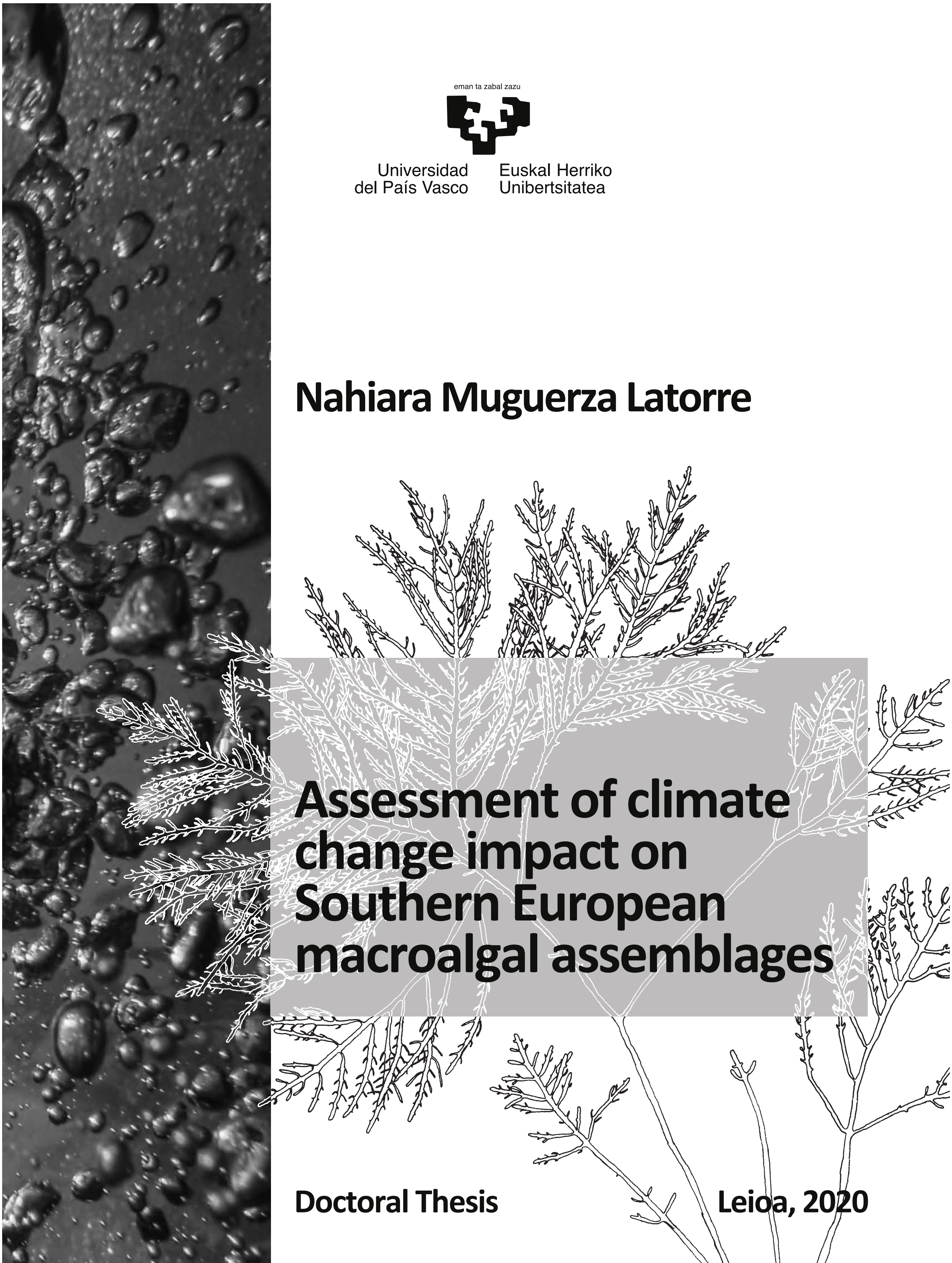

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Universidad del País Vasco
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Assessment of climate change impact on Southern European macroalgal assemblages

Doctoral Thesis
Leioa, 2020

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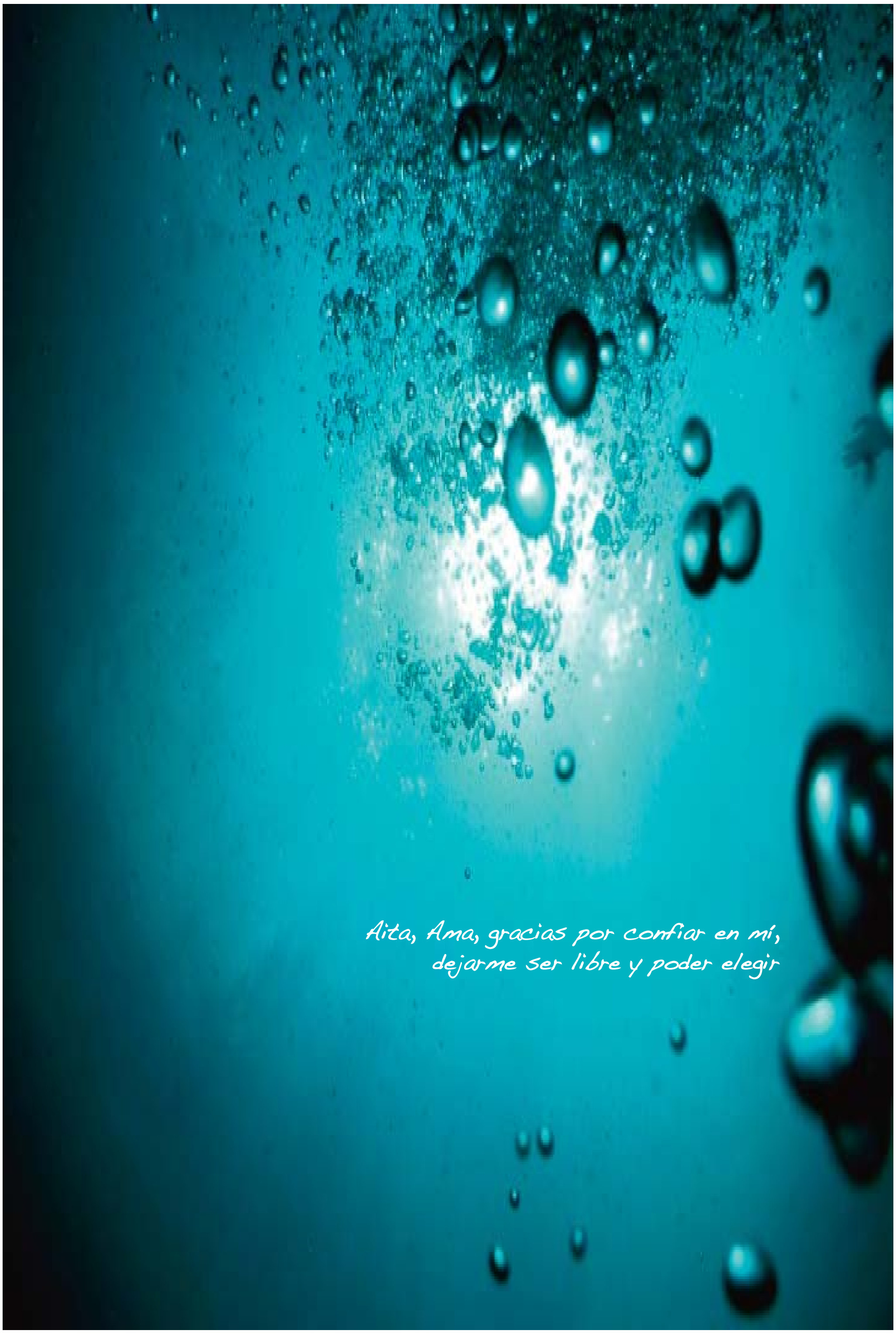

Aita, Ama, gracias por confiar en mí,
dejarme ser libre y poder elegir

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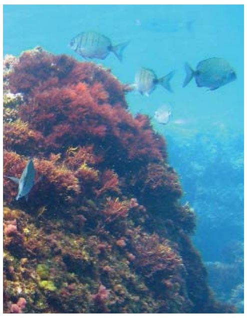

RESUMEN

El marco conceptual que sustenta esta tesis parte del existente escenario de cambio climático, cuyo efecto está ejerciendo una transformación severa en los fondos marinos a escala global. Entre los cambíos más evidentes, destaca el declive de los macrófitos formadores de copa, característicos de los fondos rocosos someros, que están siendo remplazados por algas de menor porte. Estos cambios en la comunidad algal dan lugar a una nueva fase con efectos ecológicos aún desconocidos para el ecosistema costero marino. En concreto, en la costa vasca existen incertidumbres sobre el patrón del cambio, sobre el efecto en las variables biológicas de la comunidad bentónica así como sobre cuales son las variables climáticas que ejercen un mayor efecto en el proceso de transformación de la comunidad fitobentónica. Las investigaciones llevadas a cabo en esta tesis aportan información sobre estas cuestiones, apoyándose en investigaciones previas y llevando a cabo un extenso trabajo de muestreo submareal así como métodos experimentales in situ.

Las macroalgas formadoras de copa dominan y juegan un papel importante en los ecosistemas bentónicos de la mayoría de regiones templadas del planeta. Estos grandes macrófitos perennes mantienen comunidades estructuralmente complejas, en un espacio tridimensional, proporcionando hábitat biogénico y protección para una gran variedad de organismos marinos, sirviendo de cobijo y alimento a muchas especies. Asimismo, transforman sustancialmente el medio físico en el que habitan, ya que modifican las condiciones de luz, el flujo de agua o las tasas de sedimentación. Por lo tanto, las comunidades dominadas por estas especies estructuradoras y formadoras de hábitat constituyen uno de los eslabones clave en el ecosistema costero de latitudes templadas del planeta debido a su alta diversidad y productividad. Además, estas especies biogénicas ofrecen innumerables servicios ecosistémicos, como la reducción de la erosión costera, la fijación de CO_2, reciclaje de nutrientes y sirven de materia prima para diferentes usos humanos e incluso para el control de la calidad del agua, entre otros. De modo que un cambio en su abundancia o la desaparición de las especies formadoras de copa tendrá un efecto en cascada en todo el ecosistema. Por último, también destacar que las algas bentónicas marinas son importantes bioindicadores, constituyendo una herramienta muy útil para evaluar el estado ecológico de los ecosistemas costeros. Esta característica se basa en la naturaleza sésil de las macroalgas y a las diferentes condiciones que son capaces de soportar debido a la sensibilidad de cada especie frente a los cambios en las condiciones ambientales del entorno en el que viven.

En la naturaleza, estos organismos están expuestos a las condiciones ambientales que varían de forma natural a través del tiempo y del espacio, tanto a escala global como a escala local. Así, los factores que naturalmente configuran el clima tales como la temperatura, irradiancia, oleaje, corrientes y pluviosidad determinan la naturaleza de la vegetación de cada región, y por lo tanto también la distribución de las especies de algas formadoras de copa o dosel. Sin embargo, el planeta se enfrenta actualmente a un cambio en el clima inducido por actividades antropogénicas, cuyo ritmo de cambio no tiene precedente. Asi, en las últimas décadas, se han registrado regresiones y desapariciones de macrófitos formadores de copa en muchas zonas a nivel global como consecuencia de cambios en las condiciones climáticas, expansión de especies invasoras, alteraciones y desajustes en los diferentes eslabones de las cadenas tróficas así como otros efectos derivados de la contaminación, destrucción de hábitats y sobleexplotación de recursos. Actualmente existe una gran preocupación a nivel global sobre la posibilidad de que estos hábitats bentónicos configurados por macroalgas no tengan la capacidad de mantener la biodiversidad marina asociada y los procesos ecológicos y las funciones ecosistémicas que sustentan. De hecho, la disminución de las algas que forman el dosel de vegetación marina conlleva efectos en cascada en el ecosistema. Además, la complejidad estructural y el hábitat tridimensional que ofrecen los grandes macrófitos es aprovechado eficazmente por la fauna albergando comunidades animales de gran valor ecológico y comercial. Por el contrario, en ausencia del dosel que forma la vegetación, la abundancia y la diversidad animal son muy bajas. De modo que se puede inferir que el declive de estos ingenieros ecosistémicos repercute de forma negativa en la biodiversidad, afectando a la estabilidad y resiliencia de las comunidades bentónicas.

Los cambios que se han producido en el medio marino en las últimas décadas como consecuencia del cambio climático son significativos, abarcando tanto variables físicoquímicas como biológicas y ecológicas. Las evidencias físicoquímicas del cambio quedan reflejadas principalmente por el aumento de la temperatura del agua, cambios en la circulación oceánica, cambios en la formación de masas de agua y afloramientos, aumento de la estratificación de la columna de agua, e incremento de la intensidad del oleaje. Las evidencias a nivel biológico se manifiestan principalmente por una disminución de la producción primaria y de la capacidad de absorción de CO_2, el declive de especies fundadoras, cambios en la distribución de las especies, cambios fenológicos y pérdida generalizada de biodiversidad. En concreto, el ecosistema bentónico costero ha mostrado una especial vulnerabilidad ante las nuevas condiciones climáticas.

Por otro lado, el estudio de los efectos de la radiación solar en los macrófitos marinos cobra especial relevancia, considerando que los modelos predictivos proyectan un aumento global en las próximas décadas y que la Península Ibérica es una de las regiones especialmente más afectadas. En el caso de las aguas atlánticas del norte de la península Ibérica ya se ha registrado un declive de varias especies de macroalgas formadoras de hábitat, produciéndose en consecuencia una desestructuración y pérdida de funcionalidad del ecosistema bentónico. En el caso particular de la costa vasca y como consecuencia del estancamiento estival de sus aguas, resulta ser un área especialmente vulnerable a los efectos del cambio climático debido a la mayor temperatura del agua y al menor aporte de nutrientes que en otras áreas costeras cercanas, registrándose además el mayor incremento de la radiación solar en las últimas décadas a nivel peninsular. Asimismo, el problema del declive de las especies formadoras de hábitat se agrava especialmente en la costa vasca debido a que, al ser un área rodeada de aguas más frías, queda imposibilitada la llegada natural de especies de reemplazamiento que cubran la función de las especies autóctonas. En concreto, ya ha sido documentado el declive de las poblaciones de *Gelidium corneum* (Hudson) JV Lamouroux en varias localidades. Sin embargo, la explicación a este hecho se hacía compleja ya que el incremento de temperatura detectado en aguas de la costa vasca desde el principio de los ochenta no parecía explicar por sí solo los cambios sufridos por esta especie. Así, otros factores como el aumento del oleaje (principalmente en la última década) y el efecto de las actividades humanas sobre estas comunidades se perfilaban como otras de las posibles causas del declive. Al mismo tiempo, también se ha sugerido que estos cambios podrían ser explicados por un déficit de nutrientes y un aumento de la transparencia del agua. Esta hipótesis se ve reforzada por dos hechos: por un lado, el aumento significativo de la radiación solar detectado en España (y en particular en el Cantábrico oriental) desde 1985, y por otro, la presencia de síntomas de estrés y de la existencia de zonas clareadas en las praderas de *G. corneum* en tramos de costa abierta con aguas limpias. Por lo tanto, se podría pensar que el aumento de la irradiancia en superficie junto con el incremento de la temperatura del agua superficial del mar podrían ser dos factores potenciales que expliquen en gran parte los cambios experimentados por esta especie clave en los fondos someros de la costa vasca. En cuanto a los nutrientes, es destacable el aumento generalizado de la estratificación estival en las aguas costeras superficiales, incidiendo así de una forma negativa sobre la disponibilidad de nutrientes. En este sentido, otro punto relevante es la disminución en la intensidad de los afloramientos en el noroeste peninsular frente al aumento en el suroeste. Finalmente, y apoyando esta hipótesis, en la costa vasca se ha registrado en primavera y verano una reducción de la tasa diaria de precipitación en las últimas décadas, lo cual puede incidir de forma negativa al aporte de nutrientes a través de la descarga fluvial y de escorrentías al medio costero.

En el contexto del cambio climático, uno de los retos en ecología es realizar estudios multidisciplinares con diseños observacionales y experimentales robustos que incluyan información biológica (taxonomía, fisiología y función de los organismos) y ambiental (variables físicas y químicas) enfocados a obtener un mayor conocimiento sobre la respuesta del sistema ante factores de estrés. Por lo tanto, la monitorización de las comunidades fitobentónicas aporta valiosa información sobre las condiciones ambientales en las que viven, especialmente sobre la propia variabilidad natural, así como la derivada de acciones antrópicas. Esta tesis se centra en una problemática central en el contexto del cambio climático: la pérdida de especies clave en la estructuración de los fondos marinos. La presente investigación parte de la hipótesis general de que, junto con el aumento de la temperatura del agua del mar, cambios en la radiación solar y disponibilidad de nutrientes han actuado sinérgicamente como factores de estrés, siendo parcialmente responsables de las alteraciones detectadas recientemente en la estructura de las comunidades bentónicas.

El objetivo principal de esta tesis es evaluar los cambios en la estructura taxonómica y funcional, así como en la diversidad de las comunidades submareales de macroalgas del sureste del Golfo de Vizcaya desde 1991 y su relación potencial con cambios en las condiciones ambientales de la zona, así como investigar -a una escala espacial menor- las consecuencias de la pérdida de copa en las comunidades asociadas de algas e invertebrados y en la biomasa de productores primarios.

Las consecuencias de la pérdida de la copa en las especies de fauna y flora asociadas han sido estudiadas mediante una serie temporal de datos de 21 años (1996-2017) recopilada en el extremo occidental de la costa vasca. Los resultados muestran un declive brusco de *G. corneum* acompañado de una proliferación de formas algales cespitosas e incrustantes, una disminución de invertebrados suspensívoros epífitos y epibentónicos, y la pérdida de numerosas especies asociadas de flora y fauna. Mientras la abundancia de algas e invertebrados disminuye tras la completa pérdida de la copa, tiene lugar un aumento de la densidad y riqueza de especies, así como de la equitatividad de flora y fauna. Los resultados de este estudio también identifican un aumento significativo de la variabilidad temporal de las comunidades que denota mayor estrés ambiental. Los cambios en la biomasa de las comunidades de macroalgas submareales se han evaluado para el rango de profundidad de 2 – 11 m y el periodo 1982 - 2014 con datos obtenidos también en la parte occidental de la costa vasca. La biomasa total ha disminuido principalmente como consecuencia del declive de *G. corneum*. Como excepción se ha registrado un aumento de biomasa a la profundidad de 10 m debido al notable desarrollo de la especie formadora de copa *Treptacantha baccata*.

A escala regional, se han evaluado los cambios en la estructura taxonómica y funcional, así como en la diversidad de la vegetación submareal somera (3-9 m) de 19 localidades del sureste del Golfo de Vizcaya entre 1991 y 2013. Los resultados evidencian que las comunidades tridimensionales que nos encontramos en los fondos de la zona de estudio han cambiado hacia comunidades estructuralmente menos complejas. Las algas formadoras de copa o dosel (*G. corneum, T. baccata, Saccorhiza polyschides, Laminaria ochroleuca*) han disminuido mientras que las algas cespitosas de morfología simple, entre las que destacan las especies filamentosas, polisifonadas y foliosas no corticadas, han aumentado junto con las coralináceas articuladas y varias especies incrustantes. Además, se ha observado un aumento significativo en la riqueza y diversidad, principalmente debido al desarrollo de formas simples, con carácter oportunista y afinidad meridional (de aguas más cálidas). De acuerdo a las predicciones climáticas, los cambios en las condiciones ambientales se intensificarán, por lo que la prevalencia de las nuevas especies cespitosas establecidas se mantendrá posiblemente debido a la capacidad mostrada para competir por el espacio y resistir a las perturbaciones.

Por otro lado, se han estudiado los patrones de distribución espacial actuales de las macroalgas submareales de las costas atlántica y mediterránea de la Península Ibérica mediante datos de vegetación recolectados en el campo y datos ambientales de la base de datos OCLE. Se han identificado los factores clave que influyen en la distribución de comunidades de macroalgas y se ha construido un modelo de la relación existente entre las comunidades y estas variables ambientales, con el fin de pronosticar cambios en la futura distribución de la vegetación submareal del norte de la Península Ibérica ante escenarios futuros de cambio climático (RCP4.5 y RCP8.5) para el final de siglo. Así, se ha observado que la temperatura del agua ha sido el factor más relevante en la configuración de la distribución de las comunidades de macroalgas a lo largo de las costas de la Península Ibérica, mientras que la disponibilidad de nutrientes juega un papel secundario modulando el efecto térmico en los tramos de costa con los rangos de temperatura más fríos e intermedios. Para ambos escenarios explorados, el modelo predice que las comunidades que presentan valores intermedios tanto de temperatura como de concentración de nitratos (Cantábrico central) se volverán más similares a las actualmente presentes en el Cantábrico oriental, con aguas más cálidas y oligotrofas. Además, las comunidades de macroalgas del noroeste permanecerán diferenciadas del resto de la Península Ibérica. Esta diferenciación será mayor en el escenario más pesimista (RCP 8.5), en el que las comunidades central y oriental de la Península Ibérica mostrarán un mayor parecido con las de la región mediterránea que con las del noroeste. Por tanto, estos resultados apoyan en parte la hipótesis inicial de una posible meridionalización futura de las comunidades de macroalgas de las costas de sustrato duro del norte de la Península Ibérica. En consecuencia, se producirá un simplificación del espacio tridimensional que ofrecen las macroalgas de mayor tamaño. Por otro lado, previsiblemente la costa noroeste seguirá siendo un refugio de vegetación espacialmente compleja con algas marinas de afinidad más fría. A diferencia de los datos utilizados en el modelo, existen también otros pronósticos que apuntan hacia un debilitamiento del afloramiento del NW de la Península Ibérica. Si éste tuviera lugar, es probable que las comunidades del NW también cambien hacia un fitobentos más meridional. Por lo tanto, los cambios de las comunidades del norte de la Península Ibérica ante los escenarios futuros de cambio climático podrían ser mayores de lo previsto en el modelo. Se necesita investigación futura para mejorar las proyecciones de cambio de la comunidad, incluyendo en el modelo otros factores clave, como datos sobre herbivorismo y depredación, e incluso datos sobre cambios temporales en las comunidades de macroalgas en respuesta a fluctuaciones ambientales, además de una mayor replicación espacial.

Asimismo, se ha llevado a cabo un estudio experimental de campo (*in situ*) para conocer el efecto combinado de la radiación solar y la disponibilidad de nutrientes sobre el estado fisiológico y el crecimiento de *G. corneum*, así como sus efectos sobre la composición taxonómica y la diversidad de esta comunidad bentónica. Si bien la fertilización llevada a cabo ha afectado a todo el experimento, produciéndose una difusión de los nutrientes entre las diferentes áreas, se han observado diferencias respecto al tiempo. Así, *G. corneum* ha mostrado una mayor elongación del fronde con una disponibilidad de nutrientes mayor. Respecto a su eficiencia y capacidad fotosintéticas, su capacidad fotoprotectora y el rendimiento cuántico óptimo, indicativos de su estado fisiológico, se han observado también diferencias respecto al tiempo, es decir, este macrófito acusa negativamente la mayor irradiancia acumulada recibida a lo largo del verano. Por otro lado, tanto la riqueza de especies como la diversidad presentan una gran variabilidad que dificulta obtener diferencias significativas en un experimento de este tipo.

En conclusión, los resultados de la presente investigación ayudan a comprender mejor la influencia de los factores ambientales en la distribución de la especie clave *Gelidium corneum* en el ecosistema costero de las aguas atlánticas del sur de Europa y establecer así una base científica de apoyo para su adecuada gestión en el contexto de la crisis del cambio climático. Asimismo, los resultados evidencian importantes implicaciones para el funcionamiento de los ecosistemas y la biodiversidad, ya que las especies recientemente establecidas podrían no cumplir con la función ecológica proporcionada por *G. corneum* y no se podrán mantener todos los servicios ecosistémicos proporcionados por las comunidades dominadas por especies formadoras de copa. Por otro lado, los muestreos ya realizados serán de gran ayuda para asentar una red de monitorización que facilitará el seguimiento de la evolución de las comunidades bentónicas frente a las nuevas condiciones climáticas. Todo ello permitirá establecer las bases biológicas y ecológicas para el diseño de estrategias de mitigación y adaptación frente a los efectos del cambio climático, dirigidas hacia la conservación de la función de las comunidades bentónicas de sustrato duro y la gestión de la biodiversidad en el ecosistema costero.

Finalmente, entre las futuras líneas de investigación, se hace necesario evaluar el efecto de otros factores clave en el declive de macrófitos como es la presión herbívora que ejercen los erizos, invertebrados característicos de los fondos rocosos. Asimismo, se recomiendan esfuerzos dirigidos a restaurar los fondos marinos donde haya desaparecido la copa. El trasplante de especies perennes formadoras de copa aún presentes en la costa cantábrica (*G. corneum, T. baccata*) sobre arrecifes artificiales diseñados expresamente para proporcionar condiciones ambientales óptimas de irradiancia y exposición al oleaje (teniendo en cuenta variables como la orientación, la inclinación, etc.) podría promover el aumento de la biodiversidad y de la estabilidad de las comunidades bentónicas, todo ello necesario para el correcto funcionamiento del ecosistema marino rocoso en la costa cantábrica.

LABURPENA

Tesi honen oinarrian dagoen kontzeptu-esparrua klima-aldaketaren egungo egoeratik abiatzen da, zein haren eragina mundu mailako itsas hondoetan eraldaketa larria eragiten ari bait da. Aldaketa nabarmenen artean, azpimarratzekoa da errezela eratzen duten makrofitoen gainbehera. Makrofito horiek sakonera txikiko hondo harritsuen bereizgarri diren arren, tamaina txikiagoko algek ordezkatzen dituzte. Alga-komunitatean gertatzen diren aldaketa horien ondorioz, fase berri bat sortu da, itsas ekosistemarentzat oraindik ezezagunak diren ondorio ekologikoak dituena. Zehazki, euskal kostaldean ziurgabetasunak daude aldaketa-ereduari buruz, komunitate bentonikoaren aldagai biologikoetan duen eraginari buruz eta komunitate fitobentonikoaren eraldaketa-prozesuan eragin handiena duten klima-aldagaiei buruz. Tesi honetan egindako ikerketek gai horiei buruzko informazioa ematen dute, aldez aurretik egindako ikerketetan oinarrituz eta mareaz azpiko laginketa-lan zabala eta *in situ* metodo esperimentalak eginez.

Errezela eratzen duten makroalgek paper garrantzitsua dute planetako eskualde epel gehienetako ekosistema bentonikoetan, non nagusi diren. Makrofito iraunkor handi horiek egitura aldetik konplexuak diren komunitateak osatzen dituzte, espazioaren hiru dimentsioko konplexutasuna areagotzen baitute, habitat biogenikoa eta itsas organismo askorentzako babesa emanez, espezie ugariren babesleku eta elikagai gisa. Era berean, bizi diren ingurunea nabarmen eraldatzen dute; izan ere, argi-baldintzak, ur-fluxua edo sedimentazio-tasak aldatzen dituzte eta beste organismo batzuk finkatzen laguntzen dute. Beraz, itsaspeko belardi horietan espezie asko daudenez, habitata egituratzen eta osatzen duten espezie horiek nagusi diren komunitateak munduan dibertsitate eta ekoizpen handieneko ekosistemetako bat dira eta modu esanguratsuan laguntzen diote kostaldeetako produktibitateari. Ondorioz, ekologikoki eta sozioekonomikoki habitat horiek mundu mailan garrantzitsuenetakoak dira latitude epeletan. Gainera, espezie biogeniko horiek hainbat eta hainbat zerbitzu ekosistemiko eskaintzen dituzte, hala nola itsasertzeko higadura murriztea, CO_2 finkatzea, mantenugaien zikloaren zati dira eta lehengai gisa balio dute giza erabilera desberdinetarako, baita uraren kalitatea kontrolatzeko ere besteak beste. Beraz, haien ugaritasuna aldatzeak edo errezela osatzen duten espezieak desagertzeak eragin handia izango du ekosistema osoan. Azkenik, azpimarratu behar da itsas alga bentonikoak substratuan finkaturik bizi direnez, bioadierazle garrantzitsuak direla eta baita kostaldeko ekosistemen egoera ekologikoa ebaluatzeko tresna oso erabilgarria ere. Ezaugarri hori makroalgen izaera sesilean eta espezie bakoitzaren sentikortasunaren ondorioz jasan ditzaketen baldintzetan oinarritzen da, bizi diren ingurunean gertatzen diren ingurumen- eta klima-baldintzei aurre egin behar baitiete.

Naturan, organismo horiek ingurumen-baldintzen eraginpean daude eta horiek modu naturalean denboran eta espazioan zehar aldatzen dira, bai eskala globalean bai tokiko eskalan. Honela, klima berez osatzen duten faktoreek, hala nola irradiantzia, olatuak, korronteak, euri-jasak eta tenperaturak, eskualde bakoitzeko landarediaren izaera zehazten dute eta beraz, kopa edo errezela eratzen duten alga-espezieen banaketa ere. Hala ere, planetak gaur egun jarduera antropogenikoek eragindako klima aldaketari aurre egin behar dio, horren aldaketa erritmoak aurrekaririk ez duelarik. Horrela, azken hamarkadetan, makrofito handi horiek atzera egin dute eta desagerpenak erregistratu dira eremu askotan maila globalean inpaktu antropikoen ondorioen ondorioz. Hala nola, habitataren suntsipena, kutsadura, espezie inbaditzaileak, gainpresio belarjalea edo itsasoko uraren berotzea besteak beste. Gaur egun kezka handia dago, oro har, itsasoko biodibertsitatea eta prozesu ekologikoak eta funtzio ekosistemikoak mantentzeko gaitasunik ez izatearen inguruan. Izan ere, itsas landarediaren errezela osatzen duten algak gutxitzeak kate-efektuak eragiten ditu ekosisteman. Gainera, faunak modu eraginkorrean aprobetxatzen ditu makrofito handiek eskaintzen dituzten egiturazko konplexutasuna eta hiru dimentsioko habitata, balio ekologiko eta komertzial handiko animalia-komunitateak bilduz. Aitzitik, itsas landaredia osatzen duen errezelik ez badago, animalien ugaritasuna eta dibertsitatea oso txikiak dira. Beraz, ingeniari ekosistemiko horien gainbeherak biodibertsitatean eragin negatiboa duela ondoriozta daiteke, komunitate bentonikoen egonkortasunari eta erresilientziari eraginez.

Klima-aldaketaren ondorioz azken hamarkadetan itsas ingurunean gertatu diren aldaketak esanguratsuak dira, aldagai fisikokimikoak, biologikoak eta ekologikoak barne hartzen baitituzte. Aldaketaren ebidentzia fisiko-kimikoak, batez ere, hauek islatzen dituzte: uraren tenperaturaren igoera, zirkulazio ozeanikoaren aldaketak, ur-masen eraketan eta azaleratzeetan izandako aldaketak, ur-zutabearen estratifikazioa handitzea eta olatuen intentsitatea handitzeak. Ebidentzia biologikoak, batez ere, hauek dira: ekoizpen primarioa eta CO_2 xurgatzeko gaitasuna murriztu izana, espezie fundatzaileen gainbehera, espezieen banaketan aldaketak, aldaketa fenologikoak eta biodibertsitatearen galera orokorra. Zehazki, kostaldeko ekosistema bentonikoa kalteberatasun berezia erakutsi du baldintza klimatiko berrien aurrean. Bestalde, eguzki-erradiazioak itsas makrofitoetan dituen ondorioak aztertzeak garrantzi berezia du, kontuan hartuta iragarpen-ereduek hazkunde globala aurreikusten dutela datozen hamarkadetan eta Iberiar Penintsula dela gehien kaltetutako eskualdeetako bat. Iberiar penintsularen iparraldeko ur atlantikoen kasuan, habitata osatzen duten zenbait makroalga-espezieren gainbehera erregistratu da eta ondorioz, ekosistema bentonikoaren desegituraketa eman da eta funtzionaltasuna galdu da. Euskal kostaldeari dagokionez eta udan uren geldialdiaren ondorioz, bereziki eremu kaltebera da klima-aldaketaren ondorioekiko, uraren tenperatura handiagoa delako eta inguruko kostaldeko beste eremu batzuetan baino mantenugai gutxiago ematen direlako; izan ere, penintsulan azken hamarkadetan eguzki-erradiazioak izan duen hazkunde handiena bertan erregistratu da. Era berean, habitata osatzen duten espezieen gainbeheraren arazoa bereziki larriagoa da euskal kostaldean; izan ere, ur hotzagoez inguratutako eremua denez, ezin da berez iritsi espezie autoktonoen funtzioa betetzen duten ordezko espezierik. Izan ere, dagoeneko dokumentatu da *Gelidium corneum* (Hudson) JV Lamouroux populazioen gainbehera hainbat lekuetan. Hala ere, *G. corneum* errodofizearen galera zehatzaren azalpena konplexua zen, eta laurogeiko hamarkadaren hasieratik euskal kostaldeko uretan antzeman den tenperatura-igoerak ez dirudi berez azaltzen zituenik espezie horrek jasan dituen aldaketak. Hala nola, olatuen gorakadak (batez ere azken hamarkadan) eta giza jarduerek komunitate horietan izan duten eragina besteak beste, gainbeheraren beste arrazoi batzuk izan daitezke. Era berean, aldaketa horiek mantenugaien defizitagatik eta uraren gardentasuna handitzeagatik azal litezkeela iradoki da. Hipotesi hori bi gertakarik indartzen dute: batetik, 1985etik hona Espainian (eta bereziki Kantauri Ekialdean) detektatutako eguzki-erradiazioak nabarmen gora egin duela eta bestetik, ur garbiko kostalde irekiko eremuetan *G. corneum*eko belardietan estres-sintomak eta argitutako tarteak daudela. Beraz, pentsa liteke azaleko irradiantziaren eta itsasoko uraren tenperaturaren igoerek, neurri handi batean, espezie horrek euskal kostaldeko sakonera txikiko hondoetan izandako aldaketak azaldu ditzazketen bi faktore potentzialak direla. Mantenugaiei dagokienez, nabarmentzekoa da gainazaleko kostaldeko uren estratifikazioaren igoera orokorra, eta horrek eragin negatiboa du beraien eskuragarritasunean. Ildo horretan, beste puntu garrantzitsu bat da penintsulako ipar-mendebaldeko azaleratzeen intentsitatea txikiagoa dela hego-mendebaldeko igoeraren aldean. Azkenik, hipotesi hori oinarri hartuta, euskal kostaldean, udaberrian eta udan, prezipitazio-tasa murriztu egin da azken hamarkadetan, eta horrek eragin negatiboa izan dezake ibaien deskargaren bidez mantenugaien eta itsasertzeko jariatze-uren ekarpenean.

Klima-aldaketaren testuinguruan, ekologiako erronketako bat diziplina anitzeko ikerketak egitea da, behaketa-diseinu eta diseinu esperimental sendoekin, informazio biologikoa (taxonomia, fisiologia eta organismoen funtzioa) eta ingurumenekoa (aldagai fisikoak eta kimikoak) barne hartuta, sistemak estres-faktoreen aurrean duen erantzunari buruzko ezagutza handiagoa lortzera bideratuta. Beraz, komunitate fitobentonikoen monitorizazioak informazio baliotsua ematen du bizi diren ingurumen-baldintzei buruz, batez ere berezko aldakortasunari buruz, bai eta ekintza antropikoetatik eratorritakoari buruz ere. Tesi honek klima-aldaketaren testuinguruan dagoen arazo nagusi bat du ardatz: itsas hondoen egituraketan giltzarri diren espezieen galera. Ikerketa honen abiapuntua hipotesi orokor hau da: itsasoko uraren tenperaturaren igoerarekin, eguzki-erradiazioaren eta mantenugaien eskuragarritasunaren aldaketekin batera, sinergikoki jokatu dute estres-faktore gisa eta komunitate bentonikoen egituran antzeman berri diren alterazioen erantzule dira partzialki.

Tesi honen helburu nagusia komunitate sublitoral bentonikoen aldaketak gertatzen ari diren magnitudea eta abiadura ebaluatzea da, bai tokian-tokian, bai eskualde-mailan (euskal kostaldean), bai penintsula-mailan eta azken hamarkadetan uraren tenperaturan, eguzki-erradiazioan, prezipitazioetan eta mantenugaietan izandako joerekin duten lotura. Aldaketa-maila ebaluatzeko, intereseko aldagai biologikoak aztertuko dira, hala nola espezie fundatzaileen ugaritasun erlatiboa, bai eta komunitateen osaera eta dibertsitate taxonomikoa eta funtzionala ere.

Tokian-tokian tesi honek mareaz azpiko komunitateen biomasak denboran zehar izan dituen aldaketak ebaluatzen ditu, 1982tik 2014ra arte hainbat sakoneratan euskal kostaldeko mendebaldeko muturrean. Ondorioz, *Gelidium corneum* errodofito iraunkorraren stocka nabarmen murriztu da, batez ere 3 eta 6 metroko sakoneran. Gainera, landarediaren heterogeneotasuna areagotu egin dela ikusi da, gehienbat soropila osatzen duten koralinazeo artikulatuak eta morfologikoki sinpleak eta iragankorrak diren algak ugaritzearen ondorioz. Bestalde toki berean, *Gelidium corneum*eko belardietan izandako atzerakadarekin batera urtero ikertu dira 21 urteko aldian (1996-2017) elkartutako espezie-taldeetan izandako aldaketak. Emaitzen arabera *G. corneum*-en galera ez-lineala gertatu da eta bat-bateko aldaketa bat eman da forma soropildu eta inkrustatzaileak nagusi diren komunitate berrietarantz. Morfologikoki konplexuak diren algen eta forma iraunkorren gainbehera azkarrarekin batera ornogabeak gutxitu egin dira, bai epifito eta bai epibentonikoak, flora eta fauna espezie-elkartu ugari galtzeaz gain. Errezaleran gainbeherarekin batera, algen eta ornogabeen ugaritasuna nabarmen jeitsi da. Bestalde, errezela galdu ondoren algen dentsitatea eta floraren eta faunaren aberastasuna eta ekitatibotasuna nabarmen handitu direla ikusi da. Azkenik, tokiko ikerketa honen emaitzek komunitateen denbora-aldakortasuna nabarmen handitu dela erakusten dute eta horrek aldaketaren ondoren estres handiagoa dagoela adierazten du.

Eskualde mailan, Euskal kostalde osoa hartuta 1991tik 2013ra bitartean, Bizkaiko Golkoko hego-ekialdeko kostaldeko 19 tokitan egitura taxonomikoan eta funtzionalean izandako aldaketak ebaluatu dira, baita azaleko mareaz azpiko (3-9 m) landarediaren dibertsitatean izandakoak ere. Emaitzek agerian uzten dute ikerketa-eremuaren hondoetan aurkitzen ditugun komunitateak hiru dimentsioko egiturari dagokionez konplexutasun txikiagoa duten komunitateetara aldatzen ari direla. Kopa edo errezela eratzen dituzten algak (*G. corneum, T. baccata, Saccorhiza polyschides, Laminaria ochroleuca*) gutxitzen ari dira; morfologia sinpleko alga soropilduak berriz, handitzen ari dira koralinazeo artikulatuekin eta zenbait espezie inkrustatzaileekin batera. Gainera, aberastasunak eta dibertsitateak nabarmen gora egin dutela ikusi da, batez ere forma sinpleak garatu direlako, karakter oportunista eta hegoaldeko afinitatearekin (ur beroagokoak). Iragarpen klimatikoen arabera ingurumen-baldintzen aldaketak areagotu egingo dira eta beraz, ezarritako espezie soropildu berrien nagusitasuna mantendu egingo da ziurrenik, espazioan lehiatzeko eta perturbazioei aurre egiteko erakutsi duten gaitasunaren ondorioz.

Bestalde, penintsula mailan, hau da, eskala espazial zabalagoan, Iberiar Penintsulako iparraldeko eta hego-ekialdeko mareaz azpiko komunitate bentonikoen egungo eta etorkizuneko banaketa-patroiak aztertu dira, kostalde atlantikoa eta mediterraneoa hurrenez hurren. Aztertutako eremuak eremu geografiko zabala hartzen du, maila termiko zabala hartzen duena eta espezieen banaketa espazialari buruzko informazio baliotsua ematen duena. Azterlan hau landa-datuetan (espezieen konposizioa eta ugaritasuna) eta OCLE datu-baseko ingurumen-datuetan oinarritu da. Hala, makroalga-komunitateen banaketaren konfigurazioan faktore garrantzitsuena Iberiar Penintsulako kostaldeetan uraren tenperatura izan dela ikusi da; aldiz, mantenugaien eskuragarritasunak bigarren mailako eginkizuna du, izan ere, eragin termikoa modulatzen du tenperatura-tarte hotzenetan eta bitartekoetan. Bestalde, lehen aldiz, bi azalpen-faktore horietan oinarrituta, komunitate-ingurumen erlazioaren eredu bat eraiki da, komunitateetan aldaketak proiektatzeko, klima-aldaketaren etorkizuneko 2 agertokiren arabera: RCP 4.5 eta RCP 8.5. Bi agertokietan tenperaturaren eta nitrato-kontzentrazioaren tarteko balioetan dauden komunitateak (Kantauri erdialdeko komunitateak) Iberiar Penintsulako iparraldeko eremu bero eta oligotrofikoan daudenen antzekoagoak (ekialdekoak) bihurtuko direla iragartzen dugu. Bestetik, ipar-mendebaldeko makroalgen komunitateak Iberiar Penintsulako gainerako komunitateetatik bereiztuta egongo dira. Desberdintasun hori handiagoa izango da agertoki ezkorrenean (RCP 8.5); izan ere, Iberiar Penintsulako erdialdeko eta ekialdeko komunitateek antz handiagoa izango dute Mediterraneoko eskualdekoekin ipar-mendebaldekoekin baino. Beraz, emaitza horiek neurri batean Iberiar Penintsulako iparraldeko substratu gogorreko kostaldeetako makroalgen komunitateen etorkizuneko mediterraneizazio posible baten hasierako hipotesia bermatzen dute. Ondorioz, itsas hondoko paisaia lautu egingo da; izan ere, litekeena da hiru dimentsioko (espezie egituratzaileekin) habitat biogenikoak aldatzea espezie soropildu eta inkrustatzaileak nagusi diren bi dimentsioko eremu batera. Gainera, ziurrenik, ipar-mendebaldeko kostaldeak espazioan konplexua den landarediaren babesleku izaten jarraituko du, afinitate hotzagoko itsas algekin. Bestetik, lortutako informazioarekin espezieen etorkizuneko joan-etorriak aurreikusi ahal izango dira, bai eta klima-aldaketak penintsulan duen eraginaren intentsitate eta abiadura desberdinak detektatu ere, hau da, kalteberatasun handiagoa edo txikiagoa duten eremuak. Hala ere, etorkizuneko ikerketa behar da komunitatearen aldaketa-proiekzioak hobetzeko, ereduan funtsezko beste faktore batzuk sartuz, hala nola herbiborismoari eta harrapakaritzari buruzko datuak, bai eta makroalgen komunitateetan ingurumen-gorabeherei erantzuteko aldi baterako aldaketei buruzko datuak ere, espazio-erreplikazio handiagoa izateaz gain. Era berean, landa-ikerketa esperimental bat (*in situ)* egin da eguzki-erradiazioak eta mantenugaien eskuragarritasunak *G. corneum*-en egoera fisiologikoan eta hazkundean duten eragin konbinatua ezagutzeko, bai eta komunitate bentoniko horren osaera taxonomikoan eta dibertsitatean dituen ondorioak ezagutzeko ere. Egindako ongarriketak esperimentu osoan eragina izan badu ere eta mantenugaiak eremu batetik bestera hedatu badira ere, denborari dagokionez aldeak ikusi dira. Horrela, *G. corneum*-ek areagotze handiagoa erakutsi du luzeran mantenugaien eskuragarritasun handiagoarekin. Bere efizientzia eta gaitasun fotosintetikoari, bere ahalmen fotobabesleari eta errendimendu kuantiko optimoari dagokienez, fisiologikoki landarea nola dagoen adierazten dutenak, denborarekiko ezberdintasunak ere ikusi dira, hau da, makrofito honek udan zehar irradiantzia handiagoa jasan duela erakusten du. Bestalde, espezieen aberastasunak eta dibertsitateak aldakortasun handia dute, eta horrek zaildu egiten du alde esanguratsuak lortzea mota horretako esperimentu batean.

Laburbilduz, ikerketa honen emaitzak Europa hegoaldeko ur atlantikoen kostaldeko ekosisteman ingurumen-faktoreek *Gelidium corneum* funtsezko espeziearen banaketan duten eragina hobeto ulertzeko lagungarriak dira eta horrela, klima-aldaketaren krisiaren testuinguruan oinarri zientifiko bat ezartzea eta behar bezala kudeatzea ahalbidetzen dute. Era berean, emaitzek agerian uzten dute ekosistemen eta biodibertsitatearen funtzionamenduan inplikazio garrantzitsuak daudela; izan ere, berriki ezarritako espezieek ez dute bete *G. corneum*ek emandako funtzio ekologikoa, eta errezela eratzen dituzten espezieak nagusi diren komunitateek emandako zerbitzu ekosistemiko guztiak ezin izango dira mantendu. Bestalde, dagoeneko egin diren laginketak oso lagungarriak izango dira komunitate bentonikoek klima-baldintza berrien aurrean duten bilakaeraren jarraipena erraztuko duen monitorizazio-sarea finkatzeko. Horri guztiari esker, oinarri biologiko eta ekologikoak ezarri ahal izango dira klima-aldaketaren ondorioak arintzeko eta haietara egokitzeko estrategiak diseinatzeko, substratu gogorreko komunitate bentonikoen funtzioa kontserbatzera eta kostaldeko ekosisteman biodibertsitatea kudeatzera bideratuta.

Azkenik, etorkizuneko ikerketa-ildoen artean, makrofitoen gainbeheran funtsezkoak diren beste faktore batzuen eragina ebaluatu behar da, hala nola itsas trikuek egiten duten presio belarjalea, hondo harritsuen berezko ornogabeak baitira. Era berean, errezela desagertu den itsas hondoak berrezkuratzeko ahaleginak egitea gomendatzen da. Izan ere, euskal kostaldean errezela eratzen duten espezieak, zehazki, irradiantziako eta olatuekiko esposizioko ingurumen-baldintza egokiak emateko diseinatu diren arrezife artifizialen gainean birlandatuz (orientazioa, inklinazioa eta antzeko aldagaiak kontuan hartuta) posible izango litzateke komunitate bentonikoen biodibertsitatea eta egonkortasuna areagotzea, hori guztia beharrezkoa baita euskal kostaldean itsas ekosistemak behar bezala funtziona dezan.

about this thesis

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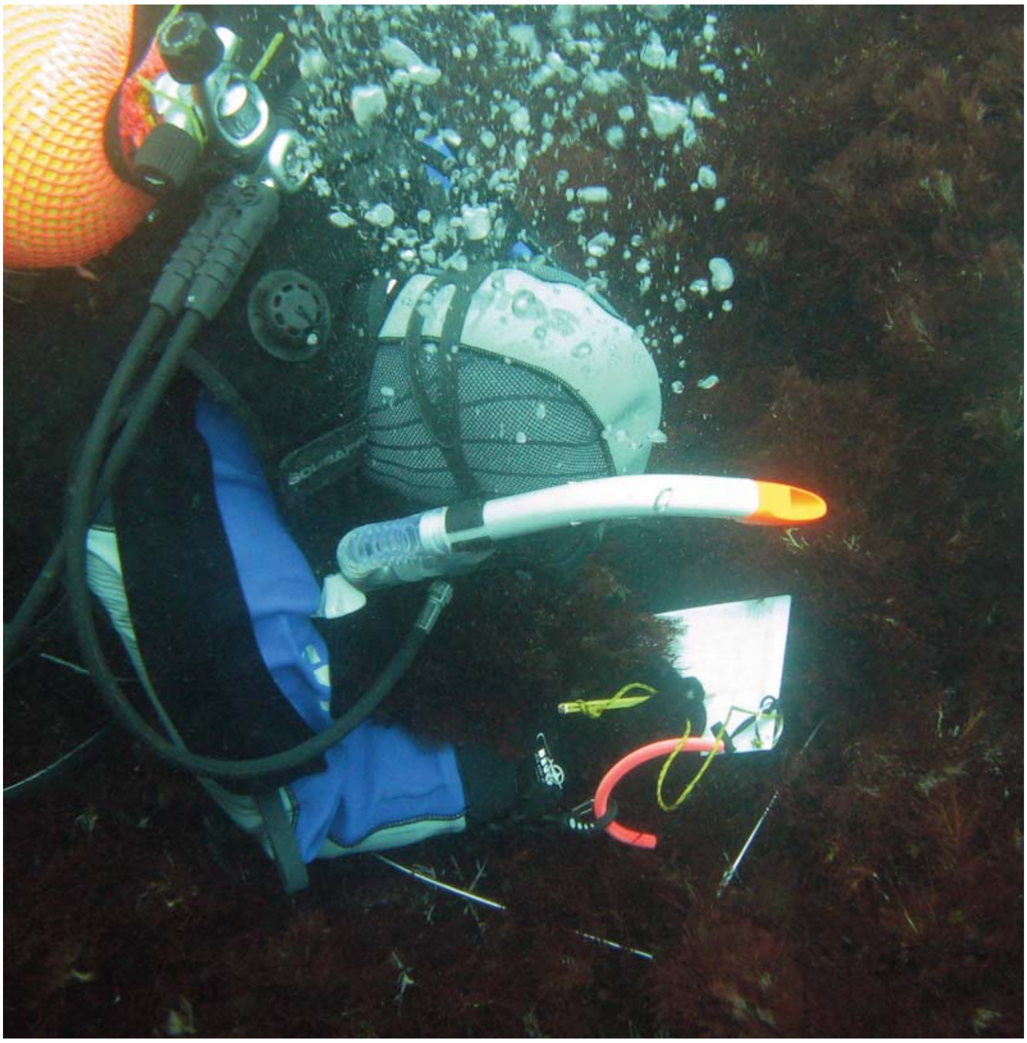


RESEARCH GROUP

The Marine Benthos Research Group UPV/EHU is formed by phycologists and zoologists. Since its beginnings in the early 1980s it has focused its research on studying the effects of human activities on marine rocky communities (Fig. 1) in order to assess the health of coastal ecosystems. As a result of numerous surveys, the team has been able to record the biodiversity of marine rocky assemblages along the Basque coast, with special attention on temporal and spatial variability. The monitoring programmes carried out have applied modern sampling techniques and impact data analysis strategies, and as a result have gathered a wide range of data and knowledge. This extensive background has focused on several key topics: 1) the effects of pollution on macroalgal assemblages (Gorostiaga and Díez, 1996; Díez et al., 1999); 2) the relationships between environmental variables and community structure (Díez et al., 2003); 3) the effect of oil spill impacts on rocky assemblages (Díez et al., 2009a); 4) the medium- and long-term recovery processes of benthic ecosystems (Gorostiaga et al., 2004; Díez et al., 2009b, 2013, 2014); 5) the effects of sampling resolution and taxonomic sufficiency on pollution assessment (Díez et al., 2010); 6) the introduction of non-indigenous species (Díez et al. 2012); 7) the use of benthic organisms as pollutant sentinels; 8) the development of biological element indicators for WFD (European Water Framework Directive) implementation (Díez et al., 2012a); 9) the effects of climate change on marine macrophytes (Díez et al., 2010; Quintano et al., 2010; Muguerza et al., 2010, 2017; Díez et al., 2012); and 10) the role of habitat-forming seaweeds in modelling benthic ecosystem properties (Bustamante et al. 2017; Muguerza et al 2020).

At the same time, the team has been involved in several competitive projects, two of which provided the spark for this thesis: 1) "K-EGOKITZEN: Climate Change: Impact and Adaptation. LT2- Marine Ecosystems. Marine Benthos (flora and fauna)" funded by the Basque Government (ETORTEK actions) from 2008 to 2010; and 2) "Monitoring the effects of Climate Change on marine communities on the Basque coast: a first assessment of the biological and ecological changes and stress factors. ECOLIFE-CAN" funded by the Spanish Ministry of Science and Innovation (MICINN) from 2010 to 2011. These projects focused on research aspects such as distributional changes in macrophytes in response to climate-driven environmental changes and their impact on the functioning of the benthos ecosystem on the Basque coast.

The main aims of these projects were not only to assess the impacts of climate change but also to design adaptative strategies for natural systems and to describe the possible future scenarios resulting from climate change on the Basque coast. To that end, firstly an exhaustive comparative analysis between the biological information on subtidal assemblages obtained in the 1990s and that recorded in the summer 2007 sampling was performed (Gorostiaga, 1994; 1995; Gorostiaga et al., 1998; Díez et al., 2003). It was at that point that I became involved in the sampling surveys with the Benthos Group. As a result of this first experience, I drew up a master's thesis project (Fig. 2).

From that point on, I gradually began to work with the research group, learning about and participating in the different projects according to their needs, until I became an active part of the team (Fig. 3). The group's work has led to the publication of several scientific papers, one of which lies at the origin of this thesis (Díez et al, 2012). That paper documented climate-change-related changes in subtidal vegetation along the coast of Bizkaia. However, there was still a need to estimate potential changes at a wider spatio-temporal scale, and to shed light on the causes and consequences of the changes observed.

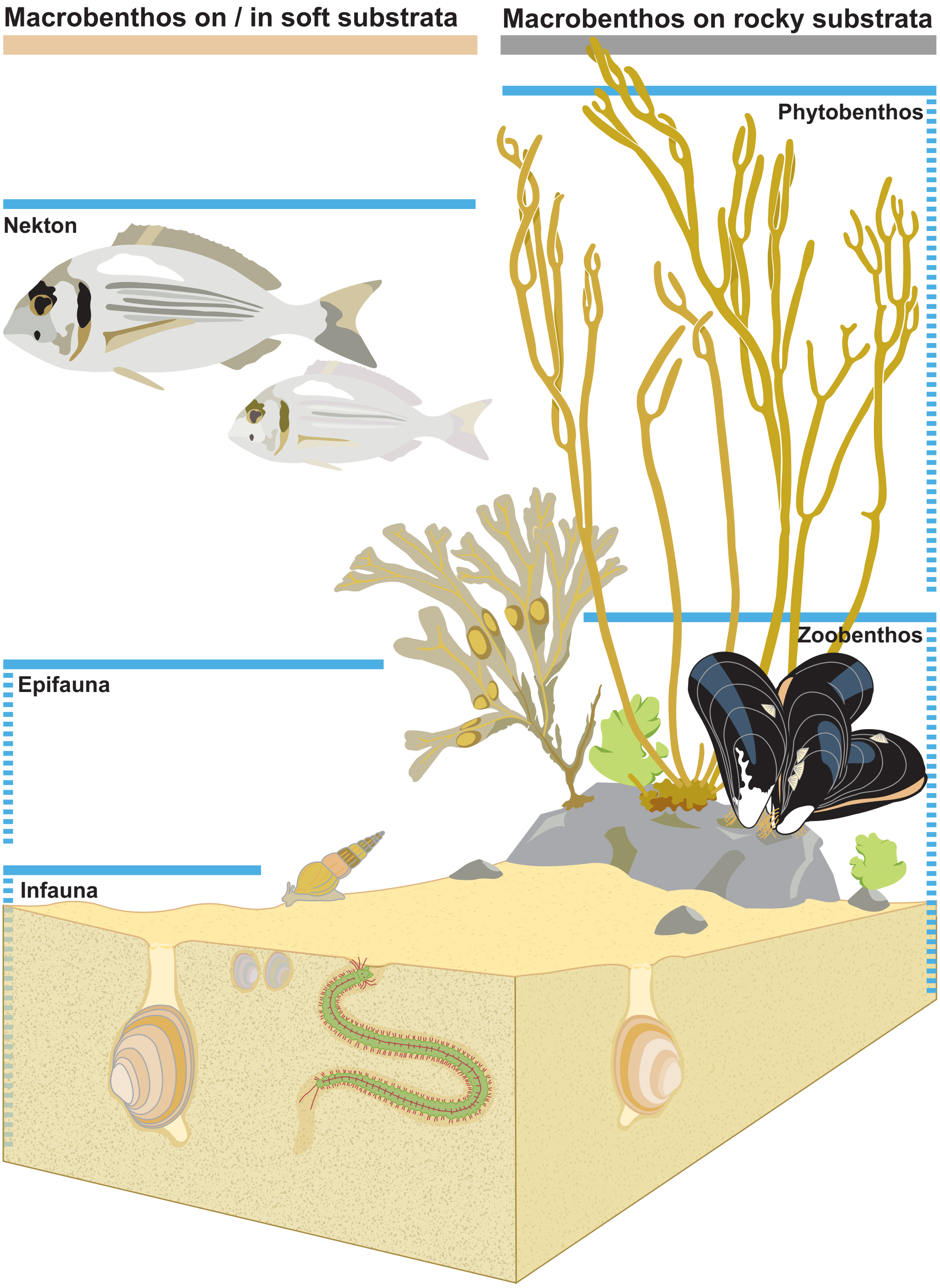


Fig. 1. Benthos. The term benthos, coined by Haeckel in 1891, comes from the Greek noun βένθος "depth of the sea", and refers to the community of organisms that live on, in, or near the sea bottom. Benthic organisms may be plants/algae or animals. Their substrate is species-specific and may be either soft sediments or hard rock. These organisms live on the surface of the substrate or inside it.

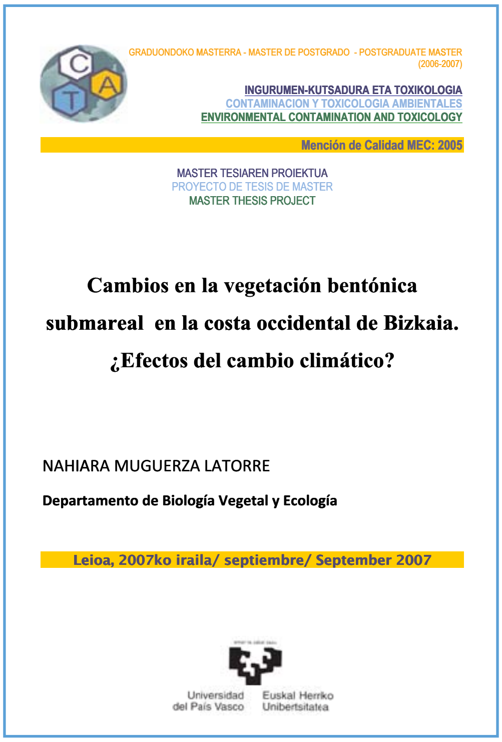
RELEVANCE

Ongoing global environmental change is expected to drive drastic alterations in community structure, biodiversity patterns and ecosystem services. One major concern is the loss of canopy-forming macroalgae that provide habitat, shelter and food for a plethora of organisms in temperate coastal rocky habitats (Wernberg et al., 2016). The phytobenthos of the southernmost part of the NE Atlantic is likely to be one of the areas most affected by the warming process around the world (Müller et al., 2009). This thesis contributes knowledge on recent changes in subtidal assemblages in that geographical area, predicts future shifts in their spatial distribution and identifies the influence of some key environmental drivers.

The information provided here on rocky subtidal communities in Southern Europe extends understanding of the impact of climate change on coastal ecosystems, which is crucial to ensure good environment management. To draw up appropriate adaptation and conservation policies with effective actions at global and local scales to safeguard ecosystem functioning and to restore marine biodiversity, it is necessary to know how the ecosystem responds to climate change and what the drivers of change are.

OBJECTIVE

This thesis aims to estimate changes in species abundance, composition and biodiversity in rocky subtidal assemblages in the southern Bay of Biscay over the last thirty years. This research also seeks to develop a mathematical model for predicting the biogeographic responses of macroalgal assemblages off the northern Iberian Peninsula to the environmental changes forecasted. The combined effect of certain changing environmental factors on the physiological performance of the canopy species *Gelidium corneum* (Hudson) J.V Lamouroux and on community structure are also tested by means of a field experiment.



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MASTER TESIAREN PROIEKTUA
PROYECTO DE TESIS DE MASTER
MASTER THESIS PROJECT

Cambios en la vegetación bentónica
submareal en la costa occidental de Bizkaia.
¿Efectos del cambio climático?

NAHIARA MUGUERZA LATORRE

Departamento de Biología Vegetal y Ecología

Leioa, 2007ko iraila/ septiembre/ September 2007

Universidad del País Vasco
Euskal Herriko Unibertsitatea

Fig. 2. Master's thesis project.

Fig. 3. Members of Marine Benthos Research Group (UPV/EHU), from left to right: Jose María Gorostiaga Garai, Nahiara Muguerza Latorre, Isabel Díez San Vicente, María Bustamante González, Francisco Javier Tajadura Martín, Endika Quintano Erraiz, José Ignacio Saiz Salinas.

chapter 1

general introduction

NAHIARA MUGUERZA (2020) DOCTORAL THESIS pp. 33-37

In the last few decades there has been widespread alarm that the biodiversity and ecological processes of coastal ecosystems are being severely threatened by increasing human pressure. Anthropogenic drivers threatening ecosystem functions include habitat destruction, pollution, over-exploitation and alien species, and further stress is induced by climate change (Bennett et al., 2015). Specifically, there is growing concern about the loss of macroalgal foundation species worldwide (Strain et al., 2014, Wernberg et al., 2016). Canopy-forming algae play a critical role on temperate rocky shores through provisions of food and a unique three-dimensional space for the settlement and protection of a wide array of marine organisms that enhance biodiversity (Steneck et al., 2002; Strain et al., 2014). Furthermore, these foundation species provide many valuable ecosystem services such as CO_2 sequestration, nursery grounds and coastal protection. Marine assemblages are being impacted across the world due to various climate events which are thought to be a consequence of climate change and are expected to intensify in the future (Harley et al., 2006, Hawkins et al., 2009). Understanding the responses of macroalgae as biogenic habitat formers to global climate change is therefore certainly important (Xiao et al., 2015).

Global warming is the variable that most conditions marine biota at all levels, from molecules to ecosystems, so it has been suggested that increasing temperature is a major driver in explaining shifts in the distribution of macroalgae (Smale et al., 2013, Wernberg et al., 2011). Rising atmospheric greenhouse gas concentrations have increased global average temperatures by ~ 0.2ºC per decade over the past 30 years (IPCC, 2014). Oceans are acting as a heat sink for the planet, storing more than 90% of the excess heat energy trapped since the 1970s. The upper layers of the ocean have warmed by 0.6ºC over the past 100 years. Oceans have also absorbed approximately one-third of CO_2 emissions, leading to a progressive acidification of seawater (Doney et al., 2009). Increased temperatures in turn host other environmental changes (Hoegh-Guldberg & Bruno, 2010). The frequency and intensity of coastal upwelling ecosystems are changing worldwide (Varela et al., 2015), water stratification has intensified, thus limiting nutrient supply to the sunlit layer (Behrenfeld et al., 2006), the salinity structure is shifting (Sjotun et al., 2015), wave power has increased globally (by 0.4% per year) since 1948 (Reguero et al., 2019) and the frequency of extreme high-intensity storms is also increasing (Meehl et al., 2000). Global-scale trends such as warming and ocean acidification, along with regional changes in storm regimes, upwelling patterns, terrigenous nutrient runoff and coastal salinity, are profoundly influencing the survival, recruitment growth and reproduction of seaweeds (Harley et al., 2012).

In the southern region of Atlantic coast of Europe, Southern Bay of Biscay, sea surface temperature (SST) increases during spring and autumn have expanded the warm season by approximately one month over the past 30 years (Costoya et al., 2015). Other local environmental factors are also changing in Iberian coastal ecosystems. A notable shift in winds has occurred over the last 20 years, resulting in a reduction in the spring-summer upwelling off the coasts of Galicia (Cabanas et al., 2003). The degree and duration

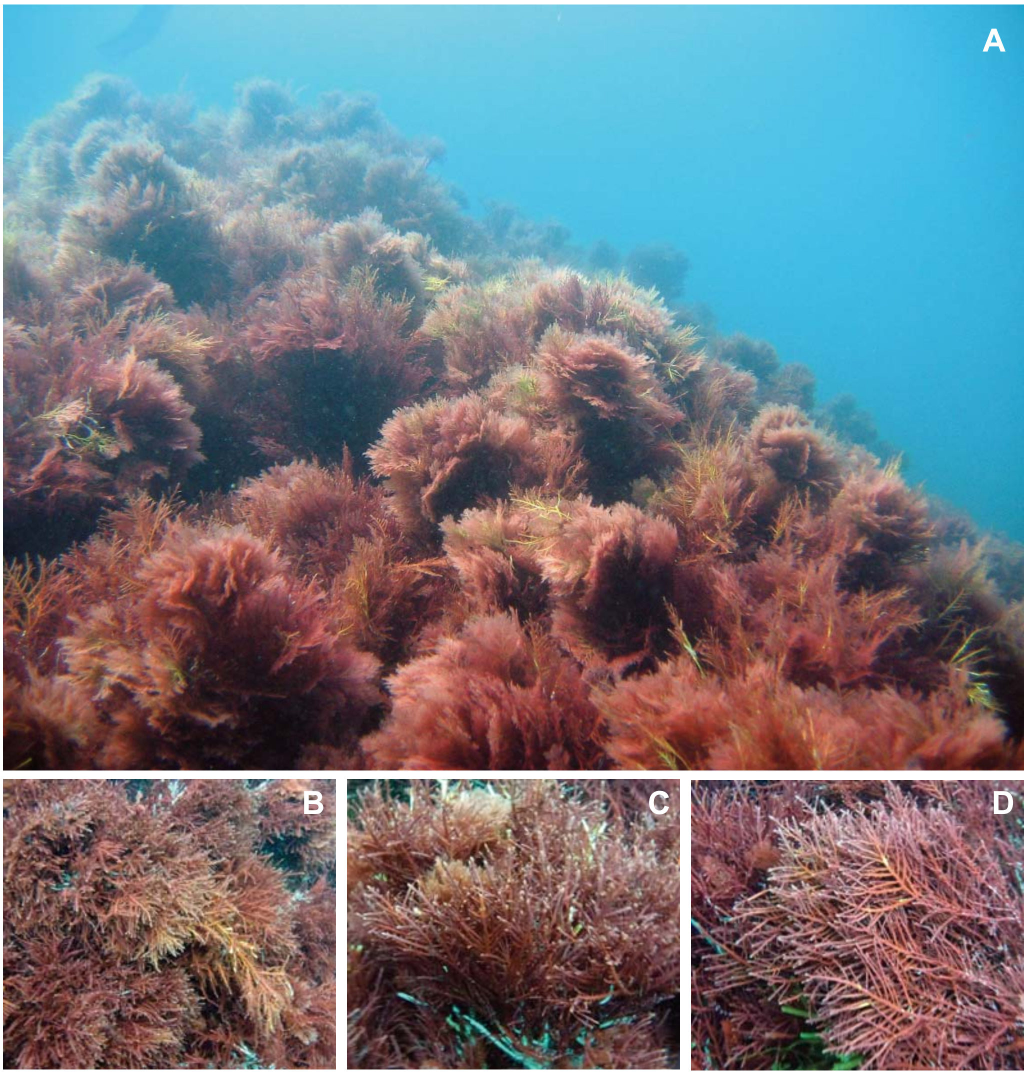

Fig. 1. Stands (A) of *Gelidium corneum* (Hudson) J.V. Lamoroux (Gelidiales, Rhodophyta), formerly *G. sesquipedale* (Clemente) Thuret. Details of the frond (B, C, D).

of water column stratification have increased off the coast of the Cantabrian Sea (Lavín et al., 1998). Authors have related these changes in upwelling intensity and water stratification to a less intense exchange of nutrients with surface layers. An increase in the intensity of storms and wave energy has also been recorded in the last 20 years (Borja et al., 2013), and overall solar radiation in the Iberian Peninsula has increased by 2.3% per decade since the 1980s (Sánchez-Lorenzo et al., 2015). Season-by-season data show that the biggest increase in irradiance (+ 6.5 W/m^2 per decade) has taken place in summer.

The northern Iberian Peninsula has been traditionally splited in two biogeographic sub-regions: a "cool-temperate" sub-region located around NW area (Galicia), that is characterized by a cold and nutrient-rich upwelling during the spring-summer, and a "warm-temperate" sub-region that encompasses the north coast which lacks this oceanographic feature (OSPAR, 2010). As a result, different seaweeds dominate their subtidal bottoms (Bárbara et al., 2005; Gorostiaga et al., 2004). In terms of abundance, there is a NW – E gradient from cold- to warm-temperate seaweeds. Therefore, historically the cold-temperate kelps *Laminaria hyperborea* and *Saccharina latissima* and the fucoid *Himanthalia elongata* have found refuge in the NW corner, whereas the warm-temperate kelps *Laminaria ochroleuca* and *Saccorhiza polyschides* progresivelly decrease from NW to E, and the red alga *Gelidium corneum* and the fucoid *Cystoseira baccata* were abundant along the Central and Eastern Cantabrian coasts. Strong retractions and even local extinctions of populations of some of these species have been detected (Casado-Amezúa et al., 2019). Marine biota along the northern Iberian Peninsula is already responding to the shifts in the physical and chemical conditions of the environment (Díez et al., 2012; Lamela-Silvarrey et al., 2012; Voermman et al., 2013; Méndez-Sandín and Fernández, 2016; Piñeiro-Corbeira et al., 2016; Ramos et al., 2020).

Within this context, the present thesis focuses in assessing the impact of recent environmental changes on the subtidal vegetation of the southeastern Bay of Biscay (Fig. 1). This region was characterised by the presence of extensive stands of the perennial macrophytes *G. corneum* and *C. baccata*. The rhodophyte thrived in exposed to very exposed coastal stretches, whereas the *C. baccata* community did in semi-exposed areas (Díez et al., 2003; Borja et al., 2004). Both canopy species play an important role in the functioning of the rocky bottom subtidal ecosystem through provisions of food, habitat and shelter for many other organisms (Borja et al., 2004, Bustamante et al., 2014). These macrophytes form dense canopies that operate as nursery grounds and as shelter from environmental stressors and predation. They create a unique three-dimensional space which favours the settlement and growth of epiphytes and other associated species of algae and invertebrates. However, in recent decades *G. corneum* populations have suffered a considerable decline on several stretches of the Basque coast, whereas *C. baccata* only experience some local retreats (Borja et al., 2013, Díez et al., 2012b). It has been suggested that these changes are related to the global warming process in combination with other changing environmental factors operating at regional scale such as decreased nutrient concentrations, increased irradiance and increased wave energy.

This thesis describes the current status of the taxonomic composition, functional structure and diversity of subtidal vegetation along the southeastern Bay of Biscay, and assesses changes since 1991. Likewise, the consequences of the canopy decline for associated assemblages of invertebrates and algae are also investigated, as well as the loss of biomass provided by primary producers.

Moreover, a present community-environment relationship model was built, that allows to identify key factors influencing macroalgal assemblage distribution along Northern Iberian Peninsula and to project their distribution shifts under future climate change scenarios. Most studies deal with predicting the impact of climate change on single species. However, community-level approaches are becoming more relevant because they can predict how the biodiversity of entire ecosystems will respond to new environmental conditions (Guisan and Rahbek, 2011).

On the other hand, field experiments (mensurative and manipulative) which enable the key environmental factors to be monitored *in situ* may substantially improve our knowledge on how species and assemblages respond to climate change and what the main drivers of change are (Figueroa and Korbee, 2010). Therefore, through a field experiment the combined effect of solar radiation and nutrients availability on the photosynthetic acclimation and growth of *G. corneum* was investigated. These two environmental factors are suggested to underly the retreat detected in *G. corneum* beds. Given that growth is affected by all environmental, biochemical and physiological variables, this attribute may be used as an integrative functional indicator (Mártinez et al., 2012). In that experiment, changes in the whole assemblage have also been studied with respect to different levels of nutrients and light availability.

The goals mentioned above are pursued as follows:

- **Chapter 2** is divided into 2 sections where changes in subtidal community biomass over the past few decades (Section **2.1**) and year-on-year changes in diversity and function of associated assemblages (flora and fauna) are investigated at local scale (Section **2.2**).

- **Chapter 3** provides evidence at regional scale of declines in canopy-forming algae over the last thirty years, resulting in the structural impoverishment of subtidal vegetation.

- **Chapter 4** examines present spatial distribution patterns based on field data on subtidal macrophyte assemblages from Atlantic and Mediterranean coasts of the Iberian Peninsula and environmental data from the open database OCLE. The key factors influencing macroalgal assemblage distribution are identified, and an assemblage-environment relationship model is built in order to forecast shifts in assemblage distribution of northern Iberian Peninsula under future climate change scenarios (RCP4.5 and RCP8.5) by the end of the century.

- **Chapter 5** sets out a field experiment carried out in open coastal waters which seeks to provide further understanding of the declines in canopy-forming populations and shed light on the environmental factors that play a crucial role. This entails investigating the response of natural assemblages of *G.corneum* to different light conditions and different nutrient levels.

- **Chapter 6** gives an overall discussion of the thesis.

- The main conclusions are set out in **Chapter 7**.

- The bibliographical references used in the study are shown in **Chapter 8**.

- The **Annex** contains references to other publications related to this thesis and pictures that provide a photographic record of the different topics covered in it.

chapter 2

local scale: Kobaron coast

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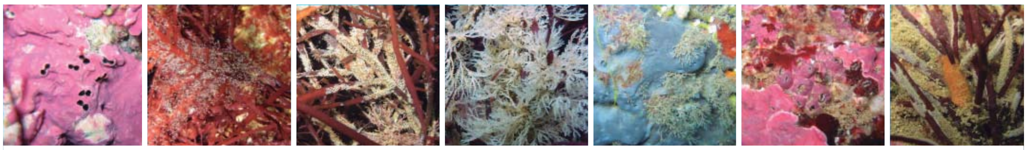

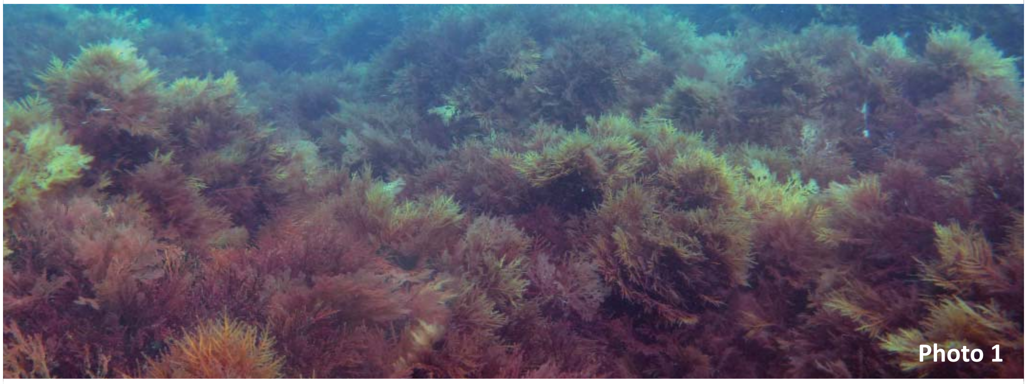

Photo 1

Photo 2

The structure of assemblages remained quite still from 1996 to 2006 displaying a complex association of algae and invertebrates species (Photo 1). Since 2008, along with the decay in canopy, the community developed to an entirely different one, dominated by morphologically simple algal forms unable to shelter well developed faunal populations (Photo 2). © Marine Benthos Research Group UPV/EHU.

chapter 2.1

NAHIARA MUGUERZA (2020) DOCTORAL THESIS pp. 39-54

Long-term surveys reveal abrupt canopy loss with immediate changes in diversity and functional traits

ABSTRACT Cumulative human pressures are threatening canopy-forming macroalgae worldwide, putting at risk the key ecosystem functions that they provide. Concurrent with declines in *Gelidium corneum* meadows, the present study investigates year-on-year changes in associated assemblages over a 21-year period (1996-2017) in the southeastern Bay of Biscay. The results show a non-linear loss of *G. corneum* that causes an abrupt shift towards new assemblages dominated by caespitose and encrusting forms. The rapid decline of morphologically complex algae and perennial forms is accompanied by a decrease in both epiphytic and epibenthic suspensivores and the loss of numerous associated species of fauna and flora. Along with the decline in canopy, a marked decrease in algae and invertebrate abundance is registered. After the canopy loss, a notable rise in algal density and a net increase in flora and fauna richness and evenness are detected. Moreover, a significant increase in the temporal variability of assemblages is identified, denoting greater stress after the shift. The implications of the changes observed and the consequences of the shift to a new state for the functioning of the ecosystem are discussed.

KEYWORDS Benthic ecology, Biogenic habitats, Climate change, Community composition, Macroalgal assemblage decline, Monitoring, Rocky invertebrates.

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LABURPENA

Denboran zehar egindako ikerketa jarraiek errezelaren galera bortitza agerian uzten dute, dibertsitatean eta ezaugarri funtzionaletan berehalako aldaketekin

Giza presioek mundu osoan errezela osatzen duten makroalgak mehatxatzen dituzte, eta ekosisteman ematen dituzten funtsezko funtzioak arriskuan jartzen ditu. *Gelidium corneum*-ek eratzen dituen belardiak izandako atzerapausoarekin batera, azterketa honek urtero 21 urtez (1996-2017) Bizkaiko Golkoko hego-ekialdean espezie elkartuen taldeetan izandako aldaketak ikertzen ditu. Emaitzen arabera, *G. corneum*-en galera ez-lineala gertatzen da, eta bat-bateko aldaketa bat ematen da forma soropilduak eta inkrustatzaileak nagusi diren komunitate berrietarantz. Morfologikoki konplexuak diren algen eta forma iraunkorren gainbehera azkarraren ondorioz, suspentsiboro epifitoak nahiz epibentonikoak gutxitu egiten dira, eta, horrez gain, alga eta ornogabeen arteko elkarte espezifikoak galtzen dira. Errezelaren gainbeherarekin batera, algen eta ornogabeen ugaritasuna nabarmen gutxitzen da. Errezela galdu ondoren, algen-dentsitatea gora egin du, flora eta faunaren aberastasuna eta ekitatibitatea egin duten bezala. Gainera, komunitateen denbora-aldakortasuna gora egin du ere, aldaketaren ondoren estres handiagoa adieraziz. Ikusitako aldaketen eraginak eta ekosistemaren funtzionamendurako egoera berri batera aldatzearen ondorioak aztertzen dira.

RESUMEN

Estudios continuados en el tiempo revelan una pérdida abrupta de la copa con cambios inmediatos en la diversidad y en los rasgos funcionales

La presión antropogénica amenaza a las macroalgas formadoras de copa en todo el mundo, poniendo en riesgo las funciones clave del ecosistema que proporcionan. En paralelo al retroceso en las praderas de *Gelidium corneum*, el presente estudio investiga de forma anual los cambios en los grupos de especies asociadas en el sureste del Golfo de Vizcaya durante un período de 21 años (1996-2017). Los resultados muestran una pérdida no lineal de *G. corneum*, que registra un cambio brusco hacia nuevas comunidades dominadas por formas cespitosas e incrustantes. El rápido declive de las algas morfológicamente complejas y las formas perennes se acompaña de una disminución tanto de los suspensivoros epífitos como epibentónicos, además de la pérdida de numerosas especies asociadas de flora y fauna. Junto con el declive de la copa, se registra una marcada disminución en la abundancia de algas e invertebrados. Después de la pérdida de la copa, se detecta un notable aumento de la densidad de algas y un aumento neto de la riqueza y equitatividad de flora y fauna. Además, se identifica un aumento significativo de la variabilidad temporal de las comunidades, lo que denota mayor estrés después del cambio. Se discuten las implicaciones de los cambios observados y las consecuencias para el funcionamiento del ecosistema del cambio hacia un nuevo estado.

1. INTRODUCTION

Global warming has caused changes across the oceans and predictions warn of the risk of abrupt, irreversible changes (IPCC, 2014b). Oceans face a cumulative impact not only from climate change but also from other anthropogenic stressors (Halpern et al., 2019). In the past few decades, investigations around the globe have reported severe declines and shifts in the geographical distribution of canopy-forming macroalgae (Harley et al., 2012; Martínez et al., 2018). In rocky shallow subtidal bottoms, turf-forming algae are replacing larger seaweeds. This entails structural and functional changes for ecosystems (Mineur et al., 2015). Under this scenario, major fields of research include processes that favor resilience in canopy forests, identifying the factors involved in the shift to turfing communities, consequences for ecosystem functions and services and for drawing up projections for the future, and management actions (Filbee-Dexter and Wernberg 2018; Strain et al. 2015).

Large perennial macroalgae act as foundation species in temperate coastal ecosystems by modulating critical ecosystem processes and promoting biodiversity in associated species. They are a fundamental biogenic habitat resource for dependent organisms such as invertebrates, fish, and other smaller algae. The three-dimensional space provided by these macrophytes offers refuge from predators or abiotic stressors and provides food resources and settlement space for many different taxa (Bertocci et al. 2014; Bulleri et al. 2012; Steneck et al. 2012). Moreover, canopy macroalgae have a major effect on the understory environment as they modify abiotic conditions (Begin et al. 2004, Russell, 2007). These engineering species play a significant role in primary production (Mann, 2000) as effective carbon sinks (Smith, 1981) and provide essential ecosystem services in coastal zones (Wernberg et al., 2011c). Canopy-forming species are key in supporting high levels of diversity in complex assemblages (Maggi et al., 2012, Piazzi et al., 2008) and the consequences of their loss include changes in species composition and a decrease in the abundance of rocky invertebrates (Bustamante et al. 2014; 2017; Christie et al. 2009; Wikström and Kautsky 2007). Canopy-forming macroalgae are being replaced by morphologically simple forms with warm-water affinity, which translates into a habitat simplification for the benthic community (Díez et al. 2013;Hawkins et al. 2009; Muguerza et al. 2017; Strain et al. 2014).

Climate change brings not just increased temperatures but other environmental shifts (Hoegh-Guldberg& Bruno, 2010). Thus, seawater is progressively acidifying (Doney et al., 2009), the frequency and intensity of coastal upwelling ecosystems are changing (Varela et al., 2015), and water stratification has intensified, limiting the supply of nutrients to the sunlit layer (Behrenfeld et al., 2006). Salinity structure is shifting (Sjøtun et al., 2015) and surface solar radiation (Wild et al 2008) has also increased all over the world. Wave power has increased globally (Reguero et al., 2019), as has the frequency of extreme high-intensity storms (Meehl et al., 2000). Other anthropogenic stressors such as pollution (Díez et al. 2014), sedimentation rates (Airoldi, 1998), and overfishing (Filbee-Dexter and Scheibling, 2014) are also co-acting factors in the process of decline of canopy forests (Benedetti-Cecchi et al., 2001a and 2001b, Harley et al., 2012; Rinne et al., 2011).

Most research on the decline of subtidal marine forests has focused on brown perennial algae such as kelps and fucoids (Filbee-Dexter and Wernerberg 2018, Mineur et al., 2015; Martínez et al., 2018; Teagle et al. 2017). There are still uncertainties and gaps to be filled by further research, but scientific efforts have provided in-depth knowledge concerning drivers and the impacts on biodiversity, ecosystem functions and services of losing these brown canopy-forming seaweeds. By contrast, the ongoing decline of the meadows formed by the red macrophyte *Gelidium corneum* still needs to be much better understood (Muguerza et al. 2017). Moreover, most research into the effect of climate change on seaweed communities has involved comparing specific sampling surveys, and there is little research based on long-term year-on-year data. Ecological responses may occur gradually or rapidly once a threshold has been reached, leading to permanent "regime shifts" (Harley and Paine, 2009). The study of large time-based datasets helps to provide a more accurate assessment of ecological variation (Hawkins et al., 2002; Magurran et al., 2010). This enables the pace of change to be identified, which is essential for predicting potential future scenarios. Moreover, an important step towards gaining a better understanding of the effect of such losses on the functioning of marine benthos is to gather information on parallel patterns of variation in benthic species composition and traits (Duffy et al., 2007). In this regard, invertebrates associated with canopy-forming macroalgae are good bioindicators of environmental conditions and play a key role in the functioning and properties of the ecosystem (Norderhaug and Christie, 2011). The combined study of the association of flora and fauna and their functional categorization is essential in efforts to link shifts in structure to ecological functions that sustain multiple ecological processes (Bremmer et al. 2005; Michaeli and Halperm 2005; Norderhaug and Christie 2011).

Previous investigations in the study area considered here, based on long term datasets, have provided evidence that the biomasss of *Gelidium corneum* has declined substantially since the 1990´s (Borja et al., 2013). Based on specific sampling surveys, other studies have revealed that the canopy decline involves increases in morphologically simple forms and subsequent increases in algal taxa richness and density (Diez et al, 2012, Muguerza et al., 2017). Our study aims to increase knowledge on the pace of change and to detect possible intermediate states by investigating the entire benthic community of algae and invertebrates. By examining changes in rocky subtidal assemblages from the southeastern Bay of Biscay over a 21-year period (1996-2017), we specifically seek to: (1) determine the pace of change in the *G. corneum* canopy; (2) assess changes in the abundance of associated invertebrates and algae; (3) estimate trends in invertebrate and algal richness, density and evenness.; and (4) assess shifts in the abundance and proportions of organisms with different functional traits. The taxonomic and functional approaches taken enable the implications of the changes observed for the ecosystem function to be discussed.

2. MATERIAL AND METHODS

2.1. Study area

The assemblages targeted in this study are located on the Basque Coast, in the southeastern Bay of Biscay (eastern Cantabrian Sea, northern Spain) (Fig. 1). Biogeographically, this area is part of the warm temperate North Eastern Atlantic Region (van den Hoek and Breeman, 1990). Specifically, the Cantabrian Sea is predicted to be one of the areas most affected by sea-temperature warming (Muller et al., 2009). This stretch of coastline is open to strong NW swell (Galparsoro et al., 2010; González et al., 2004) and its average sea-surface temperature (SST) ranges from 12°C in February to 22°C in August (Valencia et al., 2004), though in the past few decades surface waters have gradually warmed (Goikoetxea et al., 2009) by as much as 1°C in summer (Díez et al., 2012). Moreover, the southeastern Bay of Biscay is undergoing a changing wave regime with higher number of significant wave height (5 m) that is key for the detachment and breaking of *Gelidium corneum* fronds (Borja et al., 2013; 2018).

2.2. Field sampling

The data analyzed here comes from two different monitoring surveys which started in the 1990's and have a high enough temporal sampling resolution to ensure accuracy when looking for trends. Two sites separated by a few hundred meters were selected for this study (Site 1: 43° 21'13.93"N – 3° 07'47.77" W, Site 2: 43° 21'17.65"N – 3° 07'46.40"W). Both are located in non-conta-

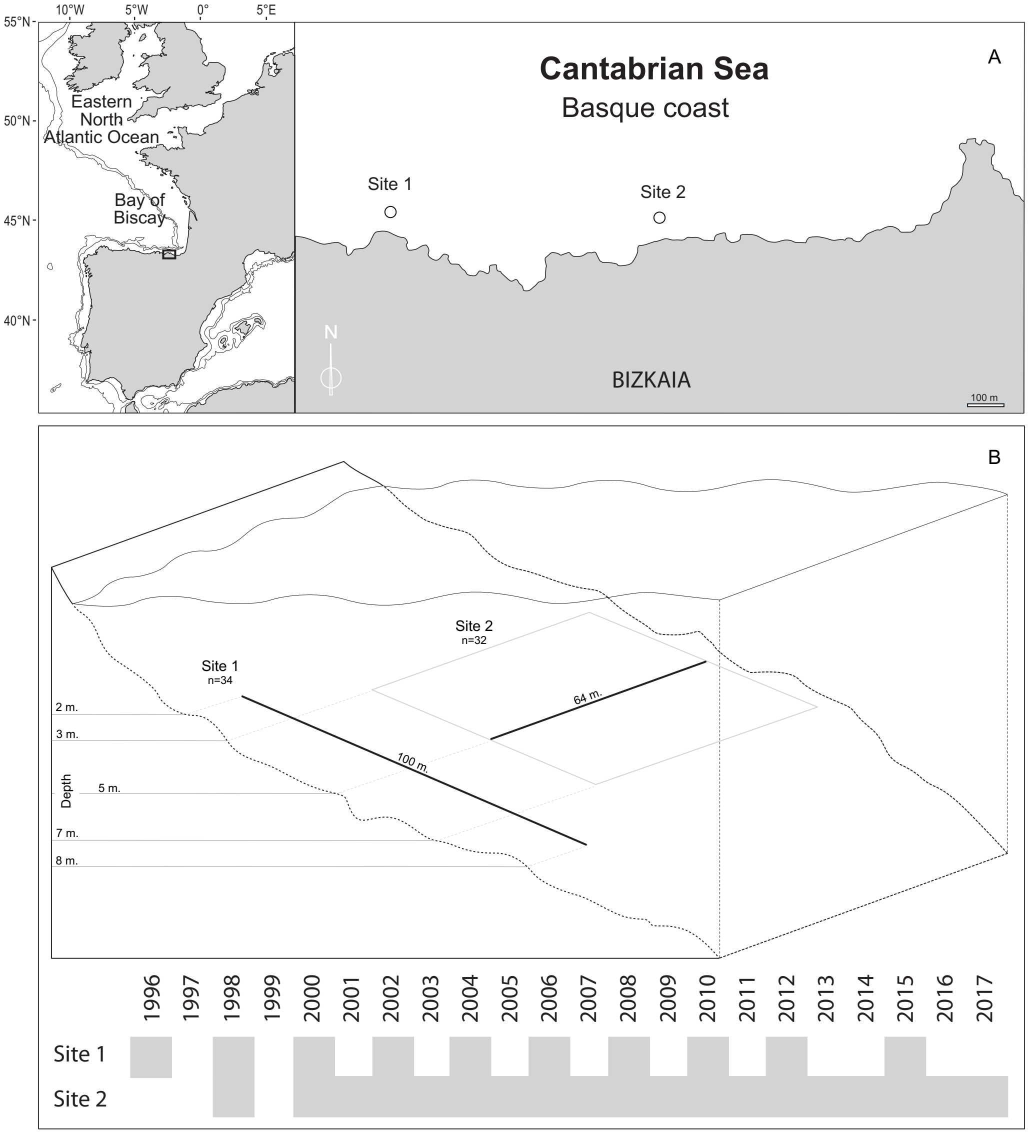


Fig. 1 Study area showing the location of the sites. The inset shows the study area (delimited by a rectangle) on the Southern Bay of Biscay (A). Visual scheme of the sampling strategy at each site. Solid black lines represent the transect (B).

minated areas that are not heavily affected by human perturbations and have good environmental conditions (Borja et al., 2018). Particularly, there has been no exploitation of *Gelidium corneum* at either site since 2000, when the Basque Government prohibited it (Borja et al., 2003). Notably, our data shows well-developed *G. corneum* assemblages with mean abundances of up to 80% in the early years of the study period (1996-2006). At Site 1 10 samplings were carried out: one every 2 years from 1996 to 2012 (9 campaigns) and the last in 2015. At Site 2 there were 19 sampling campaigns: the first in 1998, the second in 2000, and then every year until 2017. This study therefore covers data from a 21-year period (1996-2017).

At both sites, the assemblages investigated were those found on the continuous bedrock platform with gentle to moderate slopes in the shallow subtidal zone. At each sampling time the boat was anchored using a GPS device, so that the transect starting point was in approximately the same place. At Site 1 a 100 m long transect was laid out perpendicularly to the coastline, starting at a depth of 2 m below extreme low water spring tides and covering an average depth range of 2–8 m. Along the transect, quadrats of 50 x 50 cm were sampled every 3 m, making a total of 34 sampling units per year (n=34), except in 2015, for which n=21 (with quadrats every 5 m). At Site 2 a transect parallel to the coast was laid out at a depth of 5 m and quadrats on both sides were randomly located, covering an average depth range of 3–7 m. From 2001 to 2017 a total of 32 quadrats were randomly sampled per year (n=32). In 1998 and 2000, 10 quadrats were laid out every 10 m along a 100 m long transect (n=10). The data analyzed here therefore covers 887 sampling units (323 at Site 1; 564 at Site 2).

At both sites, the cover of the vegetation and macroinvertebrate taxa was estimated visually. Abundance was estimated using the cover scale proposed by Braun-Blanquet (1951): += presence; 1= 1–5%; 2= 5–25%; 3= 25–50%; 4= 50–75%; 5= 75–100%. The mean cover of invertebrate and algae species was calculated for each quadrat using the median of each range. Organisms were identified taxonomically at species level, though in a few cases higher taxonomic levels were used. Species not identified in the field were preserved in formalin or alcohol for subsequent identification.

2.3. Response variables and Statistical analyses

The spatio-temporal variability of the taxonomic structure of the community was studied in a multivariate context. Two approaches were used: Q-mode analyses to address patterns between samples (i.e. sites and time) (Clarke, 1993) and R-mode analyses to display relationships between variables (i.e. between invertebrates and algae species) (Somerfield and Clarke, 2013).

A distance-based permutational multivariate analysis of variance (PERMANOVA, Anderson et al., 2008) was performed to test for differences in the multivariate structure of assemblages attributable to time and sites. The design for the analyses involved 2 factors: Time (Ti: 19 levels; random) and Site (Si: 2 levels; random). The Bray-Curtis index was used to determine the similarity between pairs of samples. Each term in the analyses was tested using a total of 4999 random permutations of appropriate units (Anderson et al., 2008). Significant terms were investigated through pair-wise comparisons (between years within sites) using PERMANOVA t-testing and 999 permutations. The *a priori* significance level was set at a = 0.01. Non-metric Multidimensional scaling (nMDS) analyses were performed using 29 measures obtained by using overall centroids for Ti x Si. Similarity percentage analyses (SIMPER) were performed to determine which invertebrate or algae taxa contributed most to the patterns observed. The variables selected were those that accounted for up to 70% of the dissimilarity between the groups compared. Patterns indicate that samples fell into two distinct groups, so a permutation test for homogeneity of multivariate dispersion among years was performed for each site to explore the spatial heterogeneity of assemblages within groups (PERMDISP, Anderson, 2006).

Coherent Plots in combination with Shade Plots were drawn up at each site individually (Somerfield and Clarke, 2013). Coherent Plots were used to analyze significant relationships between variables (i.e. species) and thus identify clusters of species in which there is statistical support for the interpretation that they covaried consistently across samples (i.e. years). Shade Plots were plotted simultaneously to display the abundance of species over the years with rectangles whose gradual shading deepened with increasing species abundance. Analyses were performed using the Index of Association (Somerfield and Clarke, 2013). Only taxa with an abundance level of at least 1% in any of the years studied were included in the analyses. The resulting groups of taxa were tested for statistical significance using a Similarity Profiles (SIMPROF) test with 999 permutations. Given that increasing the significance level makes no difference to the overall groupings (Somerfield and Clarke, 2013), a significance level of 5% was selected in order to favor the display of groups of species that behaved similarly over the years.

For single response variables, both taxonomic and morpho-functional trait-based approaches were used. To calculate functional variables, the cover in each sample was aggregated into 3 traits for invertebrate taxa and 3 more traits for algae (Table 1). Biological traits for invertebrates reflected their behavior in terms of habitat, adult mobility and trophic strategy, which are considered to be among the main distinguishable

Table 1. Biological traits and categories used to describe ecological functioning in invertebrate and macroalgae assemblages.

Trait	**Category**
Invertebrates	
Living Habit	Epibenthic
	Epiphytic
Adult Mobility	Mobile
	Sessile
Trophic strategy	Herbivore
	Suspension feeder
	Detritivore
	Omnivore
	Carnivore
Algae	
Life Form	Annual
	Perennial
Morphology	Simple
	Complex
Vertical Layering	Canopy
	Epiphytic
	Basal
	Crustose

Table 2. PERMANOVA results and pair-wise comparisons on assemblages. Bold print indicates significant results.

Source	**df**	**MS**	***F***	***p***
Ti	19	48302	33956	**0.001**
Si	1	32227	26471	0.026
TixSi	8	13202	11453	**0.001**
Residual	858	1152.8		
Total	886			
Pair-wise comparisons				
TixSi				
		Site 1	1998 *vs* 2000	0.024
			2002 *vs* 2004	0.021
			remaining	< **0.01**
		Site 2	all	< **0.01**

features of benthic invertebrates (Wahl, 2009). To categorize each trait, the BIOTIC catalogue (MarLin, 2006) was taken as a reference. Information on the traits of invertebrates was obtained from a variety of primary and secondary literature. Vegetation traits reflected life form, vertical layering distribution, and morphology (i.e. structural complexity). Simple forms include filamentous, polysiphonated and foliose non-corticated algae, whereas complex algae include all corticated forms (foliose and terete), leathery forms, articulated calcareous and crustose forms (calcareous and non-calcareous) following the categorization in Muguerza et al., 2017 modified from Díez et al, 2010. Taxonomic variables were calculated for invertebrates and algae individually, including total abundance, taxa richness (S),density (n) (i.e. number of species per quadrat, Gotelli and Colwell, 2001), and Pielou's index for evenness (J'). Data on single variables was plotted by calculating the mean for each sampling year and separately for the two sites studied.

All statistical analyses were conducted on non-transformed data, using the PRIMER 7 (Plymouth Routines in Multivariate Ecological Research) software package (Clarke and Gorley, 2015).

3. RESULTS

3.1. Multivariate structure of assemblages

In the Permutational multivariate analysis of variance (PERMANOVA), the interaction term (Ti x Si) was significant (Table 2). Pairwise comparisons showed significant results for all years compared within each site ex-

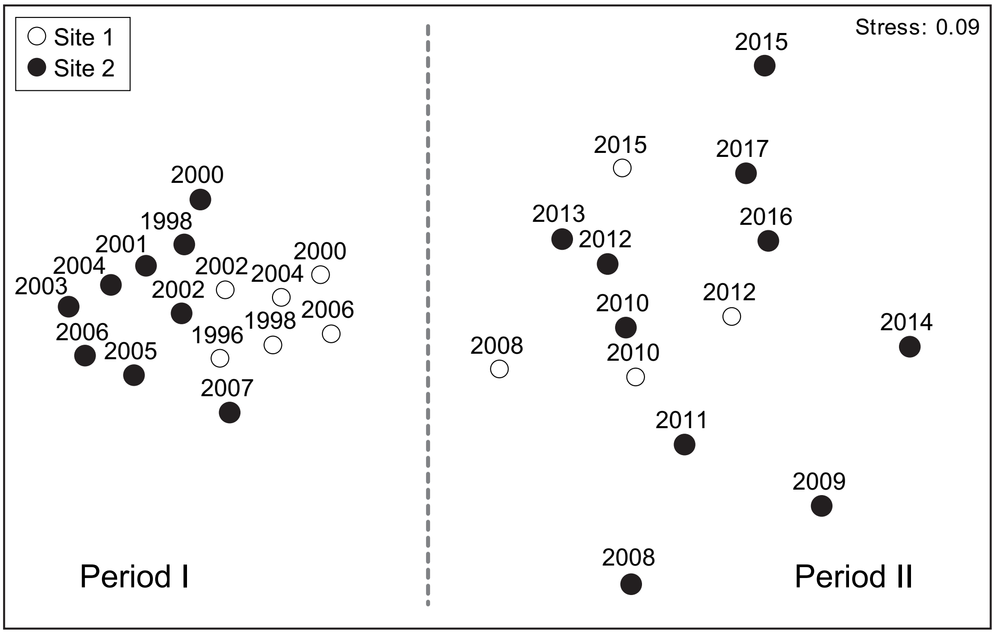


Fig. 2. Non-metric MDS ordination of taxa composition and abundance based on the Bray-Curtis dissimilarity coefficient of square-root transformed data. For the representation overall centroids for Time x Location are used.

Table 3. Average Bray-Curtis dissimilarity (untransformed data) values between ordination analysis groups and contributions of the most important taxa (δ_i).

Av. dissimilarity = 68.06	Ave. Abund Period I *vs* Period II	δ_i	δ_i /SD(δ_i)	δ_i
Taxa				
Gelidium corneum	71.0 *vs* 6.5	13.94	4.64	20.49
Mesophyllum lichenoides	66.7 *vs* 37.8	6.27	2.11	9.21
Dictyota dichotoma	18.4 *vs* 0.1	3.82	1.19	5.62
Plocamium cartilagineum	16.5 *vs* 1.6	3.17	1.76	4.65
Electra pilosa	13.8 *vs* 0.4	2.79	1.21	4.09
Aphanocladia stichidiosa	0.0 *vs* 11.8	2.51	1.97	3.69
Zanardinia typus	5.5 *vs* 16.8	2.50	1.36	3.67
Codium decorticatum	1.5 *vs* 11.0	2.08	0.92	3.05
Gastrochaena dubia	14.9 *vs* 7.3	2.01	1.40	2.95
Aglaothamnion tenuissimum	0.7 *vs* 8.2	1.70	1.10	2.50
Cystoseira baccata	5.3 *vs* 2.7	1.31	0.88	1.93
Falkenbergia rufolanosa	3.2 *vs* 6.5	1.25	0.71	1.83
Crisia spp.	5.9 *vs* 0.6	1.18	1.49	1.73
Dasysiphonia japonica	0.1 *vs* 4.1	0.91	0.64	1.33
Obelia geniculata	4.2 *vs* 1.4	0.88	0.75	1.30
Rhodymenia pseudopalmata	4.6 *vs* 0.4	0.88	1.44	1.29
Asparagopsis armata	0.4 *vs* 4.0	0.86	0.73	1.27

cept the comparisons 1998 *vs* 2000 and 2002 *vs* 2004 at Site 1. The non-metric MDS ordination diagram (Fig. 2) shows that assemblages are arranged in two separate groups with an average dissimilarity of 68% (Table 3). One group includes all the sampling campaigns from 1996 to 2007 (Period I) while the other includes all those from 2008 to 2017 (Period II). Comparatively, samples from Period I are spatially closer than those from Period II. By contrast, from 2008 onwards a greater dispersion of samples is observed. Notably, greater temporal heterogeneity of assemblages is detected at Site 2 than at Site 1, particularly in Period II. Indeed, analyses of multivariate dispersion show that from 2008 onwards the spatial heterogeneity of assemblages increased significantly at both sites (Fig. 3).

SIMPER analyses select several taxa whose abundance decreased from Period I to Period II (Table 3). These include some algae species such as *Gelidium corneum, Mesophyllum lichenoides, Dictyota dichotoma, Plocamium cartilagineum, Rhodymenia pseudopalmata* and invertebrates such as *Electra pilosa, Gastrochae nadubia, Crisia* spp. and *Obelia geniculata*. Conversely, in Period II significant increases were observed

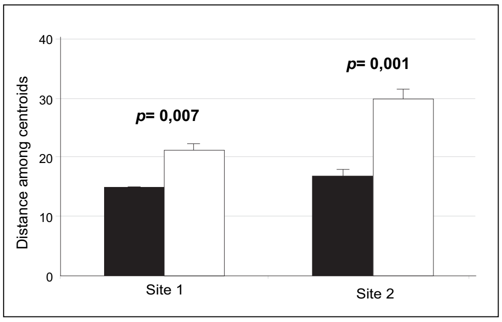


Fig. 3 Mean and standard error distance from assemblages to centroids between years in Bray-Curtis space for Site 1 and Site 2. Black bars represent Period I (1996-2007); White bars represent Period II (2008-2017).

in other species, but only for the following algae: *Aphanocladia stichidiosa, Zanardiniatypus, Codium decorticatum, Aglaothamnion* spp., *Falkenbergia rufolanosa, Dasysiphonia japonica* and *Asparagopsis armata*.

The agglomerative clustering of the inter-species association matrix, in combination with the Shade Plot, shows a quite similar pattern across the years at the two sites investigated (Fig. 4). Period I (1996-2007) is characterized by coherent groups of both algae and associated invertebrate species and Period II comprises mainly algal species that appeared and dominated from 2008 onwards. In Period I the invertebrate and algal species that characterized both sites were essentially the same. They are shown as coherent Group I at Site 1 and coherent Groups I to VI at Site 2. The associated species that differentiated Period I include the large macrophytes *Cystoseira baccata* and *Gelidium corneum* with their epiphytes *Dictyota dichotoma* and *Plocamium cartilagineum*, basal species such as *Cryptopleura ramosa*, *Acrosorium ciliolatum* and *Rhodymenia pseudopalmata,* plus the crustose species *Mesophyllum lichenoides* and invertebrate species typically growing in algae such as the bryozoans *Electra pilosa* and *Crisia* spp. However there were also other species growing in hard substrata such as *Balanus*

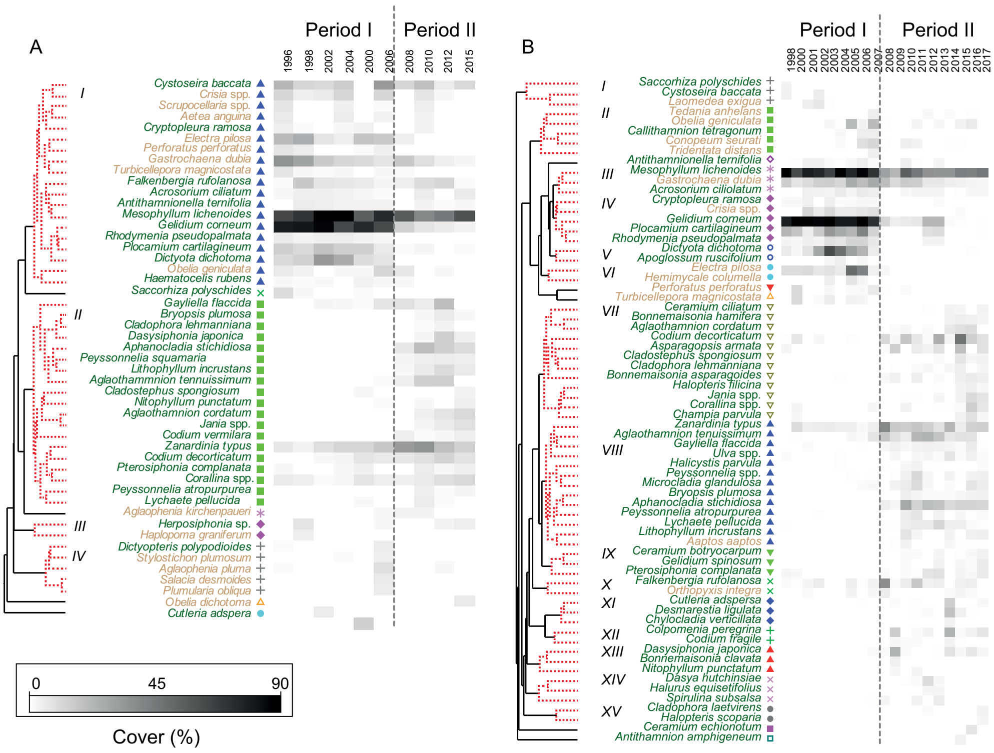


Fig. 4 Shade plots of the data matrix for the years studied and dendrogram based on the Index of Association between taxa showing 'coherent groups' at Site 1 (A) and at Site 2 (B). All data are untransformed. A blank space indicates the absence of that taxon in that year. Solid lines indicate significant groups of variables ($p < 0.05$), Dashed lines indicate groups of variables for which the null hypothesis cannot be rejected ($p > 0.05$). Green text represents algae taxa; brown text represents invertebrate taxa.

perforatus and *Gastrochaena dubia*. As shown in the shade plot, most of these species either disappear or become much less abundant in the second period.

After 2008, coherent groups (Site 1: Group II; Site 2: Groups VII to XV) comprise almost exclusively algae species that were hardle found at all in the Period I. These include several turf forming algae species such as *Aphanocladia stichidiosa*, *Aglaothamniontenuissimum*, *Dasysiphonia japonica,* the annual macrophyte *Codium decorticatum* and the non-calcareus incrusting *Zanardiniatypus*. At Site 2, the only two invertebrate taxa that accompany algae species in Group VIII and Group X are occasional and non abundant. Finally, at Site 1 Groups III, IV and singletons are formed by invertebrates or algae that appeared only sporadically at one sampling time in Period I.

3.2. Single response variables

Similar trends were detected at both sites for all the response variables studied (total abundance, taxa richness, density and evenness). The greatest change was the decrease in total abundance of both invertebrates and algae. Benthic cover varied considerably over the study period but a drastic decline in algal and animal forms in 2007, 2008, and 2009 can be observed (Fig 5 A). A slight recovery for algae cover only can be seen from 2010 onwards, whilst invertebrates remain at very low values. Several reductions in species richness can be seen but their timing does not always coincide for fauna and flora (Fig 5 B). How-

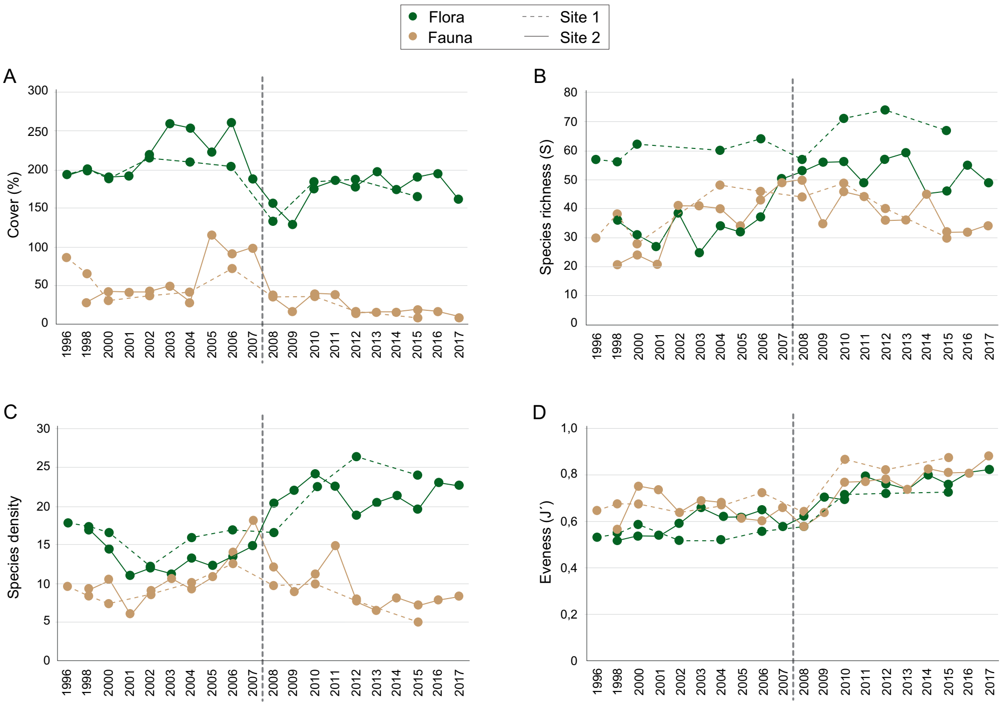
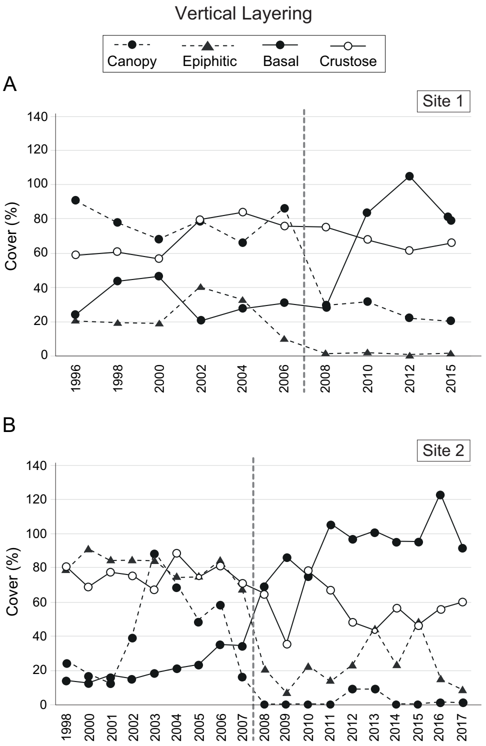


Fig. 5 Variation over time in total abundance (A), species richness (B), density (C), and Pielou's evenness (D) of algae and invertebrate assemblages at Site 1 and Site 2. Error bars are omitted to provide a better display. The thick dashed line separates years within Period I and Period II.

ever, a net increase in flora and fauna richness by the end of the study is detected. The density levels for algae and invertebrates show up as similar in Period I (1996-2007), but from 2008 onwards algal density increases whereas invertebrate density decreases (Fig. 5 C). Finally, the evenness of the community remains quite stable in Period I (Fig. 5 D), but in Period II (2008-2017) there is a continuous increase for animals and algae.

Considering the seaweed functional approach, both sites show considerable variations over the years but a distinct pattern of assemblages is evident between the periods (Figs. 6 and 7). Regarding the vertical distribution of vegetation, in Period I (1996-2006) canopy and crustose species show abundances which are quite stable and higher than those of basal species (Fig. 6). For that period, a well-structured seaweed assemblage shows up, formed by four vertical layers (Canopy, epiphytic, basal, and encrusting). By 2009, the canopy layer is almost non-existent while the basal layer has developed notably and maintains its abundance levels up to the end of the study. The crustose layer decreases but still shows fairly high abundance levels, whereas the epiphytic layer practically disappears. Similarly, major changes are detected in morphology and in life forms. Complex (Fig. 7 A)



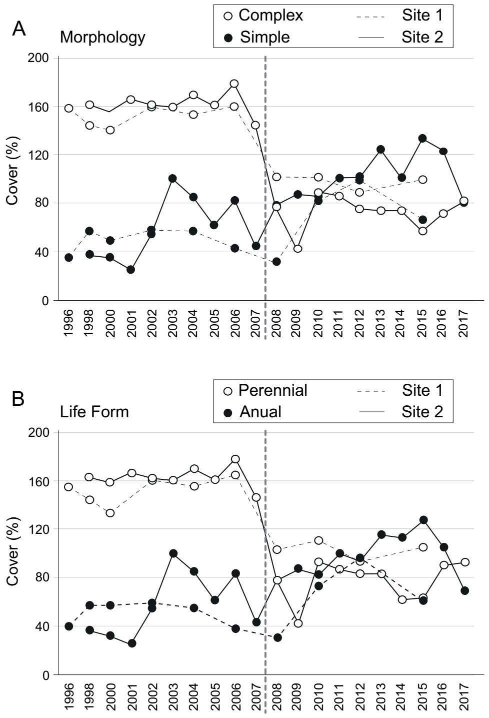


Fig. 6 Variation over time in the vertical layering distribution of macroalgae assemblages at Site 1 (A) and Site 2 (B). Error bars are omitted to provide a better display. The thick dashed line separates years within Period I and Period II.

Fig. 7 Variation over time in the morphology (A) and life forms (B) of macroalgae assemblages at Site 1 and Site 2. Error bars are omitted to provide a better display. The thick dashed line separates years within Period I and Period II.

and perennial (Fig. 7 B) species are quite stable and dominant from 1996 to 2006 but decline after 2008, while simple and annual forms increase notably.

Epiphytic and epibenthic invertebrates show quite comparable patterns at the two sites over time (Fig. 8 A). In general, before 2008 the abundance levels found for epiphytic and epibenthic forms are similar. However, in Period II epibenthic forms become comparatively more abundant, although they also show a steep decline at the end of the study. Variations in the movement capacity of invertebrates are observed over the years in sessile forms while mobile invertebrates, which are otherwise less abundant, remain markedly stable over time (Fig. 8 B). By the end of the study sessile species have declined to minimum values. Regarding trophic guilds, the same variations are displayed for suspension feeders as for adult sessile forms (Fig. 9). The suspensivore fraction is by far the most abundant trophic strategy over time. It shows significant changes, while the other strategies remain quite stable.

4. DISCUSSION

Consistently with global findings, our study reveals a retreat over the last few decades of the red alga *Gelidium corneum,* a key founda-

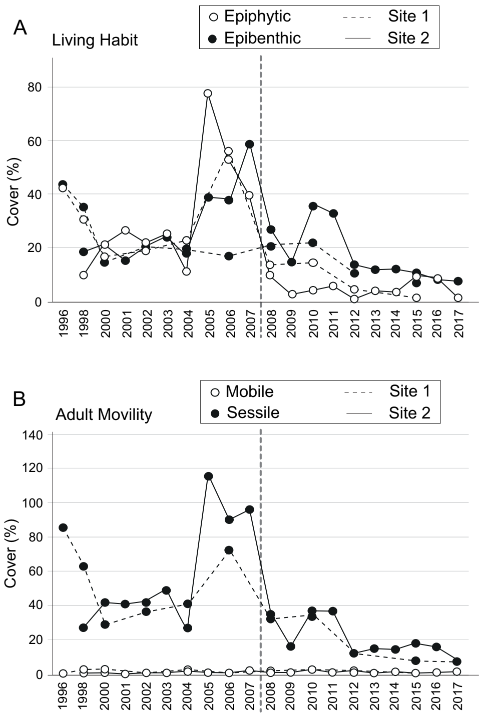


Fig. 8 Variation over time in the living habit (A) and adult mobility (B) of invertebrate assemblages at Site 1 and Site 2. Error bars are omitted to provide a better display. The thick dashed line separates years within Period I and Period II.

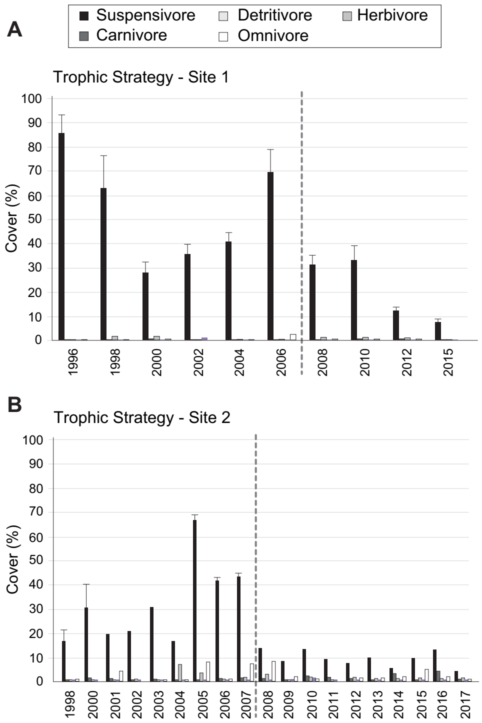


Fig. 9 Variation over time in the trophic strategy of invertebrates in faunal assemblages at Site 1 (A) and Site 2 (B). Error bars with values < 1 are omitted. The thick dashed line separates years within Period I and Period II.

tion species, involving significant changes in most of the variables studied. The decline of this species is not linear but occured abruptly in 2008, and no signs of recovery have been reported since. Several environmental factors must be considered when inferring past or future ecological responses to climate change (Harley and Paine, 2009; Stuart et al., 2010). As an adequate explanation is sought, it seems more than likely that the extreme wave energy events reported in the study area in 2007 and 2008, with wave height threshold exceedances of 5m (Borja et al., 2013), caused the sudden shift identified in our study. The decline and lack of recovery of *G. corneum* might, however, also respond to other factors. Some investigations show that responses to ocean warming may not be gradual and that shifts can take place when physiological tipping-points are overreached (Harley and Paine, 2009; Pansch et al., 2018). Indeed, previous studies carried out in the southeastern Bay of Biscay have revealed morphological and biochemical stress symptoms in *G. corneum* related to the ongoing increase in water temperature, reduction in nutrient availability, and periods of high irradiance levels (Quintano et al., 2013). When temperature is non-optimal, growth photosynthesis is negatively affected (Altamirano et al. 2003; Figueroa et al. 2009; Lüning 1990). Algae are temperature-dependent organisms so their resilience is reduced and species become more vulnerable to other stressors (Whal et al., 2015). Thus, the extreme wave events probably acted synergistically on already stressed populations of *G. corneum*, resulting in the sudden and permanent loss of this key macrophyte.

Significant temporal differences in the the multivariate structure of assemblages are found over the years. This can be explained in part by natural variability, which is a particularly relevant typical feature of rocky benthic communities (Fraschetti et al. 2005; Underwood 1994). The fact that greater variability was found at Site 2 than at Site 1 can be explained by the greater temporal resolution of data at Site 2. Remarkably, this does not mask the shift, which could have gone undetected because of the higher temporal-scale natural variability. Assemblages are arranged in two periods, with a notable increase in heterogeneity from 2008 onwards. Variations in the multivariate dispersion of assemblages have been identified as a potentially important indicator of stress in marine communities (Bevilacqua et al. 2012; Chapman et al. 1995; Warwick and Clarke 1993). Within dense, well-developed canopies of *Gelidium corneum,* greater stability is observed as this alga is competitively dominant and inhibits the growth of most other algae through physical abrasion and by reducing water flow and light (Russell 2007; Wernberg et al. 2005). At this stage, few other complex algae forms make up the community: the encrusting perennial algae *Mesophyllum lichenoides,* the basal *Rhodymenia pseudopalmata,* and the epiphytic species *Plocamium cartilagineum* and *Dictyota dichotoma*. By contrast, after the loss of the canopy new feedback processes appear as a response, favoring the development of an assemblage that is less stable over time. Several non perennial and short-lived algae such as *Aphanocladia stichidiosa*, *Codium decorticatum*, *Aglaothamnion tenuissimum*, *Falkenbergia rufolanosa*, *Dasysiphonia japonica* and *Asparagopsis armata* dominate this last stage.

Another major outcome is that rich associations of alga and invertebrate taxa are only found in the first part of the study. The principal consequence of the lack of such associations from 2008 onwards seems to be a decline in the biogenic habitat provided by *Gelidium corneum,* since most associated invertebrate forms were found growing on it. Indeed, practically no invertebrate species show up in the coherent plots after 2008. The loss of specific associations highlights particular taxa which are more likely to decrease drastically at local or even regional scale. They include algae such as *Gelidium corneum*, *Plocamium cartilagineum*, *Dictyota dichotoma*, *Rhodymenia pseudopalmata,* and *Acrosorium ciliolatum* and invertebrates such as *Electra pilosa*, *Turbicellepora magnicostata*, *Crisia* spp., *Scrupocellaria* spp., and *Aetea anguina*. Furthermore, most of these taxa are sensitive species that have been shown to be less tolerant to human stressors such as eutrophication and toxicity from sewage (Díez et al. 2009; Gorostiaga et al. 2004; Saiz-Salinas and Isasi-Urdangarin 1994).). Thus, the neighboring populations available could be important limiting factors for connectivity and recolonization, especially considering that in general macroalgae have limited dispersal (Kinlan and Gaines, 2003). To help increase the resilience and connectivity of the remaining canopy dominated assemblages, we stress the need to carry out for conservation actions already proposed by the scientific community involving the reduction of anthropogenic stressors, the implementation of protected marine areas, and active seaweed restoration plans (Jonsson et al. 2018; Mineur et al. 2015; Vergés et al. 2018).

G. corneum formed extensive stands in the 80s and 90s (Gorostiaga, 1994) but drastic declines have since been observed (Borja et al. 2013; Díez et al. 2012; Muguerza et al. 2017). Along with this loss, our findings reveal a marked decrease in benthic cover in 2008. Levels have recovered partly for algae but remain very low for invertebrates. Benthic organisms are known to be of great importance for all the processes that connect the bottom substrate and the water column (Griffiths et al., 2017). The loss of perennial algae may result in severe changes for essential ecosystem functions such as nutrient recycling and energy transfer (Kotta and Möller, 2014). Major changes in invertebrate abundance are found in suspension feeders, which remain the dominant strategy. Suspension feeding transfers available organic material from the pelagic zone to the benthos. When native suspension feeders decline, invasive species might support the persistence of suspension feeding traits (Griffths et al., 2017). However, our results indicate that no other invertebrate species or trophic traits have benefited from the new environmental conditions. Nevertheless, a wide array of processes affecting the benthic pelagic coupling might still be expected. A decline in water filtration capacity is known to cause increased phytoplankton production and reductions in water quality (Kemp et al., 2005) while an increase in the feeding strategy has the opposite effects (Cloern and Jassby, 2012). Projections for the future are difficult to make because there is limited knowledge and understanding of physical and biological effects, but our results indicate severe alterations in key organisms for benthic-pelagic processes.

The outcomes of this study coincide with the global phenomenon described in temperate reefs of flattening of subtidal forests, leading to increased dominance by turf forming algae (Filbee-Dexter and Wenberg 2018; Martínez et al. 2018; Mineur et al. 2014). Moreover, our functional approach reveals that after the decline of larger macroalgae only two layers out of four remain: the basal layer is increasing, the encrusting layer shows no changes and the canopy and epiphytic layers have practically disappeared. It is suggested that in the absence of the canopy, turf-forming algae rapidly come to use the new light conditions and nutrients available, and thus increase significantly and dominate this open space on hard subtidal substrate (Fowler-Walker and Connell 2002; Irving et al., 2004). Our results reveal that the establishment of the basal layer does not significantly affect the encrusting layer, which maintains high abundance levels. We have, however, observed specific changes in crustose species such as a decrease in the calcareous *Mesophyllum lichenoides* in favor of the non calcareous meridional *Zanardinia typus*.

Interestingly, when the basal layer becomes dominant, seaweed density increases but invertebrate levels undergo an overall net decrease. Numerous opportunistic and annual algae species with simple morphology and fast growth rates proliferate. With these new conditions, competitive interactions between the basal vegetation and invertebrates arise. As a result, sessile invertebrates (both epiphytic and epibenthic species) seem to find it hard to obtain the biological and physical resources that they need to expand locally and increase their representation. However, algal species continue to be more competitive and better colonizers than invertebrates at shallow depths. This finding reinforces the idea that the biogenic space provided by the canopy is a limiting resource for the development of invertebrates in shallow rocky subtidals (Bustamante et al., 2014, 2017).

The complexity and structure of habitat provided by canopy-forming species is known to influence the composition, abundance and richness of associated species; in this way larger thallus forms provide additional surface area to support more associated species of algae or invertebrates (Teagle and Smale, 2018). However, after the disappearance of the biogenic space provided by *Gelidium corneum* an increase in species richness is found, especially for flora species. This result has been observed previously in the study area (Muguerza et al., 2017), which could imply that communities have not yet evolved to a new steady state and that species richness is being maximized because ecological disturbance is at intermediate levels (Connell, 1978). In fact, invertebrate and seaweed evenness levels have also become higher in the absence of the canopy, indicating that no single species of animal or algae has taken advantage of the new environmental conditions during the period of the investigation.

The foregoing describes a community shift to a new phase involving major losses of large macrophytes and suspensivores and the disappearance of specific associations between algae and invertebrates. Habitat simplification due to the loss of canopy availability has changed key benthic ecosystem properties in a fairly short period of time. Data from monitoring surveys on the area reveals no signs of recovery so far, with flat subtidals dominated by turfs. Management priorities should include specific functional targets to preserve the remaining perennial marine canopy forests and associated invertebrates. Scientific efforts are required to bring about restoration by successful transplantation of key canopy seaweeds. Finally, a better understanding of the links between benthic-pelagic processes and their effects on ecosystem functioning would help to set out future management strategies.

chapter 2.2

NAHIARA MUGUERZA (2020) DOCTORAL THESIS pp. 55-71

Decades of biomass loss in the shallow rocky vegetation of the southern Bay of Biscay

ABSTRACT Canopy forming macroalgae dominate the standing biomass in temperate rocky shallow subtidal zones worldwide. This study seeks to assess changes over time in the biomass of subtidal communities at different depths on the westernmost part of the Basque coast from 1982 to 2014. A significant decline in the standing stock of the perennial rhodophyte *Gelidium corneum* is detected, especially at depths of 3 and 6 m, so that there was only a testimonial presence by the end of the study. In the place of this foundation species, large- and medium-sized species such as the canopy species *Treptacantha baccata* established themselves. In addition, an increase in the heterogeneity of the vegetation is found towards 2014, mainly as a consequence of the proliferation of turf forming articulated coralline species (*Corallina* spp.) and morphologically simple and ephemeral algae such as *Aphanocladia stichidiosa*, *Lychaete pellucida*, *Aglaothamniom pseudobyssoides* or *Microcladia glandulosa*. These results are discussed in relation to potential consequences of the loss of canopy biomass, as the newly established species might not fulfill the ecological function provided by *G. corneum*.

KEYWORDS Climate change, Macroalgal community, Productivity, Species composition, Subtidal assemblages.

LABURPENA

Hamarkadetan biomasaren galera substratu gogorreko azaleko landaredian Bizkaiko Golkoaren hegoaldean

Errezela eratzen duten makroalgek mundu osoko sakonera txikiko mareaz azpiko eremu epeletan biomasa menderatzen dute. Ikerketa honen bidez, 1982tik 2014ra bitartean mareaz azpiko komunitateen biomasan izandako aldaketak ebaluatu nahi dira hainbat sakoneratan, euskal kostaldearen mendebaldeko zatian. *Gelidium corneum* rodofito iraunkorraren stocka nabarmen murriztu da, batez ere 3 eta 6 metroko sakoneran; beraz, ikerketaren amaieran presentzia testimoniala baino ez zen izan. Espezie egituratzaile honen tokian, tamaina handi eta ertaineko espezieak ezarri ziren, *Treptacantha baccata* kasu. Gainera, landarediaren heterogeneotasuna handitu egin da 2014. urtean, batez ere soropila eratzen duten espezie koralinazeo artikulatuak (*Corallina* spp.) eta alga morfologikoki sinpleak eta iragankorrak ugaritzearen ondorioz, hala nola *Aphanocladia stichidiosa*, *Lychaete pellucida*, *Aglaothamniom pseudobyssoides* edo *Microcladia glandulosa*. Emaitza horiek errezelaren biomasaren galerak izan ditzakeen ondorioei buruz eztabaidatzen dira; izan ere, baliteke duela gutxi ezarritako espezieek *G. corneum*ek emandako funtzio ekologikoa ez betetzea.

RESUMEN

Décadas de pérdida de biomasa en la vegetación somera de sustrato rocoso en el sur del Golfo de Vizcaya

Las macroalgas formadoras de copa o dosel dominan la biomasa en las zonas someras de sustrato rocoso de zonas templadas de todo el mundo. Este estudio busca evaluar los cambios a lo largo del tiempo en la biomasa de las comunidades submareales a diferentes profundidades en la parte más occidental de la costa vasca desde 1982 hasta 2014. Se detecta una disminución significativa en el stock del rodófito perenne *Gelidium corneum*, especialmente a profundidades de 3 y 6 m, de hecho, solo hubo una presencia a modo testimonial al final del estudio. En el lugar de esta especie estructuradora, se establecieron especies de tamaño relativamente grande, como la especie de copa *Treptacantha baccata*. Además, se observa un aumento en la heterogeneidad de la vegetación hacia 2014, principalmente como consecuencia de la proliferación de especies coralináceas articuladas formadoras de césped (*Corallina* spp.) y algas morfológicamente simples y efímeras como *Aphanocladia stichidiosa*, *Lychaete pellucida*, *Aglaothamniom pseudobyssoides* o *Microcladia glandulosa*. Estos resultados se discuten en relación con las posibles consecuencias de la pérdida de biomasa de la copa, ya que las especies recientemente establecidas podrían no cumplir con la función ecológica proporcionada por *G. corneum*.

1. INTRODUCTION

Canopy-forming macroalgae are dominant and form extensive stands in rocky benthic subtidal communities in most temperate regions (Steneck et al., 2002; Smale et al., 2013; Strain et al., 2014). These large, perennial macroalgae play a very important role in marine ecosystems as they create structurally complex assemblages analogous to forests on land (Ballesteros et al., 2009; Reed and Foster, 2012; Gianni et al., 2013). In this regard, foundation species increase three-dimensional complexity by providing biogenic habitats and protection for a great variety of marine organisms (Steneck et al., 2002; Wernberg et al., 2011c; Smale et al., 2013). These macrophytes also act as ecosystem-engineers, since they substantially modify the local environment by changing light conditions (Wernberg et al., 2005), water flow (Rosman et al., 2007) and sedimentation rates (Eckman et al., 1989) in ways that favor the settlement of other organisms. Canopy dominated assemblages thus constitute one of the most diverse and productive ecosystems worldwide, contribute significantly to nearshore primary productivity and also enhance secondary productivity (Mann, 2000; Tait and Schiel, 2011, Steneck et al., 2002; Smale et al., 2013). In addition, these structuring species supply many valuable ecosystem services such as reducing coastal erosion, CO2 sinking, nutrient cycling and water quality control; they also provide raw material for different human uses (Airoldi and Beck, 2007; Smale et al., 2013; Wernberg et al., 2016).

However, in the past few decades a global decline in these foundation species has been observed (Steneck et al., 2002; Serisawa et al., 2004; Connell et al., 2008; Smale et al., 2013; Mineur et al., 2015; Perkol-Finkel and Airoldi, 2010; Wernberg et al., 2016). Ocean warming has been seen as the main driver of change, but many other abiotic and biotic factors are also related to the retreat of canopy forming species (Steneck et al., 2002; Airoldi et al., 2008; Connell et al., 2008; Tait and Schiel, 2011; Smale et al., 2013; Strain et al., 2014). Regardless of what driver is causing the decline, a shift has been observed from these large macrophytes towards structurally simpler, less productive assemblages dominated by turf-forming, filamentous or ephemeral macroalgae (Airoldi et al., 2008; Mangialajo et al., 2008; Perkol-Finkel and Airoldi, 2010; Tait and Schiel, 2011). To date there has been little evidence of foundation species recovering from disturbances (Dayton et al., 1992; Martínez et al., 2003), mainly because once simpler communities are established, they inhibit recolonisation by canopy species, resulting in alternative stable states (Strain et al., 2014; Wernberg et al., 2016). Loss of large perennial macroalgae in favour of simpler communities may have consequences for the whole ecosystem, and in this connection numerous studies have related the retreat of these ecosystem engineers to a decrease in species richness and abundance (Graham, 2004; Norderhaug et al., 2007; Schiel and Lilley, 2007; Wikström and Kautsky, 2007), homogenisation with neighbouring habitats (Mangialajo et al., 2008) and loss of productivity (Tait and Schiel, 2011; Crowe et al., 2013), among others.

In the particular case of the southeastern Bay of Biscay, local retreats in subtidal large perennial *Gelidium corneum, Laminaria ochroleuca* and *Treptacantha baccata* (former *Cystoseira baccata*) have been reported in the past few decades (Díez et al., 2012; Borja et al., 2013; 2018; Muguerza et al., 2017; 2020). In addition to the canopy decline, evidence of profound changes in community structure such as increases in coralline algae, morphologically simple forms and warm-water species has been found (Díez et al., 2012; Muguerza et al., 2017). Nevertheless, little information about the loss of productivity is available on the Basque coast, since most of the research papers mentioned provide information on species abundance in terms of cover. Only Borja et al. (2013) provides data on changes in *G. corneum* biomass for the eastern Basque coast, but they give no information on the variability over time of the standing stock of this or any other macroalgae in more western areas. The link between biomass and primary productivity may vary with the age and/or size of the algae, the successional stage of the community, the rates of tissue loss from herbivores, senescence and other local disturbances (Reed et al., 2008). Even so, biomass has usually been used as a proxy of primary productivity in macroalgae, and is determinant in per-area productivity (Reed et al., 2008; Tait and Schiel, 2011). In a recent study Quintano et al. (2019) suggest lower *G. corneum* productivity for specimens in shallower waters. We therefore seek here to assess changes over time in the standing stock of subtidal vegetation at different depths in a location in the westernmost part of the Basque coast (southern Bay of Biscay).

2. MATERIAL & METHODS

2.1. Study area

The Basque coast lies at the eastern end of the Cantabrian Sea (Northern Spain), on the southern Bay of Biscay. It is over 192 km in length and is open to strong waves coming mostly from NW, with an average height of 1.9 m (Díez et al., 2003; González et al., 2004; Galparsoro et al., 2010). This is an exposed-to-highly-exposed rocky shore, with high, mostly erosional, energy, extensive vertical cliffs and abrasion platforms interspersed with sandy beaches. In shallow waters, the rocky bottom is almost continuous, whereas it becomes sandy as depth increases (Chust et al., 2011). Its flora belongs to the warm temperate NE Atlantic Region according to the biogeographical scheme proposed by van den Hoek and Breeman (1990).

The study was carried out on a stretch of shoreline about 1.8 km long, open to NW swell, between the locations of Kobaron and Muskiz (43º35’34”N 03º15’44”W and 43º35’52”N 03º12’94”W, respectively), in the province of Bizkaia (Fig. 1).

2.2. Field sampling and processing.

In 2014 the standing stock of macroalgae assemblages was studied at six different depths (2, 3, 6, 9, 10 and 11 m) along seven transects of 100m in length, seeking to reproduce the sampling campaigns of 1982 (Gorostiaga, 1995) and 2007 (Muguerza,

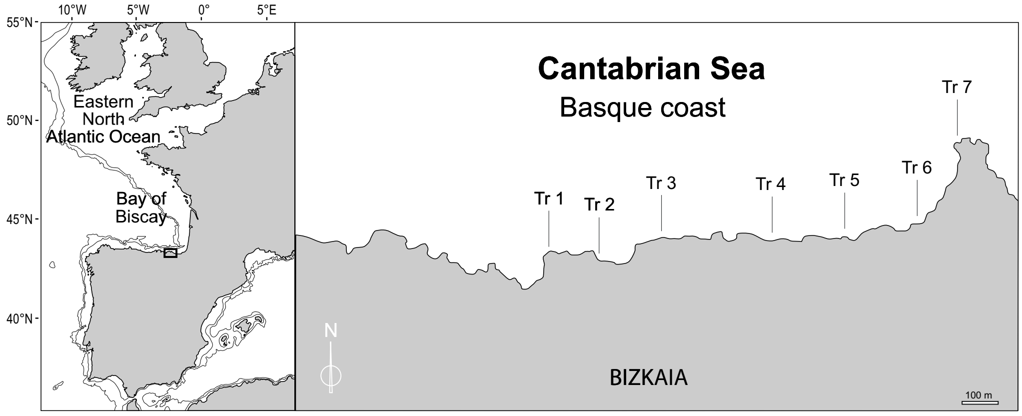


Fig. 1 Study area. Layout of the seven transects along the western end of the coast of Bizkaia.

Table 1. Summary of PERMANOVA results testing for the effect of Year (Y), Depth (D) and the interaction of both factors (Y x D) on the composition and abundance (biomass) of the vegetation. Pairwise comparisons for significant terms are shown at the bottom of the table.

PERMANOVA

	df	**SS**	**MS**	**Pseudo-F**	**p**
Y	2	59978	29989	9.929	0.0001
D	5	49146	9829.2	4.61	0.0001
Y x D	10	32517	3251.7	1.525	0.0028
Residuals	85	1,81E+05	2132.1		
Total	102	3,29E+05			

Pair-wise comparisons

2 m	3 m	6 m
1982 = 2007	1982 ≠ 2007	1982 ≠ 2007
1982 ≠ 2014	1982 ≠ 2014	1982 ≠ 2014
2007 ≠ 2014	2007 ≠ 2014	2007 ≠ 2014
9 m	**10 m**	**11 m**
1982 ≠ 2007	1982 ≠ 2007	1982 ≠ 2007
1982 ≠ 2014	1982 ≠ 2014	1982 ≠ 2014
2007 = 2014	2007 = 2014	2007 = 2014

2007, Novoa, 2008). Each transect was set perpendicular to the coastline following a north-south orientation with a starting point at 2 m below extremely low tides (Fig. 1). Within each transect, a surface area of 2000 cm^2 was delimited at each depth using quadrats of 40 x 50 cm placed systematically at the midpoint of the cross-section of the transect. This means that there were seven surface areas per depth and year (n = 7). In some transects it was not possible to sample at certain depths due to a lack of appropriate surface areas. Each surface was destructively sampled, with all flora within the quadrat being collected except the mostly calcareous crustose layer, which was not sampled. Once in the laboratory, samples were kept frozen in labelled plastic bags. For the analysis, samples were thawed and the flora was separated and identified. Algal taxonomy was updated following AlgaeBase (Guiry and Guiry 2020). Subsequently, the dry weight (DW) in g (100-110°C, 24 h) was obtained for each species.

2.3. Statistical analysis

The spatio-temporal variability of the composition of the phytobenthic communities and their abundance in terms of biomass was examined in a multivariate context, by means of a distance-based permutational multivariate analysis of variance (PERMANOVA, Anderson et al., 2008). Biomass values for each species were square root transformed to reduce the influence of the dominant taxa. The similarity between pairs of samples was calculated using the Bray-Curtis index. The design of the experiment consisted of two factors: Year (3 levels: 1982, 2007 and 2014; fixed) and Depth (6 levels: 2, 3, 6, 9, 10 and 11; random). Spatio-temporal variability was represented graphically by ordination (nMDS, non-metric multidimensional scaling) and classification (hierarchical cluster) analyses. The SIMPROF routine (similarity profile) was applied to the resulting cluster to explore the significance of the groups. In addition, a percentage similarity (SIMPER) analysis was performed to determine what species contributed most to the formation of the groups. Finally, a permutational test for homogeneity of multivariate dispersions (PERMDISP) was also performed for the Year factor (1982 *vs*. 2007 *vs*. 2014) to check for differences in the heterogeneity of multivariate dispersion between groups. All statistical analyses and the aforementioned routines were performed using the PERMANOVA+ for PRIMER6 software package (Clarke and Gorley, 2006).

3. RESULTS

The campaign carried out in 2014 identified a total of 65 taxa, 94 species were documented in 2007 and 55 species in 1982. Over all three campaigns the most widely represented phylum was Rhodophyta, with a total of 92 taxa, followed by Ochrophyta with 13 and Chlorophyta with 12 (Table A1).

Figure 2 shows the spatial variation of assemblages in terms of composition and abundance (biomass) over time. A gradual shift in the structure of the community is found between the three years studied (1982, 2007 and 2014). The significant T x D interaction indicates that the differences between the three years studied vary with depth (Table 2). The pairwise test finds significant differences between 1982 and 2007 at all depths except for 2 m. The comparison between 1982 and 2014 finds significant differences at all depths. Significant differences between 2007 and 2014 are found only for the shallow samples (2, 3 and 6 m) (Table 2). The PERMDISP analysis for the Year factor shows an increase in multivariate dispersion from 1982 to 2007 and 2014, indicating a

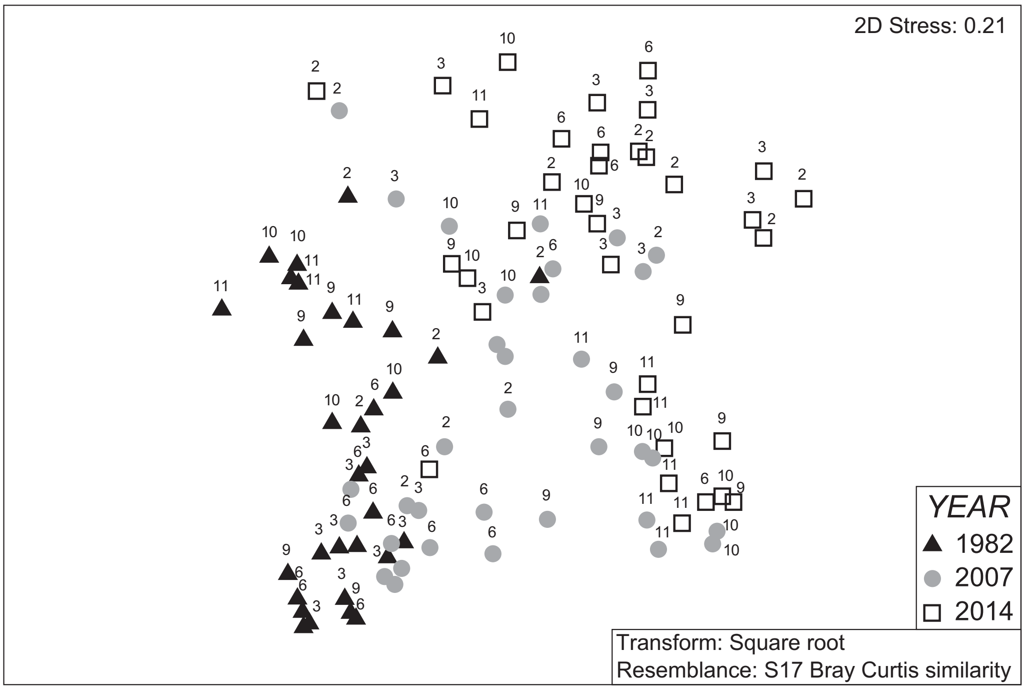


Fig. 2. MDS ordination analysis based on the Bray-Curtis dissimilarity index showing sample distribution in relation to Year (1982, 2007 and 2014) and Depth (2, 3, 6, 9, 10 and 11 m). Variables were square root transformed.

Table 2. Summary of the test of homogeneity of multivariate dispersions (PERMDISP) based on the Bray-Curtis dissimilarity matrix testing for Year. Pairwise comparisons for Year are shown.

PERMDISP

	Av. Distance	SE
1982	44.958	2.069
2007	51.076	1.077
2014	52.591	1.278

Pair-wise comparisons

	t	p
1982 vs. 2007	2.688	0.017
1982 vs. 2014	3.214	0.004
2007 vs. 2014	0.904	0.369

rise in the heterogeneity of the vegetation (Table 2; Fig. 2). However, no differences in the dispersion of samples are found between 2007 and 2014 (Table 2; Fig. 2).

In the dendrogram resulting from the composition and abundance (biomass), two main groups, A and B, are distinguished at a similarity level of 14%. Group A (average similarity between samples: 42.9%) consists mainly of samples from 1982 but also contains some samples from 2007 and one from 2014. The samples from 2007 are from depths of 3 and 6 m, except for two which come from 2 and 9 m (Fig. 3). Group B (average similarity between samples: 24.8%) comprises the rest of the samples from 2007 and 2014 and two samples from 1982 taken at a depth of 2 m (Fig. 3). The SIMPER routine points to *Gelidium corneum* as the main species responsible for the separation of these two groups, with a contribution of 26.9%. The mean biomass of this rhodophyte is higher in Group A (64.481 *vs*. 0.314 g DW ·2000 cm^{-2}). Apart from *G. corneum,* other species which make noteworthy contributions (>2%) to Group A are *Pterosiphonia complanata* (1.416 g·2000 cm^{-2}), *Plocamium cartilagineum* (0.476 g DW

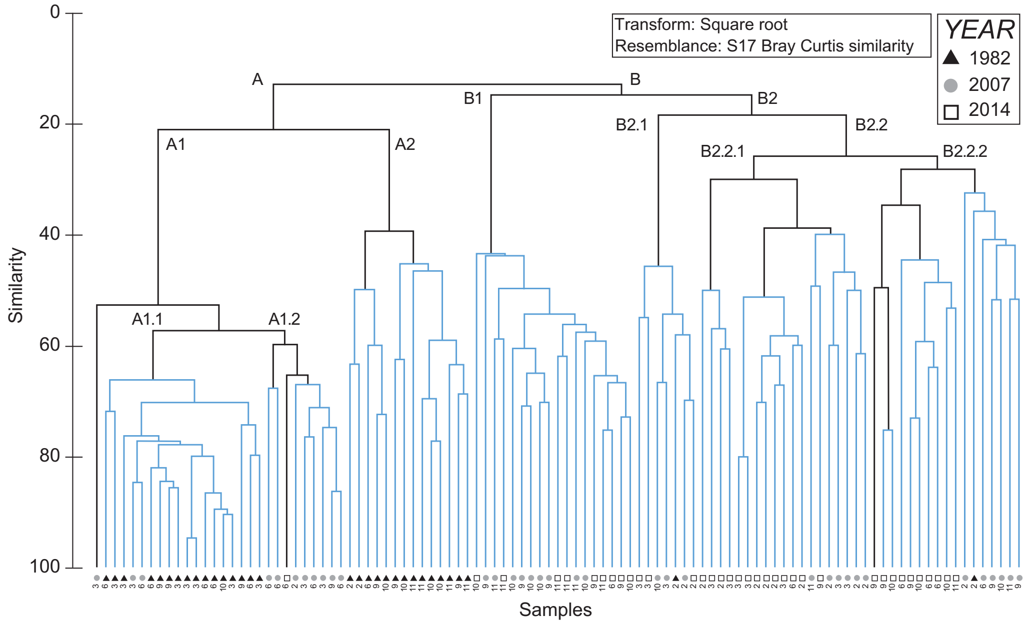


Fig. 3. Dendrogram based on Bray-Curtis dissimilarity index and square root transformed data showing sample classification. Black lines represent significantly different groups, while blue are equivalent to groups that do not differ significantly according to the SIMPROF test.

Table 3. Summary of the SIMPER test indicating the average biomass (Av.Bio; g dry weight ·2000 cm^{-2}) of each taxa and its contribution (C (%)) to the differentiation of the subgroups identified in the CLUSTER. The biomass values expressed in this table are untransformed. Only taxa that contributed more than 2% in any of the subgroups comparisons are shown. The average dissimilarity (Av. Diss.) between subgroups is also indicated. (1) *Ellisolandia elongata* and *C. officinalis*; (2) *P. harveyana* and *P. squamaria*.

	Av. Diss. = 78,86%			Av. Diss. = 42,72%			Av. Diss. = 85,15%			Av. Diss. = 81,62%			Av. Diss. = 74,24%		
Subgroups	**A1**	**A2**		**A1.1**	**A1.2**		**B1**	**B2**		**B2.1**	**B2.2**		**B2.2.1**	**B2.2.2**	
Taxa	**Av.Bio.**	**Av.Bio.**	**C(%)**	**Av.Bio.**	**Av.Bio.**	**C (%)**	**Av.Bio.**	**Av.Bio.**	**C (%)**	**Av.Bio.**	**Av.Bio.**	**C (%)**	**Av.Ab.**	**Av.Ab.**	**C (%)**
Acrosorium ciliolatum	-	-	-	0.003	0.116	2.4	-	-	-	-	-	-	-	-	-
Aglaothamnion pseudobyssoides	-	-	-	-	-	-	-	-	-	-	-	-	0.008	0.303	2.6
Aphanocladia stichidiosa	-	-	-	-	-	-	-	-	-	-	-	-	0.168	0.240	2.7
Asparagopsis armata	0.096	2.856	6.0	0.058	0.212	3.7	0.160	0.903	2.8	0.640	0.960	2.3	0.348	2.016	4.7
Calliblepharis ciliata	0.004	1.563	5.3	-	-	-	-	-	-	-	-	-	-	-	-
Callithamnion tetragonum	-	-	-	0	0.152	3.0	-	-	-	-	-	-	-	-	-
Cladostephus spongiosum	-	-	-	-	-	-	-	-	-	-	-	-	0.168	0.063	2.4
Codium decorticatum	-	-	-	-	-	-	0.006	5.808	7.6	0	8.294	9.3	25.604	0.194	22.7
Corallina spp. (1)	-	-	-	0.036	0.096	2.7	1.061	1.254	4.0	0.168	1.588	4.0	2.657	0.740	6.6
Cryptopleura ramosa	-	-	-	-	-	-	0.672	0.012	2.5	-	-	-	-	-	-
Desmarestia ligulata	-	-	-	0.176	0	3.1	-	-	-	-	-	-	-	-	-
Dictyopteris polypodioides	0.116	1.664	5.0	0.281	0	4.1	-	-	-	-	-	-	-	-	-
Dictyota dichotoma	0.144	0.096	2.0	0.026	0.723	6.1	-	-	-	0.423	0.000	2.2	-	-	-
Gelidium corneum	124.323	3.240	37.8	167.444	62.726	37.1	0.203	0.372	2.6	0.348	0.372	2.9	0.348	0.410	4.0
Gelidium spinosum	-	-	-	-	-	-	0.270	0.176	2.5	-	-	-	0.533	0.058	3.8
Halopithys incurva	-	-	-	-	-	-	0.096	4.203	6.4	102.212	0.230	34.3	0.325	0.137	3.8
Halopteris scoparia	-	-	-	-	-	-	0.006	0.792	2.8	0.372	0.884	3.6	1.716	0.281	6.4
Heterosiphonia plumosa	0.000	1.124	4.3	-	-	-	-	-	-	-	-	-	-	-	-
Jania rubens	-	-	-	-	-	-	0.102	0.922	2.8	4.884	0.518	6.3	1.145	0.109	4.5
Peyssonnelia spp. (2)	-	-	-	-	-	-	-	-	-	-	-	-	0.152	0.058	2.7
Phyllophora crispa	-	-	-	-	-	-	3.764	0.008	5.9	-	-	-	-	-	-
Plocamium cartilagineum	0.740	0.130	3.2	0.792	0.810	6.2	0.640	0.032	2.3	-	-	-	-	-	-
Pterosiphonia complanata	0.144	7.952	10.3	0.281	0.014	3.6	0.548	0.116	2.0	-	-	-	-	-	-
Rhodymenia pseudopalmata	-	-	-	0.023	0.137	2.6	-	-	-	-	-	-	-	-	-
Treptacantha baccata	-	-	-	0	1.323	7.2	71.572	0.032	27.2	-	-	-	-	-	-

·2000 cm^{-2}), *Asparagopsis armata* (0.593 g DW ·2000 cm^{-2}) and *Dictyopteris polypodioides* (0.436 g DW ·2000 cm^{-2}). Of these species *P. complanata*, *P. cartilagineum* and *D. polypodioides* are more abundant in Group A, while the biomass of *A. armata* is similar in both groups. In addition to the lower presence of *G. corneum*, Group B also shows a mosaic distribution of many species, dominated by *Treptacantha baccata* (6.864 g DW ·2000 cm^{-2}), *Codium decorticatum* (2.958 g·2000 cm^{-2}), *Halopithys incurva* (2.631 g DW ·2000 cm^{-2}) and *Corallina* spp. (1.210 g DW ·2000 cm^{-2}). It is also noteworthy that this group shows a greater abundance of morphologically simple forms such as *Aphanocladia stichidiosa*, *Lychaete pellucida*, *Aglaothamniom pseudobyssoides* or *Microcladia glandulosa*, among others (Table 3).

Group A is divided into two subgroups (A1 and A2) at a similarity level of 24% (Fig. 3). Subgroup A1 consists of samples from 1982 and the aforementioned samples from 2007 and 2014, mostly from depths of 3 and 6 m. These samples are characterised by the dominance of *G. corneum* accompanied mainly by *P. cartilagineum* (Table 3). By contrast, Subgroup A2 comprises samples from 1982, mainly from deeper waters (9, 10 and 11 m) (Fig. 3). In this case the abundance of *G. corneum* is notably lower and the species that shows the greatest abundance is *P. complanata* (Table 3). Apart from *G. corneum*, other species that show considerable biomass values are *A. armata*, *D. polypodioides*, *Calliblepharis ciliata* and *Heterosiphonia plumosa*, all of which are more abundant in Subgroup A2 than in Subgroup A1 (Table 3). The latter subgroup (samples from 3 and 6 m deep) is divided, in turn, into two groups (A1.1 and A1.2) at a similarity level of 59%. It is worth remarking that one sample from 2007 taken at a depth of 3 m that was grouped separately is not considered (Fig. 3). This sample was characterised as having a high biomass of *C. decorticatum.* Subgroup A1.1 consists of samples from 1982, except for two samples from 2007, while Subgroup A1.2 comprises the remaining samples from 2007 and the single sample from 2014 (Fig. 3). The dominant species in both subgroups is *G. corneum*, but its abundance in Subgroup A1.1 is higher (Table 3). Other significant macrophytes in terms of biomass in the latter subgroup are *P. cartilagineum*, *P. complanata*, *D. polypodioides* and *Desmarestia ligulata* (Table 3). In Subgroup A1.2 the taxa with notable abundances are *T. baccata*, *Callithamnion tetragonum*, *P. cartilagineum*, *Dictyota dichotoma*, *A. armata*, *Rhodymenia pseudopalmata* and *Corallina* spp. (Table 3). The former two species are not found in Subgroup A1.1 whilst the others all show higher biomass values in Subgroup A1.2.

Group B is divided into two subgroups (B1 and B2) at a similarity level of 17% (Fig. 3). Subgroup B1 is represented mainly by deeper (9, 10 and 11 m) samples from 2007 and 2014, with *T. baccata* as the dominant species (Table 3). Other species with noteworthy biomass values include *Phyllophora crispa*, *Corallina* spp., *Cryptopleura ramosa*, *P. complanta* and *P. cartilagineum* (Table 3). Subgroup B2 mainly comprises shallower samples (2, 3 and 6 m), most of them from 2014, and is characterized by lower figures for *T. baccata* (Fig. 3; Table 3). At a similarity level of 24%, Subgroup B2 is further divided into two groups: B2.1 and B2.2. The former has a higher biomass of *H. incurva* and *Jania rubens*, while the latter is again subdivided into two subgroups at a similarity level of 27% (Fig. 3). Subgroup B2.2.1 is represented by *C. decorticatum*, *Corallina* spp. and *Halopteris scoparia*, while the dominant species in Subgroup B2.2.2 are *A. armata* and *Corallina* spp. (Table 3).

Figure 4 depicts the trend over time of the mean biomass (g DW· 2000 cm^{-2}) at each depth for the whole vegetation and also for those species that contribute most to the spatio-temporal variability detected in the multivariate analysis. The highest total biomass records for 1982 are found at depths of 3 and 6 m with 189.36 and 149.51 g DW · cm^{-2}, respectively (Fig. 4). Intermediate values are found at depths of 9 and 10 m (63.74 and 43.66 g DW · cm^{-2}), and lower values at depths of 2 and 11 m (10.47 and 0.25 g DW · cm^{-2}) (Fig. 4). The biomass records at depths of 3 and 6 and to a lesser extent at 9 and 10 m are associated with the high-abundance *Gelidium corneum* (Fig. 4). 2007 figures show a sharp decline in the biomass of this rhodophyte at depths of 9 and 10 m, where it is replaced mainly by *Treptacantha baccata* (Fig. 4). At depths of 3 and 6 m, the decrease of *G. corneum* is smoother and its biomass loss is replaced by *Halopithys in-*

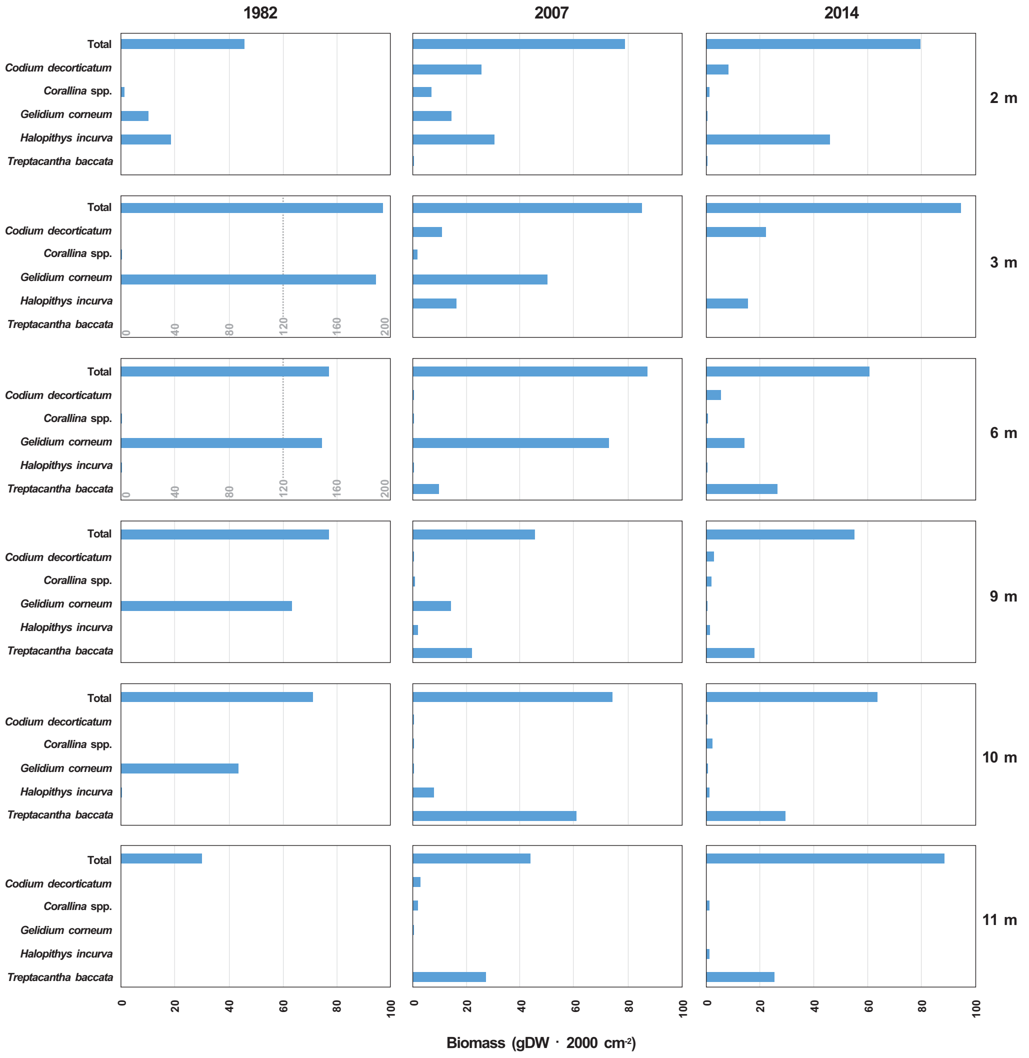


Fig. 4 Mean biomass (g dry weight · 2000 cm^{-2}) of the whole community (Total) and the five taxa that contributed most to the dissimilarity between groups in relation to Year and Depth. Discontinuous line at depths of 3 and 6 m depth indicate the boundary of 120 g dry weight · 2000 cm^{-2}. From that line on, each dividing line accounts for 40 g dry weight · 2000 cm^{-2}.

curva and *Codium decorticatum* at 3m and *T. baccata* at 6 m (Fig. 4). The total biomass decreases except at a depth of 10 m as a consequence of the noteworthy establishment of *T. bacata* (Fig. 4). In the figures for 2014 the biomass of *G. corneum* from 3 to 10 m depth is almost token and the three species mentioned above plus *Corallina* spp. increase, thus bringing the total biomass at depths of 3 and 9 m to a higher level than in 2007 (Fig. 4). However, the total biomass remain below the figures recorded in 1982. The total biomass at a depth of 2 m increases from 1982 to 2007 and 2014. In the 1982 data *H. incurva* shows the greatest biomass, followed by *G. corneum* (Fig. 4). In the 2007 data the biomass of both these species increases as do the abundances of *C. decorticatum* and *Corallina* spp. However, this last macroalgae and *G. corneum* decrease in 2014, whereas *C. decorticatum* and *H. incurva* show further increases (Fig. 4). With respect to the deepest communities (11 m), the progressive increase of *T. baccata* towards 2014 is noteworthy, bringing the total biomass to a higher level than in 1982 (Fig. 4). Finally, note that there are differences in total biomass at all depths compared to the abundance of *C. decorticatum*, *Corallina* spp., *H. incurva* and *T. baccata* in 2014. These differences are related to the higher abundance of the aforementioned morphologically simple basal macroalgae (see Table A1).

4. DISCUSSION

The results reported here reveal a significant shift in species composition and abundance of subtidal phytobenthic communities in the study area from 1982 to 2014. The main change observed is a sharp decline in the biomass of the perennial canopy-forming species *Gelidium corneum,* which in 1982 accounted for almost the entire standing stock of the community, especially at depths of 3 and 6 m. As a consequence, the total macroalgae biomass decreased in the depth range of 3 to 10 m up to 2014. In addition, the data show an increase in the heterogeneity of vegetation from 1982 to 2007 and 2014, mainly as a result of the proliferation of turf-forming articulated coralline species (*Corallina* spp.) and morphologically simple, ephemeral algae such as *Aphanocladia stichidiosa*, *Lychaete pellucida*, *Aglaothamniom pseudobyssoides* and *Microcladia glandulosa*. As a foundation species, *G. corneum* is essential for the functioning of the ecosystem: It serves as food and shelter for many associated species on the Basque coast (Borja et al., 2004). The biomass loss of this structural species in the study area may therefore have consequences for the whole benthic ecosystem.

Canopy-forming species favor the development of many associated understorey and epiphytic macroalgae species (Steneck et al., 2002). Thus, the retreat of a foundation species may be expected to result in a reduction in community biomass (Tait and Schiel, 2011). The biomass loss of *G. corneum* from 1982 to 2014 in the present study was accompanied by a reduction in the total standing stock of macroalgae in the depth range from 3 to 10 m. At depths of 6, 9, and 10 m, the niche left by *G. corneum* has been occupied to some extent by *Treptacantha baccata*, a species that forms extensive subtidal stands in subtidal areas of the southeastern Bay of Biscay along with *G. corneum* (Guinda et al., 2012). The replacement of *G. corneum* by *T. baccata* at this depth range could be related to the greater tolerance of increased temperature and irradiance levels of the latter (Miguel-Vijandi et al., 2010). It has been suggested that these two and other factors are responsible for the retreat of *G. corneum* on the Basque coast (Díez et al., 2012; Muguerza et al., 2017; Quintano et al., 2019). However, despite the ability of *T. baccata* to stand high levels of solar radiation, it has not developed satisfactorily in shallower zones (2-3 m). This could be explained by increases in wave energy since the early 90´s (Borja et al., 2013). Muguerza et al. (2017)

point to increasing hydrodynamics as a potential driver of the retreat of *T. baccata* in some locations along the Basque coast. Indeed, this canopy-forming species is linked more to sheltered and semi-exposed coastal stretches, where it finds its optimum (Díez et al., 2003; Méndez-Sandín and Fernández, 2016). At 3 m deep the biomass of *G. corneum* has been partially replaced by *Codium decorticatum* and *Halopithys incurva*, two species with a warm temperate affinity which are widely distributed in more southerly regions (Sartoni and De Biasi, 1999; Rodríguez-Prieto et al., 2013).

Several studies have linked the retreat of ecosystem engineers to the loss of one of the most important ecosystem functions: Primary productivity (Tait and Schiel, 2011; Crowe et al., 2013). Here, productivity may have been reduced since the new dominating species, mainly *T. baccata,* does not reach the biomass values shown by *G. corneum* in 1982. Moreover, the total macroalgae standing stock is also shown to be lower in 2014. It is true that biomass alone does not explain primary productivity (Reed et al., 2008; Tait and Schiel, 2011); nor have we taken specific productivity measurements. However, there are facts that may suggest a reduction in productivity: Firstly, some of the newly established species, such as *Corallina* spp*.,* are associated with low productivity rates (Litter and Arnold, 1982; Tait and Schiel, 2011). According to the latter authors, the calcium carbonate structure of these species makes them heavy relative to their photosynthetic capability. Similarly, the spread of morphologically simple, ephemeral species after canopy removal could indicate lower productivity. Although these ephemeral algae are highly productive on a per-biomass basis, their productivity on a per-area basis is relatively low (Litter and Arnold, 1982; Tait and Schiel, 2011). The second fact is that canopy associated macrofaunal assemblages as foundation species enhance secondary productivity (Edgar, 1990; Smale et al., 2013). In the study area, replacement by the perennial species *T. baccata* at depths between 6 and 11 m has not offset the loss of biomass of *G. corneum*. Moreover, although the size of *C. decorticatum* could lead to its being regarded as a canopy species, its annual nature might not allow permanent secondary production in shallow waters (3 m) in the study area.

Another consequence of canopy loss is a decline in the richness and abundance of the associated flora and fauna due to the lack of the three-dimensional space that canopies provide (Graham, 2004; Norderhaug et al., 2007; Schiel and Lilley, 2007; Wikström and Kautsky, 2007). In the study reported here, this functional role fulfilled by *G. corneum* in 1982 was not satisfactorily fulfilled in 2014 by other large- and medium-size species (*C. decorticatum*, *H. incurva* and *T. baccata*), given that their biomass in 2014 is recorded as being lower between depths of 3 and 10 m. In addition, the newly established turf-forming macroalgae typically consist of species with less ecological and functional value than those replaced (Crowe et al., 2013). A decrease in the richness and abundance of associated organisms should therefore be expected. Furthermore, recent research in the study area has shown a sharp decrease in invertebrate taxonomic and functional density and diversity after canopy loss (Bustamante et al., 2014; 2017). However, macroinvertebrate and macroalgae richness has increased (Muguerza et al., 2017; 2020). The latter authors relate these findings to the intermediate disturbance hypothesis, which predicts maximal diversity at intermediate levels of disturbance (Connell, 1978). However, partial replacement by *T. baccata* between depths of 6 and 11 m could be positive because the tree-like morphology and the leathery texture of species of the genus *Cystoseira* usually present higher epiphytic macroalgae (Otero-Schmitt and Pérez-Cirera, 1996; Quintano et al., 2015; Méndez-Sandín and Fernández, 2016).

Similarly, the increase in the biomass of the perennial *Halopithys incurva* at a depth of 2 m may also be beneficial. This species is medium-sized (up to 25 cm) and may to some extent fulfil some of the canopy functions.

Foundation species are very important for marine food webs as they capture and export carbon (Dayton 1985; Krumhansl and Scheibling 2012; Smale et al., 2013). Moreover, much of their biomass is not consumed directly by herbivores, so canopy species are a major source of nutrition for other nearshore ecosystems (Duggins et al., 1989; Mann, 2000; Steneck et al., 2002). Therefore, the loss of canopy biomass in the study area might affect the functioning of other neighboring ecosystems. In addition to changes in ecosystem functions at ecological level, the canopy loss and subsequent decrease in productivity in the study area could also impair the ecosystem services that canopy species provide. As mentioned above, these structuring macroalgae provide refuge for numerous other species, including many that are economically important for humans (Graham, 2004; Smale et al., 2013). In this regard, the fact that the species that have replaced *G. corneum* cannot easily perform its functional role means that the exploitation of some species in the study area might decline.

In summary, this study provides evidence of the low level of functional replacement of canopy forming macroalgae in the south-eastern Bay of Biscay. The loss of biomass and structure in subtidal phytobenthic assemblages may have led to a decline in primary productivity and biodiversity. In addition, the retreat of the canopy forming species *G. corneum* may have reduced the resilience of the ecosystem, making it more susceptible to future physical disturbances under ongoing climate change (IPCC, 2013). Finally, more research is needed to measure changes in productivity and better understand the consequences of canopy loss.

ANNEXES

Table A1. List of all the taxa recorded showing their mean biomass (g dry weight ·200cm^{-2}), the standard deviation (DE) and frequency in % (Fr) for the three studied years. (1) *Ellisolandia elongata* and *C. officinalis*; (2) *P. harveyana* and *P. squamaria*; (3) *P. ardreana* and *P. pennata.*

TAXA	1982			2007			2014		
	Mean	SD	Fr (%)	Mean	SD	Fr (%)	Mean	SD	Fr (%)
CHLOROPHYTA									
Bryopsis hypnoides J.V.Lamour.	0	0	0	0	0	0	<0.01	0,01	2,78
Bryopsis plumosa (Huds.) C.Agardh	0	0	0	<0.01	0,02	5,71	<0.01	0,02	2,78
Chaetomorpha linum (O.F.Müller) Kütz.	0	0	0	<0.01	<0.01	2,86	0	0	0
Cladophora lehmanniana (Lindenb.) Kütz.	0	0	0	<0.01	<0.01	5,71	0,16	0,38	50,00
Cladophora prolifera (Roth) Kütz.	0	0	0	0,05	0,15	22,86	0	0	0
Codium decorticatum (Woodw.) M.A.Howe	0	0	0	6,74	17,76	37,14	13,59	31,02	52,78
Derbesia tenuissima (Moris & De Not.) P.Crouan & H. Crouan	<0.01	<0.01	3,13	0	0	0	0	0	0
Lychaete pellucida (Hudson) M.J.Wynne	0,01	0,06	9,38	0,06	0,15	51,43	0,23	0,38	58,33
Rhizoclonium riparium (Roth) Harv.	0	0	0	<0.01	<0.01	2,86	0	0	0
Ulva pseudocurvata Koeman & Hoek	0	0	0	0	0	0	<0.01	0,02	2,78
Ulva clathrata (Roth) C.Agardh	<0.01	<0.01	6,25	0	0	0	0	0	0
Ulva rigida C.Agardh	0,13	0,60	6,25	0,06	0,20	28,57	<0.01	0,01	16,67
OCROPHYTA									
Cladostephus spongiosum (Huds.) C.Agardh	0,01	0,06	12,50	0,07	0,25	17,14	0,65	1,39	50,00
Colpomenia peregrina Sauv.	<0.01	0,01	3,13	0,04	0,24	5,71	<0.01	0,01	5,56
Desmarestia ligulata (Stackh.) J.V.Lamour.	0,54	1,76	25,00	0	0	0	<0.01	<0.01	2,78
Dictyopteris polypodioides (DC.) J.V.Lamour.	1,93	4,28	71,88	0,02	0,05	11,43	0,11	0,37	19,44
Dictyota dichotoma (Huds.) J.V.Lamour.	0,22	0,71	81,25	0,60	1,20	65,71	0,05	0,23	19,44
Halopteris filicina (Gratel.) Kütz.	0,10	0,29	65,63	0,08	0,16	60,00	0,01	0,03	11,11
Halopteris scoparia (L.) Sauv.	0,04	0,13	68,75	0,02	0,03	42,86	3,18	7,08	69,44
Hincksia granulosa (Sm.) P.C.Silva	<0.01	<0.01	3,13	0	0	0	0	0	0
Phyllariopsis brevipes (C.Agardh) E.C.Henry & South	<0.01	<0.01	3,13	0	0	0	0,01	0,03	8,33
Saccorhiza polyschides (Lightf.) Batters	0	0	0	<0.01	<0.01	5,71	0	0	0
Sphacelaria cirrosa (Roth) C.Agardh	0	0	0	0,03	0,16	22,86	0	0	0
Taonia atomaria (Woodw.) J.Agardh	0	0	0	0	0	0	0,29	1,03	27,78
Treptacantha baccata (S.G.Gmelin) Orellana & Sansón	<0.01	<0.01	3,13	18,86	37,95	42,86	22,89	46,11	50,00
RHODOPHYTA									
Acrosorium ciliolatum (Harv.) Kylin	0,05	0,18	43,75	0,35	0,54	100,00	0,03	0,06	30,56
Aglaothamnion pseudobyssoides (P.Crouan & H. Crouan) Halos	0	0	0	0	0	0	0,36	0,69	55,56
Aglaothamnion tenuissimum (Bonnem.) . Feldm.-Maz	0	0	0	0,01	0,03	48,57	<0.01	0,01	2,78

Table A1. - (cont.).

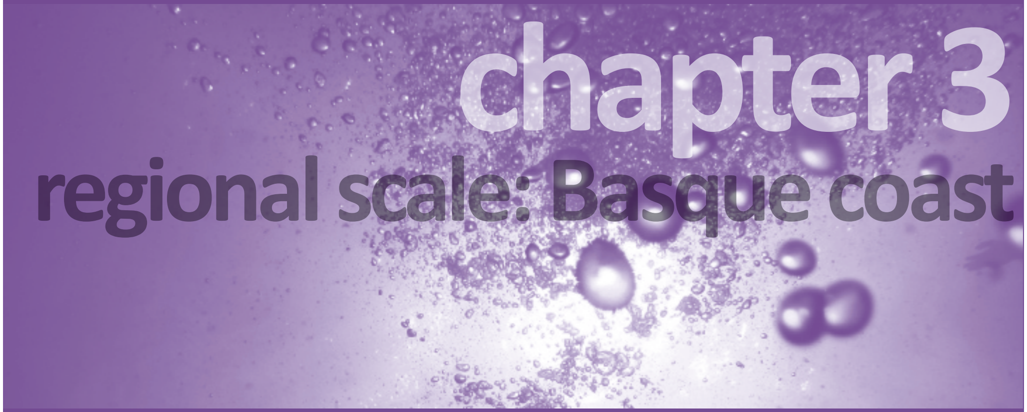
TAXA	1982			2007			2014		
	Mean	SD	Fr (%)	Mean	SD	Fr (%)	Mean	SD	Fr (%)
RHODOPHYTA									
Aglaothamnion tripinnatum (C.Agardh) . Feldm.-Maz	<0.01	<0.01	3,13	0,01	0,02	20,00	<0.01	0,01	2,78
Anotrichium furcellatum (J.Agardh) Baldock	0	0	0	<0.01	<0.01	5,71	<0.01	0,01	5,56
Antithamnion amphigeneum A. Millar	0	0	0	<0.01	<0.01	22,86	0	0	0
Antithamnion nipponicum Yamada & Inagaki	0	0	0	<0.01	<0.01	11,43	0	0	0
Antithamnion villosum (Kütz.) Athanasiadis	0	0	0	<0.01	<0.01	5,71	0	0	0
Antithamnionella ternifolia (J.D.Hooker & Harvey) Lyle	<0.01	<0.01	21,88	<0.01	<0.01	8,57	0	0	0
Aphanocladia stichidiosa (Funk) Ardré	0	0	0	0,02	0,07	28,57	0,44	0,68	63,89
Apoglossum ruscifolium (Turner) J.Agardh	0	0	0	0,03	0,04	82,86	<0.01	0,01	8,33
Asparagopsis armata Harv.	1,90	3,07	84,38	0,41	0,60	94,29	1,62	2,31	72,22
Bonnemaisonia hamifera Har.	0	0	0	0,02	0,04	40,00	<0.01	<0.01	2,78
Bonnemaisonia asparagoides (Woodw.) C.Agardh	0,09	0,17	59,38	0,04	0,07	74,29	0,01	0,03	47,22
Bornetia secundiflora (J.Agardh) Thur.	0	0	0	0,02	0,05	37,14	0,03	0,08	36,11
Calliblepharis ciliata (Huds.) Kütz.	1,61	3,71	31,25	0,05	0,23	8,57	0,14	0,45	11,11
Callithamnion tetragonum (Withering) S.F.Gray	0	0	0	0,10	0,21	68,57	<0.01	<0.01	2,78
Callithamnion corymbosum (Smith) Lyngb.	<0.01	<0.01	3,13	0,01	0,02	17,14	0	0	0
Callithamnion granulatum (Ducluz.) C.Agardh	<0.01	<0.01	9,38	0	0	0	0	0	0
Centroceras clavulatum (C.Agardh) Mont.	0	0	0	<0.01	<0.01	2,86	0	0	0
Ceramium cimbricum H.E.Petersen	0	0	0	0,01	0,05	20,00	0	0	0
Ceramium secundatum Lyngb.	0	0	0	0,01	0,04	42,86	<0.01	<0.01	5,56
Ceramium virgatum Roth	0,02	0,07	15,63	0	0	0	0	0	0
Ceramium ciliatum (J.Ellis) Ducluz.	<0.01	<0.01	28,13	<0.01	<0.01	5,71	0,01	0,03	8,33
Ceramium diaphanum (Lightf.) Roth	0,01	0,06	18,75	0	0	0	0	0	0
Ceramium echionotum J.Agardh	<0.01	<0.01	6,25	0	0	0	0,07	0,35	11,11
Champia parvula (C.Agardh) Harv.	<0.01	0,01	31,25	<0.01	0,02	31,43	0,02	0,10	19,44
Chondracanthus acicularis (Roth) Fredericq	0	0	0	0,11	0,64	5,71	0	0	0
Chondracanthus teedei (Mert. ex Roth) Kütz.	0	0	0	<0.01	0,01	5,71	0	0	0
Chondria coerulescens (J.Agardh) Falkenb.	0	0	0	<0.01	<0.01	2,86	0	0	0
Chondria dasyphylla (Woodw.) C.Agardh	0	0	0	0	0	0	<0.01	<0.01	5,56
Colaconema caespitosum (J.Agardh) Jackelman, Stegenga & J.J.Bolton	0	0	0	0,01	0,03	14,29	0	0	0
Colaconema daviesii (Dillwyn) Stegenga	0	0	0	<0.01	0,02	2,86	0	0	0
Compsothamnion gracillimum De Toni	0	0	0	0,01	0,02	11,43	0	0	0
Compsothamnion thuyoides (Sm.) Nägeli	0	0	0	<0.01	0,01	5,71	0	0	0
Corallina spp. (1)	0,28	0,75	46,88	1,68	3,78	77,14	2,75	4,34	86,11
Crouania attenuata (C.Agardh) J.Agardh	<0.01	<0.01	12,50	0,04	0,12	42,86	0	0	0

Table A1. - (cont.).

TAXA	1982			2007			2014		
	Mean	SD	Fr (%)	Mean	SD	Fr (%)	Mean	SD	Fr (%)
RHODOPHYTA									
Cryptonemia lomation (Bertol.) J.Agardh	0,06	0,17	15,63	0	0	0	0	0	0
Cryptopleura ramosa (Huds.) Kylin ex L.Newton	0,17	0,31	87,50	0,09	0,15	80,00	0,58	1,10	36,11
Dasya ocellata (Gratel.) Harv.	0	0	0	0,01	0,03	11,43	0,24	0,33	61,11
Dasya hutchinsiae Harv.	<0.01	0,01	28,13	0,02	0,07	25,71	0,04	0,09	38,89
Dasysiphonia japonica (Yendo) H.-S.Kim	0	0	0	<0.01	<0.01	2,86	<0.01	0,01	8,33
Dermocorynus dichotomus (J.Agardh) Gargiulo, M.Morabito & Manghisi	0	0	0	0	0	0	<0.01	0,01	2,78
Erythroglossum laciniatum (Lightf.) Maggs & Hommers.	0	0	0	<0.01	0,03	2,86	0	0	0
Gaillona gallica (Nägeli) Athanasiadis	0	0	0	<0.01	<0.01	5,71	0	0	0
Gayliella flaccida (Harvey ex Kützing) T.O.Cho & L.J.McIvor	<0.01	<0.01	3,13	0,01	0,02	48,57	0,02	0,07	27,78
Gelidium spinosum (S.G.Gmel.) P.C.Silva	0,33	1,19	28,13	0,08	0,38	28,57	1,36	3,55	47,22
Gelidium corneum (Huds.) J.V.Lamour.	89,57	99,02	93,75	27,22	44,83	100,00	2,69	13,38	44,44
Gelidium pusillum (Stackh.) Le Jol.	0,54	2,27	25,00	<0.01	<0.01	8,57	0	0	0
Gigartina pistillata (S.G.Gmel.) Stackh.	0,02	0,10	6,25	0,01	0,07	2,86	0	0	0
Gracilaria multipartita (Clemente) Harv.	0,01	0,05	3,13	0	0	0	0	0	0
Gymnogongrus crenulatus (Turner) J.Agardh	0,11	0,34	34,38	0	0	0	0,01	0,05	8,33
Halopithys incurva (Huds.) Batters	2,44	13,17	25,00	9,90	33,41	31,43	13,33	55,19	27,78
Halurus equisetifolius (Lightf.) Kütz.	0,03	0,12	25,00	0,08	0,20	42,86	0,16	0,52	22,22
Herposiphonia secunda (C.Agardh) Ambronn	0	0	0	0,01	0,02	34,29	0	0	0
Herposiphonia sp.	0	0	0	0	0	0	0,03	0,09	36,11
Heterosiphonia plumosa (J.Ellis) Batters	0,89	2,26	53,13	0,03	0,09	28,57	0,11	0,29	41,67
Hypoglossum hypoglossoides (Stackh.) Collins & Herv.	0	0	0	<0.01	0,01	5,71	0	0	0
Jania rubens (L.) J.V.Lamour.	0,06	0,18	37,50	0,65	1,61	68,57	2,44	7,77	69,44
Kallymenia reniformis (Turner) J.Agardh	0	0	0	<0.01	0,01	5,71	0	0	0
Lomentaria clavellosa (Lightf. ex Turner) Gaillon	<0.01	<0.01	3,13	<0.01	<0.01	22,86	0	0	0
Meredithia microphylla (J.Agardh) J.Agardh	0	0	0	0	0	0	0,05	0,28	2,78
Metacallophyllis laciniata (Hudson) A.Vergés & L.Le Gall	0	0	0	0,01	0,04	2,86	0	0	0
Microcladia glandulosa (Sol. ex Turner) Grev.	<0.01	0,02	28,13	0,05	0,09	65,71	0,16	0,56	61,11
Monosporus pedicellatus (Sm.) Solier	0	0	0	<0.01	0,01	8,57	0	0	0
Nitophyllum punctatum (Stackh.) Grev.	0	0,02	31,25	<0.01	<0.01	2,86	0	0	0
Peyssonnelia spp. (2)	<0.01	0,02	3,13	0,35	1,41	17,14	0,59	2,11	25,00
Phyllophora crispa (Huds.) P.S.Dixon	0	0	0	0,79	2,58	62,86	2,68	9,67	27,78
Pleonosporium borreri (Sm.) Nägeli	0	0	0	<0.01	<0.01	11,43	0	0	0

Table A1. - (cont.).

TAXA	1982			2007			2014		
	Mean	SD	Fr (%)	Mean	SD	Fr (%)	Mean	SD	Fr (%)
RHODOPHYTA									
Pleonosporium flexuosum (C.Agardh) Bornet ex De Toni	0	0	0	<0.01	<0.01	5,71	0	0	0
Plocamium cartilagineum (L.) P.S.Dixon	0,59	0,93	96,88	0,90	1,71	94,29	0,46	1,16	38,89
Polysiphonia brodiei (Dillwyn) Sprengel	0	0	0	0,01	0,04	28,57	0	0	0
Polysiphonia polyspora (C.Agardh) Mont.	0	0	0	<0.01	<0.01	2,86	0,00	0,02	2,78
Polysiphonia sp.	0	0	0	0	0	0	0	0	3
Polysiphonia atlantica Kapraun & J.N.Norris	0	0	0	0	0	2,86	0	0	0,00
Pterosiphonia parasitica (Huds.) Falkenb.	0	0	0	0,04	0,09	65,71	0,09	0,16	58,33
Pterosiphonia spp. (3)	0,16	0,29	78,13	0,05	0,10	68,57	0,42	0,77	63,89
Pterosiphonia complanata (Clemente) Falkenb.	4,69	7,02	90,63	0,31	0,53	91,43	0,37	0,70	75,00
Pterothamnion crispum (Ducluz.) Nägeli	0	0	0	0,08	0,23	40,00	<0.01	<0.01	8,33
Pterothamnion plumula (J.Ellis) Nägeli	0,01	0,03	37,50	0	0	0	0	0	0
Rhodophyllis divaricata (Stackh.) Papenf.	<0.01	<0.01	3,13	0,02	0,08	20,0	0	0	0
Rhodymenia holmesii Ardiss.	0	0	0	<0.01	<0.01	2,86	0	0	0
Rhodymenia pseudopalmata (J.V.Lamour.) P.C.Silva	0,03	0,05	31,25	0,11	0,26	42,86	0,14	0,40	22,22
Scageliopsis patens Wollaston	0	0	0	<0.01	<0.01	8,57	0	0	0
Schizymenia dubyi (Chauv. ex Duby) J.Agardh	0	0	0	<0.01	0,01	8,57	0	0	0
Seirospora interrupta (Sm.) F.Schmitz	<0.01	<0.01	3,13	<0.01	0,01	14,29	0	0	0
Spermothamnion repens (Dillwyn) Rosenv.	0	0	0	0,07	0,36	11,43	0	0	0
Sphaerococcus coronopifolius Stackh.	0	0	0	0,25	0,91	22,86	0,01	0,05	8,33
Sphondylothamnion multifidum (Huds.) Nägeli	0,10	0,28	56,25	0,07	0,40	8,57	0,01	0,03	30,56
Tiffaniella capitata (Schousboe ex Bornet) Doty & Meñez	0	0	0	0,01	0,04	5,71	0	0	0
Vertebrata fruticulosa (Wulfen) Kuntze	0	0	0	0	0	0	<0.01	<0.01	2,78
Vertebrata thuyoides (Harvey) Kuntze	0	0	0	<0.01	<0.01	5,71	0	0	0



chapter 3

regional scale: Basque coast

NAHIARA MUGUERZA (2020) DOCTORAL THESIS pp. 73-96

Structural impoverishment of the subtidal vegetation of southeastern Bay of Biscay from 1991 to 2013 in the context of climate change

ABSTRACT This study assesses changes in the taxonomic and functional structure and in the diversity of the shallow (3-9 m) subtidal vegetation off the southeastern coast of the Bay of Biscay by studying 19 locations between 1991 and 2013. Results provide evidence that the three-dimensional assemblages of shallow subtidal bottoms in the study area may be shifting towards less structurally complex communities. Canopy-forming algae are declining whereas simple thallus turfs composed of a combination of filamentous, polysiphonated and foliose non-corticated algae are becoming abundant along with articulated corallines and crustose species. Moreover, a significant increase in taxa richness and diversity was found, mainly due to the development of opportunistic and morphologically simple forms with warm-water affinity. The potential ecological consequences of canopy loss for coastal ecosystems are discussed. Given that changes in climate conditions are predicted to intensify, the prevalence of the new turfing space occupiers in the study area here considered seems to be realistic on the basis of their ability to compete for space and resist disturbance. Consequently, major implications for the functioning and diversity of the ecosystem and for ecosystem services may be expected.

KEYWORDS Alternative stable states; Biogenic habitats; Canopy loss; Ecological resilience; Long-term changes; Macroalgal assemblages.

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LABURPENA

Klima-aldaketaren testuinguruan 1991 eta 2013 artean Bizkaiko Golkoko hego-ekialdeko ur-azpiko landarediaren egituraren pobretzea

Ikerketa honek 1991 eta 2013 urteen artean Bizkaiko Golkoko hego-ekialdeko kostaldeko ur-azpiko (3-9 m) landarediaren egitura taxonomiko eta funtzionalean zein dibertsitatearen aldaketak baloratzen ditu. Emaitzek agerian uzten dute aztertutako azpi-hondoko hiru dimentsioko komunitateak egiturari dagokionez aldatzen ari direla hain konplexuak ez diren komunitateetarantz. Egituratzaileak edo errezela osatzen duten algak gutxitzen ari dira, eta morfologia sinpleko algak, horien artean, espezie firukarak edo hariztatuak, polisifonatuak eta hostokarak, handitzen ari dira, koralinazeo artikulatuekin eta zenbait espezie inkrustatzaileekin batera. Gainera, taxonen aberastasunean eta dibertsitatean gorakada nabarmena ikusi da, batez ere izaera oportunista eta hegoaldearekiko (ur-epeletako) afinitatea duten forma sinpleen garapenaren ondorioz. Errezela galtzeak kostaldeko ekosistemetan izan ditzakeen ondorio ekologikoak eztabaidatzen dira. Iragarpen klimatikoen arabera, ingurumen-baldintzen aldaketak areagotu egingo dira, eta, beraz, espazioa okupatzen duten espezie berrien prebalentzia mantendu egingo da ziurrenik, espazioagatik lehiatzeko eta asaldurei aurre egiteko duten gaitasuna oinarri hartuta. Ondorioz, ekosistemaren funtzionamendurako, dibertsitaterako eta zerbitzuetarako ondorio garrantzitsuak espero litezke.

RESUMEN

Empobrecimiento estructural de la vegetación submareal del sureste del Golfo de Vizcaya entre 1991 y 2013 en el contexto del cambio climático

Este trabajo evalúa los cambios en la estructura taxonómica y funcional y en la diversidad de la vegetación submareal somera (3-9 m) en 19 localidades de la costa sureste del Golfo de Vizcaya entre 1991 y 2013. Los resultados evidencian que las comunidades tridimensionales de los fondos de la zona de estudio están cambiando hacia comunidades estructuralmente menos complejas. Las algas formadoras de copa o dosel están disminuyendo mientras que las algas cespitosas de morfología simple, entre las que destacan las especies filamentosas, polisifonadas y foliosas no corticadas, están aumentando junto con las coralináceas articuladas y varias especies incrustantes. Además, se ha observado un aumento significativo en la riqueza y diversidad, principalmente debido al desarrollo de formas simples, con carácter oportunista y afinidad meridional. Se discuten las posibles consecuencias ecológicas para los ecosistemas costeros debido a la pérdida de copa. De acuerdo a las predicciones climáticas, los cambios en las condiciones ambientales se intensificarán, por lo que la prevalencia de las nuevas especies cespitosas que ocupan el espacio se mantendrá posiblemente debido a su capacidad mostrada para competir por el espacio y resistir a las perturbaciones. En consecuencia, cabe esperar importantes implicaciones para el funcionamiento, la diversidad y los servicios del ecosistema.

1. INTRODUCTION

Canopy-forming algae play a critical role on temperate rocky shores since they contribute significantly to nearshore productivity as a major component of coastal food webs (Mann, 2000; Strain et al., 2014). These species also provide a unique three-dimensional space for the settlement and protection of a wide array of marine organisms, thus resulting in enhanced biodiversity (Steneck et al., 2002; Strain et al., 2014). By providing a biogenic habitat and modifying physical factors that include light, water flow and sedimentation (Bégin et al., 2004; Irving and Connell, 2006; Løvås and Tørum, 2001), these large macrophytes substantially determine the structure of the associated communities (Smale et al., 2013). Furthermore, communities structured by these foundation species provide many valuable ecosystem services since they operate as significant CO_2 sinks, natural barriers to erosion and nursery grounds. They are also involved in nutrient cycling and water quality control and meet other human needs for food, fodder, fuel and pharmaceutical products (Airoldi and Beck, 2007; Wernberg et al., 2016; Wilmers et al., 2012).

It has been suggested that the complex interplay of a wide range of stressors underlies the retreat of canopy-forming algae (Strain et al., 2014; Wernberg et al., 2016). In combination with extreme heat events, warming is considered to be a major driver of change for Tilopteridales, Laminariales (kelps) and Fucales along temperate coastlines around the globe (Mineur et al., 2015; Schiel et al., 2004; Serisawa et al., 2004; Smale et al., 2013; Wernberg et al., 2011c). However, the effects of global changes on these autogenic species at regional scale depend on environmental features (Austin and Van Niel, 2011), and on a combination of multiple anthropogenic stressors including pollution, nutrient enrichment, over-exploitation and increased sediment loads (Benedetti-Cecchi et al., 2001b). Moreover, biotic factors such as plant-herbivore interaction, diseases and the introduction of alien species can also have significant effects on the degradation of canopy-forming macroalgae (Filbee-Dexter and Scheibling, 2014; Ling et al., 2015; Occhipinti-Ambrogi, 2007; Steneck et al., 2002).

The widespread loss of canopy species is leading to a flattening of the seabottom landscape in a shift from three-dimensional habitats towards a bidimendional space dominated by algal turfs, mussel beds or barrens (Airoldi and Beck, 2007; Mangialajo et al., 2008; Strain et al., 2014). The consequences of the loss of foundation species remain poorly understood (Airoldi et al., 2008), but numerous studies have linked the disappearance of these large macrophytes with declines in taxa richness (Graham, 2004; Schiel and Lilley, 2007), decreased abundance of rocky invertebrates (Bustamante, et al., 2017; Norderhaug et al., 2007; Wikström and Kautsky, 2007), homogenisation with neighbouring habitats (Mangialajo et al., 2008) and losses in biomass and productivity (Crowe et al., 2013; Harley et al., 2012; Tait and Schiel, 2011). This shift towards simpler communities threatens biodiversity and the functioning of coastal ecosystems (Strain et al., 2014; Tait and Schiel, 2011). Once turf-forming algae are established, they decrease the ecological resilience of the ecosystem by limiting or inhibiting recolonisation by foundation species (Airoldi and Beck, 2007; Strain et al., 2014; Wernberg et al., 2016). Some studies report a recovery of canopy forming species once unfavourable environmental conditions have returned to normal (Dayton and Tegner, 1984; Martínez et al., 2003). However, once the structure and functioning of the ecosystem are highly altered the shift might result in alternative stable states (Scheffer et al., 2001; Wernberg et al., 2016). These newly established assemblages consist of species with lower ecological and functional values that cannot provide the same ecosystem services as the species that they have replaced, which could eventually lead to significant economic losses (Wernberg et al., 2016).

Numerous authors have provided evidence of change in the distribution of habitat-forming seaweeds along the northern coast of the Iberian Peninsula (Duarte et al., 2013; Fernández, 2011; Kersting, 2016; Lamela-Silvarrey et al., 2012; Martínez et al., 2015; Voerman et al., 2013). Both intertidal (*Himanthalia elongata*, *Fucus serratus*, *F. vesiculosus* or *Ascophyllum nodosum*) and subtidal canopy forming macrophytes (*Laminaria hyperborea*, *L. ochroleuca*, *Saccorhiza polyschides* or *Gelidium corneum*) have been documented as suffering significant retreats. In the particular case of the southeastern Bay of Biscay, local declines in the habitat-forming seaweeds *Gelidium corneum* and *Cystoseira baccata* have been reported (Borja et al., 2013; Díez et al., 2012b). This paper seeks to investigate whether this is a general trend affecting the whole area. We therefore set out to estimate changes in the taxonomic and functional structure of subtidal macrophyte assemblages off the southeastern Bay of Biscay over the last thirty years by revisiting in 2008-2009 and 2013 a total of 19 locations that were first studied in 1991 (Díez et al., 2003; Gorostiaga et al., 1998).

2. MATERIAL AND METHODS

2.1. Study area

The study area is in the southeastern Bay of Biscay (from 43°21´17.65"N - 3°07´46.40"W to 43°23´42.51"N - 1°47´33.61"W (Fig. 1). Biogeographically, this area belongs to the warm temperate North Eastern Atlantic Region (van den Hoek and Breeman, 1990). The study area (about 150 km) is exposed to large fetches where swell mainly comes from the WNW (30.5%) and NW (37.9%), with 21.1% of waves reaching a mean significant height (Hs) in excess of 3 m (source: www.puertos.es; period: 1991-2013). Average sea-surface temperature (SST) on this stretch of coastline ranges from 12°C in February to 22°C in August and marked seasonality is apparent throughout the year (Borja et al., 2000). Nevertheless, surface waters have gradually warmed up (Goikoetxea et al., 2009) by as much as 1°C in summer in recent decades (1980-2008) (Díez et al., 2012b).

2.2. Data collection and treatment

The sampling methodology is adapted from previous research conducted in summer 1991 (Díez et al., 2003; Gorostiaga et al., 1998). 19 of the locations studied in 1991

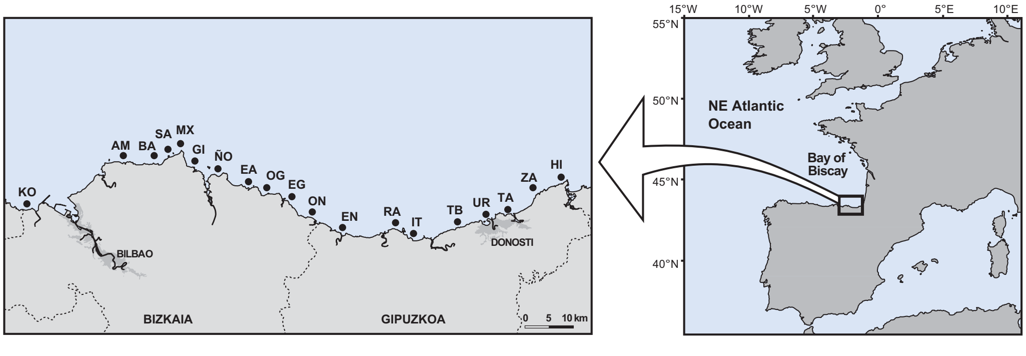

Fig. 1. Map of the study area showing the locations of transects: KO: Kobaron, AM: Armintza, BA: Bakio, SA: San Juan de Gaztelugatxe, MX: Cabo Matxitxako, GI: Gibeleko, ÑO: Ogoño, EA: Ea, OG: Ogeia, EG: Egiluz, ON: Ondarroa, EN: Punta Endata, RA: Isla San Anton, IT: Punta Iteico, TB: Tierra Blanca, UR: Urgull, TA: Tambo, ZA: Punta Zabala and HI: Cabo Higuer.

were revisited in 2008-2009 and in 2013 (Fig. 1). The three samplings were conducted between July 15th and September 30th. The locations were randomly selected from those with good environmental conditions (Borja et al., 2009; Borja et al., 2016). At each location a 100 m long transect was traced perpendicular to the coastline. The starting point of each transect was 3 m below extreme low water spring tides and an average depth range of 3-9 m was covered. The relocation of each transect was calculated using photographic records from the starting point in combination with their orientation and bathymetric profiles (see Appendix: Table A1 for georeference details). Macroalgae abundances were recorded at regular intervals of 5 m along each transect by visually estimating their cover in an area of 1 m^2 (2500 cm^2 in 2013) delimited by a quadrat. Abundance was estimated using the scale proposed by Braun-Blanquet (1951): +: presence; 1: 1-5%; 2: 5-25%; 3: 25-50%; 4: 50-75%; 5: 75-100%. 21 samples were taken in each transect and mean macroalgae cover in each quadrat was later calculated using the median of each range. Some species were grouped at genus level in order to minimise differences between years related to possible misidentification. Nomenclature follows Algaebase (www.algaebase.org).

The multivariate structure of phytobenthic assemblages was assessed from the taxonomical and morpho-functional viewpoints. For the latter purpose, the cover data of taxa in each sample were aggregated into eleven morpho-functional groups (see Appendix: Table A2) using a modification of the methodology described in Díez et al. (2010): (1) filamentous (uniseriate); (2) polysiphonated; (3) foliose non-corticated; (4) foliose slightly corticated (cortex with one or two layers); (5) foliose heavily corticated (cortex with more than two layers); (6) terete slightly corticated (cortex with one or two layers); (7) terete heavily corticated (cortex with more than two layers); (8) leathery; (9) articulated calcareous; (10) crustose calcareous; and (11) crustose non-calcareous algae. Single response variables were also calculated for each sample, including taxa richness (S) and Simpson diversity (1-λ).

2.3. Statistical analysis

The spatio-temporal variability of the multivariate structure of assemblages was examined by means of a distance-based permutational multivariate analysis of variance (PERMANOVA, Anderson et al., 2008). The experiment was designed with two factors: Time (fixed with 3 levels: T1 (1991), T2 (2008-09) and T3 (2013)) and Location (random with 19 levels). The *a priori* significant level set was $\alpha = 0.05$. For both the taxonomical and morpho-functional approaches, data were square root transformed to balance the contributions of rare and dominant taxa and morpho-functional groups. The Bray-Curtis index was used to determine similarity between pairs of samples. Each term in the analyses was tested by 4999 random permutations of appropriate units (Anderson et al., 2008). Non-metric multidimensional scaling (nMDS) ordination was used to represent the spatio-temporal variability of the data cloud. Since the number of samples was large, the data were represented multidimensionally using overall centroids for Time x Location. Similarity percentage analyses (SIMPER) were performed to identify which taxa and morpho-functional groups contributed most to the discrimination of the groups detected in the nMDS. Univariate PERMANOVA analyses of taxa density (Gotelli and Colwell, 2001) and Simpson's diversity (1-λ) were performed on the basis of Euclidean distance, applying the same experiment design described above for multivariate data. *Post-hoc* pairwise comparisons were calculated using Gosset's t-statistic after significant PERMANOVA terms (Anderson et al., 2008). All statistical analyses and the aforementioned routines were performed using PERMANOVA+ for PRIMER6 software (Anderson et al., 2008).

3. RESULTS

3.1. Taxonomic multivariate structure of assemblages

The multivariate structure of subtidal macrophyte assemblages in terms of relative abundance of taxa differed significantly from one sampling survey to another (Table 1). PERMANOVA analysis also detected significant differences between locations. The significant Time x Location (T x L) interaction indicates that differences between locations vary over time. The nMDS ordination diagram shows the spatial variation of assemblages over time (Fig. 2). Three groups were identified at a dissimilarity level of 50%. According to the similarity percentage procedure (SIMPER routine), *Cystoseira baccata* and *Mesophyllum* spp. were the taxa which contributed most to the formation of Group A, with mean covers of 49.6% and 27.1%, respectively (Table 2). Within Group A, at a dissimilarity level of 44%, the nMDS shows a temporal shift between samples from T1 (Subgroup A1) and samples from T2 and T3 (Subgroup A2).

Table 1. Summary of PERMANOVA results based on Bray-Curtis dissimilarity of square root transformed data testing for the effect of Time (T) and Location (L) on taxa composition and abundance.

Source	df	MS	Pseudo-F	P (perm)
T	2	126210	11.759	0.0001
L	18	42433	37.392	0.0001
TxL	36	10796	9.5135	0.0001
Res	1102	1134.8		

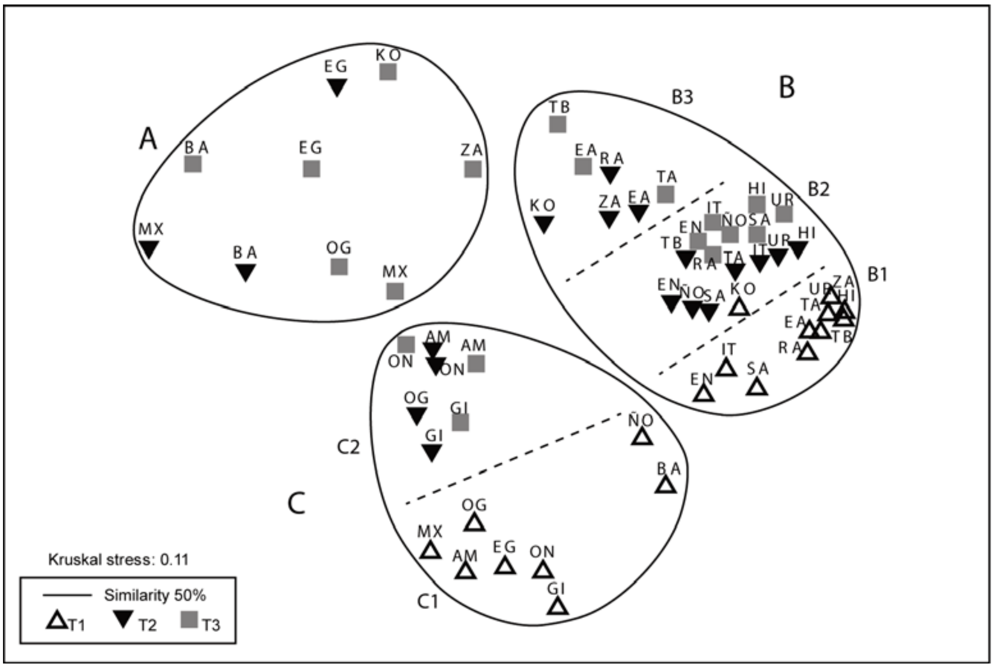

Fig. 2. Non-metric MDS ordination of taxa composition and abundance based on the Bray-Curtis dissimilarity coefficient of square-root transformed data. For the representation overall centroids for Time x Location are used.

Table 2. Summary of the results of the SIMPER routine for the three groups obtained from a dissimilarity of 50%. The average cover (Av. Cover) and percentage contribution (Contrib.) of each taxon based on a square root transformation are presented. The 24 taxa listed contribute more than 1% to the formation of groups at least in one of them. (-): Contribution < 1%. (1) *C.officinalis* and *Elisolandia elongata* (formerly C. elongata); (2) *J. rubens* and *J. Longifurca*; (3) *M. alternans* and *M. expansum*; (4) *P. cartilagineum* and *P. raphelisianum*; (5) *P. ardreana*, *P. parasitica* and *P. pennata*.

	Group A		**Group B**		**Group C**	
TAXA	**Av. Cover**	**Contrib.**	**Av. Cover**	**Contrib.**	**Av. Cover**	**Contrib.**
Acrosorium ciliolatum (Harv.) Kylin	1.6	1.3	2.3	2.0	1.2	2.1
Aglaothamnion tenuissimum (Bonnem.) Feldm.-Maz.	1.7	-	1.9	-	7.2	3.0
Centroceras clavulatum Mont.	0.0	-	0.1	-	2.3	1.0
Champia parvula (C. Agardh) Harv.	0.2	-	0.2	-	1.7	1.3
Cladostephus spongiosum (Huds.) C. Agardh	1.7	-	0.1	-	4.1	3.0
Corallina spp. (1)	13.9	10.6	3.8	-	30.4	17.9
Cryptopleura ramosa (Huds.) Kylin ex L. Newton	1.3	2.0	0.9	-	0.0	-
Cystoseira baccata (S.G. Gmel.) P.C. Silva	49.6	28.5	3.8	-	9.6	-
Dictyopteris polypodioides (A.P.De Candolle) J.V. Lamour.	0.3	1.1	0.2	-	0.1	-
Dictyota dichotoma (Hudson) J.V. Lamour.	2.1	2.2	3.5	1.9	0.4	-
Falkenbergia rufolanosa (Harv.) F. Schmitz	5.2	3.6	5.5	2.0	8.6	5.9
Gayliella flaccida (Harv. ex Kütz.) T.O.Cho & L.J.McIvor	1.8	-	1.2	-	6.5	7.3
Gelidium corneum (Huds.) J.V. Lamour.	6.2	2.5	60.1	34.6	6.6	3.3
Halurus equisetifolius (Lightfoot) Kütz.	0.7	1.5	0.1	-	0.4	-
Herposiphonia sp.	0.8	-	0.2	-	10.5	6.6
Heterosiphonia japonica Yendo	0.3	-	0.2	-	4.5	1.0
Jania spp.(2)	1.9	1.8	0.5	-	10.4	9.1
Lithophyllum incrustans Phil.	1.3	-	0.5	-	7.6	6.3
Mesophyllum spp. (3)	27.1	22.4	53.4	34.4	21.5	13.4
Plocamium spp. (4)	1.1	1.7	12.3	8.6	0.8	-
Pterosiphonia complanata (Clemente) Falkenb.	4.6	5.4	2.2	-	0.6	-
Pterosiphonia spp. (5)	1.8	1.2	0.2	-	1.9	-
Rhodymenia pseudopalmata (J.V. Lamour.) P.C. Silva	1.2	-	2.8	2.8	0.2	-
Zanardinia typus (Nardo) G. Furnari	7.9	4.6	8.2	3.8	6.2	4.7

Subgroup A2 was characterised by the absence of *Laminaria ochroleuca* and *Saccorhiza polyschides* and the presence of several taxa, such as *Acrosorium ciliolatum*, *Gayliella flaccida*, *Lithophyllum incrustans* and *Aglaothamnion tenuissimun*, that were not recorded in Subgroup A1. Group B is mainly discriminated by *Gelidium corneum* and *Mesophyllum* spp. with mean covers of 60.1% and 53.4% respectively (Table 2). Within Group B, a temporal shift was also identified (Fig. 2). At a dissimilarity level of 31%, Subgroup B1 differed from Subgroup B2 due to the lower mean cover occurof some taxa including *A. ciliolatum*, *Falkenbergia rufolanosa*, *Peyssonnelia* spp. and *Zanardinia typus*. At a dissimilarity level of 40%, Subgroup B2 was further divided into Subgroup B21 and Subgroup B22, with the latter showing lower mean cover values of *G.*

Table 3. Summary of PERMANOVA results based on Bray-Curtis dissimilarity of square root transformed data testing for the effect of Time (T) and Location (L) on morpho-functional groups.

Source	df	MS	Pseudo-F	P (perm)
T	2	80758	99.821	0.0001
L	18	37598	34.346	0.0001
TxL	36	8154.8	74.496	0.0001
Res	1102	1094.7		

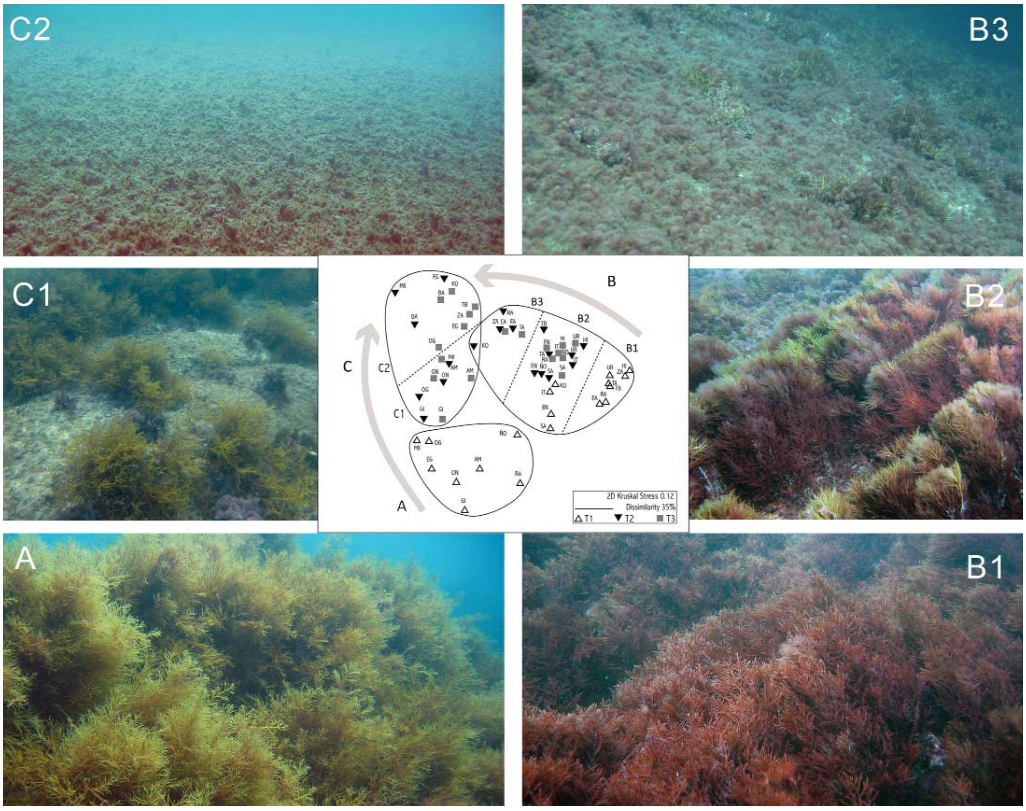

Fig. 3. Non-metric MDS ordination of morpho-functional groups based on the Bray-Curtis dissimilarity coefficient of square-root transformed data. For the representation overall centroids for Time x Location are used.

Table 4. Summary of the results of the SIMPER routine for the three groups obtained from a dissimilarity of 35%. The average cover (Av. Cover) and percentage contribution (Contrib.) of the morpho-functional groups based on a square root transformation are presented.

MORPHO-FUNCTIONAL	Group A		Group B		Group C	
GROUPS	Av. Cover	Contrib.	Av. Cover	Contrib.	Av. Cover	Contrib.
Filamentous	0.7	3.5	5.7	3.8	13.3	9.3
Polysiphonated	6.8	6.3	10.2	3.4	33.6	18.0
Foliose non-corticated	1.2	5.4	4.1	4.8	4.9	5.0
Foliose slightly corticated	3.1	6.7	3.7	2.3	2.3	1.9
Foliose heavily corticated	1.5	3.1	3.1	2.8	1.3	0.6
Terete slightly corticated	4.3	10.5	15.3	10.8	9.5	7.6
Terete heavily corticated	9.6	7.5	62.8	32.2	14.9	9.1
Leathery	46.8	28.5	5.4	0.5	27.5	5.0
Articulated calcareous	7.2	6.7	3.9	1.4	31.9	17.0
Crustose calcareous	21.7	18.8	54.8	31.1	32.4	18.8
Crustose non-calcareous	3.3	3.1	10.5	6.7	12.9	7.8

corneum (35.0%) and *Mesophyllum* spp. (39.8%). Finally, Group C was composed only of samples from T2 and T3. The taxa that contributed most to the formation of this group were *Corallina* spp. (30.4%), *Mesophyllum* spp. (21.5%), *Jania* spp. (10.4%) and *G. flaccida* (6.5%) (Table 2). The mean covers of *C. baccata* and *G. corneum* in Group C were 9.6% and 6.6%, respectively.Taking into account the mean cover of the perennial canopy-forming species detected in the study area over the study period, in the first sampling campaign (T1) 8 locations had large populations of *Cystoseira baccata*, with mean cover ranging from 15% to 80% (see Appendix: Table A3). Data collected in 2013 indicate that populations had decreased or virtually disappeared in 5 locations. Regarding *Gelidium corneum*, large populations were detected in 13 locations, with mean cover ranging between 30% and 80%, but significant decreases have been recorded in 5 of them. Finally, *Laminaria ochroleuca* and *Saccorhiza polyschides* were present in two locations, with mean covers up to 40%, but by T2 populations of both these macrophytes had disappeared.

3.2. Morpho-functional structure of assemblages

The morpho-functional multivariate structure of assemblages also differed significantly from one sampling survey and location to another (Table 3). The significant effect of the Time x Location (T x L) interaction detected by the PERMANOVA analysis indicates that changes over time depend on locations. However, according to pairwise comparisons as many as 14 of the 19 locations studied showed significant differences between the three sampling periods. In the ordination analysis (nMDS), three groups were distinguished at a dissimilarity level of 35% (Fig. 3). Group A was only composed of T1 samples. The morpho-functional groups that contributed most to the formation of this group were leathery and crustose calcareous algae with mean covers of 46.8% and 21.7%, respectively (Table 4). Group B was mainly represented by terete heavily corticated and crustose calcareous algae with mean covers of 62.8% and 54.8%, respectively. A shift over time similar to that found for the taxonomic structure of assemblages was identified within Group B (Fig. 3),

Table 5. Summary of univariate PERMANOVA results based on Euclidean distance testing for the effect of Time (T) and Location (L) on taxa density and Simpson diversity.

		TAXA DENSITY			SIMPSON DIVERSITY		
Source	**df**	**MS**	**Pseudo-F**	**P (perm)**	**MS**	**Pseudo-F**	**P (perm)**
T	2	6323.6	31309	0.0001	48583	76098	0.0001
L	18	554.03	31474	0.0001	632.96	76669	0.0001
TxL	36	203.2	11543	0.0001	642.13	77779	0.0001
Res	1089	17603			82.557		

with three subgroups distinguished at a dissimilarity level of 24%. Subgroup B1 had the highest covers of terete heavily corticated (72.3%) and crustose calcareous algae (71.2%), while the same functional forms showed intermediate levels of cover in Subgroup B2 (67.5% and 53.9%, respectively) and lower ones in Subgroup B3 (45.4% and 43.5%). By contrast, from Subgroup B1 to Subgroup B3 an increasing shift in cover was observed for crustose non-calcareous (0.9% *vs* 10.6% *vs* 18.0%) and filamentous (0.1% *vs* 6.4% *vs* 8.9%) algae. Finally, Group C was formed mainly by samples from T3 and was characterised by crustose calcareous, polysiphonated, articulated calcareous and filamentous algae (mean covers of 32.4%, 33.6%, 31.9% and 13.3% respectively) (Table 4). At a dissimilarity level of 26% two subgroups were distinguished within Group C (Fig. 3). Subgroup C1 was dominated mainly by leathery (53.8%), crustose calcareous (30.1%) and articulated calcareous (27.0%) algae, whereas in Subgroup C2 the highest covers were found in polysiphonated (43.9%), crustose calcareous (29.2%), articulated calcareous (36.1%) and filamentous algae (18.2%).

Figure 4 shows the cover of the eleven morpho-funtional groups in the study area for the three sampling periods (T1, T2 and T3). The highest covers (>35%) were recorded for terete corticated and crustose calcareous algae (Fig. 4). Filamentous, polysiphonated, foliose non-corticated, articulated calcareous and crustose non-calcareous algae increased from T1 to T2 and T3, whereas the opposite trend was found for leathery algae cover (Fig. 4).

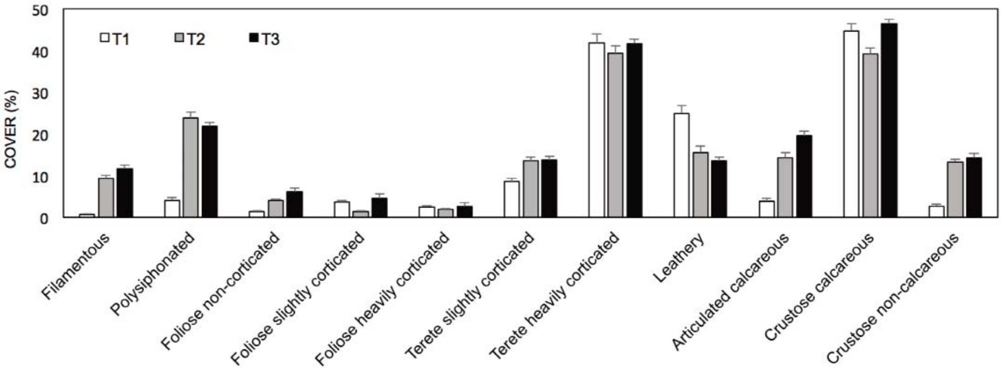

Fig. 4. Average percentage of cover of the eleven morpho-functional groups in the three sampling periods (T1: 1991; T2: 2008-09; and T3: 2013). Bars represent means ± SE.

3.3. Changes in taxa density and diversity

A total of 147 macroalgae taxa were identified over the three sampling periods: 89 in T1, 124 in T2, and 117 in T3 (see Appendix: Table A2). A general increase in taxa density was detected in 18 of the 19 locations studied from T1 to T2, but the differences between T2 and T3 depend on the location considered (Fig. 5A). Nevertheless, taxa density was higher in all locations at the end of the study than in the initial survey, with an overall mean that varied from 10.8 ± 0.7 (mean ± SE) in T1, to 17.7 ± 1.0 in T2, and 17.8 ± 1.0 in T3 (Fig. 5A). In general, the increase was higher in those locations where the canopy was totally or partially lost such as KO, BA, EA, TB, and ZA. Simpson diversity increased from T1 (0.6 ± 0.0; mean ± SE) to T2 (0.73 ± 0.0; mean ± SE) and also showed a slight increase in T3 (0.8 ± 0.0; mean ± SE) (Fig. 5B). PERMANOVA analyses detected that the taxa density and Simpson diversity of assemblages differed significantly from one sampling survey and location to another (Table 5). A significant Time x Location (T x

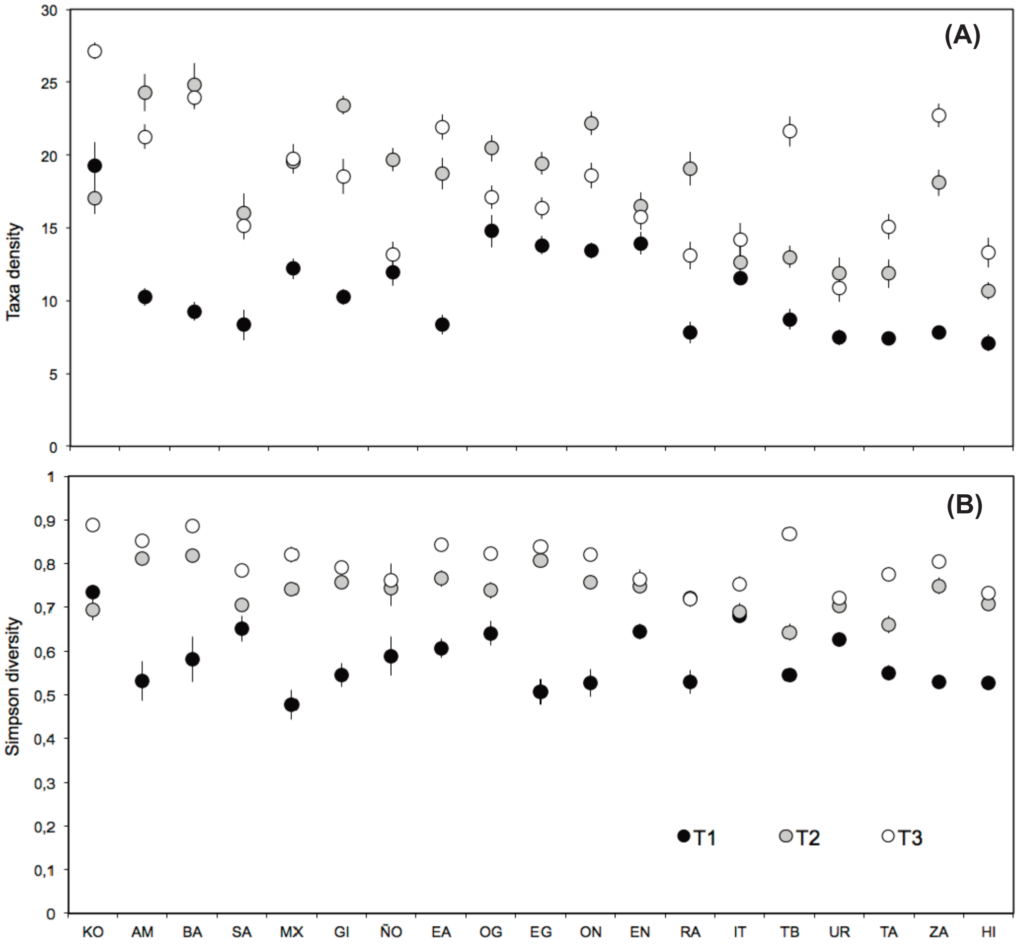

Fig. 5. Mean taxa density (A) and Simpson diversity (B) in relation to Time (T1: 1991; T2: 2008-09; and T3: 2013) and Location (see Fig.2. for location acronyms). Bars represent means ± SE.

L) interaction was also detected, indicating that changes over time in these community measures depend on locations.

4. DISCUSSION

This research provides evidence that the three-dimensional assemblages on shallow subtidal bottoms off the southeastern coast of the Bay of Biscay may be shifting towards less structurally complex communities. Canopy-forming algae are declining whereas morphologically simple forms, coralline algae and crustose species are becoming abundant. These changes might have important effects on the functioning of the marine ecosystem.

There were changes in the distribution of all the canopy-forming species from our study area (namely *Laminaria ochroleuca*, *Saccorhiza polyschides*, *Cystoseira baccata* and *Gelidium corneum*). The two first had disappeared altogether by the end of the study period, whereas *C. baccata* and *G. corneum* were lost or suffered severe reductions in some locations. By contrast, simple thallus turfs composed of a combination of filamentous (*Aglaothamnion tenuissimum*), polysiphonated (*Aphanocladia stichidiosa, Gayliella flaccida, Herposiphonia* sp.) and foliose non-corticated (*Acrosorium ciliolatum*) algae, along with articulated corallines (*Ellisolandia elongata* and *Jania* spp.) and several crustose species of the genus *Zanardinia, Peyssonnelia,* and *Lithophyllum* increased throughout the study area. These increased species were found to occur particularly in those locations where the canopy was lost.

Most studies on marine community regime shifts have been associated with single drivers but the idea of multiple drivers and their interaction (Conversi et al., 2015) seems to be a key concept to further understand the relationship between the response (species) and control variables (environmental stressors) in our study area. Specific ecological research is needed to associate drivers to the observed shifts, but the autoecology of the species involved in the changes detected might shed light on what the potential factors of change have been.

The disappearance of *L. ochroleuca* and *S. polyschides* detected in the present study coincides with the retreat of kelps documented along the coast of North Spain (Férnandez, 2011; Voerman et al., 2013). Given that *L. ochroleuca* and *S. polyschides* are two cold-temperate species, the increase in mean annual sea surface temperature (SST) of 0.26°C per decade from 1977 to 2014 in the southeastern Bay of Biscay (Costoya et al., 2015; Goikoetxea et al., 2009), along with heat events with temperatures up to 26.5°C recorded in 2003 (Díez et al., 2012b) may have been lethal for these kelps.

Cystoseira baccata is a lusitanic species that forms the canopy of subtidal vegetation in shallow subtidal assemblages on semiexposed shores on the central and eastern areas of the North coast of Spain (Díez et al., 2003; Fernández and Niell, 1982; Guinda et al., 2012). This large macrophyte is a warm-temperate species that shows a high capability for acclimation to increased temperature and irradiance (Miguel-Vijandi et al., 2010), and is therefore expected to expand northwards under ongoing climate change (Hiscock et al., 2004). In line with these predictions, its expansion along the North coast of Spain has already been detected (Martínez et al., 2015). However, contrary to expectations, *C. baccata* decreased in most of the sampling locations of the present study, showing significant losses in five of them. These contradictory results might be partially explained by differences in the degree of wave exposure at the locations studied, since wave action plays an important role in controlling *C. baccata* distribution (Díez et al., 2003). Previous reports on recent increases in *C. baccata* only refer to semiexposed sites (Méndez-Sandín and Fernández, 2016), where it finds its optimal hydrodynamic conditions (Díez et al., 2003). In our study area, an increase in the intensity of storms and wave energy has been recorded in the last two decades (Borja et al., 2013). If the force of large waves has proved too great for the supporting structure of *C. baccata* it might have resulted in breakage, dislodgement and mortality.

Gelidium corneum is another lusitanic species that is dominant in subtidal areas of the eastern part of Spain's north coast, along with *C. baccata* (Guinda et al., 2012). However, unlike the latter species, *G. corneum* forms extensive stands on highly exposed coastal stretches facing the prevailing northwesterly swell (Borja, 1987; Gorostiaga, 1994). In the particular case of *G. corneum* SST may partially explain the retreat detected for this foundation species at 5 of the sites sampled in the present study. The aforementioned extreme temperatures detected during the last decades for the study area are higher than those (23.3˚C ± 1.68) found during summer at the southern limit of the biogeographical range (northern Mauritania) of *G. corneum* (Alberto et al., 1999; Ould-Dedah et al., 1999), which suggests that this species might have exceeded its upper thermal tolerance (Lüning, 1990). Moreover, recent studies carried out in the study area relate high irradiance levels to higher bleaching and lower biomass and frond density of *G. corneum* (Quintano et al., 2017). Therefore, since the negative effects of irradiance on physiology of *G. corneum* are emphasised at temperatures above 22˚C (Torres et al., 1991), the increase in annual average solar radiation (6.2 W m^{-2} per decade) detected in the eastern part of North coast of Spain between 1985 and 2010 (Sanchez-Lorenzo et al., 2013) might also explain the decline of this foundation species. In addition, some authors have pointed to increases in wave energy (Borja et al., 2013) and reduced nutrient availability (Díez et al., 2012b) in the study area as underlying factors in the decline of the canopy-forming *G. corneum*.

The new thermal and irradiance conditions mentioned above might have favoured the development of morphologically simpler forms (*A. ciliolatum, A. stichidiosa, A. tenuissimum, G. flaccida, Herposiphonia* sp.,), since most of these increased species are algae with a warm-temperate or subtropical affinity and are commonly found in sun-exposed environments (Díez et al., 2012b). This outcome agrees with the findings of other studies, which have reported proliferations of ephemeral algae with simple undifferentiated habits (Lamela-Silvarrey et al., 2012; Méndez-Sandín and Fernández, 2016; Sangil et al., 2012) coincident with seawater warming and increased irradiance for the western part of Spain's north coast (Sanchez-Lorenzo et al., 2013; Voerman et al., 2013) and for the Canary Islands (García et al., 2014; Sangil et al., 2012). There is also experimental evidence that the recruitment of filamentous-turfs is facilitated by increased light (Connell, 2005). Similarly, the increase in articulated coralline algae (*E. elongata* and *Jania* spp) in the present study could also be induced by the rise in SST as higher temperatures foster calcification and growth in these algae (Steller et al., 2007). Regarding crustose layer, the species *Lithophyllum incrustans, Peyssonnelia* spp., and *Zanardinia typus* also increased throughout the study area. Although the causes of the spread of these taxa are not clear, the aforementioned new environmental conditions along with biotic interactions might have favored their development. As discussed for articulated coralline algae, *L. incrustans* could have benefited from increased SST (Goikoetxea et al., 2009) and irradiance (Sanchez-Lorenzo et al., 2013) in the study area since this species is abundant in sun exposed intertidal habitats along the southeastern coast of the Bay of Biscay (Díez et al., 2009b). Considering the meridional affinity of *Peyssonnelia* spp. and *Z. typus* (Boisset, 1992; Díez et al., 2012b), the new thermal conditions might have favored their increase. For all the said morpho-functional forms, the loss of canopy-forming species may have increased the speed at which they respond to new environmental conditions, since the greatest increases in simple forms, coralline algae and some crustose species occurred where the algal canopies were lost.

The concern now is to learn the potential stability of the changes observed and to identify the directions that today's subtidal communities may take in the future. Our results suggest that canopy dominated assemblages may be shifting to an alternative stable state dominated by simple turf-forming algae, coralline species and crusts. Specific ecological research is needed, but it seems reasonable to posit potential scenarios by contrasting ecological mechanisms that either enhance stability or reduce resilience in turfs and canopy dominated assemblages. In a scenario of global change, the prevalence of turf dominated subtidal bottoms in the area considered here seems to be realistic on the basis of their ability to compete for space and resist disturbance (Airoldi, 1998). Regarding species dynamics, other researchers have suggested the loss of resilience of canopy-algae since negative competitive interactions with new turfing space occupiers may have prevented canopy recovery at certain advanced stages of ecosystem alteration (Díez et al., 2014; Perkol-Finkel and Airoldi, 2010). Turf-forming algae are characterised by small body size, high reproduction rates and rapid development, enabling them to take advantage of the new environmental conditions and settle in disturbed areas (Levinton, 1970). Once established, algal-turfs modify the environmental conditions by incorporating sediment into their structure (Airoldi, 2003), which in turn appears to inhibit the recruitment of canopy-forming algae (Connell, 2003; Devinny and Volse, 1978). Differences in life-history traits between turf and canopy-forming seaweeds with the comparatively low dispersal ability of canopy-forming species may also underlie the greater resilience of turf-dominated assemblages (Airoldi, 2000; Bulleri and Benedetti-Cecchi, 2006). In particular, the success of *Ellisolandia*/*Corallina* species in establishing themselves on rocks and in persisting over time might be based on their morphological attributes (e.g. calcified thalli resistant to abrasion, grazing and prolonged burial; basal crusts increasing the surface initially occupied by a single thallus) and their life history characteristics (e.g. perennial life history, reproductive cells released for long periods, vegetative propagation coupled with dispersal by spores) (Stewart, 1989). Consequently, forecasts of environmental conditions related to climate change (i.e. increases in temperature, irradiance, storm frequencies) are likely to cause comparatively less disturbance and stress in turf-forming species than in large macrophytes. In this sense, the replication over time of the present investigation sheds light on the potential stability of the shift detected. The main changes took place between T1 (1991) and T2 (2008-2009) but the shifts remained or even increased between T2 and T3 (2013).

Primary productivity was not studied in this investigation, but it is one of the most important ecosystem functions (Harley et al., 2012; Tait and Schiel, 2011) and the loss or severe reduction of canopy-forming algae in shallow subtidal environments might alter it drastically. In the case of *Gelidium corneum*, a drastic reduction in its standing stock of about 7,800 t across 30 km of the easternmost part of our study area has been documented for the 1993-2012 period (Borja et al., 2013). The increase detected in coralline algae in this area cannot offset the loss of biomass of *G. corneum*, since corallines are some of the least productive algae because their calcium carbonate structure makes them heavy relative to their photosynthetic capability (Littler and Arnold, 1982). Likewise, the contribution of biomass to the increase in turf-forming simple algae is thought to have been low, because although they have high per-biomass productivity, their per-area productivity is low (Tait and Schiel, 2011). Indeed, in one of the sampling locations of the present study (KO), a loss of 46% of the biomass of the whole macroalgal community (with the exception of crustose species) was reported by Gorostiaga et al. (2008) between 1982 and 2007 along a coastline stretch of 2 km where the cover of the *G. corneum* canopy declined from 75% to 47%.

Losing the three-dimensional space created by canopy algae may significantly reduce the abundance of invertebrates (Norderhaug et al., 2007; Wikström and Kautsky, 2007) which also play a key role in the productivity of the system. Biomass and secondary production of macrofaunal assemblages could be favoured by the presence of larger seaweeds in shallow subtidal systems (Edgar, 1990). Considering that in the area studied here the total abundance of invertebrates shows a markedly positive relationship to the canopy layer (Bustamante et al., 2014; 2017), a decrease in productivity of the system may be expected. Particularly, the loss of space created by canopy algae drastically limits the development of the suspension feeders responsible for energy transportation (Asmus and Asmus, 2005) and key components of coastal ecosystems by coupling and transferring energy between the benthos and plankton (Gili and Coma, 1998). On the other hand, the increase in turf algae detected here might result in a shift in trophic function towards other feeding strategies such as detritivores (Bustamante et al., 2014) because turf algae form dense carpets that act as sediment traps.

Habitat-forming seaweeds also play a critical role in determining biodiversity in coastal ecosystems (Harley et al., 2012). These large macroalgae directly enhance biodiversity by providing food, habitat and refuge from environmental stressors and from predation (Airoldi et al., 2008). They are also involved in 'habitat cascades' by providing basal space for intermediate habitat formers (Thomsen et al., 2010). Losses of the protective algal canopies and the consequent increased environmental stress on associated organisms have been reported as giving rise to declines in taxa richness (Schiel and Lilley, 2007) and homogenisation with neighbouring habitats (Mangialajo et al., 2008). Therefore, the loss of algal canopies might lead to a decline in living space for a plethora of organisms and a subsequent loss of diversity (Smale et al., 2013). In the present investigation, the increase in algal species richness and diversity seems contradictory with the function that large macrophytes play in ecosystems. However, losing canopy algae may free up resources such as space and light and facilitate the settlement of opportunistic algal species with simple morphologies and short life-cycles. This plausible explanation is in line with the intermediate disturbance hypothesis, which predicts maximal diversity at intermediate levels of disturbance (Connell, 1978; Valdivia et al., 2005). However, taking into account that most of the new species detected have a warm-water affinity, the increase in species richness and diversity might be explained by physiological responses of species to warming. This hypothesis is supported by the finding that species richness increased throughout the study area. Nevertheless, the loss of canopy-forming species may have changed the speed at which species richness responds to warming, since the greatest increases occurred where the algal canopies were lost. Recent increases in simple algae richness had already been reported for intertidal assemblages in the western part of the North coast of Spain (Lamela-Silvarrey et al., 2012; Méndez-Sandín and Fernández, 2016) and on the coast of Portugal (Araújo et al., 2009). Nevertheless, regarding the potential impact of the loss of habitat-forming seaweeds on biodiversity, it should be taken into account that although a particular group of species might benefit under the loss of canopy species, a loss of biodiversity in its broadest sense is still expected. Indeed, Bustamante et al. (2014; 2017) found that the loss of canopy species (in the same study area as our own research) can result in a sharp decrease in invertebrate taxonomic and functional density and diversity. Considering the facilitating role of canopy species in sustaining ecosystem resilience (Hughes et al., 2005) the biodiversity of the benthic ecosystem studied here might be negatively impacted as a whole.

5. CONCLUSION

This study provides evidence that canopy dominated assemblages off the southern coast of the Bay of Biscay may be shifting to an alternative stable state dominated by turf-forming simple algae, coralline species and crusts, leading to a structural impoverishment of coastal ecosystems. These changes could be an ecological impact of global climate change. According to the forecasts in the latest report by the IPCC (2013) climate alterations will continue, so canopy biogenic habitats might be unlikely to recover (Wernberg et al., 2016), particularly considering that the new occupiers are likely to exhibit greater resilience to the predicted scenarios of global change. As a result, major implications for the ecosystem functioning and diversity may be expected in terms of direct and indirect losses of productivity, since macroalgae dependent organisms would also be affected. The loss of canopies may also result in significant economic losses since the ecosystem services that they provide might be also threatened.

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APPENDIX

Table 1A. Georeference of the starting point on land, direction and starting point depth of the transects.

LOCATION	Latitude	Longitude	Direction	Starting depth (m)
Kobaron (KO)	43°21'17.65"N	3° 07'46.40"W	NW 355°	3
Armintza (AR)	43°26'18.72"N	2°54'34.31"W	N 30°	4
Bakio (BA)	43°25'53.65"N	2°49'48.03"W	N 0°	3
San Juan (SA)	43°26'44.12"N	2°47'16.45"W	W 290°	4
Matxitxako (MX)	43°27'19.82"N	2°45'14.35"W	N 355°	4
Gibeleko (GI)	43°25'54.60"N	2°44'22.92"W	E 75°	2
Ogoño (ÑO)	43°24'49.73"N	2°38'58.66"W	NW 315°	3
Ea (EA)	43°23'16.89"N	2°35'00.66"W	NE 45°	3
Ogeia (OG)	43°22'55.27"N	2°33'12.60"W	NE 45°	1
Egiluz (EG)	43°21'32.79"N	2°29'06.97"W	NE 45°	2
Ondarroa (ON)	43°19'44.75"N	2°25'19.10"W	NE 45°	3
Punta Endata (EN)	43°17'56.18"N	2°18'39.52"W	N 0°	2
Isla San Antón (RA)	43°18'41.24"N	2°12'05.48"W	N 0°	4
Punta Iteico (IT)	43°17'40.61"N	2°11'01.73"W	NNE 20°	1
Tierra Blanca (TB)	43°18'39.81"N	2°04'04.53"W	NNW 325°	3
Urgull (UR)	43°19'37.58"N	1°59'26.27"W	NNW 345°	4
Tambó (TA)	43°20'18.40"N	1°54'44.23"W	NNW 320°	4
Punta Zabala (ZA)	43°22'30.49"N	1°51'27.18"W	NNW 325°	3
Cabo Higer (HI)	43°23'42.51"N	1°47'33.61"W	NNW 345°	4

Table A2. Average cover (C) in %, standard error (SE), and frequency in % (F) of the taxa in the three sampling periods (T1: 1991; T2: 2008-09; and T3: 2013). (*) Morpho-functional group: 1: filamentous; 2: polysiphonated; 3: foliose non-corticated; 4: foliose slightly corticated; 5: foliose heavily corticated; 6: terete slightly corticated; 7: terete heavily corticated; 8: leathery; 9: articulated calcareous; 10: crustose calcareous; and 11: crustose non-calcareous. (1) *C.officinalis* and *Elisolandia elongata* (formerly *C. elongata*); (2) *J. rubens* and *J. longifurca*; (3) M. alternans and M. expansum; (4) *P. harveyana* and *P. squamaria*; (5) *P. cartilagineum* and *P. raphelisianum*; (6) *P. ardreana*, *P. parasitica* and *P. pennata*; (7). *U. dangeardii*, *U. pseudocurvata* and *U. rigida*.

		T1			T2			T3		
TAXA	**(*)**	**C**	**SE**	**F**	**C**	**SE**	**F**	**C**	**SE**	**F**
Acrosorium ciliolatum (Harv.) Kylin	3	0.08	0.04	3	1.73	0.20	72	3.79	0.24	91
Aglaothamnion cordatum (Børgesen) Feldm.-Maz.	1	0.05	0.02	4	0.02	0.01	2	0.49	0.12	7
Aglaothamnion gallicum (Nägeli) Halos ex Ardré	1	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0
Aglaothamnion tenuissimum (Bonnem.) Feldm.-Maz.	1	0.01	0.00	1	5.27	0.63	48	2.70	0.29	35
Aglaothamnion tripinnatum (C. Agardh) Feldm.-Maz.	1	0.00	0.00	0	0.00	0.00	1	0.36	0.07	16
Ahnfeltia plicata (Huds.) Fr.	7	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0
Ahnfeltiopsis devoniensis (Grev.) P.C. Silva & DeCew	5	0.00	0.00	0	0.03	0.01	5	0.11	0.03	6
Anotrichium furcellatum (J. Agardh) Baldock	1	0.00	0.00	0	0.00	0.00	0	0.00	0.00	1
Antithamnion amphigeneum A. Millar	1	0.00	0.00	0	0.00	0.00	1	0.04	0.02	3
Antithamnion hubbsii E.Y.Dawson	1	0.00	0.00	0	0.00	0.00	0	0.09	0.02	5
Antithamnion nipponicum Yamada & Inagaki	1	0.00	0.00	0	0.14	0.03	15	0.16	0.07	3
Antithamnionella ternifolia (J.D.Hooker & Harvey)Lyle	1	0.05	0.02	3	0.92	0.13	39	1.60	0.18	37
Aphanocladia stichidiosa (Funk) Ardré	2	0.00	0.00	0	0.60	0.16	10	3.82	0.44	28
Apoglossum ruscifolium (Turner) J. Agardh	3	0.06	0.01	13	0.52	0.10	27	0.60	0.07	28
Asparagopsis armata Harv.	2	0.11	0.02	11	0.01	0.00	2	0.14	0.04	7
Boergeseniella fruticulosa (Wulfen) Kylin	2	0.00	0.00	0	0.00	0.00	0	0.01	0.01	0
Bonnemaisonia asparagoides (Woodw.) C. Agardh	6	0.01	0.00	2	0.18	0.09	10	0.39	0.08	16
Bonnemaisonia clavata Hamel	6	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0
Bonnemaisonia hamifera Har.	6	0.45	0.17	26	0.07	0.01	11	0.23	0.06	9
Bornetia secundiflora (J. Agardh) Thur.	1	0.01	0.00	2	0.22	0.03	27	0.24	0.04	17
Bryopsis hypnoides J.V.Lamouroux	1	0.00	0.00	0	0.00	0.00	0	0.05	0.02	2
Bryopsis pennata J.V.Lamouroux	1	0.00	0.00	0	0.01	0.01	0	0.00	0.00	0
Bryopsis plumosa (Hudson) C.Agardh	1	0.00	0.00	0	0.10	0.04	6	0.62	0.12	18
Calliblepharis ciliata (Huds.) Kütz.	5	0.12	0.04	7	0.01	0.01	0	0.02	0.01	1

Table A2. - (cont.).

TAXA	(*)	T1			T2			T3		
		C	SE	F	C	SE	F	C	SE	F
Callithamnion granulatum (Ducluz.) C. Agardh.	1	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0
Callithamnion tetragonum (With.) Gray	1	0.00	0.00	0	0.01	0.00	2	0.01	0.01	0
Callophyllis laciniata (Huds.) Kütz.	5	0.15	0.06	14	0.02	0.01	2	0.07	0.04	2
Centroceras clavulatum Mont.	2	0.00	0.00	0	0.22	0.10	8	0.91	0.20	9
Ceramium botryocarpum A.W.Griffiths ex Harvey	2	0.00	0.00	0	0.13	0.06	3	0.35	0.08	10
Ceramium ciliatum (J. Ellis) Ducluz.	2	0.09	0.04	4	0.24	0.14	2	0.58	0.15	9
Ceramium echionotum J. Agardh	2	0.00	0.00	0	0.16	0.07	3	0.33	0.09	9
Ceramium pallidum (Nägeli ex Kütz.) Maggs & Hommers.	2	0.00	0.00	0	0.01	0.01	0	0.00	0.00	0
Ceramium secundatum Lyngb.	2	0.06	0.04	1	0.03	0.01	4	0.06	0.02	5
Ceramium virgatum Roth	2	0.00	0.00	0	0.00	0.00	0	0.02	0.01	1
Chaetomorpha linum (O.F.Müller) Kützing	1	0.00	0.00	0	0.01	0.00	2	0.00	0.00	0
Champia parvula (C. Agardh) Harv.	6	0.04	0.02	4	0.28	0.07	17	0.88	0.12	27
Chondracanthus acicularis (Roth) Fredericq	7	0.05	0.04	3	0.41	0.13	9	0.66	0.13	11
Chondracanthus teedei (Mert. ex Roth) Kütz.	7	0.25	0.09	5	0.15	0.06	5	0.43	0.11	7
Chondria coerulescens (J. Agardh) Falkenb	6	0.35	0.13	7	1.14	0.34	14	0.23	0.11	4
Chrysymenia ventricosa (J.V. Lamour.) J. Agardh	6	0.01	0.00	2	0.00	0.00	0	0.03	0.01	1
Chylocladia verticillata (Lightf.) Bliding	6	0.00	0.00	0	0.00	0.00	0	0.03	0.01	3
Cladophora hutchinsiae (Dillwyn) Kützing	1	0.00	0.00	0	0.01	0.00	2	0.10	0.04	5
Cladophora laetevirens (Dillwyn) Kützing	1	0.00	0.00	0	0.01	0.00	2	0.02	0.01	2
Cladophora lehmanniana (Lindenberg) Kützing	1	0.00	0.00	0	0.04	0.01	6	0.29	0.08	11
Cladophora pellucida (Hudson) Kützing	1	0.16	0.02	21	0.45	0.11	34	1.00	0.12	48
Cladophora prolifera (Roth) Kützing	1	0.01	0.00	2	0.19	0.04	18	0.56	0.11	13
Cladostephus spongiosum (Hudson) C.Agardh	7	0.43	0.11	13	1.86	0.40	29	1.90	0.24	27
Codium adhaerens C.Agardh	11	0.00	0.00	0	0.02	0.01	1	0.05	0.04	1
Codium decorticatum (Woodward) M.Howe	2	0.14	0.06	8	0.78	0.22	18	1.30	0.30	10
Codium fragile (Suringar) Hariot	2	0.01	0.01	0	0.02	0.01	3	0.31	0.07	10
Codium vermilara (Olivi) Delle Chiaje	2	0.00	0.00	0	0.00	0.00	0	0.10	0.04	3
Colpomenia peregrina Sauvageau	4	0.00	0.00	1	0.05	0.01	8	0.05	0.01	7

Table A2. - (cont.).

		T1			T2			T3		
TAXA	**(*)**	**C**	**SE**	**F**	**C**	**SE**	**F**	**C**	**SE**	**F**
Colpomenia sinuosa (Mertens ex Roth) Derbès & Solier	4	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0
Compsothamnion thuyoides (Sm.) Nägeli	1	0.00	0.00	0	0.04	0.01	3	0.02	0.01	1
Corallina spp. (1)	9	3.78	0.57	52	12.12	1.05	70	14.04	1.01	71
Crouania attenuata (C.Agardh) J.Agardh	1	0.01	0.01	1	0.13	0.05	8	0.89	0.15	20
Cryptonemia lomation (Bertol.) J. Agardh	4	0.03	0.01	2	0.00	0.00	0	0.00	0.00	0
Cryptonemia seminervis (C.Agardh) J.Agardh	4	0.07	0.04	4	0.00	0.00	0	0.04	0.04	0
Cryptopleura ramosa (Huds.) Kylin ex L. Newton	3	0.95	0.12	63	1.02	0.17	34	0.54	0.10	13
Cystoseira baccata (S.G.Gmelin) P.C.Silva	8	20.23	1.76	40	14.76	1.49	30	13.43	1.46	26
Cystoseira tamariscifolia (Hudson) Papenfuss	8	0.02	0.01	1	0.01	0.01	0	0.04	0.04	0
Dasya hutchinsiae Harvey	2	0.01	0.01	1	0.25	0.16	5	0.37	0.09	8
Dasya ocellata (Grateloup) Harvey	2	0.00	0.00	0	0.05	0.04	1	0.01	0.01	1
Dasya rigidula (Kützing) Ardissone	2	0.00	0.00	0	0.00	0.00	0	0.69	0.17	10
Derbesia tenuissima (Moris & De Notaris) P.Crouan & H.Crouan	1	0.01	0.00	2	0.45	0.13	18	0.83	0.12	27
Desmarestia ligulata (Stackhouse) J.V.Lamouroux	4	0.04	0.01	6	0.00	0.00	0	0.04	0.04	0
Dictyopteris polypodioides (A.P.De Candolle) J.V.Lamouroux	4	0.27	0.03	37	0.13	0.02	18	0.16	0.03	8
Dictyota dichotoma (Hudson) J.V.Lamouroux	4	2.96	0.41	61	1.05	0.17	41	3.83	0.42	49
Dudresnaya verticillata (With.) Le Jol.	2	0.00	0.00	1	0.00	0.00	0	0.00	0.00	0
Erythroglossum laciniatum (Lightf.) Maggs & Hommers.	3	0.00	0.00	0	0.01	0.00	2	0.00	0.00	0
Falkenbergia rufolanosa (Harvey) F.Schmitz in F.Schmitz & Hauptfleisch	2	2.88	0.53	31	10.55	0.85	71	4.66	0.37	67
Gastroclonium ovatum (Hudson) Papenfuss	6	0.01	0.01	1	0.00	0.00	0	0.00	0.00	0
Gastroclonium reflexum (Chauvin) Kützing	6	0.00	0.00	0	0.05	0.02	6	0.13	0.03	5
Gayliella flaccida (Harvey ex Kützing) T.O.Cho & L.J.McIvor	1	0.00	0.00	0	3.53	0.36	52	3.33	0.31	49
Gelidium attenuatum (Turner) Thuret	7	0.00	0.00	0	0.09	0.05	2	0.29	0.08	7
Gelidium corneum (Hudson) J.V.Lamouroux	7	42.15	2.07	75	34.91	1.82	82	35.54	1.83	74
Gelidium pulchellum (Turner) Kützing	5	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0
Gelidium spinosum (S.G.Gmelin) P.C.Silva in Silva. Basson & Moe	7	0.15	0.06	6	0.07	0.04	4	0.31	0.09	5
Gigartina pistillata (S.G.Gmelin) Stackhouse	7	0.02	0.01	2	0.02	0.01	2	0.01	0.01	0

Table A2. - (cont.).

TAXA	(*)	T1 C	T1 SE	T1 F	T2 C	T2 SE	T2 F	T3 C	T3 SE	T3 F
Gracilaria bursa-pastoris (S.G. Gmel.) P.C. Silva	7	0.01	0.00	1	0.00	0.00	0	0.00	0.00	0
Grateloupia filicina (J.V. Lamour.) C. Agardh	5	0.14	0.10	2	0.01	0.01	0	0.00	0.00	0
Gymnogongrus crenulatus (Turner) J.Agardh	5	0.05	0.01	9	0.02	0.01	5	0.03	0.01	1
Gymnogongrus griffithsiae (Turner) Mart.	7	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0
Haematocelis rubens J.Agardh	11	0.45	0.07	41	0.92	0.15	39	0.22	0.06	7
Halicystis parvula F.Schmitz ex Murray	3	0.00	0.00	1	0.13	0.02	20	0.15	0.02	22
Halopithys incurva (Hudson) Batters	7	0.12	0.06	6	0.55	0.14	14	1.25	0.26	10
Halopteris filicina (Grateloup) Kützing	6	0.04	0.01	7	0.13	0.04	10	1.18	0.19	22
Halopteris scoparia (Linnaeus) Sauvageau	7	0.01	0.00	1	0.36	0.12	9	0.12	0.06	2
Halurus equisetifolius (Lightfoot) Kützing	1	0.17	0.03	20	0.28	0.03	27	0.42	0.07	15
Halymenia latifolia P. Crouan & H. Crouan ex Kütz.	4	0.06	0.02	5	0.00	0.00	0	0.02	0.01	1
Herposiphonia sp.	2	0.01	0.01	1	3.29	0.53	25	2.10	0.27	22
Heterosiphonia japonica Yendo	2	0.00	0.00	0	1.81	0.40	29	1.06	0.22	11
Heterosiphonia plumosa (J.Ellis) Batters	2	0.12	0.04	10	0.03	0.01	5	0.28	0.11	6
Hincksia sp.	1	0.12	0.06	2	0.00	0.00	0	0.00	0.00	0
Hypnea musciformis (Wulfen) J.V. Lamour	6	0.00	0.00	0	0.07	0.02	5	0.01	0.01	0
Hypoglossum hypoglossoides (Stackhouse) Collins & Hervey	3	0.00	0.00	0	0.10	0.02	16	0.03	0.01	4
Jania spp. (2)	9	0.16	0.05	10	1.64	0.24	41	4.96	0.43	53
Kallymenia reniformis (Turner) J. Agardh	4	0.00	0.00	0	0.01	0.01	2	0.00	0.00	0
Laminaria ochroleuca Bachelot de la Pylaie	8	2.62	0.68	11	0.00	0.00	0	0.00	0.00	0
Laurencia obtusa (Hudson) J.V.Lamouroux	6	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0
Liagora viscida (Forsskål) C.Agardh	6	0.00	0.00	0	0.08	0.05	1	0.00	0.00	0
Lithophyllum incrustans Philippi	10	0.00	0.00	0	2.16	0.28	34	3.19	0.33	36
Lomentaria clavellosa (Lightfoot ex Turner) Gaillon	6	0.00	0.00	0	0.00	0.00	1	0.00	0.00	0
Meredithia microphylla (J. Agardh) J. Agardh	3	0.00	0.00	1	0.00	0.00	0	0.00	0.00	0
Mesophyllum spp. (3)	10	44.19	1.73	92	35.77	1.36	96	43.20	1.42	99
Microcladia glandulosa (Solander ex Turner) Greville	2	0.02	0.01	1	0.43	0.10	20	0.33	0.08	13
Monosporus pedicellatus (Sm.) Solier	1	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0

Table A2. - (cont.).

		T1			T2			T3		
TAXA	**(*)**	**C**	**SE**	**F**	**C**	**SE**	**F**	**C**	**SE**	**F**
Myriogramme minuta (Kylin) Maggs & Hommers.	3	0.00	0.00	1	0.05	0.02	6	0.14	0.04	8
Naccaria wiggii (Turner) Endl.	6	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0
Nitophyllum punctatum (Stackhouse) Greville	3	0.06	0.01	11	0.13	0.02	22	0.53	0.07	30
Osmundea osmunda (S.G.Gmelin) K.W.Nam & Maggs	6	0.00	0.00	0	0.01	0.00	1	0.00	0.00	0
Padina pavonica (Linnaeus) Thivy	4	0.00	0.00	0	0.00	0.00	0	0.01	0.01	0
Peyssonnelia atropurpurea P.Crouan & H.Crouan	11	0.02	0.01	2	0.18	0.06	9	0.07	0.02	5
Peyssonnelia spp. (4)	11	0.08	0.04	5	0.62	0.08	36	3.81	0.29	60
Phyllariopsis brevipes (C.Agardh) E.C.Henry & G.R.South	8	0.01	0.00	1	0.01	0.00	1	0.01	0.01	0
Phyllophora crispa (Huds.) P.S. Dixon	7	0.00	0.00	0	0.57	0.11	17	0.63	0.12	12
Phymatolithon lenormandii (Areschoug) W.H.Adey	10	0.00	0.00	0	0.01	0.01	0	0.02	0.01	1
Pleonosporium flexuosum (C. Agardh) Bornet	1	0.00	0.00	0	0.02	0.01	1	0.01	0.00	2
Plocamium spp. (5)	6	5.05	0.56	64	9.45	0.75	76	7.74	0.69	68
Polysiphonia polyspora (C. Agardh) J. Agardh	2	0.00	0.00	0	0.03	0.01	5	0.06	0.02	5
Pseudolithoderma nigrum Hollenberg	11	0.00	0.00	0	0.00	0.00	0	0.02	0.01	1
Pterocladiella capillacea (S.G. Gmel.) Santelices & Hommers.	7	0.01	0.01	1	0.00	0.00	0	0.00	0.00	0
Pterosiphonia spp. (6)	2	0.10	0.02	11	2.23	0.26	35	0.95	0.21	27
Pterosiphonia complanata (Clemente) Falkenberg	6	2.65	0.42	41	1.93	0.27	40	2.84	0.29	44
Pterothamnion crispum (Ducluz.) Nägeli	1	0.01	0.00	1	0.27	0.13	14	0.33	0.07	12
Pterothamnion plumula (J. Ellis) Nägeli	1	0.08	0.04	5	0.00	0.00	1	0.01	0.01	1
Radicilingua thysanorhizans (Holmes) Papenf	3	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0
Rhodophyllis divaricata (Stackh.) Papenf.	4	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0
Rhodothamniella floridula (Dillwyn) Feldmann	2	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0
Rhodymenia holmesii Ardiss.	5	0.00	0.00	0	0.03	0.01	4	0.05	0.02	2
Rhodymenia pseudopalmata (J.V. Lamour.) P.C. Silva	5	1.97	0.27	55	1.66	0.22	49	2.11	0.20	43
Saccorhiza polyschides (Lightf.) Batters	8	0.87	0.29	16	0.00	0.00	0	0.00	0.00	0
Sargassum vulgare C. Agardh	8	0.00	0.00	0	0.00	0.00	0	0.01	0.01	0
Scageliopsis patens Wollaston	1	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0
Schimmelmannia schousboei (J.Agardh) J.Agardh	4	0.00	0.00	0	0.00	0.00	0	0.17	0.07	2

Table A2. - (cont.).

TAXA	(*)	T1			T2			T3		
		C	**SE**	**F**	**C**	**SE**	**F**	**C**	**SE**	**F**
Schizymenia dubyi (Chauv. ex Duby) J. Agardh	5	0.02	0.01	4	0.01	0.00	2	0.11	0.03	6
Scinaia furcellata (Turner) J.Agardh	6	0.01	0.00	1	0.00	0.00	1	0.01	0.01	0
Seirospora interrupta (Smith) F.Schmitz	1	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0
Spatoglossum solieri (Chauv. ex Mont.) Kütz.	4	0.01	0.01	1	0.00	0.00	0	0.12	0.06	2
Spermothamnion repens (Dillwyn) Rosenv	1	0.00	0.00	0	0.01	0.01	1	0.00	0.00	0
Sphacelaria cirrosa (Roth) C.Agardh	2	0.00	0.00	0	0.01	0.01	0	0.00	0.00	0
Sphaerococcus coronopifolius Stackh.	7	0.06	0.01	10	0.22	0.06	13	0.57	0.12	11
Sphondylothamnion multifidum (Huds.) Nägeli	1	0.03	0.01	7	0.01	0.00	2	0.00	0.00	0
Stenogramme interrupta (C. Agardh) Mont. ex Harv.	5	0.00	0.00	1	0.00	0.00	0	0.00	0.00	0
Taonia atomaria (Woodw.) J. Agardh	4	0.02	0.01	2	0.05	0.01	8	0.19	0.05	8
Trailliella intricata Batters	1	0.00	0.00	0	0.48	0.11	16	0.70	0.11	20
Ulva spp. (7)	3	0.20	0.04	25	0.33	0.10	25	0.35	0.12	10
Zanardinia typus (Nardo) G. Furnari	11	2.05	0.38	38	11.47	0.84	68	10.13	0.58	73

Table A3. Average cover at each location for the four canopy species present in the study area, for the three sampling periods.

	Cystoseira baccata			*Gelidium corneum*			*Laminaria ochroleuca*			*Saccorhiza polyschides*		
	T1	**T2**	**T3**	**T1**	**T2**	**T3**	**T1**	**T2**	**T3**	**T1**	**T2**	**T3**
KO	7.9	9.9	1.4	76.9	9.3	2.1	0.0	0.0	0.0	8.5	0.0	0.0
AM	30.9	31.4	23.9	6.2	10.1	10.3	0.0	0.0	0.0	0.3	0.0	0.0
BA	43.2	9.2	1.0	36.3	0.6	7.1	19.5	0.0	0.0	0.0	0.0	0.0
SA	2.4	22.7	10.0	45.0	56.5	69.9	39.3	0.0	0.0	0.0	0.0	0.0
MX	40.8	0.0	41.8	0.4	0.6	2.3	0.3	0.0	0.0	0.1	0.0	0.0
GI	79.2	82.1	82.9	0.0	0.1	1.7	0.0	0.0	0.0	0.2	0.0	0.0
ÑO	6.6	15.7	2.1	30.5	60.3	67.5	0.2	0.0	0.0	0.0	0.0	0.0
EA	1.9	0.0	0.1	65.7	35.4	36.3	0.0	0.0	0.0	0.1	0.0	0.0
OG	40.2	58.7	26.3	0.2	3.7	4.3	0.0	0.0	0.0	0.9	0.0	0.0
EG	44.9	1.9	1.9	0.6	12.3	6.9	0.0	0.0	0.0	0.0	0.0	0.0
ON	63.8	46.2	59.0	0.5	0.8	1.7	0.0	0.0	0.0	2.4	0.0	0.0
EN	18.5	19.5	4.1	34.2	56.7	69.6	0.0	0.0	0.0	0.0	0.0	0.0
RA	2.8	0.0	0.7	61.3	37.0	67.6	0.0	0.0	0.0	0.0	0.0	0.0
IT	6.6	0.5	0.3	49.5	68.3	68.2	0.0	0.0	0.0	0.0	0.0	0.0
TB	4.6	0.0	0.0	71.7	65.0	24.4	0.0	0.0	0.0	0.0	0.0	0.0
UR	0.0	0.0	0.0	77.2	70.4	79.9	0.0	0.0	0.0	0.0	0.0	0.0
TA	0.0	0.0	0.0	71.7	66.5	60.4	0.0	0.0	0.0	0.0	0.0	0.0
ZA	0.0	0.0	0.0	83.5	40.5	21.9	0.0	0.0	0.0	0.0	0.0	0.0
HI	0.0	0.1	0.0	75.6	78.6	82.7	0.0	0.0	0.0	0.0	0.0	0.0

chapter 4

Iberian Peninsula

NAHIARA MUGUERZA (2020) DOCTORAL THESIS pp. 97-125

A spatially-modelled photo of future marine algal communities in southern Europe: towards a broader Mediterranean region?

ABSTRACT The effect of climate change on species distribution has been the focus of much recent research, but the community-level approach remains poorly studied. Our investigation applies a present community-environment relationship model for the first time to the exploring of future spatial distributions of subtidal macrophyte assemblages from the northern Iberian Peninsula under the RCP 4.5 and RCP 8.5 climate scenarios by 2100. Water temperature is the most relevant factor in shaping assemblage distribution, whilst nutrient availability plays a secondary role. The results partially support our hypothesis that there may well be a meridionalization of northern Iberian communities in the future. Under the most pessimistic scenario, the model projects that the north-western assemblages will remain distinct from the rest, whereas the central and eastern communities of the northern Iberian Peninsula will come to resemble those of the Mediterranean region more closely than those of the north-west coast.

KEYWORDS Ecosystem restoration; Macroalgal assemblages; Ecological quality assessment; Long-term changes; Human impacts, Ecological resilience.

LABURPENA

Etorkizuneko Europaren hegoaldeko itsas algen komunitateen espazialki modelatutako argazkia: eskualde mediterraneo zabalago baterantz?

Klima-aldaketak espezieen banaketan izan duen eragina ikerketa berrienetako askoren ardatza izan da, baina komunitate-mailako ikuspegia gutxi aztertu da oraindik. Gure ikerketak lehen aldiz,komunitatea eta ingurumena erlazionatzen dituen eredu bat aplikatzen du Iberiar Penintsulako iparraldeko mareaz azpiko makrofitoen komunitateen etorkizuneko banaketa espazialak esploratzeko RCP 4.5 eta RCP 8.5 agertoki klimatikoetan, 2100 urterako. Komunitateen banaketan faktore garrantzitsuena uraren tenperatura da, eta mantenugaien eskuragarritasuna berriz, bigarren mailakoa da. Emaitzek, neurri batean, gure hipotesia onesten dute: Iberiar Penintsulako iparraldeko komunitateek etorkizunean hegoaldeko joera erakutsi dezakete. Agertoki ezkorrenean, Ipar-mendebaldeko komunitateek gainerakoetatik bereizten jarraituko dutela dio ereduak; Penintsularen iparraldeko erdi eta ekialdeko komunitateek, berriz, antzekotasun gehiago azalduko dituzte Mediterraneo hurbileko komunitateekin, ipar-mendebaldekoekin baino.

RESUMEN

Una instantánea, modelada espacialmente, de las futuras comunidades de algas submareales del sur de Europa: ¿se va hacia una región mediterránea más amplia?

El efecto del cambio climático en la distribución de especies ha sido el foco de muchas de las investigaciones más recientes, pero el enfoque a nivel de comunidad sigue estando poco estudiado. Nuestra investigación aplica por primera vez un modelo que relaciona comunidad y medio ambiente para la exploración de futuras distribuciones espaciales de las comunidades de macrófitos submareales del Norte de la Península Ibérica en los escenarios climáticos RCP 4.5 y RCP 8.5 para 2100. La temperatura del agua es el factor más relevante en la distribución de las comunidades, mientras que la disponibilidad de nutrientes juega un papel secundario. Los resultados apoyan parcialmente nuestra hipótesis que considera que en el futuro puede darse una meridionalización de las comunidades del norte de la Península Ibérica. En el escenario más pesimista, el modelo proyecta que las comunidades noroccidentales seguirán diferenciándose del resto, mientras que las comunidades centrales y orientales del Norte de la Península Ibérica presentarán más similitudes con las de la región mediterránea más cercana que con las comunidades del noroeste.

1. INTRODUCTION

Understanding and anticipating future climate-driven changes in marine ecosystems is now a major theme in science. Macroalgae sustain highly diverse, productive ecosystems on temperate rocky seashores by supplying food and shelter for a large number of associated invertebrates and fish (Harley et al., 2012). Seaweeds help maintain biodiversity, which in turn has positive effects on invasion resistance and stability (Boyer et al., 2009). They function as nursery grounds and as shelter from environmental stressors and predation (Steneck et al., 2002). Furthermore, algae provide many ecosystem goods and services including food, medicine, CO2 emissions sinks, raw materials, storm protection and natural barriers to erosion (Harley et al., 2012).

The spatial distribution of seaweeds results from a complex interaction of biotic and abiotic factors (Knox, 2000). On a global geographic scale, sea surface temperature (SST) is considered the most important range-limiting factor which, in combination with day length, sets biogeographical boundaries for survival, growth and reproduction of algae (Lüning, 1990). Local factors, including nutrient availability (Pineiro-Corbeira et al., 2019), salinity (Schubert et al., 2011), solar radiation (Figueroa et al., 2010), pollution (Díez et al., 2014), sedimentation rates (Airoldi, 1998) and hydrodynamic forces (i.e. wave action and currents) (Burrows, 2008) interact with water temperature in establishing (or not) the habitat suitability required for each species. In addition, interspecific interactions such as competition, herbivory and predation may determine spatial distributions by complementing or modulating the effects of environmental conditions (Foster, 1990).

Organisms are exposed to environmental conditions that naturally vary across time and space at different scales (Connell et al., 1997). However, the planet is currently facing a change in climate induced by anthropogenic activities which is progressing at an unprecedented pace (IPCC, 2014). Marine biota is already responding to these shifts in the physical and chemical conditions of oceans (Hoegh-Guldberg & Bruno, 2010). In coastal areas, climate change-driven alterations are having substantial negative implications for the functioning and biodiversity of ecosystems (Jueterbock et al., 2013). In several regions these changes are already sufficiently abrupt and permanent to be termed “regime shifts”, involving biogenic habitat loss (Wernberg et al., 2016), alteration of species interactions within trophic pathways (O’Connor, 2009) and spread of non-indigenous species (Sorte et al., 2010). Following species distribution shifts, novel species interactions such as competition (Harley et al., 2012), herbivory (Vergés et al., 2016) and disease (Qiu et al., 2009) may lead to more detrimental consequences for ecosystem functioning than direct physiological responses to changes in environmental conditions. Wernberg et al. (2016) point out that an intensification of reinforcing feedback mechanisms would provide resilience to the new alternative community configuration, often with profound ecological, social, and economic consequences.

Warming rates vary from one latitude and region to another. The warming of the Atlantic Ocean since 1970 almost matches that of the Pacific Ocean and Indian Ocean combined (Lee et al., 2011). In the Bay of Biscay in particular, a warming of 0.26 ± 0.03°C every ten years was detected for the period 1982–2014 (Costoya et al., 2015). Under this scenario of environmental change, the range of macroalgal species is shifting along the coast of the Iberian Peninsula (Martínez et al., 2015). Strong retractions and even local extinctions of some temperate-cold species have been detected (Casado-Amezúa et al., 2019). The biggest changes in the northern Iberian Peninsula are the retreat of habitat-forming species such as *Laminaria hyper-*

borea, *Laminaria ochroleuca*, *Saccorhiza polyschides*, *Saccharina latissima* and the red alga *Gelidium corneum* (Borja et al., 2013; Duarte et al., 2013; Fernández, 2011; Muguerza et al., 2017; Piñeiro- Corbeira et al. 2018; Voerman et al., 2013). In addition to the loss of biogenic species, in the past few decades there has been an increase in richness and abundance of warm-affinity species (mainly ephemeral forms with simple morphology), coralline algae and crustose species have become abundant and non-indigenous species have expanded (Díez et al., 2012b; Lamela-Silvarrey et al., 2012; Muguerza et al., 2017). Most of these studies point out that higher temperatures are likely the main driver of the changes observed. Nevertheless, other local factors such as nutrient availability, solar radiation, sunlight hours, and wave height have been suggested as potential co-acting factors of change in combination with warming (Borja et al., 2013, 2018; Fernández, 2011; Muguerza et al., 2017).

Global climate is projected to continue to change over the 21st century (IPCC, 2014) and predictions state that sea surface temperature isotherms will shift up to 600 km northwards by its end (Jueterbock et al., 2013). These changes are expected to have profound impacts on the distribution of seaweeds (Martínez et al., 2018). In the Bay of Biscay, the RCP 8.5 scenario projects a 1.5ºC to 3.0ºC warming above mean for 2050–2099 (IPCC, 2014). Solar radiation is expected to increase by up to 5% by the end of the century (Ruosteenoja and RaÅNisaÅNnen, 2013). Projections also suggest changes in the coastal upwelling system of the NW Iberian Peninsula, showing trends of both intensification and weakening (Santos et al., 2011). Similarly, predictions for future wave energy are variable (Charles et al., 2012; Ulazia et al., 2017).

Research into future redistribution of seaweeds typically focuses on commercially important macroalgae (Khan et al., 2018) or large macrophytes with a habitat-forming function (Jueterbock et al., 2013), while research at community level receives much less attention (Harley et al., 2006). For the northern Iberian Peninsula, several models dealing with targeted macroalgal species have concluded that some species will become extinct or dramatically reduced, while others are predicted to expand their range under future climate projections (de la Hoz et al., 2019; Franco et al., 2018; Pineiro-Corbeira et al., 2019). It is suggested that the expansion or retraction of these species is modulated mainly by temperature (Franco et al., 2018; Pineiro-Corbeira et al., 2019). Nevertheless, nutrient availability may also be a crucial contributor to maintaining optimal physiological performance (Franco et al., 2018), and some projections even indicate that nutrient limitation might influence the performance of both upward and downward seaweeds more strongly than warming (Pineiro-Corbeira et al. 2019).

This study examines present and future spatial distribution patterns based on field data on subtidal macrophyte assemblages (composition and species abundance) from the Atlantic and Mediterranean coasts of the Iberian Peninsula and environmental data from the OCLE open database (de la Hoz et al., 2018). The aims of this research are to: (1) determine the key factors influencing macroalgal assemblage distribution; (2) build an assemblage-environment relationship model; and (3) forecast assemblage distribution shifts under future climate change scenarios (RCP4.5 and RCP8.5) by the end of the century. As oceans become warmer, evidence of redistribution from many species show expansion at their poleward range boundaries and contraction at their equatorward boundaries (Wernberg et al. 2011b). This study therefore hypothesises that, at community level, climate change will drive a meridionalisation of the Atlantic coast of the Iberian Peninsula.

Most studies deal with predicting the impact of climate change on single species. Individual species responses are connected and interact among one another and between themselves and their physical environment, so considering only species responses explains just a small portion of the community elements that compose the whole ecosystem (Lavergne et al., 2010). Spatial predictions of community composition are a major challenge. As the scale of global change increases, community-level approaches are becoming more relevant because they can predict how the biodiversity of entire ecosystems will respond to new environmental conditions (Guisan and Rahbek, 2011).

To our knowledge, this is the first study to draw up an assemblage-environment relationship model for the subtidal vegetation of the Iberian Peninsula with a view to forecasting the impact of climate change on the seaweed communities of the Bay of Biscay. Community-level models would permit a better prediction of the whole ecosystem response and would also shed light on where valued habitats may be found under climate change scenarios. This information is essential for the proper management and conservation of coastal ecosystems. This study also provides a unified framework of survey sampling methodology to be used as the first step of a monitoring plan. Together with integrated modelling and experimental work, there is a need for monitoring studies to better highlight the consequences of climate change so as to ensure the resilience of ecosystems in a changing world (Dutra Silva et al., 2019).

2. MATERIAL AND METHODS

2.1 Study area

Along the Atlantic coast, the tide wave enters from the west and propagates towards the east, increasing its amplitude as it enters the Cantabrian Sea. As a result the mean spring tide on the Galician coast is approximately 3.5 m whilst in the Basque Country it is 4.5 m. By contrast, the Mediterranean coast is microtidal with astronomic tidal amplitudes of less than 25 cm.

Wave energy regimes also vary substantially from one region to the other. In winter, significant wave heights (Hs) can exceed 5 m during storms on the Galician coast, coming with westerly winds that often have a southerly component (Fernández-Salas et al., 2015). The summer wave regime has less energy, with Hs of about 2 m (Vitorino et al., 2002). The Cantabrian Sea is also exposed to large storms, with north-westerly waves of more than 2 m over more than 50% of the wintertime. Under extreme conditions, Hs can exceed 5 m several times a year, and may occasionally reach 10 m (Liria et al., 2009). The summer wave regime has less energy, with wave heights of 1.5 m over 75% of the time. In the Mediterranean, wave heights are much lower than on the Atlantic coast because swell plays a lesser role and waves are caused mostly by strong winds (wind sea). In the northern Alboran Sea alternating winds generate equally prevailing waves (40%) from the east and west, with Hs < 1 m over 80% of the year (Puertos del Estado, 2019). On the south-eastern coast, waves come from the SE in summer and from the NW in winter, generating a low to moderate wave climate (Fernández-Salas et al. 2015) with Hs < 1 m over 75% of the year.

The Atlantic coast studied here has a marked thermal gradient running from west (Galicia) to east (Basque Country), with different seasonal cycles in sea surface temperature (SST) at both extremes (Lavín et al., 2006). In the west, SST ranges from 19.5°C during summer downwelling conditions to 14°C in winter (Gómez-Gesteira et al., 2008), though summer upwelling events can cool waters to 16°C (Ospina-Álvarez et al., 2010). The difference between summer and winter SST in the east is reported as being about 10°C, with 22°C in august and 12°C in February (Valencia et al., 2004). In the Mediterranean region there are also differences between the northern Alboran Sea and the South-eastern coast. SST in the Alboran Sea behaves seasonally, averaging 15.5°C in winter and 22.8°C in summer (Shaltout and Omstedt, 2014). However, the inflow of Atlantic waters through the Strait of Gibraltar (the Atlantic Jet) and westerly upwelling-favourable winds may cool summer SST down to 17°C (Echevarría et al., 2009). Winter SST on the south-eastern coast is also around 15°C, but summer SST is more stable and 2°C warmer than in the northern Alboran Sea (Shaltout and Omstedt, 2014).

Mediterranean waters are saltier than Atlantic waters. Evaporation exceeds precipitation plus river runoff in the Mediterranean (Talley et al., 2011). Salt is conserved but there is a net loss of volume due to evaporation that results in a salinity increase. This denser water flows out of the Mediterranean at the bottom of the Strait of Gibraltar. The outflow, with a salinity of 38.4, is balanced by the inflow of less salty (36.1) water from the North Atlantic in the upper layer (Talley et al., 2011). On the other hand, wind forcing, heating, rainfall and river runoff make the salinity of upper waters of the Atlantic highly variable (Lavín et al., 2006).

Nitrate concentration at the surface is highest in winter and lowest during the stratified period, especially in summer. However, on some coastal stretches of the study area seasonal upwelling events inject colder nutrient-rich deeper waters into the surface layers in the spring-summer period (Lavín et al., 2006). North-easterly winds between Cape Finisterre and Ortegal (Galicia) and easterly winds on the Cantabrian shelf produce upwellings mainly in late spring and summer (Lavín et al., 2006). The intensity and frequency of upwelling events decreases eastward as temperature and stratification increase, so they have little or no effect at the eastern end. On the Mediterranean coast studied there is also an upwelling area in the northern Alboran Sea (Echevarría et al., 2009), but nutrient input to the surface layers depends on the nutrient content of the waters at the source of the upwelling, which is lower in relation to the Atlantic coast.

These oceanographic and hydrographic differences between the two regions are accompanied by differences in climate. Solar radiation has a crucial influence on macroalgae (Häder and Figueroa, 1997). There is a strong annual cycle in global solar radiation in the Iberian Peninsula. In the north-western part of the Atlantic coast (A Coruña), seasonal mean irradiance for 1991–2010 ranges from 69.7 to 258.2 W m^{-2} in winter and summer, respectively, whilst in the east (San Sebastian) it varies from 65.9 to 224.1 W m^{-2} (Sanchez-Lorenzo et al., 2013). In the northern Alboran Sea (Malaga) (121.9 vs 317.4 W m^{-2}) and on the south-eastern coast (Cabo Palos) (109.2 vs 309.0 W m^{-2}) irradiances are significantly higher than on the Atlantic coast (Sanchez-Lorenzo et al., 2013).

2.2. Data collection

2.2.1. Field data collection

In summer 2015, data on macroalgal assemblages at 5m depth were collected from 10 locations: Malpica (L1) and Cedeira (L2) on the Galician coast; Luarca (L3), Lastres (L4), San Vicente (L5), Somocuevas (L6), Kobaron (L7) and Ea (L8) on the Cantabrian Sea; La Herradura (L9) on the northern Alboran Sea; and Cabo Palos (L10) on the South-eastern Mediterranean coast of Spain (Figure 1; Table 1). Each location is represented by two randomly selected sites separated by at least 15 m. At each site, a set of eight quadrats (50 x 50 cm) was randomly chosen. All quadrats were separated from each other by at least

1 m and laid out on stable substrates (continuous bedrock) with slight to moderate slopes (<30°). For each quadrat, a SCUBA-diver estimated in situ the macroalgal species cover following a 5% interval scale (from 5 to 100%). Values < 5% were estimated at 1% intervals. For taxa present at less than < 1%, a symbolic value of 0.5% was assigned. Sampling was conducted at species level when possible, and for those species that could not be identified in situ specimens were collected for further identification in the laboratory. The identification was carried out with the Marine Benthos Research Group of the UPV/EHU by means of stereoscopic and optical microscopes, guides and taxonomic books. Specimens collected from L9 and L10 were identified in collaboration with the Department of Plant Biology I (Botany and Plant Physiology) of the Complutense University of Madrid (UCM).

As regards environmental data, for each site SST (°C), photosynthetically active radiation (PAR: 400-700 nm, µmol m^{-2} s^{-1}) and ultraviolet-A radiation (UVA: 315-400 nm; W m^{-2}) were continuously logged every 5 min over 1 month (09/2015) at a depth of 5 m. Each sensor and the corresponding data logger were placed inside a polycarbonate box and attached to the bedrock using a stainless-steel structure. Problems with the maintenance of the box led to the data on radiation not being included in the subsequent analyses.

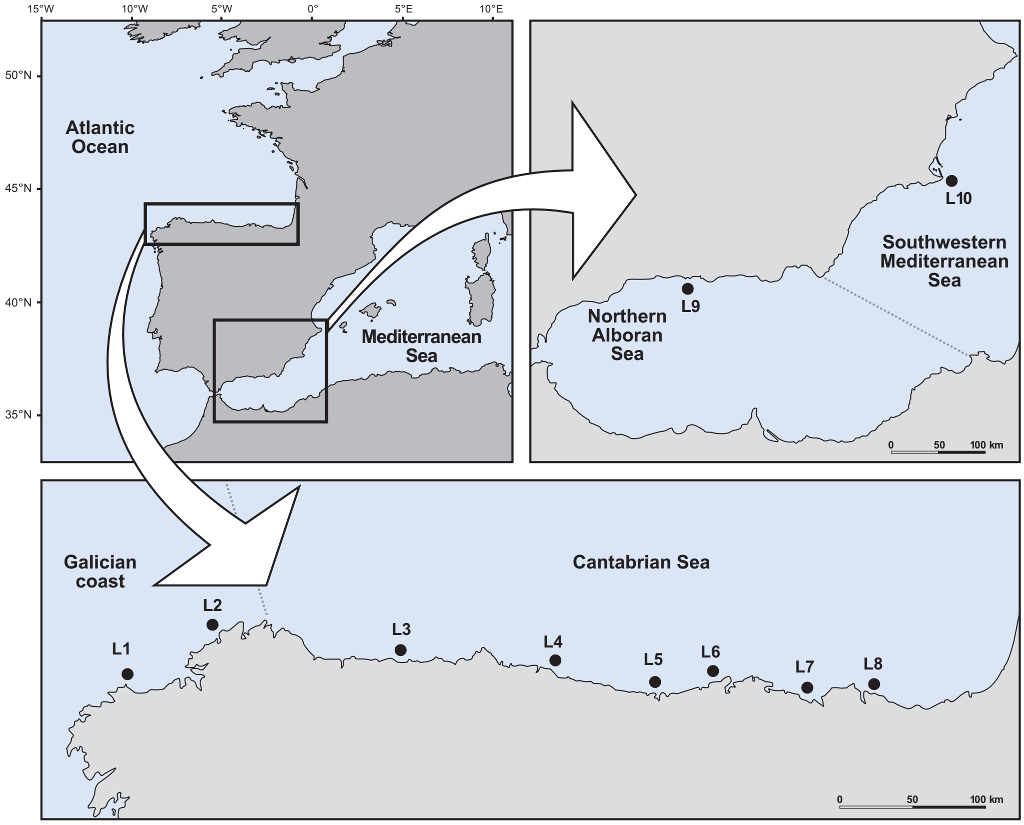

Fig. 1. Map of the study area showing the sampling locations.

2.2.2. Environmental data from databases

The environmental data used in this study were obtained from the OCLE database (de la Hoz et al., 2018). OCLE is an open access database set up to generate an observatory of climate change effects on littoral ecosystems in Europe for both the present and the future. The data are obtained from reanalysis. Satellite-derived data and in situ measurements are compiled at a 0.1º spatial resolution. The environmental variables included in the study were SST (°C), solar radiation (W/m^2), nitrate (mol/m^3), bottom shear stress (N/m^2), significant wave height (m), salinity and tidal range (m), all factors known to influence the distribution of seaweeds (Lüning, 1990). Seasonal means for each variable were extracted for a period that varied from 2010 to 2013, 2014 or 2015, according to the information available (Annex 2). Since there were no data on the exact coordinates of sampling sites, we chose the closest coordinates for every location, trying always to keep a similar distance and positioning from land. To confirm that these coordinates provided an adequate representation of the sampling points, we conducted a correlation analysis between the SST measured in situ by the sensors and that of the database. The results showed that there was a good correlation (R2=0.916).

Environmental data for projections of assemblage distribution shifts under future climate change scenarios were also obtained from the OCLE database. Of the four representative concentration pathways (RCPs) developed by the IPCC (2014), RCP 4.5 and RCP 8.5 were chosen. RCP 4.5 corresponds to a medium stabilisation scenario (mitigation actions resulting in medium emissions more-or-less stable throughout the century) with no overshoot radiative forcing pathway to 4.5 W/m^2 (~650 ppm CO_2 eq) by the end of the century. In contrast, RCP 8.5 is a 'business-as-usual' scenario with continued increases in emissions over time that would lead to radiative forcing levels of 8.5 W/m^2 (~1370 ppm CO_2 eq) by 2100. The time frame considered in the present study was 2070-2100.

2.3. Data analyses

2.3.1. Macroalgal assemblage composition

To explore the assemblages potentially present in the study area, macroalgal species cover data were square-root transformed and similarity between pairs of averaged site samples was calculated using the Bray-Curtis index. Using a group average cluster analysis, we represented the similarity matrix as a dendrogram. To identify the taxa that contributed most to the similarity within the groups detected by the cluster analysis, we performed a similarity percentage analysis (SIMPER).

2.3.2. Assemblage-environment relationship modelling

In order to obtain a graphic visualisation of the spatial distribution of communities, a non-metric multidimensional scaling (nMDS) was performed. The analysis was based on Bray–Curtis similarities calculated on square root-transformed data to reduce the weight of dominant taxa in the multivariate pattern. The site average for each location was plotted with their respective 95% confidence intervals (CI95). The spatial distribution detected in the nMDS was modelled by a polynomial regression.

Environmental data were normalised and log-transformed prior to analyses to obtain comparable scales and reduce skewness (Anderson et al., 2008). Of the total of 28 variables initially considered, we retained for possible inclusion in the model only those for which the pairwise Spearman correlations were R < 0.894 (R2 < 80%) in order to reduce redundancy. A similarity matrix between locations in relation to these latter environmental variables was generated based on Euclidean distance.

To perform a preliminary exploration of how closely similarities in macroalgal assemblage structure were linked to similarities in environmental data, a RELATE test was conducted (Clarke and Warwick, 2001) using 9999 permutations. Distance-based linear model permutation tests (DistLM) were performed to identify the set of environmental variables that best predicted the variation in macroalgal assemblage structure (McArdle and Anderson, 2001).

Given the parabolic-shaped model detected in the nMDS, the curve was split into two parts separated by the vertex and each of them was modelled by a linear regression to obtain a more accurate model. Then the DistLM routine was run for each part of the parabolic-shaped pattern using 9999 permutations and the BEST procedure, as it selects the best model for all possible combinations of predictor variables based on a selection criterion (Anderson et al., 2008). The selection criterion was AICc (Akaike's Information Criterion corrected), a modification of the AIC criterion for models with small numbers of samples in relation to the number of predictor variables. AICc, like the AIC criterion, tends to incorporate more predictor variables within the model than other stricter selection criteria. This enables all predictor variables to be considered in the quantitative partitioning of the multivariate variability and determines how much of the variability is attributable to each one (either acting alone or in pre-defined sets) (Anderson et al., 2008). We plotted distance-based redundancy analyses (dbRDA) to illustrate these relationships, constrained by the best fit-explanatory variables from the DistLM.

With the best predictor variables identified by DistLM for each part of the parabolic-shaped distribution model, two regressions were run. The dependent variable was the distance between the centroids of localities detected in the nMDS (based on the matrix of similarities between macroalgal assemblages), which were considered as 'ecological distance observations'. As for the environmental variables, we used the absolute values of differences -calculated from the original data- between locations. We also ran a third regression to estimate the relationships between predictor variables and those 'ecological distance observations' not considered in these two previous regression models, i.e. between locations from each part of the polynomial distribution model. Subsequently, all predicted values of ecological distance obtained from these three regression equations were plotted against the observed ecological distances to assess the predictive power of the overall model. Predicted distances between locations were then turned into similarity values (by subtracting this distance from 100) to construct a nMDS based on the model.

2.3.3. Projections

We estimated assemblage distribution shifts under future climate change scenarios (RCP4.5 and RCP8.5) for 2070-2100 using the model described above. Future differences between locations in relation to the predictor variables included in the model were calculated from forecast environmental data obtained from the OCLE database. Once the predicted ecological distances were obtained after running the model, two n-MDS were built and compared with the one inferred from the model for the present scenario.

The analyses were performed using PERMANOVA+ for PRIMER software (Anderson et al., 2008) and the open source software 'R' (see www.r-project.org).

3. RESULTS

3.1. Macroalgal assemblage's composition

A total of 174 taxa were identified (Annex 1): Rhodophyta was found to be the dominant phylum, represented by 127 taxa (~73%), followed by Chlorophyta and Ochrophyta with 23 taxa each and Cyanobacteria with a single taxon.

Cluster analysis separated five assemblages at a 43% similarity (Figure 2). Similarity percentage analysis (SIMPER) showed that each assemblage was dominated by one or two particular species (Table 1).

Group A, which brings together the sites at the three westernmost Atlantic locations, is characterised by high covers of the annual kelp *Saccorhiza polyschides* (68%) and the geniculate calcareous alga *Corallina officinalis* (45%). The three central Atlantic locations form Group B, where *Gelidium corneum* (69%) and the encrusting calcareous alga *Mesophyllum expansum* (65%) are co-dominant species. Group C corresponds to the easternmost Atlantic locations, characterised by high covers of *M. expansum* (65%). Group D includes the sites from the Alboran Sea location, where *Halopteris scoparia* (57%) is the dominant species, while Group E comprises the sites from the south-eastern Mediterranean location, where *Padina pavonica* (49%) is the most abundant species. Overall, it can be observed that Atlantic locations are separated from the Mediterranean ones at a similarity level of 20%.

3.2. The assemblage-environment relationship model

The nMDS plot (Figure 3) shows a clear separation between all locations, while replicates of each location were consistent with each other, as shown by CI95. The spatial distribution follows a parabolic-shaped curve (R=0.86; p=0.001 for 2nd order polynomial regression test) from the westernmost Atlantic locations to Spain's south-eastern Mediterranean coast.

The average values of the 28 environmental variables for each locality initially included in the study are summarised in Annex 3. Once the co-linearity between them was ex-

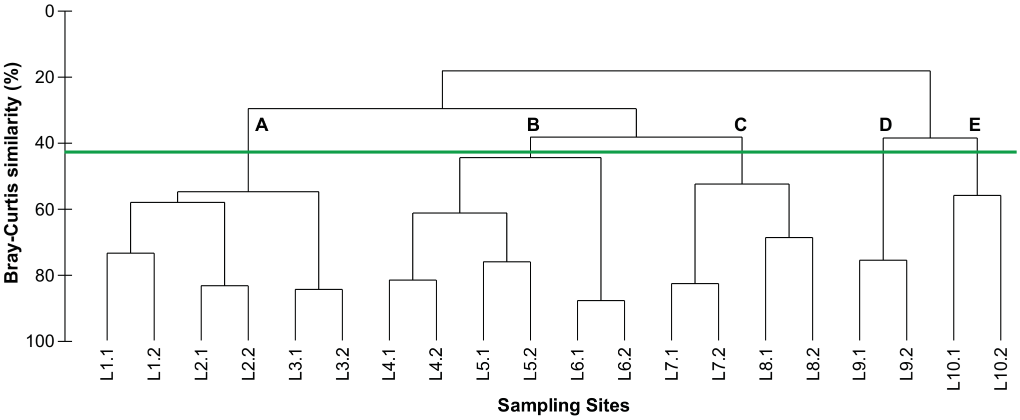

Fig. 2. Dendrogram for hierarchical clustering of sampling sites, using group-average linking of Bray-Curtis similarities calculated on √-transformed abundance data. Green line indicates a 43% similarity level.

Table 1. Mean cover(%), contribution (%), and acumulative contribution (%) of the taxa to the average similarity within each group according to the SIMPER routine. Only taxa with a contribution >4% to the average similarity of the group has been included.

SIMPER results – similarity percentage – species contribution			
Taxa list	**Mean cover (%)**	**Contribution (%)**	**Cumulative contribution (%)**
Group A – average similarity 75.67% –			
Saccorhiza polyschides	68.13	16.42	16.42
Corallina officinalis	44.69	15.16	31.58
Pterosiphonia complanata	11.65	6.07	37.65
Chondracanthus teedei	6.34	5.00	42.64
Jania squamata	10.56	4.77	47.41
Falkenbergia rufolanosa	5.69	4.52	51.93
Lithophyllum incrustans	27.40	4.33	56.25
Group B – average similarity 56.04% –			
Gelidium corneum	69.18	21.25	21.25
Mesophyllum expansum	65.10	21.02	42.26
Plocamium cartelagineum	16.72	8.52	50.79
Cryptopleura ramosa	9.82	5.63	56.42
Falkenbergia rufolanosa	15.67	4.29	60.71
Group C – average similarity 60.90% –			
Mesophyllum expansum	64.69	18.58	18.58
Aphanocladia stichidiosa	25.16	10.83	29.41
Zanardinia typus	10.16	5.67	35.08
Codium decorticatum	13.69	5.16	40.23
Group D – average similarity 60.32% –			
Halopteris scoparia	56.56	15.80	15.80
Mesophyllum expansum	38.75	15.42	31.21
Ellisondia elongata	11.25	7.45	38.66
Lithophyllum incrustans	8.44	6.89	45.55
Zanardinia typus	5.66	5.63	51.18
Halopteris filicina	6.16	5.03	56.22
Group E – average similarity 56.51% –			
Padina pavonica	49.06	19.98	19.98
Lithophyllum incrustans	14.69	10.68	30.66
Caulerpa racemosa	2.94	5.14	35.82
Wrangelia penicillata	4.03	4.43	40.25

amined, seven variables (R < 0.894 among them) were maintained for further analyses: SST in spring (SSTSP), SST in winter (SSTW), nitrate concentration in spring (NITSP), nitrate concentration in winter (NITW) and shear stress in winter (SHSW). The variables that showed a collinearity of R>0.894 were not included for analysis (Annex 4).

The results of a RELATE test indicated that there was a significant link (R = 66.8%, p = 0.0011) between the spatial pattern of macroalgal assemblages and the seven environmental variables maintained. The polynomial regression demonstrated that assemblage spatial distribution followed a parabolic-shaped model in the nMDS analysis, so DistLM tests were performed separately for each part of the curve (from L1 to L6, and from L7 to L10) to obtain a more accurate model. The parabolic-shaped distribution model indicates that each part of the curve corresponds to a different environmental gradient driven by different environmental factors or by a combination of factors.

For the first gradient (locations from L1 to L6), DistLM identifies a model with three environmental variables (SSTSP, NITW and SHSW) which explain 81.91% of the variation in the spatial pattern of macroalgal distribution (R2 = 0.88, AICc = 79.30) (Figure 4A). However, when the relationship between assemblage distribution and these three explanatory variables is modelled by means of a multiple regression, SHSW is no longer found to be significant (p = 0.1572) (Table 2A). The DistLM model excluding SHSW (R2 = 0.81, AICc = 51.97) still explains more than 80% of the variation (Figure 4B). The dbRDA ordination plot shows that NITW is strongly correlated with the Y axis (0.902) and SSTSP with the X axis (0.761) (Figure 4B). The regression model that describes the relationship between these predictor variables and macroalgae distribution is shown in Table 2B. For the second gradient of the

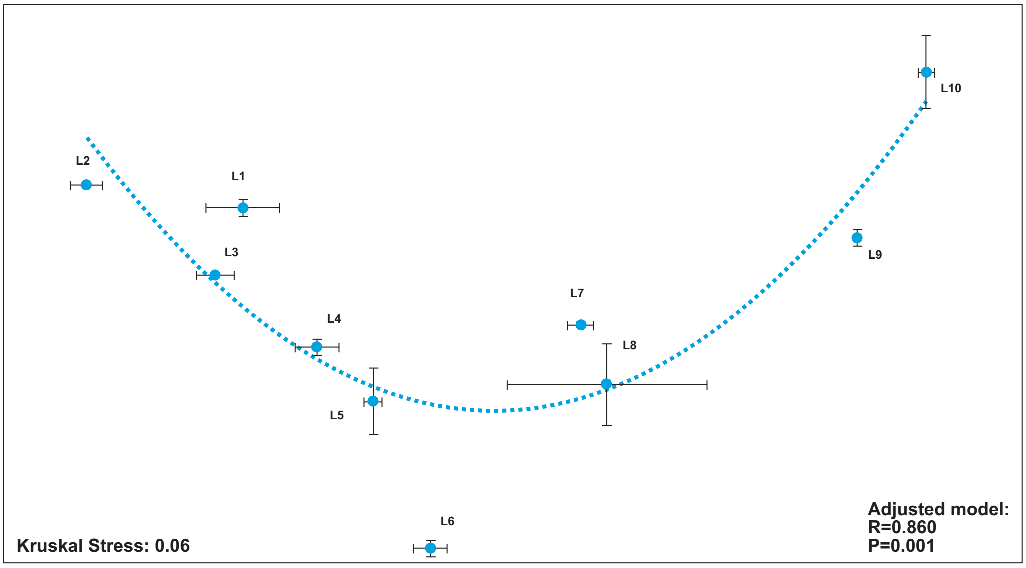

Fig. 3. n-MDS ordination of macroalgal based on Bray-Curtis similarity index of √-transformed data. Error bars represents 95% confidence intervals for site average of each locality. Blue dashed line corresponds to the adjusted polynomial model.

Table 2. Summary of multiple regression analysis for enviromental variables predicting the observed gradient in the spatial distribution of macroalgal assemblages from L1 to L6: A) including three explanatory variables (SSTSP, SST of spring; NITW, nitrate concetration of winter; SHSW, shear stress of winter); B) including two variables.

	Estimate	SE	t	P
A				
Intercept	30.820	2.662	11.577	1.68e-07
SSTSP	99.399	13.888	7.157	1.85e-05
NITW	-32.530	10.694	-3.042	0.0112
SHSW	-5.995	3.949	-1.518	0.1572
B				
Intercept	30.408	2.788	10.905	1.39e-07
SSTSP	82.526	8.768	9.412	6.87e-07
NITW	-24.836	9.916	-2.505	0.0277

polynomial regression model (locations from L7 to L10), DistLM test (R2 = 0.64, AICc = 41.76) identifies only SSTSP as a significant explanatory variable, which explains 64% of the variation in assemblage distribution (Figure 5).

The regression model that describes the relationship between SSTSP and the macroalgal spatial distribution is shown in Table 3. To explore the relationship between locations from the two gradients described above, a third multiple regression was run including the environmental variables that best explained the pattern in the previous analyses (SSTSP and NITW). NITW appeared not to be significant (Table 4A), so the regression equation for these combinations

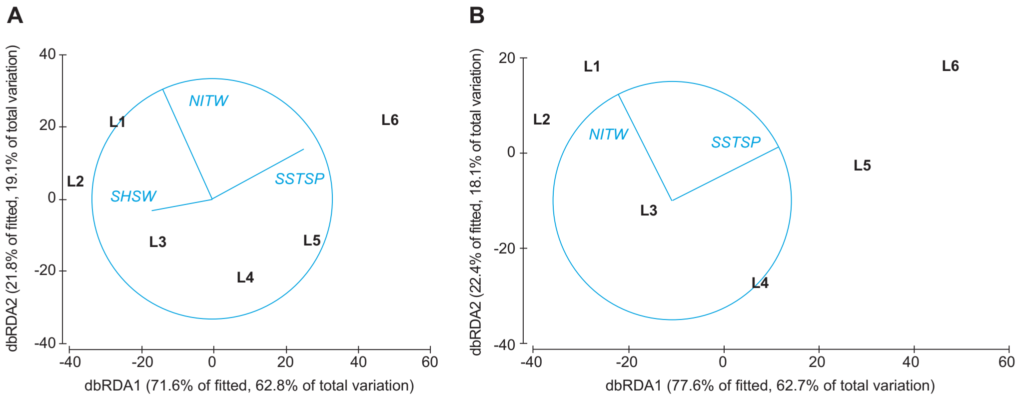

Fig. 4. dbRDA ordination plots illustrating the relationship between the enviromental variables that best explain the variation of macroalgal assemblages from L1 to L6. The dbRDA was constrained by the best-fit explanatory variables from a multivariate multiple regresion analysis (DISTLM). A) Including three explanatory variables (SSTSP, SST of spring; NITW, nitrate concentration of winter; SHSW, shear stress of winter). B) Results excluding SHSW.

Table 3. Summary of the regression analysis for enviromental variable SSTSP predicting the observed gradient in the distribution of macroalgal assemblages from L7 to L10.

	Estimate	SE	t	P
Intercept	44.056	1.420	31.03	6.42e-06
SSTSP	11.351	0.614	18.50	5.02e-05

was based on a simple linear regression (Table 4B). The model was built by combining the 3 equations which, as a whole, provided the predicted ecological distances between all pairs of localities. The goodness-of-fit of the final model is R2 = 0.855, which can be considered very good (Figure 6). The ecological data predicted by the model are based on distances to centroids. These data were converted into a similarity matrix in order to build an n-MDS based on the model (Figure 7B). The power of the model is high, so the spatial distribution pattern of macroalgal assemblages is similar in both the observed and the predicted n-MDSs (Figure 7).

3.3. Projections

Predicted distributions of Iberian macroalgal assemblages according to the model for the year A2100 based on the RCP 4.5 and RCP 8.5 scenarios are shown in Figure 8. Output based on the medium stabilisation scenario (RCP 4.5) indicates that assemblages from the Mediterranean locations (L9, L10) are still the most different from the study area, as observed in the present data. However, Cantabrian location L3 is no longer grouped with the colder Galician localities (L1 and L2) but instead with L4, which in turn becomes further away from L5 and L6. It can also be observed that the locations from Galicia (L1 and L2) differ more from the rest of the northern locations, with an average similarity of only 15% (compared to 35% for the present) (Figure 8A).

By contrast, under the RCP 8.5 scenario (Figure 8B) with continued increases in emissions over time, predicted changes in the spatial distribution of macroalgal assemblages are more noticeable. The locations on the Cantabrian Sea (L3 to L8) are more similar to those in the Mediterranean region (L9, L10) than to those on the Galician coast (L1,

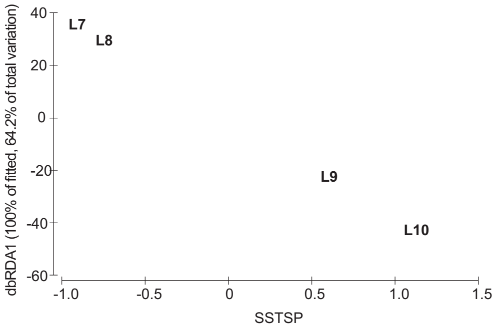

Fig. 5. dbRDA ordination plots illustrating the relationship between SSTSP that best explain the variation of the spatial distribution of macroalgal assemblages from L7 to L10.

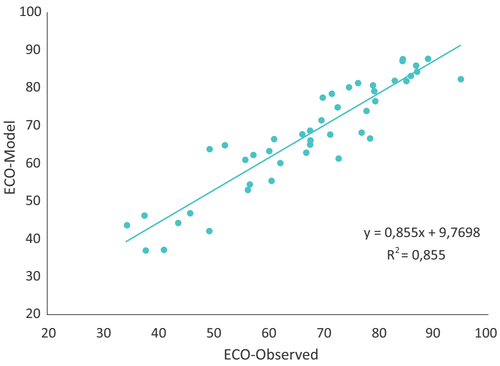

Fig. 6. Regresion between the observed ecological data and the ecological data predicted from the model.

Table 4. Summary of the regression analysis for enviromental variables predicting the observed pattern of the communities for the combination of the localities 1-6 and 7-10. A) including two explanatory variables (SSTSP, SST of spring; NITW, nitrate concetration of winter); B) including a single variable (SSTSP).

	Estimate	SE	t	P
A				
Intercept	58.837	2.792	21.075	1.31e-15
SSTSP	5.268	1.245	4.231	3.74e-04
NITW	9.726	6.868	1.416	0.171
B				
Intercept	60.342	2.640	22.857	2.00e-16
SSTSP	6.293	1.036	6.075	4.09e-06

L2), suggesting a future meridionalization of the Atlantic assemblages. It can also be observed that spatial variability among Cantabrian locations is greater and that Galician assemblages (L1 and L2) are becoming separated from the rest.

4. DISCUSSION

Our hypothesis is that at community level climate change will drive a meridionalization of the Atlantic coast of the Iberian Peninsula, so our study seeks to determine the key factors influencing macroalgal assemblage distribution, build an assemblage-environment relationship model for subtidal vegetation and project assemblage distribution shifts under future climate change scenarios.

4.1 SST and nutrients explaining the spatial distributional pattern of communities

The first main finding of our study is that water temperature is the most relevant factor in shaping macroalgal assemblage distribution along the coasts of the Iberian Peninsula, whilst nutrient availability plays a secondary role by modulating the thermal effect on coastal stretches with the coldest

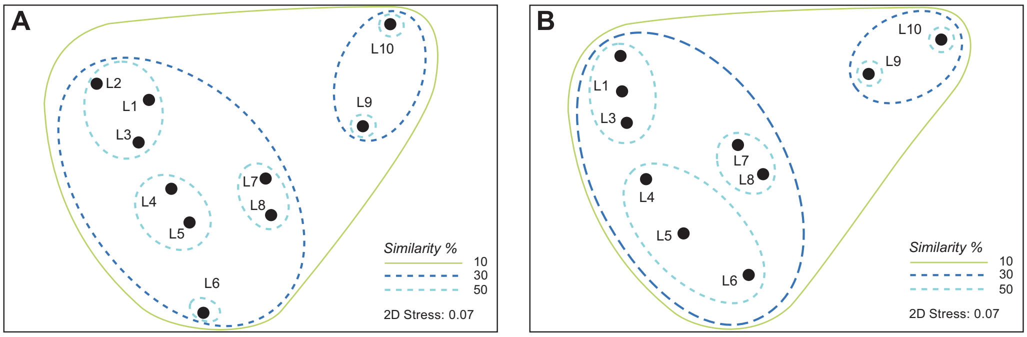

Fig. 7. n-MDS ordination plots of the 10 localities based on √-transformed abundance and Bray-Curtis similarities . A) Observed pattern. B) Model (three similarity levels between localities are ploted: 10, 30 and 50%).

and intermediate temperature ranges. These results are as expected since temperature and nutrient availability interact to control the pathways and rates at which energy and materials move through ecosystems (Cross et al. 2015).

By controlling biological activity through its fundamental effect on metabolic rates, temperature has a strong influence on the survival, growth, reproduction and recruitment of macroalgae, and consequently on their distribution patterns (Hoek, 1982; Husa et al., 2008; Lima et al., 2007; Lüning, 1990; Müller et al., 2009; Sjøtun et al., 2015). Many studies have pointed to temperature increase as the main driver of recent changes detected in the distribution of marine flora in coastal ecosystems throughout the Iberian Peninsula (Casado-Amezúa et al., 2019; Díez et al., 2012b; Duarte et al., 2013; Fernández, 2011; Gorostiaga et al., 2004; Voerman et al., 2013). Together with temperature, nutrients are essential for physiological performance (Harrison and Hurd, 2001). Nitrogen is a main component of the catalyst capacity of algal proteins and enzymes which often limits growth and biomass (Lapointe, 1987; Hecky & Kilham, 1988).

The two main explanatory environmental factors –water temperature and nitrate concentration– that most likely determine community structure in the study area show a high negative correlation (R = - 0.83). This means that there is an environmental gradient from nutrient-rich cold water to nutrient-poor warm ambient water. On that gradient, five macroalgal assemblages have been identified, whose dominant species from the coldest habitat to the warmest are *Saccorhiza polyschides*, *Gelidium corneum*, *Aphanocladia stichidiosa*, *Halopteris scoparia* and *Padina pavonica*. This distribution pattern shows that in general the thallus size of the dominant species decreases as temperature increases, ranging from 2m to few centimetres, which means that the vertical layering of the community also becomes simplified.

As a foundation species, the kelp *S. polyschides* creates complex, highly diverse assemblages and provides important goods and ecosystem services (Fernández, 2011). Our study finds that *S. polyschides* only shows conspicuous cover west of Cape Peñas, in accordance with earlier studies (Fernández, 2011). Kelps are distributed from the Arctic to Brittany, though they can also be present further south in areas asso-

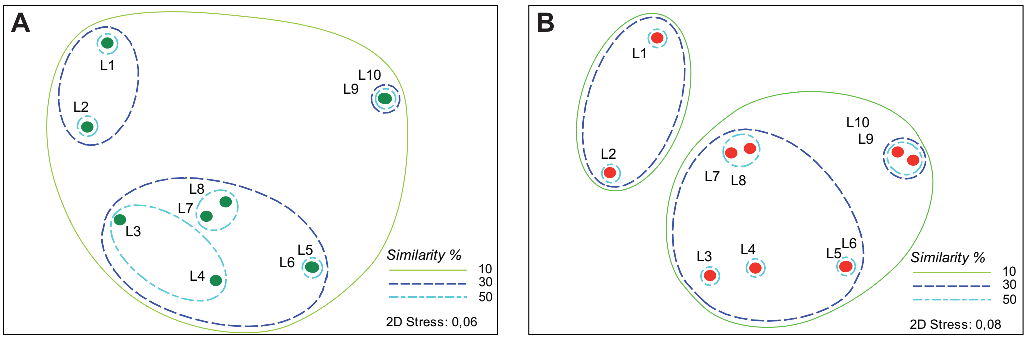

Fig. 8. n-MDS ordinations of macroalgal assemblages predicted by the model based on Bray-Curtis similarity matrix of the √-transformed data. A) Scenario RCP 4.5. B) RCP 8.5 (three similarity levels between localities are ploted: 10, 30 and 50%).

ciated with strong upwelling events (Lüning, 1990). This is the case of *S. polyschides* which, with a survival interval of between 5 and 23ºC (Hoek, 1982), finds refuge in the NW Iberian Peninsula, where summer upwellings lower SST and increase nutrient availability (Fraga et al., 1981). In the central Cantabrian locations of this study, meadows of *G. corneum* were found to be the dominant subtidal vegetation. This economically important macrophyte (a resource for high quality agar; Melo, 1998) plays a key role in coastal ecosystems along the Atlantic coast of the Iberian Peninsula and in Morocco (Santelices, 1991), since it operates as an ecosystem engineer providing habitat and food for many organisms (Borja et al., 2004; Bustamante et al., 2017; Gorostiaga, 1994).

A. stichidiosa, an ephemeral, morphologically simple species, is the most abundant species in the easternmost area of the Eastern Cantabrian coast. It is an endemic species from the warm-temperate region of the eastern Atlantic (Hoek, 1982) whose known distribution includes the western Mediterranean and the nearby Atlantic coasts. This study shows that within ~ 65 km there is a drastic difference in vegetation structure, shown by the presence or absence of a *G. corneum* canopy layer. One plausible explanation for this abrupt spatial difference is that a maximum temperature threshold and/or minimum nutrient threshold had been exceeded for *G. corneum*, leading to a new stable state. Some ecosystems may respond gradually to environmental changes (Scheffer et al., 2001). However, if a critical threshold for one or more species is exceeded for a certain environmental condition, abrupt changes are likely to occur (Perry et al., 2010). *G. corneum* forms dense populations (of 3.4 kg m-2) in Sidi Bouzid (Morocco) (Givernaud et al., 2005), where the summer mean SST is 23°C and a weak permanent annual upwelling provides nutrients to the upper layers all year round (Benazzouz et al., 2014). Given that summer mean SST in the easternmost area of the Cantabrian Sea is not higher than at Sidi Bouzid, a minimum nutrient threshold has probably been exceeded for *G. corneum*.

The perennial alga *H. scoparia* is the most abundant species in the shallow subtidal vegetation of the northern Alboran area (Rodríguez et al., 2013). The dominance of *H. scoparia* in shallow subtidal bottoms in the northern Alboran Sea and in some intertidal habitats in the north-eastern Iberian Peninsula (Díez et al., 2012a) suggests that the two environments may share some environmental features. Another smaller brown alga, *P. pavonica*, is the most abundant species in the south-western Mediterranean location. This is a warm-temperate affinity species with an annual life cycle whose distribution includes temperate and tropical areas of the Atlantic Ocean and the Indo-Pacific Ocean (Rodríguez et al., 2013). It is also a frequent seasonal component of intertidal vegetation of the Eastern Cantabrian coast (Borja et al. 2004).

Hein et al. (1995) observe a relationship between nitrogen uptake rate and algal size, which suggests that small algae are generally better at acquiring nitrogen. Previously, other researchers have reported that the combination of large algae, high resource acquisition and high growth rates imply that smaller algae may be competitively superior under low nitrogen availability (Laws, 1975; Malone, 1980). Consistently with this observation, small algae such as *A. stichidiosa*, *P. pavonica*, and *H. scoparia* dominate the warmest, most oligotrophic environments in this study.

4.2 The potential role of other environmental variables

Multiple environmental factors co-vary seasonally or along latitudinal gradients and can therefore interact as potential drivers of responses to future climate change scenarios

(Martins et al., 2017). In this study solar radiation, salinity and tidal range were found to be closely correlated with temperature, whereas bottom shear stress and significant wave height were closely correlated with nitrate concentration.

Solar radiation is an essential source of energy for primary producers, but excessive irradiance (especially UVA) can have deleterious effects on macroalgae at biochemical, physiological and morphological levels (Figueroa and Gomez, 2001). In this study the maximum irradiance level was found to be concurrent with the warmest temperatures in the Mediterranean region, where two photophilic species, *H. scoparia* and *P. pavonica*, were dominant (Cholbi & Sala, 1996). The oligotrophic conditions of this region result in clear waters that enable solar radiation to go deeper into the column. Macroalgae living under these conditions have developed efficient photoprotective mechanisms to tolerate light stress (Figueroa and Gomez, 2001). According to the OCLE database, surface solar radiation in the Atlantic locations is similar from one to another but smaller than in the Mediterranean region. However, Quintano et al. (2017) find significant differences in ambient light at depths of 5 m between locations on the eastern Cantabrian coast. They report that during the warm, oligotrophic conditions of summer the density and biomass of *G. corneum* populations were significantly lower under higher irradiances, suggesting a potential negative interaction between SST, nutrients and irradiance.

Average salinity ranged from 35.2 to 37.8 in the study area, with the Mediterranean locations being saltier than the Atlantic ones, especially the south-eastern location. Seasonal fluctuations were also low, with the northern Alboran location showing the greatest variation (36.5 vs 36.63). The salinity of open-ocean water is generally in the range of 34 to 37, and the response of algae to moderate salinity changes is a well-regulated process (Kirst 1989). As long as seaweeds have an adequate supply of nutrients they are able to deal with variations in salt concentrations by regulating the content of substances such as ions, sugars and amino acids in their cells. Most species prefer high salinity and only few can survive in salt-deficient waters (Mouritsen 2013). Therefore, salinity seems to be a weak contributor to the spatial distribution observed.

The subtidal habitat studied (-5m) may undergo stronger daily environmental fluctuations in the Atlantic locations than in the Mediterranean ones in water temperature, water pressure and hydrodynamism as a consequence of differences in tidal amplitude. For instance, communities thriving at stable depths of 5m in the Mediterranean location of the northern Alboran Sea could not stand the 9 m depth environmental conditions imposed by the Atlantic spring high tides. According to Cebrián and Ballesteros (2004), rocky subtidal bottoms in this area show a marked vertical zoning pattern with high spatial variability within a few meters. These authors find a discontinuity at a depth of 5 m that may be related to the change from highly rheophilic species that withstand heavy surf and hydrodynamics (upper infralittoral zone) to species not adapted to surf or to strong water movement (lower infralittoral zone). Nevertheless, the potential effect of ‘environmental fluctuation’ associated with tidal amplitude in regard to the effects of the main explanatory variables identified in this study remains unclear.

The effect of water movement on the distribution of macroalgae is hard to identify because of the complex interactions with other environmental factors that affect their biochemical performance, especially temperature, nutrients and light (Hurd, 2000). Thus, water movement may counteract community shading or self-shading by directly moving fronds, allowing light to penetrate into the understory layer and optimising conditions for photosynthesis (Kregting et al., 2016). In this study, we included two parameters related to hydrodynamism: Hs and shear stress, which is the force of friction from the interaction of waves and currents acting on the bed sea. In the study area, both parameters were found to be considerably higher in the Atlantic region than in the Mediterranean, especially in the western area, where *S. polyschides* and *G. corneum* were abundant. These seaweeds are adapted to highly hydrodynamic conditions and take advantage of water movement, which enhances nutrient uptake by reducing or breaking the boundary layer (Hurd et al., 1996; Wheeler, 1980) and removes epiphytes and waste products (Kain & Norton, 1990).

Interactions between algae and herbivores are not considered in this paper, even though they may play a pivotal role in the distribution and abundance of seaweeds (Franco et al., 2018; Korpinen et al., 2007; Steneck et al., 2002; Vergés et al., 2016).

4.3 Projections

This is the first study that predicts shifts at community level based on an assemblage-environment-relationship model for future climate change scenarios (RCP 4.5 and RCP 8.5). Under both scenarios, we predict that assemblages occurring at intermediate temperatures and nitrate concentrations (central Cantabrian communities) will become more similar to those occurring in the warmest, most oligotrophic area of the northern Iberian Peninsula, i.e. the easternmost part. Moreover, north-western macroalgal assemblages will remain differentiated from the rest of the Iberian Peninsula. This differentiation will be greater under the most pessimistic scenario (RCP 8.5), under which the central and eastern communities of the Iberian Peninsula will come to resemble those of the Mediterranean region more closely than those of the north-west. Our results thus partially support the study hypothesis of a potential meridionalization of macroalgae assemblages on northern Iberian rocky shores.

The warming rate of the SST on the northern coast of the Iberian Peninsula from 1982 to 2014 has been recorded as increasing towards the east, and greatest on the Basque coast (Costoya et al., 2015). Here, profound structural shifts in the community have already occurred, including the decline of canopy-forming algae and the enrichment of warm-temperate affinity species with simple morphologies and annual life cycles. These structural changes have led to a flattening of the sea bottom landscape in a shift from three-dimensional habitats towards a bidimensional space dominated by algal turfs, coralline species and crusts (Díez et al., 2012b; Muguerza et al., 2017). Our study finds that the communities currently occurring at intermediate temperatures and nutrient levels are likely to suffer the same structural and functional shift due to the increasing trend in SST and decreasing nutrient availability, which will lead to a meridionalization of Cantabrian macroalgal assemblages.

Based on our model and the OCLE database, assemblages from the north-western coast (Galicia) will remain differentiated. Under the most pessimistic scenario (RCP 8.5), the model predicts that the north-western phytobenthos will have a similarity level with the rest of communities of only about 10%. Our model is based on winter nitrate concentrations, which according to OCLE database are expected to increase in future scenarios in most of the locations studied. However, future simulations for the summer coastal upwelling along the north-western Iberian Peninsula should be taken into account, since this oceanographic feature of the region is essential in maintaining its kelp forest ecosystems (Franco et al., 2018).

Some authors have concluded that upwelling phenomena in spring and summer along the Galician coast will increase (Alvarez et al., 2017; Casabella et al., 2014), but most studies suggest a weakening in the upwelling process in relation to changes in wind regimes mainly attributed to climate change (Gómez-Gesteira et al., 2011; Lemos and Pires, 2004; Pérez et al., 2010). Consequently, a future scenario for north-west Iberia that combines warmer waters with a reduced nutrient supply may be expected (Piñeiro-Corbeira et al., 2019). Likewise, summer nutrient concentrations are likely to decrease in the central and north-eastern parts of the northern Iberian Peninsula as result of dryer seasons with decreased precipitation and river runoff (Gómez-Gesteira et al., 2008). Another plausible explanation for the decrease in nutrient concentrations in the north-eastern Cantabrian Sea is the intensification of water column stratification, which may supress nutrient exchange through vertical mixing (Lavín et al., 1998).

Based on the foregoing, we suggest that community shifts under future climate change scenarios could be greater than predicted in our model. If the summer upwelling system in the north-west of the Iberian Peninsula becomes weaker, even the seaweed assemblages of Galicia are likely also to suffer a meridionalization process. Each macroalgal species has a demand for nutrients for growth, maintenance and reproduction (Lobban and Harrison 1994). If the upwelling intensity decreases, nutrient limitation may become more critical than temperature for some algae (Piñeiro-Corbeira et al., 2019).

At a global scale a tropicalization of temperate communities is occurring, which could be the equivalent of the meridionalization foreseen in our model. According to Vergés et al., (2019), warm water affinity species are shifting their distribution toward the poles in response to warming, while cool-water species are retracting. This situation has been observed all over the globe, from eastern and western Australia to Japan and the Mediterranean Sea (Bianchi and Morri, 2003; Kumagai et al., 2018; Vergés et al., 2014, 2019; Wernberg et al., 2016).

The new arrivals which are colonising warming temperate ecosystems are leading to new interactions. Depending on which new species colonise an area, abrupt changes will occur in the ecosystem. For instance, some authors highlight the overgrazing of temperate foundation seaweed species by tropical herbivores, leading to barren spaces or ecosystems dominated by turf algae (Vergés et al., 2014, 2019). In this new community structure, biodiversity is likely to decline (Vergés et al., 2014), since these species are unable to sustain a whole ecosystem. By contrast, if the replacement is by another biogenic species with warmer affinity, the associated community is going to reflect this change but it will not necessarily lead to a decrease in biodiversity (Vergés et al., 2019; Wernberg et al., 2016). In this regard, Méndez-Sandín & Fernández (2016) observe an increase in the biomass of Cystoseira baccata in semi-exposed areas from 1977 to 2007 in the northern Iberian Peninsula. This canopy-forming fucoid can grow up to 1 meter, and it has a complex structure which can sustain a large number of associated species (García-Fernández and Bárbara, 2016). This seaweed could be a good alternative to offset the loss of the current canopy-forming species, since it is a warmer-affinity species which can stand higher temperature and irradiance levels (Miguel-Vijandi et al., 2010). However, according to Díez et al. (2003), it cannot tolerate heavy hydrodynamics. The future wave regime will therefore determine whether or not this species becomes the future substitute of cooler-affinity biogenic species. Some authors have detected an increase in wave activity (Borja et al., 2013: Ulazia et al., 2017) that would make it difficult for this species to settle, at least in exposed and shallow waters. Under a warming scenario, other algae that may increase their rates of subtidal bottom occupancy include species of the genus Halopteris, since there is already some evidence of their extension (Fernández 2016; Muguerza et al., 2017). These brown macroalgae form dense populations in intertidal habitats on the Eastern Cantabrian coast (Díez et al., 2012a) and a downward extension into the subtidal zone may be expected.

Siuatations such as those predicted in our model have occurred in the past. Over the last few decades, numerous macroalgae range shifts and changes in the community composition have been observed in all ocean basins (Díez et al., 2012b; Duarte et al., 2013; Husa et al., 2008; Lima et al., 2007; Sjøtun et al., 2015; Wernberg et al., 2016, 2011a,b). In the particular case of the Iberian Peninsula, Casado-Amezúa et al. (2019) document distributional contractions of canopy-forming seaweeds from the Atlantic coasts. These range shifts are reported to be more pronounced in the east of the Cantabrian Sea than along the western coast of the Iberian Peninsula. The cold-temperate fucoids *Himanthalia elongata* and *Fucus serratus*, the cold-temperate kelps *Saccharina latissima* and *Laminaria hyperborea* and the warm-temperate kelps *S. polyschides* and *Laminaria ochroleuca* have suffered contractions (Casado-Amezúa et al. 2019). These shifts show Peñas Cape as the new biogeographic boundary between colder and warmer waters (Fernández, 2016). A substantial decline has also been reported for *G. corneum* on the coast of the eastern Cantabrian Sea (Borja et al. 2018; Muguerza et al. 2017). The warming trend in SST, radiation stress, lower nutrient availability and increased wave energy have been suggested as causes of this retreat in *G. corneum* (Borja et al. 2018; Díez et al. 2012b; Muguerza et al. 2017; Quintano et al. 2017). Macroalgal assemblages have also shown an increase in coralline, crustose and morphologically simple algae with warm affinity (Díez et al. 2012b; Voerman et al., 2013).

The meridionalization foreseen in our model is likely to have dramatic effects on subtidal communities. Coastal systems dominated by canopy-forming seaweeds comprise one of the most ecologically and socio-economically important habitats in temperate waters (Bennett et al., 2016; Steneck et al., 2002) They are habitat formers that support many species, including economically important fish and lobsters. Hence, a change in their abundance or even the disappearance of some of these biogenic species will have a cascade effect throughout the ecosystem (Vergés et al., 2016). Among the ecosystem services they provide, climate regulation, sequestration of CO2, nutrient cycling and coastline protection are of great importance in the new climate change scenarios. They also provide food, shelter and habitat for other species. From the economic point of view some species are of major importance: for instance, *G. corneum* is the main natural resource for the extraction of agar (Gorostiaga, 1994), which is used in the pharmaceutical industry and to produce biodegradable films (Guerrero et al., 2014; Juanes and Borja, 1991).

To learn the potential impact of the disappearance of these ecosystems on society, it would be useful to quantify the value of the ecosystem services and goods that they provide (Bennett et al., 2016). This would also help to create an appropriate management plan, since we believe that such plans are not often based on the community level.

4.4 Conclusions

To our knowledge, this is the first study to develops an assemblage-environment relationship model for the subtidal vegetation of the Iberian Peninsula to forecast the impact of climate change on the seaweed communities of the Bay of Biscay. We find that water temperature is the main factor in shaping macroalgal assemblage distribution along the coast of the Iberian Peninsula, whilst nutrient availability plays a secondary role by modulating the thermal effect on stretches of coast with the coldest and intermediate temperature ranges. Based on our model, projections under future climate change RCP scenarios (4.5 and 8.5) predict that Cantabrian assemblages will become more similar to those of the Mediterranean region, and more strongly so under the RCP 8.5 scenario. Therefore, the study hypothesis of a potential future meridionalization of northern Iberian marine vegetation is partially supported by our results. This meridionalization entails a shift from a three-dimensional biogenic habitat towards a bidimensional space dominated by algal turfs and crusts that may entail drastic consequences for ecosystem functioning and biodiversity. By contrast, north-western (Galicia) subtidal vegetation will remain differentiated from the rest of communities under both RCP scenarios (4.5 and 8.5), serving as a refuge for colder affinity species. Nevertheless, evidence and forecasts exist that suggest a weakening of the upwelling system off the NW Iberian Peninsula. Under this scenario, north-western communities are also likely to shift towards a more Mediterranean-like phytobenthos. This shift would have profound ecological and socio-economic impacts due to all the ecosystem services that they provide.

Further research is needed to improve forecasts of community-level shifts. The top-down effects of the ecosystem, including predation and herbivory, should be considered in the model to take into account potential changes in grazing pressure. Earlier studies have reported that alterations in species interactions may cause the most profound effects of climate change on ecosystems, rather than direct physiological effects due to changing environmental conditions (Franco et al., 2018; Korpinen et al., 2007; Steneck et al., 2002; Vergés et al., 2016). New interactions of tropical fish (Vergés et al., 2019) and sea urchins (Ling et al. 2009) with temperate seaweed ecosystems are already having profound impacts on macroalgae assemblages. The model also has limitations in terms of spatial replication. For further studies it would be interesting to increase the study area to the coast of Portugal and increase the sampling locations in the Mediterranean Sea.

ANNEXES

Annex 1. Average abundance in percentage of cover of the identified taxa for each locality.

TAXA	ABUNDANCE (% of cover)									
	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10
CHLOROPHYTA										
Anadyomene stellata	0	0	0	0	0	0	0	0	0	1.38
Bryopsis hypnoides	0	0	0	0	0	0	0.22	0.03	0.03	0
Bryopsis pennata	0	0	0	0	0	0	0	0	0.16	0
Bryopsis plumosa	0	0	0	0	0	0	0.22	0.19	0	0
Caulerpa racemosa	0	0	0	0	0	0	0	0	0	2.94
Cladophora coelothrix	0	0	0	0	0	0	0	0	0.34	0.66
Cladophora hutchinsiae	0	0	0	0	0	0	1.47	0.56	0	0
Cladophora lehmanniana	0	0	0.13	0.06	0	0	0	0.06	0	0
Cladophora prolifera	0	0	0	0	6.56	0	0.50	1.94	0.06	0.75
Cladophora sericea	0	0	0	0	0	0	0	0	0	0.28
Cladophora socialis	0	0	0	0	0	0	0	0	0	1.81
Codium adhaerens	1.25	0	0	0	0	0	0	0	0	0.03
Codium decorticatum	2.63	4.19	2.19	0.38	0.84	0	24.88	2.50	0	0
Codium fragile	0	0	2.03	2.28	0	0	0	0	0	0
Codium vermilara	0	0	0	0	0	0	0	0.06	0	0.34
Derbesia tenuissima	0	0.03	0	0	0.34	0	0.03	0.19	0	0
Halimeda tuna	0	0	0	0	0	0	0	0	0	0.03
Lychaete pellucida	0	0	0	0.44	0.16	0.22	5.00	2.63	0.09	0.31
Parvocaulis parvulus	0	0	0	0	0	0	0	0	0	0.34
Pseudochlorodesmis furcellata	0	0	0	0	0	0	0	0	0.19	0.03
Ulva clathrata	0	0	0	0	0	0	0	0	0.28	4.69
Ulva rigida	2.06	0.88	5.31	2.81	0.06	0	0.94	0.03	0	0
Valonia utricularis	0	0	0	0	0	0	0	0	0.06	0.19
CYANOBACTERIA										
Phormidium sp.	0	0.03	0	0	0	0	0	0.50	0	0
OCROPHYTA										
Cladostephus spongiosus	0.13	2.31	4.50	0.31	0.25	0	0.63	2.25	0	0
Colpomenia peregrina	0	0	0	0	0	0	3.84	0.94	0	0
Colpomenia sinuosa	0	0	0	0	0.03	0	0	0	0.03	0
Cutleria multifida	0	0	0	0	0	0	0	0	0.44	0
Cystoseira baccata	0	3.44	3.44	6.25	0.69	0	0	0	0	0
Cystoseira compressa	0	0	0	0	0	0	0	0	0.06	0.44
Cystoseira tamariscifolia	0	0	0	0.63	0	0	0	0.63	0	0
Desmarestia ligulata	1.13	0.63	0	0.31	0	0	2.59	0	0	0
Dictyopteris polypodioides	0.31	0.22	0	0	0	0	0	0	0.06	0.22
Dictyota dichotoma	1.63	0.50	0	0.59	7.28	0.69	0	1.25	0.81	0.63
Dictyota spiralis	0	0	0	0	0	0	0	0	0	0.41

Annex 1. - (cont.).

TAXA	**ABUNDANCE (% of cover)**									
	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10
OCROPHYTA										
Halopteris filicina	0.06	0.06	0.22	0	0.03	0	0	0	6.16	3.09
Halopteris scoparia	1.41	0.06	2.44	0.47	0.34	0	1.69	2.72	56.56	5.59
Laminaria ochroleuca	2.63	0	0	0	0	0	0	0	0	0
Lobophora variegata	0	0	0	0	0	0	0	0	0.06	0.44
Padina pavonica	0	0	0	0	0	0	0	0	0.03	49.06
Phyllariopsis brevipes	1.94	0	0	0.38	0	0	0	0	0	0
Saccorhiza polyschides	55.94	100	48.44	9.41	0	0	0	0	0	0
Sargassum vulgare	0	0	0	0	0	0	0	0	0.03	1.41
Sphacelaria cirrosa	0	0	0	0	0	0	0	0	0.97	0.50
Sphacelaria sp.	0	0	0	0	0	0	0.06	0	0	0
Taonia atomaria	2.06	0.28	0	0	0	0.06	0.88	3.06	0.28	0
Zanardinia typus	2.50	3.44	5.31	12.81	8.81	0	3.75	16.56	5.66	2.03
RHODOPHYTA										
Acrosorium ciliolatum	4.06	1.75	6.50	1.06	2.16	1.28	0.53	2.59	0.06	0
Aglaothamnion pseudobyssoides	0	0	0.16	0.28	10.22	0	5.75	0	0	0
Aglaothamnion sp.	0	0.06	0	0	0	0	0	0	0	0
Aglaothamnion tenuissimum	0	0	0	0	0.03	0	0.31	0.09	0	0
Ahnfeltiopsis devoniensis	0	0	0	2.38	0	0	0	0	0	0
Amphiroa rigida	0	0	0	0	0	0	0	0	1.25	3.84
Anotrichium furcellatum	0	0	0	0	0	0	0	0.06	0	0
Anotrichium tenue	0	0	0	0	0	0	0	0	0.06	0.13
Antithamnion amphigeneum	0	0	0	0	0.03	0	0	0	0	0
Antithamnion cruciatum	0	0	0	0	0	0	0	0	0.09	0
Antithamnion decipiens	0	0	0	0	0	0	0	0	0	0.13
Antithamnion hubbsii	0	0	0	0	0.09	0	0	0	0	0
Antithamnionella ternifolia	0.13	0.03	0	0.34	2.84	0.13	0	0.06	0	0
Aphanocladia stichidiosa	0	0	0	0	0	0	15.94	34.38	0	0
Apoglossum ruscifolium	0.03	0.25	0.13	0.22	0.28	1.19	0.06	0.59	0	0
Asparagopsis armata	5.97	0	0.72	2.81	0.91	0	12.59	0.31	3.13	0.69
Asparagopsis taxiformis	0	0	0	0	0	0	0	0	6.16	0
Bonnemaisonia asparagoides	0	0	0	0.72	0	0	2.81	0.66	0	0
Bonnemaisonia clavata	0	0	0	0	0	0	0	0	0	0.03
Bonnemaisonia hamifera	1.72	0	0	0	0.19	13.75	10.31	1.25	0	0
Bornetia secundiflora	0	0	0.03	0	0.03	0	0	0	0	0
Botryocladia botryoides	0	0	0	0	0	0	0	0	0	0.03
Calliblepharis ciliata	0	0.69	0.09	0.31	0.31	3.19	0	0	0	0
Callithamnion tetragonum	0.03	0	0	0.16	0.16	0	0	0	0	0
Caulacanthus ustulatus	0	0	0	0	0	0	0	0	0.09	0.06
Centroceras clavulatum	0	0	0	0	0	0	0	0	0.38	0

Annex 1. - (cont.).

TAXA	**ABUNDANCE (% of cover)**									
	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10
RHODOPHYTA										
Ceramium botryocarpum	0	0	0	0	0.03	0	0	0	0	0
Ceramium ciliatum	0	0.03	0	0.03	0	0	0.19	2.53	0	4.75
Ceramium cingulatum	0	0	0	0	0	0	0	0	0.03	0
Ceramium circinatum	0	0	0	0	0	0	0	0	0.03	0.50
Ceramium codii	0	0	0	0	0	0	0	0	0.28	0.34
Ceramium echionotum	0	0	0.19	0.09	0.25	0	0.56	2.50	0.13	0
Ceramium mazudo	0	0	0	0	0	0	0	0	0	0.03
Ceramium secundatum	0.06	0.09	0.31	0.09	0.09	0	0.22	2.00	0	0
Champia parvula	0	0	0.03	0.91	0.13	0	0.16	2.50	0.53	0.59
Chondracanthus acicularis	0	0	0	0	0	0	0	0	0.13	0
Chondracanthus teedei	9.50	6.25	3.28	3.25	0.34	0	0	0	0	0
Chondria capillaris	0	0	0	0	0	0	0	0	0	0.16
Chondria coerulescens	0	1.19	0.19	0	0	0	0	0	0	0.09
Chondria scintillans	0	0	2.94	0	0	0	0	0	0	0
Chondria sp.	0	0	0	0	0	0	0	0.16	0	0
Chrysymenia ventricosa	0	0	0	0	0	0	0	0.06	0	0
Chylocladia verticillata	0	0	0	0	0	0	0	0	0	0.03
Compsothamnion thuioides	0	0	0	0	0	0	0	0	0.06	0
Corallina officinalis	52.19	40	41.88	8.16	1.81	0	0	0	0	0
Crouania attenuata	0	0.53	0.22	1.28	0.94	0	0	0.31	0.06	0.13
Cryptonemia lomation	0	0	0	0	0	0	0	0	0	0.03
Cryptopleura ramosa	0.88	0.06	7.81	2.81	4.16	22.50	0	0	0	0
Dasya corymbifera	0	0	0	0	0	0	0	0	0.06	0.16
Dasya hutchinsiae	0	0	0.03	1.44	0.88	0	0	0	0	0
Dasya ocellata	0.03	0.03	0.47	0.63	0.06	0	0.47	0.81	0	0.09
Dasya rigidula	0	0	0	0	0	0	0	0	0.03	0.19
Dumontia contorta	0	1.13	0.06	0	0	0	0	0	0	0
Ellisolandia elongata	0.31	0.31	5.00	14.25	12.56	0	0.47	9.44	11.25	1.16
Falkenbergia rufolanosa	8.84	5.00	3.22	25.94	21.06	0	11.44	0.66	0	0
Gaillona gallica	0	0	0	0	0	0	0.03	0	0	0
Gastroclonium ovatum	0	0	0.03	0	0	0	0	0.13	0	0
Gastroclonium reflexum	0	0	0	0	0	0	0	0.13	0	0
Gayliella flaccida	0	0.47	6.94	15.13	0.56	0	0.25	0.66	0.28	1.53
Gelidiella sp.	0	0	0	0	0	0	0	0.06	0	0
Gelidium attenuatum	0.66	1.72	6.88	5.94	0	0	0	0	0	0
Gelidium corneum	0	0	0	54.38	59.09	94.06	0	21.75	0	0
Gelidium pusillum	0	0	0	0	0	0	0	0	0.25	0.25
Gelidium spinosum	0	0	0	0	0	0.03	0.28	4.59	0	0
Gigartina pistillata	0.31	0.25	0.94	0.44	0	0	0	0	0	0

Annex 1. - (cont.).

TAXA	**ABUNDANCE (% of cover)**									
	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10
RHODOPHYTA										
Grateloupia filicina	0	0	0	0	0	0	0	0	0	0.69
Griffithsia schousboei	0	0	0	0	0	0	0	0	0.03	0
Gymnogongrus (crustose-phase)	0	8.31	0.66	0	0.03	0	0	0	0	
Gymnogongrus crenulatus	1.25	3.63	0.16	0	0.03	0	0	0	0	0
Halopithys incurva	0	0	0	0	0	0	0	0.06	0	0
Halurus equisetifolius	3.63	3.50	3.03	0.72	0.44	0	0	0	0	0
Herposiphonia secunda	0	0	0	0	0	0	0	0	0.47	0.97
Herposiphonia secunda f. *tenella*	0	0	0	0.91	0	0	0	0.06	0	0
Heterosiphonia crispella	0	0	0	0	0	0	0	0	0.53	0.22
Heterosiphonia plumosa	0.19	5.19	1.91	0.03	0	0	0	0	0	0
Hypoglossum hypoglossoides	0.03	0.19	0.03	0.09	0	0	0	0	0.34	0.03
Jania rubens	0.06	0.13	2.53	3.53	0.91	0	0.81	7.50	0	0.25
Jania squamata	10.94	1.38	19.38	4.25	0	0	0	0	0	0
Jania virgata	0	0	0	0	0	0	0	0	0.44	6.81
Kallymenia reniformis	0.03	0.03	0.03	0.22	0.41	0.13	0	0	0	0
Laurencia obtusa	0	0	0	0	0	0	0	0	0.19	0.47
Liagora viscida	0	0	0	0	0	0	0	0.31	0	0
Lithophyllum incrustans	12.19	70	0	0	0	0	0.13	0.38	8.44	14.69
Lomentaria chylocladiella	0	0	0	0	0	0	0	0	0.06	0
Lomentaria clavellosa	0	0	0	0	0	0	0.09	0.47	0	0
Lomentaria verticillata	0	0	0	0	0	0	0	0	0.09	0
Lophocladia lallemandii	0	0	0	0	0	0	0	0	0.03	1.81
Lophosiphonia obscura	0	0	0	0	0	0	0	0	0.03	0.47
Meredithia microphylla	0	0	0	0	0.06	0	0	0	0	0
Mesophyllum lichenoides	12.81	0	26.56	75.00	64.06	56.25	79.69	49.69	38.75	0
Metacallophyllis laciniata	0.03	0.94	0	0	0	0.06	0	0	0	0
Microcladia glandulosa	0	0.06	2.91	5.84	0.50	0	6.16	2.22	0	0
Nitophyllum micropunctatum	0	0	0	0	0	0	0	0	0	0.19
Nitophyllum punctatum	0.13	0.03	0	0	0	0.03	0	0.47	0	0.19
Osmundea pinnatifida	0	0	0	0	0	0	0	0	0.09	0
Osmundea sp.	0	0	0	0	0	0	0	0.03	0	0
Peyssonnelia atropurpurea	0	0	1.25	1.25	0.47	3.97	0.59	1.03	1.59	0.72
Peyssonnelia rubra	5.94	0	0	0	0	0	0	0	0	0
Peyssonnelia squamaria	0	0	0	0	0	0	2.47	0.63	1.00	10.34
Plocamium cartilagineum	3.00	0.06	0.31	9.41	8.88	31.88	0.03	0.50	0.31	0.03
Polysiphonia breviarticulata	0	0	0	0	0	0	0	0.03	0	0
Polysiphonia brodiei	0	0	0	0	0	0	0	0	0	0.06
Polysiphonia macrocarpa	0	0	0	0.03	0	0	0.91	0	0	0
Polysiphonia sertularioides	0	0	0	0	0	0	0	0	0	0.41

Annex 1. - (cont.).

TAXA	ABUNDANCE (% of cover)									
	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10
RHODOPHYTA										
Polysiphonia sp.	0.03	0	0	0.03	0	0	0.13	0	0.13	0
Pterosiphonia complanata	16.44	5.69	12.81	3.50	0.75	1.25	0.16	4.78	0	0
Pterothamnion crispum	0	0.06	0.03	0.47	1.91	0.72	0	0.03	0	0
Pterothamnion plumula	0	0	0	0	0	0	0	0	0.03	0
Rhodophyllis divaricata	0	0	0	0.03	0	0.63	0.41	0	0.44	0.06
Rhodymenia ardissonei	0	0	0	0	0	0	0	0	1.47	0
Rhodymenia pseudopalmata	0	0	0.97	0.13	1.91	6.75	0.03	0	0	0
Scageliopsis patens	0	0	0	0	0	0	0	0.03	0	0
Schizymenia dubyi	0	0	0	0.34	0	0	0	0	0	0
Scinaia furcellata	0	0	0	0	0	0	0	0.06	0	0
Seirospora interrupta	0	0	0	0.03	0	0	0.03	0	0	0
Seirospora sphaerospora	0	0	0	0	0	0	0	0	0	0.03
Spermothamnion flabellatum	0	0	0	0	0	0	0	0	0	0.06
Sphaerococcus coronopifolius	0	0	2.03	2.50	0.63	0	0	0.63	0	0
Sphondylothamnion multifidum	0	0	0.03	0	0	0	0.03	0.25	0	0
Spyridia filamentosa	0	0	0	0	0	0	0	0	0	0.15
Symphyocladia parasitica	0	0	0.06	0.03	0.28	0	0.16	1.22	0	0
Vertebrata fruticulosa	0	0	3.50	5.44	0.03	0	0	0	1.34	0
Vertebrata furcellata	0	0	0	0	0	0	0	0	0.06	0
Vertebrata reptabunda	0	0	0	0.31	0	0	0	0.06	0	0
Wrangelia penicillata	0	0	0	0	0	0	0	0	1.03	4.03
Xiphosiphonia ardreana	0	0	0.63	1.44	0.16	0	0	0.41	0	0
Xiphosiphonia pennata	0	0	0	0.09	0	0	0	0	0	0

Annex 2. Acronym and the time-frame of the environmental variables included in the study.

Variables	Acronym	Time frame
Sea surface temperature (°C)	SST	2010-2015
Radiation (W/m^2)	RAD	2010-2015
Attenuation coefficient (m^{-1})	ATT	2010-2014
Nitrate (mol/m^3)	NIT	2010-2015
Bottom shear stress (N/m^2)	SHS	2010-2015
Significant wave height (m)	SWH	2010-2013
Salinity (psu)	SAL	2010-2015
Tidal range (m)	TID	2010-2013

Annex 3. Average values of the environmental variables for each locality. The time-frame and the units are specified in Annex 2.

	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10
SSTW	13.121	13.026	12.605	12.612	12.526	12.61	12.51	12.495	14.872	14.309
SSTSP	14.559	14.476	14.740	15.003	15.173	15.322	15.477	15.718	17.891	18.811
SSTSU	17.335	18.447	19.223	20.154	20.503	20.696	20.978	21.36	23.129	25.439
SSTAU	12.161	12.194	12.421	12.817	12.829	12.977	12.930	13.054	14.102	15.277
RADW	104.806	104.144	110.868	114.892	118.954	113.484	110.22	111.332	162.440	152.489
RADSP	246.801	246.803	242.539	256.107	267.023	261.296	254.007	253.899	308.999	293.483
RADSU	235.754	231.076	235.388	244.919	250.841	243.873	237.747	238.514	290.693	280.034
RADAU	82.461	80.920	88.168	93.989	97.239	92.176	89.358	89.091	140.478	127.187
NITW	1.231	1.220	0.912	0.666	0.696	0.720	0.607	0.679	0.454	0.393
NITSP	1.215	0.961	0.086	0.094	0.263	0.375	0.426	0.676	0.211	0.139
NITSU	2.473	1.967	0.080	0.275	0.618	0.753	0.941	0.889	0.116	0.101
NITAU	1.133	1.042	0.201	0.173	0.318	0.377	0.272	0.386	0.351	0.167
SHSW	1.679	1.656	1.322	1.185	0.028	0.132	1.430	0.303	0.002	0.046
SHSSP	0.658	0.599	0.669	0.745	0.008	0.084	0.639	0.101	0.001	0.027
SHSSU	0.363	0.316	0.394	0.533	0.004	0.061	0.374	0.048	0.001	0.020
SHSAU	1.732	1.733	1.546	1.352	0.032	0.152	1.678	0.345	0.002	0.040
WAVW	2.869	2.961	1.918	1.228	1.208	1.869	1.221	1.061	0.571	0.884
WAVSP	1.916	1.951	1.379	0.921	0.868	1.302	0.881	0.749	0.515	0.748
WAVSU	1.589	1.609	1.156	0.796	0.744	1.137	0.784	0.651	0.424	0.648
WAVAU	2.689	2.770	1.882	1.191	1.219	1.892	1.196	1.034	0.442	0.747
SALW	35.623	35.607	35.563	35.474	35.401	35.359	35.299	35.277	36.632	37.184
SALSP	35.619	35.603	35.539	35.442	35.371	35.329	35.274	35.261	36.598	37.164
SALSU	35.599	35.583	35.513	35.429	35.369	35.332	35.286	35.275	36.506	37.153
SALAU	35.621	35.604	35.559	35.472	35.405	35.365	35.308	35.285	36.570	37.186
TIDW	2.576	2.682	2.808	2.927	2.940	2.947	2.997	2.912	0.367	0.132
TIDSP	2.529	2.635	2.756	2.869	2.889	2.895	2.942	2.859	0.346	0.115
TIDSU	2.572	2.683	2.812	2.931	2.946	2.952	2.999	2.914	0.340	0.109
TIDAU	2.592	2.699	2.827	2.946	2.960	2.966	3.016	2.928	0.354	0.127

Annex 4. Summary of the correlations between the selected and the discarded variables, based on the selection criterion of R>0.894.

	SSTW	SSTSP	NITW	NITSP	SHSW
SSTSU	·	0.930	·	·	·
SSTAU	·	0.982	·	·	·
RADW	·	0.939	·	·	·
RADSP	·	0.913	·	·	·
RADSU	·	0.922	·	·	·
RADAU	·	0.930	·	·	·
NITSU	·	·	·	0.959	·
NITAU	·	·	·	0.926	·
SHSSP	·	·	·	·	0.975
SHSSU	·	·	·	·	0.933
SHSAU	·	·	·	·	0.998
WAVW	·	·	0.948	·	·
WAVSP	·	·	0.935	·	·
WAVSU	·	·	0.927	·	·
WAVAU	·	·	0.941	·	·
SALW	0.927	·	·	·	·
SALSP	0.927	·	·	·	·
SALSU	0.914	·	·	·	·
SALAU	0.918	·	·	·	·
TIDW	-0.950	-0.935	·	·	·
TIDSP	-0.950	-0.935	·	·	·
TIDSU	-0.950	-0.935	·	·	·
TIDAU	-0.950	-0.935	·	·	·

chapter 5

Experiment

NAHIARA MUGUERZA (2020) DOCTORAL THESIS pp. 127-151

Split-plot marine experiment to assess ecophysiological responses of *Gelidium corneum* assemblages

ABSTRACT Canopy-forming macroalgae are facing large declines due to climate change worldwide. The foundation species *Gelidium corneum* (Hudson) J.V. Lamouroux has shown a long-term decline in the Southeastern Bay of Biscay. We conducted an in situ experiment to investigate the combined effect of solar radiation and nutrient availability on the photosynthetic acclimation and growth of this macrophyte, and the effects on the species richness and diversity of the assemblages that it forms. Photochemical stress in *G. corneum* was found to be greater at the end of the study, probably as a result of a prolonged exposure to high irradiance (PAR and UVR) and due to high temperatures during summer. We found an acclimation of *G. corneum* specimens to summer light and thermal conditions through dynamic/reversible photoinhibition and a decrease in efficiency. Nutrients may also have had a positive effect in dealing with the negative effects of these stressors. Under ongoing global climate change and projections for the future, further research will be needed to better understand the effects not only on canopy forming species but also on the whole community and thus on the functioning of the ecosystem.

KEYWORDS Canopy-forming algae, Climate Change, Diversity, Foundation species, Growth, Irradiance, Macroalgae, Nutrients

LABURPENA

Split-plot esperimentua *Gelidium corneum* komunitatearen erantzun ekofisiologikoak ebaluatzeko

Errezela eratzen duten makroalgak asko ari dira murrizten mundu mailan, klima-aldaketaren ondorioz. *Gelidium corneum* (Hudson) J.V. Lamouroux espezie sortzaileak gainbehera bat izan du denboran zehar Bizkaiko Golkoaren hego-ekialdean. In situ egindako esperimentu baten bidez, eguzki-erradiazioak eta mantenugaien eskuragarritasunak aklimatazio fotosintetikoan eta makrofito horren hazkundean duten efektu konbinatua ikertzen dugu, bai eta espezieen aberastasunean eta osatzen duen komunitatearen dibertsitatean duten eragina ere. Emaitzek erakusten dutenez, *G. corneum*-en estres fotokimikoa handiagoa izan zen ikerketaren amaieran, ziurrenik, udako irradiantzia altuaren (PAR eta UVR) eta tenperatura altuen eraginpean luzaro egotearen ondorioz. *G. corneum*-en espezimenak erradiaziora eta udako baldintza termikoetara egokitzen direla fotoinhibizio dinamiko/itzulgarri baten bidez ikusi da, eta baita eraginkortasun fotosintetikoa murrizten dela. Horrez gain, nutrienteek estresatzaile horien ondorio negatiboen aurrean izan dezaketen eragin positiboa ere ikusi da. Klima-aldaketa globalaren arabera eta etorkizuneko proiekzioen arabera, ikerketa handiagoa nahitaezkoa izango da hauen ondorioak errezela eratzen dituzten espezieengan ez ezik, komunitate osoan ere hobeto ulertzeko eta ondorioz, ekosistemaren funtzionamenduan.

RESUMEN

Evaluación de respuestas ecofisiológicas en la comunidad de *Gelidium corneum* mediante un experimento Spli-plot

Las macroalgas formadoras de copa están registrando grandes disminuciones a nivel mundial debido al cambio climático. La especie fundadora *Gelidium corneum* (Hudson) J.V. Lamouroux ha mostrado un declive a lo largo del tiempo en el sureste del Golfo de Vizcaya. Mediante un experimento *in situ* investigamos el efecto combinado de la radiación solar y la disponibilidad de nutrientes sobre la aclimatación fotosintética y el crecimiento de este macrófita, así como sus efectos sobre la riqueza de especies y la diversidad de la comunidad que forma. Los resultados muestran que el estrés fotoquímico de *G. corneum* fue superior al final del estudio, probablemente como resultado de una exposición prolongada a una alta irradiancia (PAR y UVR) y también a las altas temperaturas durante el verano. Se ha observado una aclimatación de los especímenes de *G. corneum* a la radiación y a las condiciones térmicas estivales mediante una fotoinhibición dinámica/reversible y una disminución de la eficiencia fotosintética, además del efecto positivo que los nutrientes podrían tener frente a los efectos negativos de estos estresores. A tenor del cambio climático global y según las proyecciones futuras, una mayor investigación será imperativa para comprender mejor sus efectos no solo en las especies formadoras de copa sino también en toda la comunidad y en consecuencia en el funcionamiento del ecosistema.

1. INTRODUCTION

Canopy-forming macroalgae are ecologically key species on temperate rocky shores since they act as ecosystem engineers, providing biogenic habitat, protection and shelter for a wide variety of marine organisms (Wernberg et al., 2011c). These foundation species contribute significantly to nearshore productivity (Airoldi and Beck, 2007) and provide a unique three-dimensional space that enhances biodiversity (Strain et al., 2014). However, there is rising concern worldwide about the loss of these important species since it might cause changes in the whole benthic ecosystem (Schiel and Lilley, 2011). In this regard, the widespread loss of canopy-forming macroalgae has been observed to entail a change towards a bidimensional habitat (Airoldi and Beck, 2007; Strain et al., 2014) where the space becomes dominated by algal turfs made up of morphologically simple forms (Smale et al., 2013; Wernberg et al., 2016). Furthermore, this shift towards simpler communities threatens biodiversity and the functioning of the coastal ecosystem (Strain et al., 2014), since these new assemblages are occupied by species with lower ecological and functional values (Wernberg et al., 2016).

Apart from local anthropogenic stressors (Lilley and Schiel, 2006; Perkol-Finkel and Airoldi, 2010; Pocklington et al., 2017), rising sea-surface temperature has been suggested as the major driver in explaining shifts in the distribution of this canopy-forming macroalgae (Smale et al., 2013; Wernberg et al., 2011c, Mineur et al., 2015). However, in the context of climate change not only global warming but also other factors such as ocean acidification, increasing irradiance and storminess, among others, are changing environmental conditions (Kroecker et al., 2013; Hawkins et al., 2009; Wild et al., 2005). The most apparent changes occur at the population and community levels, but changes in environmental conditions first affect individuals themselves at biochemical and physiological levels. In this sense, numerous studies have shown effects from most of the aforementioned environmental factors on these perennial macroalgae (Hanelt et al., 2003; Figueroa et al., 2014).

The macrophyte *Gelidium corneum* (Hudson) J. V. Lamoroux (Gelidiales, Rhodophyta) used to form extensive stands on rocky shores off the Basque coast (Borja et al., 2004; Gorostiaga et al., 1995), but in recent decades a decline in this canopy-forming species has been reported (Borja et al., 2013; Díez et al., 2012; Muguerza et al., 2017). Among the factors responsible for this retreat, increased sea surface temperature, solar radiation and wave energy and decreased nutrient availability have been suggested (Quintano et al., 2019; Borja et al., 2013; Díez et al., 2012; Muguerza et al., 2017). However, most research on this matter consists of observational studies with no manipulation of the factors suggested. Only Quintano et al. (2019) carry out an *in situ* experiment transplanting *G. corneum* individuals between two depths as a proxy for two different irradiance levels. These authors report biochemical and physiological stress in *G. corneum* individuals at higher irradiances and suggest lower nutrient availability as a factor exacerbating the negative effects on the species. However, they did not carry out any nutrient manipulation. In this regard, it has been observed that at high light intensities photoinhibition can be intensified with rising temperatures and nutrient limitation (Tait and Schield, 2011). In fact, there is an overall consensus that solar ultraviolet radiation (UVR) negatively affects aquatic organisms (Häder et al., 2003), causing photoinhibition and oxidative stress (Bischof et al., 2006; Figueroa and Gómez, 2001; Wiencke et al., 2000). Increased irradiance may also encourage damage at different stages with effects on growth, reproduction and settlement of macroalgae (Figueroa and Korbee, 2010) and may therefore affect the whole community. Conversely, these marine primary producers show several physiological mechanisms for withstanding high light levels (Hanelt and Figueroa, 2012; Celis-Plá et al., 2017). It is also important to highlight that good nutrient availability can mitigate the stressful conditions caused by high irradiance and water temperature since it increases the production of protective substances and accelerates biochemical recovery from damage (Figueroa et al., 2006; Figueroa et al., 2010).

To help explain these declines in *G. corneum* assemblages and shed light on the consequences of their loss, starting from the initial hypothesis that the irradiance conditions and nutrient availability of recent years are stressful for the species, this study seeks to explore the combined effect of solar radiation and nutrient availability on the physiological state of *G. corneum,* and their effects on the taxonomic composition and diversity of this benthic community. To that end, an experimental approach with an *in situ* field experiment was used 1) to determine the combined effect of irradiance and nutrient concentration on the physiological and morphological performance of the canopy-forming species *Gelidium corneum;* and 2) to explore the variation in the structure and taxonomic diversity of the benthic community. The results provide a better understanding of the influence of both factors on the distribution of this key species in the coastal ecosystem of the Atlantic waters of southern Europe and thus establish a scientific basis of support for its proper management in the context of the climate change crisis.

2. MATERIAL AND METHODS

2.1. Study area and sampling location

This study was carried out from 07/06/2018 to 09/10/2018 on the Basque coast, the eastern part of the Cantabrian Sea (Northern Spain), in the south-eastern Bay of Biscay. This stretch of coastline is exposed to large fetches where the swell mainly comes from the NW (Galparsoro et al., 2010). Mean sea-surface temperature here formerly ranged between 12ºC in February and 22ºC in August, but recently a gradual warming has been reported (Goiekoetxea et al., 2009, Díez et al., 2012). Nutrient concentration during summer in the surface layer directly above the thermocline (above 10 m) is comparable to areas with oligotrophic conditions (Valencia & Franco, 2004).

The location chosen for the experiment is at 43°41’98’’ N, 2°95’31’’ W (Fig. 1).

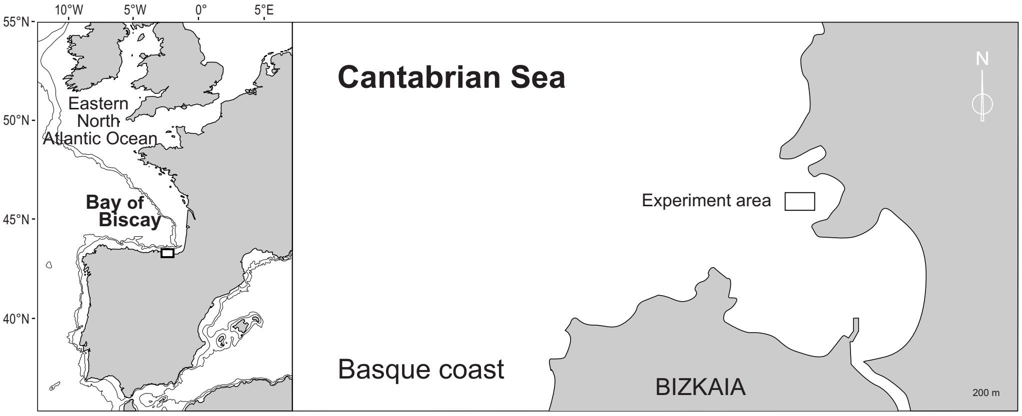

Fig. 1. Map of the study area showing the sampling location and/or the zone where the field experiment has been carried out.

2.2. Design of the Experiment

An *in situ* “split split-plot design” experiment was carried out in 2018 lasting 4 months, from June to October to test the effects of fertilisation (nutrients) and light availability (irradiance) on algae. Four fragments of habitat (whole plots) were randomly assigned to each of two levels for the Nutrients factor (unfertilised and fertilised), making a total of eight (whole) Plots. Four levels (non-manipulated control, procedural control, shaded negative and shaded positive) for the second treatment factor - Light - were randomised in each whole plot, thereby splitting them (Fig. 2). The entire set-up, with a total of 32 plots or parcels, was placed on the bedrock at a depth of 5 m (Fig. 3). The structure used for each light treatment comprised 3 legs fixed in the substrate as support for methacrylate, which was used together with a mesh material to remove light or shade the algae. The nutrients were placed in perforated tubes in each leg of the structure and released continuously. In unfertilised blocks the tubes were filled with stones. Photos illustrating the *in situ* experiment are attached in the Annex. Different univariate responses (*Gelidium corneum* length, species richness, species diversity) and several physiological response variables were recorded on two occasions in each split plot, one at the outset of treatment application (“before” level) and the other after four months of treatment application (“after” level).

2.3. Environmental conditions

Throughout the experiment Photosynthetically Active Radiation (PAR, 400–700 nm) and Ultraviolet A Radiation (UVA, 315–400 nm) were continuously recorded in the ex-

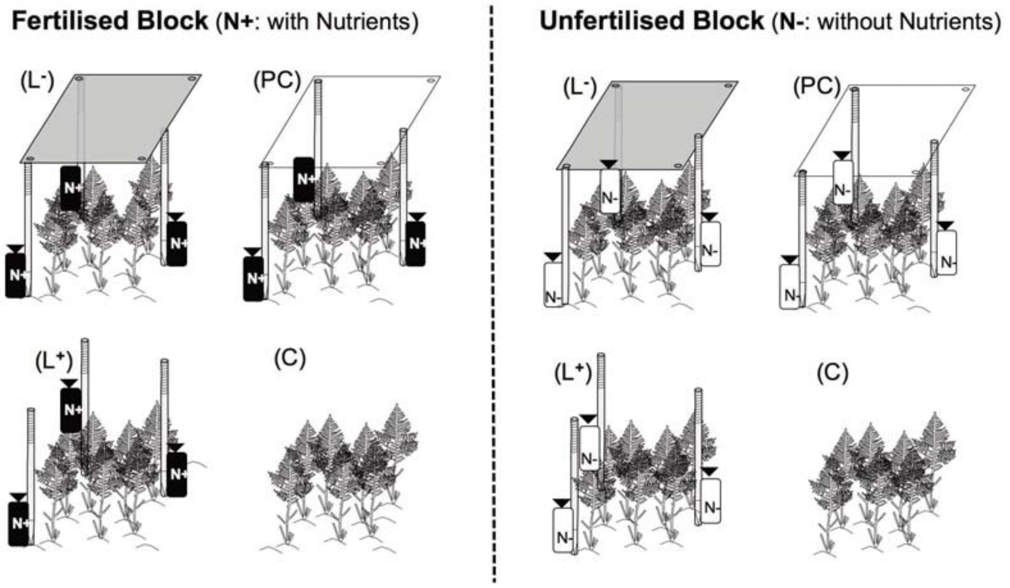

Fig. 2. Schematic layout of the two main blocks of the experiment: Fertilised (with addition of nutrients) and unfertilised (without nutrients). Each block or parcel is subdivided into 4 subplots.: L- , L+, PC and C. (L- : Shadow = shaded positive; L+ : light = shaded negative; PC : Procedural Control; C : Unmanipulated Control).

periment area at depth of 5 m using QSO-SUN 2.5 V and USB-SU 100 sensors, respectively. Water temperature was also monitored using a TMC1-HD sensor (Onset Computer Products, USA). Data from solar radiation and temperature sensors were recorded using a HOBO U12-006 data logger. Each sensor and each corresponding data logger were placed inside a polycarbonate box (OtterBox 3000) and attached to the bedrock using a stainless-steel structure.

2.4. Macroalgal material

Six fronds were marked *in situ* in each plot using numbered metal tags, and frond length was measured as a proxy of growth. The term "Frond" is understood as any erect axis stemming from the prostrate system of the macrophyte (Santos & Nyman, 1998). Performing this procedure under water is complex, so to ensure maximum data and to minimise data loss, 3 measurements were taken

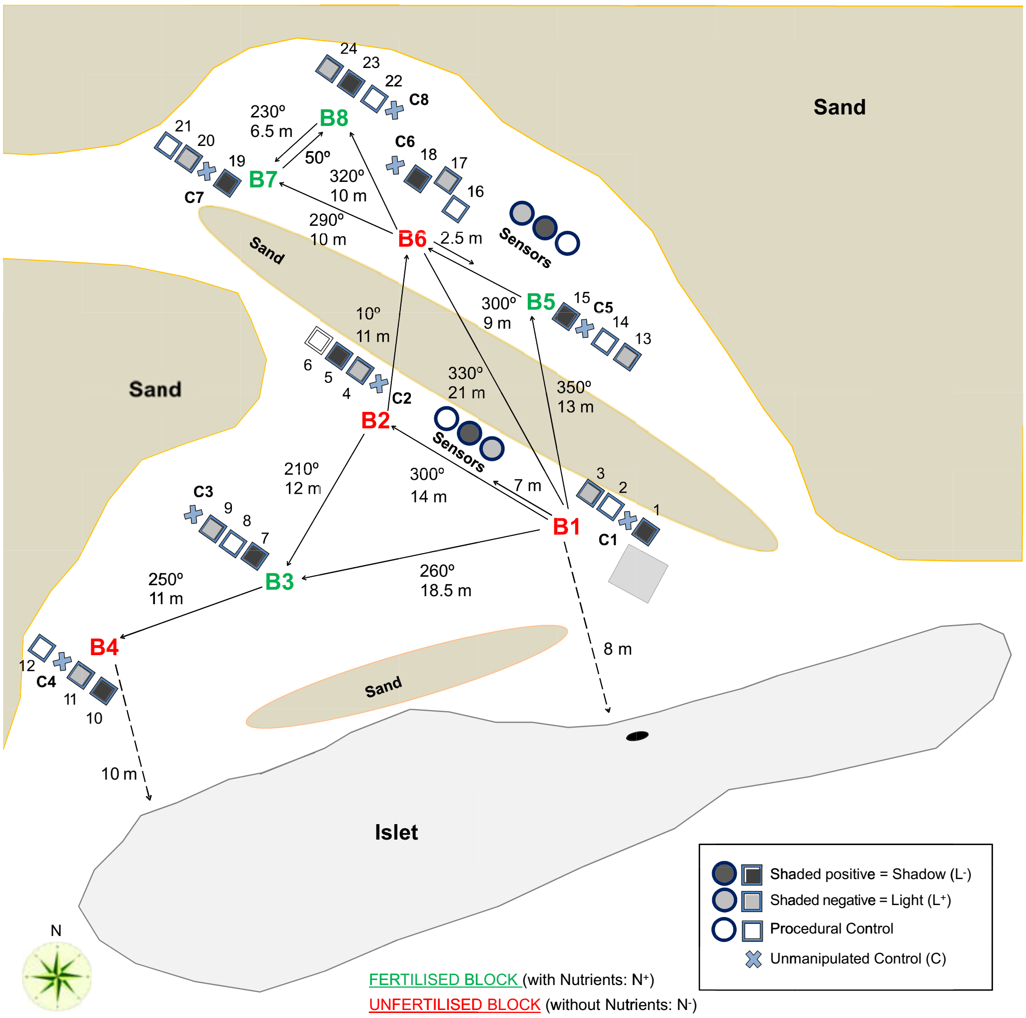

Fig. 3. The experimental area: the layout of the "Split Split-Plot" experiment setup and the distribution of the different blocks in the study area.

for this variable: at the beginning of the experiment, an intermediate measurement 2 months after the beginning (06/08/2018) and at the end. Additionally, three apical parts of the fronds were randomly collected at each plot to assess the physiological response of *G. corneum* by means of physiological variables.

2.5. Physiological response variables

In vivo chlorophyll-a fluorescence associated with photosystem II was determined using two pulse amplitude modulated fluorometers (Water-PAM, Walz GmbH, Germany) to characterise the photosynthetic status of the algae in response to changes in irradiance conditions. Apical pieces of fronds were placed in 10 ml steel incubation chambers with seawater to obtain rapid light curves for each treatment. F_o and F_m were measured after 15 min in darkness to obtain the maximum quantum yield (F_v/F_m). This process enables the reaction centres to oxidise completely so as to establish the basal fluorescence, with $F_v=F_m- F_o$, F_o being the basal fluorescence of 15 min dark adapted thalli and F_m maximal fluorescence after a saturation light pulse of>4000 µmol m^{-2} s^{-1}, with a duration of a few seconds (Schreiber et al., 1995). The electron transport rate (*ETR*), in µmol electrons per square-m per second, after 20s of exposure to 12 incremental irradiance levels of actinic blue light was calculated according to Schreiber et al. (1995) as follows:

> (equation 1) *ETR* =ium length, species richness and species diversity) according to equation 3, we used function lme() from the R package nlme (Pinheiro, Bates et al. 2018) in R software v. 3.6.1 (R Core Team 2019). Variance function structures (Davidian & Giltinan 1995) were introduced as appropriate via the *weights* argument of lme(). Additionally, the R libraries sjPlot (Lüdecke 2018) and visreg (Breheny & Burchett 2017) were used to plot the models, and the R library MuMIn (Barton 2018) to estimate coefficients of determination (R^2).

On the other hand, the efficacy of the experiment was analysed according to the repeated measurements statistical model, which in the case of only two repeated measurements is analogous to the split-plot model described in equation 4 (Casella 2008).

3. RESULTS

3.1. Efficacy of the experiment

An analysis of ammonium concentration (Fig. 4) shows that Time is significant, but Nutrients and the interaction between Nutrients and Time are not. The experimental fertilisation applied in half of the plots increased ammonium levels in both the unfertilised and the fertilised plots by 5.40 µmol L^{-1} with a 95% confidence interval (1.75, 9.05).

Nonetheless, three additional features of the data are worth noting in Fig. 4. First, the observed variability in ammonium concentration in the fertilised level of the Nutrients factor is about three times that in the unfertilised level for the same factor. Second, the initial (Time level before) mean concentration of ammonium in the fertilised level of the Nutrients treatment (34.92 µmol L^{-1}) was found to be higher than in the unfertilised level (31.04 µmol L^{-1}), though the difference is not statistically significant. Third (albeit not significantly, since the interaction term is not significant), the final (Time level after) mean concentration of ammonium in the fertilised level for the Nutrients factor (38.11 µmol L^{-1}) was observed to be slightly higher than in the unfertilised level for Nutrients (36.44 µmol L^{-1}).

3.2. Environmental conditions

Average temperature (mean ± SE, n=125) at a depth of 5 m was 20.50 ± 0.20, while temperature ranged from 15.0 ºC to 24,16 ºC. (Fig. 5). Daily maximum solar irradiance values are shown in Fig. 5. They peaked at 320 μmol m^{-2} s^{-1} for PAR and 27 W m^{-2} for UVA.

3.3. *Gelidium corneum* length

We found strong evidence against the null hypothesis of no effect of Time (Table 1; Fig. 6). The average increase in *G. corneum* length from 07/06/2018 (before) to 06/08/2018 (after) was estimated to be 1.5 cm with a 95% confidence interval (1.0, 2.0) (Table 2).

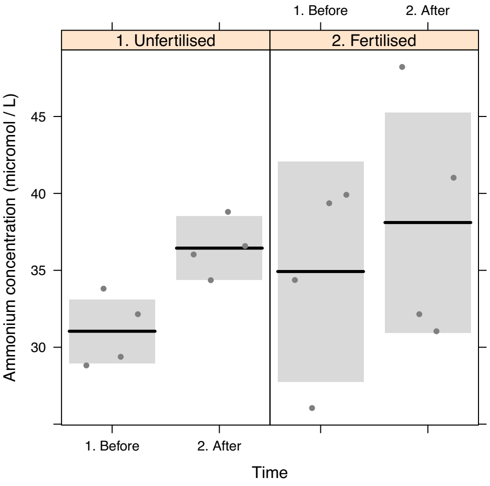

Fig. 4. Ammonium concentration in sea water before (24/05/2018) and after (10/10/2018) the application of experimental fertilisation (with two levels: fertilised and unfertilised): observed and fitted relationship. The effect of the experimental manipulations was tested according to the repeated measures statistical model and controlling for the observed heterogeneity of variances through an imbedded variance function structure (different deviations per Nutrients stratum). The hypothesis testing procedure yielded the next statistics: $F_{1,6}$ (Nutrients) = 1.07, with p-value = 0.342; $F_{1,6}$ (Time) = 13.34, with p-value = 0.011; $F_{1,6}$ (Nutrients x Time) = 0.17, with p-value = 0.694. R^2 = 62.14%.

We also found moderate evidence against the null hypotheses of no effect of Nutrients x Time, which suggests that the increase in length of *G. corneum* over time in the fertilised level was 1.2 cm larger with a 95% confidence interval (-1.2, 3.5) than in the unfertilised level (Fig. 7). *G. corneum* length was measured again on 09/10/2018, but growth in the species from 06/08/2018 to 09/10/2018 was null in all experiment plots.

3.4. Species richness and species diversity (macroalgae)

We also found strong evidence against the null hypothesis of no effect of Time (Table 1; Fig. 8) on species richness. The average species richness decrease, however, was estimated to be very small (-0.3, which represents a loss of less than one species) (Table 3). We also found weak evidence ($F_{1,24}$ = 2.58, p-value = 0.121) against the null hypotheses of no effect of Time x Nutrients (Table 1), with an estimate of 4 species lost (i.e. -4) after fertilisation, with a 95% CI (-9.6, 1.6) (Table 3). The statistical evidence is weak, but the graphical representation is suggestive (Fig. 9).

In the case of species diversity, we found strong evidence in line with the Shannon Index ($F_{3,24}$ = 9.19 with p-value < 0.001) against the null hypothesis of no effect of Nutrients x Light x Time (Table 1; Fig. 10). In the unfertilised plots diversity remained stable throughout the experiment, but in the fertilised plots it decreased significantly by 0.25 with a 95% confidence interval (-0.36, -0.15) (Table 4, Figure 11). Similarly, before the beginning of the experiment diversity was approximately similar in all the split-plot units (i.e. under each level of the Light treatment), whereas at the end of the experiment it had dropped by c. 0.30 in the procedural control, shaded positive and shaded negative Light treatment levels (Table 4, Figure 12).

3.5. Photosynthetic acclimation

In fluorescence measurements we found strong evidence against the null hypothesis of no change over Time for maximum quantum yield (F_v/F_m) (Table 5, Fig. 13). The significant average decrease in F_v/F_m, was nevertheless estimated to be quite small (0.13) (Table 6). Similarly, we found evidence against the null hypothesis of no Time effect on the photosynthetic efficiency of *Gelidium corneum* (initial slope of *ETR vs*. irradiance; α_{ETR}) (Table 5, Fig. 14); the estimate of the average decrease over time was 0.01 with a

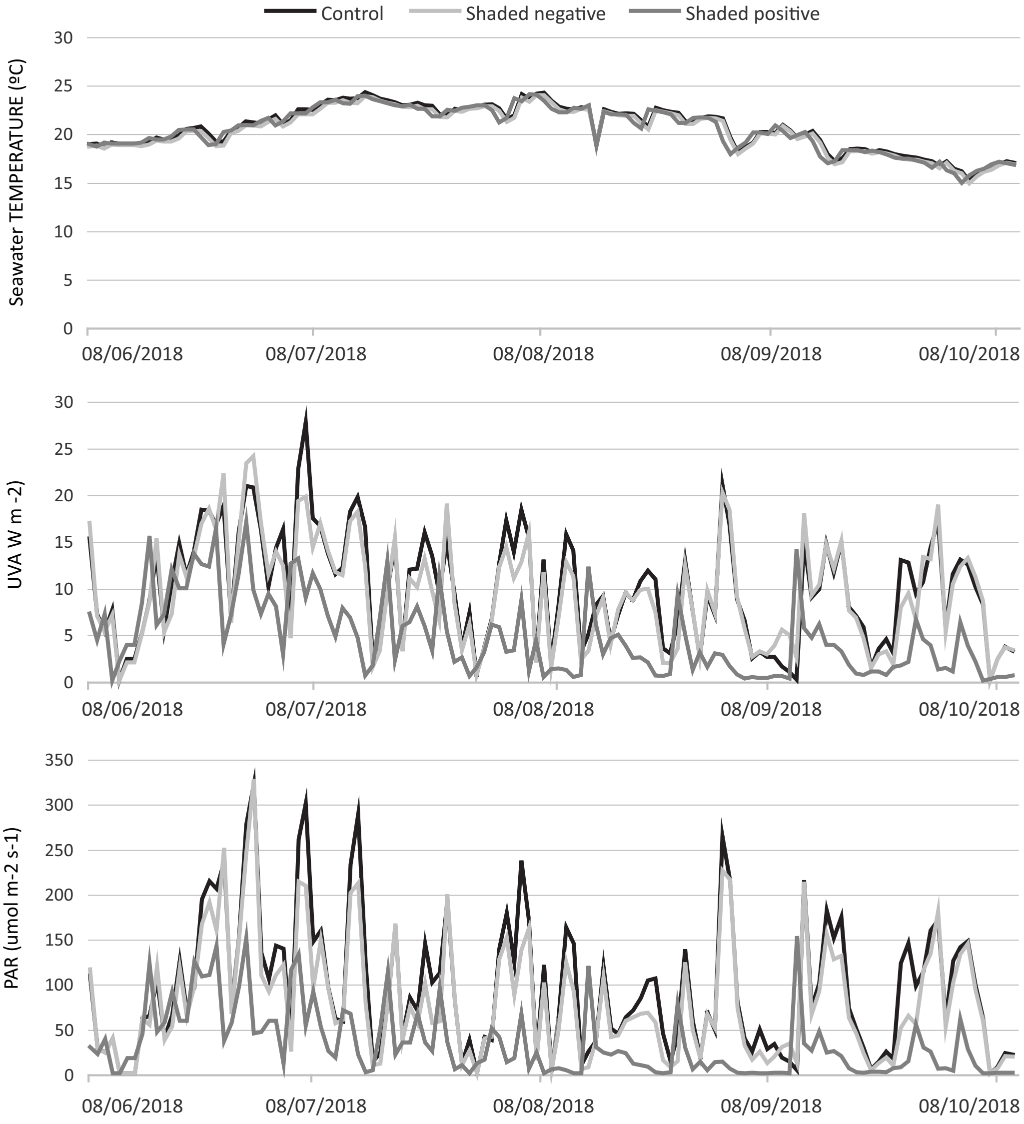

Fig. 5. Maximum daily values at depths of 5m for Temperature (°C), Photosynthetically active radiation (PAR; µmol m^{-2} s^{-1}) and Ultraviolet radiation A (UVA; W m^{-2}) during the experiment.

95% confidence interval (-0.02, 0.01) (Table 7). We also found significant differences over time in the variable NPQ_{max} (maximal non-photochemical quenching) (Table 5, Fig. 15), with an average decrease of 0.26 with a 95% confidence interval (-0.47, +0.06) (Table 8). Finally, photosynthesis capacity, measured as the maximal electron transport rate (ETR_{max}), showed moderate evidence ($F_{1,6} = 9.19$ with p-value = 0.053) against the null hypothesis of no effect of Nutrients (Table 5, Fig. 16), with an estimated average of 6.2 and a 95% confidence interval of (4.7, 7.7), as detailed in Table 9.

4. DISCUSSION

In this study we found that at the end of the summer the stress responses measured in *Gelidium corneum* were significantly higher. More specifically, our study focused on the effect of irradiance and nutrients not only on the growth and photosynthetic acclimation of the canopy-forming algae *G.corneum* but also on the species richness and diversity of the assemblages that it forms. However, the results no significant effect of the manipulation of irradiance levels on any of the variables studied. For nutrient manipulation significant increases and decreases were observed in the lengths of individuals and in Shannon diversity, respectively, in those experiment units in the fertilization treatment (in the case of length this happened only between the beginning and the middle of the experiment). A decrease (albeit not a significant one) in the number of species was also observed in the same experiment units. Moreover, no significant effect of fertilisation was observed since the ammonium concentration increased in both treatments, possibly due to the proximity between them or to the dynamics of the bay currents. Nor was the manipulation of radiation satisfactory. Consequently, it is not possible to draw any conclusions regarding the differences found between the combinations of irradiance level and nutrients. In this respect, even though it is not possible to attribute variations in the variables studied to the manipulation of nu-

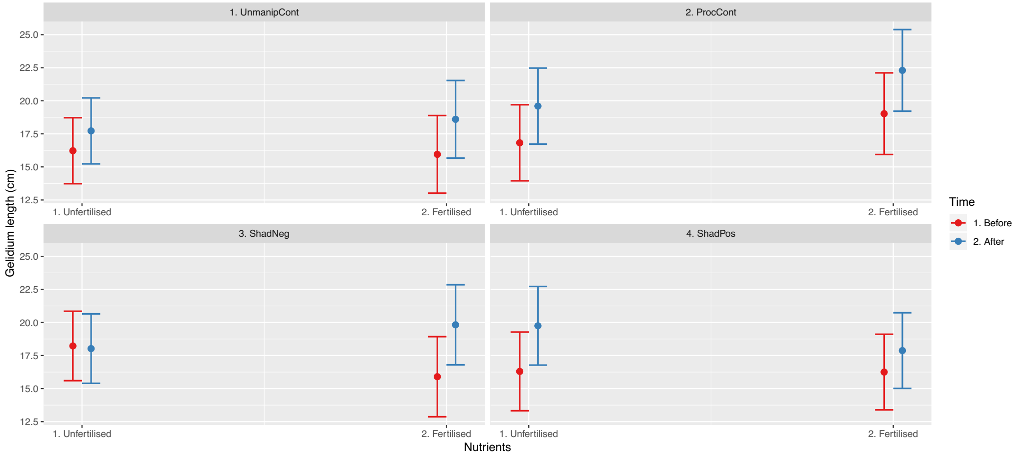

Fig. 6. *Gelidium corneum* length before (07/06/2018) and after (09/10/2018) the application of experimental fertilisation (factor Nutrients, with two levels: unfertilised and fertilised) and light experimental manipulation (factor Light, with four levels: unmanipulated control, procedural control, shading negative and shading positive): marginal effects. Hypothesis testing and parameter estimation are reported in Tables 1 and 2, respectively.

trients and irradiance levels it is worth noting that there was a significant decrease in optimal quantum yield, photosynthetic efficiency and photoprotection (non-photochemical quenching) over the course of the study period, which suggests that the *Gelidium corneum* specimens might be exposed to environmental stress.

One of the most important environmental factors for macroalgae is solar radiation, since it is essential for photosynthesis. Furthermore, solar radiation is a vital source of energy for primary producers and an essential factor that controls multiple processes in macroalgae at biochemical, physiological, morphological and population levels (Bischof et al., 2006; Figueroa and Gómez, 2001; Huovinen and Gómez, 2011). Light stimulates growth and photosynthesis, but algae often receive more sunlight than they can use for photosynthesis, so they have several strategies for protecting against excessive light and are able to acclimatize photosynthetically (Häder and Figueroa, 1997; Lüder et al., 2002). In our study we observed that the photosynthesis efficiency of *G.*

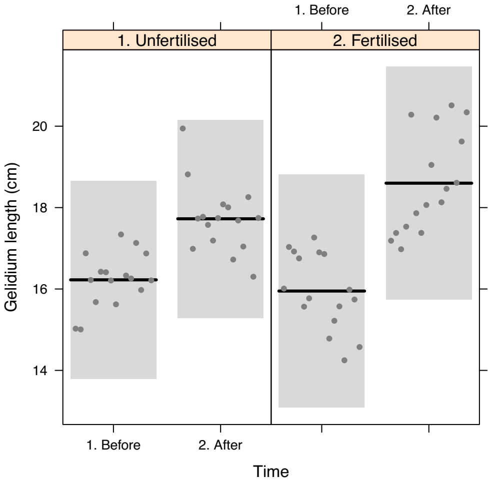

Fig. 7. The effect of the interaction between factor Nutrients (two levels: unfertilised and fertilised) and Time (before: 07/06/2018; after: 09/10/2018) on Gelidium corneum length: observed data and fitted model. See also Tables 1-2.

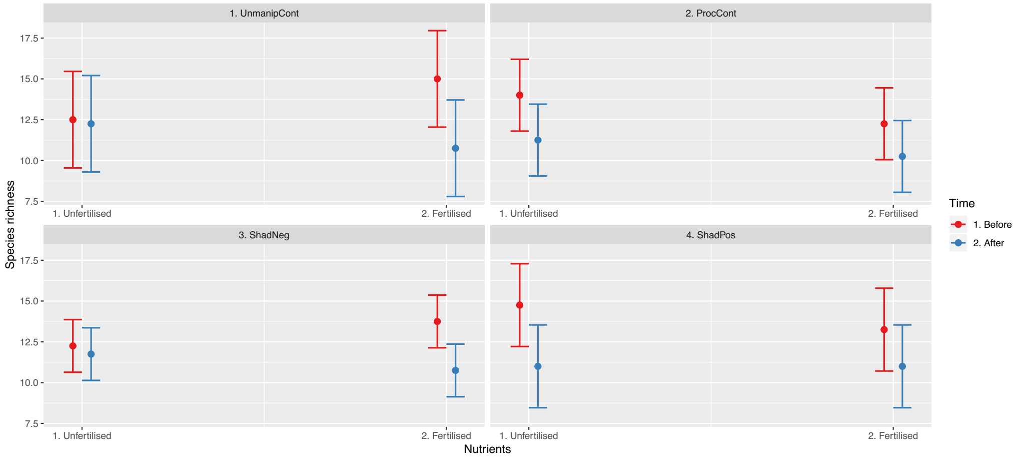

Fig. 8. Species richness before (29/05/2018) and after (26/10/2018) the application of experimental fertilisation (factor Nutrients, with two levels: unfertilised and fertilised) and light experimental manipulation (factor Light, with four levels: unmanipulated control, procedural control, shading negative and shading positive): marginal effects. Hypothesis testing and parameter estimation are reported in Tables 1 and 3, respectively.

corneum had decreased significantly, indicating an acclimation of its photosynthetic apparatus to the higher radiation levels prevailing in summer (Hanelt & Figueroa 2012). Reduced photosynthesis efficiency towards midday is certainly a widespread phenomenon in natural aquatic plants (Figueroa and Gómez, 2001; Häder and Figueroa, 1997; Hanelt et al., 2003), which may explain why the highest photosynthesis efficiency figures (α_{ETR}) were observed at the beginning of the experiment, coinciding with the start of summer. Moreover, reductions in α_{ETR} can be caused by greater heat dissipation (Alvarez-Gómez et al., 2019). On the other hand, while increasing irradiance levels are positively correlated with photosynthesis and growth (Coutinho and Zingmark, 1993), excessive light levels may cause reversible/dynamic photoinhibition of photosynthesis, consisting of an adjustable decrease in the photosynthetic electron transport chain (Häder and Figueroa, 1997; Häder et al., 2007; Hanelt and Figueroa, 2012). During the experiment significant differences were observed in photosynthesis production (ETR_{max}) in fertilised plots, which

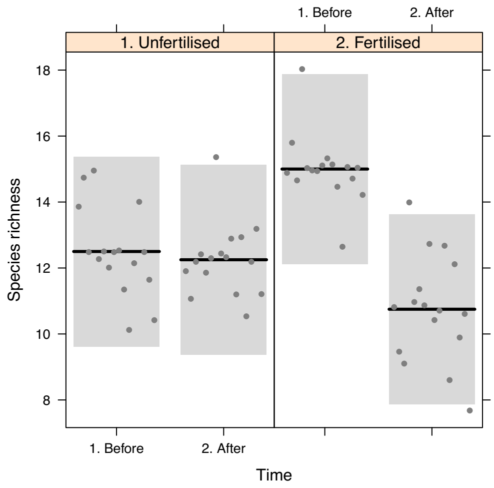

Fig. 9. The effect of the interaction between factor Nutrients (two levels: unfertilised and fertilised) and Time (before: 29/05/2018; after: 26/10/2018) on species richness: observed data and fitted model. See also Tables 1 and 3.

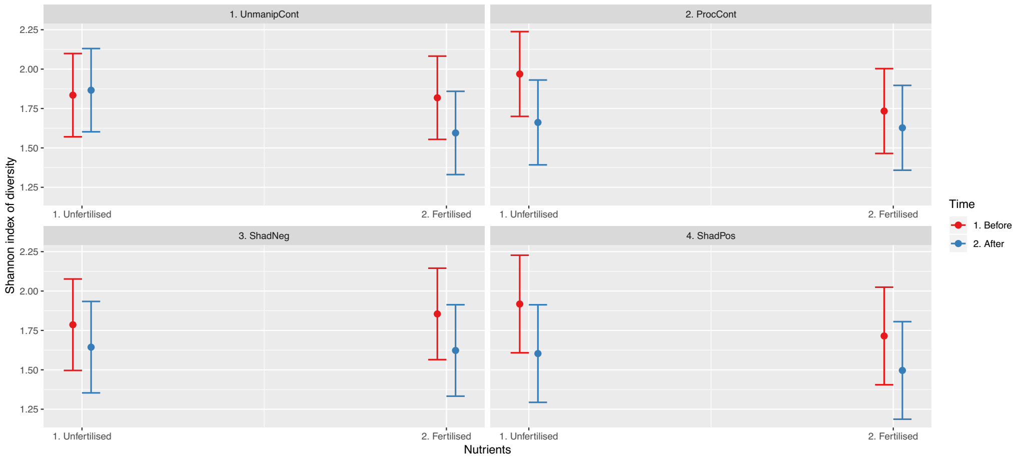

Fig. 10. Species diversity before (29/05/2018) and after (26/10/2018) the application of experimental fertilisation (factor Nutrients, with two levels: unfertilised and fertilised) and light experimental manipulation (factor Light, with four levels: unmanipulated control, procedural control, shading negative and shading positive): marginal effects. Hypothesis testing and parameter estimation are reported in Tables 1 and 4, respectively.

would indicate that *G.corneum* exploits nutrients not only for growth but also for photosynthesis. ETR_{max} may also indicate the energy available for investment in photoprotection and repair mechanisms (Raven, 2010). Our results for maximum nonphotochemical quenching (NPQ_{max}), which is considered a photoprotection mechanism, are higher at the beginning of the summer, which is consistent with the general trend that harmful effects on production and growth increase when the exposure dose is increased (Altamirano et al., 2003). Hence, as expected, NPQ_{max} values decrease over the course of the experiment. In general, optimal quantum yield (F_v/F_m) is used as an indicator of photoinhibition and is related to acclimation capacity (Figueroa et al., 2014). In this sense our results show a significant decrease in F_v/F_m over the period of the experiment. Indeed, populations of *G. corneum* on the Basque coast showed declines in optimal quantum yield (F_v/F_m) under high temperature and nitrogen limitation conditions, while under high nutrient supply the F_v/F_m decrease was less marked (Miguel-Vijandi et al., 2010). In a recent study carried out in an area close to the area of our experiment, Quintano et al. (2019) have observed symptoms of photodamage in specimens of *G. corneum*. Our figures for solar radiation are lower than those of that study. It should also be noted that the decrease observed in the present study for F_v/F_m and α_{ETR} contrasts with the reduction in PAR and UVA values recorded towards the end of the experiment. On the other hand, in comparison with the findings of Quintano et al. (2013) for the same location, although our outcomes are lower in terms of PAR values, they are significantly higher for UVA. Populations of this canopy forming macrophyte may therefore have been subjected to non-optimal environmental conditions and probably to stress conditions. In fact, the photoinhibition irradiance level for *G.corneum* in PAR is 250 µmol m^{-2} s^{-1} at 22ºC (Torres et al., 1991). The photoinhibition recorded for this macrophyte could therefore be explained by the high temperatures

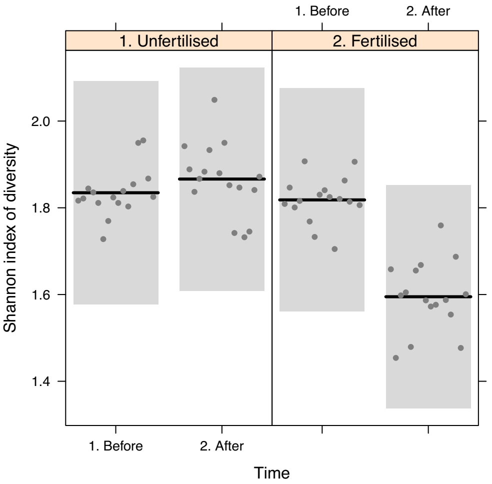

Fig. 11. The effect of the interaction between factor Nutrients (two levels: unfertilised and fertilised) and Time (before: 29/05/2018; after: 26/10/2018) on species diversity: observed data and fitted model. See also Tables 1 and 4.

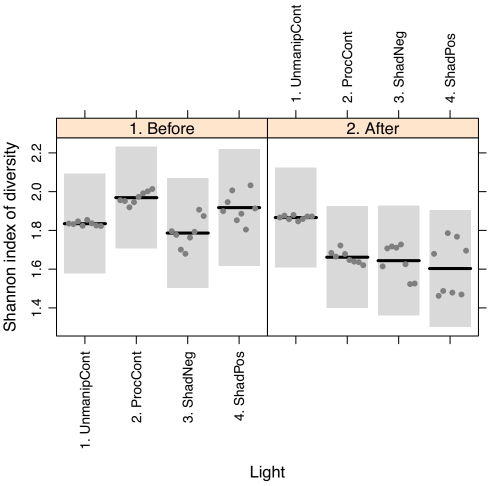

Fig. 12. The effect of the interaction between factor Light (four levels: unmanipulated control, procedural control, shading negative and shading positive) and Time (before: 29/05/2018; after: 26/10/2018) on species diversity: observed data and fitted model. See also Tables 1 and 4.

recorded during the study (up to 24.16ºC), which were close to the maximums recorded in recent decades (Diéz et al. 2012) and could interact with high radiation levels.

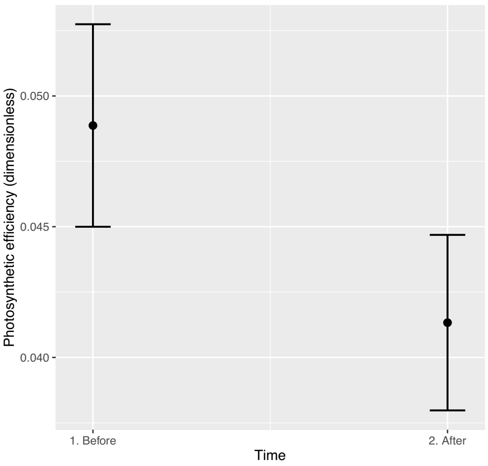

Fig. 13. The effect of the Time (before: 29/05/2018; after: 26/10/2018) on Maximum quantum yield (Fv/Fm): observed data and fitted model. See also Tables 5 and 6.

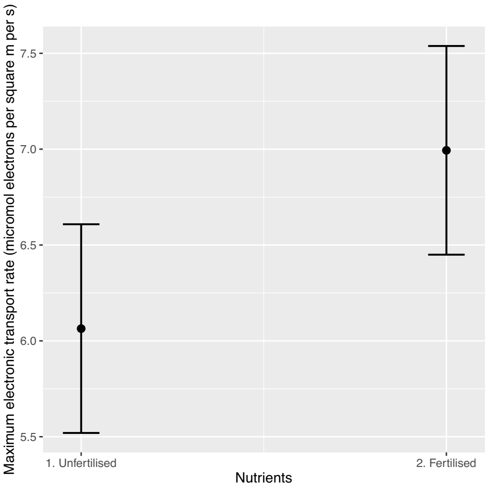

Fig. 14. The effect of the Time (before: 29/05/2018; after: 26/10/2018) on Photosynthetic efficiency (αETR): observed data and fitted model. See also Table 5 and Table 7.

Despite the photoinhibition observed, *G. corneum* specimens increased their length by an average of 1.5 cm, which suggests that photoinhibition could be dynamic/reversible

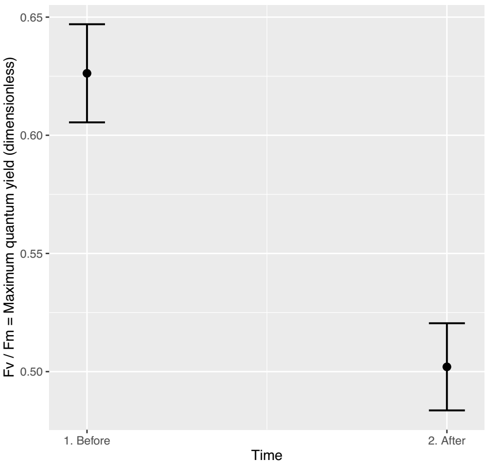

Fig. 15. The effect of the Time (before: 29/05/2018; after: 26/10/2018) on maximum nonphotochemical quenching (NPQ_{max}): observed data and fitted model. See also Tables 5 and 8.and 8.

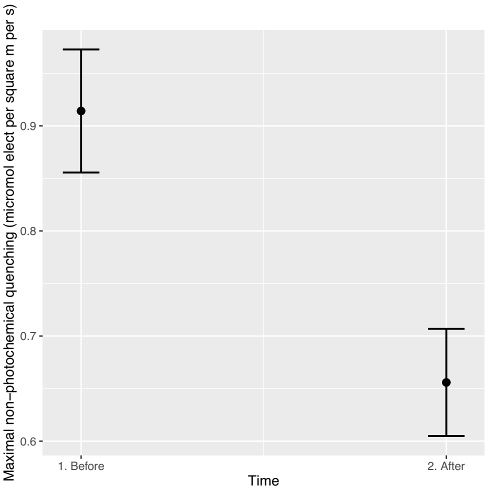

Fig. 16. The effect of the Time (before: 29/05/2018; after: 26/10/2018) on maximal electronic transport rate (ETR_{max}): observed data and fitted model. See also Table 5 and Table 9.

and be a response to the greater irradiance typical of the summer season. *G. corneum* is a perennial species with apical growth (7–10 cm yr^{-1}). Its maximum growth rate coincides with high light availability and temperatures in summer (Borja, 1994; Borja et al., 2004; Gorostiaga, 1994). As mentioned above, the PAR and UVA values obtained were not as high as in other summers in the study area (Quintano et al. 2013; 2019), so photodamage can be ruled out, even without studying other variables that could shed light on the matter such as antioxidant capacity and pigment composition. No significant changes were found in growth measured as an increase in length, but in all treatment levels the increase in length over time in the fertilised level was greater than in the unfertilised level. This reinforces the idea that nutrients are really vital for frond elongation. It should however be noted that, contrary to expectations, there was nutrient diffusion during the experiment from the fertilised to the unfertilised plots. This could explain why no differences were found between treatments. However, from the beginning to the end of the experiment the mean concentrations of ammonium in the fertilised level were higher than in the unfertilised level. It is known that nitrogen favours the metabolism of *G. corneum* and even helps it protect itself. However, it must be taken into account that this higher growth is not supported by a better physiological response in the aforementioned specimens, with the exception of productivity (ETR_{max}), which was slightly higher in the fertilised specimens (those exposed to higher nutrient concentrations from the outset).

Conversely, changes occurring at individual level could be being reflected at community level. In this regard, the results for the variables related to the community associated with *G. corneum* showed a generalised decrease in the number of species towards the end of the summer. No statistical significance was found between treatments for species richness, but this might be due to the large variability observed, and this trend might have held had a larger experiment been carried out. Nevertheless, diversity before the beginning of the experiment, as per the Shannon Index, was approximately similar in all the split-plot units, but by the end of the experiment it had dropped in the Light treatment levels. However, 4 months is probably not long enough to detect changes in diversity because species richness, community structure and turn-over of other macroalgae are more associated with seasonal changes in canopy biomass than with environmental variables *per se* (Wernberg and Goldberg, 2008). In fact, seasonal changes in environmental conditions drive changes in the canopy, which in turn drive changes in species richness and assemblage structure, so habitat-formers can exert a strong influence over time on associated communities (Wernberg and Goldberg, 2008).

The physiological performance of macroalgae and as a result their survival are strongly related to irradiance and temperature exposure (Rothäusler et al., 2011), so one relevant outcome of the present study is that the photochemical stress of *G. corneum* was found to be greater at the end of the study, probably as a result of a prolonged exposure to high irradiance (PAR and UVR) and to high temperatures during summer, even though there was no deficit in nutrient availability. In conclusion, the results of this study show an acclimation of *G. corneum* specimens to summer light and thermal conditions through dynamic/reversible photoinhibition and a decrease in efficiency. A potentially positive effect of nutrients on the aforementioned stressors is also observed. In fact, this study highlights the importance of nutrients for *G. corneum* in dealing with the negative effects of other stressors. However, further physiological and biochemical variables need to be explored to obtain a more detailed response. Given that photoinhibition may cause several stress symptoms

(Quintano et al., 2019), future research on the effect of *G. corneum* physiology should be carried out to determine what physiological mechanisms are associated with changes in the community. In regard to the community, it would be useful for future studies to increase the experimentation time since 4 months may not be long enough to obtain answers. Thus, under ongoing global climate change and with forecasts for the south-eastern Bay of Biscay of increases in irradiance and ocean warming and greater stratification (Chust et al., 2011; Ruosteenoja and Räisänen, 2013), it would be also important to investigate and better understand the effects of interactions between abiotic (nutrients, irradiance, temperature, wave energy) and biotic (grazing pressure, pollution) factors that affect *G. corneum* and hence the whole assemblage that it forms. In line with this, it is necessary to obtain an understanding of the processes and factors that regulate the distribution of habitat-forming macrophytes in order to predict future fluctuations in coastal ecosystems and their ecological consequences.

Table 1. Hypothesis testing (Restricted Maximum Likelihood approach) for the univariate responses Gelidium length, species richness, and species diversity, according to the split split plot statistical model. df (num) = degrees of freedom (numerator); df (den) = degrees of freedom (denominator).

Response is *Gelidium* length: hypothesis testing

Source	df (num)	df (den)	F-value	p-value
(Intercept)	1	24	1038.44	< 0.001
Nutrients	1	6	0.11	0.754
Light	3	18	1.25	0.321
Time	1	24	61.92	< 0.001
Nutrients x Light	3	18	0.68	0.575
Nutrients x Time	1	24	4.50	0.044
Light x Time	3	24	1.81	0.172
Nutrients x Light x Time	3	24	2.84	0.059

Response is species richness: hypothesis testing

Source	df (num)	df (den)	F-value	p-value
(Intercept)	1	24	1007.19	< 0.001
Nutrients	1	6	0.14	0.723
Light	3	18	0.28	0.842
Time	1	24	23.76	< 0.001
Nutrients x Light	3	18	0.62	0.609
Nutrients x Time	1	24	2.58	0.121
Light x Time	3	24	0.36	0.783
Nutrients x Light x Time	3	24	1.57	0.224

Response is species diversity (Shannon index): hypothesis testing

Source	df (num)	df (den)	F-value	p-value
(Intercept)	1	24	671.82	< 0.001
Nutrients	1	6	0.60	0.469
Light	3	18	0.25	0.858
Time	1	24	55.63	< 0.001
Nutrients x Light	3	18	0.28	0.838
Nutrients x Time	1	24	5.47	0.028
Light x Time	3	24	3.02	0.049
Nutrients x Light x Time	3	24	9.19	< 0.001

Table 2. Parameter point and 95% confidence interval estimation for *Gelidium* length. Fixed-factors-R^2 = 33.2%; random-factors R^2 = 66.7%. LB and UB = lower and upper bounds.

Fixed terms	Estimate	SE	95% LB	95% UB
Intercept	16.2	1.2	13.7	18.8
Nutrients				
Unfertilised	REF			
Fertilised	-0.3	1.9	-5.0	4.4
Light				
Unmanipulated Control	REF			
ProceduralControl	0.6	1.8	-3.1	4.3
ShadedNegative	2.0	1.7	-1.5	5.5
ShadedPositive	0.1	1.8	-3.7	3.9
Time				
Before	REF			
After	1.5	0.2	1.0	2.0
Nutrients x Light				
Unfertilised x Unmanipulated Control	REF			
Fertilised x Procedural Control	2.5	2.7	-3.1	8.1
Fertilised x Shaded Negative	-2.1	2.6	-7.5	3.4
Fertilised x Shaded Positive	0.2	2.6	-5.3	5.7
Nutrients x Time				
Unfertilised x Before	REF			
Fertilised x After	1.2	1.1	-1.2	3.5
Light x Time				
Unmanipulated Control x Before	REF			
ProceduralControl x After	1.3	1.1	-0.9	3.5
ShadedNegative x After	-1.7	0.7	-3.1	-0.3
ShadedPositive x After	2.0	1.2	-0.5	4.4
Nutrients x Light X Time				
Unfertilised x Unmanipulated Control x Before	REF			
Fertilised x Procedural Control x After	-0.7	2.0	-4.8	3.5
Fertilised x Shaded Negative x After	3.0	1.8	-0.7	6.7
Fertilised x Shaded Positive x After	-3.0	1.9	-6.9	1.0

Random terms: $\sigma^2_{\varepsilon} = 1.0^2$; $\sigma^2_{\delta} = 2.3^2$; $\sigma^2_{\omega} = 0.3^2$; residuals = 0.1^2. The parameter estimates for the variance function structure (different deviations for each Nutrients x Light stratum) are as follows: 1.0 (unfert. x unmanip. control); 12.9 (unfert. x proc. control); 7.4 (unfert. x shaded neg.); 14.6 (unfert. x shaded pos.); 13.9 (fert. x unmanip. control); 16.3 (fert. x proc. control); 15.4 (fert. x shaded neg.); 12.6 (fert. x shaded pos.).

Table 3. Parameter point and 95% confidence interval estimation for species richness. Fixed-factors-R^2 = 19.5%; random-factors R^2 = 22.8%. LB and UB = lower and upper bounds.

Fixed terms	Estimate	SE	95% LB	95% UB
Intercept	12.5	1.5	9.5	15.5
Nutrients				
Unfertilised	REF			
Fertilised	2.5	2.1	-2.6	7.6
Light				
Unmanipulated Control	REF			
ProceduralControl	1.5	1.7	-2.2	5.2
ShadedNegative	-0.3	1.6	-3.6	3.1
ShadedPositive	2.3	1.9	-1.7	6.2
Time				
Before	REF			
After	-0.3	1.9	-4.2	3.7
Nutrients x Light				
Unfertilised x Unmanipulated Control	REF			
Fertilised x Procedural Control	-4.3	2.5	-9.4	0.9
Fertilised x Shaded Negative	-1.0	2.2	-5.7	3.7
Fertilised x Shaded Positive	-4.0	2.6	-9.5	1.5
Nutrients x Time				
Unfertilised x Before	REF			
Fertilised x After	-4.0	2.7	-9.6	1.6
Light x Time				
Unmanipulated Control x Before	REF			
ProceduralControl x After	-2.5	2.4	-7.4	2.4
ShadedNegative x After	-0.3	2.1	-4.6	4.1
ShadedPositive x After	-3.5	2.5	-8.7	1.7
Nutrients x Light X Time				
Unfertilised x Unmanipulated Control x Before	REF			
Fertilised x Procedural Control x After	4.8	3.3	-2.1	11.6
Fertilised x Shaded Negative x After	1.5	3.0	-4.6	7.6
Fertilised x Shaded Positive x After	5.5	3.6	-1.8	12.8

Random terms: $\sigma^2_\varepsilon = 0.8^2$; $\sigma^2_\delta = 0.8^2$; $\sigma^2_\omega = 1.1^2$; residuals = 2.5^2. The parameter estimates for the variance function structure (different deviations per Light stratum) are as follows: 1.0 (unmanip. control); 0.6 (proc. control); 0.1 (shaded neg.); 0.8 (shaded pos.).

Table 4. Parameter point and 95% confidence interval estimation for species diversity. Fixed-factors-R^2 = 19.97%; random-factors R^2 = 79.03%. LB and UB = lower and upper bounds.

Fixed terms		Estimate	SE	95% LB	95% UB
Intercept		1.83	0.13	1.56	2.11
Nutrients					
	Unfertilised	REF			
Fertilised	-0.02	0.19	-0.47	0.44	
Light					
	Unmanipulated Control	REF			
	ProceduralControl	0.13	0.15	-0.19	0.46
	ShadedNegative	-0.05	0.16	-0.39	0.29
	ShadedPositive	0.08	0.17	-0.28	0.44
Time					
	Before	REF			
	After	0.03	0.04	-0.04	0.11
Nutrients x Light					
	Unfertilised x Unmanipulated Control	REF			
	Fertilised x Procedural Control	-0.22	0.22	-0.67	0.24
	Fertilised x Shaded Negative	0.09	0.23	-0.40	0.57
	Fertilised x Shaded Positive	-0.19	0.24	-0.69	0.32
Nutrients x Time					
	Unfertilised x Before	REF			
	Fertilised x After	-0.25	0.05	-0.36	-0.15
Light x Time					
	Unmanipulated Control x Before	REF			
	ProceduralControl x After	-0.34	0.06	-0.47	-0.21
	ShadedNegative x After	-0.17	0.10	-0.38	0.03
	ShadedPositive x After	-0.35	0.12	-0.60	-0.09
Nutrients x Light x Time					
	Unfertilised x Unmanipulated Control x Before	REF			
	Fertilised x Procedural Control x After	0.46	0.09	0.27	0.64
	Fertilised x Shaded Negative x After	0.17	0.14	-0.12	0.45
	Fertilised x Shaded Positive x After	0.35	0.18	-0.01	0.71

Random terms: $\sigma^2_\varepsilon = 0.15^2$; $\sigma^2_\delta = 0.21^2$; $\sigma^2_\omega = 0.04^2$; residuals = 0.03^2. The parameter estimates for the variance function structure (different deviations per Light stratum) are as follows: 1.0 (unmanip. control); 2.0 (proc. control); 4.2 (shaded neg.); 5.5 (shaded pos.).

Table 5. Hypothesis testing (Restricted Maximum Likelihood approach) for the univariate responses ETR_{max} (Maximun electronic transport rate), F_v/F_m (Maximum quantum yield), α_{ETR} (photosynthetic efficiency) and NPQ_{max} (Maximal non-photochemical quenching), according to the split split plot statistical model. df (num) = degrees of freedom (numerator); df (den) = degrees of freedom (denominator).

Response is ETR_{max}: hypothesis testing

Source	df (num)	df (den)	F-value	p-value
(Intercept)	1	18	1179.62	< 0.001
Nutrients	1	6	5.78	0.053
Light	3	18	0.75	0.535
Time	1	16	2.02	0.175
Nutrients x Light	3	18	1.00	0.417
Nutrients x Time	1	16	1.64	0.218
Light x Time	3	16	1.21	0.340
Nutrients x Light x Time	3	16	2.11	0.139

Response is F_v/F_m: hypothesis testing

Source	df (num)	df (den)	F-value	p-value
(Intercept)	1	18	4726.96	< 0.001
Nutrients	1	6	1.78	0.230
Light	3	18	0.86	0.482
Time	1	16	133.84	< 0.001
Nutrients x Light	3	18	1.58	0.229
Nutrients x Time	1	16	0.37	0.551
Light x Time	3	16	0.17	0.914
Nutrients x Light x Time	3	16	0.38	0.767

Response is NPQ_{max}: hypothesis testing

Source	df (num)	df (den)	F-value	p-value
(Intercept)	1	18	1369.85	< 0.001
Nutrients	1	6	1.95	0.212
Light	3	18	2.17	0.127
Time	1	16	54.87	< 0.001
Nutrients x Light	3	18	0.67	0.580
Nutrients x Time	1	16	0.01	0.945
Light x Time	3	16	0.05	0.983
Nutrients x Light x Time	3	16	0.32	0.812

Response is α_{ETR}: hypothesis testing

Source	df (num)	df (den)	F-value	p-value
(Intercept)	1	18	1184.53	< 0.001
Nutrients	1	6	0.06	0.815
Light	3	18	1.15	0.356
Time	1	16	9.44	0.007
Nutrients x Light	3	18	0.52	0.672
Nutrients x Time	1	16	0.34	0.571
Light x Time	3	16	1.13	0.367
Nutrients x Light x Time	3	16	2.42	0.104

Table 6. Parameter point and 95% confidence interval estimation for F_v/F_m. Fixed-factors-R^2 = 70.3%; random-factors R^2 = 29.7%. LB and UB = lower and upper bounds.

Fixed terms		Estimate	SE	95% LB	95% UB
Intercept		0.62	0.02	0.57	0.67
Nutrients					
	Unfertilised	REF			
	Fertilised	-0.01	0.03	-0.09	0.08
Light					
	Unmanipulated Control	REF			
	ProceduralControl	0.02	0.03	-0.05	0.08
	ShadedNegative	-0.02	0.03	-0.09	0.05
	ShadedPositive	-0.02	0.03	-0.09	0.05
Time					
	Before	REF			
	After	-0.13	0.03	-0.19	-0.07
Nutrients x Light					
	Unfertilised x Unmanipulated Control	REF			
	Fertilised x Procedural Control	0.01	0.04	-0.08	0.11
	Fertilised x Shaded Negative	0.05	0.04	-0.04	0.15
	Fertilised x Shaded Positive	0.08	0.04	-0.02	0.17
Nutrients x Time					
	Unfertilised x Before	REF			
	Fertilised x After	0.01	0.04	-0.08	0.10
Light x Time					
	Unmanipulated Control x Before	REF			
	ProceduralControl x After	0.00	0.04	-0.09	0.08
	ShadedNegative x After	0.04	0.04	-0.05	0.13
	ShadedPositive x After	0.01	0.04	-0.08	0.10
Nutrients x Light X Time					
	Unfertilised x Unmanipulated Control x Before	REF			
	Fertilised x Procedural Control x After	0.00	0.06	-0.12	0.13
	Fertilised x Shaded Negative x After	-0.05	0.06	-0.18	0.07
	Fertilised x Shaded Positive x After	-0.03	0.06	-0.15	0.10

Random terms: $\sigma^2_\varepsilon = 0.0^2$; $\sigma^2_\delta = 0$; $\sigma^2_\omega = 0.0^2$; residuals = 0.0^2.

Table 7. Parameter point and 95% confidence interval estimation for α_{ETR}. Fixed-factors-R^2 = 30.8%; random-factors R^2 = 69.1%. LB and UB = lower and upper bounds.

Fixed terms	Estimate	SE	95% LB	95% UB
Intercept	0.05	0.01	0.04	0.06
Nutrients				
Unfertilised	REF			
Fertilised	-0.01	0.01	-0.02	0.01
Light				
Unmanipulated Control	REF			
ProceduralControl	0.00	0.01	-0.02	0.01
ShadedNegative	0.01	0.01	-0.01	0.03
ShadedPositive	0.00	0.01	-0.02	0.01
Time				
Before	REF			
After	-0.01	0.01	-0.02	0.01
Nutrients x Light				
Unfertilised x Unmanipulated Control	REF			
Fertilised x Procedural Control	0.02	0.01	0.00	0.04
Fertilised x Shaded Negative	0.00	0.01	-0.02	0.02
Fertilised x Shaded Positive	0.01	0.01	-0.02	0.03
Nutrients x Time				
Unfertilised x Before	REF			
Fertilised x After	0.01	0.01	-0.01	0.04
Light x Time				
Unmanipulated Control x Before	REF			
ProceduralControl x After	0.01	0.01	-0.01	0.03
ShadedNegative x After	-0.01	0.01	-0.03	0.02
ShadedPositive x After	0.00	0.01	-0.02	0.02
Nutrients x Light X Time				
Unfertilised x Unmanipulated Control x Before	REF			
Fertilised x Procedural Control x After	-0.04	0.01	-0.07	-0.01
Fertilised x Shaded Negative x After	-0.01	0.01	-0.04	0.02
Fertilised x Shaded Positive x After	-0.02	0.01	-0.05	0.01

Random terms: $\sigma^2_{\varepsilon} = 0.0^2$; $\sigma^2_{\delta} = 0.0$; $\sigma^2_{\omega} = 0.0^2$; residuals = 0.0^2.

Table 8. Parameter point and 95% confidence interval estimation for NPQ_{max}. Fixed-factors-R^2 = 54.1%; random-factors R^2 = 45.8%. LB and UB = lower and upper bounds.

Fixed terms	Estimate	SE	95% LB	95% UB
Intercept	0.85	0.08	0.69	1.01
Nutrients				
Unfertilised	REF			
Fertilised	-0.03	0.11	-0.29	0.23
Light				
Unmanipulated Control	REF			
ProceduralControl	0.10	0.10	-0.12	0.32
ShadedNegative	0.02	0.10	-0.20	0.24
ShadedPositive	0.03	0.10	-0.19	0.24
Time				
Before	REF			
After	-0.26	0.10	-0.47	-0.06
Nutrients x Light				
Unfertilised x Unmanipulated Control	REF			
Fertilised x Procedural Control	0.04	0.15	-0.27	0.35
Fertilised x Shaded Negative	0.11	0.15	-0.20	0.41
Fertilised x Shaded Positive	0.19	0.15	-0.12	0.50
Nutrients x Time				
Unfertilised x Before	REF			
Fertilised x After	0.03	0.14	-0.26	0.32
Light x Time				
Unmanipulated Control x Before	REF			
ProceduralControl x After	-0.05	0.14	-0.34	0.24
ShadedNegative x After	0.04	0.14	-0.25	0.33
ShadedPositive x After	0.02	0.14	-0.28	0.31
Nutrients x Light X Time				
Unfertilised x Unmanipulated Control x Before	REF			
Fertilised x Procedural Control x After	0.07	0.19	-0.34	0.49
Fertilised x Shaded Negative x After	-0.08	0.19	-0.49	0.34
Fertilised x Shaded Positive x After	-0.09	0.19	-0.51	0.32

Random terms: $\sigma^2_\varepsilon = 0.0^2$; $\sigma^2_\delta = 0.0$; $\sigma^2_\omega = 0.1^2$; residuals = 0.0^2.

Table 9. Parameter point and 95% confidence interval estimation for ETR_{max}. Fixed-factors-R^2 = 30.5%; random-factors R^2 = 69.5%. LB and UB = lower and upper bounds.

Fixed terms	Estimate	SE	95% LB	95% UB
Intercept	6.2	0.7	4.7	7.7
Nutrients				
Unfertilised	REF			
Fertilised	-0.7	1.0	-3.2	1.7
Light				
Unmanipulated Control	REF			
ProceduralControl	-0.8	1.0	-2.9	1.4
ShadedNegative	-0.7	1.0	-2.9	1.4
ShadedPositive	-0.6	1.0	-2.8	1.5
Time				
Before	REF			
After	0.2	0.8	-1.5	1.8
Nutrients x Light				
Unfertilised x Unmanipulated Control	REF			
Fertilised x Procedural Control	1.6	1.4	-1.4	4.7
Fertilised x Shaded Negative	2.8	1.4	-0.2	5.8
Fertilised x Shaded Positive	3.9	1.4	0.9	6.9
Nutrients x Time				
Unfertilised x Before	REF			
Fertilised x After	1.5	1.1	-0.8	3.9
Light x Time				
Unmanipulated Control x Before	REF			
ProceduralControl x After	0.8	1.1	-1.6	3.2
ShadedNegative x After	1.1	1.1	-1.3	3.5
ShadedPositive x After	0.5	1.1	-1.9	2.9
Nutrients x Light X Time				
Unfertilised x Unmanipulated Control x Before	REF			
Fertilised x Procedural Control x After	-2.4	1.6	-5.8	1.0
Fertilised x Shaded Negative x After	-2.8	1.6	-6.1	0.6
Fertilised x Shaded Positive x After	-3.9	1.6	-7.2	-0.5

Random terms: $\sigma^2_{\varepsilon} = 0.0^2$; $\sigma^2_{\delta} = 0.7^2$; $\sigma^2_{\omega} = 1.0^2$; residuals = 0.1^2.

chapter 6

General Discussion

GENERAL DISCUSSION

Above all, the most noteworthy outcome lies in the significant long-term changes revealed in the shallow rocky subtidal bottoms in the southeastern Bay of Biscay, where turf-forming algae have replaced larger macrophytes, leading to structural and functional simplification of the coastal ecosystem. Similarly, severe declines and shifts have been reported globally in the distribution of canopy-forming macroalgae in the last few decades (Harley et al., 2012, Martínez et al., 2015). Considering that coastal marine areas feature amongst the most ecologically sensitive and economically important ecosystems (Kennish 2001, Halpern 2007) and that rocky assemblages are the most productive and diverse worldwide (Whal, 2009), this investigation provides a warning that proper actions at global and local are needed to ensure the correct funcioning of the coastal ecosystem and maintain the resources and services that it provides.

Gelidium corneum (Hudson) J.V. Lamouroux is a canopy forming species that used to form extensive stands and dominate exposed coastal stretches, playing a major ecological role as an autogenic ecosystem engineer (Borja et al.,2004) along the coasts of southern Europe. The first main finding of this thesis reveals an abrupt retreat for this species in 2008 and no signs of recovery have been reported since. The extreme wave energy events reported in this area in 2007 and 2008 (Borja et al., 2013) may well have caused increased mortality of *G. corneum* through stipe breakage or attachment failure. However, the fast decline could also be due to other factors given that algae are temperature-dependent organisms and ocean warming reduces their resilence, making them more vulnerable to other stressors (Whal et al., 2015). In fact, several environmental factors must be considered when inferring ecological responses to climate change (Harley and Paine 2009; Stuart et al., 2010). Extreme temperatures detected in the study area during the last few decades, higher than those found during summer at the southern limit of the biogeographical range of *G. corneum* (Alberto et al., 1999; Ould-Dedah et al., 1999), suggest that this species might have occasionally exceeded its upper thermal tolerance (Lünning, 1990). Moreover, studies carried out in the study area relate high irradiance levels and a reduction in nutrient availability to stress symptoms in *G. corneum,* such as higher bleaching, lower biomass and lower frond density (Quintano et al., 2013; 2017). Given that the negative effects of irradiance on the physiology of *G. corneum* are heightened at temperatures above 22°C (Torres et al., 1991), the increase in annual average solar radiation detected in the eastern part of the northern Iberian Peninsula since the 1980s (Sanchez-Lorenzo et al., 2013) might also explain the decline in this foundation species. In this regard, the extreme wave events probably acted synergistically on already stressed populations of *G. corneum*. In addition, well-developed communities dominated by *G. corneum* showed high stability before 2007, whereas after the loss of the canopy the assemblages became less stable over time. This can be considered as a symptom of stress since variations in the multivariate dispersion of assemblages have been identified as an indicator of stress in marine communities (Bevilacqua et al., 2012).

The significant decline detected in the biomass of the perennial canopy-forming species *G. corneum* in the depth range of 3 to 10 m has led to an increase in a heterogeneus vegetation, mainly as a result of the proliferation of morphologically simple ephemeral algae and turf-forming articulated coralline species. The niche left by *G. corneum* has been occupied to some extent by *T. baccata* but only in the deepest zones (depth range 9-10 m). Although this canopy forming species may be more tolerant to increased temperature and solar radiation, it has not developed in shallower zones (2-3m). The increasing wave energy in the area (Borja et al., 2013) may well have limited its expansion towards shallower areas, given that *T. baccata* finds its optimum in semi-exposed and sheltered coastal stretches (Díez et al., 2003; Méndez-Sandín and Fernandez, 2016). Instead, at 3 m *Codium decorticatum* and *Halopithys incurva* have partially replaced the biomass of *G. corneum.* These are two species with a warm temperate affinity which are widely distributed in more southerly regions (Rodríguez-Prieto et .al., 2013).

The thesis outcomes also suggest that all the canopy-forming species in the shallow subtidal bottoms of southeastern Bay of Biscay have shown changes in their distributions. *Laminaria ochroleuca* and *Saccorhiza polyschides* have entirely disappeared while *Treptacantha baccata* and *G. corneum* have suffered severe reductions in some locations. By contrast, simple thallus turfs composed of a combination of filamentous, polysiphonated and foliose non-corticated algae, along with articulated corallines and several crustose species, have increased throughout the study area. These changes may be reflecting the occurrence of a regime shift that involve the crossing of a tipping point to enter into a new alternative state. Most studies on marine community regime shifts have been associated with single drivers but the idea of multiple drivers and the interaction between them (Conversi et al., 2015) seems to be key in further understanding the relationship between the response (species) and control variables (environmental stressors). In this sense, the disappearance of *L. ochroleuca* and *S. polyschides* coincides with the retreat of kelps documented along the northern Iberian Peninsula (Fernández, 2011; Voerman et al., 2013). Given that both are cold-temperate species, the increase in sea surface temperature and with heat events in the study region (Costoya et al., 2015; Goikoetxea et al., 2009; Díez et al., 2012) might have been lethal for these kelps. The large macrophyte *T. baccata* is a warm-temperate species that shows a high capability for acclimation to increased temperature and irradiance (Miguel-Vijandi et al., 2010) and finds its optimal hydrodynamic conditions in semiexposed areas (Méndez-Sandín and Fernández, 2016; Díez et al., 2003). Accordingly, *T. baccata* is expected to expand northwards under ongoing climate change (Hiscock et al., 2004), as indeed has been already detected (Martínez et al., 2015). However, contrary to expectations, a decrease in *T. baccata* is observed in this study. These results might be due to the increase in the intensity of storms and wave energy recorded in the region (Borja et al., 2013), since wave action plays an important role in controlling *T. baccata* distribution (Díez et al., 2003).

The development of morphologically simple forms might have been favoured by seawater warming and increased irradiance since most of them are algae with a warm-temperate affinity (Díez et al., 2012). This result is consistent with other studies carried out in north western Spain (Lamela-Silvarrey et al., 2012; Méndez-Sandín and Fernández, 2016;) and southernmost areas (Sangil et al., 2012) that also report proliferations of ephemeral algae. There is evidence that the recruitment of filamentous turfs is facilitated by increased irradiance (Connell, 2005). The rise detected in articulated coralline algae could be due to the increase in sea surface temperature, as higher temperatures foster calcification and development in these algae (Steller et al., 2007).

Accordingly, the environmental conditions related to climate change forecast are likely to cause comparatively less disturbance and stress in turf-forming species than in large macrophytes. Turf-forming algae are characterised by small body size, high reproduction rates and rapid development, enabling them to take advantage of new environmental conditions. Once established, turf-forming algae modify the environment by incorporating sediment into their structure (Airoldi, 2003), which seems to inhibit the recruitment and consequently the recovery of canopy-forming algae (Connell, 2003; Devinny and Volse, 1978). Added to this is the fact that the canopy's ability to recover is naturally limited since in general macroalgae have limited dispersal (Kinlan and Gaines 2003).

The retreat of ecosystem engineers has been linked to the loss of primary production, one of the most important ecosystem functions (Tait and Schield, 2011; Crowe et al., 2013). In this regard, biomass measures do not quantify productivity and no other specific investigation has been conducted in this study to measure productivIty, but a loss of primary production could be infered. Some of the newly established species, such as *Corallina spp*. are known to be associated with low productivity rates because their calcium carbonate structure makes them heavy, namely, less efficient in their photosynthetic capability (Litter and Arnold, 1982; Tait and Schield, 2011). The spread of morphologically simple ephemeral algae after canopy removal could also indicate lower productivity, given that although these ephemeral algae are highly productive on a per-biomass basis, their productivity on a per-area basis is relatively low (Litter and Arnold, 1982; Tait and Schield, 2011). Moreover, foundation species are very important for marine food webs as they capture and export carbon (Dayton 1985; Krumhansl and Scheibling 2012; Smale et al., 2013) and much of their biomass is not consumed directly by herbivores. Canopy species are thus a major source of nutrition for other nearshore ecosystems (Duggins et al., 1989; Mann, 2000; Steneck et al., 2002). The loss of these structuring macrophytes that provide refuge for numerous species (Graham, 2004; Smale et al., 2013) might also affect the functioning of other neighbouring ecosystems.

The functional approach of the present research reveals that after the decline of larger macrophytes, only two or the four layers of vegetation remain: the encrusting layer and the basal one. The canopy and the epiphytic layer practically disappear. In the crustose layer, *Lithophyllum incrustans*, *Peyssonnelia* spp. and *Zanardinia typus* have increased throughout the study area, so new environmental conditions and biotic interactions might have favoured their expansion. New assemblages dominated by the increase of tuf-forming algae in the basal layer have been reported globally in temperate reefs (Mineur et al., 2014, Martínez et al., 2018). Interestingly, with these new conditions the algal fraction of the benthos continues to be predominant over the zoobenthos. The proliferation of opportunistic and annual algae species with simple morphologies and fast growth rates that comprise the basal layer are clearly more competitive and better colonisers than invertebrates. This finding reinforces the idea that the biogenic space provided by the canopy is a limiting resource for the development of invertebrates, at least at shallow depths (Bustamante et al., 2014, 2017). In fact, the loss of canopy might lead to a decline in living space for a plethora of organisms and a subsequent loss of diversity (Smale et al., 2013). Along with the decline in canopy, a marked decrease in algae and invertebrate abundance has also been recorded. Furthermore, rich associations of algae and invertebrates are only found before the decline of the biogenic habitat provided by *G. corneum*, since most associated invertebrates grow on it. In this regard, benthic organisms are known to be of great importance for all the processes that connect the bottom substrate and the water column (Griffiths et al. 2017). The loss of perennial algae may therefore result in severe changes for essential ecosystem functions such as nutrient recycling and energy transfer (Kottaand Möller 2014) among others.

Notably, the increase in algal species richness and diversity observed in the present investigation seems to run counter to the function that large macrophytes play in ecosystems. However, it should be noted that in the study area the loss of the canopy has released resources such as space and light and facilitated the settlement of a variety of opportunistic algae with simple morphologies and short life-cycles. This possible explanation is in line with the intermediate disturbance hypothesis, which predicts maximal diversity at intermediate levels of disturbance (Connell, 1978; Valdivia et al., 2005).

An assemblage-environment relationship model has been built to forecast shifts in the distribution of macroalgal assemblages of Northern Iberian Peninsula under future climate change scenarios (RCP4.5 and RCP8.5) by the end of the century. The analyses indicate that water temperature is the main factor in determining macroalgal assemblage distribution along the coasts of the Peninsula, whilst nutrient availability plays a secondary role by modulating the thermal effect on the stretches of coast with the coldest and intermediate temperature ranges. In this regard, temperature not only controls biological activity through its fundamental effect on metabolic rates, but also has a strong influence on the survival, growth, reproduction and recruitment of macroalgae, and thus on their distribution patterns (Hoek, 1982; Husa et al., 2008; Lima et al., 2007; Lüning, 1990; Müller et al., 2009; Sjøtun et al., 2015). Nutrients are considered essential for physiological performance (Harrison and Hurd, 2001). Furthermore, these two main explanatory environmental factors show a high negative correlation, which means that there is an environmental gradient from nutrient-rich cold water to nutrient-poor warm ambient water. In that gradient, five macroalgal assemblages have been identified, the dominant species in which are, from the coldest habitat to the warmest, *Saccorhiza polyschides*, *Gelidium corneum*, *Aphanocladia stichidiosa*, *Halopteris scoparia* and *Padina pavonica*.

Multiple environmental factors co-vary seasonally along latitudinal gradients and therefore interact as potential drivers of responses to future climate change scenarios (Martins et al., 2017). In this study, solar radiation, salinity and tidal range were found to be closely correlated with temperature, whereas bottom shear stress and significant wave height were closely correlated with nitrate concentration. So, based on the OCLE database and projections under future climate change RCP scenarios (4.5 and 8.5), our model predicts that Cantabrian assemblages will become more similar to those of the Mediterranean region. Therefore, the initial hypothesis of a potential future meridionalization of northern Iberian Peninsula vegetation is partially supported by our results. This meridionalization entails a shift from a three-dimensional biogenic habitat towards a two-dimensional space dominated by algal turfs that may have drastic consequences for ecosystem functioning and biodiversity. By contrast, north-western (Galicia) subtidal vegetation will remain differentiated from the rest of the communities, serving as a refuge for colder affinity species. Nevertheless, there are forecasts and evidence that suggest a weakening of the upwelling system off the NW Iberian Peninsula (Gómez-Gesteira et al., 2011; Lemos and Pires, 2004; Pérez et al., 2010). Under this scenario, north-western communities are also likely to shift towards a more Mediterranean-like phytobenthos. On that basis, we suggest that community shifts under future climate change scenarios could be greater than predicted in our model. Moreover, at global scale a tropicalisation of temperate communities is occurring, which could be the equivalent of the meridionalization foreseen in our model. According to Vergés et al., (2019), warm water affinity species are shifting their distribution toward the poles in response to warming, while cool-water species are retracting. This has been observed worldwide (Bianchi and Morri, 2003; Kumagai et al., 2018; Vergés et al., 2014, 2019; Wernberg et al., 2016). Coastal systems dominated by canopy-forming species comprise one of the most ecologically and socio-economically important habitats in temperate waters (Bennett et al., 2016; Steneck et al., 2002). Hence, the disappearance of some of these biogenic engineers or even a change in their abundance will probably have a cascade effect throughout the ecosystem (Vergés et al., 2016). Among the ecosystem services that they provide, climate regulation, sequestration of CO_2, nutrient cycling and coastline protection are of great importance taking into account the new climate change scenarios.

Finally, the *in situ* experiment carried out in the present thesis has been helpful in furthering understanding of the combined effect of irradiance and nutrient availability on the physiological state of *G. corneum,* and of its effects on the taxonomic composition and diversity of the benthic community. The results indicate that the stress responses measured in *G. corneum* at the end of the summer were significantly higher. Nevertheless, the results do not show evidence of a significant effect of irradiance for any of the variables studied. In relation to nutrients, a significant increase was observed in the length of individuals and a decrease in Shannon diversity in the experimental units which underwent fertilisation treatment. However, no significant effect of fertilisation can be definitely said to exist since water analyses during the experiment revealed that nutrient diffusion occurred from the fertilised to the unfertilised plots.

The physiological performance of macroalgae and in consequence their survival are strongly related to irradiance and temperature exposure (Rothäusler et al., 2011). Consequently, even if it is not possible to attribute variations in the variables studied to the manipulation of nutrients and irradiance, it is worth noting that there is a significant decrease in optimal quantum yield, photosynthetic efficiency and photoprotection (non-photochemical quenching) over the course of the experiment, which suggests that the *G. corneum* specimens might be exposed to environmental stress. Thus, one relevant outcome of the present study is that the photochemical stress of *G. corneum* was found to be higher at the end of the experiment, probably as a result of a prolonged exposure to high irradiance (PAR and UVR) and to high temperatures during summer, even though there was no deficit in nutrient availability.

Light is essential for primary producers because it stimulates growth and photosynthesis, but algae often receive more solar radiation than they can use, so they have several strategies for protecting against excessive light and can acclimatise photosynthetically (Häder and Figueroa, 1997; Lüder et al., 2002). In fact, our results show a significant decrease in the photosynthetic efficiency of *G. corneum*, indicating an acclimatisation of its photosynthetic apparatus to the greater radiation that occurs during summer. Too much light may also cause photoinhibition of photosynthesis, which consists of an adjustable decrease in the ETR (photosynthetic electron transport chain) (Häder and Figueroa, 1997; Häder et al., 2007; Hanelt and Figueroa, 2012). During the experiment significant differences were observed in photosynthetic production (ETR_{max}) in fertilised plots, which would indicate that *G.corneum* exploits nutrients not only for growth but also for photosynthesis. Moreover, maximum nonphotochemical quenching (NPQ_{max}), which is considered a photoprotection mechanism, was higher at the beginning of the summer. This result is consistent with the general trend for harmful effects on production and growth to increase when exposure is increased (Altamirano et al., 2003). In the same way, optimal quantum yield (F_v/F_m), which is an indicator of photoinhibition related to acclimatisation capacity (Figueroa et al., 2014), shows a significant decrease at the end of the experiment. These results could be explained by the high temperature values recorded during the experiment (up to 24.16ºC), close to the maximums detected in recent decades (Díez et al. 2012), which might have interacted with high levels of summer irradiance to result in non-optimal environmental conditions for *G. corneum* populations in the bay.

No significant changes in growth in *G. corneum* specimens, measured as frond elongation, were found between treatments, but the increase in length in the fertilised level was greater than in the unfertilised level, which supports the idea that nutrients are necessary for growth. However, this greater frond elongation was not supported by a better physiological response in the aforementioned specimens except in productivity, which was slightly higher in the fertilised specimens. Nitrogen favours the metabolism of *G. corneum* and self-protection, so this may suggest that the photoinhibition detected could be dynamic/reversible and may occur as a response to the greater irradiance typical of the summer season.

Changes that occur at individual level could be reflected in the whole community, but in the light of the results of this investigation, 4 months is probably not long enough to detect changes in diversity. Species richness, community structure and the turnover of other macroalgae seem to be associated more with seasonal changes in canopy biomass than with changes in environmental variables *per se* (Wernberg and Goldberg, 2008). In fact, seasonal changes in environmental conditions drive changes in the canopy, which in turn drive changes in species richness and assemblage structure, so habitat-formers can exert a strong temporal influence on associated biota (Wernberg and Goldberg, 2008).

In summary, the aforomentioned long-term changes in the rocky subtidal phytobenthic asemblages, in which canopy-forming species have been replaced by turf-forming algae, have led to not only structural but also functional shifts which have the potential to affect the whole marine ecosystem of the area studied. In other words, the impoverishment of vegetation due to the loss of canopy has caused a habitat simplification that has changed important benthic ecosystem properties in a fairly short period of time. In addition, there are many uncertainties regarding biotic interactions, such as the effect of herbivory, which are not studied in this thesis. Thus, further research and experimentation are needed to shed light on these points and to better understand the response of benthic assemblages to climate change. Also noteworthy is the need to increase the resilience and connectivity of the remaining canopy-dominated assemblages. To preserve them, good future management and conservation actions are needed. In this sense, management priorities should include actions to reduce anthropogenic stressors, to implement protected marine areas and to active macroalgae restoration plans through transplants of key canopy species.

chapter 7

Conclussions

CONCLUSIONS:

The main conclusions of this thesis can be summed up as follows:

- Canopy dominated assemblages off the southeastern coast of the Bay of Biscay are shifting to communities dominated by simple, turf-forming algae, coralline species and crusts, leading to a structural impoverishment of coastal ecosystems.

- The sharp decline observed locally in *Gelidium corneum* occurred abruptly in 2008 and no signs of recovery have been reported to date.

- The greater temporal variability of shallow assemblages after the decline of *G. corneum* indicates environmental stress conditions and a reduction in the resilience of the ecosystem, making it more vulnerable to future physical disturbances under ongoing climate change.

- Rich associations of alga and invertebrate taxa were found only before the decline in the biogenic habitat provided by *G. corneum.*

- Under this new scenario, turf-forming algae are more competitive than invertebrates in colonising shallow rocky benthos.

- Turf-forming species are able to take advantage of the new environmnetal conditions (i.e. increases in temperature, irradiance and storm frequencies) and settle, showing high resilience.

- The general retreat of *G. corneum* might affect the functioning of ecosystems and impair the ecosystem services that this canopy species provides.

- The loss of biomass in subtidal phytobenthic assemblages may have led to a decline in one of the most important ecosystem functions: primary production.

- The increase in algal species richness and diversity observed is due to the proliferation of a variety of simple, oportunistic species. This is understood as a symptom of stress.

- Based on the assemblage-environment relationship model developed in this thesis, projections under future climate change scenarios predict that Cantabrian assemblages will become more similar to those of the Mediterranean region whereas north-western subtidal vegetation (Galicia) will remain differentiated from the rest.

- Even if it is not possible to draw any conclusion regarding combinations of irradiance and nutrients in the plots in the fiel manipulative experiment, significant decreases in optimal quantum yield, photosynthetic efficiency and photoprotection were detected at the end of the summer, which shows that *G. corneum* specimens were exposed to environmental stress.

chapter 8

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Annexes

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Annex I: Other publications related to this thesis

Annex II: Photographs

Annex I: Other publications related to this thesis

1 **Muguerza N., Díez I., Santolaria A., Gorostiaga J.M.** (2012) Euskal Herriko Kostaldean azkeneko hogei urteetan (1991-2009) Komunitate Fitobentikoetan izan diren egiturazko aldaketak: klima-aldaketak izan al du eraginik? Ekaia, 25: 73-88.

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Laburpena: Azkeneko hiru hamarkadetan, ur-azaleko tenperaturak gora egin du gure kostaldean, bereziki udaberri eta uda sasoian. Halaxe dago jasota. Fitobenkton komunitateetan aldaketa nabarmenak izan dira, bai dibertsitateari dagokionez eta bai kopuruari dagokionez ere. Kontu hauek ikusmiran izanik, 1991. urteko udan lagindu ziren lekuak berriz ikusi genituen 2009. urtean. Egiturazko espezieen banaketan ere aldaketa esanguratsua gertatu da, baina joera hori ez da berdina izan kostalde osoan. Ikerketa-emaitzek erakutsi dute aldaketak nabarmenak izan direla. Alga koralinazeoak eta hegoaldearekiko afinitatea duten morfologia sinpleko espezieak orohar ugaritu egin dira, eta kanpoko espezieen ugaritasuna ere emendatu egin da. Gainera, nabarmena da espezie gehiago daudela eta dibertsitatea handitu egin dela azterketa-eremu osoan. Ekoizle primarioetan eta habitat-sortzaileetan antzeman diren aldaketek eragin handia izan dezakete gure kostaldeko ekosisteman. Hain zuzen ere, antzeman diren aldaketa horien atzean arrazoi asko egon daitezke, besteak beste klima-aldaketa. Nahiz eta elikagaien kontzentrazioan gertatu diren aldaketen edota korronteen eta olatuen inguruko datuak oso mugatuak izan, baliteke horiek ere antzemandako aldaketekin lotuta egotea.

Abstract: Increased trend in sea surface temperature during the last three decades has been documented for the Basque coast (Northern Spain), particularly for spring and summer seasons. Evidence of changes in key structural phytobenthic communities detected at local scale let us to evaluate changes in species abundance and diversity along the Basque coast. For that purpose, several locations studied in summer 1991 were revisited in 2009. Strong changes in the distribution of the main canopy species were detected, although a trend for the whole coast could not be established. Results also showed widespread increases of coralline algae, increases of morphologically simple forms of meridional affinity, introduction and expansion of non-indigenous species. On the other hand, species richness and diversity significantly increased at all studied locations. These changes in major primary producers and habitat formers could signifi-

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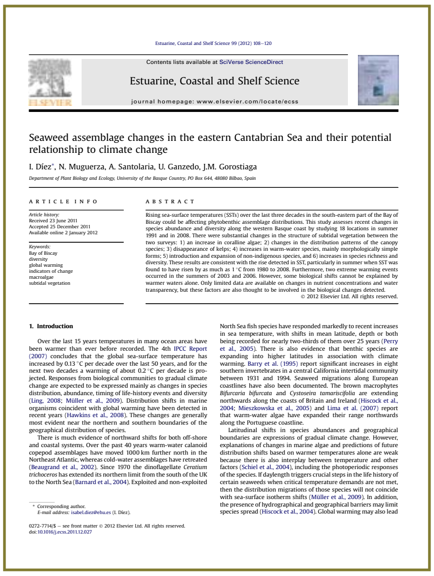
2 **Díez I., Muguerza N., Santolaria A., Ganzedo U., Gorostiaga J.M.** (2012) Seaweed assemblage changes in the eastern Cantabrian Sea and their potential relationship to climate change. Estuarine, Coastal and Shelf Science 99: 108-120.



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Seaweed assemblage changes in the eastern Cantabrian Sea and their potential relationship to climate change

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A B S T R A C T

Rising sea-surface temperatures (SSTs) over the last three decades in the south-eastern part of the Bay of Biscay could be affecting phytobenthic assemblage distributions. This study assesses recent changes in species abundance and diversity along the western Basque coast by studying 18 locations in summer 1991 and in 2008. There were substantial changes in the structure of subtidal vegetation between the two surveys: 1) an increase in coralline algae; 2) changes in the distribution patterns of the canopy species; 3) disappearance of kelps; 4) increases in warm-water species, mainly morphologically simple forms; 5) introduction and expansion of non-indigenous species, and 6) increases in species richness and diversity. These results are consistent with the rise detected in SST, particularly in summer when SST was found to have risen by as much as 1 °C from 1980 to 2008. Furthermore, two extreme warming events occurred in the summers of 2003 and 2006. However, some biological shifts cannot be explained by warmer waters alone. Only limited data are available on changes in nutrient concentrations and water transparency, but these factors are also thought to be involved in the biological changes detected.

1. Introduction

Over the last 15 years temperatures in many ocean areas have been warmer than ever before recorded. The 4th IPCC Report (2007) concludes that the global sea-surface temperature has increased by 0.13 °C per decade over the last 50 years, and for the next two decades a warming of about 0.2 °C per decade is projected. Responses from biological communities to gradual climate change are expected to be expressed mainly as changes in species distribution, abundance, timing of life-history events and diversity (Ling, 2008; Müller et al., 2009). Distribution shifts in marine organisms coincident with global warming have been detected in recent years (Hawkins et al., 2008). These changes are generally most evident near the northern and southern boundaries of the geographical distribution of species.

There is much evidence of northward shifts for both off-shore and coastal systems. Over the past 40 years warm-water calanoid copepod assemblages have moved 1000 km further north in the Northeast Atlantic, whereas cold-water assemblages have retreated (Beaugrand et al., 2002). Since 1970 the dinoflagellate *Ceratium trichoceros* has extended its northern limit from the south of the UK to the North Sea (Barnard et al., 2004). Exploited and non-exploited North Sea fish species have responded markedly to recent increases in sea temperature, with shifts in mean latitude, depth or both being recorded for nearly two-thirds of them over 25 years (Perry et al., 2005). There is also evidence that benthic species are expanding into higher latitudes in association with climate warming. Barry et al. (1995) report significant increases in eight southern invertebrates in a central California intertidal community between 1931 and 1994. Seaweed migrations along European coastlines have also been documented. The brown macrophytes *Bifurcaria bifurcata* and *Cystoseira tamariscifolia* are extending northwards along the coasts of Britain and Ireland (Hiscock et al., 2004; Mieszkowska et al., 2005) and Lima et al. (2007) report that warm-water algae have expanded their range northwards along the Portuguese coastline.

Latitudinal shifts in species abundances and geographical boundaries are expressions of gradual climate change. However, explanations of changes in marine algae and predictions of future distribution shifts based on warmer temperatures alone are weak because there is also interplay between temperature and other factors (Schiel et al., 2004), including the photoperiodic responses of the species. If daylength triggers crucial steps in the life history of certain seaweeds when critical temperature demands are not met, then the distribution migrations of those species will not coincide with sea-surface isotherm shifts (Müller et al., 2009). In addition, the presence of hydrographical and geographical barriers may limit species spread (Hiscock et al., 2004). Global warming may also lead

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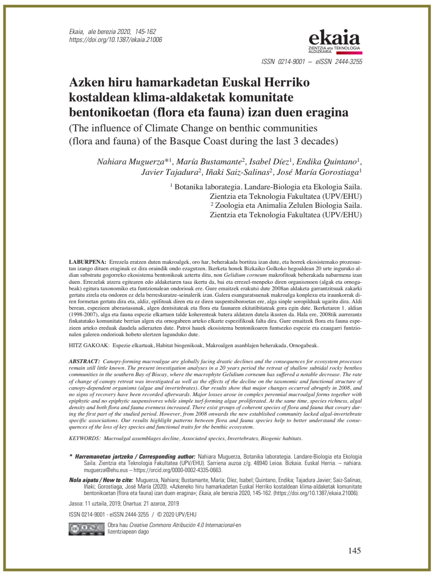
3 **Muguerza N., Bustamante M., Díez I., Quintano E., Tajadura J., Saiz-Salinas I., Gorostiaga J.M.** (2020) Azken hiru hamarkadetan Euskal Herriko kostaldean klima-aldaketak komunitate bentonikoetan (flora eta fauna) izan duen eragina. Ekaia https://doi.org/10.1387/ekaia.21006.



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Azken hiru hamarkadetan Euskal Herriko kostaldean klima-aldaketak komunitate bentonikoetan (flora eta fauna) izan duen eragina

(The influence of Climate Change on benthic communities
(flora and fauna) of the Basque Coast during the last 3 decades)

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LABURPENA: Errezela eratzen duten makroalgek, oro har, beherakada bortitza izan dute, eta horrek ekosistemako prozesuetan izango dituen eraginak ez dira oraindik ondo ezagutzen. Ikerketa honek Bizkaiko Golkoko hegoaldean 20 urte inguruko aldian substratu gogorreko ekosistema bentonikoak aztertu ditu, non *Gelidium corneum* makrofitoak beherakada nabarmena izan duen. Errezelak atzera egitearen edo aldaketaren tasa ikertu da, bai eta errezel-menpeko diren organismoen (algak eta ornogabeak) egitura taxonomiko eta funtzionalean ondorioak ere. Gure emaitzek erakutsi dute 2008an aldaketa garrantzitsuak zakarki gertatu zirela eta ondoren ez dela berreskuratze-seinalerik izan. Galera esanguratsuenak makroalga konplexu eta iraunkorrak diren formetan gertatu dira eta, aldiz, epifitoak diren eta ez diren suspentsiboroetan ere, alga sinple soropilduak ugaritu dira. Aldi berean, espezieen aberastasunak, algen dentsitateak eta flora eta faunaren ekitatibitateak gora egin dute. Ikerketaren 1. aldian (1998-2007), alga eta fauna espezie elkartuen talde koherenteak batera aldatzen dutela ikusten da. Hala ere, 2008tik aurrerantz finkatutako komunitate berrian algen eta ornogabeen arteko elkarte espezifikoak falta dira. Gure emaitzek flora eta fauna espezieen arteko ereduak daudela adierazten dute. Patroi hauek ekosistema bentonikoaren funtsezko espezie eta ezaugarri funtzionalen galeren ondorioak hobeto ulertzen lagunduko dute.

HITZ GAKOAK: Espezie elkartuak, Habitat biogenikoak, Makroalgen asanblajen beherakada, Ornogabeak.

ABSTRACT: *Canopy-forming macroalgae are globally facing drastic declines and the consequences for ecosystem processes remain still little known. The present investigation analyses in a 20 years period the retreat of shallow subtidal rocky benthos communities in the southern Bay of Biscay, where the macrophyte Gelidium corneum has suffered a notable decrease. The rate of change of canopy retreat was investigated as well as the effects of the decline on the taxonomic and functional structure of canopy-dependent organisms (algae and invertebrates). Our results show that major changes occurred abruptly in 2008, and no signs of recovery have been recorded afterwards. Major losses arose in complex perennial macroalgal forms together with epiphytic and no epiphytic suspensivores while simple turf-forming algae proliferated. At the same time, species richness, algal density and both flora and fauna evenness increased. There exist groups of coherent species of flora and fauna that covary during the first part of the studied period. However, from 2008 onwards the new established community lacked algal-invertebrate specific associations. Our results highlight patterns between flora and fauna species help to better understand the consequences of the loss of key species and functional traits for the benthic ecosystem.*

KEYWORDS: Macroalgal assemblages decline, Associated species, Invertebrates, Biogenic habitats.

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1

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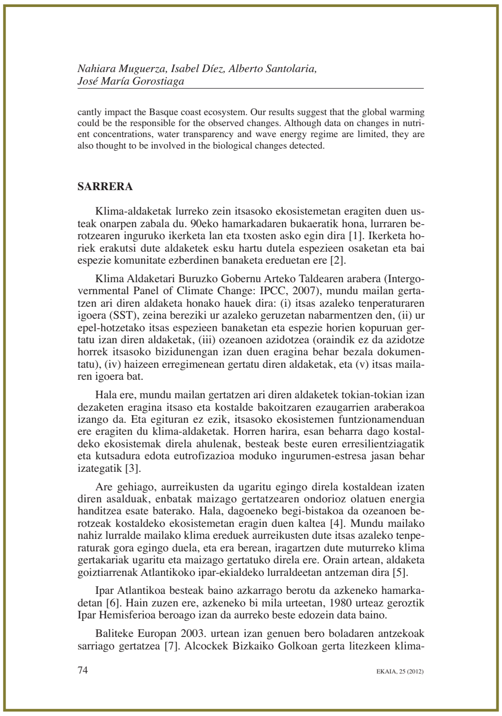
Laburpena: Azkeneko hiru hamarkadetan, ur-azaleko tenperaturak gora egin du gure kostaldean, bereziki udaberri eta uda sasoian. Halaxe dago jasota. Fitobenkton komunitateetan aldaketa nabarmenak izan dira, bai dibertsitateari dagokionez eta bai kopuruari dagokionez ere. Kontu hauek ikusmiran izanik, 1991. urteko udan lagindu ziren lekuak berriz ikusi genituen 2009. urtean. Egiturazko espezieen banaketan ere aldaketa esanguratsua gertatu da, baina joera hori ez da berdina izan kostalde osoan. Ikerketa-emaitzek erakutsi dute aldaketak nabarmenak izan direla. Alga koralinazeoak eta hegoaldearekiko afinitatea duten morfologia sinpleko espezieak orohar ugaritu egin dira, eta kanpoko espezieen ugaritasuna ere emendatu egin da. Gainera, nabarmena da espezie gehiago daudela eta dibertsitatea handitu egin dela azterketa-eremu osoan. Ekoizle primarioetan eta habitat-sortzaileetan antzeman diren aldaketek eragin handia izan dezakete gure kostaldeko ekosisteman. Hain zuzen ere, antzeman diren aldaketa horien atzean arrazoi asko egon daitezke, besteak beste klima-aldaketa. Nahiz eta elikagaien kontzentrazioan gertatu diren aldaketen edota korronteen eta olatuen inguruko datuak; oso mugatuak izan, baliteke horiek ere antzemandako aldaketekin lotuta egotea.

Abstract: Increased trend in sea surface temperature during the last three decades has been documented for the Basque coast (Northern Spain), particularly for spring and summer seasons. Evidence of changes in key structural phytobenthic communities detected at local scale let us to evaluate changes in species abundance and diversity along the Basque coast. For that purpose, several locations studied in summer 1991 were revisited in 2009. Strong changes in the distribution of the main canopy species were detected, although a trend for the whole coast could not be established. Results also showed widespread increases of coralline algae, increases of morphologically simple forms of meridional affinity, introduction and expansion of non-indigenous species. On the other hand, species richness and diversity significantly increased at all studied locations. These changes in major primary producers and habitat formers could signifi-



cantly impact the Basque coast ecosystem. Our results suggest that the global warming could be the responsible for the observed changes. Although data on changes in nutrient concentrations, water transparency and wave energy regime are limited, they are also thought to be involved in the biological changes detected.

SARRERA

Klima-aldaketak lurreko zein itsasoko ekosistemetan eragiten duen usteak onarpen zabala du. 90eko hamarkadaren bukaeratik hona, lurraren berotzearen inguruko ikerketa lan eta txosten asko egin dira [1]. Ikerketa horiek erakutsi dute aldaketek esku hartu dutela espezieen osaketan eta bai espezie komunitate ezberdinen banaketa ereduetan ere [2].

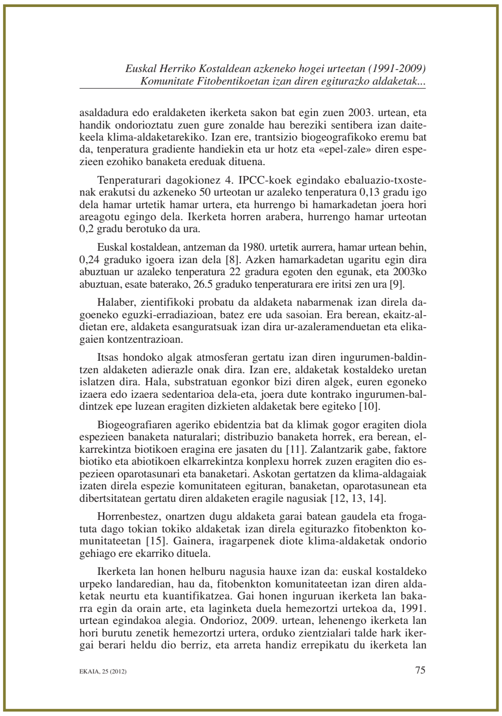
Klima Aldaketari Buruzko Gobernu Arteko Taldearen arabera (Intergovernmental Panel of Climate Change: IPCC, 2007), mundu mailan gertatzen ari diren aldaketa honako hauek dira: (i) itsas azaleko tenperaturaren igoera (SST), zeina bereziki ur azaleko geruzetan nabarmentzen den, (ii) ur epel-hotzetako itsas espezieen banaketan eta espezie horien kopuruan gertatu izan diren aldaketak, (iii) ozeanoen azidotzea (oraindik ez da azidotze horrek itsasoko bizidunengan izan duen eragina behar bezala dokumentatu), (iv) haizeen erregimenean gertatu diren aldaketak, eta (v) itsas mailaren igoera bat.

Hala ere, mundu mailan gertatzen ari diren aldaketek tokian-tokian izan dezaketen eragina itsaso eta kostalde bakoitzaren ezaugarrien araberakoa izango da. Eta egituran ez ezik, itsasoko ekosistemen funtzionamenduan ere eragiten du klima-aldaketak. Horren harira, esan beharra dago kostaldeko ekosistemak direla ahulenak, besteak beste euren erresilientziagatik eta kutsadura edota eutrofizazioa moduko ingurumen-estresa jasan behar izategatik [3].

Are gehiago, aurreikusten da ugaritu egingo direla kostaldean izaten diren asalduak, enbatak maizago gertatzearen ondorioz olatuen energia handitzea esate baterako. Hala, dagoeneko begi-bistakoa da ozeanoen berotzeak kostaldeko ekosistemetan eragin duen kaltea [4]. Mundu mailako nahiz lurralde mailako klima ereduek aurreikusten dute itsas azaleko tenperaturak gora egingo duela, eta era berean, iragartzen dute muturreko klima gertakariak ugaritu eta maizago gertatuko direla ere. Orain artean, aldaketa goiztiarrenak Atlantikoko ipar-ekialdeko lurraldeetan antzeman dira [5].

Ipar Atlantikoa besteak baino azkarrago berotu da azkeneko hamarkadetan [6]. Hain zuzen ere, azkeneko bi mila urteetan, 1980 urteaz geroztik Ipar Hemisferioa beroago izan da aurreko beste edozein data baino.

Baliteke Europan 2003. urtean izan genuen bero boladaren antzekoak sarriago gertatzea [7]. Alcockek Bizkaiko Golkoan gerta litezkeen klima-



asaldadura edo eraldaketen ikerketa sakon bat egin zuen 2003. urtean, eta handik ondorioztatu zuen gure zonalde hau bereziki sentibera izan daitekeela klima-aldaketarekiko. Izan ere, trantsizio biogeografikoko eremu bat da, tenperatura gradiente handiekin eta ur hotz eta «epel-zale» diren espezieen ezohiko banaketa ereduak dituena.

Tenperaturari dagokionez 4. IPCC-koek egindako ebaluazio-txostenak erakutsi du azkeneko 50 urteotan ur azaleko tenperatura 0,13 gradu igo dela hamar urtetik hamar urtera, eta hurrengo bi hamarkadetan joera hori areagotu egingo dela. Ikerketa horren arabera, hurrengo hamar urteotan 0,2 gradu berotuko da ura.

Euskal kostaldean, antzeman da 1980. urtetik aurrera, hamar urtean behin, 0,24 graduko igoera izan dela [8]. Azken hamarkadetan ugaritu egin dira abuztuan ur azaleko tenperatura 22 gradura egoten den egunak, eta 2003ko abuztuan, esate baterako, 26.5 graduko tenperaturara ere iritsi zen ura [9].

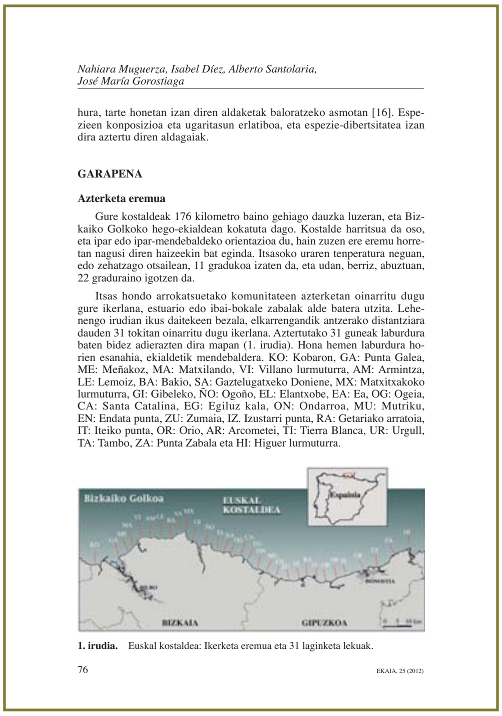
Halaber, zientifikoki probatu da aldaketa nabarmenak izan direla dagoeneko eguzki-erradiazioan, batez ere uda sasoian. Era berean, ekaitz-aldietan ere, aldaketa esanguratsuak izan dira ur-azaleramenduetan eta elikagaien kontzentrazioan.

Itsas hondoko algak atmosferan gertatu izan diren ingurumen-baldintzen aldaketen adierazle onak dira. Izan ere, aldaketak kostaldeko uretan islatzen dira. Hala, substratuan egonkor bizi diren algek, euren egoneko izaera edo izaera sedentarioa dela-eta, joera dute kontrako ingurumen-baldintzek epe luzean eragiten dizkieten aldaketak bere egiteko [10].

Biogeografiaren ageriko ebidentzia bat da klimak gogor eragiten diola espezieen banaketa naturalari; distribuzio banaketa horrek, era berean, elkarrekintza biotikoen eragina ere jasaten du [11]. Zalantzarik gabe, faktore biotiko eta abiotikoen elkarrekintza konplexu horrek zuzen eragiten dio espezieen oparotasunari eta banaketari. Askotan gertatzen da klima-aldagaiak izaten direla espezie komunitateen egituran, banaketan, oparotasunean eta dibertsitatean gertatu diren aldaketen eragile nagusiak [12, 13, 14].

Horrenbestez, onartzen dugu aldaketa garai batean gaudela eta frogatuta dago tokian tokiko aldaketak izan direla egiturazko fitobenkton komunitateetan [15]. Gainera, iragarpenek diote klima-aldaketak ondorio gehiago ere ekarriko dituela.

Ikerketa lan honen helburu nagusia hauxe izan da: euskal kostaldeko urpeko landaredian, hau da, fitobenkton komunitateetan izan diren aldaketak neurtu eta kuantifikatzea. Gai honen inguruan ikerketa lan bakarra egin da orain arte, eta laginketa duela hemezortzi urtekoa da, 1991. urtean egindakoa alegia. Ondorioz, 2009. urtean, lehenengo ikerketa lan hori burutu zenetik hemezortzi urtera, orduko zientzialari talde hark ikergai berari heldu dio berriz, eta arreta handiz errepikatu du ikerketa lan



hura, tarte honetan izan diren aldaketak baloratzeko asmotan [16]. Espezieen konposizioa eta ugaritasun erlatiboa, eta espezie-dibertsitatea izan dira aztertu diren aldagaiak.

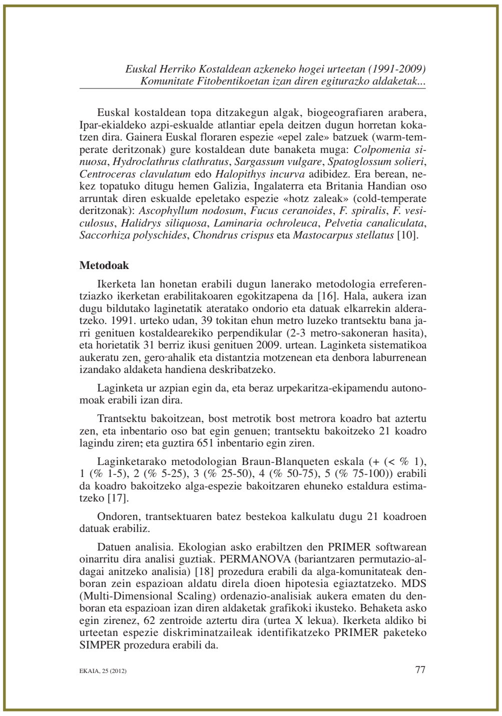
GARAPENA

Azterketa eremua

Gure kostaldeak 176 kilometro baino gehiago dauzka luzeran, eta Bizkaiko Golkoko hego-ekialdean kokatuta dago. Kostalde harritsua da oso, eta ipar edo ipar-mendebaldeko orientazioa du, hain zuzen ere eremu horretan nagusi diren haizeekin bat eginda. Itsasoko uraren tenperatura neguan, edo zehatzago otsailean, 11 gradukoa izaten da, eta udan, berriz, abuztuan, 22 graduraino igotzen da.

Itsas hondo arrokatsuetako komunitateen azterketan oinarritu dugu gure ikerlana, estuario edo ibai-bokale zabalak alde batera utzita. Lehenengo irudian ikus daitekeen bezala, elkarrengandik antzerako distantziara dauden 31 tokitan oinarritu dugu ikerlana. Aztertutako 31 guneak laburdura baten bidez adierazten dira mapan (1. irudia). Hona hemen laburdura horien esanahia, ekialdetik mendebaldera. KO: Kobaron, GA: Punta Galea, ME: Meñakoz, MA: Matxilando, VI: Villano lurmuturra, AM: Armintza, LE: Lemoiz, BA: Bakio, SA: Gaztelugatxeko Doniene, MX: Matxitxakoko lurmuturra, GI: Gibeleko, ÑO: Ogoño, EL: Elantxobe, EA: Ea, OG: Ogeia, CA: Santa Catalina, EG: Egiluz kala, ON: Ondarroa, MU: Mutriku, EN: Endata punta, ZU: Zumaia, IZ. Izustarri punta, RA: Getariako arratoia, IT: Iteiko punta, OR: Orio, AR: Arcometei, TI: Tierra Blanca, UR: Urgull, TA: Tambo, ZA: Punta Zabala eta HI: Higuer lurmuturra.

1. irudia. Euskal kostaldea: Ikerketa eremua eta 31 laginketa lekuak.



Euskal kostaldean topa ditzakegun algak, biogeografiaren arabera, Ipar-ekialdeko azpi-eskualde atlantiar epela deitzen dugun horretan kokatzen dira. Gainera Euskal floraren espezie «epel zale» batzuek (warm-temperate deritzonak) gure kostaldean dute banaketa muga: *Colpomenia sinuosa*, *Hydroclathrus clathratus*, *Sargassum vulgare*, *Spatoglossum solieri*, *Centroceras clavulatum* edo *Halopithys incurva* adibidez. Era berean, nekez topatuko ditugu hemen Galizia, Ingalaterra eta Britania Handian oso arruntak diren eskualde epeletako espezie «hotz zaleak» (cold-temperate deritzonak): *Ascophyllum nodosum*, *Fucus ceranoides*, *F. spiralis*, *F. vesiculosus*, *Halidrys siliquosa*, *Laminaria ochroleuca*, *Pelvetia canaliculata*, *Saccorhiza polyschides*, *Chondrus crispus* eta *Mastocarpus stellatus* [10].

Metodoak

Ikerketa lan honetan erabili dugun lanerako metodologia erreferentziazko ikerketan erabilitakoaren egokitzapena da [16]. Hala, aukera izan dugu bildutako laginetatik ateratako ondorio eta datuak elkarrekin alderatzeko. 1991. urteko udan, 39 tokitan ehun metro luzeko trantsektu bana jarri genituen kostaldearekiko perpendikular (2-3 metro-sakoneran hasita), eta horietatik 31 berriz ikusi genituen 2009. urtean. Laginketa sistematikoa aukeratu zen, gero-ahalik eta distantzia motzenean eta denbora laburrenean izandako aldaketa handiena deskribatzeko.

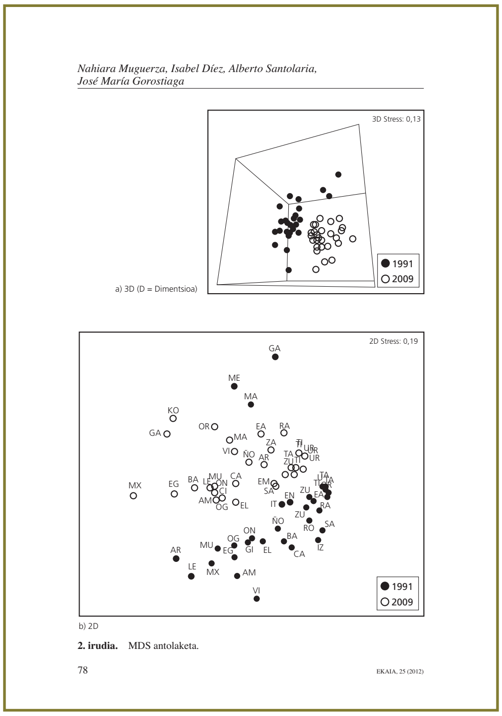
Laginketa ur azpian egin da, eta beraz urpekaritza-ekipamendu autonomoak erabili izan dira.

Trantsektu bakoitzean, bost metrotik bost metrora koadro bat aztertu zen, eta inbentario oso bat egin genuen; trantsektu bakoitzeko 21 koadro lagindu ziren; eta guztira 651 inbentario egin ziren.

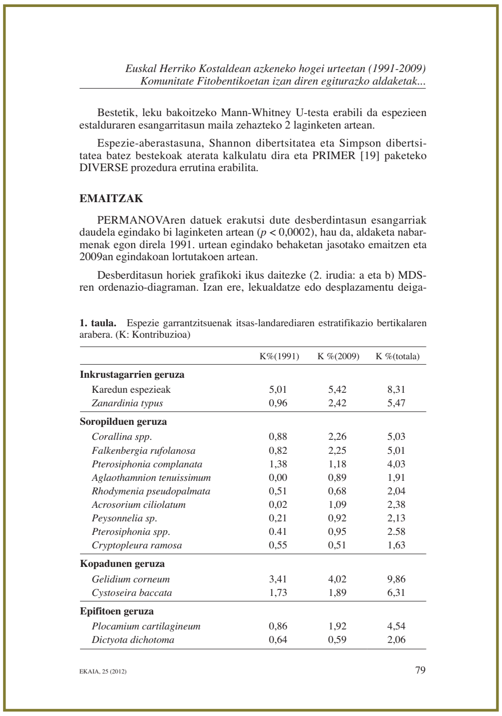
Laginketarako metodologian Braun-Blanqueten eskala (+ (< % 1), 1 (% 1-5), 2 (% 5-25), 3 (% 25-50), 4 (% 50-75), 5 (% 75-100)) erabili da koadro bakoitzeko alga-espezie bakoitzaren ehuneko estaldura estimatzeko [17].

Ondoren, trantsektuaren batez bestekoa kalkulatu dugu 21 koadroen datuak erabiliz.

Datuen analisia. Ekologian asko erabiltzen den PRIMER softwarean oinarritu dira analisi guztiak. PERMANOVA (bariantzaren permutazio-aldagai anitzeko analisia) [18] prozedura erabili da alga-komunitateak denboran zein espazioan aldatu direla dioen hipotesia egiaztatzeko. MDS (Multi-Dimensional Scaling) ordenazio-analisiak aukera ematen du denboran eta espazioan izan diren aldaketak grafikoki ikusteko. Behaketa asko egin zirenez, 62 zentroide aztertu dira (urtea X lekua). Ikerketa aldiko bi urteetan espezie diskriminatzaileak identifikatzeko PRIMER paketeko SIMPER prozedura erabili da.



2. irudia. MDS antolaketa.



Bestetik, leku bakoitzeko Mann-Whitney U-testa erabili da espezieen estalduraren esangarritasun maila zehazteko 2 laginketen artean.

Espezie-aberastasuna, Shannon dibertsitatea eta Simpson dibertsitatea batez bestekoak aterata kalkulatu dira eta PRIMER [19] paketeko DIVERSE prozedura errutina erabilita.

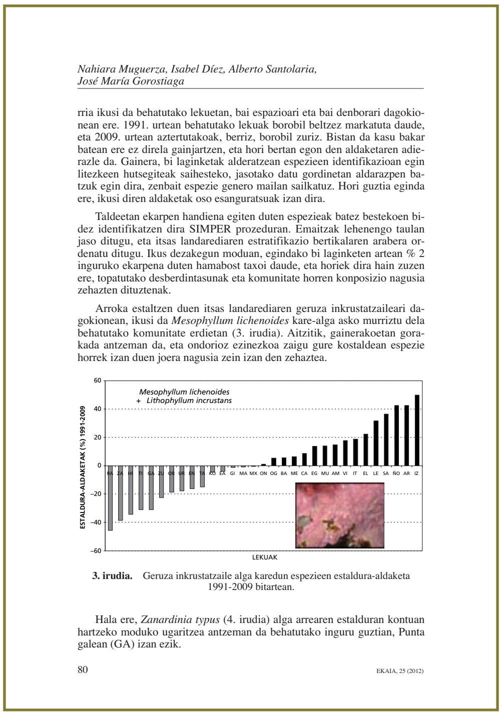
EMAITZAK

PERMANOVAren datuek erakutsi dute desberdintasun esangarriak daudela egindako bi laginketen artean ($p < 0{,}0002$), hau da, aldaketa nabarmenak egon direla 1991. urtean egindako behaketan jasotako emaitzen eta 2009an egindakoan lortutakoen artean.

Desberditasun horiek grafikoki ikus daitezke (2. irudia: a eta b) MDS-ren ordenazio-diagraman. Izan ere, lekualdatze edo desplazamentu deiga-

1. taula. Espezie garrantzitsuenak itsas-landarediaren estratifikazio bertikalaren arabera. (K: Kontribuzioa)

	K%(1991)	K %(2009)	K %(totala)
Inkrustagarrien geruza			
Karedun espezieak	5,01	5,42	8,31
Zanardinia typus	0,96	2,42	5,47
Soropilduen geruza			
Corallina spp.	0,88	2,26	5,03
Falkenbergia rufolanosa	0,82	2,25	5,01
Pterosiphonia complanata	1,38	1,18	4,03
Aglaothamnion tenuissimum	0,00	0,89	1,91
Rhodymenia pseudopalmata	0,51	0,68	2,04
Acrosorium ciliolatum	0,02	1,09	2,38
Peysonnelia sp.	0,21	0,92	2,13
Pterosiphonia spp.	0.41	0,95	2.58
Cryptopleura ramosa	0,55	0,51	1,63
Kopadunen geruza			
Gelidium corneum	3,41	4,02	9,86
Cystoseira baccata	1,73	1,89	6,31
Epifitoen geruza			
Plocamium cartilagineum	0,86	1,92	4,54
Dictyota dichotoma	0,64	0,59	2,06



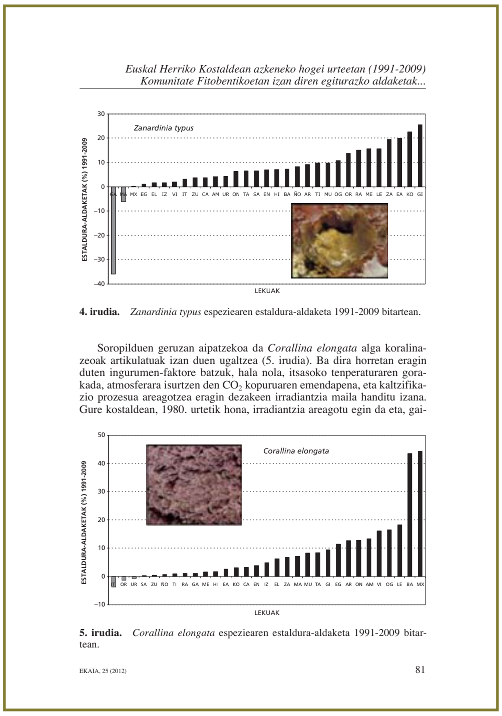
rria ikusi da behatutako lekuetan, bai espazioari eta bai denborari dagokionean ere. 1991. urtean behatutako lekuak borobil beltzez markatuta daude, eta 2009. urtean aztertutakoak, berriz, borobil zuriz. Bistan da kasu bakar batean ere ez direla gainjartzen, eta hori bertan egon den aldaketaren adierazle da. Gainera, bi laginketak alderatzean espezieen identifikazioan egin litezkeen hutsegiteak saihesteko, jasotako datu gordinetan aldarazpen batzuk egin dira, zenbait espezie genero mailan sailkatuz. Hori guztia eginda ere, ikusi diren aldaketak oso esanguratsuak izan dira.

Taldeetan ekarpen handiena egiten duten espezieak batez bestekoen bidez identifikatzen dira SIMPER prozeduran. Emaitzak lehenengo taulan jaso ditugu, eta itsas landarediaren estratifikazio bertikalaren arabera ordenatu ditugu. Ikus dezakegun moduan, egindako bi laginketen artean % 2 inguruko ekarpena duten hamabost taxoi daude, eta horiek dira hain zuzen ere, topatutako desberdintasunak eta komunitate horren konposizio nagusia zehazten dituztenak.

Arroka estaltzen duen itsas landarediaren geruza inkrustatzaileari dagokionean, ikusi da *Mesophyllum lichenoides* kare-alga asko murriztu dela behatutako komunitate erdietan (3. irudia). Aitzitik, gainerakoetan gorakada antzeman da, eta ondorioz ezinezkoa zaigu gure kostaldean espezie horrek izan duen joera nagusia zein izan den zehaztea.

3. irudia. Geruza inkrustatzaile alga karedun espezieen estaldura-aldaketa 1991-2009 bitartean.

Hala ere, *Zanardinia typus* (4. irudia) alga arrearen estalduran kontuan hartzeko moduko ugaritzea antzeman da behatutako inguru guztian, Punta galean (GA) izan ezik.



4. irudia. *Zanardinia typus* espeziearen estaldura-aldaketa 1991-2009 bitartean.

Soropilduen geruzan aipatzekoa da *Corallina elongata* alga koralinazeoak artikulatuak izan duen ugaltzea (5. irudia). Ba dira horretan eragin duten ingurumen-faktore batzuk, hala nola, itsasoko tenperaturaren gorakada, atmosferara isurtzen den CO_2 kopuruaren emendapena, eta kaltzifikazio prozesua areagotzea eragin dezakeen irradiantzia maila handitu izana. Gure kostaldean, 1980. urtetik hona, irradiantzia areagotu egin da eta, gai-

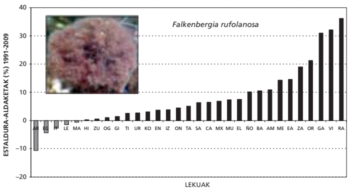
5. irudia. *Corallina elongata* espeziearen estaldura-aldaketa 1991-2009 bitartean.

nera, zenbait koralinazeotan estres zantzuak nabaritu dira, esate baterako zuritzeak edo bleachingak, erradiazio handiekin edota ur bareekin lotura izan dezaketenak. Baliteke gure kostaldean antzemandako tenperatura-igoera horrek kaltzifikazio-prozesua azkartzea. Izan ere, azkeneko hamarkadetan gero eta udako egun gehiagotan gainditu du itsasoko uraren tenperaturak 22-23 graduko muga Donostiako Aquariumeko datuen arabera.

Alga soropilduen gainean hazten diren alga zeramiazeoak asko ugaldu dira, eta horien artean bi dira nabarmendu diren espezieak: *Aglaothamnion tenuissimum* eta *Gayliella flaccida*.

Ziurrenik berotze efektu horrek erraztu du kanpoko espezieak gure kostaldean horren erraz ezarri izana.

Esate baterako, uste da *Falkenbergia rufolanosa* (6. irudia) Australiatik zetozen itsasontzietan sartu zela Ipar Hemisferioan. Atlantikoko uretan 1925. urtean topatu zen lehenengoz alga hori, hain zuzen ere Miarritzeko kostaldean. Hala, tenperaturaren igoera eta landare horrek inguru berrietara egokitzeko duen erraztasuna izan dira bi faktoreak, ziurrenik, behatutako leku guztietan alga horrek izan duen ugaltze azkarra azaltzen dutenak.



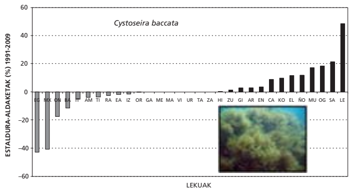
6. irudia. *Falkenbergia rufolanosa* espeziearen estaldura-aldaketa 1991-2009 bitartean.

Era berean, ustez kanpotik ekarritakoa den beste espezie bat ere nabarmen ugaritu da behatutako puntu askotan (EA, GI, EL, ON, LE, BA, EG eta MX). Oraingoz, ez dugu lortu espezie mailan identifikatzea, baina nolanahi ere, garbi dago *Herposiphonia* generoaren baitakoa dela.

Ugaritu diren beste alga soropildu edo basal batzuk *Pterosiphonia* generokoak dira, bereziki *Pterosiphonia ardreana* delakoa. Aldiz, *Pterosiphonia complanatak*, gure kostaldean ugarienetakoak diren alga basal bat denak, aldaketak jasan ditu, bai, baina ezin esan daiteke behatutako leku guztietan modu berean aldatu denik.

Acrosorium ciliolatum alga basal gorri bat da, eta nabarmen ugaritu da ikerketak iraun duen denboran.

Kopadunen geruzan, hau da ikertutako guneetako espezie egituratzaileen barruan, aipamen berezia merezi du *Cystoseira baccata* espezie arreak. Espezie honi kalte handia egiten dio kutsadurak, baina aldiz, ondo jasaten edo toleratzen du sedimentazioa, eta hain zuzen ere, horixe da bai gure kostaldean itsas hondo arrokatsu eta garbietan, bai olatuek gogor jotzen duten inguruetan nagusi den makrofitoa. Hala ere, ikertutako bi aldiak alderatuz gero, ikustekoa da kokapenari dagokionean zer nolako aldaketak izan dituen. Ugariago dago leku batzuetan, eta hori ulertzeko bi azalpen nagusi egon daitezke: batetik, aztertutako zenbait tokitan ur garbiagoa egon liteke orain, eta bestetik, baliteke *Cystoseira baccata* ugaritu den lekuetan (CA, KO, EL, ÑO, MU, OG, SA eta LE) uraren tenperatura nahiz irradiantzia igo izana. Bestalde, baliteke espezie hori gutxitu den lekuetan (EG, MX, ON eta BA) denborale edo enbata gogorrek eragin duten higaduragatik gertatu izana (7. irudia).

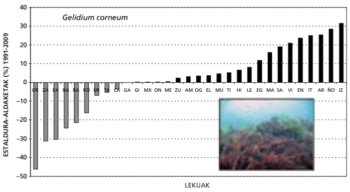


7. irudia. *Cystoseira baccata* espeziearen estaldura-aldaketa 1991-2009 bitartean.

Gainera, ikerketa hau egin den aldi berean laborategian egin diren saioek erakutsi dute espezie hau, *C.baccata* alegia, ondo egokitu dela tenperaturaren eta irradiantziaren igoerara [20].

Gelidium corneum oso espezie garrantzitsua da. Espezie egituratzaile hau nagusi da olatuek gogor edo oso gogor jotzen duten itsas hondo arrokatsuetan, eta belardi zabalak osatzen ditu gure kostaldean.

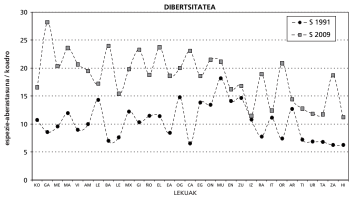
Emaitzek ez dute kostalde osora orokortu daitekeen joerarik adierazi (8. irudia). Izan ere, aldatu den arren eta ikertutako leku guztietan aldaketak nabarmenak izan diren arren, ezin da esan eredu bera erakutsi duenik leku guztietan. Hala, *Gelidium corneum* gutxitu egin da ur garbi eta gardenetan, irradiantzia handiko lekuetan ahulagoa delako (ZA, EA, BA, RA eta KO); aldiz, ur uherretan, ibai aho edo bokaletan esate baterako, ugaritu egin da (HI, LE, EG, MA, SA, VI, EN, IT, AR, ÑO, eta IZ), irradiantziatik babestuago dagoelako. Era berean, ur-kalitatea hobetu den lekuetan ere ugaritu egin da. Ikerketa paraleloek adierazi dute *G. corneum* espeziea ez dela ondo egokitu irradiantzia handitu den lekuetara.



8. irudia. *Gelidium corneum* espeziearen estaldura-aldaketa 1991-2009 bitartean.

Geruza epifitoetan, *Plocamium cartilagineum* espeziea da ugariena. *G. corneum* espeziearen frondeetan hazten da bereziki. *P. cartilagineum* espeziea asko ugaritu den bi lekutan izan ezik, gainerako aldaketak ziurrenik urtaro bakoitzean izaten diren aldaketei egotzi behar zaizkie.

Dibertsitateari dagokionez, egindako bi laginketak alderatzen baditugu, argi ikusiko dugu azken hogei urteotan espezieak nabarmen ugaritu direla ikerketutako eremuan. Bestela esanda, gure kostaldeko alga-espezieen kopuruak (S) handitu egin da (9. irudia). Dibertsitate indizeei dagokienean, bai espezieen aberastasunaren adierazle den Shannon indizeari eta bai nagusitasunaren adierazle den Simpson indizeari dagokienean, esan behar dugu bata zein bestea handiagoak direla 2009an 1991. urtean baino. Ingurumen-baldintzak aldatzen badira, baliteke espezieen arteko oreka haustea eta dibertsifikazioa handitzea. Izan ere, espezie jakin batzuek egoera hori baliatzen dute bertan ezartzeko; aldiz, egoera hori egonkortzen denean eta berriz ere espezieen arteko oreka lortzen denean, gerta daiteke dibertsifikazioan atzerapausua ematea.



9. irudia. Dibertsitatea: espezieen aberastasunarean arabera.

ONDORIOAK

Ikerketa honetako emaitzak eskuartean ditugula, honako hau ondoriozta dezakegu azken hogei urteotan gure kostaldean gertatu denaz:

— Alga koralinazeoak oro har ugaritu egin dira: *Corallina elongata, Jania rubens,* eta *Lithophyllum incrustans*.
— Hegoaldearekiko afinitatea duten morfologia sinpleko espezieak ugaritu egin dira:

Gayliella flaccida, Aglaothamnion tenuissimum, eta *Acrosorium ciliolatum*.

— Kanpoko espezieen ugaritasuna emendatu egin da: *Falkenbergia rufolanosa* eta *Herposiphonia sp*.

- — Gure kostaldeko espezie egituratzaileen kokapen-patroietan aldaketa esanguratsuak gertatu dira: *Gelidium corneum* eta *Cystoseira baccata*.
- — Espezie gehiago daude eta dibertsitatea handitu egin da.

Ekoizle primarioetan eta habitat eratzaileetan antzeman diren aldaketek eragin handia izan dezakete gure kostaldeko ekosisteman. Hain zuzen ere, antzeman diren aldaketak bat datoz azken hamarkadetan ingurumen-baldintzetan gertatu diren ageriko aldaketekin. Ikertu dugun eremuan, uraren tenperatura igo eta irradiantzia handitu egin da; horrek iradoki du berotze efektua, hau da, klima-aldaketa izan dela aldaketa horien erantzuleetako bat. Gainera, frogatua dago itsas gainazaleko tenperaturaren gorakadaren asaldua espezie exotikoak ezartzea errazten duela [4].

Hala ere, elikagaien kontzentrazioan gertatu diren aldaketen edota uraren gardentasunari edo itsasoaren dinamikari dagokionean eman diren aldaketen inguruko datuak, hau da, korronteen edo olatuen inguruko datuak, oso mugatuak dira, eta baliteke horiek ere antzemandako aldaketekin lotuta egotea.

Ipar itsasoan ere ingurumen-aldaketak garrantzitsuak izan dira eta zonalde horrek antzekotasun handia du gure kostaldean gertatu denarekin. Han, fitobenkton komunitateetan egitura-aldaketa esanguratsuak ikusi dira, kopadunen geruzaren galera nabarmena izanik [2].

Era berean gure emaitzekin bat dator Cloernen lana, non adierazi baitzen makroalgen komunitateetan elikagai-aberastasunaren efektu nagusia hautazko baldintzen aldaketa dela. Hazkuntza motela duten alga iraunkorrek nagusitasuna galtzen dute hazkuntza azkarra eta morfologia sinplea duten algen onurako, eta beraz komunitatearen egitura eta dibertsitatea guztiz aldatzen da [21].

Klima-aldaketaren testuinguru honetan (berotze efektua), badakigu azkarra dela algek ingurumenean gertatutako aldaketen aurrean emandako erantzuna, eta beraz algak erabil daitezke klima-aldaketak itsasoko ekosistemetan eragin ditzakeen aldaketen ebaluazio azkarra egiteko [22]. Horregatik dira hain egokiak komunitateen jarraipen-azterketak («monitoring»).

ESKER ONAK

Egileek bereziki eskertu nahi diogu Arantza Aldezabali egindako irakurketa eta zuzenketa, zeren eta berak egindako lana dezente nahiko hobetu duelako gure idazlana. Aipamen berezia merezi du Ainara Argoitiak, egindako lana eta laguntzagatik.

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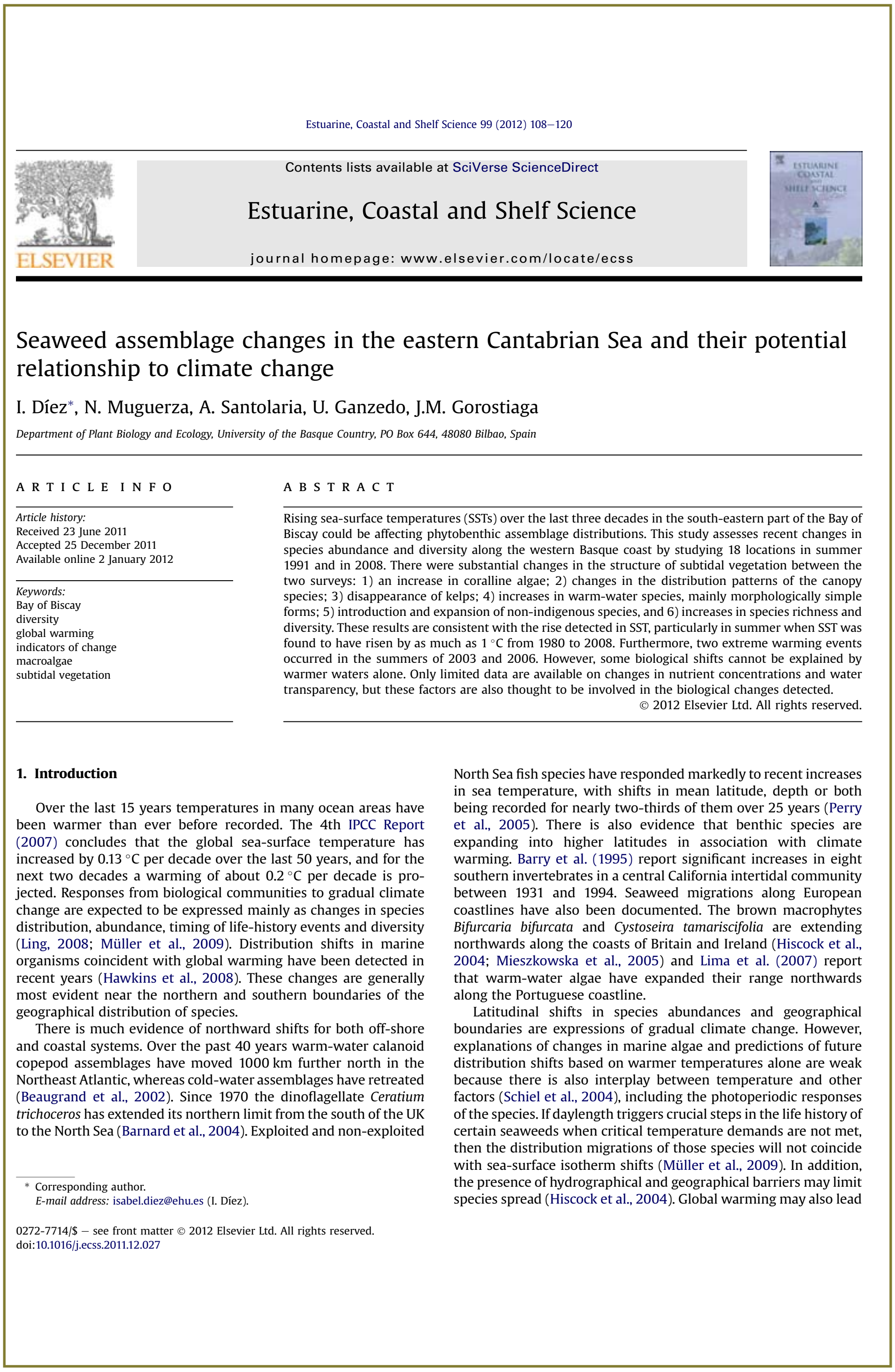

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Seaweed assemblage changes in the eastern Cantabrian Sea and their potential relationship to climate change

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A B S T R A C T

Rising sea-surface temperatures (SSTs) over the last three decades in the south-eastern part of the Bay of Biscay could be affecting phytobenthic assemblage distributions. This study assesses recent changes in species abundance and diversity along the western Basque coast by studying 18 locations in summer 1991 and in 2008. There were substantial changes in the structure of subtidal vegetation between the two surveys: 1) an increase in coralline algae; 2) changes in the distribution patterns of the canopy species; 3) disappearance of kelps; 4) increases in warm-water species, mainly morphologically simple forms; 5) introduction and expansion of non-indigenous species, and 6) increases in species richness and diversity. These results are consistent with the rise detected in SST, particularly in summer when SST was found to have risen by as much as 1 °C from 1980 to 2008. Furthermore, two extreme warming events occurred in the summers of 2003 and 2006. However, some biological shifts cannot be explained by warmer waters alone. Only limited data are available on changes in nutrient concentrations and water transparency, but these factors are also thought to be involved in the biological changes detected.

1. Introduction

Over the last 15 years temperatures in many ocean areas have been warmer than ever before recorded. The 4th IPCC Report (2007) concludes that the global sea-surface temperature has increased by 0.13 °C per decade over the last 50 years, and for the next two decades a warming of about 0.2 °C per decade is projected. Responses from biological communities to gradual climate change are expected to be expressed mainly as changes in species distribution, abundance, timing of life-history events and diversity (Ling, 2008; Müller et al., 2009). Distribution shifts in marine organisms coincident with global warming have been detected in recent years (Hawkins et al., 2008). These changes are generally most evident near the northern and southern boundaries of the geographical distribution of species.

There is much evidence of northward shifts for both off-shore and coastal systems. Over the past 40 years warm-water calanoid copepod assemblages have moved 1000 km further north in the Northeast Atlantic, whereas cold-water assemblages have retreated (Beaugrand et al., 2002). Since 1970 the dinoflagellate *Ceratium trichoceros* has extended its northern limit from the south of the UK to the North Sea (Barnard et al., 2004). Exploited and non-exploited North Sea fish species have responded markedly to recent increases in sea temperature, with shifts in mean latitude, depth or both being recorded for nearly two-thirds of them over 25 years (Perry et al., 2005). There is also evidence that benthic species are expanding into higher latitudes in association with climate warming. Barry et al. (1995) report significant increases in eight southern invertebrates in a central California intertidal community between 1931 and 1994. Seaweed migrations along European coastlines have also been documented. The brown macrophytes *Bifurcaria bifurcata* and *Cystoseira tamariscifolia* are extending northwards along the coasts of Britain and Ireland (Hiscock et al., 2004; Mieszkowska et al., 2005) and Lima et al. (2007) report that warm-water algae have expanded their range northwards along the Portuguese coastline.

Latitudinal shifts in species abundances and geographical boundaries are expressions of gradual climate change. However, explanations of changes in marine algae and predictions of future distribution shifts based on warmer temperatures alone are weak because there is also interplay between temperature and other factors (Schiel et al., 2004), including the photoperiodic responses of the species. If daylength triggers crucial steps in the life history of certain seaweeds when critical temperature demands are not met, then the distribution migrations of those species will not coincide with sea-surface isotherm shifts (Müller et al., 2009). In addition, the presence of hydrographical and geographical barriers may limit species spread (Hiscock et al., 2004). Global warming may also lead

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to nutrient input alterations due to changes in water column stratification (Roemmich and McGowan, 1995; Llope et al., 2006) and to changes in the geographical or seasonal distributions of rainfall and upwelling (Llope et al., 2006) with subsequent changes in primary production (Bakun, 1990; Llope et al., 2007). Similarly, changes in the carbon chemistry of seawater due to CO_2 emissions may have large-scale impacts on calcifying macroalgae, which are key species in a wide range of ecosystems (Beardall et al., 1998; Nelson, 2009). In addition, global warming may facilitate the spread of exotic species (Stachowicz, 2002). Climate-driven changes may affect the dispersion of non-indigenous species due to the alteration of current patterns and to competitive interactions between alien and native species as a result of the onset of new thermal optima and/or different water chemistry (Occhipinti-Ambrogi, 2007). Climate-induced changes may well be exacerbated by the synergistic effects between climate and other anthropogenic variables, particularly pollution and the over-exploitation of biological resources (Nelson, 2009). The overall response of a community to the complex interplay of various stress factors in combination with key ecological interactions is therefore unpredictable (Schiel et al., 2004).

Simulations for 2080–2099 show that the phytobenthos of northern Spain is likely to be one of those most affected by future sea-surface temperature increases around the world (Müller et al., 2009). The Basque coast extends over approximately 192 km at the eastern end of the Cantabrian Sea, northern Spain. Increases of about 0.26 °C per decade in SST for this area have been documented since 1977 (Goikoetxea et al., 2009). Recent surveys have revealed the disappearance of *Gelidium corneum* beds at the western end of the coast of Bizkaia (Gorostiaga et al., 2009). These local alterations led us to assess changes in species abundance and diversity along the whole western part of the Basque coast. The first quantitative study dealing with the sublittoral vegetation of this area was conducted in 1991 by the present research team (Díez et al., 2003) and then 17 years later we repeated our study to estimate changes in species composition, relative abundance of species and diversity.

2. Materials and methods

2.1. Study area

The Cantabrian Sea is the southernmost part of the Bay of Biscay, in the North-eastern Atlantic (Fig. 1). The sample area, which extends approximately 108 km along the eastern Cantabrian Sea, corresponds to the western part of the Basque coast. This is an open coastline exposed to a large fetch where swell comes mainly from the WNW and NW. Rocky bottoms are almost continuous in shallow waters and soft ground is scarce. Mean water surface temperature off the Basque coast used to range between 12 °C in February and 22 °C in August (Valencia et al., 2004). The flora falls within the warm-temperate NE Atlantic sub-region according to the phytogeographical scheme proposed by Hoek and Breeman (1990).

2.2. Climate variables

The data used in this study include measurements of mean daily precipitation at the surface (expressed in $\mathrm{kg\,m^{-2}\,s^{-1}}$) and mean daily visible beam downward solar flux at the surface (expressed in $\mathrm{W/m^2}$) from January 1948 to December 2008. The data are reanalysis daily averages (Kalnay et al., 1996) obtained from the National Centers for Environmental Prediction (NOAA/NCEP, http://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis.surfaceflux.html). Data are centred on an area from 42.8564°N to 44.7611°N and 3.750°W to 1.875°W with 1.9° × 1.9° resolution. Wave energy flux was also obtained from NOAA/NCEP (http://polar.ncep.noaa.gov/waves/index2.shtml). WAVEWATCH III™ (Tolman, 2009) is a third-generation wave model developed at NOAA/NCEP in the spirit of the WAM model (WAMDIG, 1988; Komen et al., 1994). The data used run from January 1998 to December 2008. Wave energy flux (henceforth called *E* and expressed in $\mathrm{kW\,m^{-1}}$) is the rate at which energy is transmitted in the direction of wave propagation, across a vertical plane perpendicular to the direction of wave advance and extending down the entire ocean depth (Dean and Dalrymple, 1991). The three-hourly data from the wave model and buoy data were used to compute *E* at the original three-hourly sampling rate, by means of the approximate equation $E = 0.5Hs2Tp$ (Dean and Dalrymple, 1991; Hagerman, 2001; Beyene and Wilson, 2006). The SST data, provided by the Fundación Oceanográfica de Guipúzcoa - Aquarium de Donostia-San Sebastián, run from January 1980 to December 2008 and were recorded daily at 10 a.m.

To provide an accurate indicator of the climate behaviour of each variable, the 25th and 75th percentiles were calculated on the basis of the longest available data series. The period and number of missing values (above 98% in all periods) differ from one variable to another: (a) Climate data (obtained from NCEP) for 1948–2008, (b) wave energy flux for 1998–2008 (WAVEWATCH model), (c) SST data for 1947–2008 (Aquarium data). The relationships between variables were analysed on the basis of Pearson's correlation and Linear Models (LM) (Verzani, 2005). The correlation coefficient was checked against the hypothesis that it was zero with a 95% confidence level (Wilks, 2006).

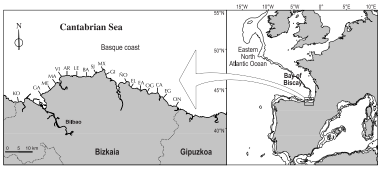

Fig. 1. Map of the study area showing locations of transects: Kobaron (KO); La Galea (GA); Meñakoz (ME); Matxilando (MA); Cabo Villano (VI); Arminza (AR); Lemoiz (LE); Bakio (BA); San Juan de Gaztelugatxe (SJ); Matxitxako (MX); Gibeleko (GI); Ogoño (ÑO); Elantxobe (EL); Ea (EA); Ogeia (OG); Santa Catalina (CA); Egiluz (EG); and Ondarroa (ON).

2.3. Biological data

The methods used were adapted from earlier research (Díez et al., 2003) to ensure comparable datasets. In the reference study, sampling was carried out in the summer of 1991 using SCUBA. Twenty-one 100 m long equidistant transects were set up perpendicularly along 108 km of coastline and 18 of these transects were revisited in the summer of 2008 (from July 14 to September 19) (Fig. 1). The relocation of each transect was calculated using photographic records of the starting point in combination with the transect orientation and bathymetric profile (see Annex Table A1 for georeference details). Each transect started at 2–4 m below mean low water at spring tide, with depth being determined with a digital gauge, and the tide tables were corrected for the diving time. The average depth range covered by transects was 3–9 m (2 m minimum; 13 m maximum depth). Macrophyte abundances were assessed by visually estimating their cover (%) in 1 m^2 quadrats at 5 m intervals along each transect, according to the scale of Braun-Blanquet (1951). Average species cover among quadrats was calculated using the median value for each Braun-Blanquet interval. To minimise the differences between the years and prevent possible misidentification of species, some species were aggregated into genera.

Permutational multivariate analysis of variance (PERMANOVA) was performed to test the hypothesis that assemblages differed from one year to the other. Non-metric multidimensional scaling (nMDS) ordination on the basis of a Bray–Curtis dissimilarity matrix calculated for square-root transformed data was used to provide a graphic visualisation of variation over time in communities. The SIMPER (Similarity Percentage Analysis) routine was applied to identify species that could discriminate between the two years. For each site the significance levels of the differences in species cover from one year to the other were evaluated by the Wilcoxon signed-rank test. Species richness (*S*), Shannon diversity (H', $\log_e$), Simpson ($1 - \lambda$) diversity and Pielou J' evenness were calculated for each quadrat. The PRIMER software package (Anderson et al., 2008) was used to perform the analyses.

3. Results

3.1. Climate variable trends

Annual increases in SST occurred from 1980 to 2008 (Fig. 2a), particularly in Spring and Summer (Table 1). The number of days in summer with SST over the 75th percentile value (22.1 °C) increased from less than 9.88 to 36.67 over this period (Fig. 2b). The average SST in this season increased from 20.8 °C to 21.7 °C. The average summer temperatures above the 75th percentile significantly increased from 22.4 °C to 23.2 °C (Fig. 2c). The maximum temperatures reached in summer also increased, with the summers of 1997, 2003 and 2006 being especially hot (Maximum SST > 25 °C) (Fig. 2d). The daily precipitation rate at surface suffered a significant (99%) annual decline over the period 1980–2008, which was significant (99%) in both spring and summer (Table 1). The mean daily visible (photosynthetically active, PAR) beam downward solar flux at surface showed no significant changes (1980–2008) (Table 1). Only an annual increase of 2.9 days per decade of radiation above the 75th percentile (beam PAR > 95.9 W/m^2) at 90% significance was detected. No significant change in wave energy was detected, although it should be noted that the time series (1998–2008) is too short to confirm trends.

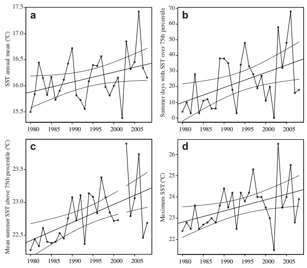

Fig. 2. Time series of sea-surface temperature: annual mean (a), number of summer days exceeding the 75th percentile (b), summer mean of values over 75th percentile (c), and maxima (d) over the period 1980–2008. The dashed lines represent the 95% confidence intervals.

Table 1
Linear trends (slope and significance: 90%·, 95%*, 99%**) of seasonal (Winter: January–March; Spring: April–June; Summer: July–September; Autumn: October–December) and annual sea-surface temperature (SST), mean daily precipitation rate (DPR), and mean daily visible beam downward solar flux at surface (PAR beam) over the period 1980–2008. Mean = Average of all values; Mean (*P* > 75) = Average of values over 75th percentile; Days (*P* > 75) = Number of days exceeding the 75th percentile; Max = Maximum value of SST.

	Winter	Spring	Summer	Autumn	Annual
SST					
Mean	0.016	0.036*	0.033*	0.001	0.019*
Mean (*P* > 75)	0.001	0.023	0.028**	0.015	0.017·
Days (*P* > 75)	0.735	0.499*	0.957**	0.131	1.278**
Max	0.019	0.043	0.052*	0.002	0.052*
DPR					
Mean	−2.4245e−07	−6.2430e−07·	−6.3307e−07*	−8.60522e−08	−3.9678e−07**
PAR beam					
Mean	0.037	0.065	0.104	0.069	0.069
Mean (*P* > 75)	0.059	−0.009	0.033	0.020	0.008
Days (*P* > 75)	0.097	0.091	0.116	−0.037	0.294·

3.2. Changes in vegetation structure

Permutational multivariate analysis of variance (PERMANOVA) detected significant differences between the two years (Table 2). The diagram resulting from nMDS ordination graphically represents the variation of assemblages over time (Fig. 3). The ordination analysis shows clear differences between the two surveys and the species contributing most to the discrimination of the time pattern detected were identified by the similarity percentage procedure (SIMPER routine). Each of the 28 taxa listed in Table 3 contributes in excess of 1% to the average dissimilarity between the two years (59.5%), and their cumulative contribution is 68%. Changes in the abundance of these taxa are detailed below.

The only encrusting calcareous species reported in 1991 was *Mesophyllum* spp. (reported as *Mesophyllum licheoides*), whereas in 2008 *Lithophyllum incrustans* (average cover: 3.2 ± 0.4 SE) was also found in 54% of the quadrats. *Mesophyllum* spp., the dominant species of the crustose layer, showed no significant changes in most of the sites (Fig. 4). A widespread increase was detected in the brown alga *Zanardinia typus*, which showed significant increases at ten sampling sites. In general terms, the crustose layer of subtidal vegetation in the study area has experienced greater development.

The results show increases in the abundance of articulated coralline algae. The most abundant genus *Corallina* showed significant increases at 15 sampling sites (Fig. 4) with a mean increase of 14.5% ± 3.8% (mean ± SE). Two species were found, *Corallina officinalis* and *Corallina elongata*, with the latter being more abundant. Similarly, the genus *Jania*, including the species *Jania rubens* and *Jania longifurca*, showed significant increases at 15 locations. Epiphytic filamentous forms, mainly ceramiaceous algae, also showed significant increases, e.g. *Gayliella flaccida* and *Aglaothamnion tenuissimum*. Another taxon that discriminates between the two surveys is the genus *Pterosiphonia*. The species *Pterosiphonia ardreana* and *Pterosiphonia pennata*, treated as a group (*Pterosiphonia* spp.), showed significant increases at eleven sampling sites. However, changes in *Pterosiphonia complanata* varied from site to site. Other basal species that increased along the coast, albeit with low cover values, were *Acrosorium ciliolatum*, *Cladostephus spongiosus*, *Cladophora pellucida*, *Chondria coerulescens* and *Bornetia secundiflora*.

Table 2
PERMANOVA results based on Bray–Curtis dissimilarities of square-root transformed data showing the effect of Year (Y) on algal assemblages (140 variables). *P* values were obtained using 9999 permutations of given permutable units.

PERMANOVA – permutational multivariate analysis of variance						
Source	df	SS	MS	Pseudo-*F*	*P*(perm)	Unique perms
Y	1	10,878	10,878	8.4823	0.0001	9928
Res	34	43,601	1282.4			
Total	35	54,479				

The key structural seaweeds *Cystoseira baccata* and *Gelidium corneum* (formerly *G. sesquipedale*) underwent significant distributional changes between 1991 and 2008. *Cystoseira baccata* significantly increased at four sites (KO, LE, SJ, ÑO) but decreased at three (BA, MX, EG) (Fig. 4). The agarophyte *G. corneum* decreased in clean, transparent waters (KO, BA, EA) but increased at those sites where water quality had improved (MA, VI, SJ, ÑO) (Díez et al., 2010; Gorostiaga et al., 2010). *Plocamium cartilagineum* growing epiphytically on canopy species increased. In 1991 two populations of the kelp *Laminaria ochroleuca* were detected in Bakio (cover: 20%, frequency: 80%) and San Juan de Gaztelugatze (cover: 39%, frequency: 78%), along with scattered specimens along the coast, whereas in 2008 was not found. Similarly, the annual kelp *Saccorhiza polyschides* was present in 24.6% of the quadrats sampled in 1991 but was not observed at all in 2008.

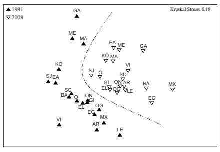

Fig. 3. Non-metric MDS ordination based on the Bray–Curtis dissimilarity coefficient applied to square-root transformed data. Each symbol is the 'average sample' obtained by averaging across site quadrats in each sampling survey. Black triangles: 1991 survey; white triangles: 2008 survey. For site abbreviations, see legend to Fig. 1.

Table 3
Average cover in % (C) and frequency in % (F) of the species in 1991 and 2008 and contribution of each taxon to the average dissimilarity between the two surveys according to the SIMPER routine. The 28 taxa listed have a contribution of over 1% of the total dissimilarity. They are ordered on the basis of their cold or warm-water affinity. Northern distribution limit: (a) Scandinavia; (b) British Isles. (1) *C. elongata* and *C. officinalis*; (2) *M. expansum* and *M. alternans*; (3) *P. pennata* and *P. ardreana*; (4) *P. cartilagineum* and *P. raphelisianum*; (5) *J. rubens* and *J. longifurca*.

SIMPER results – similarity percentages – species contributions					
Taxa list	1991		2008		Contrib.%
	C	F	C	F	
Lusitanic species					
Cystoseira baccata (S.G. Gmel.) P.C. Silva	23.6	39.0	23.2	41.5	6.31
Gelidium corneum (Huds.) J.V. Lamour.	13.4	45.5	15.0	69.8	5.06
Pterosiphonia complanata (Clemente) Falkenb.	9.2	58.8	5.8	61.9	3.19
Laminaria ochroleuca Bach. Pyl.	2.9	11.6	–	–	1.10
Warm-water species (a)					
Cladostephus spongiosus (Huds.) C. Agardh	0.6	15.0	2.2	40.7	1.81
Dictyota dichotoma (Huds.) J.V. Lamour.	2.4	44.6	1.6	50.3	1.76
Phyllophora crispa (Huds.) P.S. Dixon	–	–	0.9	18.6	1.06
Warm-water species (b)					
Corallina spp. (1)	4.1	47.2	15.8	86.4	4.26
Zanardinia typus (Nardo) G. Furnari	7.5	50.6	13.3	77.1	4.00
Aglaothamnion tenuissimum (Bonnem.) Feldm.-Maz.	–	–	7.00	64.1	3.95
Mesophyllum spp. (2)	28.0	85.0	32.5	96.0	3.51
Codium decorticatum (Woodw.) M.A.Howe	6.0	18.2	6.1	25.1	3.28
Gayliella flaccida (Harv. ex Kütz.) T.O.Cho & L.J.McIvor	0.0	2.5	4.0	61.9	2.78
Lithophyllum incrustans Phil.	–	–	3.2	54.5	2.77
Pterosiphonia spp. (3)	0.5	15.0	4.0	50.3	2.36
Plocamium spp. (4)	0.7	38.4	3.6	68.4	2.07
Acrosorium ciliolatum (Harv.) Kylin	0.0	5.1	1.8	73.7	1.94
Jania spp. (5)	0.2	11.6	2.2	61.0	1.77
Chondria coerulescens (J. Agardh) Falkenb.	0.6	15.3	1.7	18.6	1.45
Haematocelis rubens J. Agardh	1.1	21.5	1.3	37.9	1.43
Rhodymenia pseudopalmata (J.V. Lamour.) P.C. Silva	1.2	27.7	0.8	32.2	1.41
Cladophora pellucida (Huds.) Kütz.	0.3	30.5	1.2	42.9	1.08
Bornetia secundiflora (J. Agardh) Thur.	0.0	1.1	0.4	49.4	1.04
Cryptopleura ramosa (Huds.) Kylin ex L. Newton	0.8	44.9	0.8	50.8	1.03
Peyssonnelia atropurpurea P. Crouan & H. Crouan	–	–	0.9	24.0	1.00
Alien species					
Falkenbergia rufolanosa (Harv.) F. Schmitz	3.7	51.7	12.5	83.9	3.18
Herposiphonia sp.	–	–	4.3	30.8	2.28
Heterosiphonia japonica Yendo	–	–	1.9	31.9	1.37

The study reveals the introduction and expansion of non-indigenous species. The alien species *Heterosiphonia japonica* was found at 17 sampling sites, although its abundance was high at only one location (EG). Several recently introduced species of Ceramiaceae were also found, such as *Antithamnion amphigeneum*, *Antithamnion nipponicum* and *Scageliopsis patens*, all with low cover values. Likewise, an unidentified species of the genus *Herposiphonia* whose abundance ranges from occasional presence to 26% cover (Fig. 4) is probably a newly introduced species. The tetrasporophitic phase (*Falkenbergia rufolanosa*) of the established non-indigenous species *Asparagopsis armata* was significantly greater at ten of the eighteen locations studied (Fig. 4). Its mean cover change in the study area was 8.9% ± 2.4% (SE). Similarly, the tetrasporophitic phase (*Trailliella intricata*) of the non-native species *Bonnemaisonia hamifera*, which was not recorded in 1991, was found in eight locations.

In total 140 macroalgal taxa were found, 86 in 1991 and 133 in 2008 (see Annex Table A2 for full species list with their relative abundances). Seventy-nine of them were recorded in both surveys and 54 species were new additions, distributed as follows: 44 Rhodophyceae, 6 Chlorophyceae, and 4 Phaeophyceae. The total number of species per site found was higher at 17 of the 18 sampling sites in 2008 (Fig. 5a). The increases ranged from 4.3% (2 species) to 126.7% (38 species). Similarly, the species richness per quadrat was higher at all sampling sites, with an average increase of 10.6 ± 4.3 SD (Fig. 5b). Changes in the number of species per sampling unit were also estimated, considering only conspicuous species (cover higher than 1%). Increases were detected at all locations, with an average increase of 5.9 ± 1.7 SD (Fig. 5c). Diversity also increased throughout the study area. Shannon diversity measurements gave figures of over 1.5 in all cases in 2008, whereas only subtidal vegetation at Matxilando (MA) showed such a figure in 1991 (Fig. 5d). Simpson diversity measurements were significantly higher at 17 sites in 2008 (Fig. 5e). It was also observed that differences in Simpson diversity from site to site were lower in 2008. Similarly, Pielou's evenness was higher at most sites in 2008 (Fig. 5f).

4. Discussion

The results obtained in this study reveal significant changes in the structure of subtidal vegetation along the western Basque coast from 1991 to 2008. The most important results are: 1) an increase in coralline algae; 2) changes in the distributional patterns of the canopy-forming species; 3) disappearance of kelps; 4) increases of meridional affinity species, mainly morphologically simple forms; 5) introduction and expansion of non-indigenous species, and 6) increases in species richness and diversity. All these biological changes have coincided with upward trends in sea-surface temperature over the last three decades, particularly in summer.

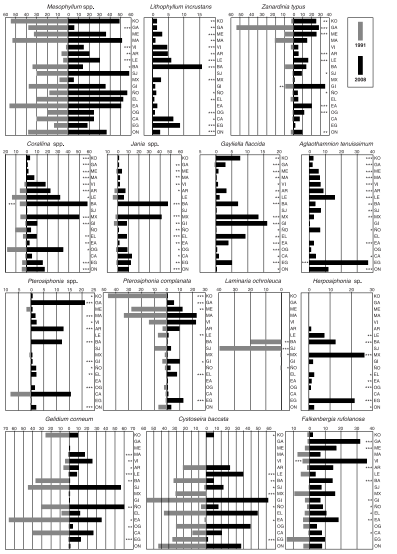

Fig. 4. Percentage cover of the most discriminant species in differences detected between 1991 and 2008. Asterisks *, ** and *** indicate significance levels $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively, for the Wilcoxon signed-rank test of differences between means. For site abbreviations, see legend to Fig. 1.

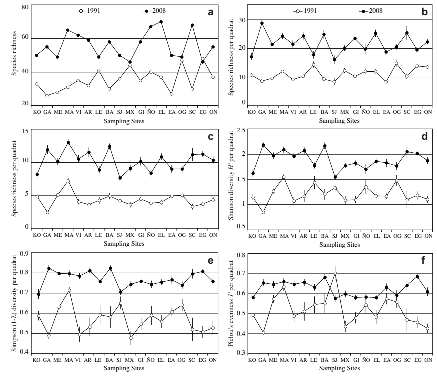

Fig. 5. Cumulative species richness (a), mean values of species richness derived from full species dataset (b), species richness after the removal of occasional species (c), Shannon–Wiener H' diversity (d), Simpson $(1-\lambda)$ diversity (e) and Pielou evenness J' (f) for each sampling site and year. Bars show standard error (SE). For site abbreviations, see legend to Fig. 1.

4.1. Increase in coralline algae

The study reveals increases in the cover of coralline algae, mainly *Corallina elongata*, *Jania rubens* and *Lithophyllum incrustans*. These changes may be related to the warming trend detected since 1980 (0.21 °C per decade in mean annual SST). Stimulation of calcification and growth by increasing temperature has already been documented for coralline algae (Mohamed and Khaled, 2005; Steller et al., 2007; Jian-Zhang et al., 2010). Nevertheless, given that these species are common macrophytes thriving in sun-exposed intertidal habitats along the Basque coast (Díez et al., 2009), their downward extension into the subtidal zone may also be attributable to increases in light availability. The interactive effects of temperature and irradiance levels are known to exert control over the rate of calcification of temperate coralline algae (Martin et al., 2006). Our results show no evidence that PAR radiation levels have changed significantly since 1980, so we suggest that there may have been increases in water transparency. The combination of the decrease suggested in the productivity of the inner Bay of Biscay (Llope et al., 2007; Valdés et al., 2007), pollution abatement (Gorostiaga and Díez, 1996; García-Barcina et al., 2006; Díez et al., 2010; Gorostiaga et al., 2010) and the decrease detected in rainfall could have resulted in greater clarity of seawater. Changes in depth distributions of seaweeds concordant with water transparency increases have been reported recently for other European areas (Pehlke and Bartsch, 2008).

On the other hand, changes in the carbonate chemistry of seawater are predicted to have profound negative consequences for calcifying algae (Gao et al., 1993; Martin and Gattuso, 2009). According to the IPCC, for a three-fold increase in atmospheric CO_2 from the pre-industrial level (a rise to 840 ppm), dissolved CO_2 would cause a decrease in average ocean surface pH to ca. 7.77 (assuming a temperature of 18 °C) by 2100 (Raven et al., 2005). Studies on volcanic hydrothermal vents (Hall-Spencer et al., 2008; Couto et al., 2010) report large-scale decreases in the abundance of coralline algae at lowered pH levels of 7.6. The current seawater pH in the study area (8.2–8.3) is far from levels that would inhibit calcification, but it is possible that by the end of this century net dissolution may exceed net calcification in coralline algae along the Basque coast.

4.2. Changes in the distribution patterns of canopy species

The impact of climate change on key species is expected to have major negative consequences in coastal ecosystems (Breeman, 1990; Hiscock et al., 2004). Seaweed vegetation in unpolluted shallow waters throughout the study area was characterised in 1991 by the presence of a perennial canopy of *Gelidium corneum* or *Cystoseira baccata* (Díez et al., 2003) and significant changes in the distribution of both species have been detected. The macrophyte *G. corneum* exhibited high covers at six locations in 1991 (KO, BA, SJ, ÑO, EA, CA), all of them exposed to high wave action. Our results show that this agarophyte has significantly decreased in three of these locations (KO, BA, EA), and shows stress symptoms such as partial frond yellowing and an unusual branch breakdown pattern. By contrast, *G. corneum* has increased in those exposed sites where extra loads of nutrients and turbidity are available but water quality has improved as result of pollution mitigation (MA, VI, SJ, ÑO) (Díez et al., 2010; Gorostiaga et al., 2010). These results suggest that warming of the waters in the past three decades does not fully explain the decline of *G. corneum* beds. Miguel-Vijandi et al. (2010) conducted multifactorial experiments to examine the effects of the interaction between temperature, photosynthetic irradiance, UV radiation, and nutrient availability on the acclimation capacity of *G. corneum* collected from Basque populations. They found that nitrogen supply exerts a positive effect on photosynthesis performance, as opposed to the stress factors of increased temperature and irradiance, as reported for other macrophytes such as *Gracilaria conferta* (Figueroa et al., 2010). Some studies (Llope et al., 2007; Valdés et al., 2007) have suggested that the Cantabrian Sea is becoming less productive, for example, a decreasing trend in nitrate availability has been reported for the southern Bay of Biscay, as result of decreases in upwelling intensity and an increase in the period of summer stratification (Llope et al., 2007). In addition, the decrease in summer rainfall recorded on the Basque coast since 1980, and the consequent decrease in the input of nutrient-rich continental waters during the stratification period, may also have contributed to the hypothetical decline in nutrient availability in waters off that coast. Nutrient depletion, increased temperature and water transparency in summer may be acting synergetically as a complex stress factor for those *G. corneum* populations that live in clean coastal stretches.

The key structural seaweed *Cystoseira baccata* also underwent significant distributional changes in the study area from 1991 to 2008. It significantly increased at four sites (KO, LE, SJ, ÑO) but significantly decreased at three others (BA, MX, EG). Multifactorial laboratory experiments carried out to examine the effects of the interaction between several stress factors suggest that *C. baccata* shows a high acclimation capacity to increased temperature and irradiance (Miguel-Vijandi et al., 2010). This brown macrophyte is predicted to migrate northwards along European coastlines (Hiscock et al., 2004). This shift seems to be occurring now as this species has became dominant on the neighbouring coast of Asturias in those habitats where kelps beds have retreated (J. Rico in Müller et al., 2009).

4.3. Disappearance of kelps

Two dense populations of *Laminaria ochroleuca* were detected in Bakio and San Juan de Gaztelugatxe in 1991, as well as scattered individuals of *Saccorhiza polyschides* along the coast. Neither of these two species was observed in 2008. According to Fernández (2011) these kelps have been retreating westward on the north coast of Spain since the 1980s, and they are currently reduced to small patches and isolated individuals east of Cabo Peñas. *Laminaria ochroleuca* is considered to be a warm-temperate species since it exhibits optimum growth at between 15 and 20 °C and an upper lethal temperature of 22–23 °C for its sporophytes (tom Dieck, 1992). Similarly, *S. polyschides* has a survival interval of between 5 and 23 °C (van den Hoek, 1982). Our results suggest that the number of summer days with temperatures above 22.1 °C has increased from less than 10 to more than 35 from 1980 to 2008. These long warm periods in combination with the pronounced warming up to 26.5 °C in 2003 and 25.5 °C in 2006 probably had a lethal effect on both species. The regression of kelps has already been documented along European coastlines (Cosson, 1999; Husa, 2007). However, although kelps are considered particularly vulnerable to climate change due to their cold-water affinities, there is no evidence of a worldwide shift to higher latitudes (Merzouk and Johnson, 2011).

4.4. Introduction and expansion of non-indigenous species

This study also detected the alien species *Antithamnion amphigeneum*, *Scageliopsis patens*, *Antithamnion nipponicum* and *Heterosiphonia japonica*, recently introduced into Atlantic European waters (Secilla et al., 1997, 2007, 2008; Husa et al., 2004; Rueness et al., 2007), as well as the proliferation of one unidentified exotic species of the genus *Herposiphonia*. The introduction of species into new ecosystems is a major threat to biodiversity because it may lead to biotic homogenisation, especially in synergy with other anthropogenic disturbances such as climate change and coastal pollution (Schaffelke et al., 2006). Currently none of the alien species detected in this study is considered invasive because they all have low cover values. However, it is important that they are closely tracked because as climate-driven changes ensue, the new environmental conditions could alter the competitive interactions between alien and native species (Occhipinti-Ambrogi, 2007). In this sense, we have detected a significant spread of the established alien *Falkenbergia rufolanosa* (tetrasporophytic phase of *Asparagopsis armata*), mainly at those sites where the vegetation has no canopy. Although no disappearance of native species can be related to the increase in *F. rufolanosa*, its expansion may be affecting the relative abundance of native species. Our finding agrees with that of Lima et al. (2007), who estimate that *Asparagopsis armata* has shifted 287 km northwards along the Portuguese coast over the last 50 years.

4.5. Increases in species with meridional affinity

Warm-temperate species have increased significantly throughout the study area, a result consistent with the increases detected in SST. While warming may have allowed some species such as *Aglaothamnion tenuissimum*, *Aphanocladia stichidiosa* or *Centroceras clavulatum* to migrate northwards, the new thermal conditions could have enhanced the growth and/or reproduction of some warm-temperate species already recorded in 1991 such as *Gayliella flaccida*, *Acrosorium ciliolatum*, and *Zanardinia typus*. Most of the species that exhibit increased cover are filamentous or polysiphonated annual forms. The northward expansion of warm-temperate species has already been observed along European coasts. According to Helmuth et al. (2006) the poleward range limits of intertidal biota have shifted by as much as 50 km per decade, faster than recorded shifts of most terrestrial species. Most of the changed documented in algae distributions coinciding with global warming are focussed on large-sized species such as *Bifurcaria bifurcata*, *Cystoseira tamariscifolia*, *Halopithys incurva* and *Hypnea musciformis* (Hiscock et al., 2004; Mieszkowska et al., 2005; Lima et al., 2007). In contrast, reports on changes in the distribution of small, inconspicuous species are scarce. Araújo et al. (2009) report northwards expansion in the distributional range of the southern warm-temperate small

species *A. stichidiosa*, *Ctenosiphonia hypnoides* and *Griffithsia schousboei* in northern Portugal.

4.6. Changes in species richness and diversity

Our results reveal that subtidal phytobenthic assemblages along the western Basque coast underwent large-scale increases in species richness and diversity from 1991 to 2008. Approximately 70% of the species that account for the increase in taxon richness are morphologically simple forms with short life-cycles and warm-water affinity. Such changes could be due to physiological responses of species to new environmental conditions, but may also be related to shifts in interspecific interactions. The first explanation is consistent with the evidence of the positive relationship between SST and marine biodiversity (Tittensor et al., 2010). Higher temperatures increase metabolic rates, resulting in latitudinal gradients of increasing species richness from polar to equatorial regions (Gaston and Spicer, 2004). But the instability shown by the perennial canopy species *Cystoseira baccata* and *Gelidium corneum* could also have benefited opportunistic species. Underlying this non-equilibrium approach is the intermediate disturbance hypothesis, which predicts maximal diversity at intermediate levels of disturbance (Connell, 1978; Valdivia et al., 2005). Nevertheless, global climate change is predicted to have major negative consequences for marine biodiversity, particularly if important habitat-modifying species undergo range shifts (Ling, 2008). In addition, warming is expected to reduce compositional stability and increase temporal species turnover (Hillebrand et al., 2010).

The present study suggests that global warming could already be affecting the eastern Cantabrian coastal ecosystems. Most of the changes detected are probably attributable to the observed increase in SST, but changes in water clarity and nutrient availability may also have had an effect. There is great uncertainty in forecasting future trends in seaweed distributions since global climate change involves the interplay of ocean warming with other environmental factors plus indirect effects that operate through ecological interactions such as trophic relationships and competition. Hence biological and modelling studies are needed to identify sentinel species and sites in order to track future changes and build more accurate predictive models for the responses of benthic assemblages to climate change.

Acknowledgements

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Annex

Table A1
Georeference of the starting point on land, direction and starting point depth of the transects.

Location	Latitude	Longitude	Direction	Starting depth
Kobaron (KO)	43°21′17.65″N	3°07′46.40″O	NW 355°	−3 m
La Galea (GA)	43°22′24.06″N	3°02′11.88″O	NW 315°	−3 m
Meñakoz (ME)	43°23′37.70″N	2°59′25.44″O	NW 315°	−3 m
Matxilando (MA)	43°24′51.44″N	2°58′00.39″O	NW 315°	−4 m
Cabo Villano (VI)	43°26′09.80″N	2°56′47.94″O	N 330°	−4 m
Arminza (AR)	43°26′18.72″N	2°54′34.31″O	N 30°	−4 m
Lemoiz (LE)	43°25′54.18″N	2°52′05.95″O	N 30°	−2 m
Bakio (BA)	43°25′53.65″N	2°49′48.03″O	N 0°	−3 m
San Juan de Gaztelugatxe (SJ)	43°26′44.12″N	2°47′16.45″O	W 290°	−4 m
Matxitxako (MX)	43°27′19.82″N	2°45′14.35″O	N 355°	−4 m
Gibeleko (GI)	43°25′54.60″N	2°44′22.92″O	E 75°	−2 m
Ogoño (ÑO)	43°24′49.73″N	2°38′58.66″O	NW 315°	−3 m
Elantxobe (EL)	43°23′38.50″N	2°37′18.49″O	NE 45°	−4 m
Ea (EA)	43°23′16.89″N	2°35′00.66″O	NE 45°	−3 m
Ogeia (OG)	43°22′55.27″N	2°33′12.60″O	NE 45°	−2 m
Santa Catalina (CA)	43°22′34.17″N	2°30′51.85″O	NW 315°	−3 m
Egiluz (EG)	43°21′32.79″N	2°29′06.97″O	NE 45°	−2 m
Ondarroa (ON)	43°19′44.75″N	2°25′19.10″O	NE 45°	−3 m

Table A2
Average cover in % (C), standard error (SE) and frequency in % (F) of the species in 1991 and 2008.

Taxa list	1991			2008		
	C	SE	F	C	SE	F
RHODOPHYTA						
Acrosorium ciliolatum (Harv.) Kylin	0.0	0.0	5.1	1.8	0.2	73.7
Aglaothamnion cordatum (Børgesen) Feldm.-Maz.	0.1	0.0	10.5	0.1	0.0	6.5
Aglaothamnion gallicum (Nägeli) Halos ex Ardré	–		–	0.0	0.0	0.3
Aglaothamnion tenuissimum (Bonnem.) Feldm.-Maz.	–	–	–	7.0	0.8	64.1
Aglaothamnion tripinnatum (C. Agardh) Feldm.-Maz.	–	–	–	0.0	0.0	2.5
Ahnfeltia plicata (Huds.) Fr.	0.0	0.0	0.3	–	–	–
Ahnfeltiopsis devoniensis (Grev.) P.C. Silva & DeCew	0.0	0.0	1.1	0.0	0.0	1.7

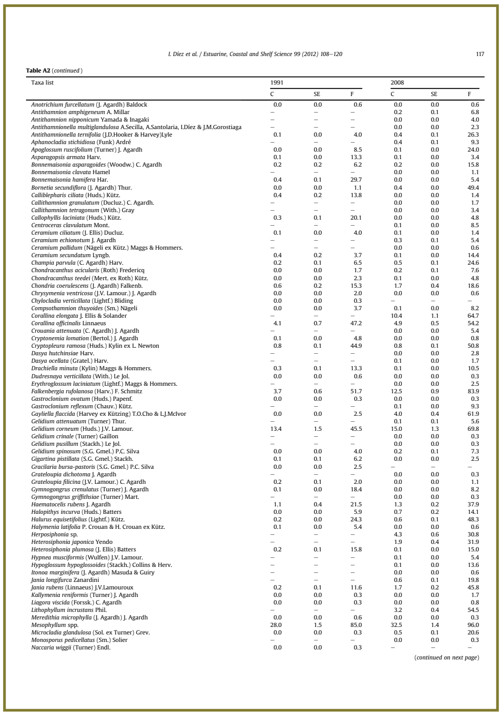

Table A2 (*continued*)

Taxa list	1991			2008		
	C	SE	F	C	SE	F
Anotrichium furcellatum (J. Agardh) Baldock	0.0	0.0	0.6	0.0	0.0	0.6
Antithamnion amphigeneum A. Millar	–	–	–	0.2	0.1	6.8
Antithamnion nipponicum Yamada & Inagaki	–	–	–	0.0	0.0	4.0
Antithamnionella multiglandulosa A.Secilla, A.Santolaria, I.Díez & J.M.Gorostiaga	–	–	–	0.0	0.0	2.3
Antithamnionella ternifolia (J.D.Hooker & Harvey)Lyle	0.1	0.0	4.0	0.4	0.1	26.3
Aphanocladia stichidiosa (Funk) Ardré	–	–	–	0.4	0.1	9.3
Apoglossum ruscifolium (Turner) J. Agardh	0.0	0.0	8.5	0.1	0.0	24.0
Asparagopsis armata Harv.	0.1	0.0	13.3	0.1	0.0	3.4
Bonnemaisonia asparagoides (Woodw.) C. Agardh	0.2	0.2	6.2	0.2	0.0	15.8
Bonnemaisonia clavata Hamel	–	–	–	0.0	0.0	1.1
Bonnemaisonia hamifera Har.	0.4	0.1	29.7	0.0	0.0	5.4
Bornetia secundiflora (J. Agardh) Thur.	0.0	0.0	1.1	0.4	0.0	49.4
Calliblepharis ciliata (Huds.) Kütz.	0.4	0.2	13.8	0.0	0.0	1.4
Callithamnion granulatum (Ducluz.) C. Agardh.	–	–	–	0.0	0.0	1.7
Callithamnion tetragonum (With.) Gray	–	–	–	0.0	0.0	3.4
Callophyllis laciniata (Huds.) Kütz.	0.3	0.1	20.1	0.0	0.0	4.8
Centroceras clavulatum Mont.	–	–	–	0.1	0.0	8.5
Ceramium ciliatum (J. Ellis) Ducluz.	0.1	0.0	4.0	0.1	0.0	1.4
Ceramium echionotum J. Agardh	–	–	–	0.3	0.1	5.4
Ceramium pallidum (Nägeli ex Kütz.) Maggs & Hommers.	–	–	–	0.0	0.0	0.6
Ceramium secundatum Lyngb.	0.4	0.2	3.7	0.1	0.0	14.4
Champia parvula (C. Agardh) Harv.	0.2	0.1	6.5	0.5	0.1	24.6
Chondracanthus acicularis (Roth) Fredericq	0.0	0.0	1.7	0.2	0.1	7.6
Chondracanthus teedei (Mert. ex Roth) Kütz.	0.0	0.0	2.3	0.1	0.0	4.8
Chondria coerulescens (J. Agardh) Falkenb.	0.6	0.2	15.3	1.7	0.4	18.6
Chrysymenia ventricosa (J.V. Lamour.) J. Agardh	0.0	0.0	2.0	0.0	0.0	0.6
Chylocladia verticillata (Lightf.) Bliding	0.0	0.0	0.3	–	–	–
Compsothamnion thuyoides (Sm.) Nägeli	0.0	0.0	3.7	0.1	0.0	8.2
Corallina elongata J. Ellis & Solander	–	–	–	10.4	1.1	64.7
Corallina officinalis Linnaeus	4.1	0.7	47.2	4.9	0.5	54.2
Crouania attenuata (C. Agardh) J. Agardh	–	–	–	0.0	0.0	5.4
Cryptonemia lomation (Bertol.) J. Agardh	0.1	0.0	4.8	0.0	0.0	0.8
Cryptopleura ramosa (Huds.) Kylin ex L. Newton	0.8	0.1	44.9	0.8	0.1	50.8
Dasya hutchinsiae Harv.	–	–	–	0.0	0.0	2.8
Dasya ocellata (Gratel.) Harv.	–	–	–	0.1	0.0	1.7
Drachiella minuta (Kylin) Maggs & Hommers.	0.3	0.1	13.3	0.1	0.0	10.5
Dudresnaya verticillata (With.) Le Jol.	0.0	0.0	0.6	0.0	0.0	0.3
Erythroglossum laciniatum (Lightf.) Maggs & Hommers.	–	–	–	0.0	0.0	2.5
Falkenbergia rufolanosa (Harv.) F. Schmitz	3.7	0.6	51.7	12.5	0.9	83.9
Gastroclonium ovatum (Huds.) Papenf.	0.0	0.0	0.3	0.0	0.0	0.3
Gastroclonium reflexum (Chauv.) Kütz.	–	–	–	0.1	0.0	9.3
Gayliella flaccida (Harvey ex Kützing) T.O.Cho & L.J.McIvor	0.0	0.0	2.5	4.0	0.4	61.9
Gelidium attenuatum (Turner) Thur.	–	–	–	0.1	0.1	5.6
Gelidium corneum (Huds.) J.V. Lamour.	13.4	1.5	45.5	15.0	1.3	69.8
Gelidium crinale (Turner) Gaillon	–	–	–	0.0	0.0	0.3
Gelidium pusillum (Stackh.) Le Jol.	–	–	–	0.0	0.0	0.3
Gelidium spinosum (S.G. Gmel.) P.C. Silva	0.0	0.0	4.0	0.2	0.1	7.3
Gigartina pistillata (S.G. Gmel.) Stackh.	0.1	0.1	6.2	0.0	0.0	2.5
Gracilaria bursa-pastoris (S.G. Gmel.) P.C. Silva	0.0	0.0	2.5	–	–	–
Grateloupia dichotoma J. Agardh	–	–	–	0.0	0.0	0.3
Grateloupia filicina (J.V. Lamour.) C. Agardh	0.2	0.1	2.0	0.0	0.0	1.1
Gymnogongrus crenulatus (Turner) J. Agardh	0.1	0.0	18.4	0.0	0.0	8.2
Gymnogongrus griffithsiae (Turner) Mart.	–	–	–	0.0	0.0	0.3
Haematocelis rubens J. Agardh	1.1	0.4	21.5	1.3	0.2	37.9
Halopithys incurva (Huds.) Batters	0.0	0.0	5.9	0.7	0.2	14.1
Halurus equisetifolius (Lightf.) Kütz.	0.2	0.0	24.3	0.6	0.1	48.3
Halymenia latifolia P. Crouan & H. Crouan ex Kütz.	0.1	0.0	5.4	0.0	0.0	0.6
Herposiphonia sp.	–	–	–	4.3	0.6	30.8
Heterosiphonia japonica Yendo	–	–	–	1.9	0.4	31.9
Heterosiphonia plumosa (J. Ellis) Batters	0.2	0.1	15.8	0.1	0.0	15.0
Hypnea musciformis (Wulfen) J.V. Lamour.	–	–	–	0.1	0.0	5.4
Hypoglossum hypoglossoides (Stackh.) Collins & Herv.	–	–	–	0.1	0.0	13.6
Itonoa marginifera (J. Agardh) Masuda & Guiry	–	–	–	0.0	0.0	0.6
Jania longifurca Zanardini	–	–	–	0.6	0.1	19.8
Jania rubens (Linnaeus) J.V.Lamouroux	0.2	0.1	11.6	1.7	0.2	45.8
Kallymenia reniformis (Turner) J. Agardh	0.0	0.0	0.3	0.0	0.0	1.7
Liagora viscida (Forssk.) C. Agardh	0.0	0.0	0.3	0.0	0.0	0.8
Lithophyllum incrustans Phil.	–	–	–	3.2	0.4	54.5
Meredithia microphylla (J. Agardh) J. Agardh	0.0	0.0	0.6	0.0	0.0	0.3
Mesophyllum spp.	28.0	1.5	85.0	32.5	1.4	96.0
Microcladia glandulosa (Sol. ex Turner) Grev.	0.0	0.0	0.3	0.5	0.1	20.6
Monosporus pedicellatus (Sm.) Solier	–	–	–	0.0	0.0	0.3
Naccaria wiggii (Turner) Endl.	0.0	0.0	0.3	–	–	–

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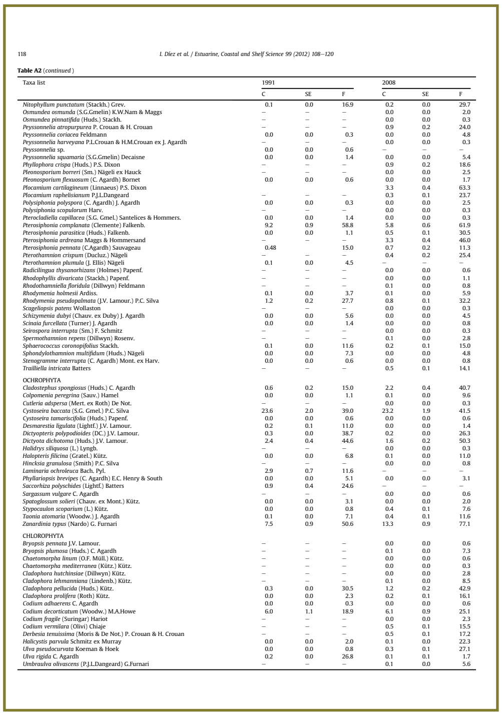

Table A2 (*continued*)

Taxa list	1991			2008		
	C	SE	F	C	SE	F
Nitophyllum punctatum (Stackh.) Grev.	0.1	0.0	16.9	0.2	0.0	29.7
Osmundea osmunda (S.G.Gmelin) K.W.Nam & Maggs	–	–	–	0.0	0.0	2.0
Osmundea pinnatifida (Huds.) Stackh.	–	–	–	0.0	0.0	0.3
Peyssonnelia atropurpurea P. Crouan & H. Crouan	–	–	–	0.9	0.2	24.0
Peyssonnelia coriacea Feldmann	0.0	0.0	0.3	0.0	0.0	4.8
Peyssonnelia harveyana P.L.Crouan & H.M.Crouan ex J. Agardh	–	–	–	0.0	0.0	0.3
Peyssonnelia sp.	0.0	0.0	0.6	–	–	–
Peyssonnelia squamaria (S.G.Gmelin) Decaisne	0.0	0.0	1.4	0.0	0.0	5.4
Phyllophora crispa (Huds.) P.S. Dixon	–	–	–	0.9	0.2	18.6
Pleonosporium borreri (Sm.) Nägeli ex Hauck	–	–	–	0.0	0.0	2.5
Pleonosporium flexuosum (C. Agardh) Bornet	0.0	0.0	0.6	0.0	0.0	1.7
Plocamium cartilagineum (Linnaeus) P.S. Dixon				3.3	0.4	63.3
Plocamium raphelisianum P.J.L.Dangeard	–	–	–	0.3	0.1	23.7
Polysiphonia polyspora (C. Agardh) J. Agardh	0.0	0.0	0.3	0.0	0.0	2.5
Polysiphonia scopulorum Harv.	–	–	–	0.0	0.0	0.3
Pterocladiella capillacea (S.G. Gmel.) Santelices & Hommers.	0.0	0.0	1.4	0.0	0.0	0.3
Pterosiphonia complanata (Clemente) Falkenb.	9.2	0.9	58.8	5.8	0.6	61.9
Pterosiphonia parasitica (Huds.) Falkenb.	0.0	0.0	1.1	0.5	0.1	30.5
Pterosiphonia ardreana Maggs & Hommersand	–	–	–	3.3	0.4	46.0
Pterosiphonia pennata (C.Agardh) Sauvageau	0.48		15.0	0.7	0.2	11.3
Pterothamnion crispum (Ducluz.) Nägeli	–	–	–	0.4	0.2	25.4
Pterothamnion plumula (J. Ellis) Nägeli	0.1	0.0	4.5	–	–	–
Radicilingua thysanorhizans (Holmes) Papenf.	–	–	–	0.0	0.0	0.6
Rhodophyllis divaricata (Stackh.) Papenf.	–	–	–	0.0	0.0	1.1
Rhodothamniella floridula (Dillwyn) Feldmann	–	–	–	0.1	0.0	0.8
Rhodymenia holmesii Ardiss.	0.1	0.0	3.7	0.1	0.0	5.9
Rhodymenia pseudopalmata (J.V. Lamour.) P.C. Silva	1.2	0.2	27.7	0.8	0.1	32.2
Scageliopsis patens Wollaston	–	–	–	0.0	0.0	0.3
Schizymenia dubyi (Chauv. ex Duby) J. Agardh	0.0	0.0	5.6	0.0	0.0	4.5
Scinaia furcellata (Turner) J. Agardh	0.0	0.0	1.4	0.0	0.0	0.8
Seirospora interrupta (Sm.) F. Schmitz	–	–	–	0.0	0.0	0.3
Spermothamnion repens (Dillwyn) Rosenv.	–	–	–	0.1	0.0	2.8
Sphaerococcus coronopifolius Stackh.	0.1	0.0	11.6	0.2	0.1	15.0
Sphondylothamnion multifidum (Huds.) Nägeli	0.0	0.0	7.3	0.0	0.0	4.8
Stenogramme interrupta (C. Agardh) Mont. ex Harv.	0.0	0.0	0.6	0.0	0.0	0.8
Trailliella intricata Batters	–	–	–	0.5	0.1	14.1
OCHROPHYTA						
Cladostephus spongiosus (Huds.) C. Agardh	0.6	0.2	15.0	2.2	0.4	40.7
Colpomenia peregrina (Sauv.) Hamel	0.0	0.0	1.1	0.1	0.0	9.6
Cutleria adspersa (Mert. ex Roth) De Not.	–	–	–	0.0	0.0	0.3
Cystoseira baccata (S.G. Gmel.) P.C. Silva	23.6	2.0	39.0	23.2	1.9	41.5
Cystoseira tamariscifolia (Huds.) Papenf.	0.0	0.0	0.6	0.0	0.0	0.6
Desmarestia ligulata (Lightf.) J.V. Lamour.	0.2	0.1	11.0	0.0	0.0	1.4
Dictyopteris polypodioides (DC.) J.V. Lamour.	0.3	0.0	38.7	0.2	0.0	26.3
Dictyota dichotoma (Huds.) J.V. Lamour.	2.4	0.4	44.6	1.6	0.2	50.3
Halidrys siliquosa (L.) Lyngb.	–	–	–	0.0	0.0	0.3
Halopteris filicina (Gratel.) Kütz.	0.0	0.0	6.8	0.1	0.0	11.0
Hincksia granulosa (Smith) P.C. Silva	–	–	–	0.0	0.0	0.8
Laminaria ochroleuca Bach. Pyl.	2.9	0.7	11.6	–	–	–
Phyllariopsis brevipes (C. Agardh) E.C. Henry & South	0.0	0.0	5.1	0.0	0.0	3.1
Saccorhiza polyschides (Lightf.) Batters	0.9	0.4	24.6	–	–	–
Sargassum vulgare C. Agardh	–	–	–	0.0	0.0	0.6
Spatoglossum solieri (Chauv. ex Mont.) Kütz.	0.0	0.0	3.1	0.0	0.0	2.0
Stypocaulon scoparium (L.) Kütz.	0.0	0.0	0.8	0.4	0.1	7.6
Taonia atomaria (Woodw.) J. Agardh	0.1	0.0	7.1	0.4	0.1	11.6
Zanardinia typus (Nardo) G. Furnari	7.5	0.9	50.6	13.3	0.9	77.1
CHLOROPHYTA						
Bryopsis pennata J.V. Lamour.	–	–	–	0.0	0.0	0.6
Bryopsis plumosa (Huds.) C. Agardh	–	–	–	0.1	0.0	7.3
Chaetomorpha linum (O.F. Müll.) Kütz.	–	–	–	0.0	0.0	0.6
Chaetomorpha mediterranea (Kütz.) Kütz.	–	–	–	0.0	0.0	0.3
Cladophora hutchinsiae (Dillwyn) Kütz.	–	–	–	0.0	0.0	2.8
Cladophora lehmanniana (Lindenb.) Kütz.	–	–	–	0.1	0.0	8.5
Cladophora pellucida (Huds.) Kütz.	0.3	0.0	30.5	1.2	0.2	42.9
Cladophora prolifera (Roth) Kütz.	0.0	0.0	2.3	0.2	0.1	16.1
Codium adhaerens C. Agardh	0.0	0.0	0.3	0.0	0.0	0.6
Codium decorticatum (Woodw.) M.A.Howe	6.0	1.1	18.9	6.1	0.9	25.1
Codium fragile (Suringar) Hariot	–	–	–	0.0	0.0	2.3
Codium vermilara (Olivi) Chiaje	–	–	–	0.5	0.1	15.5
Derbesia tenuissima (Moris & De Not.) P. Crouan & H. Crouan	–	–	–	0.5	0.1	17.2
Halicystis parvula Schmitz ex Murray	0.0	0.0	2.0	0.1	0.0	22.3
Ulva pseudocurvata Koeman & Hoek	0.0	0.0	0.8	0.3	0.1	27.1
Ulva rigida C. Agardh	0.2	0.0	26.8	0.1	0.1	1.7
Umbraulva olivascens (P.J.L.Dangeard) G.Furnari	–	–	–	0.1	0.0	5.6

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Azken hiru hamarkadetan Euskal Herriko kostaldean klima-aldaketak komunitate bentonikoetan (flora eta fauna) izan duen eragina

(The influence of Climate Change on benthic communities (flora and fauna) of the Basque Coast during the last 3 decades)

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LABURPENA: Errezela eratzen duten makroalgek, oro har, beherakada bortitza izan dute, eta horrek ekosistemako prozesuetan izango dituen eraginak ez dira oraindik ondo ezagutzen. Ikerketa honek Bizkaiko Golkoko hegoaldean 20 urte inguruko aldian substratu gogorreko ekosistema bentonikoak aztertu ditu, non *Gelidium corneum* makrofitoak beherakada nabarmena izan duen. Errezelak atzera egitearen edo aldaketaren tasa ikertu da, bai eta errezel-menpeko diren organismoen (algak eta ornogabeak) egitura taxonomiko eta funtzionalean ondorioak ere. Gure emaitzek erakutsi dute 2008an aldaketa garrantzitsuak zakarki gertatu zirela eta ondoren ez dela berreskuratze-seinalerik izan. Galera esanguratsuenak makroalga konplexu eta iraunkorrak diren formetan gertatu dira eta, aldiz, epifitoak diren eta ez diren suspentsiboroetan ere, alga sinple soropilduak ugaritu dira. Aldi berean, espezieen aberastasunak, algen dentsitateak eta flora eta faunaren ekitatibitateak gora egin dute. Ikerketaren 1. aldian (1998-2007), alga eta fauna espezie elkartuen talde koherenteak batera aldatzen dutela ikusten da. Hala ere, 2008tik aurrerantz finkatutako komunitate berrian algen eta ornogabeen arteko elkarte espezifikoak falta dira. Gure emaitzek flora eta fauna espezieen arteko ereduak daudela adierazten dute. Patroi hauek ekosistema bentonikoaren funtsezko espezie eta ezaugarri funtzionalen galeren ondorioak hobeto ulertzen lagunduko dute.

HITZ GAKOAK: Espezie elkartuak, Habitat biogenikoak, Makroalgen asanblajen beherakada, Ornogabeak.

ABSTRACT: *Canopy-forming macroalgae are globally facing drastic declines and the consequences for ecosystem processes remain still little known. The present investigation analyses in a 20 years period the retreat of shallow subtidal rocky benthos communities in the southern Bay of Biscay, where the macrophyte Gelidium corneum has suffered a notable decrease. The rate of change of canopy retreat was investigated as well as the effects of the decline on the taxonomic and functional structure of canopy-dependent organisms (algae and invertebrates). Our results show that major changes occurred abruptly in 2008, and no signs of recovery have been recorded afterwards. Major losses arose in complex perennial macroalgal forms together with epiphytic and no epiphytic suspensivores while simple turf-forming algae proliferated. At the same time, species richness, algal density and both flora and fauna evenness increased. There exist groups of coherent species of flora and fauna that covary during the first part of the studied period. However, from 2008 onwards the new established community lacked algal-invertebrate specific associations. Our results highlight patterns between flora and fauna species help to better understand the consequences of the loss of key species and functional traits for the benthic ecosystem.*

KEYWORDS: Macroalgal assemblages decline, Associated species, Invertebrates, Biogenic habitats.

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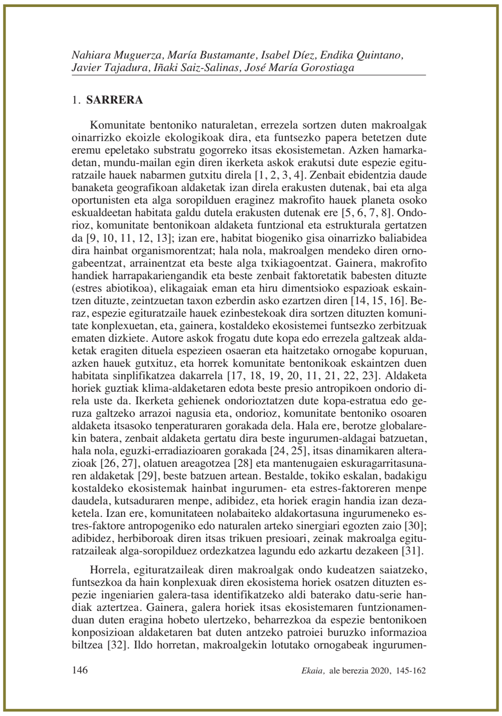
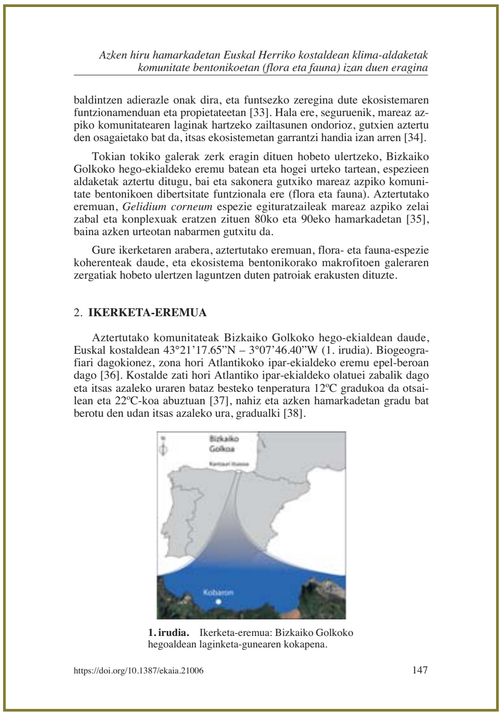


1. SARRERA

Komunitate bentoniko naturaletan, errezela sortzen duten makroalgak oinarrizko ekoizle ekologikoak dira, eta funtsezko papera betetzen dute eremu epeletako substratu gogorreko itsas ekosistemetan. Azken hamarkadetan, mundu-mailan egin diren ikerketa askok erakutsi dute espezie egituratzaile hauek nabarmen gutxitu direla [1, 2, 3, 4]. Zenbait ebidentzia daude banaketa geografikoan aldaketak izan direla erakusten dutenak, bai eta alga oportunisten eta alga soropilduen eraginez makrofito hauek planeta osoko eskualdeetan habitata galdu dutela erakusten dutenak ere [5, 6, 7, 8]. Ondorioz, komunitate bentonikoan aldaketa funtzional eta estrukturala gertatzen da [9, 10, 11, 12, 13]; izan ere, habitat biogeniko gisa oinarrizko baliabidea dira hainbat organismorentzat; hala nola, makroalgen mendeko diren ornogabeentzat, arrainentzat eta beste alga txikiagoentzat. Gainera, makrofito handiek harrapakariengandik eta beste zenbait faktoretatik babesten dituzte (estres abiotikoa), elikagaiak eman eta hiru dimentsioko espazioak eskaintzen dituzte, zeintzuetan taxon ezberdin asko ezartzen diren [14, 15, 16]. Beraz, espezie egituratzaile hauek ezinbestekoak dira sortzen dituzten komunitate konplexuetan, eta, gainera, kostaldeko ekosistemei funtsezko zerbitzuak ematen dizkiete. Autore askok frogatu dute kopa edo errezela galtzeak aldaketak eragiten dituela espezieen osaeran eta haitzetako ornogabe kopuruan, azken hauek gutxituz, eta horrek komunitate bentonikoak eskaintzen duen habitata sinplifikatzea dakarrela [17, 18, 19, 20, 11, 21, 22, 23]. Aldaketa horiek guztiak klima-aldaketaren edota beste presio antropikoen ondorio direla uste da. Ikerketa gehienek ondorioztatzen dute kopa-estratua edo geruza galtzeko arrazoi nagusia eta, ondorioz, komunitate bentoniko osoaren aldaketa itsasoko tenperaturaren gorakada dela. Hala ere, berotze globalarekin batera, zenbait aldaketa gertatu dira beste ingurumen-aldagai batzuetan, hala nola, eguzki-erradiazioaren gorakada [24, 25], itsas dinamikaren alterazioak [26, 27], olatuen areagotzea [28] eta mantenugaien eskuragarritasunaren aldaketak [29], beste batzuen artean. Bestalde, tokiko eskalan, badakigu kostaldeko ekosistemak hainbat ingurumen- eta estres-faktoreren menpe daudela, kutsaduraren menpe, adibidez, eta horiek eragin handia izan dezaketela. Izan ere, komunitateen nolabaiteko aldakortasuna ingurumeneko estres-faktore antropogeniko edo naturalen arteko sinergiari egozten zaio [30]; adibidez, herbiboroak diren itsas trikuen presioari, zeinak makroalga egituratzaileak alga-soropilduez ordezkatzea lagundu edo azkartu dezakeen [31].

Horrela, egituratzaileak diren makroalgak ondo kudeatzen saiatzeko, funtsezkoa da hain konplexuak diren ekosistema horiek osatzen dituzten espezie ingeniarien galera-tasa identifikatzeko aldi baterako datu-serie handiak aztertzea. Gainera, galera horiek itsas ekosistemaren funtzionamenduan duten eragina hobeto ulertzeko, beharrezkoa da espezie bentonikoen konposizioan aldaketaren bat duten antzeko patroiei buruzko informazioa biltzea [32]. Ildo horretan, makroalgekin lotutako ornogabeak ingurumen-



baldintzen adierazle onak dira, eta funtsezko zeregina dute ekosistemaren funtzionamenduan eta propietateetan [33]. Hala ere, seguruenik, mareaz azpiko komunitatearen laginak hartzeko zailtasunen ondorioz, gutxien aztertu den osagaietako bat da, itsas ekosistemetan garrantzi handia izan arren [34].

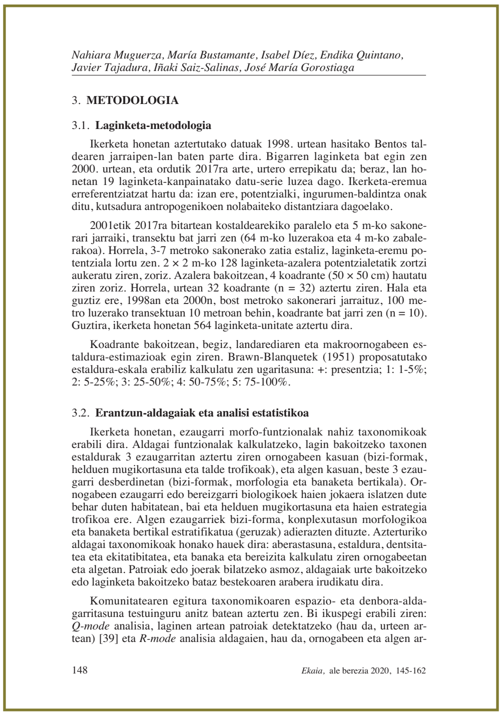
Tokian tokiko galerak zerk eragin dituen hobeto ulertzeko, Bizkaiko Golkoko hego-ekialdeko eremu batean eta hogei urteko tartean, espezieen aldaketak aztertu ditugu, bai eta sakonera gutxiko mareaz azpiko komunitate bentonikoen dibertsitate funtzionala ere (flora eta fauna). Aztertutako eremuan, *Gelidium corneum* espezie egituratzaileak mareaz azpiko zelai zabal eta konplexuak eratzen zituen 80ko eta 90eko hamarkadetan [35], baina azken urteotan nabarmen gutxitu da.

Gure ikerketaren arabera, aztertutako eremuan, flora- eta fauna-espezie koherenteak daude, eta ekosistema bentonikorako makrofitoen galeraren zergatiak hobeto ulertzen laguntzen duten patroiak erakusten dituzte.

2. IKERKETA-EREMUA

Aztertutako komunitateak Bizkaiko Golkoko hego-ekialdean daude, Euskal kostaldean 43°21’17.65”N – 3°07’46.40”W (1. irudia). Biogeografiari dagokionez, zona hori Atlantikoko ipar-ekialdeko eremu epel-beroan dago [36]. Kostalde zati hori Atlantiko ipar-ekialdeko olatuei zabalik dago eta itsas azaleko uraren bataz besteko tenperatura 12ºC gradukoa da otsailean eta 22ºC-koa abuztuan [37], nahiz eta azken hamarkadetan gradu bat berotu den udan itsas azaleko ura, gradualki [38].

1. irudia. Ikerketa-eremua: Bizkaiko Golkoko hegoaldean laginketa-gunearen kokapena.



3. METODOLOGIA

3.1. Laginketa-metodologia

Ikerketa honetan aztertutako datuak 1998. urtean hasitako Bentos taldearen jarraipen-lan baten parte dira. Bigarren laginketa bat egin zen 2000. urtean, eta ordutik 2017ra arte, urtero errepikatu da; beraz, lan honetan 19 laginketa-kanpainatako datu-serie luzea dago. Ikerketa-eremua erreferentziatzat hartu da: izan ere, potentzialki, ingurumen-baldintza onak ditu, kutsadura antropogenikoen nolabaiteko distantziara dagoelako.

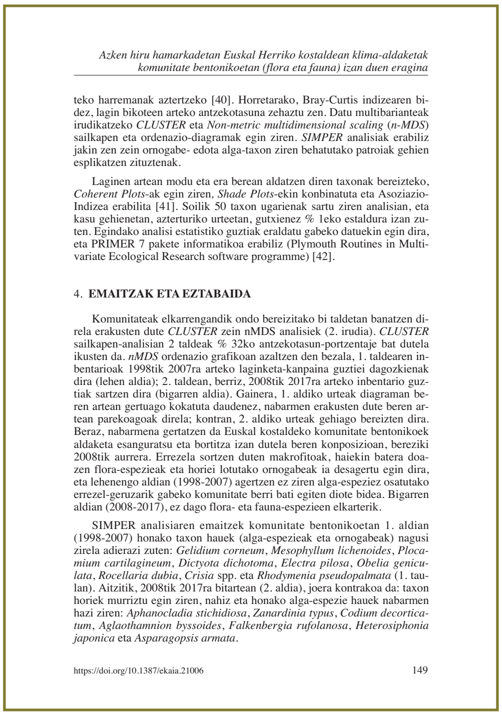
2001etik 2017ra bitartean kostaldearekiko paralelo eta 5 m-ko sakonerari jarraiki, transektu bat jarri zen (64 m-ko luzerakoa eta 4 m-ko zabalerakoa). Horrela, 3-7 metroko sakonerako zatia estaliz, laginketa-eremu potentziala lortu zen. 2 × 2 m-ko 128 laginketa-azalera potentzialetatik zortzi aukeratu ziren, zoriz. Azalera bakoitzean, 4 koadrante (50 × 50 cm) hautatu ziren zoriz. Horrela, urtean 32 koadrante (n = 32) aztertu ziren. Hala eta guztiz ere, 1998an eta 2000n, bost metroko sakonerari jarraituz, 100 metro luzerako transektuan 10 metroan behin, koadrante bat jarri zen (n = 10). Guztira, ikerketa honetan 564 laginketa-unitate aztertu dira.

Koadrante bakoitzean, begiz, landarediaren eta makroornogabeen estaldura-estimazioak egin ziren. Brawn-Blanquetek (1951) proposatutako estaldura-eskala erabiliz kalkulatu zen ugaritasuna: +: presentzia; 1: 1-5%; 2: 5-25%; 3: 25-50%; 4: 50-75%; 5: 75-100%.

3.2. Erantzun-aldagaiak eta analisi estatistikoa

Ikerketa honetan, ezaugarri morfo-funtzionalak nahiz taxonomikoak erabili dira. Aldagai funtzionalak kalkulatzeko, lagin bakoitzeko taxonen estaldurak 3 ezaugarritan aztertu ziren ornogabeen kasuan (bizi-formak, helduen mugikortasuna eta talde trofikoak), eta algen kasuan, beste 3 ezaugarri desberdinetan (bizi-formak, morfologia eta banaketa bertikala). Ornogabeen ezaugarri edo bereizgarri biologikoek haien jokaera islatzen dute behar duten habitatean, bai eta helduen mugikortasuna eta haien estrategia trofikoa ere. Algen ezaugarriek bizi-forma, konplexutasun morfologikoa eta banaketa bertikal estratifikatua (geruzak) adierazten dituzte. Azterturiko aldagai taxonomikoak honako hauek dira: aberastasuna, estaldura, dentsitatea eta ekitatibitatea, eta banaka eta bereizita kalkulatu ziren ornogabeetan eta algetan. Patroiak edo joerak bilatzeko asmoz, aldagaiak urte bakoitzeko edo laginketa bakoitzeko bataz bestekoaren arabera irudikatu dira.

Komunitatearen egitura taxonomikoaren espazio- eta denbora-aldagarritasuna testuinguru anitz batean aztertu zen. Bi ikuspegi erabili ziren: *Q-mode* analisia, laginen artean patroiak detektatzeko (hau da, urteen artean) [39] eta *R-mode* analisia aldagaien, hau da, ornogabeen eta algen ar-



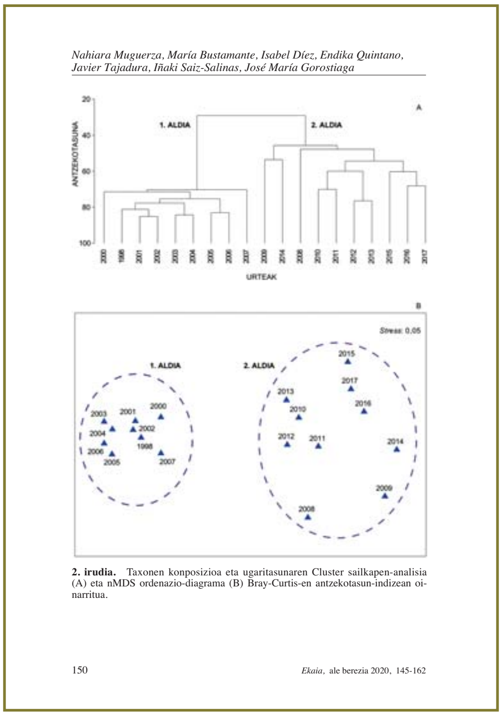
teko harremanak aztertzeko [40]. Horretarako, Bray-Curtis indizearen bidez, lagin bikoteen arteko antzekotasuna zehaztu zen. Datu multibarianteak irudikatzeko *CLUSTER* eta *Non-metric multidimensional scaling* (*n-MDS*) sailkapen eta ordenazio-diagramak egin ziren. *SIMPER* analisiak erabiliz jakin zen zein ornogabe- edota alga-taxon ziren behatutako patroiak gehien esplikatzen zituztenak.

Laginen artean modu eta era berean aldatzen diren taxonak bereizteko, *Coherent Plots*-ak egin ziren, *Shade Plots*-ekin konbinatuta eta Asoziazio-Indizea erabilita [41]. Soilik 50 taxon ugarienak sartu ziren analisian, eta kasu gehienetan, azterturiko urteetan, gutxienez % 1eko estaldura izan zuten. Egindako analisi estatistiko guztiak eraldatu gabeko datuekin egin dira, eta PRIMER 7 pakete informatikoa erabiliz (Plymouth Routines in Multivariate Ecological Research software programme) [42].

4. EMAITZAK ETA EZTABAIDA

Komunitateak elkarrengandik ondo bereizitako bi taldetan banatzen direla erakusten dute *CLUSTER* zein nMDS analisiek (2. irudia). *CLUSTER* sailkapen-analisian 2 taldeak % 32ko antzekotasun-portzentaje bat dutela ikusten da. *nMDS* ordenazio grafikoan azaltzen den bezala, 1. taldearen inbentarioak 1998tik 2007ra arteko laginketa-kanpaina guztiei dagozkienak dira (lehen aldia); 2. taldean, berriz, 2008tik 2017ra arteko inbentario guztiak sartzen dira (bigarren aldia). Gainera, 1. aldiko urteak diagraman beren artean gertuago kokatuta daudenez, nabarmen erakusten dute beren artean parekoagoak direla; kontran, 2. aldiko urteak gehiago bereizten dira. Beraz, nabarmena gertatzen da Euskal kostaldeko komunitate bentonikoek aldaketa esanguratsu eta bortitza izan dutela beren konposizioan, bereziki 2008tik aurrera. Errezela sortzen duten makrofitoak, haiekin batera doazen flora-espezieak eta horiei lotutako ornogabeak ia desagertu egin dira, eta lehenengo aldian (1998-2007) agertzen ez ziren alga-espeziez osatutako errezel-geruzarik gabeko komunitate berri bati egiten diote bidea. Bigarren aldian (2008-2017), ez dago flora- eta fauna-espezieen elkarterik.

SIMPER analisiaren emaitzek komunitate bentonikoetan 1. aldian (1998-2007) honako taxon hauek (alga-espezieak eta ornogabeak) nagusi zirela adierazi zuten: *Gelidium corneum*, *Mesophyllum lichenoides*, *Plocamium cartilagineum*, *Dictyota dichotoma*, *Electra pilosa*, *Obelia geniculata*, *Rocellaria dubia*, *Crisia* spp. eta *Rhodymenia pseudopalmata* (1. taulan). Aitzitik, 2008tik 2017ra bitartean (2. aldia), joera kontrakoa da: taxon horiek murriztu egin ziren, nahiz eta honako alga-espezie hauek nabarmen hazi ziren: *Aphanocladia stichidiosa*, *Zanardinia typus*, *Codium decorticatum*, *Aglaothamnion byssoides*, *Falkenbergia rufolanosa*, *Heterosiphonia japonica* eta *Asparagopsis armata*.



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2. irudia. Taxonen konposizioa eta ugaritasunaren Cluster sailkapen-analisia (A) eta nMDS ordenazio-diagrama (B) Bray-Curtis-en antzekotasun-indizean oinarritua.

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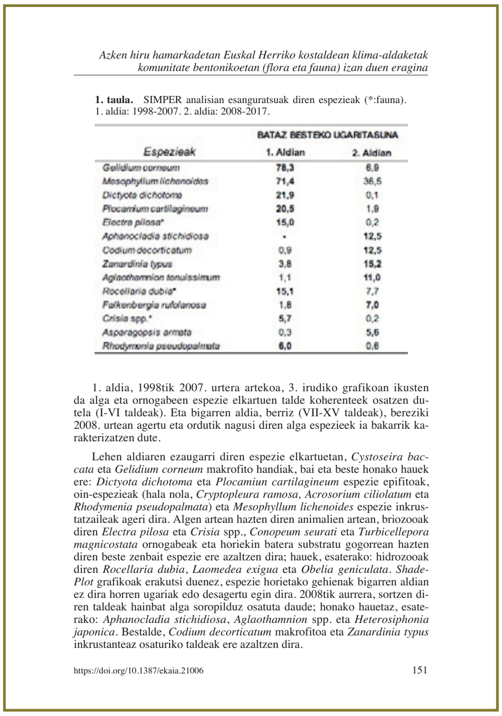

Azken hiru hamarkadetan Euskal Herriko kostaldean klima-aldaketak
komunitate bentonikoetan (flora eta fauna) izan duen eragina

1. taula. SIMPER analisian esanguratsuak diren espezieak (*:fauna). 1. aldia: 1998-2007. 2. aldia: 2008-2017.

Espezieak	BATAZ BESTEKO UGARITASUNA	
	1. Aldian	2. Aldian
Gelidium corneum	**78,3**	6,9
Mesophyllum lichenoides	**71,4**	36,5
Dictyota dichotoma	**21,9**	0,1
Plocamium cartilagineum	**20,5**	1,9
*Electra pilosa**	**15,0**	0,2
Aphanocladia stichidiosa	-	**12,5**
Codium decorticatum	0,9	**12,5**
Zanardinia typus	3,8	**15,2**
Aglaothamnion tenuissimum	1,1	**11,0**
*Rocellaria dubia**	**15,1**	7,7
Falkenbergia rufolanosa	1,8	**7,0**
*Crisia spp.**	**5,7**	0,2
Asparagopsis armata	0,3	**5,6**
Rhodymenia pseudopalmata	**6,0**	0,6

1. aldia, 1998tik 2007. urtera artekoa, 3. irudiko grafikoan ikusten da alga eta ornogabeen espezie elkartuen talde koherenteek osatzen dutela (I-VI taldeak). Eta bigarren aldia, berriz (VII-XV taldeak), bereziki 2008. urtean agertu eta ordutik nagusi diren alga espezieek ia bakarrik karakterizatzen dute.

Lehen aldiaren ezaugarri diren espezie elkartuetan, *Cystoseira baccata* eta *Gelidium corneum* makrofito handiak, bai eta beste honako hauek ere: *Dictyota dichotoma* eta *Plocamiun cartilagineum* espezie epifitoak, oin-espezieak (hala nola, *Cryptopleura ramosa, Acrosorium ciliolatum* eta *Rhodymenia pseudopalmata*) eta *Mesophyllum lichenoides* espezie inkrustatzaileak ageri dira. Algen artean hazten diren animalien artean, briozooak diren *Electra pilosa* eta *Crisia* spp., *Conopeum seurati* eta *Turbicellepora magnicostata* ornogabeak eta horiekin batera substratu gogorrean hazten diren beste zenbait espezie ere azaltzen dira; hauek, esaterako: hidrozooak diren *Rocellaria dubia*, *Laomedea exigua* eta *Obelia geniculata*. *Shade-Plot* grafikoak erakutsi duenez, espezie horietako gehienak bigarren aldian ez dira horren ugariak edo desagertu egin dira. 2008tik aurrera, sortzen diren taldeak hainbat alga soropilduz osatuta daude; honako hauetaz, esaterako: *Aphanocladia stichidiosa*, *Aglaothamnion* spp. eta *Heterosiphonia japonica*. Bestalde, *Codium decorticatum* makrofitoa eta *Zanardinia typus* inkrustanteaz osaturiko taldeak ere azaltzen dira.

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3. irudia. Taxonen arteko Asoziazio-Indizean oinarritutako datu-matrizearen *Shade-plot*-a, non 15 talde koherente erakusten diren (I-XV) aztertutako 19 urteetarako. Taxon berdeak alga-espezieak dira eta laranjak ornogabeak. Marra eten moreak bi aldiak bereizten ditu sailkapen- eta ordenazio-analisietan erakusten den moduan. Espazio hutsek urte jakin baterako taxon baten falta adierazten dute. Marra beltz etengabeak aldagai-multzo esanguratsuak (p > 0,05) adierazten ditu eta marra eten gorriak zein taxon taldetan hipotesi nulua ezin den baztertu (p > 0,05) adierazten du.

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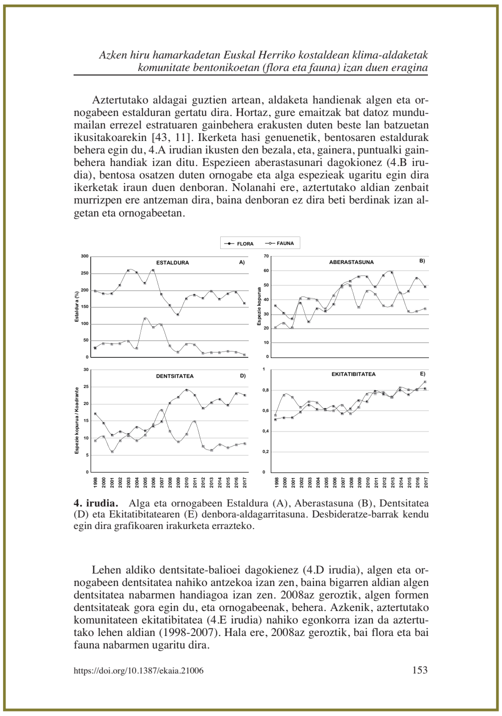

Azken hiru hamarkadetan Euskal Herriko kostaldean klima-aldaketak
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Aztertutako aldagai guztien artean, aldaketa handienak algen eta ornogabeen estalduran gertatu dira. Hortaz, gure emaitzak bat datoz mundu-mailan errezel estratuaren gainbehera erakusten duten beste lan batzuetan ikusitakoarekin [43, 11]. Ikerketa hasi genuenetik, bentosaren estaldurak behera egin du, 4.A irudian ikusten den bezala, eta, gainera, puntualki gainbehera handiak izan ditu. Espezieen aberastasunari dagokionez (4.B irudia), bentosa osatzen duten ornogabe eta alga espezieak ugaritu egin dira ikerketak iraun duen denboran. Nolanahi ere, aztertutako aldian zenbait murrizpen ere antzeman dira, baina denboran ez dira beti berdinak izan algetan eta ornogabeetan.

4. irudia. Alga eta ornogabeen Estaldura (A), Aberastasuna (B), Dentsitatea (D) eta Ekitatibitatearen (E) denbora-aldagarritasuna. Desbideratze-barrak kendu egin dira grafikoaren irakurketa errazteko.

Lehen aldiko dentsitate-balioei dagokienez (4.D irudia), algen eta ornogabeen dentsitatea nahiko antzekoa izan zen, baina bigarren aldian algen dentsitatea nabarmen handiagoa izan zen. 2008az geroztik, algen formen dentsitateak gora egin du, eta ornogabeenak, behera. Azkenik, aztertutako komunitateen ekitatibitatea (4.E irudia) nahiko egonkorra izan da aztertutako lehen aldian (1998-2007). Hala ere, 2008az geroztik, bai flora eta bai fauna nabarmen ugaritu dira.

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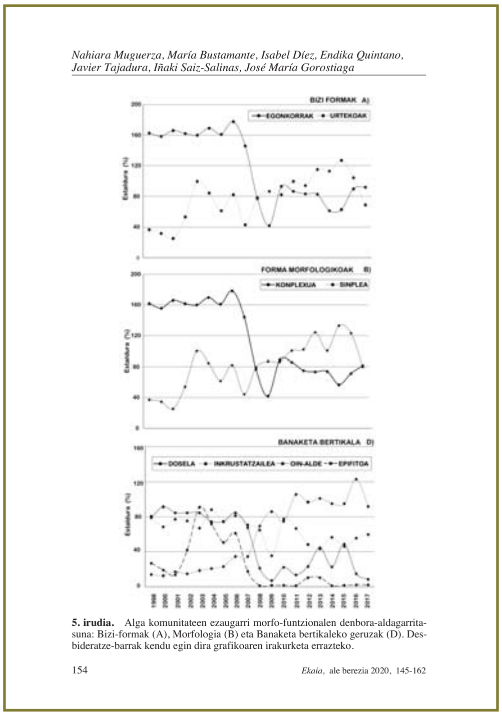

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5. irudia. Alga komunitateen ezaugarri morfo-funtzionalen denbora-aldagarritasuna: Bizi-formak (A), Morfologia (B) eta Banaketa bertikaleko geruzak (D). Desbideratze-barrak kendu egin dira grafikoaren irakurketa errazteko.

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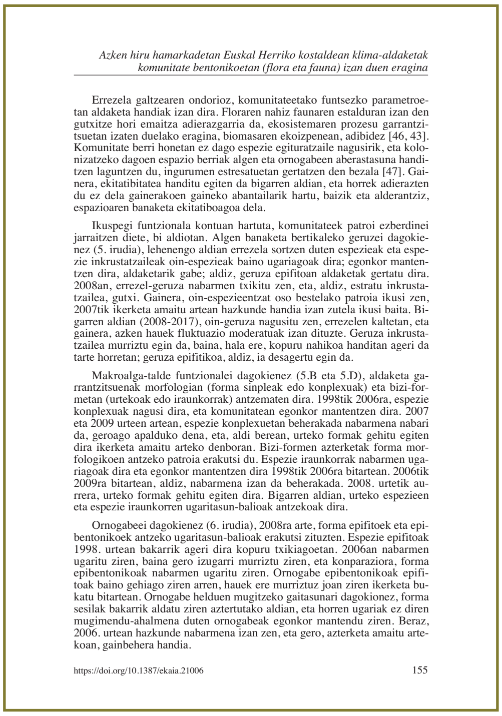

Azken hiru hamarkadetan Euskal Herriko kostaldean klima-aldaketak
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Errezela galtzearen ondorioz, komunitateetako funtsezko parametroetan aldaketa handiak izan dira. Floraren nahiz faunaren estalduran izan den gutxitze hori emaitza adierazgarria da, ekosistemaren prozesu garrantzitsuetan izaten duelako eragina, biomasaren ekoizpenean, adibidez [46, 43]. Komunitate berri honetan ez dago espezie egituratzaile nagusirik, eta kolonizatzeko dagoen espazio berriak algen eta ornogabeen aberastasuna handitzen laguntzen du, ingurumen estresatuetan gertatzen den bezala [47]. Gainera, ekitatibitatea handitu egiten da bigarren aldian, eta horrek adierazten du ez dela gainerakoen gaineko abantailarik hartu, baizik eta alderantziz, espazioaren banaketa ekitatiboagoa dela.

Ikuspegi funtzionala kontuan hartuta, komunitateek patroi ezberdinei jarraitzen diete, bi aldiotan. Algen banaketa bertikaleko geruzei dagokienez (5. irudia), lehenengo aldian errezela sortzen duten espezieak eta espezie inkrustatzaileak oin-espezieak baino ugariagoak dira; egonkor mantentzen dira, aldaketarik gabe; aldiz, geruza epifitoan aldaketak gertatu dira. 2008an, errezel-geruza nabarmen txikitu zen, eta, aldiz, estratu inkrustatzailea, gutxi. Gainera, oin-espezieentzat oso bestelako patroia ikusi zen, 2007tik ikerketa amaitu artean hazkunde handia izan zutela ikusi baita. Bigarren aldian (2008-2017), oin-geruza nagusitu zen, errezelen kaltetan, eta gainera, azken hauek fluktuazio moderatuak izan dituzte. Geruza inkrustatzailea murriztu egin da, baina, hala ere, kopuru nahikoa handitan ageri da tarte horretan; geruza epifitikoa, aldiz, ia desagertu egin da.

Makroalga-talde funtzionalei dagokienez (5.B eta 5.D), aldaketa garrantzitsuenak morfologian (forma sinpleak edo konplexuak) eta bizi-formetan (urtekoak edo iraunkorrak) antzematen dira. 1998tik 2006ra, espezie konplexuak nagusi dira, eta komunitatean egonkor mantentzen dira. 2007 eta 2009 urteen artean, espezie konplexuetan beherakada nabarmena nabari da, geroago apalduko dena, eta, aldi berean, urteko formak gehitu egiten dira ikerketa amaitu arteko denboran. Bizi-formen azterketak forma morfologikoen antzeko patroia erakutsi du. Espezie iraunkorrak nabarmen ugariagoak dira eta egonkor mantentzen dira 1998tik 2006ra bitartean. 2006tik 2009ra bitartean, aldiz, nabarmena izan da beherakada. 2008. urtetik aurrera, urteko formak gehitu egiten dira. Bigarren aldian, urteko espezieen eta espezie iraunkorren ugaritasun-balioak antzekoak dira.

Ornogabeei dagokienez (6. irudia), 2008ra arte, forma epifitoek eta epibentonikoek antzeko ugaritasun-balioak erakutsi zituzten. Espezie epifitoak 1998. urtean bakarrik ageri dira kopuru txikiagoetan. 2006an nabarmen ugaritu ziren, baina gero izugarri murriztu ziren, eta konparaziora, forma epibentonikoak nabarmen ugaritu ziren. Ornogabe epibentonikoak epifitoak baino gehiago ziren arren, hauek ere murriztuz joan ziren ikerketa bukatu bitartean. Ornogabe helduen mugitzeko gaitasunari dagokionez, forma sesilak bakarrik aldatu ziren aztertutako aldian, eta horren ugariak ez diren mugimendu-ahalmena duten ornogabeak egonkor mantendu ziren. Beraz, 2006. urtean hazkunde nabarmena izan zen, eta gero, azterketa amaitu artekoan, gainbehera handia.

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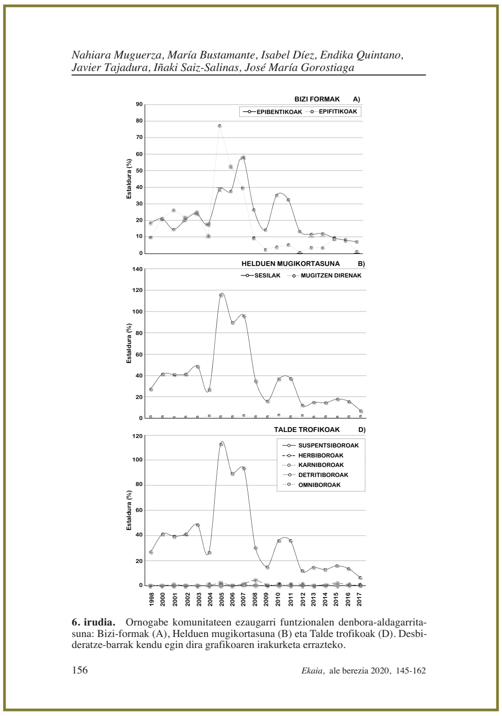

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6. irudia. Ornogabe komunitateen ezaugarri funtzionalen denbora-aldagarritasuna: Bizi-formak (A), Helduen mugikortasuna (B) eta Talde trofikoak (D). Desbideratze-barrak kendu egin dira grafikoaren irakurketa errazteko.

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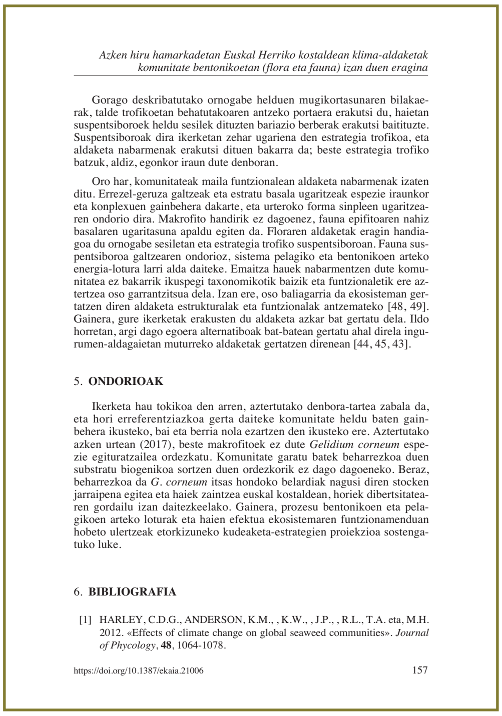

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Gorago deskribatutako ornogabe helduen mugikortasunaren bilakaerak, talde trofikoetan behatutakoaren antzeko portaera erakutsi du, haietan suspentsiboroek heldu sesilek dituzten bariazio berberak erakutsi baitituzte. Suspentsiboroak dira ikerketan zehar ugariena den estrategia trofikoa, eta aldaketa nabarmenak erakutsi dituen bakarra da; beste estrategia trofiko batzuk, aldiz, egonkor iraun dute denboran.

Oro har, komunitateak maila funtzionalean aldaketa nabarmenak izaten ditu. Errezel-geruza galtzeak eta estratu basala ugaritzeak espezie iraunkor eta konplexuen gainbehera dakarte, eta urteroko forma sinpleen ugaritzearen ondorio dira. Makrofito handirik ez dagoenez, fauna epifitoaren nahiz basalaren ugaritasuna apaldu egiten da. Floraren aldaketak eragin handiagoa du ornogabe sesiletan eta estrategia trofiko suspentsiboroan. Fauna suspentsiboroa galtzearen ondorioz, sistema pelagiko eta bentonikoen arteko energia-lotura larri alda daiteke. Emaitza hauek nabarmentzen dute komunitatea ez bakarrik ikuspegi taxonomikotik baizik eta funtzionaletik ere aztertzea oso garrantzitsua dela. Izan ere, oso baliagarria da ekosisteman gertatzen diren aldaketa estrukturalak eta funtzionalak antzemateko [48, 49]. Gainera, gure ikerketak erakusten du aldaketa azkar bat gertatu dela. Ildo horretan, argi dago egoera alternatiboak bat-batean gertatu ahal direla ingurumen-aldagaietan muturreko aldaketak gertatzen direnean [44, 45, 43].

5. ONDORIOAK

Ikerketa hau tokikoa den arren, aztertutako denbora-tartea zabala da, eta hori erreferentziazkoa gerta daiteke komunitate heldu baten gainbehera ikusteko, bai eta berria nola ezartzen den ikusteko ere. Aztertutako azken urtean (2017), beste makrofitoek ez dute *Gelidium corneum* espezie egituratzailea ordezkatu. Komunitate garatu batek beharrezkoa duen substratu biogenikoa sortzen duen ordezkorik ez dago dagoeneko. Beraz, beharrezkoa da *G. corneum* itsas hondoko belardiak nagusi diren stocken jarraipena egitea eta haiek zaintzea euskal kostaldean, horiek dibertsitatearen gordailu izan daitezkeelako. Gainera, prozesu bentonikoen eta pelagikoen arteko loturak eta haien efektua ekosistemaren funtzionamenduan hobeto ulertzeak etorkizuneko kudeaketa-estrategien proiekzioa sostengatuko luke.

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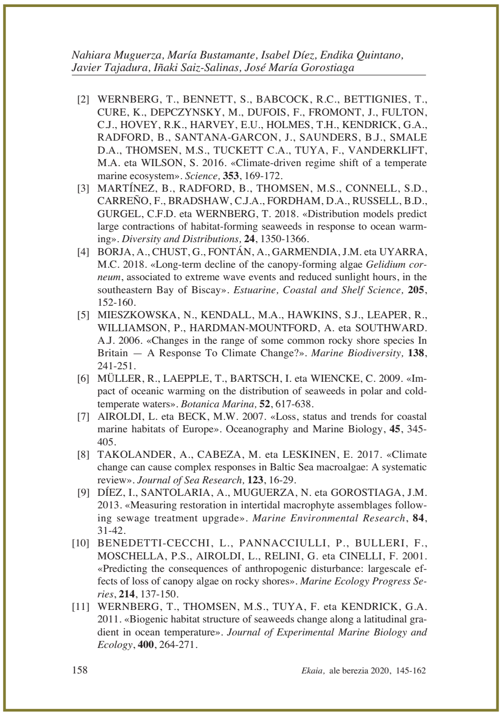

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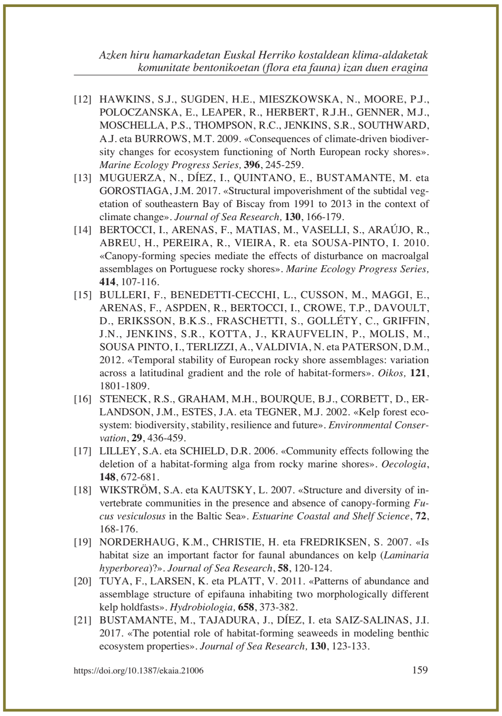

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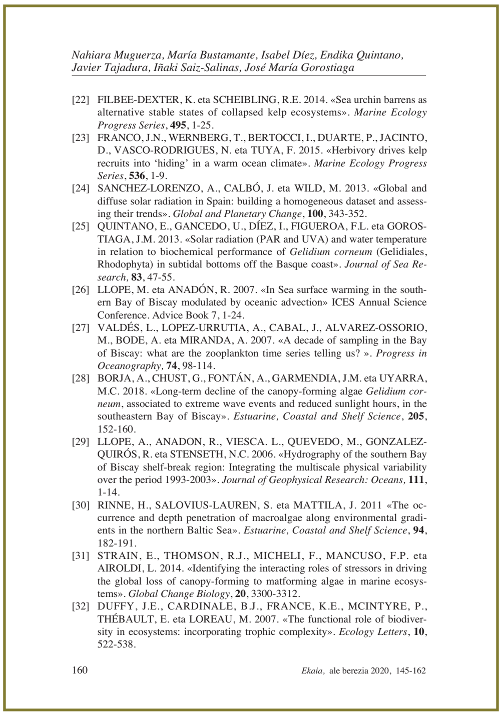

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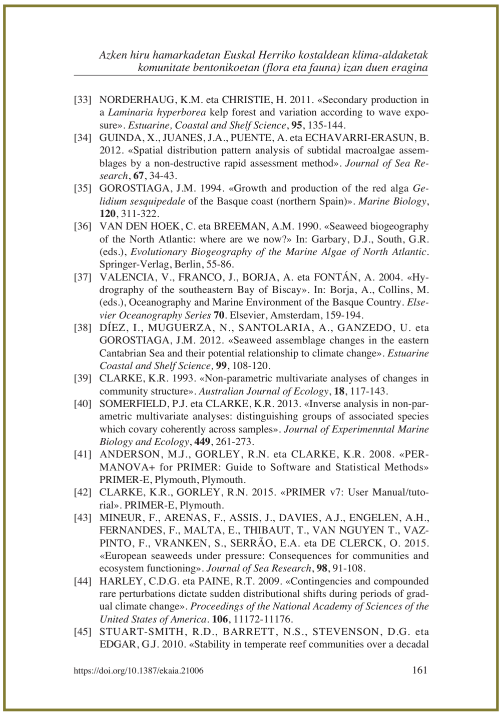

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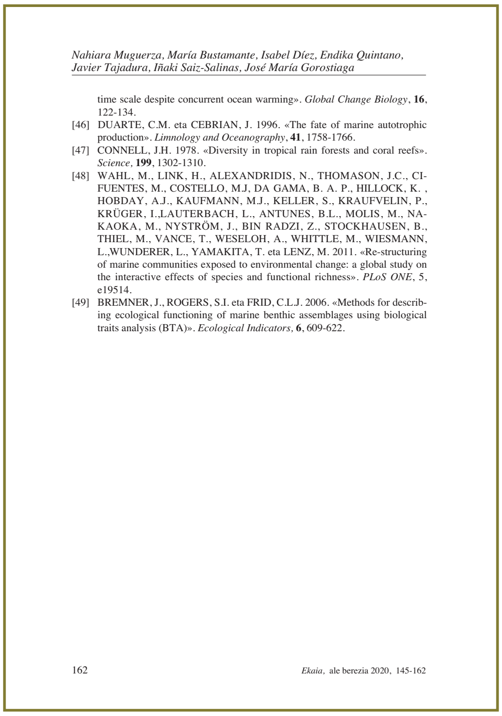

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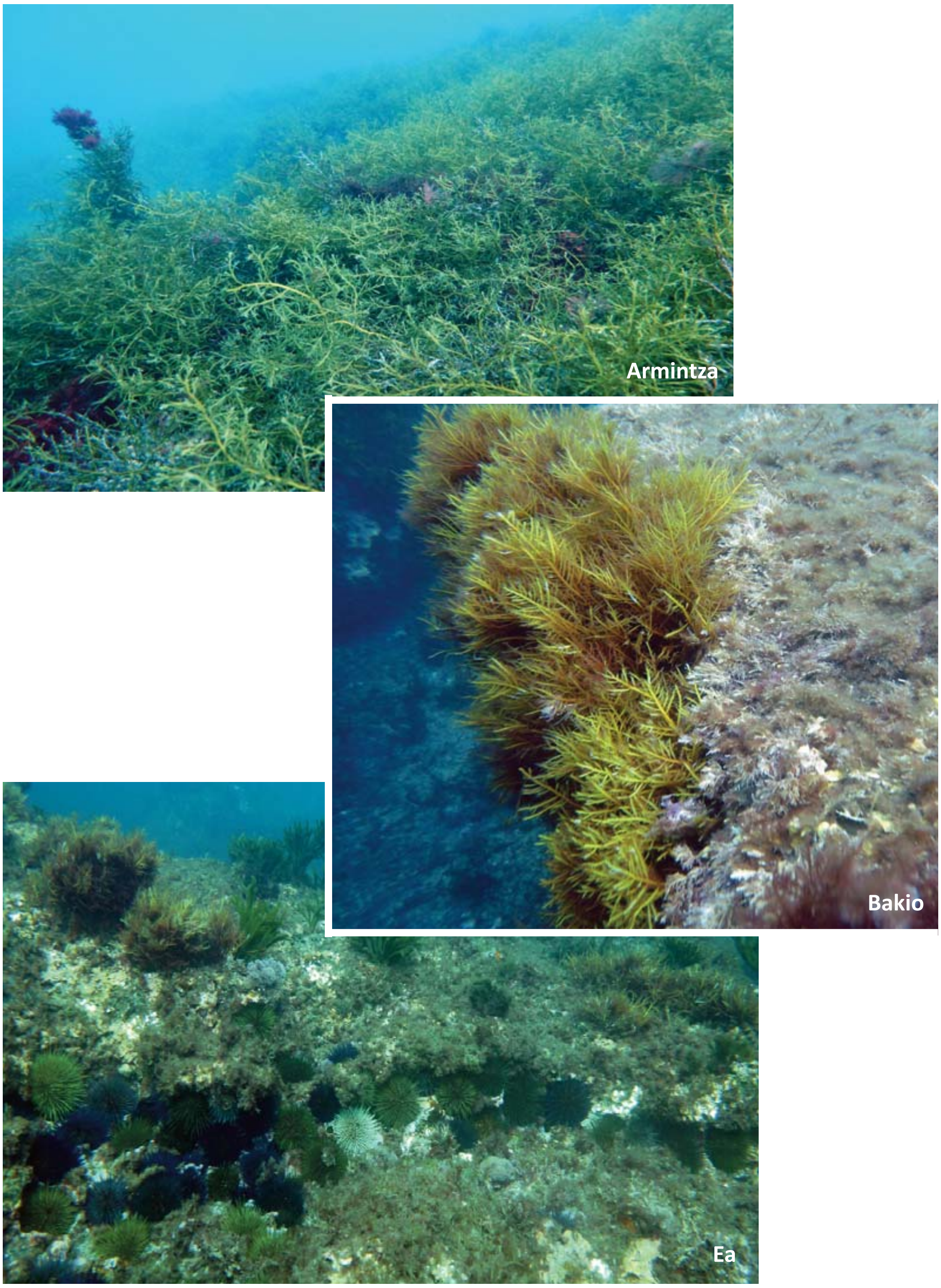
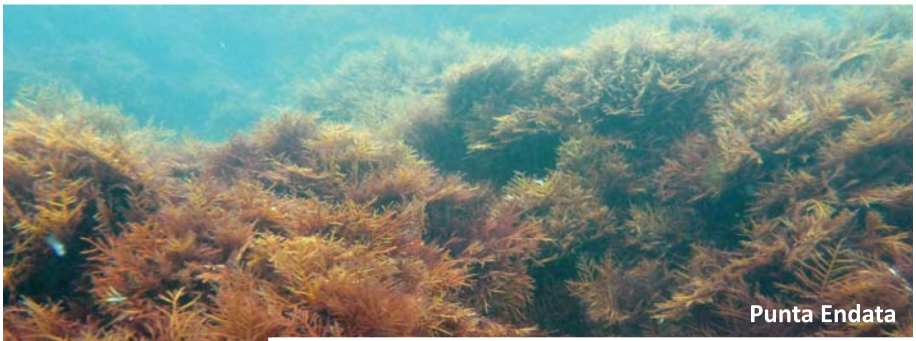
Annex II: Photographs

General aspect of the subtidal rocky benthos at sampling locations





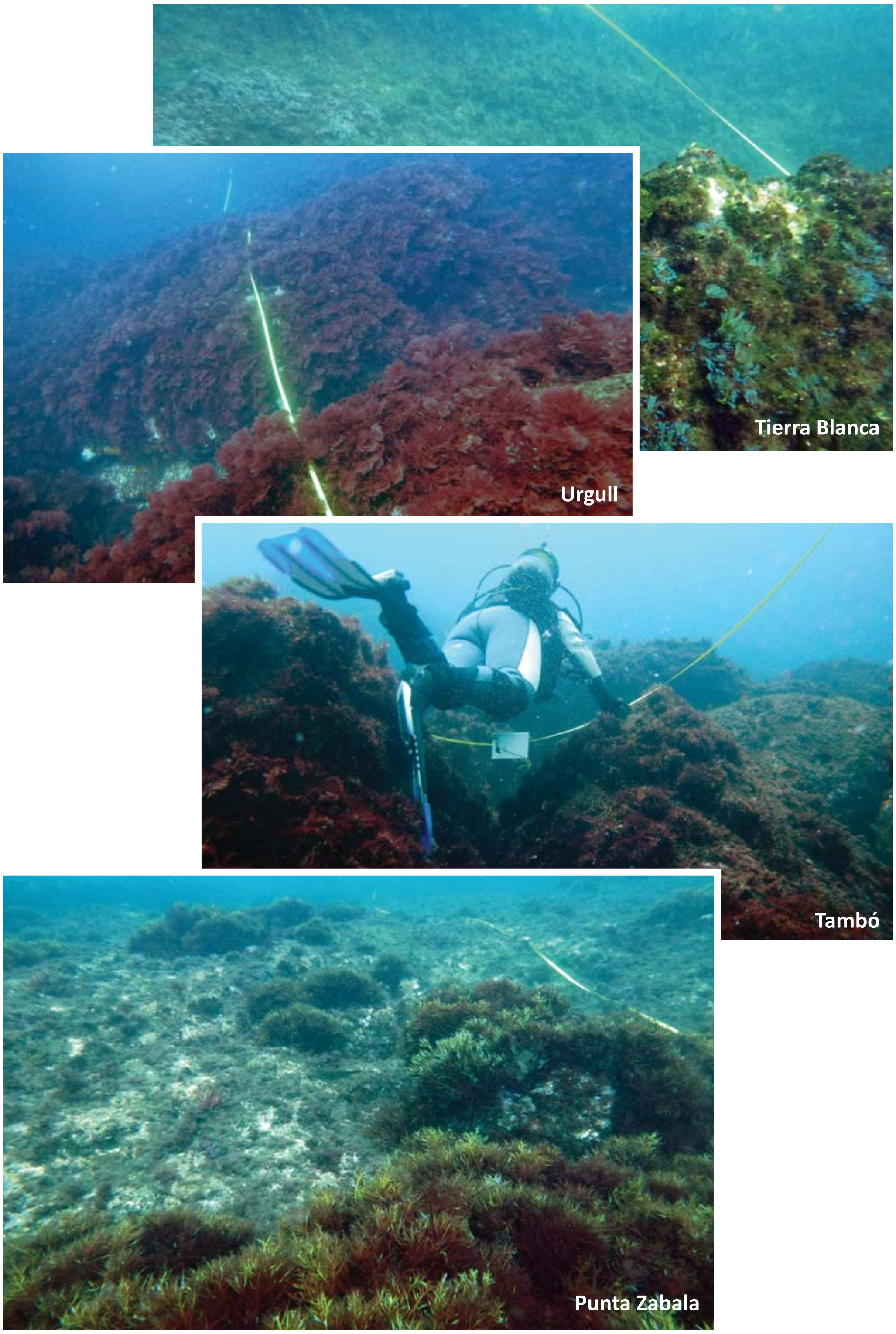
Punta Endata

Punta Iteiko

Punta Zabala

Higuer

Placement of the transect in the subtidal

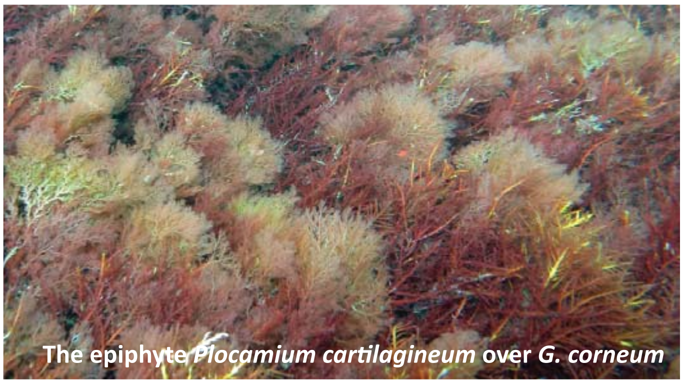

Tierra Blanca
Urgull
Tambó
Punta Zabala

Details of subtidal communities

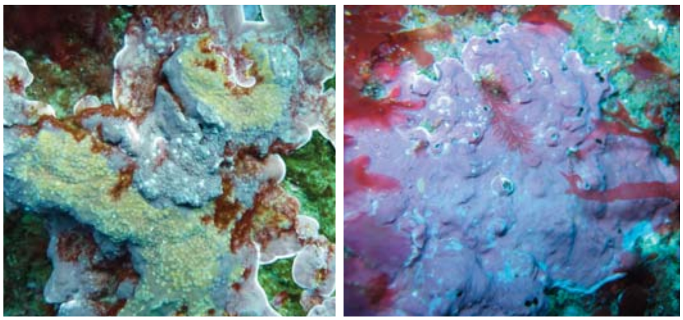
Extensive canopy stands

G. corneum with the epiphyte *Dictyota dichotoma*

Stand of *Cystoseira baccata*

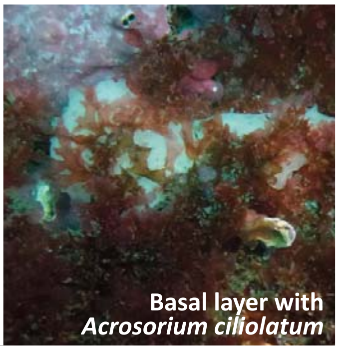


The epiphyte *Plocamium cartilagineum* over *G. corneum*



Crustose layer

Basal layer with *Corallina officinalis*

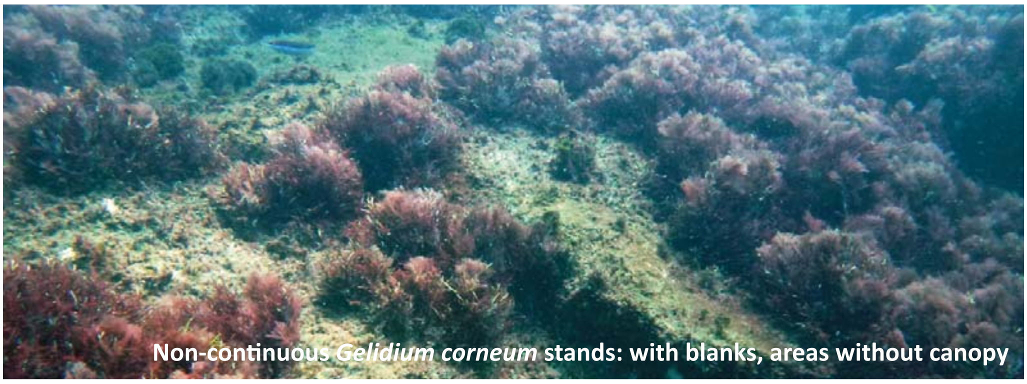


Basal layer with *Acrosorium ciliolatum*

Basal layer with *Rhodymenia pseudopalmata*

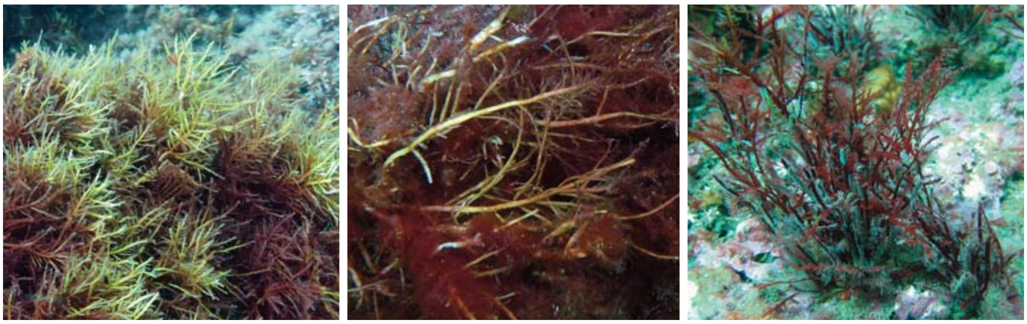
Details of subtidal communities

The decline of the canopy

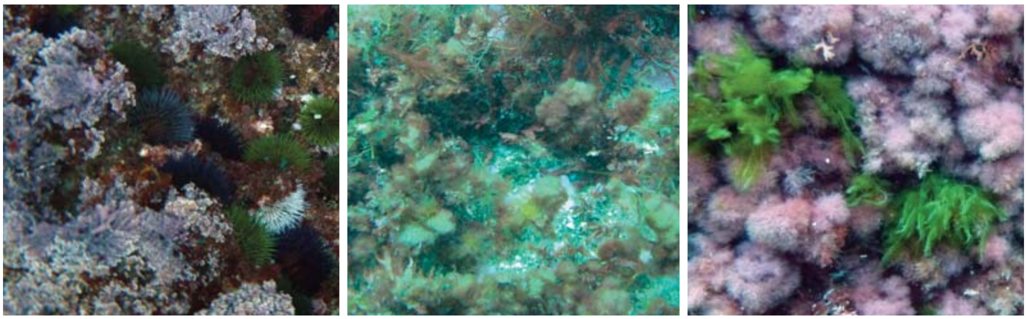


Non-continuous *Gelidium corneum* stands: with blanks, areas without canopy

The entry of non perennial species such as *Codium decorticatum* and *Asparagopsis armata*



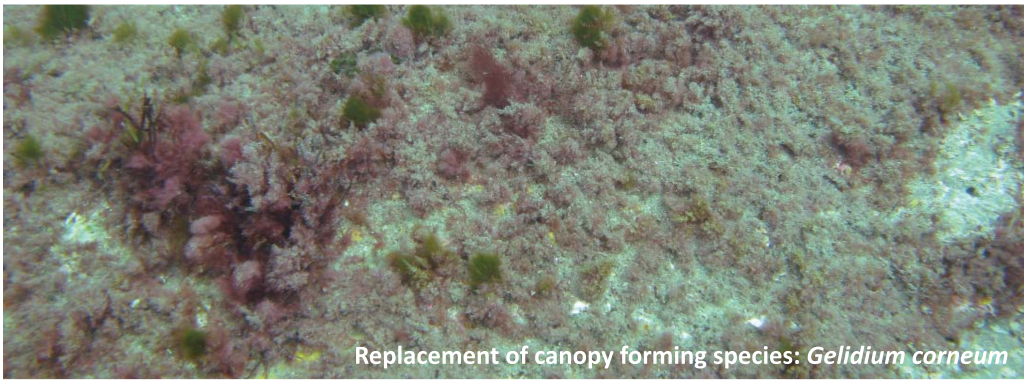
Stress symptoms in *Gelidium corneum*

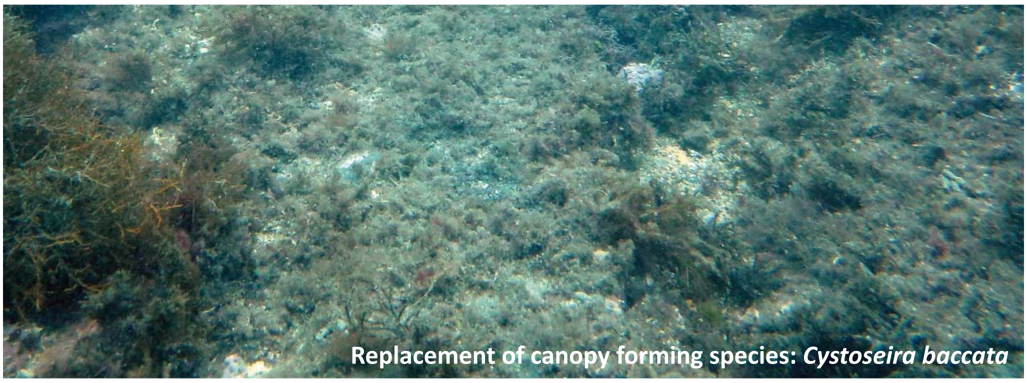


Proliferation of the basal layer

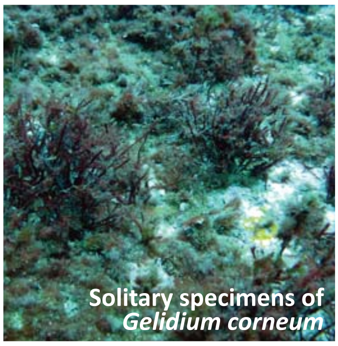
Details of subtidal communities

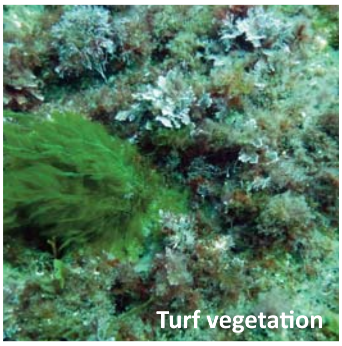
In the absence of the canopy


Replacement of canopy forming species: *Gelidium corneum*

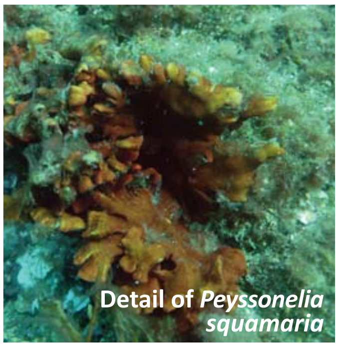

Replacement of canopy forming species: *Cystoseira baccata*

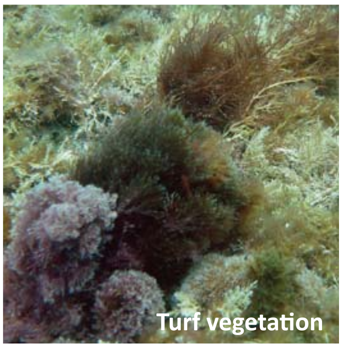

Codium spp.
no perennial canopy


Solitary specimens of
Gelidium corneum


Turf vegetation


Detail of *Ellisondia elongata*


Detail of *Peyssonelia*
squamaria


Turf vegetation

Underwater data colletion


Punta Zabala


Ea

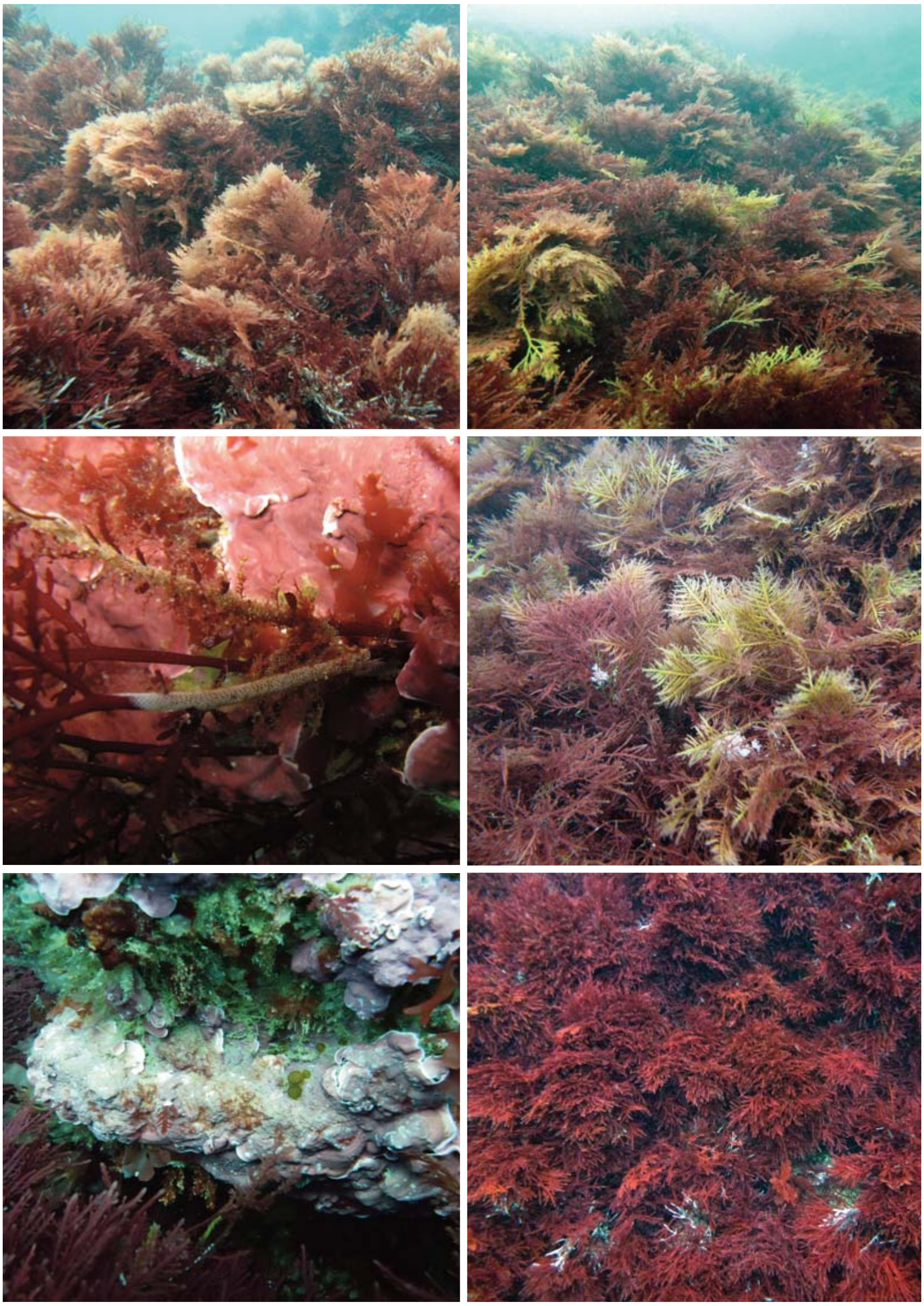

Getaria


Tambó


Tierra Blanca

KOBARON: Before and After (Photos illustrate the change from 2002 to 2017)

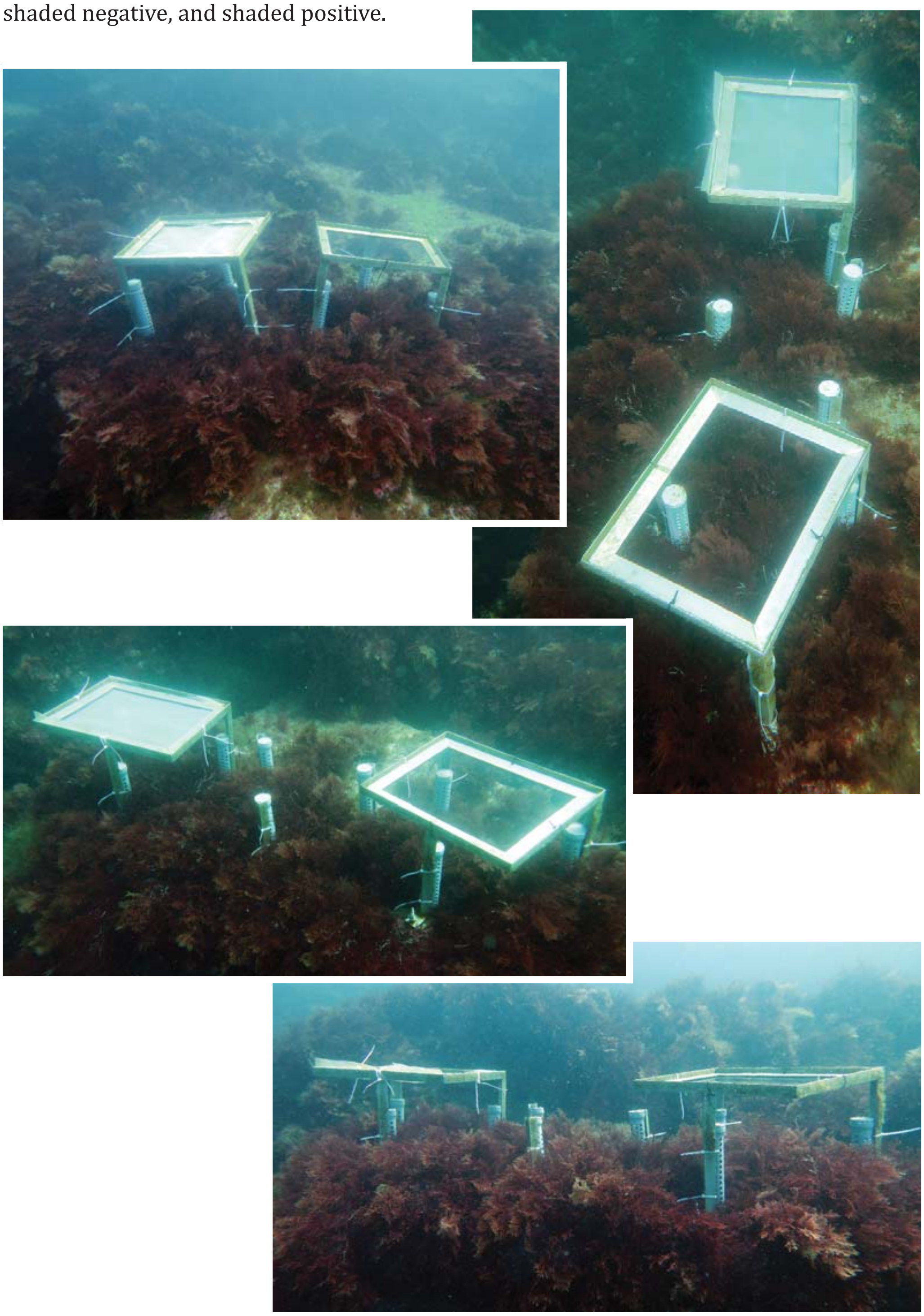
Before



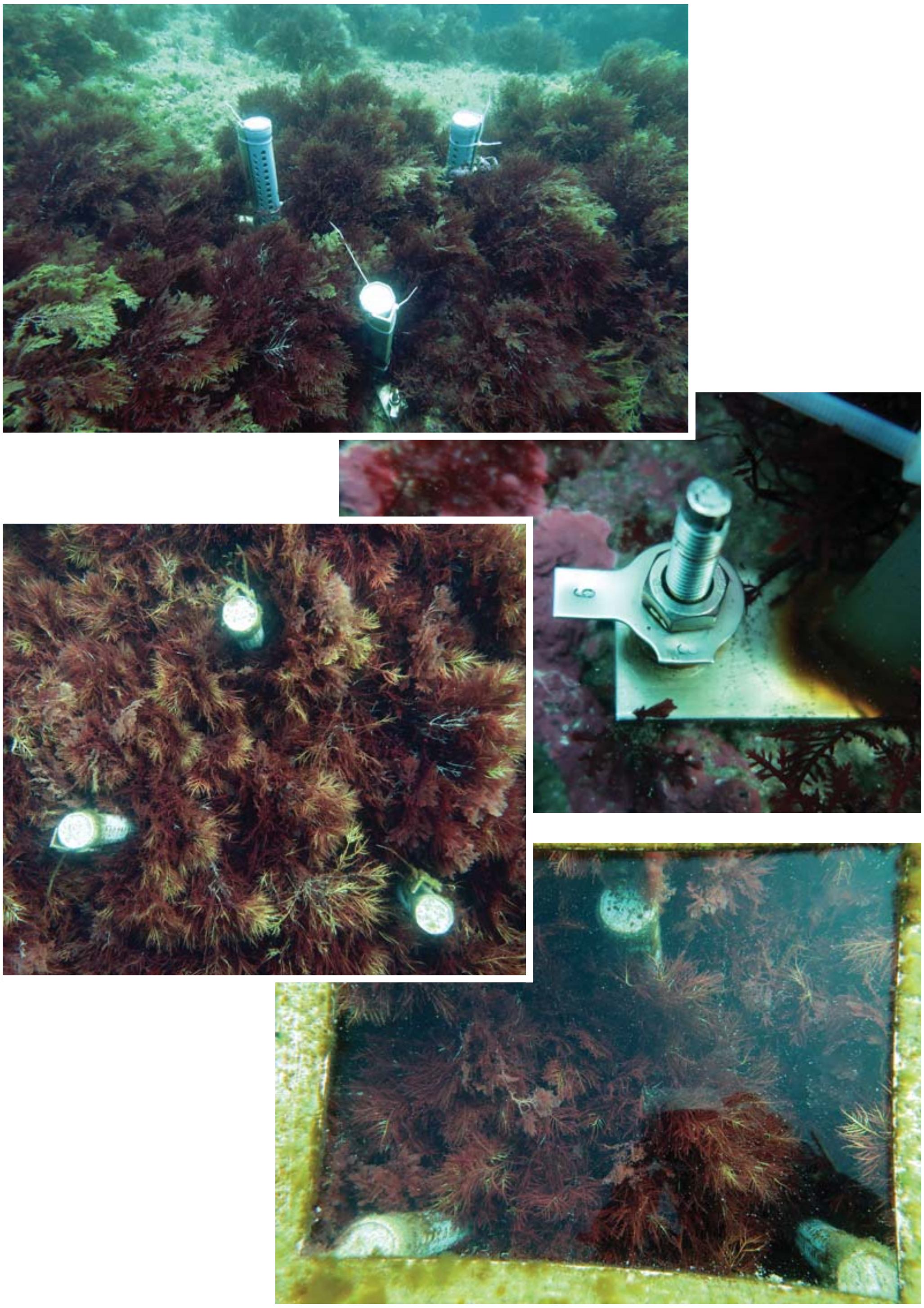
KOBARON: Before and After (Photos illustrate the change from 2002 to 2017)
After

Split-plot marine experiment

Fragments of habitat (Wholeplots) with 4 plots: unmanipulated control, procedural control, shaded negative, and shaded positive.

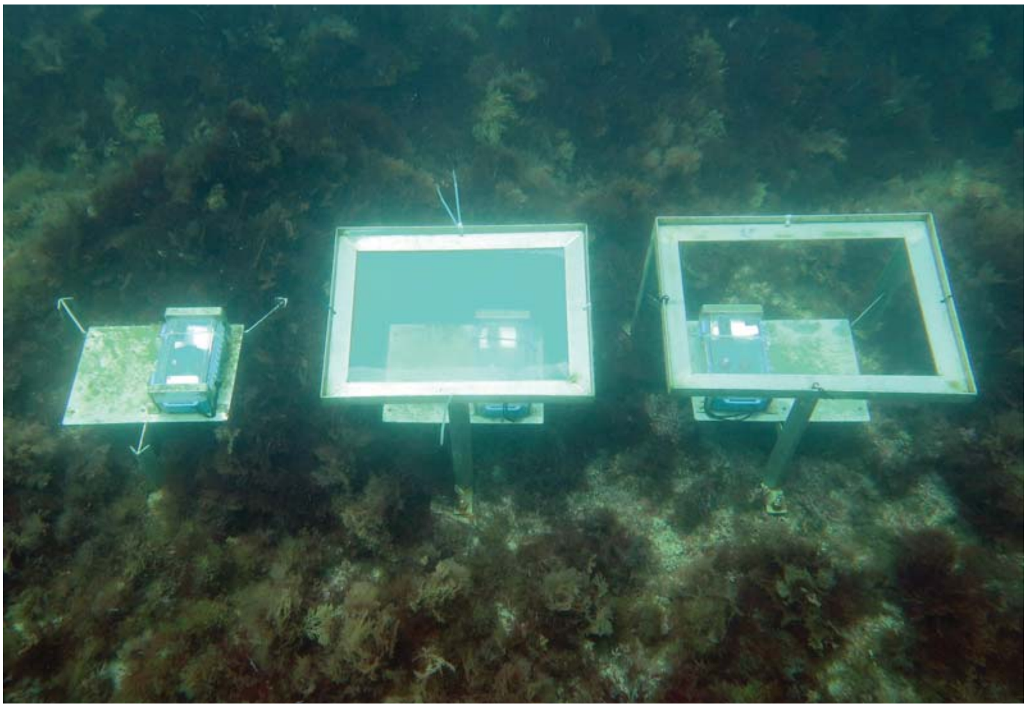


Split-plot marine experiment
Details of the plots or parcels

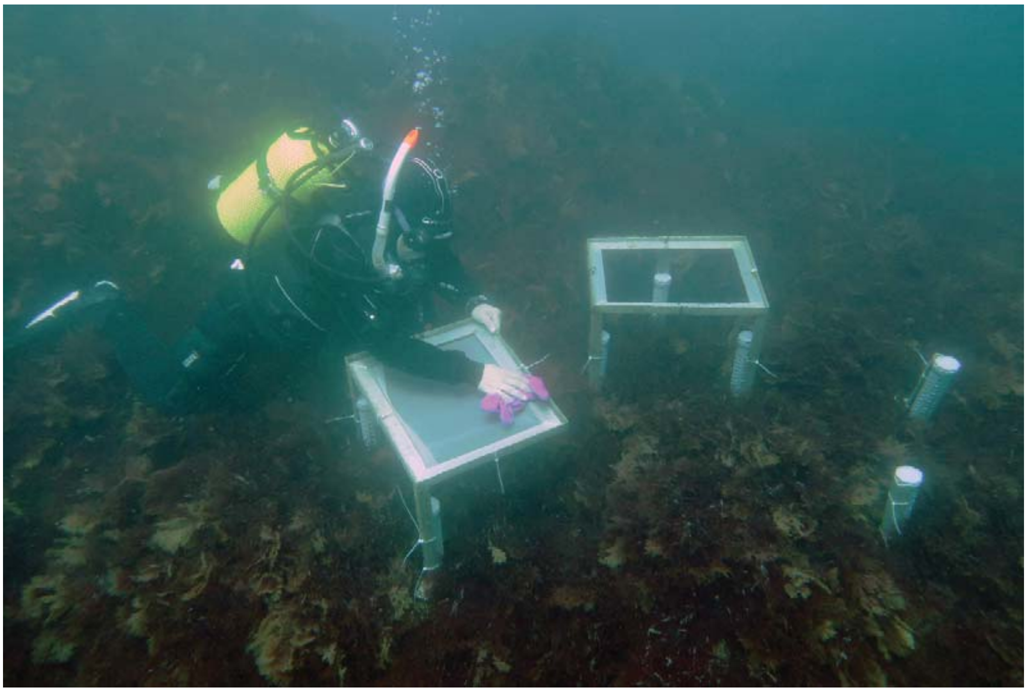


Split-plot marine experiment

PAR and UVA sensors installed in situ in the experimentation area

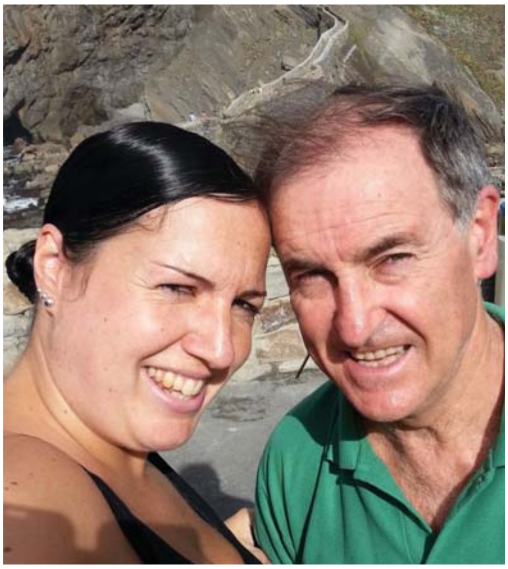


Performing maintenance (cleaning) of the installed device



Agradecimientos

NAHIARA MUGUERZA (2020) DOCTORAL THESIS pp. 217-224



Si finalmente llegaba el momento de hacerlo… siempre había pensado que me resultaría sencillo escribir los agradecimientos de mi tesis. No sé muy bien el porqué, pero es un ejercicio que he repetido muchas veces en mi cabeza. Me he imaginado haciéndolo en situaciones muy diferentes… de hecho, mentalmente he "escrito" mis agradecimientos mientras nadaba… tanto en el mar como en la piscina, paseando por el monte o incluso en la cama antes de dormir. Sin embargo, sentada ante una hoja en blanco las palabras no fluyen tan fácilmente, aunque los sentimientos están claros y lo vivido durante todo el proceso también.

Esta tesis ha sido posible sin duda, gracias a mis directores, Jose M. Gorostiaga e Isabel Díez; Txema e Isa. ¡GRACIAS!

Cada uno me ha aportado cosas muy diferentes desde el principio, pero que unidas han hecho posible que yo me haya podido desarrollar profesionalmente en la uni y a la vez ir haciendo esta tesis. De hecho, por un lado, quiero darle las gracias a Txema, que después de hacer el trabajo fin de master con él, confió en mí y me dio la oportunidad de formar parte de su grupo de investigación, de su equipo, y sin duda, sin esa apuesta inicial por mí nada de esto hubiera sido posible ¡Gracias de corazón Txema! Y, por otro lado, quiero darle las gracias a Isabella que me dedicó muchísimas horas en el campo, enseñándome en exclusiva con mucha paciencia y pasión prácticamente todo lo que sé sobre las algas y que me ha permitido poco a poco no solo ser, sino sentirme y trabajar como bióloga marina. ¡Muchísimas gracias Isa por enseñarme tanto!

Dicho con otras palabras, habéis hecho posible que ese sueño, mi sueño viendo los documentales de Cousteau sea una realidad. Sinceramente, muchísimas gracias a los dos por ser un ejemplo al que poder seguir en muchísimos aspectos, pero, sobre todo, si algo os caracteriza a ambos es el amor hacia las algas y al medio ambiente en su conjunto y vuestra lucha y trabajo por intentar preservarlo. Esa dedicación, pasión y/ o vocación que demostráis siempre por el bentos ha hecho posible que ese tandem que formáis haya dado y siga dando muchos frutos, y uno de ellos es sin duda esta tesis, una tesis que comparto con vosotros porque también es vuestra. Eskerrik asko!

Después siempre está el equipo, el grupo de trabajo, mis compañeros de este viaje, un equipo único e imprescindible para poder realizar esta tesis. El Bentos, un grupo de 5 personas que más que compañeros de trabajo somos amigos. Todos muy diferentes pero muy unidos por lo que hacemos y como lo hacemos. ¡Gracias! Eskerrik asko! Es una gran SUERTE poder trabajar con vosotros. Me siento muy afortunada, mucho y agradecida por poder formar parte del Bentos Team, FloFa, el equipo Gorostiaga o GG, cualquiera de nuestros nombres me gusta.

Individualmente os tengo mucho que agradecer a todos y cada uno de vosotros. Y aquí Isa vuelve a estar presente, pero esta vez como mi compañera. Alguien que trabaja duro y con pasión por lo que hace, que mima hasta el último detalle, y que contagia esa energía y lucha por intentar aportar nuestro granito de arena a mejorar el mar, el medio ambiente, la naturaleza. ¡Es un verdadero placer y honor trabajar contigo, gracias de nuevo Isa!

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Pasando al género masculino: Javi Tajadura, tu forma de ser hace que trabajar contigo sea una fiesta, te sale la gracia por los poros, sin quererlo, de forma innata, y a mí la sonrisa de forma permanente. Porque sin perder profesionalidad haces que todo sea más sencillo y placentero. Eskerrik asko Javi!

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Ongoing global environmental change is expected to drive drastic alterations in community structure, biodiversity patterns and ecosystem services. One major concern is the loss of canopy-forming macroalgae that provide habitat, shelter and food for a plethora of organisms in temperate coastal rocky habitats.The phytobenthos of the southernmost part of the NE Atlantic is likely to be one of the areas most affected by the warming process around the world. This thesis contributes knowledge on recent changes in subtidal assemblages in that geographical area, predicts future shifts in their spatial distribution and identifies the influence of some key environmental drivers.

The information provided here on rocky subtidal communities in Southern Europe extends understanding of the impact of climate change on coastal ecosystems, which is crucial to ensure good environment management. To draw up appropriate adaptation and conservation policies with effective actions at global and local scales to safeguard ecosystem functioning and to restore marine biodiversity, it is necessary to know how the ecosystem responds to climate change and what the drivers of change are.