3	S-4	S-5	S-6	S-7	S-8	S-9	S-10	S-11	S-12	S-13	S-14
Cryptonemia lomation														
Cystoseira balearica				33										
Cystoseira barbata							394						7	
Cystoseira compressa v. *compressa*											110			
Cystoseira compressa v. *pustulata*	3		8											
Cystoseira corniculata														
Cystoseira crinita	2060	3000	2456	1364	2968	1628	1144	1914	1611	1892	1210	1518	1804	1724
Cystoseira foeniculacea v. *tenuiramosa*														
Cystoseira jabukae														
Cystoseira spinosa v. *tenuior*							7					5		
Dasya corymbifera				0.2							0.3			
Dasya rigidula				1.5	1.3							0.3		
Dasycladus vermicularis	1	0.6			0.7					105				1
Delesseriaceae unidentified 1														
Delesseriaceae unidentified 2														
Dictyopteris polypodioides			10									11		
Dictyota dichotoma														
Dictyota dichotoma v.*intricata*							4.3					2		
Dictyota fasciola			6	0.5										
Dictyota spiralis														
Dictyotaceae unidentified	300		3	336	24		506	4	0.5	90	1	257	6	8
Digenea simplex	1													
Dipterosiphonia rigens											25		2	0.7
Discosporangium mesarthrocarpum														
Encrusting Corallinaceae (unidentified)														
Erythrocystis montagnei														0.1
Falkenbergia cf. *hillebrandii*-stadium											1.5			
Falkenbergia rufolanosa-stadium														
Feldmannia cf. *irregularis*														
Feldmannia lebelii		0.1												
Feldmannia sp.											20			
Flabellia petiolata	0.2								0.7		0.5			
Gastroclonium clavatum														

	S-1	S-2	S-3	S-4	S-5	S-6	S-7	S-8	S-9	S-10	S-11	S-12	S-13	S-14
Gayliella flaccida					0.1						0.2			
Gelidiella sp.														
Gelidium crinale			1.3											
Gelidium latifolium														
Gelidium pusillum														
Gelidium spathulatum														
Grateloupia dichotoma														
Halimeda tuna	0.6													
Haliptilon virgatum	8	3.5	135	15	1870	94	5.3	374	1489	483	114	7	1.5	15
Halopithys incurva														
Halopteris filicina						1								
Halurus flosculosus														0.1
Herposiphonia secunda	2			4			0.1	1			4		1	1
Heterosiphonia crispella														
Hildenbrandia crouaniorum			5											
Hydrolithon farinosum		20	225	40	40	110	40	250	140	110	60	42	150	60
Hypnea musciformis														
Hypnea sp.														
Hypoglossum hypoglossoides														
Janczewskia verrucaeformis														
Jania adhaerens	0.5	1									1			
Jania longifurca														
Jania rubens		1				4	0.7	9	60				2.5	3
Jania rubens v. *corniculata*														
Jania sp.														
Laurencia cf. *obtusa*														1.5
Laurencia chondrioides														
Laurencia microcladia			0.2	0.2	1		1.5	154				3	11	
Laurencia sp. 1								2				0.5	0.2	
Laurencia sp. 2														
Laurencia sp. 3														
Laurencia sp. 4														
Lejolisia mediterranea														

	S-1	S-2	S-3	S-4	S-5	S-6	S-7	S-8	S-9	S-10	S-11	S-12	S-13	S-14
Leptofauchea coralligena														
Liebmannia leveillei														
Lithophyllum incrustans														
Lithophyllum pustulatum														
Lithophyllum sp.														
Lobophora variegata														
Lophosiphonia cristata												1	3	
Lophosiphonia obscura														
Lophosiphonia reptabunda														
Lophosiphonia sp.														
Melobesiae unidentified														
Mesophyllum alternans														
Mesophyllum sp.														
Miryactula rivulariae														
Myriogramme sp.														
Neogoniolithon brassica-florida	500	250	420	450	62	460	94	187,5	437	8	250	562	437	160
Nitophyllum micropunctatum														
Osmundea truncata													0.5	
Padina pavonica	90		7.4	5			0.7				0.5	2.5	0.5	
Palisada papillosa			4											
Palisada patentirramea														
Palisada tenerrima													1	
Parviphycus tenuissimus			2			1								
Pedobesia lamourouxii														
Peyssonnelia cf. *armorica*														
Peyssonnelia dubyi														
Peyssonnelia harveyana														
Peyssonnelia rosa-marina					35									
Peyssonnelia sp.														
Peyssonnelia squamaria														
Phyllophora crispa														
Plocamium cartilagineum														
Polysiphonia flocculosa														

	S-1	S-2	S-3	S-4	S-5	S-6	S-7	S-8	S-9	S-10	S-11	S-12	S-13	S-14
Polysiphonia opaca													9	
Polysiphonia scopulorum														
Polysiphonia setigera														
Polysiphonia sp. 1											0.2			
Polysiphonia sp. 2													4	
Polysiphonia sp. 3														
Polysiphonia sp. 4														
Polystrata fosliei														
Porphyra sp.														
Pseudochlorodesmis furcellata														
Pseudolithoderma adriaticum		25	10	60	240	40	102.5	187.5		3	62.5	31	3	80
Pterocladiella melanoidea														
Rhodophyllis divaricata														
Rhodophyllis strafforelloi														
Rytiphloea tinctoria	0.2						401					38.8	721	162
Sargassum vulgare														
Siphonocladus pusillus														
Spermothamnion irregulare														
Spermothamnion repens		4												
Spermothamnion sp.														
Sphacelaria cirrosa	320	1000	60	50	15	170	0.7	90			2	42		60
Sphacelaria rigidula														
Spyridia filamentosa												0.2	2	20
Stypocaulon scoparium	49		0.3				2.3					2.1		
Taonia atomaria														
Titanoderma trochanter														
Ulva multiramosa														
Ulva pseudolinza														
Ulva ramulosa														
Ulva rigida														
Ulva sp.														
Valonia aegagropila			65	4										
Valonia utricularis			225	15		171	4.5				1		1.5	0.5

	S-1	S-2	S-3	S-4	S-5	S-6	S-7	S-8	S-9	S-10	S-11	S-12	S-13	S-14
Vickersia baccata														
Womersleyella setacea														
Wrangelia penicillata														0.1
Wurdermannia miniata														
Sessile macroinvertebrates														
Aetea anguina		5												
Aglaophenia kirchenpaueri		0.1									1.5			
Aiptasia diaphana				1										
Amathia lendigera											2			
Amathia sp.														
Anemonia sulcata														
Arca noae														
Balanophyllia europaea				4										
Campanulariidae (unidentified)		3												
Chiton sp.										1.5				
Chlidonia pyriformis														
Clavularia crassa														
Crisia sp.														
Cystodites dellechiajei														
Didemnidae unidentified 1			0.4											
Didemnidae unidentified 2														
Didemnidae unidentified 3														
Didemnidae unidentified 4													2.5	0.5
Didemnum granulosum														
Didemnum maculosum														
Encrusting bryozoan (unidentified)														
Filicrisia geniculata														
Guanchia sp.														
Haliclona sp.														
Hymedesmia versicolor														
Ircinia fasciculata				4										
Ircinia variabilis														
Ostraea edulis														

	S-1	S-2	S-3	S-4	S-5	S-6	S-7	S-8	S-9	S-10	S-11	S-12	S-13	S-14
Pherusella tubulosa														
Porifera unidentified														
Sarcotragus spinosula														
Scrupocellaria sp.														
Spondylus spinosus														
Turbicellepora magnicostata											2	3		

Appendix 1.4. Species horizontal cover (in cm^2) at the sites from Sardinia.

	I-1	I-2	I-3	I-4	I-5	I-6	I-7	I-8	I-9	I-10	I-11	I-12	I-13	I-14	I-15	I-16	I-17
Cyanobacteriae																	
Calothrix confervicola										3		1					
Lyngbya semiplena																	
Lyngbya sp.																	
Phormidium sp.																	
Symploca hydnoides																	
Actiniaria (unidentified)																	
Macroalgae																	
Acetabularia acetabulum				2												33.25	
Acrothamnion preissii			1.5														
Aglaothamnion scopulorum			0.3		0.1	0.8	2			0.1			0.8	5	70		
Aglaozonia parvula (stadium)																	
Alsidium corallinum	26																
Alsidium helminthochorton																	
Amphiroa cryptarthrodia																	
Amphiroa rigida												5	6.25				
Anadyomene stellata																	
Anotrichium barbatum																	
Boergeseniella fruticulosa		135	120	100	6	375	20	90	190	80				40			
Botryocladia botryoides																	
Botryocladia sp.															9.7	3	
Bryopsis duplex						0.1											
Bryopsis sp.									0.1								
Callithamnion corymbosum																	
Caulerpa racemosa v. *cylindracea*																	
Ceramiaceae unidentified																	
Ceramium ciliatum																	
Ceramium circinatum																	
Ceramium codii																	
Ceramium deslongchampsii							0.1									0.2	
Ceramium diaphanum									0.5								0.3
Ceramium siliquosum v. *zostericola*																	

	I-1	I-2	I-3	I-4	I-5	I-6	I-7	I-8	I-9	I-10	I-11	I-12	I-13	I-14	I-15	I-16	I-17
Ceramium sp.						0.1											
Ceramium tenerrimum				0.3			0.1							1		0.5	
Chaetomorpha linum	1	0.5		0.8					1.1	0.5	1.9	0.3		0.1		1	2.5
Champia parvula		0.2	1		5		0.3							0.1			
Chondracanthus acicularis		3						6	8		6						
Chondria capillaris																	0.6
Chondria dasyphylla																	
Chondria sp.																	
Choreonema thuretii											0.1						
Chrisonephos lewisii																	
Chylocladia verticillata					17	2.3	10						1.5	12			
Cladophora albida										3							
Cladophora cf. *sericea*																	
Cladophora coelothrix																3.2	
Cladophora dalmatica																	10
Cladophora hutchinsiae	6			8					1		1.5						
Cladophora laetevirens																	
Cladophora lehmanniana																	
Cladophora nigrescens		0.8															
Cladophora pellucida																	
Cladophora prolifera	1.8	11	15.5	8							13.5	2		6		40	
Cladophora rupestris																	
Cladophora socialis																	
Cladophora sp. 1						0.2	15							3	40	50.75	
Cladophora sp. 2																	
Cladophora vagabunda				20													
Cladophoropsis membranacea																	
Cladosiphon sp.																	
Cladostephus spongiosus				8.5													
Codium bursa																	
Contarinia peyssonneliaeformis																	
Corallina elongata	0.2	412	385	12	432	248	1.5	125	40	2	55.5	24	15	15		0.1	
Corallophila cinnabarina														0.1			

	I-1	I-2	I-3	I-4	I-5	I-6	I-7	I-8	I-9	I-10	I-11	I-12	I-13	I-14	I-15	I-16	I-17
Crouania attenuata														0.1			0.2
Cryptonemia lomation										1							
Cystoseira balearica																	
Cystoseira barbata	1505			132													
Cystoseira compressa v. *compressa*						45	252			6	25		25		70	100	
Cystoseira compressa v. *pustulata*																	
Cystoseira corniculata																	
Cystoseira crinita	1071	2550	1581	3105	1862	1913	1428	2244	1862	2040	2372	2474	1798	2015	1531	1454	2372
Cystoseira foeniculacea v. *tenuiramosa*																	
Cystoseira jabukae																	
Cystoseira spinosa v. *tenuior*																	
Dasya corymbifera			1			0.8				8				2	3.5		1.2
Dasya rigidula					0.2						0.2						
Dasycladus vermicularis	4																
Delesseriaceae unidentified 1																	
Delesseriaceae unidentified 2																	
Dictyopteris polypodioides		1.5	15	45	30			0.6			22				328.5		
Dictyota dichotoma	16			25	15	0.6	7	0.5	35		30	2.5			191.3		
Dictyota dichotoma v.*intricata*	6			12.5						30							
Dictyota fasciola		4.5															
Dictyota spiralis	3												0.6				1.2
Dictyotaceae unidentified									0.5					5			
Digenea simplex																	
Dipterosiphonia rigens																	
Discosporangium mesarthrocarpum																	
Encrusting Corallinaceae (unidentified)																	
Erythrocystis montagnei																	

	I-1	I-2	I-3	I-4	I-5	I-6	I-7	I-8	I-9	I-10	I-11	I-12	I-13	I-14	I-15	I-16	I-17
Falkenbergia cf. *hillebrandii*-stadium																	
Falkenbergia rufolanosa-stadium																	
Feldmannia cf. *irregularis*																	
Feldmannia lebelii																	
Feldmannia sp.																	
Flabellia petiolata	25	54								1					12		
Gastroclonium clavatum	0.5					6											
Gayliella flaccida																0.2	0.3
Gelidiella sp.																	
Gelidium crinale		1.5							187								
Gelidium latifolium																	
Gelidium pusillum				20		84.5		15					0.4		19.5	62.5	
Gelidium spathulatum																	
Grateloupia dichotoma																	
Halimeda tuna	327	40			1	18	1.5		37	80	16				105	121.5	
Haliptilon virgatum	396	481	136	75	15	134	14	28	45	90	209	2.5	30	112	67.3	283.5	248
Halopithys incurva																	
Halopteris filicina																	
Halurus flosculosus																	
Herposiphonia secunda					0.3	1	1			0.1				0.1		0.7	
Heterosiphonia crispella																	
Hildenbrandia crouaniorum																	
Hydrolithon farinosum	140	76	16	15	56	57	71.4	15	9	102	24	25	18	20	90	29	48
Hypnea musciformis																	
Hypnea sp.						0.2											
Hypoglossum hypoglossoides						0.2											
Janczewskia verrucaeformis																	
Jania adhaerens																	
Jania longifurca											4						
Jania rubens		255			255						13					50	
Jania rubens v. *corniculata*																	
Jania sp.																	

	I-1	I-2	I-3	I-4	I-5	I-6	I-7	I-8	I-9	I-10	I-11	I-12	I-13	I-14	I-15	I-16	I-17
Laurencia cf. *obtusa*									79								
Laurencia chondrioides																	
Laurencia microcladia																	
Laurencia sp. 1	1		63			1				0.2				39			13
Laurencia sp. 2						12	5							2	5	7	
Laurencia sp. 3																	
Laurencia sp. 4																	
Lejolisia mediterranea																	
Leptofauchea coralligena															20		
Liebmannia leveillei											0.1						
Lithophyllum incrustans																	
Lithophyllum pustulatum																	
Lithophyllum sp.																	
Lobophora variegata																	
Lophosiphonia cristata				0.3													
Lophosiphonia obscura																0.4	
Lophosiphonia reptabunda																	
Lophosiphonia sp.																	
Melobesiae unidentified										6							
Mesophyllum alternans																	
Mesophyllum sp.																	
Miryactula rivulariae		0.5								0.1							0.5
Myriogramme sp.													0.3				
Neogoniolithon brassica-florida	35		250	62.5	94	62.5	312.5		375	94	190	330	437	93.75	262.5	187.5	145
Nitophyllum micropunctatum	5			6	10	0.1	1		6	40	2.5			2	25		
Osmundea truncata								1	3	0.2			2	0.5			
Padina pavonica	6.3	7.5	1.5	3.5			54									10.5	
Palisada papillosa																6	
Palisada patentirramea																	
Palisada tenerrima																	
Parviphycus tenuissimus										4	6	1.2		63			
Pedobesia lamourouxii																	
Peyssonnelia cf. *armorica*																	

	I-1	I-2	I-3	I-4	I-5	I-6	I-7	I-8	I-9	I-10	I-11	I-12	I-13	I-14	I-15	I-16	I-17
Peyssonnelia dubyi																	
Peyssonnelia harveyana																	
Peyssonnelia rosa-marina	5																
Peyssonnelia sp.			3	5	6		18					55	10	12	40		
Peyssonnelia squamaria			38		30					3				9	35		
Phyllophora crispa																	
Plocamium cartilagineum																	
Polysiphonia flocculosa																	
Polysiphonia opaca																	
Polysiphonia scopulorum																	
Polysiphonia setigera																	
Polysiphonia sp. 1																	
Polysiphonia sp. 2																	
Polysiphonia sp. 3																	
Polysiphonia sp. 4																	
Polystrata fosliei																	
Porphyra sp.																	
Pseudochlorodesmis furcellata																	
Pseudolithoderma adriaticum																	
Pterocladiella melanoidea																	
Rhodophyllis divaricata																	
Rhodophyllis strafforelloi			2.5		1		2	0.6	4	4	2	3		2.5			
Rytiphloea tinctoria																	
Sargassum vulgare			40														
Siphonocladus pusillus																	
Spermothamnion irregulare																	
Spermothamnion repens																	
Spermothamnion sp.					0.5												
Sphacelaria cirrosa	42.5	112	1186	2050	931	57	142.8	1833	1489	102	403	30	9			0.5	1889
Sphacelaria rigidula																	
Spyridia filamentosa																	
Stypocaulon scoparium	4		5	100		4			0.3					0.8	1.5		
Taonia atomaria															4		

	I-1	I-2	I-3	I-4	I-5	I-6	I-7	I-8	I-9	I-10	I-11	I-12	I-13	I-14	I-15	I-16	I-17
Titanoderma trochanter																	
Ulva multiramosa				0.1													
Ulva pseudolinza																	
Ulva ramulosa																	
Ulva rigida						3	1	10	40	9	7	78	50				0.6
Ulva sp.																	
Valonia aegagropila	374			40		15	6	42	13	20				2		195	
Valonia utricularis		101	7.5		23	5	1	55	9	10	13.5	60	37	3	10	6	0.7
Vickersia baccata					0.1	0.1											
Womersleyella setacea																	
Wrangelia penicillata																	
Wurdermannia miniata																	
Sessile macroinvertebrates																	
Aetea anguina																	
Aglaophenia kirchenpaueri																	
Aiptasia diaphana																	
Amathia lendigera																	
Amathia sp.	0.2															80	93.5
Anemonia sulcata																	
Arca noae																	
Balanophyllia europaea																	
Campanulariidae (unidentified)																	
Chiton sp.																	
Chlidonia pyriformis																	
Clavularia crassa																	
Crisia sp.					3												
Cystodites dellechiajei													90				
Didemnidae unidentified 1																	
Didemnidae unidentified 2																	
Didemnidae unidentified 3																	
Didemnidae unidentified 4																	
Didemnum granulosum																	

	I-1	I-2	I-3	I-4	I-5	I-6	I-7	I-8	I-9	I-10	I-11	I-12	I-13	I-14	I-15	I-16	I-17
Didemnum maculosum																	
Encrusting bryozoan (unidentified)																	
Filicrisia geniculata				1													0.7
Guanchia sp.																	
Haliclona sp.																	
Hymedesmia versicolor																	
Ircinia fasciculata																	
Ircinia variabilis	20	8		36													
Ostraea edulis		3															
Pherusella tubulosa		22			30												
Porifera unidentified																	
Sarcotragus spinosula																	
Scrupocellaria sp.	25	48	161	0.7			0.5				86	4.5	16	3			
Spondylus spinosus																	
Turbicellepora magnicostata																	

Appendix 1.5. Species horizontal cover (in cm^2) at the sites 1 to 17 from Istria.

	I-18	I-19	I-20	I-21	I-22	I-23	I-24	I-25	I-26	Cy-1	Cy-2	Do-3	Do-4	Ly-1	Ly-2	Ly-3
Cyanobacteriae																
Calothrix confervicola			109	56												
Lyngbya semiplena																
Lyngbya sp.																
Phormidium sp.																
Symploca hydnoides																
Actiniaria (unidentified)															3.1	
Macroalgae																
Acetabularia acetabulum							0.2		0.2	0.8						
Acrothamnion preissii																
Aglaothamnion scopulorum	123.2	0.1	5													
Aglaozonia parvula (stadium)						8										
Alsidium corallinum					0.2											
Alsidium helminthochorton	13				0.5											
Amphiroa cryptarthrodia																
Amphiroa rigida				0.3							0.8		4.1			
Anadyomene stellata										0.8						
Anotrichium barbatum																
Boergeseniella fruticulosa				25						0.8					1.6	
Botryocladia botryoides														54.7	7.8	
Botryocladia sp.																
Bryopsis duplex																
Bryopsis sp.																
Callithamnion corymbosum																
Caulerpa racemosa v. *cylindracea*										10.9						
Ceramiaceae unidentified																
Ceramium ciliatum					21											
Ceramium circinatum																
Ceramium codii																
Ceramium deslongchampsii							0.1									
Ceramium diaphanum	3				52										1.6	
Ceramium siliquosum v. *zostericola*																

	I-18	I-19	I-20	I-21	I-22	I-23	I-24	I-25	I-26	Cy-1	Cy-2	Do-3	Do-4	Ly-1	Ly-2	Ly-3
Ceramium sp.							0.1									
Ceramium tenerrimum			1													
Chaetomorpha linum	0.2				1			0.1	0.1							
Champia parvula						0.1	0.1									
Chondracanthus acicularis							0.5									
Chondria capillaris																
Chondria dasyphylla																
Chondria sp.																
Choreonema thuretii											0.2					1.6
Chrisonephos lewisii																
Chylocladia verticillata				0.3	2											
Cladophora albida																
Cladophora cf. *sericea*						10		31								
Cladophora coelothrix						4			5							
Cladophora dalmatica	1.5									1.6						
Cladophora hutchinsiae									23							
Cladophora laetevirens										1.6						
Cladophora lehmanniana																
Cladophora nigrescens																
Cladophora pellucida											28.1					
Cladophora prolifera					30	8	33	13	15	3.1						
Cladophora rupestris																
Cladophora socialis																
Cladophora sp. 1			20			0.5	136									
Cladophora sp. 2																
Cladophora vagabunda																
Cladophoropsis membranacea																
Cladosiphon sp.																
Cladostephus spongiosus																
Codium bursa																
Contarinia peyssonneliaeformis																
Corallina elongata	3	2	15	3	7	14	3	12	7		12.5		11.7			14.1

	I-18	I-19	I-20	I-21	I-22	I-23	I-24	I-25	I-26	Cy-1	Cy-2	Do-3	Do-4	Ly-1	Ly-2	Ly-3
Corallophila cinnabarina																
Crouania attenuata	2	0.5														
Cryptonemia lomation															46.9	
Cystoseira balearica																
Cystoseira barbata																
Cystoseira compressa v. *compressa*				98		1.5		1			81.3					3.6
Cystoseira compressa v. *pustulata*									206.5							
Cystoseira corniculata								1.5								
Cystoseira crinita	1767	1326	3621	2805	1449	1811	1173	1581	1505	1248	2489	1392	1498	1938	1688	1764
Cystoseira foeniculacea v. *tenuiramosa*																
Cystoseira jabukae																
Cystoseira spinosa v. *tenuior*																
Dasya corymbifera		0.3				150	1				1.6		109	139.1	87.5	67.2
Dasya rigidula								0.7								4.7
Dasycladus vermicularis					0.7	2	3	0.8				21.9	233			
Delesseriaceae unidentified 1																
Delesseriaceae unidentified 2																
Dictyopteris polypodioides						120		4.5							156.3	26.6
Dictyota dichotoma					9	45	3.5	1								3.1
Dictyota dichotoma v.*intricata*																
Dictyota fasciola									28							20.3
Dictyota spiralis																
Dictyotaceae unidentified	0.5			0.7												
Digenea simplex																
Dipterosiphonia rigens																
Discosporangium mesarthrocarpum																
Encrusting Corallinaceae (unidentified)												3.1		93.8		
Erythrocystis montagnei																
Falkenbergia cf. *hillebrandii*-stadium											0.2					
Falkenbergia rufolanosa-stadium																
Feldmannia cf. *irregularis*																

	I-18	I-19	I-20	I-21	I-22	I-23	I-24	I-25	I-26	Cy-1	Cy-2	Do-3	Do-4	Ly-1	Ly-2	Ly-3
Feldmannia lebelii	35.2		2													
Feldmannia sp.																
Flabellia petiolata			25		75	15	46	279	134	35.9				23.4		
Gastroclonium clavatum																
Gayliella flaccida	0.5	0.3		0.2	10					3.1						3.1
Gelidiella sp.																
Gelidium crinale																
Gelidium latifolium																
Gelidium pusillum		0.3			0.2		2.5		0.3							
Gelidium spathulatum																
Grateloupia dichotoma																
Halimeda tuna		36	77	112	60	160	16.25	336	250	7.8						
Haliptilon virgatum	72	465	66	282.5	85.25	437	433.5	178.5	242	719		1013		39.1	40.6	1688
Halopithys incurva																
Halopteris filicina																
Halurus flosculosus																
Herposiphonia secunda						8	0.2	1	2		23.4		12.5	234.4	46.9	226.6
Heterosiphonia crispella																
Hildenbrandia crouaniorum																
Hydrolithon farinosum	70	13	109	70.5	72.45	18		8	30							
Hypnea musciformis																
Hypnea sp.																
Hypoglossum hypoglossoides														62.5		
Janczewskia verrucaeformis													1.6			
Jania adhaerens																
Jania longifurca																
Jania rubens							3				7.8					7.8
Jania rubens v. *corniculata*														562.5		
Jania sp.				2.7												
Laurencia cf. *obtusa*																
Laurencia chondrioides																
Laurencia microcladia																

	I-18	I-19	I-20	I-21	I-22	I-23	I-24	I-25	I-26	Cy-1	Cy-2	Do-3	Do-4	Ly-1	Ly-2	Ly-3
Laurencia sp. 1	20	25	9	7	32	0.1										
Laurencia sp. 2			0.8	3			1		0.4							
Laurencia sp. 3										3.1					7.8	
Laurencia sp. 4													7.8			
Lejolisia mediterranea																
Leptofauchea coralligena																
Liebmannia leveillei																
Lithophyllum incrustans														39.1		
Lithophyllum pustulatum																
Lithophyllum sp.																
Lobophora variegata											21.9					13.44
Lophosiphonia cristata																
Lophosiphonia obscura							0.1									
Lophosiphonia reptabunda																
Lophosiphonia sp.																
Melobesiae unidentified																
Mesophyllum alternans																
Mesophyllum sp.										78.1						
Miryactula rivulariae				3												
Myriogramme sp.																
Neogoniolithon brassica-florida	290	187	125	22.5	187.5	156.3	93.75	250	406.3	125	62.5		453	31.3		390.6
Nitophyllum micropunctatum		1			2.5				4							
Osmundea truncata	1	3		1	7											
Padina pavonica			0.5		0.6	2	1	1	18	9.4	9.4					
Palisada papillosa																
Palisada patentirramea										7.8			31.3			
Palisada tenerrima																
Parviphycus tenuissimus							10									
Pedobesia lamourouxii									11.7							
Peyssonnelia cf. *armorica*																
Peyssonnelia dubyi																
Peyssonnelia harveyana											6.6					

	I-18	I-19	I-20	I-21	I-22	I-23	I-24	I-25	I-26	Cy-1	Cy-2	Do-3	Do-4	Ly-1	Ly-2	Ly-3
Peyssonnelia rosa-marina		88								7.8			85.9			
Peyssonnelia sp.	105	94	250	187.5					12							
Peyssonnelia squamaria		5						3								
Phyllophora crispa																
Plocamium cartilagineum																
Polysiphonia flocculosa																
Polysiphonia opaca																
Polysiphonia scopulorum																
Polysiphonia setigera																
Polysiphonia sp. 1																
Polysiphonia sp. 2																
Polysiphonia sp. 3																
Polysiphonia sp. 4										0.3	0.2					
Polystrata fosliei																
Porphyra sp.																
Pseudochlorodesmis furcellata																
Pseudolithoderma adriaticum																
Pterocladiella melanoidea																
Rhodophyllis divaricata																
Rhodophyllis strafforelloi			3	1.5	4	6	1.6	2								
Rytiphloea tinctoria			40									198				
Sargassum vulgare											23.4				18.7	
Siphonocladus pusillus										3.1						
Spermothamnion irregulare																
Spermothamnion repens						0.3				0.6						
Spermothamnion sp.																
Sphacelaria cirrosa	37			0.5	3	482.6	470.7	672.4	454	46.9	23.4	4.7	18.8			
Sphacelaria rigidula																
Spyridia filamentosa																
Stypocaulon scoparium	2				0.4	1.5	10									
Taonia atomaria		2.5							1.5							73.4
Titanoderma trochanter														3.1		

	I-18	I-19	I-20	I-21	I-22	I-23	I-24	I-25	I-26	Cy-1	Cy-2	Do-3	Do-4	Ly-1	Ly-2	Ly-3
Ulva multiramosa																
Ulva pseudolinza																
Ulva ramulosa																
Ulva rigida					1											
Ulva sp.	0.2															
Valonia aegagropila			9	40		20										
Valonia utricularis	2	19.25	6	3	0.3	1	30	20	70							
Vickersia baccata																
Womersleyella setacea										6.3						
Wrangelia penicillata																
Wurdermannia miniata																
Sessile macroinvertebrates																
Aetea anguina																
Aglaophenia kirchenpaueri										4.7	39.1			34.4	39.1	
Aiptasia diaphana																
Amathia lendigera																
Amathia sp.			2	29		70	60	8	5							
Anemonia sulcata																
Arca noae																
Balanophyllia europaea																
Campanulariidae (unidentified)																
Chiton sp.																
Chlidonia pyriformis																46.9
Clavularia crassa											25			7.8	26.6	3.1
Crisia sp.									1	1.6	31.3			15.6	23.4	14.06
Cystodites dellechiajei	158	13	15	84										6.3	62.5	25
Didemnidae unidentified 1																
Didemnidae unidentified 2																
Didemnidae unidentified 3																
Didemnidae unidentified 4																
Didemnum granulosum										15.6	37.5					
Didemnum maculosum																

	I-18	I-19	I-20	I-21	I-22	I-23	I-24	I-25	I-26	Cy-1	Cy-2	Do-3	Do-4	Ly-1	Ly-2	Ly-3
Encrusting bryozoan (unidentified)														12.5	23.44	
Filicrisia geniculata				0.4	1	0.5	0.1									
Guanchia sp.										1.6						
Haliclona sp.																
Hymedesmia versicolor																
Ircinia fasciculata																
Ircinia variabilis										7.8	23.1					
Ostraea edulis						3			4							
Pherusella tubulosa																
Porifera unidentified																
Sarcotragus spinosula										7						
Scrupocellaria sp.				48		240			1							
Spondylus spinosus														23.4		
Turbicellepora magnicostata												1.6				39.06

Appendix 1.6. Species horizontal cover (in cm^2) at the sites 18 to 26 from Istria and the sites from Cyclades, Dodecanese and Lycia.

Appendix 2

Values of environmental factors used in Chapter 3

Details on how the parameters were measured are given in Table 1 of chapter 3. MF1: Morphological factor 1 (% of rocky littoral); MF2: Morphological factor 2 (littoral height); MF3: Morphological factor 3 (% of coastline constituted by blocks); BF1: Bottom factor 1 (% of vegetated bottom); BF2: Bottom factor 2 (% of bottom covered by seagrass); BF3: Bottom factor 3 (% of rocky bottom); Urb Dist (Urbanisation distance).

Site	Slope	Exposure	MF1	MF2	MF3	BF1	BF2	BF3	Urb Dist	$[PO_4]$	$[NH_4]$	$[NO_2]$	$[NO_3]$	$[SiO_4]$
1	32.22	26	100	1.90	30.00	100.00	16.58	83.42	1000	0.04	0.42	0.04	0.28	1.38
2	34.86	68	100	1.00	50.00	90.11	39.25	50.86	1	0.05	0.34	0.04	0.52	1.09
3	37.60	41	100	1.00	1.00	69.84	32.08	37.75	1	0.05	0.30	0.05	0.31	0.94
4	34.67	50	41	1.00	1.00	21.44	12.29	9.16	1	0.06	0.33	0.02	0.28	0.67
5	15.00	55	100	1.00	1.00	100.00	1.00	100.00	400	0.04	0.82	0.03	0.32	0.68
6	51.97	12	100	1.90	30.00	89.96	74.41	15.54	170	0.08	1.26	0.03	0.52	1.37
7	40.84	13	70	1.14	44.29	19.72	8.69	11.03	1	0.08	0.55	0.03	0.49	1.16
8	21.94	1	75	1.40	26.67	65.65	21.94	43.71	730	0.07	0.69	0.04	0.34	0.99
9	38.77	1	85	1.35	5.88	70.21	47.77	22.44	1300	0.05	0.57	0.05	0.37	0.76
10	28.78	14	80	1.00	18.75	86.12	37.63	48.49	830	0.04	0.45	0.07	0.31	0.83
11	15.00	1	65	1.00	38.46	71.85	50.26	21.59	1200	0.04	0.99	0.06	0.37	0.79
12	15.00	48	60	1.00	100.00	32.46	17.00	15.46	1800	0.04	0.86	0.06	0.21	0.72
13	29.41	43	100	1.10	84.00	98.98	54.31	44.68	3100	0.04	0.42	0.06	0.22	0.71
14	17.54	63	85	1.18	69.41	100.00	62.83	37.17	3500	0.07	0.57	0.03	0.26	0.49
15	20.56	48	70	1.00	28.57	34.74	2.84	31.90	4200	0.09	1.04	0.03	0.27	0.54
16	22.16	17	85	1.12	29.41	100.00	31.90	68.10	4800	0.10	0.77	0.03	0.18	0.91
17	32.46	44	75	1.00	97.33	47.31	5.99	41.31	2000	0.07	0.72	0.02	0.11	0.33
18	28.43	9	80	1.00	80.00	36.58	14.99	21.59	1700	0.07	0.89	0.02	0.18	0.52
19	24.29	1	29	1.01	27.00	100.00	100.00	1.00	200	0.08	1.03	0.06	0.36	0.76
20	32.55	1	30	1.00	10.00	100.00	100.00	1.00	200	0.06	1.15	0.05	0.30	0.75
21	51.31	10	50	2.28	56.00	34.18	25.78	8.40	1	0.07	0.77	0.05	1.03	1.34
22	57.28	5	70	1.93	28.57	18.75	2.46	16.29	40	0.07	0.64	0.03	0.53	1.28
23	49.10	28	100	1.10	91.00	95.65	22.22	73.43	760	0.06	0.88	0.05	0.22	0.61
24	15.00	1	60	1.08	90.00	17.03	8.55	8.48	1000	0.04	0.99	0.04	0.34	0.91
25	56.09	1	80	1.69	25.00	75.55	56.07	19.47	2500	0.11	1.26	0.06	0.25	1.85
26	24.27	1	75	1.00	40.00	64.76	47.69	17.07	600	0.17	0.91	0.02	0.18	0.42
27	43.40	1	90	1.00	11.11	64.05	41.48	22.56	700	0.11	1.01	0.03	0.22	0.64
28	20.27	1	85	1.00	47.06	96.09	74.20	21.88	1000	0.08	0.68	0.03	0.20	1.53

Site	Slope	Exposure	MF1	MF2	MF3	BF1	BF2	BF3	Urb Dist	[PO_4]	[NH_4]	[NO_2]	[NO_3]	[SiO_4]
29	15.00	1	50	1.00	52.94	100.00	96.21	3,79	1100	0.10	0.81	0.01	0.19	1.66
30	15.00	1	10	1.00	9.33	100.00	100.00	1.00	1200	0.05	0.47	0.02	0.16	2.19
31	15.00	1	25	1.00	21.05	93.55	92.14	1.41	1300	0.06	0.40	0.04	0.22	1.01
32	15.00	1	15	1.00	12.00	100.00	100.00	1.00	1100	0.05	0.97	0.04	0.17	1.19
33	15.00	1	8	1.00	4.00	63.83	63.83	1.00	800	0.07	0.45	0.03	0.17	0.67
34	15.00	1	2	1.00	1.00	92.54	92.54	1.00	700	0.08	0.75	0.05	0.20	1.17
35	31.45	46	95	1.00	100.00	100.00	40.23	59.77	600	0.11	0.91	0.02	0.22	1.34
36	23.09	23	100	1.00	30.00	31.72	1.00	31.72	800	0.04	0.92	0.03	0.20	0.89
37	32.82	35	100	1.00	54,00	100.00	1.00	100.00	1500	0.01	0.51	0.04	0.22	0.53
38	37.40	1	100	1.40	20.00	100.00	1.00	100.00	1600	0.06	0.73	0.04	0.25	0.80
39	35.25	1	97	1.00	7.22	100.00	26.56	73.44	1800	0.03	0.65	0.05	0.32	0.97
40	48.05	15	85	1.06	58.82	72.09	33.88	38.21	3000	0.06	0.63	0.03	0.28	0.79
41	15.00	3	65	1.01	59.60	89.49	78.01	11.48	2500	0.11	0.62	0.03	0.17	0.23
42	15.00	1	75	1.00	48.00	69.29	13.07	56.22	2900	0.02	0.75	0.04	0.31	0.86
43	19.27	70	40	1.00	87.50	42.92	1.00	42.92	2900	0.07	0.86	0.03	0.16	0.86
44	24.80	48	70	1.00	50.00	100.00	1.00	100.00	3500	0.09	1.03	0.02	0.16	0.80
45	44.82	39	70	1.01	50.00	87.89	9.04	78.85	4500	0.05	0.80	0.07	0.70	1.02
46	20.80	42	95	1.00	68.42	100.00	32.29	67.71	4800	0.02	0.63	0.04	0.15	0.77
47	41.61	1	75	1.00	65.33	60.90	16.44	44.46	5300	0.03	0.47	0.03	0.18	0.70
48	30.72	27	70	1.00	28.57	15.36	1.00	15.05	5500	0.09	0.70	0.03	0.21	0.63
49	20.58	28	100	1.05	75.00	89.23	55.04	34.19	6800	0.12	0.77	0.05	0.12	0.75
50	53.55	20	85	1.24	88.24	100.00	3.55	96.45	7800	0.06	0.87	0.04	0.19	0.74
51	30.99	34	100	1.60	60.00	100.00	33.00	67.00	7900	0.07	0.78	0.03	0.11	0.49
52	39.07	74	50	1.00	70.00	22.52	1.00	22.52	7300	0.04	0.85	0.03	0.13	0.57
53	66.55	2	70	2.43	14.29	5.70	2.94	2.77	2700	0.09	0.65	0.05	0.27	0.65
54	18.13	33	85	1.12	29.41	6.75	1.37	5.38	2500	0.07	0.77	0.04	0.13	0.43
55	36.90	6	85	1.65	35.29	82.29	41.05	41.23	2000	0.03	0.71	0.05	0.15	0.48
56	31.19	1	85	1.76	41.18	66.56	17.50	49.05	1	0.06	0.95	0.07	7.83	2.77
57	48.81	1	99	3.51	1.00	84.59	59.65	24.94	1	0.09	0.84	0.05	1.13	0.78

Site	Slope	Exposure	MF1	MF2	MF3	BF1	BF2	BF3	Urb Dist	$[PO_4]$	$[NH_4]$	$[NO_2]$	$[NO_3]$	$[SiO_4]$
58	60.38	9	99	2.75	1.00	56.55	56.55	1.00	1	0.06	1.10	0.18	6.77	1.72
59	80.14	3	99	3.00	1.00	91.18	85.63	5.55	1	0.11	1.02	0.06	1.58	1.04
60	89.41	1	96	2.35	1.04	84.63	75.06	9.57	1	0.09	1.11	0.09	3.28	1.58
61	92.91	52	99	2.21	2.02	64.90	64.90	1.00	1	0.14	0.66	0.03	2.63	2.03
62	39.84	1	100	1.60	40.00	1.00	1.00	1.00	1	0.10	0.97	0.11	13.38	3.19
63	91.66	1	95	2.00	1.00	37.84	37.84	1.00	1	0.09	1.06	0.08	7.83	1.92
64	61.87	18	98	1.97	1.02	26.33	11.69	14.65	1	0.11	0.96	0.03	6.99	1.12
65	90.06	1	97,5	1.82	15.38	13.85	10.13	3.73	1	0.16	0.91	0.15	75.26	13.97
66	78.99	4	93	1.99	1.08	48.58	29.46	19.12	1	0.09	0.90	0.03	1.08	1.06
67	18.37	70	36	1.56	13.89	44.32	24.31	20.02	1	0.04	0.71	0.02	0.16	0.76
68	45.00	55	55	1.00	1.00	49.52	36.43	13.09	3500	0.10	1.09	0.03	0.36	1.17
69	75.00	18	90	2.00	1.00	63.97	48.80	15.17	4600	0.07	0.52	0.03	0.36	0.82
70	50.89	15	85	1.71	5.88	44.98	44.98	1.00	3500	0.02	0.39	0.06	0.53	1.15
71	71.80	6	85	2.94	17.65	51.44	23.92	27.52	1700	0.14	0.91	0.04	1.18	1.10
72	74.36	27	70	2.71	35.71	25.78	2.92	22.87	1500	0.11	0.92	0.06	5.98	2.53
73	83.20	19	61	3.08	6.56	28.59	11.33	17.26	1	0.11	0.93	0.03	0.84	1.55
74	92.74	41	85	3.18	5.88	46.79	45.04	1.75	600	0.06	0.66	0.04	0.42	1.09
75	72.20	46	85	2.18	2.35	55.15	51.85	3.30	2200	0.11	0.93	0.07	0.44	1.50
76	74.05	18	95	1.93	6.32	63.21	51.03	12.18	2800	0.02	0.31	0.05	0.36	1.31
77	35.83	57	65	2.15	38.46	39.30	22.12	17.18	2600	0.10	0.87	0.04	0.47	1.09
78	50.14	70	100	1.70	30.00	53.35	23.50	29.86	200	0.08	0.81	0.04	0.36	1.04
79	95.51	17	85	3.44	18.82	28.71	14.73	13.98	1	0.14	1.33	0.21	6.44	5.30
80	66.87	18	95	2.74	36.84	61.28	38.28	23.00	600	0.07	0.79	0.09	6.68	2.28
81	60.49	18	95	2.84	15.79	46.40	21.74	24.66	1	0.14	0.88	0.12	19.94	6.93
82	75.00	8	90	2.00	1.00	48.28	9.90	38.37	70	0.12	0.88	0.03	2.74	1.00
83	75.00	1	95	3.00	1.00	69.06	23.64	45.42	1	0.07	0.69	0.07	7.60	2.64
84	75.00	2	90	2.00	1.00	63.68	27.40	36.28	1	0.15	0.97	0.07	30.57	9.41
85	15.00	1	36	1.56	13.89	84.54	1.00	84.54	1	0.15	1.09	0.05	5.08	1.99
86	25.73	42	80	1.00	1.00	60.65	51.83	8.82	100	0.10	0.74	0.04	4.77	1.36

Site	Slope	Exposure	MF1	MF2	MF3	BF1	BF2	BF3	Urb Dist	[PO_4]	[NH_4]	[NO_2]	[NO_3]	[SiO_4]
87	47.02	1	95	1.00	5.26	50.84	36.42	14.42	1	0.07	0.74	0.06	4.14	1.99
88	20.14	60	85	1.06	1.00	70.52	2.39	68.13	1	0.40	0.33	0.10	4.12	1.72
89	36.30	3	95	2.11	1.00	70.47	4.64	65.84	300	0.14	0.24	0.10	10.81	2.23
90	66.74	1	95	1.84	21.05	71.25	9.04	62.21	1	0.17	1.13	0.18	95.35	18.52
91	45.74	1	100	1.85	30.00	56.76	28.97	27.80	1	0.13	0.88	0.10	2.84	1.07
92	83.14	1	100	2.80	5.00	4.87	1.00	4.87	1	0.11	0.56	0.11	6.14	1.65
93	81.93	1	100	2.40	1.00	1.00	1.00	1.00	1	0.13	0.51	0.08	3.07	1.07
94	87.51	1	100	2.55	1.00	1.00	1.00	1.00	1	0.12	0.57	0.09	3.47	1.04
95	78.96	1	100	1.70	30.00	1.00	1.00	1.00	1	0.11	0.60	0.13	5.75	0.93
96	38.85	1	100	1.55	45.00	1.00	1.00	1.00	1	0.12	0.55	0.17	3.08	1.44
97	15.00	1	100	1.00	100.00	1.00	1.00	1.00	1	0.09	0.92	0.17	1.71	1.07
98	15.00	1	95	1.53	47.37	1.00	1.00	1.00	1	0.07	0.46	0.11	0.86	0.61
99	21.18	1	100	1.00	75.00	1.00	1.00	1.00	1	0.08	0.66	0.08	0.48	0.55
100	15.00	1	100	1.00	100.00	1.00	1.00	1.00	1	0.07	0.51	0.06	0.82	0.46
101	15.00	1	65	1.15	84.62	31.20	24.75	6.45	1	0.06	0.45	0.05	0.28	1.77
102	15.00	1	100	1.50	50.00	1.00	1.00	1.00	300	0.10	0.36	0.04	0.10	0.64
103	15.00	1	80	1.38	68.75	9.58	4.52	5.06	1000	0.08	0.39	0.03	0.12	1.03

Appendix 2.1. Values of the environmental factors used for DistlM and dbRDA analyses.