Université Montpellier II-Sciences et techniques du Languedoc

THESE

pour obtenir le grade de

DOCTEUR DE L'UNIVERSITE MONTPELLIER II

Discipline : Biologie des Populations et Ecologie

*Ecole Doctorale : SIBAGHE, **S**ystèmes **I**ntégrés en **B**iologie, **A**gronomie, **G**éosciences, **H**ydrosciences et **E**nvironnement*

présentée et soutenue publiquement

par
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Le 20/12/2012

Modélisation de scénarios pour la biodiversité ichtyologique en mer Méditerranéenne : influence du changement global et conséquences trophiques, application aux réserves marines et aux écosystèmes exploités

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Résumé

Un des enjeux majeurs en écologie est de comprendre les effets du changement climatique sur la biodiversité et le fonctionnement des écosystèmes. En milieu marin, la surexploitation des ressources par l'homme est un autre facteur de forçage sur les assemblages d'espèces. La thèse propose, par une approche multi-composantes de la biodiversité, de projeter les modifications attendues sur la structure des assemblages de poissons côtiers méditerranéens soumis au changement climatique mais aussi aux différentes pressions de pêche. L'originalité de ce travail est de considérer la dynamique de la structure en taille, de la diversité des espèces mais aussi des lignées (diversité phylogénétique), des traits fonctionnels (diversité fonctionnelle) et des interactions (diversité des liens trophiques) des assemblages de poissons à différentes échelles au sein du bassin méditerranéen, ces trois dernières composantes étant largement ignorées dans les projections face au changement climatique alors qu'elles sont essentielles pour le maintien de la viabilité des écosystèmes et des services associées au delà du simple nombre d'espèces.

Nous avons donc projeté les futures aires de répartition des poissons côtiers méditerranéens grâce à l'implémentation d'un nouveau modèle climatique (NEMOMED8) et de modèles de niche basés sur les enveloppes bioclimatiques. Les projections des aires de distribution des poissons côtiers méditerranéens mettent en évidence que pour la fin du siècle (*i*) 54 espèces devraient perdre leur niche climatique, (*ii*) la richesse en espèces pourrait diminuer sur 70,4% du plateau continental, en particulier en Méditerranée occidentale et en mer Égée, et (*iii*) la taille maximale moyenne des assemblages de poissons pourrait augmenter dans 74,8% des cellules du plateau continental. Les espèces de petite taille non ciblées par la pêche pourraient être les espèces les plus menacées par le changement climatique alors que les espèces de grande taille seraient les plus vulnérables face à l'effort de pêche. Nos projections, au niveau de l'ensemble de la Méditerranée, révèlent une diminution de 13,6% de la diversité phylogénétique (PD) des poissons côtiers et de 12,6% de leur diversité fonctionnelle (FD) suggérant l'érosion importante de quelques lignées comme la famille des gobidae. Même si l'érosion de PD et de FD est en partie liée à la perte de richesse spécifique (moins d'espèces moins de lignées ou de fonctions) nous avons simulé, notamment dans le bassin Ouest, que les assemblages de poissons perdraient plus de diversité phylogénétique et fonctionnelle que prévu simplement suite à l'érosion de la richesse spécifique.

Pour appréhender les effets du changement climatique sur la structure du réseau trophique nous avons mis en place une méthodologie basée sur la robustesse d'une relation entre la taille des proies et des prédateurs. Nous avons pu ainsi mettre en évidence les modifications potentielles des réseaux trophiques au sein des assemblages de poissons face au changement global pour l'ensemble du plateau continental méditerranéen. Nous avons constaté qu'une partie importante du plateau continental méditerranéen serait confrontée à une diminution du nombre de liens trophiques, de la vulnérabilité (nombre de prédateur par proie) et de généralité (nombre de proie par prédateur) moyenne des espèces, tandis que la connectance et le niveau trophique dans les assemblages de poissons pourraient augmenter d'ici la fin du XXI$^{\text{ème}}$ siècle.

Au dela des modifications de richesse spècifique, les assemblages de posissons méditerranéens côtiers pourraient être modifiés dans les fonctions qu'ils jouent au sein de l'écosystème, dans l'histoire évolutive qu'ils contiennent ainsi que dans les intéractions structurant les réseaux trophiques. La thèse est donc une ouverture vers la biogéographie du fonctionnement des écosystèmes à partir de modèles parsimonieux et hybrides permettant d'intégrer différentes composantes de la biodiversité, l'océanographie physique, et le niveau d'exploitation des ressouces pour inférer le devenir des systèmes marins côtiers face aux pressions multiples qui s'y exercent déjà.

Mots Clés : Changement climatique ; Mer Méditerranée, Poissons côtiers, modèle d'enveloppes bioclimatiques, BIOMOD, NEMOMED8, Diversité fonctionelle, diversité phylogénétique, diversité de liens, réseau trophique.

Abstract

One of the main goals in ecology is to understand the effects of climate change on biodiversity and ecosystem functionning. In marine environments the overexploitation of ressources by human activities is another forcing factor on species assemblages. This Phd thesis poposed, within a multi-components biodiversity approach, to project expected changes in the structure of Mediterranean coastal fish assemblages under climate change but also under different fishing pressures.

The originality of this work is to consider the dynamics of size structure, diversity of species, but also lineages (phylogenetic diversity), functional traits (functional diversity) and interactions (diversity of trophic links) in fish assemblages at different scales within the Mediterranean basin, the latter three components being largely ignored in climate change projections whereas they are essential for maintaining the viability of ecosystems and associated services beyond the simple number of species.

We therefore projected future geographic ranges of Mediterranean coastal fish through the implementation of a new climate model (NEMOMED8) and based on bioclimatic envelopes models. Projected range shifts of Mediterranean coastal fish show that for the end of the century (*i*) 54 species would lose their climatic niche, (*ii*) species richness may decline on 70.4% of the continental shelf, particularly in the Western Mediterranean basin and in the Aegean Sea, and (*iii*) the average maximum size of fish assemblages would increase on 74.8% of the continental shelf. The small species, not targeted by fishing activities, would be the species most threatened by climate change, while larger species are most vulnerable to fishing effort.Our projections at the whole Mediterranean scale, show a decrease of 13.6% for the phylogenetic diversity (PD) of coastal fish and 12.6% for their functional diversity (FD) by the end of this century and suggest a significant erosion of some lineages like the gobidae family. While erosion of PD and FD is partly due to the loss of species richness (fewer species implies less lineage and functions) we obseved, especially in the western basin, that the fish assemblages would loss more phylogenetic and functional diversity than expected simply due to the erosion of species richness.

These two components, were largely ignored in conservation of marine species assemblages and appear to be strongly impacted by global change.To understand the effects of climate change on food web structure we developed a new methodology based on the robust relationship between the size of prey and predators. We were able to highlight potential changes in food webs of fish assemblages under climate change for the Mediterranean continental shelf. We found that a significant portion of the Mediterranean continental shelf would face a reduction in the number of trophic links, vulnerability (number of predators per prey) and generality (number of prey per predator) of species on average, while connectance and trophic level within fish assemblages would increase by the end of the XXIth century.

Beyond changes in species richness, the Mediterranean coastal fish assemblages may be modified, in the functions that they play in ecosystem, in the amount evolutionary history they support, as well as in their interactions structuring food webs. This Phd thesis paves the way towards the biogeography of ecosystem functioning using parsimonious and hybrid models to integrate different components of biodiversity, physical oceanography, and the level of exploitation of ressouces to infer the futur of marine systems cfunctioning facing multiple pressures that are already there.

Keywords: Climate Change, Mediterranean Sea, coastal fishes, bioclimatic model, BIOMOD, NEMOME8, functional diversity, phylogenetic diversity, diversity of links, trophic network.

Remerciements

Je profite des premières lignes de ce manuscrit de thèse pour remercier l'ensemble des personnes qui ont contribué de près ou de loin à l'élaboration de ce projet.

Je tiens à exprimer, en premier lieu mes remerciements aux membres du jury qui ont pris le temps d'évaluer mon travail de thèse. Je remercie Mr Kostantinos Stergiou et Mr Eric Rochard, d'avoir accepté d'être rapporteur de ce travail de thèse. Je remercie également l'ensemble du jury de s'être déplacé pour assister à la soutenance.

Un tel travail ne peut se faire sans l'appui de nombreuses personnes, que ce soit des étudiants, des chercheurs, ou des ingénieurs. Sans une équipe soudée sur laquelle j'ai pu compter tous les jours et sans le soutien indéfectible de mes proches, je n'aurais jamais réussi à accomplir un tel travail.
Je tiens particulièrement à remercier mes directeurs de thèse David Mouillot et François Le Loc'h pour avoir supporté mon mauvais caractère, mon entêtement et m'avoir soutenu et défendu lorsque cela était nécessaire, merci de m'avoir permis de découvrir le monde de la recherche dans un environnement aussi serein. Merci également de m'avoir laissé une place importante dans l'élaboration de ce projet et d'avoir été là aux moments opportuns pour réorienter, commenter et corriger mon travail.

Un MERCI à Fabien Leprieur, lorsque tu es arrivé à Ecolag (maintenant Ecosym), David venait de partir en Australie pour 2 ans, tu es tombé à pic, ta bonne humeur, ton expérience, tes explications statistiques m'ont permis de prendre confiance en moi et de m'épanouir dans mon travail de recherche. Tu as su me guider et me conseiller lors de la finalisation des principaux manuscrits de cette thèse et pour cela je te remercie encore.
Pour ce qui est du privé, ca restera privé et l'on aura le temps de discuter par skype durant l'hiver Canadien.

Un MERCI à JAT, je sais que nous avons une grande différence d'âge, mais je sais aussi que tu ne te vexeras pas si je t'appelle mon pote. On en aura passé du temps ensemble, à préparer des Tp de statistiques, toi à nous raconter l'histoire de la fac moi à écouter, à râler (Fab aussi d'ailleurs). Je te remercie pour tout ce que tu as fait pour moi, je te remercie également pour la relecture de ce manuscrit, tu as su trouver un peu de temps. Je te souhaite de finir tranquillement ta carrière.

Un MERCI à « Yo mon geek », on en aura raconté des histoires (pour parler poliment) sur gmail pendant ces deux années durant lesquelles tu étais en postdoc... On a passé suffisamment de temps ensemble depuis mon arrivé en master à Ecolag, pour ne pas que j'en écrive des tartines, on se connaît bien on a plaisir à travailler ensemble bien que des fois tu sois une vrai tête de mule alors j'espère que cela va continuer avec ton récent recrutement.

Un MERCI à Laure Velez, tu as été d'une aide précieuse tout au long de ces trois années de thèse. J'ai pris plaisir à travailler avec toi et j'espère qu'avec François nous avons réussi à réveiller le petit geek qui sommeillait en toi. Car maintenant les mots ssh, ftp, grub, batch, sql, sata ou ram que le commun des mortels ne comprend pas, n'ont plus de secret pour toi. Bon courage pour ta recherche de poste et à bientôt.

A Delphine, aux moments agréables passés ensembles en Corse, j'ai admiré ton enthousiasme et ta détermination à aller chaque matin compter les poissons auprès des pêcheurs. J'espère que l'on pourra se faire des tas de plongées aux 4 coins de la planète et descendre ensemble en dessous des 40 m. La prochaine étape c'est l'Espagne puis j'espère que tu viendras faire de la plongée sous la glace à Rimouski avec Santi.

Je tiens à remercier Marta Coll et Dominique Gravel pour m'avoir accueilli lors de mes deux séjours au Canada. Un merci à Samuel Somot pour avoir pris du temps sur son emploi du temps surchargé pour venir m'expliquer ses travaux de recherche et m'avoir fais confiance en me donnant les sorties de ses modèles climatiques. Merci à Frida pour ses conseils avisés en SIG et pour avoir été présente au début de cette thèse. Merci à joanne pour sa participation à ce travail de thèse, bon courage pour ta thèse.

Je tiens également à remercier tous mes collègues de l'équipe DEP que j'ai pu côtoyer pendant ces trois années, Maud, le petit Seb, Jean DO, David, Arthur, Franck, Jennifer, Awa, Kiki, Audrey, Élodie, Charlotte, Julien, Mariana, sans qui les burgers de Fred pizza n'auraient pas eu la même saveur. Bon courage aux thésards, si vous lisez ces mots je vous conseille de commencer à penser à vos remerciements ce n'est pas si facile à écrire.

Un Merci aux collègues d'EME, Morgane, Philippe, Tarek, j'espère que l'on continuera à travailler ensemble.

Aux amis, un Merci à Loulou, Ben pour tous ces bons moments passés ensemble. A Leny et Anna et leur petit bout pour leur soutien et leur relécture des manuscrits, Adrien, Séb, Aurore, David, Titoune, Rémy, Nico, Nico, Greg pour toutes les fiestas et bons moments partagés ensembles.
A Pierrot et Jeannette mes potes depuis le collège, merci pour votre soutien et vos encouragements. Merci pour tout, les amis.

Merci à ma belle famille pour les bons repas du dimanche. Papa, maman merci de m'avoir laisser du temps pour trouver ma route. Merci de m'avoir soutenu tout au long de ces années d'études, et d'avoir cru en moi. Un petit coucou a mon frangin, qui m'a tellement apporté jusqu'ici. Plein de gros bisous à ma frangine et toute sa petite famille.

Et pour terminer je voudrais remercier celle qui au début de cette thèse était ma compagne et qui est devenue ma femme, on a traversé ces trois années en se serrant les coudes et en profitant du mieux possible des temps libres que nos recherches nous ont accordés. Séverine sans ton soutien et ta compréhension pour les longues heures passées derrière mon ordinateur je n'aurai pas pu réaliser l'ensemble de ce travail.

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Chapitre 1

Introduction générale

I.1 La Mer Méditerranée : bilan des connaissances

I.1.1 Caractéristiques de la Mer Méditerranée

Au carrefour de trois continents (Afrique, Asie et Europe), la Mer Méditerranée est la plus vaste Mer semi-fermée du monde. Connectée à l'océan Atlantique par le détroit de Gibraltar, à la Mer Noire par le détroit du Bosphore et à la Mer Rouge par le canal de Suez (Fig. 1) elle constitue le bassin le plus étendu (2 969 000 km²) et le plus profond (moyenne: 1 460 m, maximum: 5 267 m) du monde. Avec 17 000 espèces recensées (Coll et al. 2010) qui représentent 7% de la biodiversité marine mondiale, et un taux d’endémisme à 25% pour seulement 0,82% de la surface océanique globale (Bianchi & Morri 2000), la mer Méditerranée est un « point chaud » de biodiversité (Bianchi & Morri 2000, Myers et al. 2000, Coll et al. 2010).

Figure 1 : La mer Méditerranée, les pays la bordant, ses subdivisions maritimes et ses connexions. Le plateau continental (0-200m) est en gris foncé.

I.1.2 Genèses et crises de la biodiversité méditerranéenne

La forte biodiversité en mer Méditerranée résulte d'épisodes paléogéographiques et géologiques particuliers. Avant le Miocène (23 millions d'années), ce vestige de la Téthys (mer reliant l'océan Atlantique à l'océan Indopacifique au Crétacé) abritait une faune plutôt thermophile similaire à celle retrouvée actuellement dans l'océan Indien. La formation de l'isthme de Suez durant l'orogenèse du Miocène obtura la communication entre la Méditerranée et l'océan Indopacifique, puis à la fin du Miocène (5,3 millions d'années), celle avec l'océan Atlantique. La mer Méditerranée, ainsi isolée, les apports en eau ne compensant plus l'évaporation, il s'ensuivit une période d'assèchement sévère qui entraîna la disparition de nombreux taxons à l'exception de certaines espèces de faible profondeur qui survécurent dans quelques plans d'eau rémanents (Bouchet & Taviani 1992). La biodiversité méditerranéenne fut donc largement réduite jusqu'au Pliocène (5 millions d'années), période durant laquelle l'ouverture du détroit de Gibraltar remis en eau la totalité du bassin méditerranéen. Cette crise majeure d'une durée 0,4 million d'années, n'a cependant pas provoqué une forte diversification des taxons. En effet, la diversification des poissons méditerranéens daterait du Cénomanien (95-100 millions d'années), période géologique marquée par une forte augmentation de la température et du niveau des océans (Meynard et al. 2012). Par conséquent, la Mer Méditerranée serait plus un réceptacle d'espèces (puits), à l'interface entre l'océan Atlantique et Indien plutôt qu'une source de diversité.

I.1.3 Une mer sous contraintes

De nos jours, la Mer Méditerranée est l'une des régions marines les plus menacées au monde et subit de profonds changements tant environnementaux que biologiques (Ben Rais Lasram et al. 2010, Coll et al. 2010, de Madron et al. 2011; Manuscrit A). Ces changements résultent d'une combinaison de diverses pressions anthropiques directes telles que la surpêche, l'aquaculture, la pollution des eaux et l'urbanisation (Claudet & Fraschetti 2010) auxquelles s'ajoutent les inroductions d'espèces (Ben Rais Lasram & Mouillot 2009) et les changements climatiques (Giorgi 2006). Depuis plus d'un siècle, ces perturbations ont provoqué un profond remaniement des assemblages d'espèces ayant pour conséquence, en conjonction avec les modifications environnementales, une modification du fonctionnement des écosystèmes (Lejeusne et al. 2010) et donc une altération potentielle des biens et services fournis aux sociétés humaines (apport de protéines *via* la pêche). Par exemple les espèces envahissantes d'origine lessepsienne *Siganus luridus* ou *Siganus rivulatus* sont capables de modifier les assemblages algaux et de transforMer un habitat riche en un habitat pauvre en algues et par conséquent de modifier la complexité des habitats et la biodiversité associée (Fig. 2).

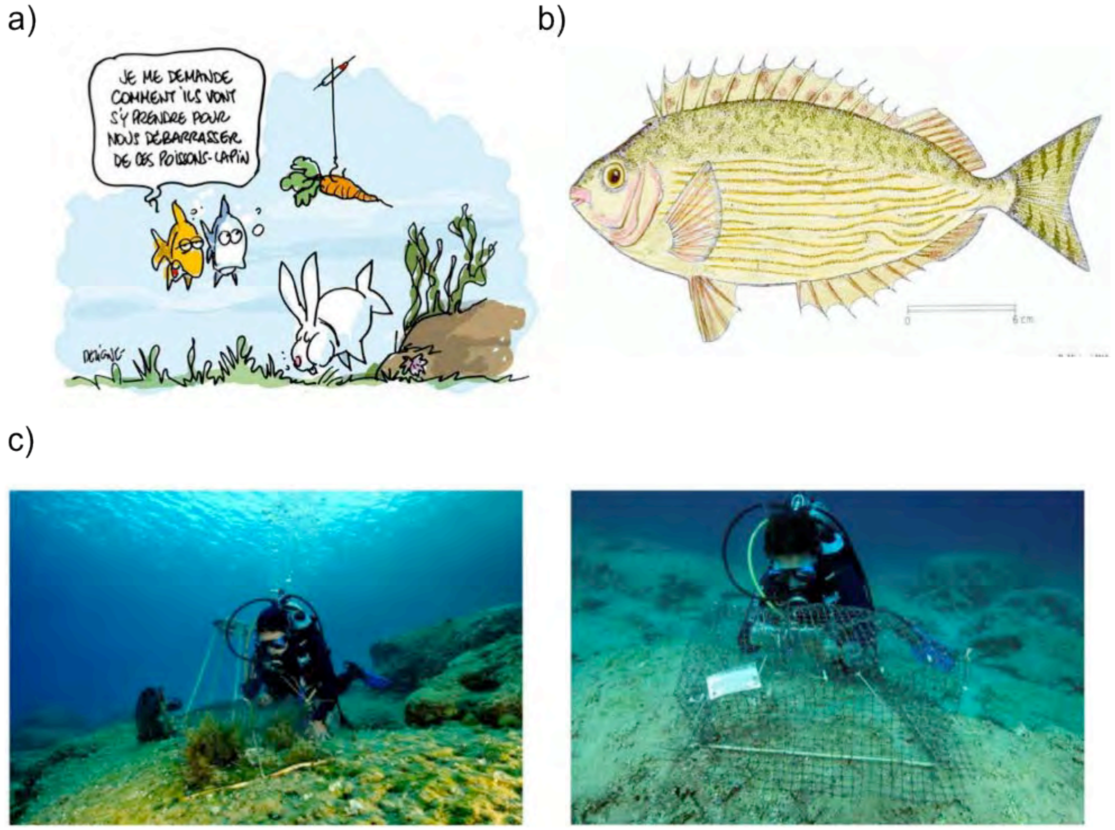


Figure 2 : a)Dessin humoristique traduisant l'influence des Siganidae sur l'écosystème (source Nice Matin) b) Dessin du poisson lapin (*Siganus rivulatus*) espèce herbivore d'origine lessepsienne c) Expérimentation d'exclusion des poissons herbivores sur les assemblages algaux de Méditerranée. Au bout de 5 mois à l'intérieur de la cage un assemblage d'algues bien développé est présent (photo droite) ; puis dans cette même cage introduction d'un jeune *Siganus,* en un mois plus aucune algue n'est présente dans la cage (Sala et al. 2011).

I.1.4 Les Aires Marines Protégées

Ayant pour but prioritaire de protéger les espèces emblématiques et les habitats remarquables, tel que l'herbier à posidonies (*Posidonia oceanica*), contre les menaces croissantes, une centaine d'Aires Marines Protégées (AMP) ont été créées et renforcées depuis les années 1960 en Méditerranée. Elles ont pour objectif de maintenir les fonctions et l'intégrité de l'écosystème marin, en offrant un refuge spatial permanent (Worm et al. 2006). Les bénéfices des AMP ne concernent pas uniquement la conservation ou la restauration de la biodiversité à l'intérieur de la réserve mais, également, le soutien des pêcheries adjacentes par des échanges de type sources-puits. Ces derniers peuvent être assurés par deux mécanismes liés à l'augmentation des tailles de populations pour les espèces exploitées (principalement poissons et crustacées) du fait de leur protection : (*i*) le *spill over* qui désigne la migration de l'excédent de poissons juvéniles ou adultes depuis les zones protégées vers les zones adjacentes (Forcada et al. 2009, Claudet et al. 2010); (*ii*) une production plus élevée d'œufs à l'intérieur des AMP, grâce à une forte densité de géniteurs de grande taille, donc de futurs individus potentiels, dont une partie sera entraînée vers les zones exploitées pour les ensemencer (Perez-Ruzafa et al. 2008). En favorisant l'augmentation du nombre de larves et du recrutement en leur sein, conduisant à des densités de populations plus importantes qu'à l'extérieur, les AMP jouent un rôle dans la résilience des écosystèmes face aux perturbations notamment celles induites par le changement climatique (Micheli et al. 2012).

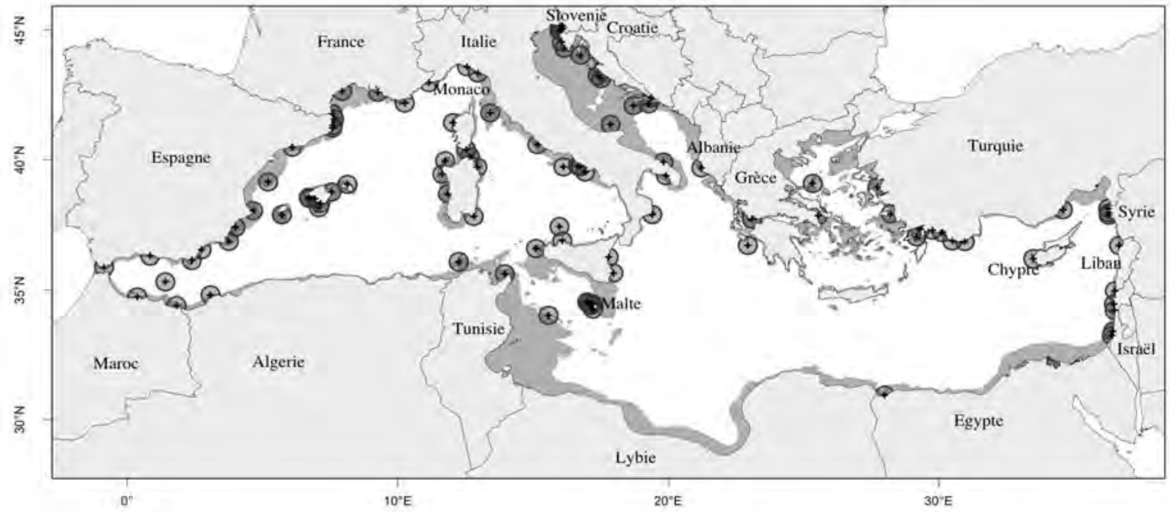


Figure 3 : Localisation des aires marines protégées en Mer Méditerranée.

Néanmoins le système d'AMP méditerranéen ne couvre que 0,5% du plateau continental (en excluant le sanctuaire pelagos ; Fig. 3) et il n'a été implanté qu'en fonction de décisions économiques et politiques locales (nationales ou régionales; Francour et al. 2001). Aucune stratégie de conservation à l'échelle du bassin méditerranéen n'a été établie et le système actuel présente un fort déséquilibre entre le nord et le sud. Actuellement 73% des AMP sont situées le long des côtes nord méditerranéennes. Cela correspond davantage à un décalage sociopolitique avec les pays du sud qu'à une répartition réfléchie et efficace des efforts de conservation. C'est donc un véritable défi qui a été lancé en 2010 lors de la conférence pour la biodiversité de Nagoya : d'ici 2020, les zones marines et côtières abritant une forte biodiversité ou soutenant des services écosystémiques importants devront être protégées par un réseau d'AMP couvrant 10% de leur surface ; ce qui concerne la Mer Méditerranée au premier plan. Malgré l'urgence, aucune étude n'a été entreprise pour définir les sites où doivent être concentrés les futurs efforts pour à la fois contrecarrer les menaces et protéger les zones à forte valeur de biodiversité.

I.2 Les différentes composantes de la biodiversité

Les années 1990 ont vu l'émergence de nouveaux enjeux concernant la conservation de la biodiversité (Loreau 2010). En effet, si la préservation de la biodiversité n'a été pendant longtemps justifiée que sur des critères éthiques, patrimoniaux ou esthétiques, cette vision a changé avec les travaux reliant la biodiversité au fonctionnement des écosystèmes : la biodiversité est devenue « utile ». Ainsi des premières études ont montré, en manipulant la richesse spécifique d'espèces végétales, que la productivité était positivement influencée par la biodiversité (Tilman & Downing 1994, Tilman et al. 2001). Par la suite d'autres études ont montré que la richesse en espèces induit, entre autres, une meilleure résilience des écosystèmes (Loreau & Behera 1999) et une meilleure lutte contre les espèces envahissantes (Naeem et al. 2000). Même si ces études ont permis de placer la biodiversité au centre des préoccupations, la seule richesse spécifique ne suffit pas à expliquer le fonctionnement des écosystèmes car les relations prédictives restent faibles dans les études précédemment citées (Fig. 4).

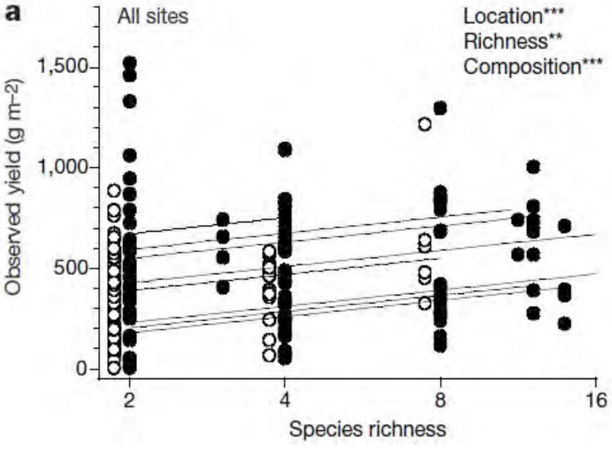


Figure 4 : Relation entre productivité et biodiversité (richesse spécifique) pour toute les localités de l'expérimentation BIODEPTH (Loreau & Hector 2001).

La littérature récente a mis en évidence la nécessité d'utiliser, pour expliquer le fonctionnement des écosystèmes de manière plus robuste et donc plus convaincante la diversité des caractères qui rendent uniques les espèces en termes de traits biologiques (Mouillot et al. 2008, Flynn et al. 2009) ou de gènes (Mace et al. 2003, Redding et al. 2010). En effet l'étude de Cadotte et al. (2009) démontre que parmi 16 variables potentiellement explicatives, la présence de certains traits fonctionnels (pouvant être définis comme une mesure des caractéristiques biologiques des espèces) ainsi que leurs relations avec l'environnement et la diversité phylogénétique (définie comme la diversité des lignées présentes dans l'assemblage) sont plus importants que la richesse spécifique pour expliquer la productivité d'un écosystème terrestre (Tableau 1).

Tableau 1 : Importance des variables dans les modèles expliquant la productivité d'un écosystème terrestre, extrait de la publication de Cadotte et al. (2009)

Variables	Ordonnée à l'origine	Pente	DF	P-value	AIC	R^2	Rang
Fixation d'azote	111.99	147.50	149	< 0.001	1747.47	0.436	1
Diversité phylogénétique	123.76	29.37	149	< 0.001	1752.78	0.415	2
Poids des graines	154.44	- 5126.37	149	< 0.001	1758.56	0.392	3
log(Richesse spécifique)	123.30	62.51	149	< 0.001	1764.20	0.369	4

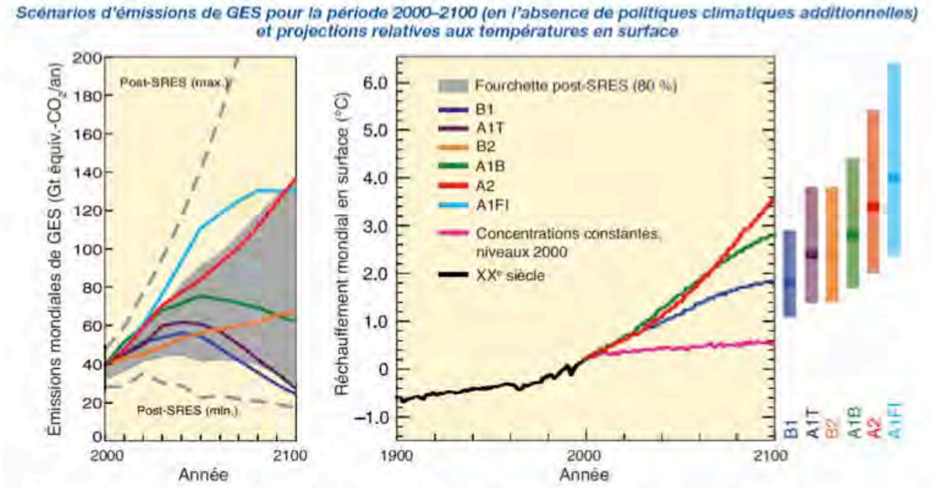
Cependant, la biodiversité telle qu'elle a été étudiée par les écologues terrestres, n'englobe qu'une partie du réseau trophique (un seul niveau trophique, les producteurs primaires). Or les écosystèmes sont composés d'espèces interagissant entre elles suivant différents types d'interactions telles que la prédation, le parasitisme, la symbiose, le mutualisme, la compétition ou encore le commensalisme et l'amensalisme. Même si ces relations entre espèces sont critiques pour le fonctionnement des écosystèmes (Worm & Duffy 2003), leur biodiversité, c'est-à-dire la diversité des liens interspécifiques, est rarement envisagée comme une composante à part entière. Pourtant, la connaissance de cette diversité de liens apporte une information sur la nature des interactions interspécifiques et leur intensité (flux de matière au sein d'un écosystème) et, par conséquent, nous informe sur la structuration de la biodiversité. Or, la connaissance à large échelle de cette composante de la biodiversité est encore largement méconnue et ses projections suite au changement global restent marginales et souvent locales (Kirby & Beaugrand 2009).

C'est la raison pour laquelle nous avons adopté, afin d'étudier la dynamique de la biodiversité des poissons méditerranéens face au changement climatique ainsi que sa conservation par le réseau d'AMP, une approche multi-composantes de la biodiversité en considérant la richesse totale, celle en espèces endémiques et menacées (UICN) ainsi que les diversités fonctionnelle (traits) et phylogénétique (lignées) des assemblages ainsi que la diversité de leur interactions trophiques. Les trois dernières composantes ont été largement ignorées dans la planification des AMP (mais voir Rodriguez et al. 1998, Devictor et al. 2010) et dans les scénarios face au changement climatique (mais voir Thuiller et al. 2011), mais elles sont toutes trois essentielles à la diversité de la vie sur Terre (Mace et al. 2003, Flynn et al. 2009) et au fonctionnement des écosystèmes (Cadotte et al. 2008, Clemente et al. 2010). L'originalité de la thèse a donc été de projeter le devenir des assemblages de poissons côtiers méditerranéens non plus comme un simple remaniement taxonomique mais comme une restructuration de la diversité de lignées, de traits fonctionnels, et des interactions.

I.3 Le changement climatique en Mer Méditerranée

Si l'histoire de la Terre a été ponctuée par l'alternance de périodes glacières et de périodes chaudes, l'augmentation de la température observée actuellement (+ 0,6°C en 100 ans) peut être considérée comme anormalement rapide (IPCC, 2007). Elle est, au moins en partie, liée à l'augmentation dans l'atmosphère de gaz à effet de serre provoquée par l'utilisation des énergies fossiles et plus globalement par l'activité humaine des XIX^{éme} et

Encart 1 : Les scénarios SRES



Scénarios d'émissions de GES pour la période 2000–2100 (en l'absence de politiques climatiques additionnelles) et projections relatives aux températures en surface

Le sigle SRES renvoie aux scénarios décrits dans le rapport spécial du GIEC sur les scénarios d'émissions de Gaz à Effet de Serre (GES) dans l'atmosphère (SRES, 2000). Ceux ci sont regroupés en quatre familles (A1, A2, B1 et B2), qui étudient différentes voies de développement en fonction d'un large éventail de facteurs démographiques, économiques et technologiques ainsi que des émissions de gaz à effet de serre qui en résultent. Le canevas A1 fait l'hypothèse d'un monde caractérisé par une croissance économique très rapide, un pic de la population mondiale au milieu du siècle et l'adoption rapide de nouvelles technologies plus efficaces. Cette famille de scénarios se répartit en trois groupes qui correspondent à différentes orientations de l'évolution technologique du point de vue des sources d'énergie : à forte composante fossile (A1FI, scenario le plus pessimiste), non fossile (A1T, scenario optimiste) et équilibrant les sources (A1B). Le canevas B1 (scénario le plus optimiste) décrit un monde convergent présentant les mêmes caractéristiques démographiques que A1, mais avec une évolution plus rapide des structures économiques vers une économie de services et d'information. Le canevas B2 décrit un monde caractérisé par des niveaux intermédiaires de croissances démographique et économique, privilégiant l'action locale pour assurer une durabilité économique, sociale et environnementale. Enfin, le canevas A2, l'un des plus pessimiste, décrit un monde très hétérogène caractérisé par une forte croissance démographique, un faible développement économique et de lents progrès technologiques.

XX^{ème} siècles. Les preuves de ce changement climatique sont sans équivoque, mais les causalités ainsi que les scénarios futurs sont encore très débattus. Un groupe d'experts intergouvernemental sur l'évolution du climat (GIEC) propose des projections sur l'évolution de la température terrestre à long terme. Ils se basent sur des outils de modélisation climatique et des scénarios d'évolution de l'utilisation des ressources par l'homme. Comme le reste du monde, la Méditerranée n'échappe pas à ce phénomène de changement climatique avec, par exemple, une température moyenne des eaux de surface qui s'est élevée de 1,1°C depuis les années 1970 (Salat & Pascual 2002). En utilisant un modèle climatique adapté à la mer Méditerranée et le scénario A2 proposé par le GIEC (voir Encart 1 : les scénarios SRES), Somot et al. (2006) on prédit une augmentation moyenne des températures des eaux de surface de 3,1°C et de la salinité de 0,48 d'ici la fin du XXI^{ème} siècle.

La température est un facteur ayant une influence majeure sur le recrutement, la reproduction, la physiologie, la croissance, le métabolisme et le comportement des animaux à sang froid tels que les poissons (Burreson & Sypek 1981, Mann & Blackburn 1991). Cette augmentation de température a pour effet de modifier les aires de répartitions des espèces de poissons en mer Méditerranée, notamment en favorisant l'expansion et l'augmentation en abondance des espèces thermophiles (Raitsos et al. 2010, Azzurro et al. 2011). Elle peut aussi conduire à des extinctions locales si elle est supérieure au seuil létal de l'espèce (Reist et al. 2006).

Pour prédire les modifications d'aire de répartition des espèces terrestres ou marines en fonction du changement climatique, il est essentiel de modéliser la niche réalisée des espèces à l'aide de modèles statistiques, puis, grâce à des données issues de modèles climatiques, de prédire la distribution potentielle future. La niche réalisée peut être définie comme l'hyper-volume des variables dans lequel l'espèce peut assurer sa croissance et sa reproduction contraintes par les paramètres biotiques ou physiologiques (Hutchinson 1957). Cette méthodologie nous permet de prédire les changements potentiels pouvant affecter les différentes composantes de la biodiversité (Cheung et al. 2009, Ben Rais Lasram et al. 2010, Lenoir et al. 2011) et le fonctionnement des écosystèmes marins (Beaugrand et al. 2003, Cheung et al. 2010). Cette approche est peu développée en milieu marin, notamment en mer Méditerranée. Elle nous a permis d'aborder les modifications induites par le changement climatique sur les composantes fonctionnelles, phylogénétiques et trophiques de la biodiversité pour le fin du XXI^{éme} siècle.

I.4 Synthèse des travaux préliminaires à la thèse

Dans cette synthèse introductive j’ai incorporé les études auxquelles j’ai collaboré en début de thèse mais pour lesquelles je n’ai pas assuré un rôle de premier auteur. J’y ai apporté une contribution sur les hypothèses à tester, les traitements statistiques, la manipulation de la base de données et sur les illustrations sans avoir eu en charge la rédaction des publications. Ces études font le bilan des connaissances sur la Mer Méditerranée et m’ont permis d’acquérir un socle important pour la suite de mes travaux. Ces études ont aussi initié la mise en place de la base de données que j'ai d’abord utilisée et puis complétée et améliorée. Cette synthèse s’articule autour de trois thèmes, (*i*) la biodiversité, les menaces et les zones à protéger, (*ii*) la protection des différentes composantes de la biodiversité et (*iii*) une première approche de modélisation des effets du changement climatique sur les poissons endémiques de Méditerranée. Chacun de ces thèmes est illustré par une publication à laquelle j’ai participé au sein d’un groupe de travail international.

I.4.1 Biodiversité, menaces et zones à protéger

En nous fondant sur les répartitions géographiques de 706 espèces marines réparties en 5 groupes taxonomiques (les poissons, les mammifères marins et les tortues, les oiseaux marins, les invertébrés, et les grands prédateurs incluant oiseaux, tortues, mammifères marin et poissons), nous avons estimé la distribution spatiale de la richesse spécifique en mer

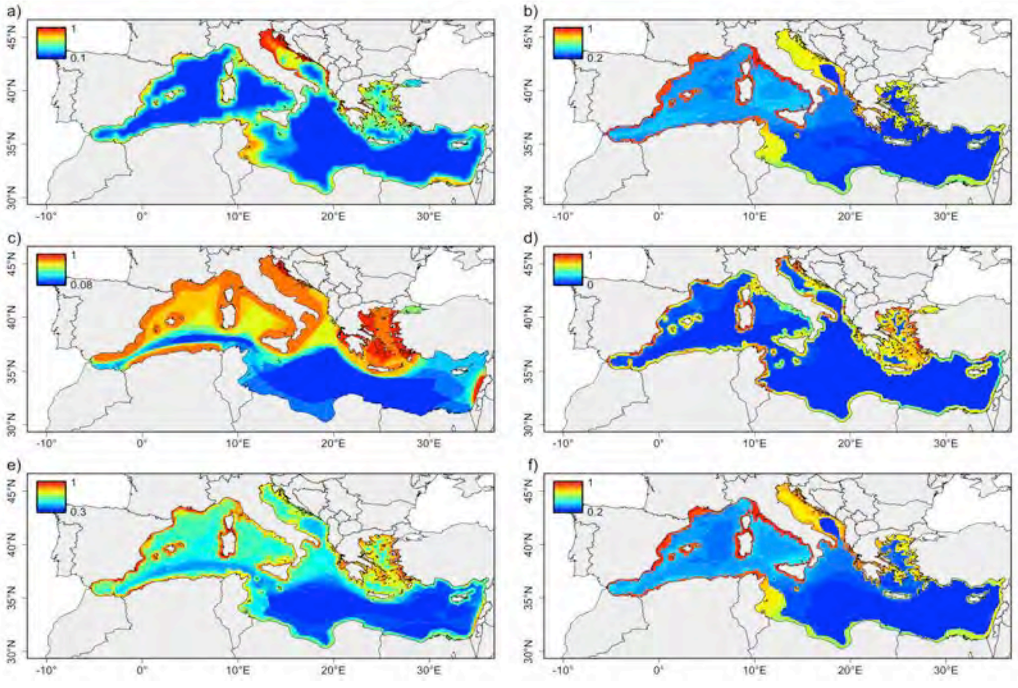


Figure 5 : Biodiversité relative pour a) les invertébrés, b) les poissons, c) les mammifères marins et les tortues, d) les oiseaux marins, e) les grands prédateurs, f) pour l’ensemble des taxons, en mer Méditerranée.

Méditerranée (Manuscrit A). La répartition de la biodiversité est hétérogène : elle est davantage concentrée dans les zones côtières et suit un gradient de biodiversité nord-ouest–sud-est décroissant (Fig. 5f).

A partir de la compilation de 18 variables représentant les pressions anthropiques en Méditerranée (Manuscrit A), six variables synthétiques ont été créées : (*i*) les menaces côtières regroupant la pollution côtière inorganique et organique, le ruissellement des éléments nutritifs et l'hypoxie, l'aquaculture et la présence d'espèces envahissantes, (*ii*) les perturbations liées au chalutage et au dragage, (*iii*) la pollution océanique regroupant les déchets toxiques, les déchets radioactifs, la pollution liée au trafic maritime, les dépôts de métaux lourds et d'azote inorganique, (*iv*) l'exploitation des ressources marines par les pêches industrielles ou semi-industrielles et artisanales, (*v*) les activités maritimes liées au trafic maritime et la présence de plates-formes pétrolières, et (*vi*) le changement climatique (Fig. 6). Chacune de ces menaces a été standardisée afin de pouvoir comparer leur intensité.

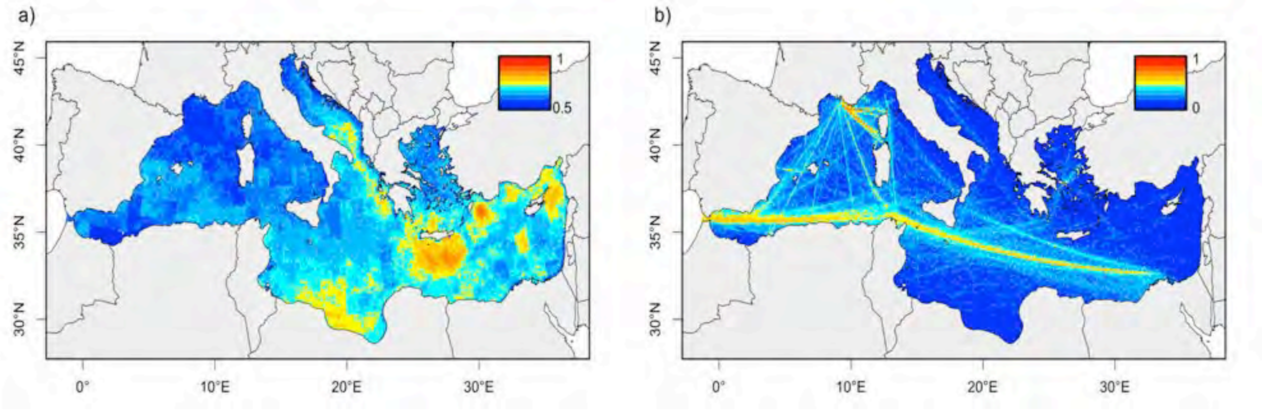


Figure 6 : Exemple de perturbation anthropique affectant la Méditerranée a) Effets du changement climatique b) Effets du trafic maritime.

Afin de créer une carte cumulant l'ensemble de ces menaces pour chacun des 5 groupes d'espèces, ces 6 variables ont été pondérées en fonction de leur importance vis à vis du groupe d'espèces considéré. Grâce à la distribution spatiale de la biodiversité et l'agrégation des menaces pour chaque groupe taxinomique, nous avons construit un indice de chevauchement (OI) permettant d'identifier les zones où les menaces et la biodiversité sont conjointement importantes. Pour les invertébrés, les poissons et les grands animaux les zones identifiées comme étant des zones critiques donc prioritaires du point de vue de la conservation sont les zones côtières espagnoles, du golfe du Lion, de la mer Adriatique, de la mer Égée, du nord est de la mer Ligurienne, du sud est de la Turquie et des régions proches de l’embouchure du Nil et du plateau continental tunisien (Fig. 7). Ces zones critiques ne sont protégées qu'à hauteur de 2% par le système d'AMP actuel et devraient faire l'objet d'un effort particulier pour les activités de recherche, de gestion et de protection. Cette étude montre pour la première fois en Mer Méditerranée les zones où les pressions, la biodiversité et les réserves sont spatialement congruentes ou non.

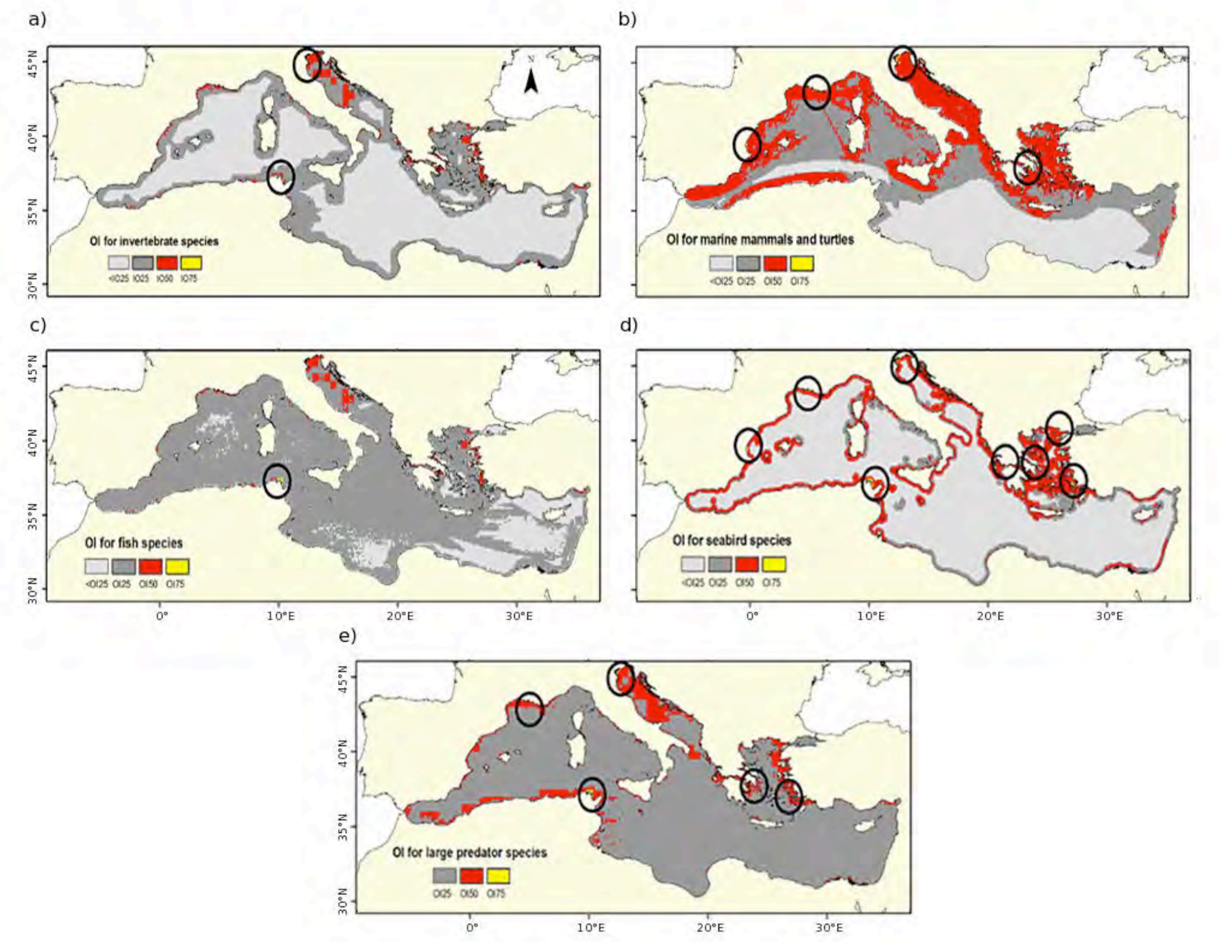


Figure 7 : Identification des zones importantes d’un point de vue de la conservation pour a) les invertébrés, b) les mammifères marins et les tortues, c) les poissons, d) les oiseaux marins e) et les grands prédateurs.

I.4.2 Quelle protection pour les différentes composantes de la biodiversité des poissons méditerranéens ?

Il est maintenant largement reconnu qu'il est indispensable, pour analyser les processus qui déterminent la distribution et le maintien de la biodiversité ainsi que le fonctionnement des écosystèmes, de prendre en considération d'autres composantes de la biodiversité que la seule richesse spécifique. Il est admis que la diversité phylogénétique et fonctionnelle des assemblages permet d'améliorer notre compréhension des mécanismes sous-jacents aux distributions de la biodiversité et au fonctionnement des écosystèmes (par exemple Faith 1992, Petchey & Gaston 2002, Hooper et al. 2005, Villéger et al. 2011). Ces deux composantes de la biodiversité peuvent être évaluées grâce à l'utilisation des deux indices régulièrement utilisés, la diversité phylogénétique (PD; Faith 1992) et son homologue fonctionnel (FD; Petchey & Gaston 2002).

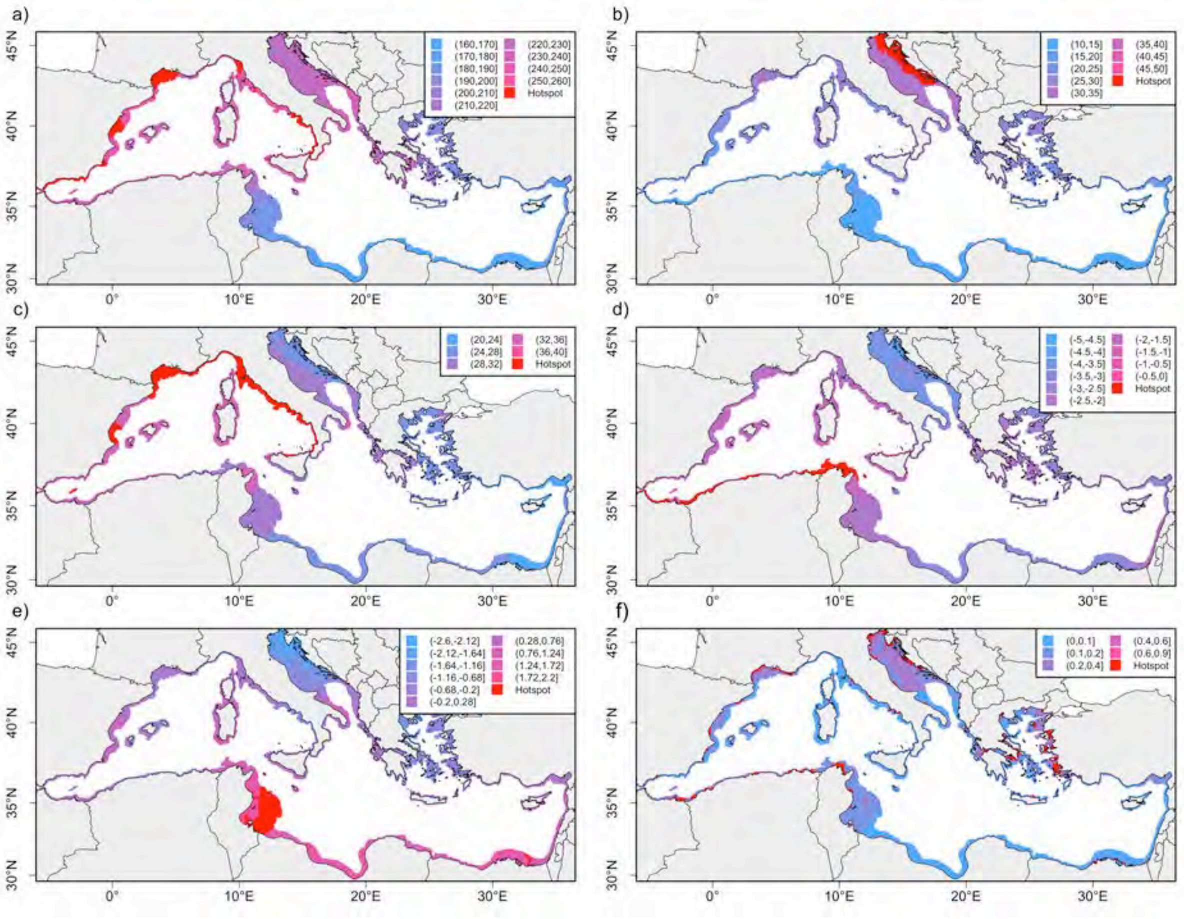


Figure 8 : Représentation de la distribution spatiale des différentes composantes de la biodiversité pour les poissons côtiers méditerranéens a) Richesse spécifique totale b) Richesse en espèces endémiques c) Richesse en espèces classées sur la liste rouge de l'UICN d) Diversité phylogénétique indépendante de la richesse spécifique totale e) Diversité fonctionnelle indépendante de la richesse spécifique totale estimée f) Pression de pêche côtières.

La mesure du PD décrit la diversité de l'histoire évolutive représentée par un ensemble d'espèces en cumulant la longueur des branches les reliant à la racine sur un arbre phylogénétique. L'indice FD mesure les différences fonctionnelles entre les espèces d'un assemblage en prenant en compte leurs traits morphologiques, physiologiques et écologiques (Petchey & Gaston 2006). Dans cette étude, des mesures de diversité fonctionnelle et phylogénétique indépendantes de la richesse spécifique, les SES (pour plus de détails voir Manuscrit B), ont été utilisées.

Afin d'étudier la protection des différentes composantes de la biodiversité des poissons côtiers méditerranéens par le système actuel d'AMP nous avons utilisé une base de données comprenant les localisations des 101 AMP, les aires de répartitions des espèces de poissons côtiers ainsi qu'une phylogénie datée (Meynard et al. 2012). Dans cette étude (Manuscrit B), nous avons montré que le système d'aires marines protégées convient pour préserver les points chauds (5% des valeurs les plus fortes) de richesse spécifique, d'espèces endémiques et d'espèces enregistrées sur la liste rouge de de l'Union internationale pour la conservation de la nature et des ressources naturelles (UICN ; Fig. 8a, b, c). Cependant ce système d'AMP est inadéquat pour préserver les points chauds de diversité fonctionnelle et phylogénétique. En effet, ces points chauds ont été identifiés dans le golfe de Gabès et le long des côtes des pays du Maghreb, là où l'effort de protection est faible (Fig. 8d,e). Les différentes composantes de la biodiversité des poissons on été confrontées aux menaces des pêches côtières. Il en ressort que les points chauds de pêche sont spatialement congruents avec ceux de richesse en espèces endémiques et de diversité phylogénétique (Fig. 8f). Nos résultats mettent en évidence que les futures stratégies de conservation et d'évaluation des systèmes de réserves devront prendre en compte la protection des différentes composantes de la biodiversité dont certaines sont largement ignorées par le système actuel de réserves.

I.4.3 Modélisation biogéographique des espèces endémiques de poissons méditerranéens côtiers face au changement climatique

Les effets attendus du changement climatique sur la biodiversité comprennent (*i*) un déplacement des espèces vers les pôles ou des altitudes plus élevées pour suivre un environnement froid (Hickling et al. 2005, Parmesan 2006, Dulvy et al. 2008, Lenoir et al. 2008), (*ii*) des extinctions lorsque les espèces n'ont plus les capacités de suivre leur niche climatique (Thomas et al. 2004, Cheung et al. 2009), et (*iii*) une réorganisation des communautés locales qui pourrait donner lieu à des extinctions d'espèces natives et favoriser l'expansion d'espèces exotiques thermophiles (Mills et al. 2004, Olden et al. 2006). En conséquence, le réchauffement des eaux de surface devrait entraîner un déplacement vers le nord des aires de distribution des poissons en Mer Méditerranée conduisant au remplacement progressif des espèces d'eau froides ou tempérée par des espèces thermophiles.

Les zones les plus froides de la Mer Méditerranée (le nord de l'Adriatique, de la Mer Égée et le Golfe du Lion) pourraient, dans un premier temps, servir de sanctuaire pour les espèces d'eau froides ou tempérées. Cependant, avec l'intensification du réchauffement, ces zones pourraient devenir un « cul-de-sac » d'où les espèces d'eaux froides ou tempérées ne pourraient s'échapper. Ce phénomène serait critique pour les espèces endémiques car l'effet de piège pourrait conduire à l'extinction des espèces se situant majoritairement au nord de la Méditerranée (Fig. 9b). Les niches réalisées de 75 poissons endémiques de mer Méditerranée ont été modélisées grâce à une approche multi-modèle, puis les futures aires de distributions ont été projetées en utilisant un scénario de réchauffement climatique (SERS A2) mis en œuvre grâce au modèle méditerranéen OPAMED8 (Manuscrit C).

Les données de températures observées ont été obtenues pour la période 1981-1984 à partir du NCDC (National Climatic Data Center). Les données de température projetées suivant le Scénario A2 du GIEC pour deux périodes (2041-2060 ; 2070-2099) ont été obtenues à partir du modèle climatique régional OPAMED8 (Somot et al. 2006, Beuvier et al. 2010). Les données de présences-absences des 75 espèces endémiques ont été compilées à partir du FNAM (Fishes of the Northern Atlantic and Mediterranean ; Whitehead *et al.* 1986). Les espèces endémiques étant à 93% présentes exclusivement sur le plateau continental, notre

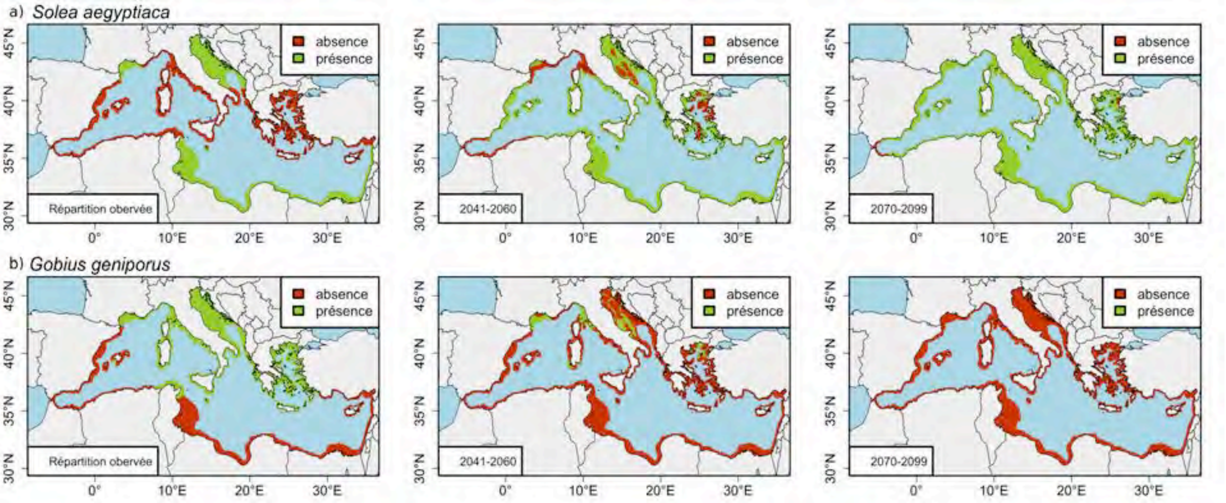


Figure 9 : Aires de répartitions de deux espèces de poissons, *Solea aegyptiaca*, et *Gobius geniporus,* observées et projetées pour deux périodes (2041-2060 ; 2070-2099). *Solea aegyptiaca* pourrait voir augmenter son aire de répartition, et *Gobius geniporus* pourrait voire son aire de répartition diminuée.

étude a été conduite en utilisant une grille de 0,1° de résolution couvrant la zone de 0 à 200 mètres de profondeur. Les distributions d'espèces ont été modélisées en utilisant sept techniques disponibles dans le package BIOMOD (Thuiller et al. 2009). Pour chaque espèce, les sept modèles ont été calibrés à l'aide d'un échantillon aléatoire des données (80% des cellules). Ensuite, chaque modèle a été évalué sur les 20% restant en utilisant l'indice proposé par Allouche et al. (2006), le TSS (*True Skill Statistic*). Les sept modèles de niche peuvent fournir des prévisions très différentes pour le même ensemble de données, et les évaluations des modèles ne permettent pas toujours de déterminer le meilleur modèle (Araújo & New 2007). Pour surmonter ces limitations, une méthode statistique permettant d'obtenir un consensus en pondérant les sorties de chaque modèle par le critère d'évaluation relatif (Marmion et al. 2009, Thuiller et al. 2009) a été utilisée.

En 2070-2099, la température moyenne des eaux de surface de la Mer Méditerranée pourrait se réchauffer de 3,1°C. Les projections pour 2041-2060 prédisent que 25 espèces pourraient être inscrites sur la liste rouge de l'UICN, et six pourraient être éteintes. En 2070-2099, 45 espèces pourraient être inscrites sur la Liste rouge de l'UICN et 14 pourraient disparaître. En outre, les aires de distribution des espèces endémiques pourraient subir une fragmentation importante (discontinuité des habitats), ce qui est un facteur potentiellement aggravant (Opdam & Wascher 2004). Dans l'ensemble, 25% du plateau continental de la Mer Méditerranée pourrait être affecté par une modification complète des assemblages d'espèces endémiques d'ici la fin du XXI^{ème} siècle avec des conséquences fonctionnelles encore largement méconnues (Fig. 10) mais certaines expérimentations laissent penser que les changements seront majeurs (Fig. 2).

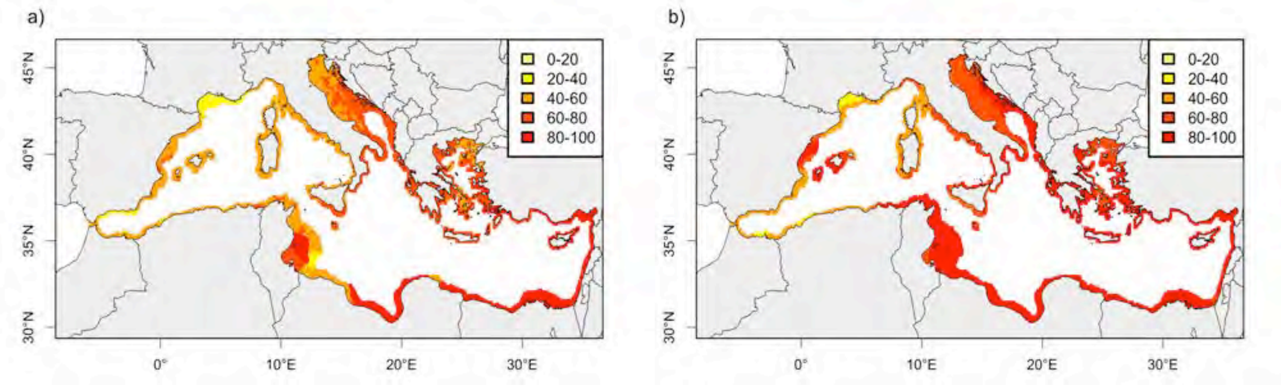


Figure 10 : Quantification du pourcentage de remplacement d'espèces endémiques sur l'ensemble du plateau méditerranéen pour deux périodes a) 2041-2060, b) 2070-2099.

I.5 Enjeux et problématiques

Les chapitres à venir sont structurés autour de 7 publications (dont 6 en premier auteur) constituant les travaux majeurs de cette thèse. Le défit était de projeter, à partir d'un ensemble de modèles et d'une base données historique, les conséquences liées au changement climatique sur l'ensemble des composantes de la biodiversité des assemblages de poissons côtiers méditerranéens et de prendre en compte les pressions anthropiques telles que la pêche (Figure 11).

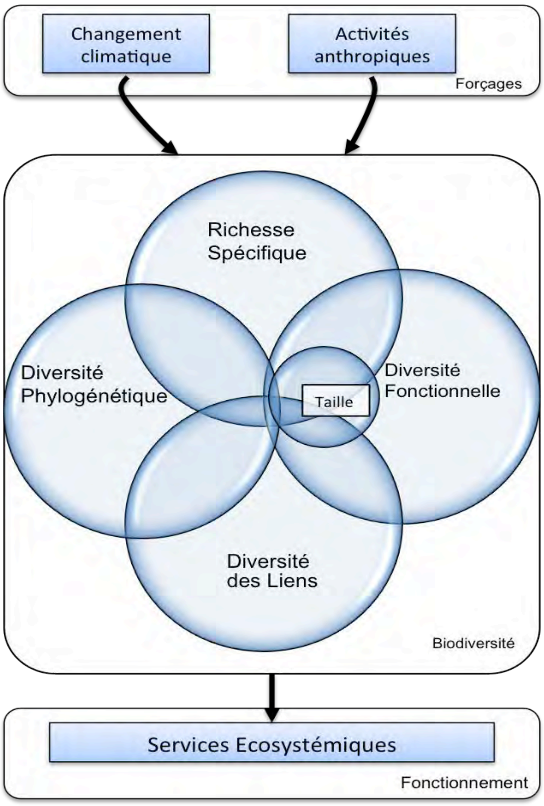


Figure 11 : Enjeux et Problématiques de la thèse.

Une première étude concernant les poissons endémiques a montré que d'ici la fin du XXI^{ème} siècle, 14 espèces pourraient disparaître parmi les 75 étudiées. Un des enjeux de cette thèse est d'étendre cette analyse à l'ensemble des poissons côtiers et de comprendre les mécanismes affectant la biodiversité en explorant la dynamique temporelle des changements de richesse et de taille moyenne des assemblages.

Même si l'étude des variations de richesse spécifique est un point de départ nécessaire, cela n'est pas suffisant pour étudier les modifications de biodiversité associées au changement global. Il est important de prendre en compte (*i*) la diversité phylogénétique qui décrit l’histoire évolutive portée par un groupe d’espèces, (*ii*) la diversité fonctionnelle qui illustre la diversité des fonctions assurées par les espèces au sein des assemblages. Par conséquent il s’agit d’évaluer, au delà des modifications de richesse spécifique, comment la diversité des lignées et des traits fonctionnels pourrait être affectée par le changement climatique. Chez les poissons, parmi les traits biologiques, la taille est le trait décrivant le mieux le métabolisme, la survie ou la croissance des espèces. Pour l’ensemble de ces raisons, les effets du changement climatique sur ce trait intégrateur ont été étudiés.

Si la modélisation des aires de répartition permet actuellement de mieux appréhender l’impact des changements climatiques sur la biodiversité, nous en savons beaucoup moins sur les conséquences écosystémiques qu'il génère et les services associés. Il est un fait établi : les modèles de niche négligent les interactions entre espèces (Woodward et al. 2010). Or, il est évident que la structure et la composition des réseaux d’interactions seront remaniées à la suite des changements globaux du fait de l’arrivée et de la disparition d’espèces. Les organismes migreront à des rythmes différents, ce qui entraînera une réorganisation des communautés et, par conséquent les nouveaux écosystèmes qui pourraient émerger comporteront des espèces qui n'ont jamais interagi auparavant (Woodward et al. 2010). Le second enjeu de cette thèse est de comprendre comment les assemblages futurs seront réorganisés à la suite des réponses individuelles des espèces au changement climatique et comment la structure des ces écosystèmes émergents pourraient être modifiés.

I.6 Objectifs

Dans le but de répondre aux enjeux abordés ci-dessus nous avons construit une base de données comprenant des informations sur les aires de répartitions, les traits biologiques et écologiques, et la phylogénie des espèces de poissons méditerranéens. Des données annexes ont été également récoltées comme le positionnement des réserves et les données climatiques actuelles et futures.

Cette thèse s'articule autour de trois chapitres en dehors des chapitres d'introduction et de conclusion :

- ✓ le premier chapitre présente la stratégie d'élaboration et la structuration de la base de données qui a été créée à partir de données dispersées et hétérogènes.
- ✓ le deuxième chapitre met en évidence, à travers trois publications, les effets potentiels du changement climatique sur les aires de répartitions des poissons côtiers méditerranéens, le remplacement d'espèces au sein des assemblages de poissons et comment, indépendamment de la richesse spécifique, la perte de diversité phylogénétique et fonctionnelle pourrait être induite par le changement climatique en Méditerranée.
- ✓ Dans le troisième chapitre, nous avons développé une méthodologie fondée sur l'étude des réseaux écologiques pour prédire l'effet du changement climatique sur la structure des réseaux trophiques des assemblages de poissons suite à la modification des aires de répartition des espèces et donc de la composotion en espèces.

Chapitre 2

Construction et utilisation de la base de données

Afin d’étudier la dynamique des différentes composantes de la biodiversité en Mer Méditerranée (taxonomique, fonctionnelle, phylogénétique et trophique) et sa protection dans un contexte de changement global, nous avons, durant plusieurs années au sein du laboratoire, élaboré et alimenté une base de données permettant de centraliser, de structurer et d'homogénéiser l'information. Ses droits et son utilisation s'effectuent dans le cadre du Consortium pour l'Exploration des Facettes de la Diversité en Méditerranée (CEFDEM) que j'ai mis en place en 2011. Par ailleurs, l'ensemble du travail n’est pas de mon seul fait mais résulte d'une collaboration avec d’autres membres du CEFDEM. Cette base de données en construction depuis 5 ans arrive aujourd’hui à maturité. Dans ce chapitre sont présentés les différents maillons constitutifs de cette base ainsi que la valorisation déjà effectuée et celle à venir en précisant ma contribution personnelle par rapport à celles des membres du consortium.

II.1 Aires Marines Protégées et écorégions

En dépit de la mise en place d’une centaine d’AMP en Mer Méditerranée, seule une liste inventoriant ces AMP et quelques informations parcellaires sur leur localisation étaient disponibles auprès de l’association MEDPAN (Mediterranean protected area network ; http://www.medpan.org/) au début de la thèse en 2009. Aucune donnée géoréférencée, recensant les emplacements des réserves avec coordonnées spatiales, n’avait été établie. Pour pallier ce manque d’informations géographiques sur les emplacements et la forme des réserves, nous avons collecté les cartes et les coordonnées GPS (*Global Position System*) pour établir les polygones représentant la frome et la surface des réserves. Ces données ont été obtenues en contactant les gestionnaires ou les autorités nationales par enquête, courrier et courriel. 101 AMP ont été identifiées (Fig. 9) et localisées dans 18 pays du pourtour méditerranéen : Albanie (1), Algérie (1), Croatie (8), Chypre (1), Egypte (1), France (8), Grèce (4), Israël (5), Italie (25), Liban (1), Malte (5), Monaco (1), Maroc (1), Slovénie (3), Espagne (22), Syrie (3), Tunisie (2), Turquie (9)

Nous avons également intégré les écorégions définies comme les plus petites unités du système MEOW (Marine Ecoregions of the World) qui comprend 12 domaines, 62 provinces et 232 écorégions (Spalding et al. 2007). Une écorégion est une aire homogène en terme de composition d'espèces et distincte des systèmes adjacents. Elles sont au nombre de 7 en mer Méditerranée : la mer Adriatique, la mer Egée, le bassin Levantin, le plateau Tunisien et le golfe de Syrte, la mer Ionienne, la mer d'Alboran et la partie ouest de la Méditerranée (Fig. 12). L'intérêt de ces écorégions est qu'elles permettent d'estimer la dynamique des composantes de la biodiversité par entité géographique homogène.

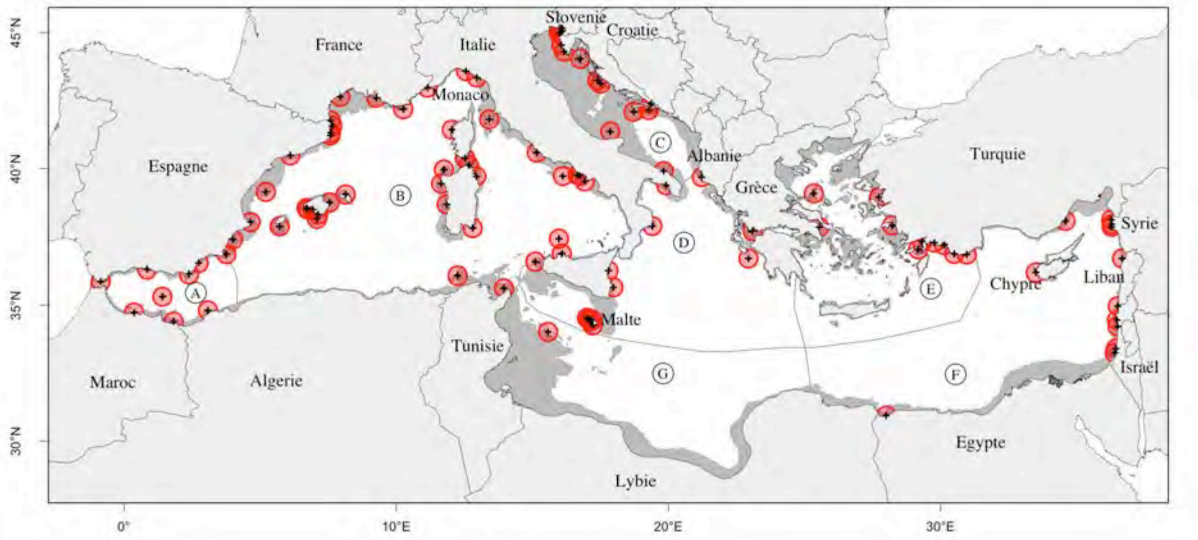


Figure 12 : Localisation des 101 Aires Marines Protégées en Méditerranée (cercle rouge); les lettres entourées représentes les écorégions A : la Mer d'Alboran; B : partie ouest de la Méditerranée ; C : la Mer Adriatique ; D : la Mer Ionienne ; G : le Plateau Tunisien/et le Golfe de Syrte ; E : la Mer Egée ; F : le Bassin Levantin. Le gris foncé correspond à la zone de 0-200 mètres qui a été identifiée comme le plateau continental dans nos études.

II.2 Traits biologiques et écologiques

Chaque espèce occupe et utilise le milieu (habitat, écosystème) d'une manière qui lui est propre, c'est la notion de niche écologique (MacArthur & Levins 1967). Cette niche est définie, entre autre, par des gammes de tolérance pour les facteurs écologiques de l'écosystème, correspondant aux besoins de l'espèce considérée (pour la nutrition, la reproduction, tolérance physiologique, etc...) et sa façon d'occuper le milieu (habitat, température, etc..). Cette niche est par définition multidimensionnelle où chaque dimension serait un facteur du milieu; la dimensionnalité de cette niche correspondrait idéalement au très grand nombre de facteurs indépendants pouvant affecter la survie de l'espèce. En pratique l'ensemble de ces axes de niche est difficile voire impossible à appréhender quantitativement. Une alternative est d'utiliser les traits biologiques et écologiques des espèces pour mieux comprendre leur utilisation du milieu (Mouillot et al. 2011). Pour les poissons méditerranéens, nous avons ainsi recueilli des traits biologiques et écologiques en rapport avec leur utilisation de l'habitat, leur type de reproduction, leur régime alimentaire, et leur comportement. Même si ces traits sont loin d'être assez exhaustifs pour prétendre englober l'ensemble de la niche des espèces ils semblent suffisamment pertinents et étoffés pour approximer "qui fait quoi ?" dans le milieu.

- La taille

La taille des animaux est un trait intégrateur, elle est indicatrice de leur rôle au sein des écosystèmes et conditionne leur physiologie, leur écologie et, par conséquent, leur comportement (Peters & Wassenberg 1983). Allant de la blennie à tête noire (*Lipophrys nigriceps,* 4cm) au requin pèlerin (*Cetorhinus maximus,* 1200 cm), la taille des poissons méditerranéens varie considérablement. Cette diversité de taille implique une structuration complexe du réseau trophique (Jennings & Brander 2010).

- Les régimes alimentaires

Les régimes alimentaires des poissons sont très divers. Cependant, classiquement, trois grandes catégories sont distinguées : les herbivores, les omnivores, et les carnivores. Pour cette dernière catégorie, une distinction entre les piscivores et les autres carnivores moins spécialisés a été réalisée.

- L'habitat

Afin de définir l'habitat, trois catégories d'espèces aquatiques ont été identifiées : les espèces dites «démersales» qui se nourrissent sur le fond mais qui se déplacent au dessus, les espèces dites «benthiques» qui vivent et se nourrissent sur le fond et les espèces dites «pélagiques» qui évoluent et se nourrissent en pleine eau. Quatre autres variables spatiales qualifient également la distribution des poissons dans la colonne d'eau : le littoral, le plateau continental, le talus continental et la haute mer. Nous avons également considéré les trois substrats les plus communément retrouvés en mer Méditerranée, à savoir les fonds meubles, les fonds rocheux et les herbiers à Posidonie (*Posidonia Oceanica*).

- La reproduction

Chez les poissons, trois stratégies reproductives sont observées : l'oviparité (les espèces pondant des œufs dans l’eau), la viviparité (les espèces dont les œufs se développent à l’intérieur du corps maternel, l'alimentation de l'embryon étant assurée par une annexe embryonnaire faisant fonction de placenta), l'ovoviviparité (les espèces dont les œufs se développent à l'intérieur du corps maternel, l'alimentation de l'embryon par la mère se faisant en l'absence d'une annexe embryonnaire). L’oviparité est le mode de reproduction le plus répandu. Chez les ovipares il existe deux types principaux de larves : les larves dites planctotrophiques (qui se nourrissent de plancton), et celles dites lécitotrophiques (qui se nourrissent de leurs propres ressources vitellines).

La possibilité de changement de sexe au cours de la vie (hermaphrodisme séquentiel) chez certaines espèces de poisson a également été intégrée à la base de données. Dans le cas de l'hermaphrodisme successif, chez les espèces protogynes, les individus, femelles durant les premières années de leur vie, deviennent ensuite mâles. Chez les espèces protandres, c'est l'inverse qui se produit : les individus d'abord mâles deviennent ensuite femelles. Nous avons également pris en considération comme caractère reproducteur le nombre de cycles de reproduction au cours de la vie et fait la distinction entre espèces itéropares qui pondent à plusieurs reprises au cours de leur vie et espèces semelpares qui ne se reproduisent qu'une fois au cours de leur vie, ce qui est souvent une caractéristique d'espèces migratrices comme le saumon ou l'anguille.

- La migration

Un certain nombre de poissons effectuent des migrations tout en restant en Mer (océanodrome), d’autres vivent alternativement en eau de Mer et en eau douce. Les espèces anadromes vivent généralement en Mer et se reproduisent en eau douce, les catadromes vivent le plus souvent en eau douce et se reproduisent en Mer. Quant aux espèces amphidromes, elles migrent, selon leurs différents stades de vie, entre Mer et eau douce sans que cela ne soit lié obligatoirement à la reproduction.

- Le comportement social

Trois grands types de comportements sociaux existant chez les poissons ont été pris en compte : solitaire, grégaire, ou mixte.

- Degré de vulnérabilité

Afin de classer les espèces en fonction de leur degré de vulnérabilité, l'UICN a établi une liste rouge (*Red list*) qui distingue différentes catégories allant de potentiellement en danger jusqu'à éteinte (UICN 2008 ; http://www.iucnredlist.org). Ces différentes catégories sont : préoccupation mineure (LC), quasi menacée (NT), vulnérable (VU), en danger (EN), danger critique d'extinction (CE), éteint à l'état sauvage (EW), éteint (EX), manque de données (DD), aucun statut UICN (NP).

La majorité des données proviennent de plusieurs sources (Whitehead et al. 1986, Louisy 2005, Froese & Pauly 2012). Nous avons accordé la même importance aux différents ouvrages consultés.

II.3 Aire de répartition de 635 espèces de poissons méditerranéens.

La première étape de l'élaboration de la base de données a été la digitalisation des aires de répartition (Ben Rais Lasram 2009) de 635 espèces de poissons méditerranéens à partir de deux sources, le FNAM (Whitehead et al. 1986) et le site internet de la CIESM (Commission Internationale pour l'Exploration Scientifique de la mer Méditerranée ; Golani et al. 2002). Ceci a permis d'obtenir 635 polygones représentant la répartition de chaque espèce de poissons sur l'ensemble de la Méditerranée. Les résultats de ce travail préalable ont été ensuite améliorés en apportant des modifications afin d'intégrer un nouveau trait de côte

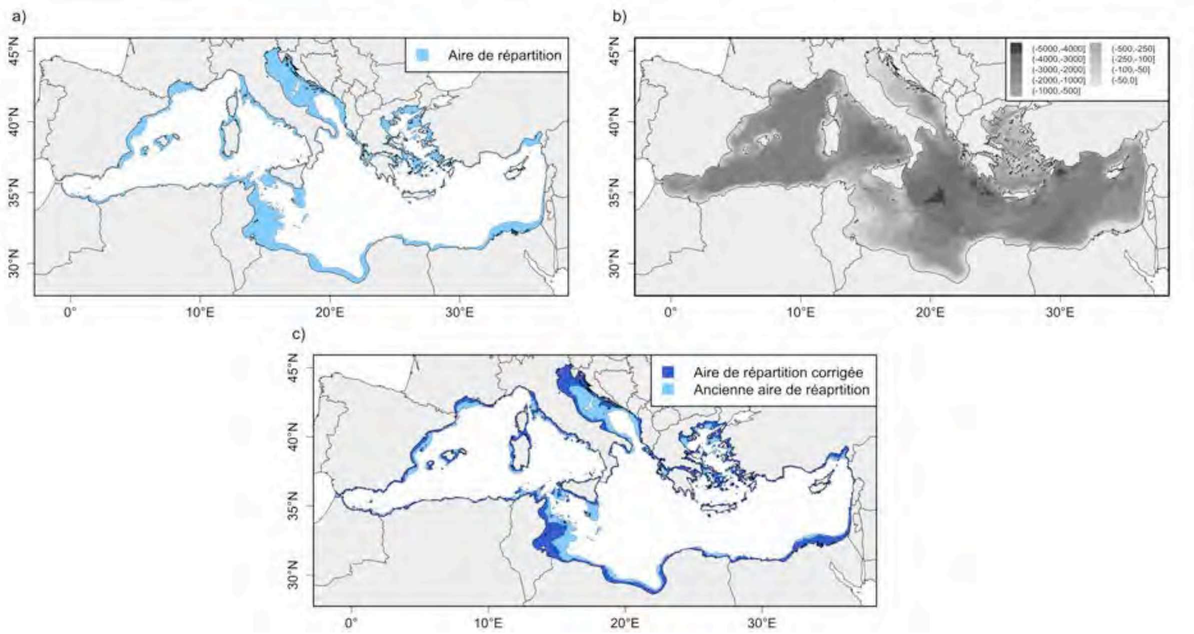


Figure 13: a) Aire de répartition initiale de *Coris julis*; b) Bathymétrie pour la méditerranée suivant ETOPOV2; c) Aire de répartition modifiée pour *Coris Julis*.

plus précis et largement utilisé par la communauté scientifique : le trait de côte des écorégions terrestres (Olson et al. 2001). Les polygones de présence des espèces ont été par la suite corrigés en prenant en considération les limites bathymétriques de vie de chaque espèce, ceci afin de réduire les incohérences entre les informations figurant dans les atlas et les caractéristiques biologiques des différentes espèces. Ainsi, la base de données sur les traits d'histoire de vie fournit, pour l'ensemble des espèces, les profondeurs maximales et minimales entre lesquelles elles évoluent habituellement. La cartographie bathymétrique de la Méditerranée provient des données ETOPOV2 (ETOPOV2, 2010) et nous renseigne sur les profondeurs en tous points. Par exemple, la girelle (*Coris Julis*) n'est, en réalité, présente qu'entre 1 et 60 mètres alors qu'elle figurait initialement, avant que nous corrigions sa répartition, sur l'ensemble du plateau continental défini par Ben Rais Lasram (2009) de 0 à 200 mètres (Fig. 13a). Après correction par la bathymétrie (Fig. 13b) et prise en compte de son aire de répartition, le polygone modifié de la girelle (Fig. 13c) présente son aire de répartition corrigée par son intervalle bathymétrique sur l'ensemble de la Méditerranée. Cette rectification conduit à un changement de 41% de l'aire de répartition de la girelle sur le plateau continental.

Les polygones ont ensuite été superposés sur une grille de mailles de 0,1° de longitude par 0,1° de latitude afin de créer une matrice de présence-absence couvrant toute la Mer Méditerranée. Nous avons opté pour un maillage fin qui est un compromis entre la dimension de la Mer Méditerranée et la localisation précise des espèces. En effet un maillage trop fin ne serait pas cohérent avec les données d'atlas et un maillage plus grossier ne permettrait pas d'estimer correctement la surface des espèces et ne serait pas cohérent avec le trait de côte.

II.4 Arbre phylogénétique des poissons méditerranéens

Afin d'appréhender la diversité des assemblages de poissons méditerranéens dans son ensemble, il était nécessaire d'étudier la diversité phylogénétique qui est une composante cruciale en conservation (Cadotte et al. 2010). Cependant aucune phylogénie des poissons méditerranéens n'était disponible. Pour remédier à l'absence de ces données, une phylogénie datée des poissons téléostéens (Fig. 14) a été réalisée dans le cadre du CEFDEM. L'arbre phylogénétique initial regroupe 363 espèces méditerranéennes réparties en 110 familles et 237

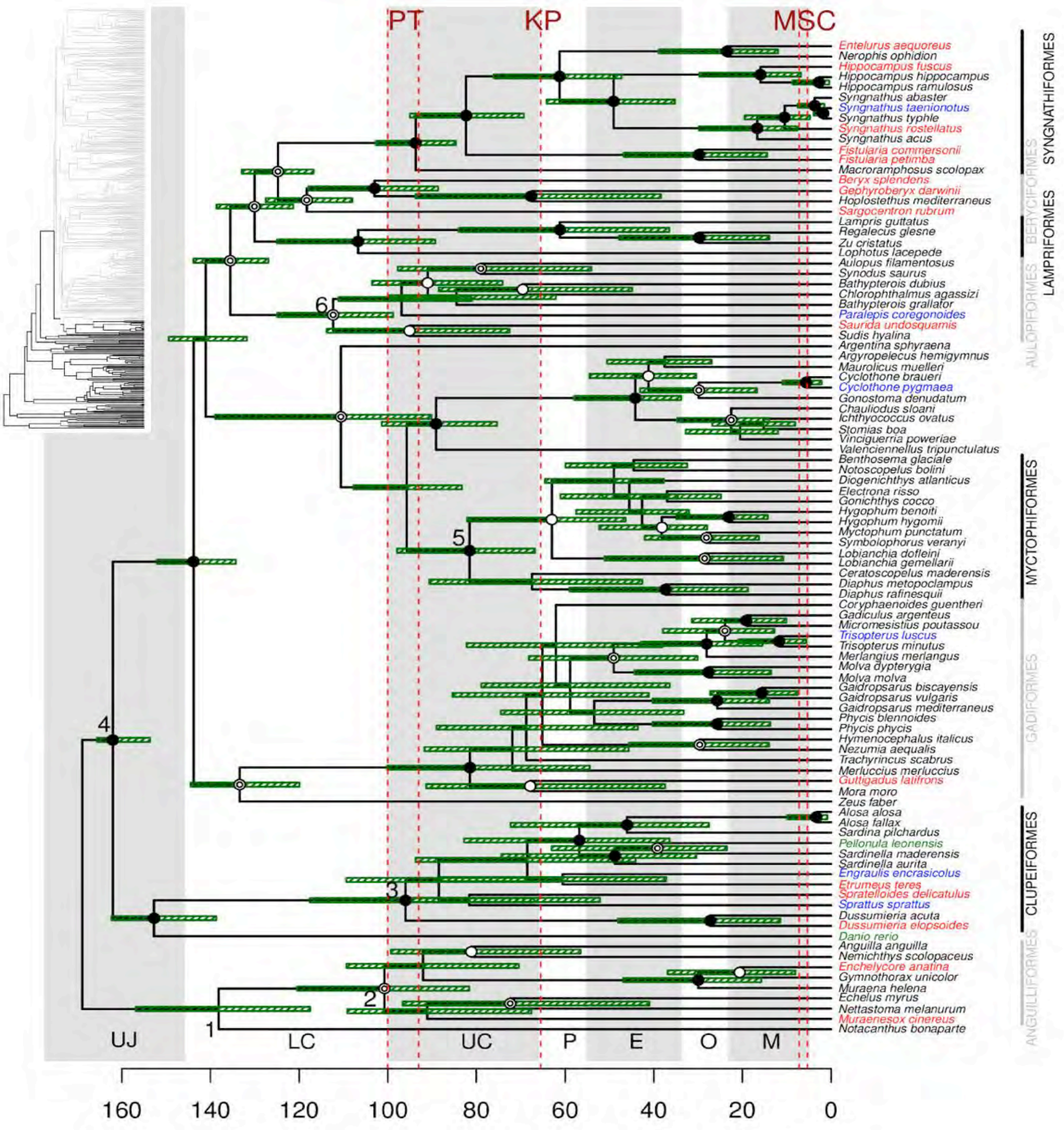


Figure 14 : Extrait de la phylogénie datée des poissons téléostéens de Méditerranée (Meynard et al. 2012). Les couleurs pour les noms des espèces indiquent l'origine de celle-ci (rouge : espèces exotiques, bleu : espèces endémiques, noir : espèces ubiquistes, vert : espèces extra-méditerranéennes). Les boîtes vertes indiquent l'intervalle de confiance à 95% sur l'âge des nœuds. Les lettres indiquent les temps géologiques UJ : Jurassique supérieure, LC : Crétacé inférieure, UC : Crétacé supérieur, P : Paléocène, E : Eocène, O : Oligocène, M : Miocène. Les lignes rouges représentent les principaux événements biogéographiques (PT : pic de température du Cénomanien; KP : extinction massives Crétacé/Paléocène ; MSC : crise messénienne).

séquences nucléotidiques, collectées sur GenBank ont permis de construire une super matrice composée de quatre gènes mitochondriaux (ADN 12S ribosomal, ADN 16S ribosomal, cytochrome C oxydase I, cytochrome b) ainsi que deux gènes nucléaires (rhodopsine et gène activant la recombinaison 1). Le temps de divergence entre les différents taxons a été estimé à l'aide de la méthode du maximum de vraisemblance et de statistiques bayésiennes en se fondant sur les âges de poissons fossiles déjà utilisés dans différentes publications (Meynard et al. 2012). Les données génétiques n'étant pas disponibles pour l'ensemble des poissons, 124 espèces ont été ajoutées *a posteriori* sur le chronogramme phylogénétique. La phylogénie finale intègre 496 espèces de poissons téléostéens méditerranéens et extra-méditerranéens, ces derniers ayant été inclus pour calibrer l'arbre. Cette phylogénie nous a servi à explorer les patrons de diversité phylogénétique observés, mais aussi les modifications de ces patrons induites par le changement climatique.

II.5 Données climatiques

Pour explorer les impacts potentiels du changement climatique sur les différentes composantes de la diversité des poissons méditerranéens, il est indispensable d'avoir des données climatiques provenant de modèles recréant, de la manière la plus correcte, la complexité des variations de paramètres physico-chimiques en mer Méditerranée. Les

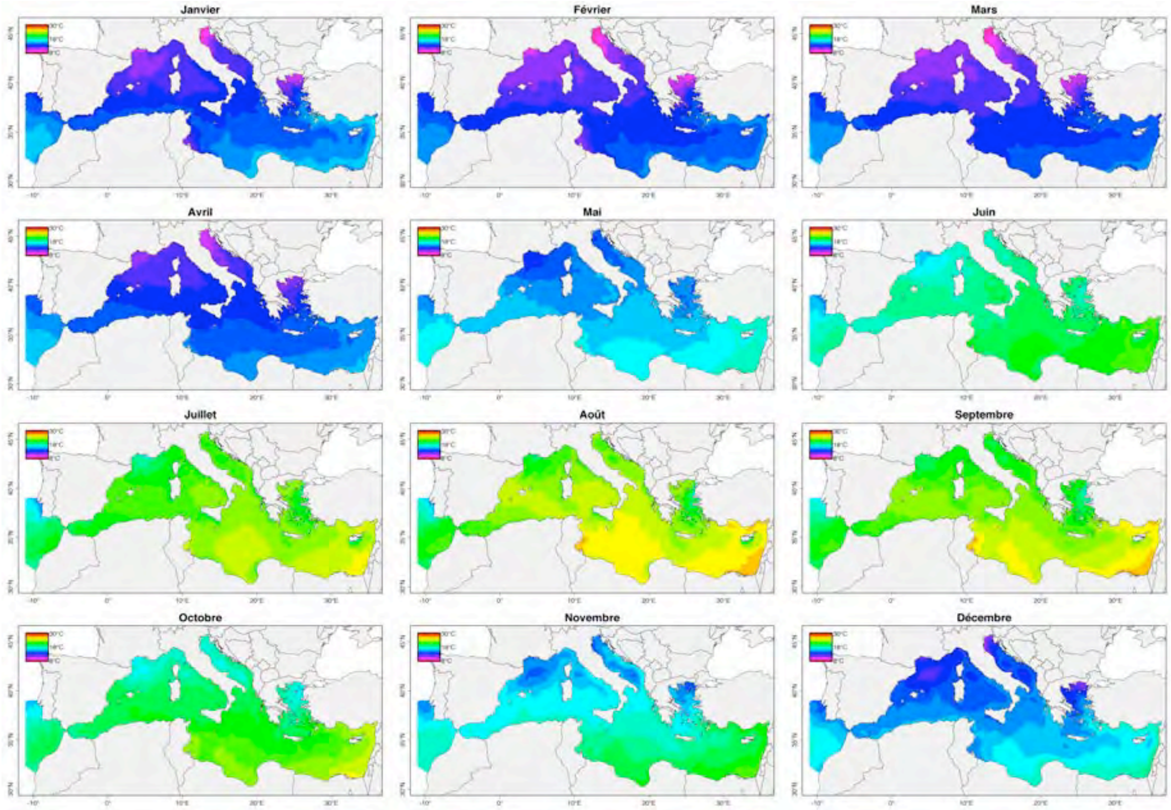


Figure 15 : Températures mensuelles de surface moyennées sur une période de 20 ans (1961-1980) issues du modèle NEMOMED8.

données de température de surface, extraites de simulations numériques faites avec un modèle dédié exclusivement à la mer Méditerranée, ont été fournies par Samuel Somot, chercheur à Météo France. Il s'agit d'une adaptation du modèle NEMO océan (Madec 2008) qui peut être considérée comme une version actualisée du modèle OPAMED8 (Somot et al. 2006) déjà utilisé par Ben Rais Lasram et al. (2010). Le modèle NEMOMED8 est un modèle océanique régional qui prédit les températures de surface à partir de différents facteurs : les échanges de chaleur et d'eau entre l'air et la mer, les débits fluviaux, et les échanges de chaleur et d'eau avec l'océan Atlantique et la mer Noire (Beuvier et al. 2010).

NEMOMED8 couvre l'ensemble de la Méditerranée et une zone tampon incluant une partie de l'océan Atlantique (Fig. 15). La résolution horizontale est de 1/8° ce qui équivaut à une fourchette de 9 à 12 km du nord au sud. La grille en trois dimensions comprend 43 niveaux verticaux avec une distribution hétérogène de 6 m d'épaisseur en surface à 200 m au fond et avec 25 niveaux dans les 1000 premiers mètres. La profondeur maximale est de 4100 m dans le bassin est (Fig. 13b). La profondeur du dernier niveau est ajustée en fonction de la bathymétrie réelle. Le débit mensuel ou bien interannuel des 33 principaux fleuves se jetant en Méditerranée a été utilisé pour caractériser les apports d'eau douce qui s'élèvent à 7696

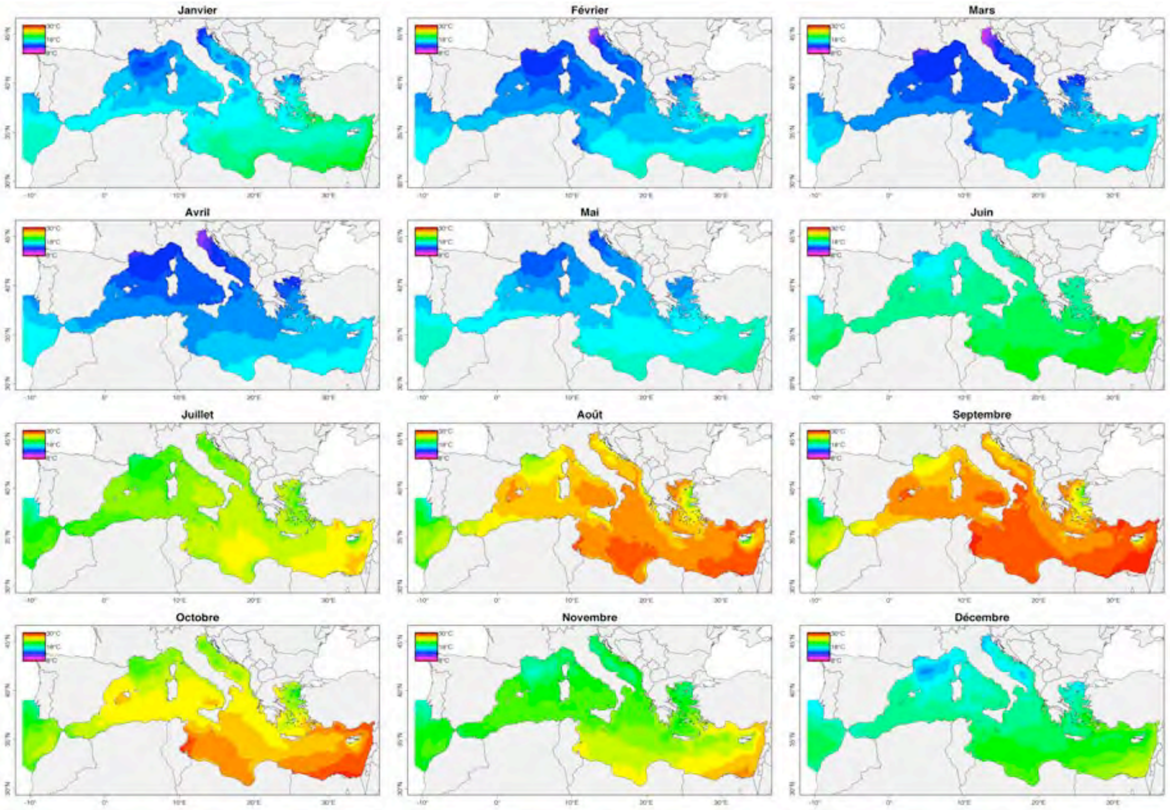


Figure 16 : Températures mensuelles de surface moyennées sur une période de 20 ans (2080-2099) issues du modèle NEMOMED8.

m^3.s^{-1}. La mer Noire n'est pas comprise dans la grille du modèle car elle est très peu salée, et de ce fait est considérée comme un fleuve.

Les données journalières nous ont été transmises sous la forme de fichiers « Netcdf » pour trois périodes de vingt ans, l'une observée (1961-1980 ; Fig. 15) et les deux autres projetées suivant le scénario A2 du GIEC (2040-2059; 2080-2099 ; Fig. 16). Ce scénario décrit un monde très hétérogène caractérisé par une forte croissance démographique, un faible développement économique et de lents progrès technologiques (Encart 1, Chapitre 1). Les températures ont été ensuite compilées pour obtenir des données mensuelles pour chacune des trois périodes. Elles ont été modifiées pour être en adéquation avec la grille de présence/absence des poissons.

II.6 Construction d'une base de données relationnelle

Une base de données relationnelle permettant de lier une partie des données présentées dans les sous-chapitres précédents a été construite. Afin qu'elle soit utilisable en ligne, un protocole précis a été suivi, à savoir la réalisation d'un cahier de données dans lequel sont décrits tous les objectifs de la base ainsi que toutes les données. Dans un premier temps, un Modèle Conceptuel des Données a été réalisé (MCD; Fig. 17). Il expose de façon formelle les données qui seront utilisées par le système d'information. Il s'agit d'une représentation des données, permettant de décrire le système d'information à l'aide d'entités et de liens logiques. Le MCD est ensuite traduit en Modèle Logique des Données (MLD ; Fig. 18). Le MLD intègre comme contraintes techniques la prise en compte de l'outil logiciel d'implantation du MCD. Afin d'automatiser le processus de création et de remplissage de la base de donnée un script a été implémenté en langage Phyton.

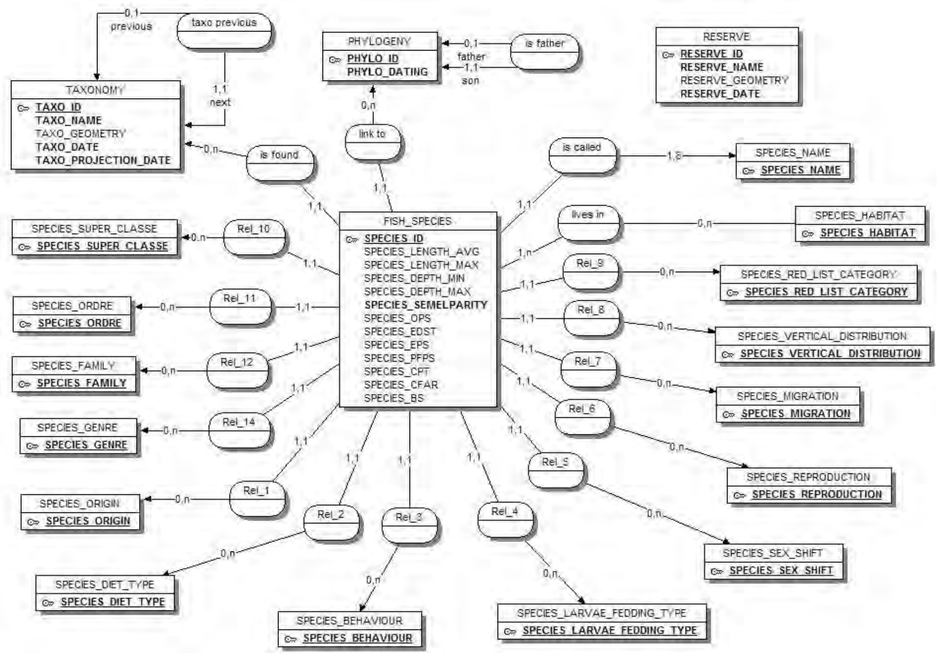


Figure 17 : Représentation schématique d'un modèle conceptuel de base de donnée.

La base de données a été placée sur un serveur « PostgresSQL 8.4.12 » à l'aide du logiciel « phpPgAdmin ». A ce jour cette base de données est accessible en local. Un des points fort de cette base est l'incorporation de données spatialisées tels que les polygones des espèces, les polygones des réserves ainsi que les polygones permettant de réaliser les opérations courantes comme les polygones des écorégions, ceux du plateau continental ou de la bathymétrie. Il est en effet possible de réaliser des requêtes (SQL ; Structured Query Language) depuis le logiciel R comme par exemple : « Combien d'espèces sont présentes dans l'écorégion de la mer Ionienne ? » ou encore « Quel est l'arbre phylogénétique pour les espèces présentes en mer Adriatique ? » ou bien encore « Quels sont les traits écologiques et fonctionnels pour un genre d'espèces donné ? » (Fig. 19).

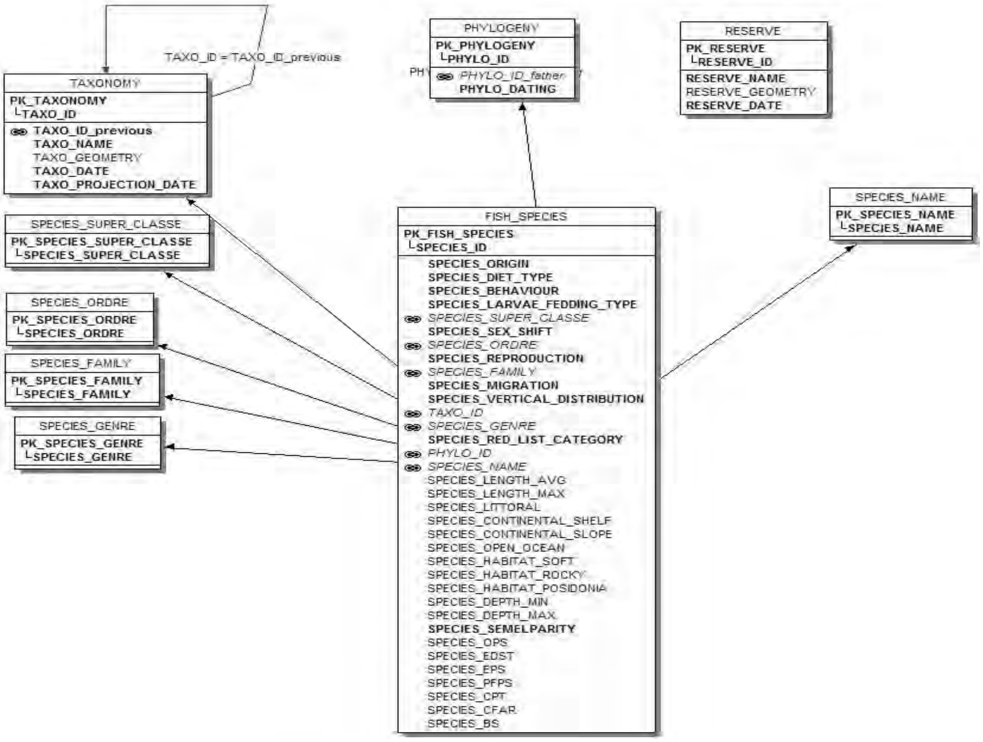


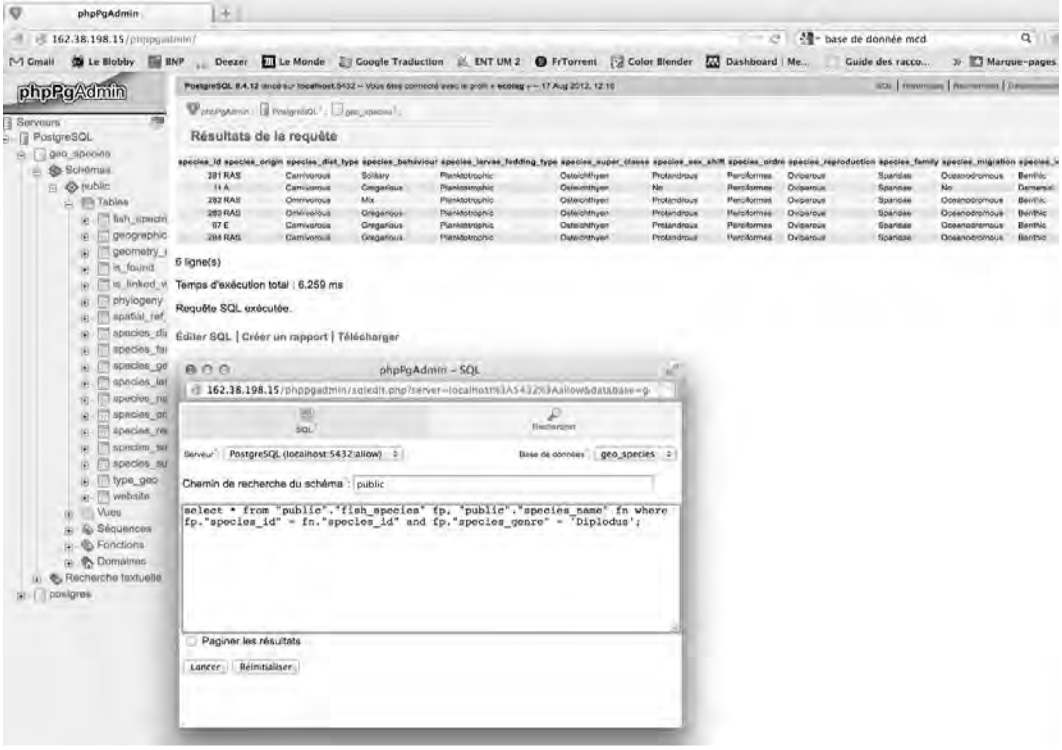
Figure 18 : Représentation schématique du modèle logique de données.

II.7 Partage de la base de données

Dans un souci de transfert de connaissances vers la communauté scientifique ainsi que vers les organisations impliquées dans la conservation du milieu marin en Méditerranéen, nous avons pris la décision de rendre la base de données publique. Elle sera prochainement consultable et téléchargeable en ligne et fera l'objet d'une publication scientifique dans la revue *Ecology* qui possède une section dédiée aux présentations des bases de données « Data Papers ». La priorité d'utilisation d'une grande partie de cette base de données a été accordée au CEFDM ainsi qu'à l'association MEDPAN qui a pour objectif de faciliter les échanges entre les gestionnaires des AMP en Mer Méditerranée afin d'améliorer l'efficacité de la gestion des territoires. Ainsi, les données fournies vont servir à l'élaboration du rapport d'activité MEDPAN pour l'année 2012. Dès que cela sera possible les données publiées seront accessibles en ligne (voir interface ; Fig. 19).

II.8 Utilisation de la base de données pour la thèse

Dans le cadre de l'accord de consortium, les données de la base ont servi à réaliser 7 articles (Manuscrit A, B, D, E, F, H, J) dont 4 ont été publiés dans des revues internationales à comité de lecture (Manuscrit A,B,D,F). Ces données m'ont permis de co-encadrer deux stages, un de Master 2 et un stage de Master 1. Cependant, la totalité des informations de la base n'a pas été exploitée pour chacune des publications. Pour les premières publications (Manuscrits A, B, C), nous avons utilisé une base de données dans laquelle les aires de répartitions n'étaient pas encore corrigées par la bathymétrie et où le trait de côte était moins précis que dans la base actuelle.



Résultats de la requête

species_id	species_origin	species_diet_type	species_behaviour	species_larvae_fedding_type	species_super_classe	species_sex_shift	species_ordre	species_reproduction	species_family	species_migration	species_
281	RAS	Carnivorous	Solitary	Planktotrophic	Osteichthyen	Protandrous	Perciformes	Oviparous	Sparidae	Oceanodromous	Benthic
11	A	Carnivorous	Gregarious	Planktotrophic	Osteichthyen	No	Perciformes	Oviparous	Sparidae	No	Demersal
282	RAS	Omnivorous	Mix	Planktotrophic	Osteichthyen	Protandrous	Perciformes	Oviparous	Sparidae	Oceanodromous	Benthic
283	RAS	Omnivorous	Gregarious	Planktotrophic	Osteichthyen	Protandrous	Perciformes	Oviparous	Sparidae	Oceanodromous	Benthic
67	E	Carnivorous	Gregarious	Planktotrophic	Osteichthyen	Protandrous	Perciformes	Oviparous	Sparidae	Oceanodromous	Benthic
284	RAS	Carnivorous	Gregarious	Planktotrophic	Osteichthyen	Protandrous	Perciformes	Oviparous	Sparidae	Oceanodromous	Benthic

6 ligne(s)

Temps d'exécution total : 6.259 ms

Requête SQL exécutée.

Éditer SQL | Créer un rapport | Télécharger

phpPgAdmin – SQL

162.38.198.15/phppgadmin/sqledit.php?server=localhost%3A5432%3Aallow&database=g

Serveur : PostgreSQL (localhost:5432:allow)

Base de données : geo_species

Chemin de recherche du schéma : public

```
select * from "public"."fish_species" fp, "public"."species_name" fn where
fp."species_id" = fn."species_id" and fp."species_genre" = 'Diplodus';
```

☐ Paginer les résultats

Figure 19 : Interface de la base de données SQL, avec un exemple de requête SQL pour accéder à l'ensemble des données fonctionnelle pour le genre Diplodus.

Tableau 2 : Synthèse des différents éléments de la base de données utilisés dans le cadre des publications présentent dans ce manuscript de thèse.

<table>
<tr><th rowspan="2"></th><th rowspan="2">Manuscrits</th><th colspan="8">Données utilisées</th><th rowspan="2">Commentaires</th></tr>
<tr><th>Nombre d'espèces</th><th>Traits fonctionnels</th><th>Réserves</th><th>Présence /absence</th><th>Phylogénie</th><th>Données climatiques</th><th>Menaces</th><th>Projections</th></tr>
<tr><td rowspan="3">Ancienne base de données Méditerranée</td><td>A</td><td>282</td><td></td><td>✔</td><td>✔</td><td></td><td></td><td>✔</td><td></td><td>Pas de correction par la bathymétrie. Ancien trait de côte. Poissons ayant au moins 40% de leur aire de répartition sur le plateau continental.</td></tr>
<tr><td>B</td><td>282</td><td>✔</td><td>✔</td><td>✔</td><td>✔</td><td></td><td>✔</td><td></td><td>Pas de correction par la bathymétrie. Ancien trait de côte. Poissons ayant au moins 40% de leur aire de répartition sur le plateau continental.</td></tr>
<tr><td>C</td><td>75</td><td></td><td></td><td>✔</td><td></td><td>✔</td><td></td><td>✔</td><td>Pas de corrections par la bathymétrie. Ancien trait de côte. Poissons endémiques</td></tr>
<tr><td colspan="11"></td></tr>
<tr><td rowspan="5">Nouvelle base de donnée Méditerranée</td><td>D</td><td>288</td><td>✔</td><td></td><td>✔</td><td></td><td>✔</td><td></td><td></td><td>Espèces strictement sur le plateau continental. Contraintes de projections.</td></tr>
<tr><td>E</td><td>230</td><td>✔</td><td></td><td>✔</td><td>✔</td><td>✔</td><td></td><td>✔</td><td>Espèces strictement plateau. Contraintes de projections. Contrainte de phylogénie.</td></tr>
<tr><td>F</td><td>288</td><td>✔</td><td></td><td>✔</td><td></td><td>✔</td><td></td><td></td><td>Espèces strictement plateau. Contraintes de projections.</td></tr>
<tr><td>H</td><td>256</td><td></td><td></td><td>✔</td><td></td><td>✔</td><td></td><td>✔</td><td>Espèces strictement plateau. Contraintes de projections. Exclusion des chondrichtyens.</td></tr>
<tr><td>J</td><td>256</td><td></td><td></td><td>✔</td><td></td><td>✔</td><td></td><td>✔</td><td>Espèces strictement plateau. Contraintes de projections. Exclusion des chondrichtyens.</td></tr>
<tr><td colspan="11"></td></tr>
<tr><td rowspan="3">Autre Bases</td><td rowspan="2">G</td><td colspan="9">Commentaires</td></tr>
<tr><td colspan="2">35</td><td colspan="7">Données provenant de la réserve des Bouches de Bonifacio (2004)+ données bibliographiques sur les contenus stomacaux</td></tr>
<tr><td>I</td><td colspan="2">n</td><td colspan="7">Modèle écosystémique, sources multiples</td></tr>
</table>

Pour les études se concentrant sur la protection des poissons côtiers, nous avons considéré qu'une espèce ayant au moins 40% de son aire de répartition sur le plateau continental faisait partie du plateau. En ce qui concerne les données de la seconde série de publications (Manuscrits D, E, F, I, J), les polygones ont été modifiés par la bathymétrie des espèces, et le nouveau trait de côte a été intégré. La phylogénie établie dans le cadre du CEFDM n'ayant pris en compte que les poissons téléostéens, les chondrichtyens n'ont pas été inclus dans les analyses faisant appel aux informations phylogénétiques. Pour les analyses concernant les projections des aires de distributions futures, seules les espèces strictement côtières ont été prises en considération. En outre le nombre d'espèces a été considérablement réduit en raison des nombreuses contraintes liées à la modélisation.

II.9 Implication personnelle et collaborations dans la mise en place de la base de données

La constitution d'une base de données intégrant l'ensemble des composantes de la biodiversité ne peut se faire sans collaboration, et la part de mon travail dans les différents volets de la base est résumée dans le Tableau 2. En fonction des thématiques, mon implication a varié depuis l'intégration directe des données jusqu'à la gestion des projets. Par exemple pour la compilation des traits biologiques, pour la correction des aires de répartitions par la bathymétrie des espèces ou pour structurer une base de donnée accéssible en ligne, j'ai entiérement supervisé le travail. La réalisation de la base m'a permis de travailler en collaboration avec des étudiants, des ingénieurs et des chercheurs de plusieurs nationalités.

Tableau 3: Pourcentage d'implication, responsabilité et collaboration pour la mise en place de la base de donnée.

	AMP	**Traits biologiques**	**Données climatiques**	**Aire de répartition**	**Structuration de la base de donnée**	**Menaces**
Camille Albouy	10%	50%	100%	40%	40%	-
Laure Velez	80%	45%	-	40%	-	-
François Guilhaumon	10%	-	-	-	-	-
Frida Ben Rais Lasram	-	-	-	20%	-	-
Etudiants L3	-	5%	-	-	-	-
Fabien Retif	-	-	-	-	60%	-
Responsabilité	Conseils techniques	Recherche, gestion du projet, vérification	Traitement des données brutes	Gestion du projet/correction/réalisation	Gestion du projet/réalisation	-
Collaboration	MEDPAN / France	-	Samuel Somot / France	Frida Ben Rais Lasram/ Tunisie	-	Marta Coll/ Espagne

Chapitre 3

Projections des impacts du changement climatique sur la structure des assemblages de poissons côtiers méditerranéens

III.1 Introduction

Comme tous les écosystèmes marins, la mer Méditerranée subit les impacts anthropiques tels que la pêche, le transport maritime ou encore la pollution (Coll et al. 2012; Manuscrit A). Au delà de ces pressions exercées localement, la Méditerranée est, et restera, une des régions les plus affectées par le changement climatique au point d'être qualifiée de « points chaud » du changement climatique (Fig. 20 ; Giorgi 2006).

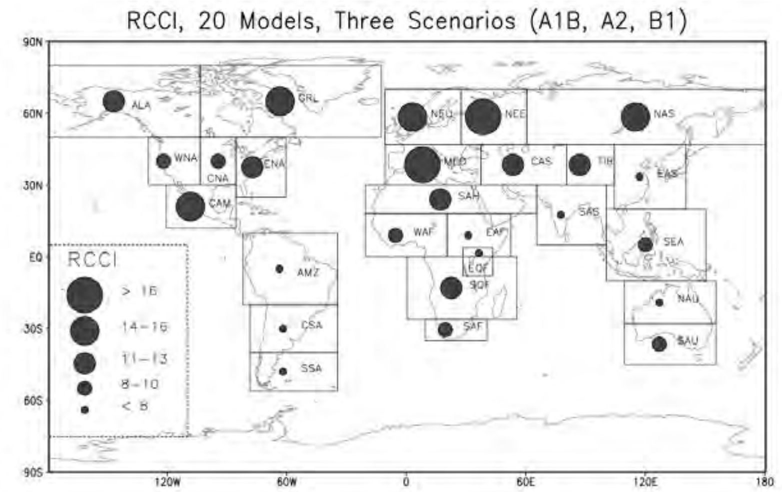


Figure 20 : Cartographie d'un indice d'impact du changement climatique suivant trois scénarios (pour plus de détails voir Encart 1 Chapitre 1) du GIEC et 20 modèles climatiques globaux (Giorgi, 2006).

In fine, l'ensemble de ces menaces peuvent conduire à une modification des assemblages de poissons, en favorisant certaines espèces alors que d'autres disparaissent (Harborne & Mumby 2011). Ces modifications dans la composition et la structure des assemblages ne sont pas anodines pour le fonctionnement des écosystèmes marins côtiers, mais les prédictions de ces fonctionnements futurs restent très délicates avec des assemblages d'espèces qui jusqu'alors n'avaient jamais coexisté. Ces prédictions sont d'autant plus difficiles que les modifications d'assemblages sont aussi accompagnées de changement de température et d'impact de la pêche. La prédiction de l'effet de ces forçages multiples et de leur interactions sur les écosystèmes constitue certainement l'un des enjeux majeurs en écologie. Par exemple, Kirby and Beaugrand (2009) démontre que la température est un moteur important de la trophodynamie de la mer du Nord. En utilisant une approche de modélisation allant des producteurs primaires jusqu'aux poissons, ils ont constaté que la température pouvait avoir le même effet que la pêche à savoir favoriser l'apparition de méduses (pour le compartiment plancton) et des décapodes et détritivores (pour le compartiment benthique). Ces changements contribuent à diminuer l'abondance de la morue (Fig. 21). Ce cas d'étude illustre très bien la complexité des interactions et la difficulté de modéliser le fonctionnement des écosystèmes sous forçages multiples. Nous allons, plus modestement, modéliser les effets potentiels du changement climatique sur la structure des assemblages de poissons côtiers en adoptant une approche multifacette de la biodiversité incluant les liens trophiques.

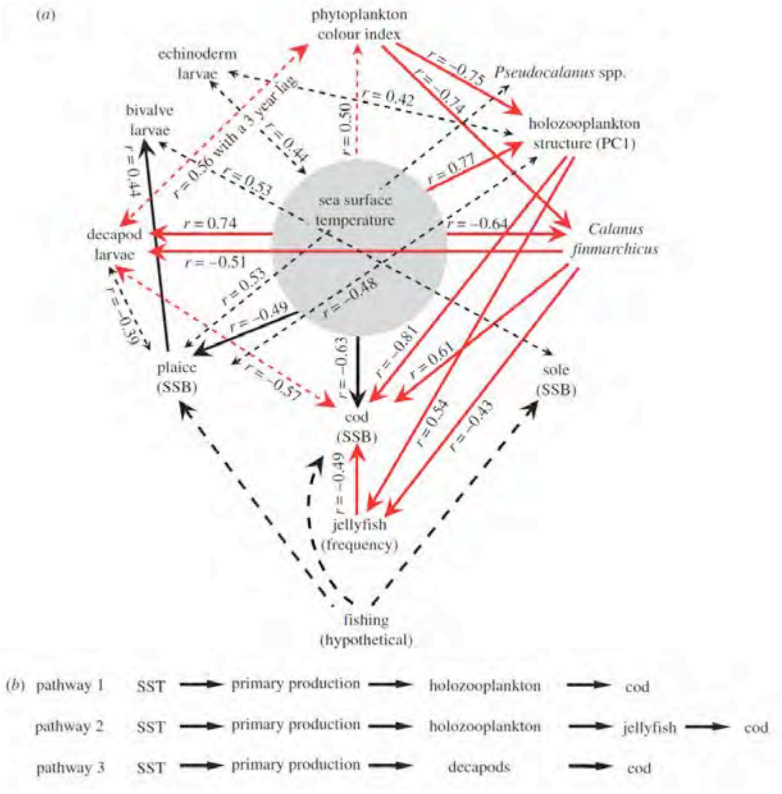


Figure 21 : Schéma des relations permettant de déterminer les voies par lesquelles l'effet de l'augmentation de température se propage en mer du Nord. a) Modèle de causalité basé sur les coefficients de corrélation significatifs. Les flèches pleines unidirectionnelles indiquent un lien de causalité entre les variables avec une indication de direction. Les flèches bidirectionnelles en pointillés indiquent une corrélation entre variables sans direction. Les flèches rouges indiquent les voies qui contribuent à l'amplification trophique liée à la température pour la morue. Les flèches noires unidirectionnelles en pointillés indiquent les effets *top-down* liés à la pêche. b) Trois voies indirectes conduisant à l'amplification trophique liées à l'augmentation de température sur la morue.

D’un point de vue sociétal, les poissons constituent la clef de voûte d’une économie locale et régionale importante regroupant différentes activités de pêche (artisanale, industrielle et récréative) qui représentent des milliers d’emplois autours du bassin méditerranéen. Si les effets de la pêche sont bien étudiés (capture des prédateurs et des espèces de grande taille), il paraît désormais essentiel d’anticiper les effets que pourrait avoir le changement climatique sur la restructuration des assemblages de poissons côtiers méditerranéens. Une des méthodes couramment utilisée pour prévoir les impacts du changement climatique sur la biodiversité est fondée sur les modèles d'enveloppes bioclimatiques (Thuiller 2003, Araújo & Peterson 2012). Ce type de modèle quantifie, en premier lieu, l’association entre la répartition géographique actuelle d'une espèce et les conditions climatiques de la zone d’étude. Les relations obtenues sont ensuite utilisées pour prévoir les répartitions futures des espèces en fonction de scénarios de changement climatique. La composition ainsi que la structure des assemblages locaux peuvent alors être déduites en agrégeant les projections d’aire de répartition des espèces. Cette méthodologie relève de la stratégie suivante « prédire abord, assembler plus tard » (Ferrier & Guisan 2006). Afin de caractériser les modifications potentielles de la composition taxinomique des assemblages, nous avons en premier lieu étudié les changements de richesse spécifique entre une période observée (1961-1980) et deux périodes futures (2040-2059 ; 2080-2099). Ces changements ont été analysés pour l'ensemble des poissons méditerranéens côtiers mais aussi pour les poissons exploités par différents types de pêcherie.

Cependant, étudier les changements de richesse ne permet pas de révéler les changements de composition pouvant affecter les nouveaux assemblages de poissons attendus sous la contrainte du changement climatique. L’une des étapes de ce travail de thèse a donc été de développer une méthode permettant de mesurer et de visualiser graphiquement les changements de composition taxinomique des assemblages causés par le changement climatique. La métrique couramment utilisée est le « S*pecies Temporal Turnover* » (STT) qui peut être traduit par « renouvellement temporel des espèces » (Peterson et al. 2002, Thuiller et al. 2005). Par analogie, cette métrique est équivalente dans sa formulation à l’indice de Jaccard (Anderson et al. 2011), utilisé en écologie pour quantifier les différences de composition en espèces entre deux localités (Nekola & White 1999). Plus précisément cet indice permet de quantifier la diversité β (Whittaker 1977), laquelle correspond dans son sens le plus large au changement de composition en espèces dans l’espace. Un inconvénient majeur du STT est qu’il n’intègre pas les récents développements méthodologiques sur la diversité β. Baselga (2010, 2012) a en effet proposé une méthode qui permet d'identifier deux composantes importantes pour comprendre les modifications dans la composition taxinomique des assemblages. La première composante reflète la perte (ou le gain d'espèces) entre deux localités (composante emboîtée), alors que la deuxième composante reflète le remplacement d'espèces entre deux localités indépendamment des différences de richesse entre ces localités (composante de remplacement). Ces deux composantes, souvent exprimées à l'intérieur d'un seul indice, méritent d'être étudiées séparément afin de mieux expliquer les patrons de diversité β à larges échelles (Leprieur et al. 2011). Dans notre cas d'étude, nous avons adapté cette décomposition mesurant le changement de composition en espèces à la dynamique temporelle des assemblages avec une application aux poissons côtiers méditerranéens (Manuscrit F).

Même si la richesse en espèces reste l'un des déterminants du fonctionnement des écosystèmes dans une grande variété de biomes (Balvanera et al. 2006), cette facette de la biodiversité possède une capacité d'explication des processus écologiques bien moindre que les facettes incluant les différences et les particularités des espèces liées notamment à leurs traits ou à leurs lignées (voir Tableau 1 ; Loreau & Hector 2001). La taille corporelle est, probablement, le trait fonctionnel le plus intégrateur concernant les mécanismes physiologiques et écologiques chez les poissons (Brown et al. 2004). En effet, elle influe par exemple sur le taux métabolique, la croissance, la masse des œufs, l'âge à première maturité, la survie (Hildrew & Townsend 2007), ou encore sur la densité de population (Blackburn et al. 1993). Elle est également un facteur structurant des interactions trophiques pour les poissons (Jennings 2001, Fisher et al. 2010)

Nous avons donc projeté les modifications de la distribution des tailles maximales moyennes au sein des assemblages de poissons du plateau méditerranéen entre la période observée et les deux périodes futures (2040-2059 ; 2080-2099). Même si ces changements de taille moyenne au sein des assemblages de poissons sont importants pour le fonctionnement des systèmes marins, le rôle des espèces, leur niche fonctionnelle, doit s'appréhender dans un espace multidimensionnel de traits (Villéger et al. 2011). En effet deux espèces de même taille peuvent remplir des rôles très distincts (par exemple *Sarpa salpa* et *Pagellus erythrinus*). C'est pourquoi il est important d'étudier la dynamique de la diversité fonctionnelle des assemblages de poissons, qui comprend un ensemble de traits (Mouchet et al. 2010) et celle de leur diversité phylogénétique qui peut déterminer, en partie, les relations trophiques (Naisbit et al. 2012) et potentiellement intégrer de nombreux traits suivant le niveau de conservatisme phylogénétique (Wiens et al. 2010).

Une analyse a donc été conduite à différentes échelles spatiales afin d'étudier l'érosion de la diversité phylogénétique mais aussi fonctionnelle des poissons côtiers méditerranéens face au changement climatique. Nous avons tout d'abord évalué les modifications attendues des aires de répartitions de 288 espèces de poissons côtiers sous l'effet du changement climatique, ainsi que les changements de richesse spécifique mais aussi de distribution en taille (Manuscrit D). Nous avons ensuite analysé l'érosion des différentes composantes de la biodiversité ichtyologique côtière en fonction du changement climatique (Manuscrit E). Enfin une méthodologie permettant d'interpréter de manière plus précise les modifications des assemblages d'espèces a été développée (Manuscrit F).

III.2 Dynamique des assemblages de poissons côtiers méditerranéens face au changement climatique

III.2.1 Projections des aires de répartitions futures

Dans le Manuscrit D, nous avons estimé les futures aires de répartitions de 288 poissons côtiers méditerranéens en nous basant sur le scénario A2 du GIEC (Chapitre 1 Encart1), lequel est implémenté avec le modèle de circulation générale spécifique à la Méditerranée NEMOMED8 (Manuscrit D). Les projections d'aire de répartition de chaque espèce ont ensuite été agrégées à l'échelle du pixel (0,1 x 0,1°) afin de quantifier : (*i*) les changements de richesse spécifique, (*ii*) les changements moyens de taille corporelle à l'échelle de l'assemblage, ansi que (*iii*) les changements pouvant altérer les composantes fonctionnelles et phylogénétiques de la biodiversité. Pour cela, plusieurs modèles

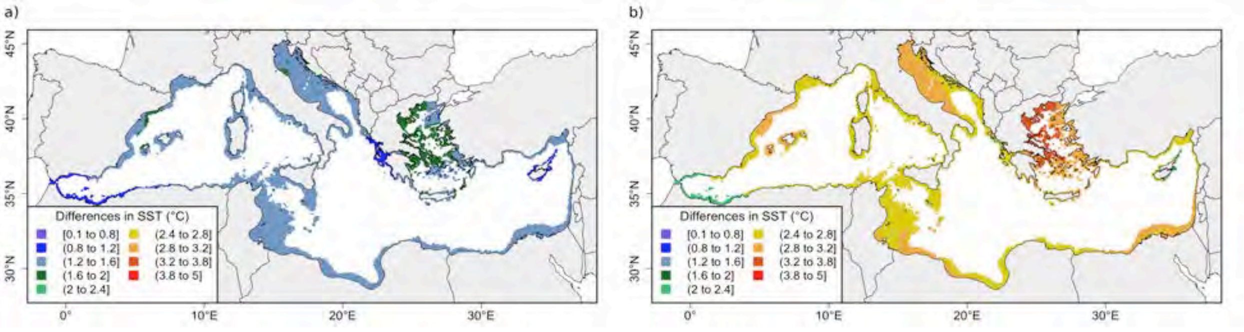


Figure 22 : Différence de température de surface moyenne entre la période 1960-1980 et a) 2040-2059, b) 2080-2099. Ces données sont extraites du modèle NEMOMED8.

d'enveloppes bioclimatiques ont été mis en place. Les données extraites de la base ont été corrigées par la bathymétrie à laquelle les espèces pouvaient être rencontrées (voir Chapitre II.2 pour plus de détails ou Manuscrit D). Les espèces exotiques ont été exclues car elles présentent une évolution spatiale actuelle rapide (Ben Rais Lasram et al. 2008), elles ne peuvent donc pas être considérées à l'équilibre avec les variables environnementales ce qui empêche toute modélisation fondée sur les niches (Guisan & Thuiller 2005). Les espèces sélectionnées sont strictement côtières et leurs présences sont définies, à partir d'un atlas, sur une grille de 0,1° de résolution couvrant l'ensemble du plateau continental et comprenant 8154 cellules. Plusieurs variables de température ont été considérées car les poissons sont des organismes ectothermes dépendant des caractéristiques environnementales liées à la température notamment pour la reproduction et le développement (Mann & Blackburn, 1991). Par exemple, le recrutement des larves et des juvéniles est fortement dépendant de la température maximale annuelle (Burreson & Sypek, 1981).

Les valeurs de température de surface prédites par NEMOMED8 (voir Chapitre II.5 pour plus de détails) pour la période 1961-1980 ont été utilisées comme base de référence pour calibrer les modèles de distribution des espèces (Beuvier et al. 2010) afin d'être en adéquation avec les données d'occurrences récoltées durant cette période. Le modèle NEMOMED8 prédit pour la mer Méditerranée une augmentation de la température de surface moyenne de l'ordre de 1,4°C d'ici le milieu du XXI$^{\text{ième}}$ siècle et de 2,8 °C d'ici la fin du XXI$^{\text{ième}}$ siècle. Les données quotidiennes ont été moyennées pour chaque période afin d'obtenir des données mensuelles, conduisant à la création de 15 variables : 12 valeurs moyennes mensuelles de température de surface, le minimum absolu annuel, le maximum absolu annuel et la différence entre ces deux dernières variables (Fig. 22). Pour éviter la sur-paramétrisation des modèles et pour réduire la colinéarité entre variables (Thuiller 2004), les variables de température ont été agrégées sur la base d'une partition « K-means » (Legendre & Legendre 1998). La partition fournit huit variables synthétiques et relativement indépendantes. Les données de températures utilisées pour projeter les aires de distributions ont également été fournies par le modèle NEMOMED8 pour les périodes 2040-2059 et 2080-2099, évitant ainsi tout biais possible entre les sources d'informations. La salinité a été exclue des variables car elle n'était pas, au regard d'une analyse OMI (Outlying mean Index ; Doledec et al. 2000), une variable structurante pour les aires de répartition des poissons côtiers méditerranéens (voir Manuscrit D, Annexe2).

À partir de l'ensemble de ces données, des méthodes de modélisation des enveloppes bioclimatiques (Guisan & Thuiller 2005, Buisson et al. 2008, Thuiller et al. 2009) ont été appliquées grâce au logiciel BIOMOD (Thuiller et al. 2009). Sept différentes modèles statistiques ont été utilisés (Fig. 23).

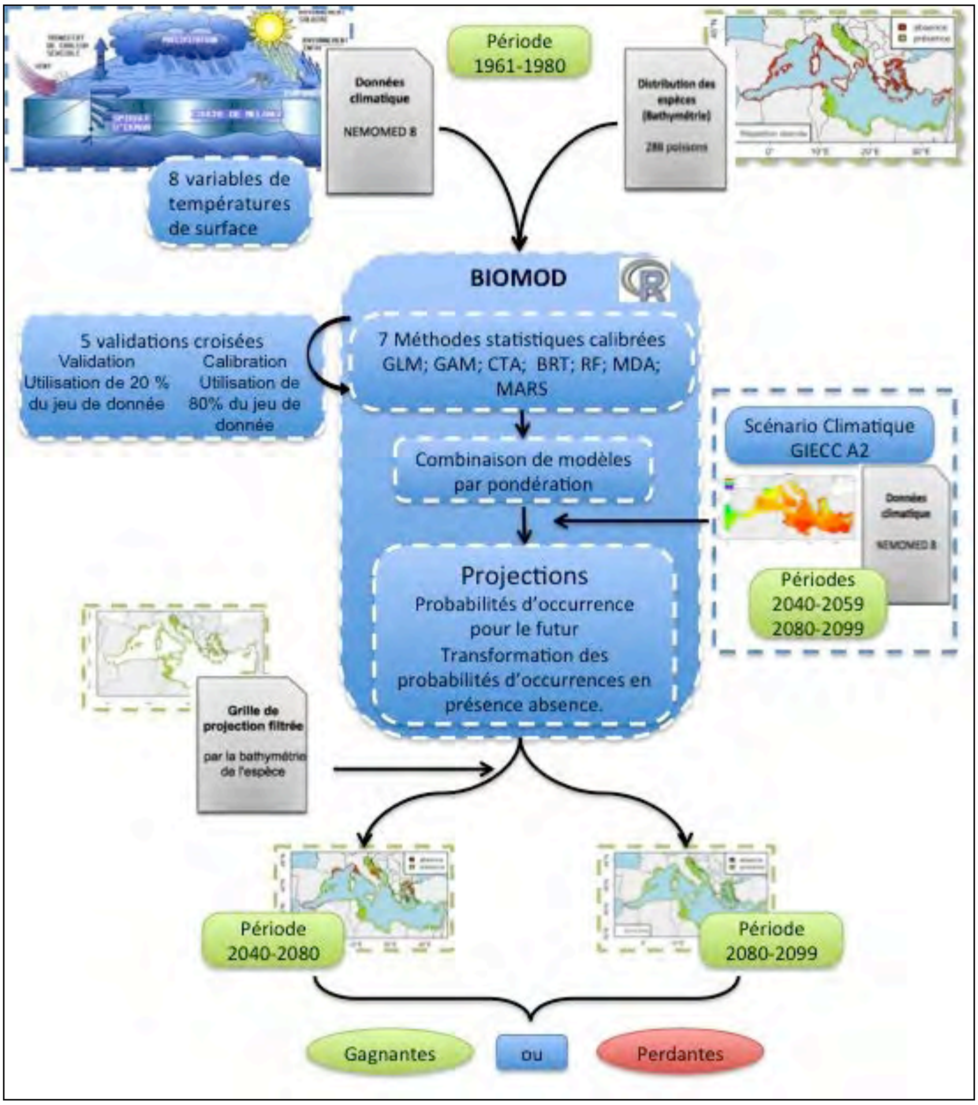


Figure 23 : Processus de modélisation des enveloppes bioclimatiques pour les poissons côtiers méditerranéens et projections de leurs aires de répartition futures suivant le changement climatique.

Dans un premier temps ces modèles ont été calibrés puis évalués. La procédure de calibration utilise 80% des observations prises au hasard et permet la paramétrisation du modèle. Les 20% restant sont réservés pour la phase d'évaluation, qui permet de vérifier que la variable réponse est bien modélisée, en évitant la circularité : prédire les réponses des objets utilisés pour la mise en place du modèle. Pour évaluer un modèle, il existe différents critères qui consistent à évaluer la concordance entre ce qui a été modélisé (prédit) et ce qui est réellement observé (Ben Rais Lasram 2009). Un consensus a émergé sur l'indice à considérer et il est recommandé d'utiliser le TSS (True Skill Statistic ; Allouche et al. 2006). Une fois les sept modèles calibrés et validés, sachant qu'aucun consensus sur la supériorité prédictive d'un modèle par rapport à un autre n'existe, nous avons utilisé une combinaison de modèles par pondération afin de réaliser les projections des aires de répartitions dans le futur pour deux périodes de temps (2040-2059 ; 2080-2099 voir Encart 2).

Ensuite, chaque espèce a été classée en fonction du type de pêche qui la ciblait, à savoir la pêche professionnelle, récréative ou les deux. Connaissant les tailles maximales (plus grandes tailles enregistrées en Méditerranée) de ces 288 espèces (Chapitre II.1) et les types de pêche, celles-ci ont été subdivisées en quatre groupes: les espèces de petites et de grandes tailles non pêchées (PENP et GENP respectivement), et les espèces de petites et de grandes tailles pêchées (PEP et GEP respectivement). Une espèce est considérée comme petite lorsque sa taille maximale est inférieure à 20 cm.

Encart 2 : Comment prédire les aires de répartition futures ?

Les types de modèles

Tous les modèles nécessitent deux entrées : une ou plusieurs variables prédictives (explicatives) et une variable réponse. Ils permettent de modéliser les relations espèce-milieu. Il existe quatre grandes catégories de modèles : les régressions multiples (GLM, GAM, MARS), les arbres de régression (BRT, RF, CTA), les analyses discriminantes (LDA, MDA) et les méthodes d'apprentissage.

Les régressions multiples

Les modèles linéaires généralisés (GLM) nécessitent la prise en compte de trois composantes, une variable réponse, des variables explicatives et un ensemble de fonctions de lien décrivant les relations entre la variable réponse et les variables prédictives. Ils permettent de modéliser des relations paramétriques complexes entre une variable réponse et des variables prédictives (linéaires, quadratiques ou polynomiales) en recherchant la relation la plus parcimonieuse.

Les modèles additifs généralisés (GAM) constituent la version non paramétrique des GLM : ils estiment la courbe de réponse de la variable prédite avec une fonction de lissage (« *smoothing spline* ») non paramétrique. Le principal avantage des GAM est leur capacité à traiter des relations largement non linéaires et non monotones entre la variable prédite et les prédicteurs.

Les régressions multivariées par *spline* adaptatif (MARS) combinent la régression linéaire, la construction mathématique de splines et la partition binaire récursive des données afin de produire un modèle où les relations entre variables explicatives et variables réponses peuvent être aussi bien linéaires que non-linéaires (Heikkinen et al. 2006).

Les arbres de régression

Les arbres de régression forment des partitions itératives de l'espace des variables en groupes grâce à l'utilisation d'une série de règles. Les « nœuds » des arbres, qui séparent les groupes résultant d'une partition, sont choisis de manière à minimiser les erreurs de prédiction. Il s'agit donc de maximiser l'homogénéité intergroupe tout en minimisant les erreurs. Lorsqu'un nœud n'a pas de successeur il est appelé « feuille ». Le meilleur arbre est un compromis entre la déviance minimale et le nombre de feuilles minimales (Elith et al. 2008). Dans cette catégorie sont classés les CTA (*Classification Trees Analysis*), les BRT (*Boosting Regression Trees*) et les RF (*Random Forest*).

Les analyses discriminantes

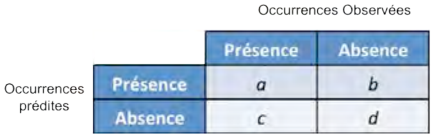
L'analyse discriminante linéaire (LDA) est la plus connue et la plus utilisée des méthodes de classification L'objectif de la LDA est de prédire la composition des unités statistiques à des classes prédéfinies en construisant des axes discriminants qui sont des combinaisons linéaires des variables explicatives (Fisher 1936). Ce modèle s'est avéré insuffisamment complexe, d'où le recours à un « mélange » de plusieurs modèles, ce qui a donné naissance à une extension de l'analyse discriminante linéaire, la MDA (Mixture Discriminant Analysis ; Hastie et al. 1995).

Les méthodes d'apprentissage

Il existe d'autres modèles n'appartenant à aucune des catégories décrites plus haut. Parmi eux nous pouvons citer le SRE (Surface Range Envelops) qui utilise l'intervalle de valeurs des variables explicatives afin de définir l'enveloppe climatique de l'espèce. Lors de la prédiction, chaque pixel de la grille de présence dont la valeur du prédicteur est comprise entre le maximum et le minimum ainsi identifiés, est considéré comme appartenant à l'enveloppe. Il existe aussi un autre modèle récemment développé par Phillips et al. (2006) : MAXENT. Ce type de modèle estime la variable réponse (distribution d'une espèce) en trouvant la distribution de l'entropie maximale sous la contrainte que la valeur attendue de chaque variable environnementale sous cette distribution corresponde à sa moyenne empirique.

Calibration et évaluation

Pour être utilisé notamment à des fins prédictives, un modèle doit être validé en validation croisée. Pour ce faire, le jeu de données initial est divisé en deux sous-groupes : un sous-groupe qui sert à la calibration, l'autre à l'évaluation qui permet de valider ou non le pouvoir prédictif du modèle. Cependant, les sorties des modèles nous donnent des probabilités. Elles seront modifiées en données présence/absence en utilisant un seuil qui est sélectionné de manière à maximiser le critère d'évaluation des modèles : le TSS (Allouche et al. 2006). Ce critère d'évaluation consiste à étudier la concordance entre ce qui a été modélisé (prédit) et ce qui est observé. Cette opération se base sur une matrice de confusion qui comporte deux colonnes rapportant, les absences et les présences observées, et deux lignes rapportant les absences et les présences prédites.



		Occurrences Observées	
		Présence	**Absence**
Occurrences prédites	**Présence**	*a*	*b*
	Absence	*c*	*d*

$$Sensibilité = \frac{a}{a+c} \qquad TSS = Sensibilité + Spécificité - 1$$

$$Spécificité = \frac{d}{b+d} \qquad TSS = \frac{ad - bc}{(a+c)(d+b)}$$

a représente le nombre d'unités spatiales où la présence d'une espèce est bien prédite par le modèle ; *b* représente le nombre d'unités spatiales où l'absence d'une espèce est observée mais le modèle prédit une présence ; *c* représente le nombre d'unités spatiales où la présence d'une espèce est observée mais le modèle prédit une absence ; *d* représente le nombre d'unités spatiales où l'absence d'une espèce est bien prédite par le modèle

Projection

Comme la supériorité d'aucun de ces types de modèle n'a émergé dans la littérature, nous avons utilisé une méthodologie prenant en compte l'ensemble de ces méthodes statistiques (Weigthed Average Consensus). Cette méthode permet de projeter les distributions des espèces dans le futur en se basant sur un scénario de changement global. Une probabilité moyenne d'occurrence pour chaque espèce a été établie en fonction de l'ensemble des modèles et de leur critère d'évaluation. Ensuite cette probabilité a été transformée en présence/absence en appliquant un seuil correspondant à la moyenne des TSS des modèles.

Il est important de souligner que les modèles statiques (ne prenant pas en considération les facteurs dynamiques intrinsèques aux populations tel que la compétition et la dispersion) projettent des enveloppes futures potentielles et non des enveloppes futures réalisées. Ces modèles ne font qu'extrapoler les occurrences des espèces à partir de scénarios qui influencent les variables prédictives préalablement identifiées dans le processus de prédiction.

III.2.2 Projections des changements de structure taxinomique, fonctionnelle et phylogénétique

Les projections des aires de distribution des poissons côtiers méditerranéens mettent en évidence que pour la fin du siècle (*i*) 54 espèces devraient perdre leur niche climatique, (*ii*) la richesse en espèces pourrait diminuer dans 70,4% des 8154 cellules composant le plateau continental (Fig. 24a), en particulier en Méditerranée occidentale et en mer Égée, et (*iii*) la taille maximale moyenne des assemblages de poissons pourrait augmenter dans 74,8% des cellules du plateau continental (Fig. 24b). Parmi les quatre catégories d'espèces présentées plus haut, ce sont les poissons de petite taille non ciblés par la pêche commerciale ou récréative qui présentent, en moyenne, la plus forte diminution de leur aire de répartition géographique (Fig. 25).

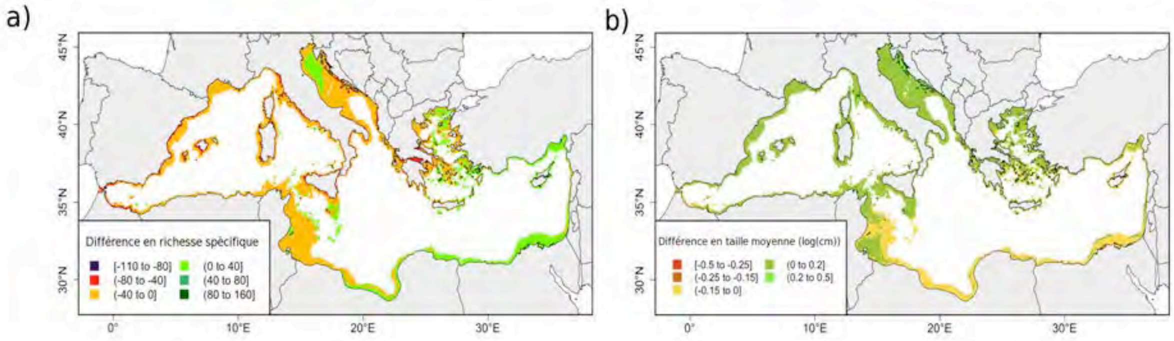


Figure 24 : Différence en richesse spécifique (a) en taille moyenne maximale (b) pour les assemblages de poissons côtiers entre les périodes 1960-1980 et 2080-2099

Les changements climatiques en Méditerranée pourraient avoir des effets sévères sur la diversité des poissons côtiers, y compris sur les espèces de poissons endémiques, même si la pression de pêche n'est pas prise en compte. Dans l'ensemble, les poissons de Méditerranée pourraient être pris en étau entre ces deux menaces majeures que sont la pêche et le changement climatique. Ce dernier semble affecter les petites espèces non ciblées par la pêche en réduisant leur aire de répartition géographique. Cette tendance observée pour les deux périodes modélisées peut avoir des répercussions à l'échelle des écosystèmes en réduisant l'offre alimentaire pour les plus gros poissons, oiseaux et mammifères marins (Cury et al. 2011, Pinsky et al. 2011). En outre, la pêche agit comme une pression sélective, qui entraîne une diminution de la taille moyenne des individus dans les assemblages exploités en prélevant dans le milieu les prédateurs supérieurs (Kuparinen & Merila 2007). Cela peut affecter la dynamique des populations de bas niveaux trophiques et, éventuellement, perturber le fonctionnement des écosystèmes. Ainsi, le changement climatique et la pêche pourraient agir conjointement et conduire, directement ou indirectement, à des extinctions directes ou indirectes, ces dernières restant difficiles à prédire.

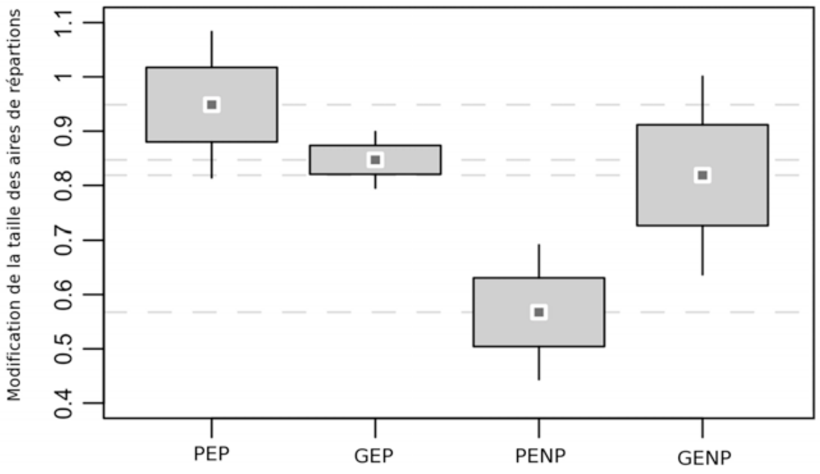


Figure 25 : Rapport des aires de répartitions entre la période (1961-1980) et la seconde période modélisée (2080-2099) pour les quatre groupes d'espèces, les petites ou les grandes espèces non pêchées (PENP,GENP) et les petites ou les grandes espèces pêchées (PEP,GEP)

Au delà des modifications de richesse spécifique et de taille maximale au sein des assemblages, l'érosion de la diversité phylogénétique (lignées) et de la diversité fonctionnelle (traits) reste peu étudiée. Les organismes marins sont d'ailleurs largement ignorés dans ce domaine de recherche. Pour évaluer l'impact potentiel du changement climatique sur les diversités phylogénétique et fonctionnelle des poissons côtiers méditerranéens, nous avons utilisé les aires de répartition de 230 espèces de poissons téléostéens du plateau continental. Pour ces espèces, une phylogénie datée et fondée sur des données moléculaires (Meynard et al. 2012) ainsi qu'un dendrogramme fonctionnel basé sur 15 traits fonctionnels ont été construits pour évaluer les états actuels et futurs des diversités phylogénétiques et fonctionnelles (voir Chapitre II.2 pour plus de détails ou Manuscrit E).

` Nos projections, au niveau de l'ensemble de la Méditerranée, révèlent une diminution de 13,6% de la diversité phylogénétique (PD) et de 12,6% de la diversité fonctionnelle (FD) d'ici la fin de ce siècle (Fig. 26). La perte de richesse spécifique à toute les échelles induit une diminution en PD et en FD mais dans certaines régions les assemblages de poissons perdent plus de diversité phylogénétique et fonctionnelle que prévu simplement suite à l'érosion de la richesse. Cela signifiue que les assemblages perdent des espèces soutenant une grande quantité d'histoire évolutive ou de combinaisons unique de traits.

En se plaçant à l'échelle des écorégions méditerranéennes, les projections montrent une perte de PD et FD dans toutes à l'exception de la mer Égée. C'est en mer Ionienne (-18,2%) et en mer Adriatique (-15,4%) que les projections révèlent les baisses en PD les plus importantes. Pour le FD, il est également prévu une nette diminution dans la plupart des écorégions excepté en mer Égée. La diminution la plus importante du FD est observée en mer Ionienne (-16,9%) et en Méditerranée occidentale (-12,1% ; Manuscrit E).

À l'échelle locale, pour la période 2080-2099, les projections montrent une diminution du PD et du FD pour respectivement 74,6% et 72,8% de la superficie du plateau continental présentent (Fig. 27c, d). A une plus petite échelle, c'est-à-dire au niveau des assemblages locaux, les patrons d'érosion de FD et PD montrent une forte hétérogénéité avec quelques zones du plateau continental méditerranéen perdant une forte proportion d'histoire évolutive ou d'espace fonctionnel, notamment dans le bassin Occidental. Du point de vue de la conservation de la biodiversité, les écorégions perdant le plus de diversité phylogénétique et fonctionnelle, indépendamment de la perte en richesse spécifique (par exemple l'ouest de la Méditerranée et la mer d'Alboran), sont aussi surexploitées par la pêche.

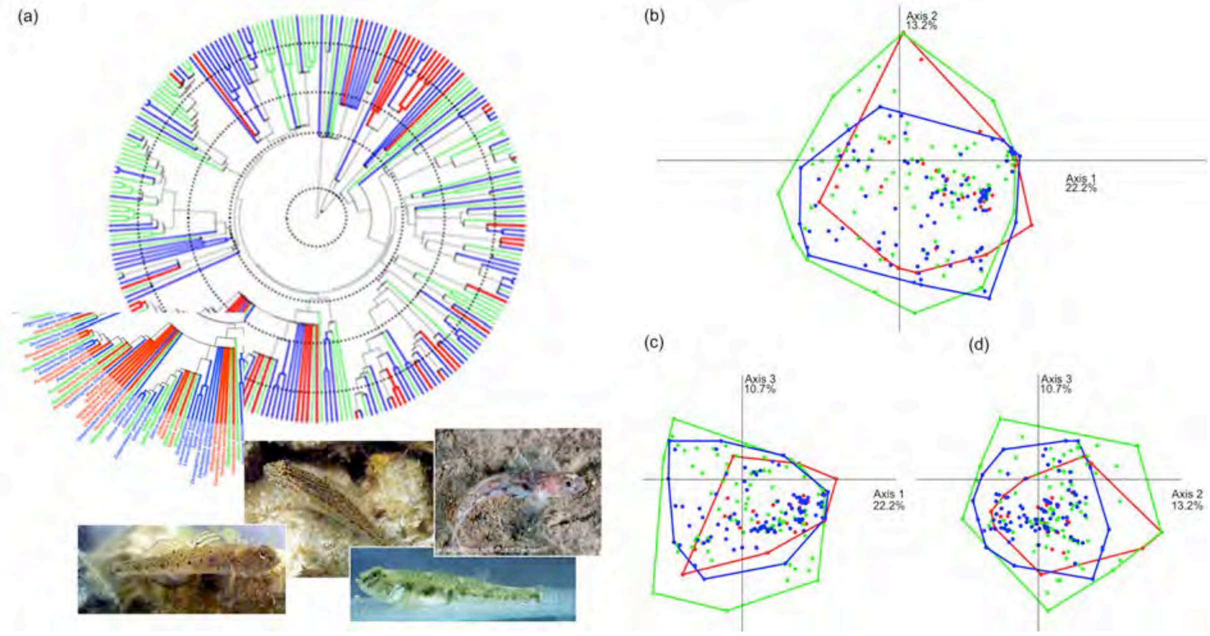


Figure 26: Variation des aires de répartitions représentées sur l'arbre phylogénétique et l'espace fonctionnel pour le scénario A2 du GIEC, pour un assemblage de 230 espèces de poissons côtiers de Méditerranée entre le scénario de référence (1961-1980) et la période modélisée (2080-2099). a) Variation de l'aire de répartition des espèces représentées sur la phylogénie des poissons méditerranéens. Les branches vertes indiquent une expansion de l'aire de répartition, les autres couleurs indiquent une contraction : bleu pour une diminution et rouge pour la disparition totale. b) Variation de l'aire de répartition des espèces représentée sur l'espace fonctionnel des poissons du littoral méditerranéen. Les polygones indiquent l'espace fonctionnel occupé par les espèces. L'espace 3D fonctionnel a été représenté en (b) avec le premier et le deuxième axe de la « Principal Coordinates Analysis » (PCoA) effectuée sur les traits, (c) avec le premier et le troisième axe de la PCoA, en (d) avec le second et le troisième axe. La couleur vertes indiquent une expansion de l'aire de répartition, les autres couleurs indiquent une contraction : bleu pour une diminution et rouge pour la disparition totale.

Nous avons démontré que les petites espèces non ciblées par la pêche peuvent disparaître en premier sous influence du changement climatique. Ici nous montrons que la perte probable des niches climatiques est concentrée sur l'arbre phylogénétique, plus particulièrement sur la famille des Gobidea. Comme la plupart des petites espèces dans les écosystèmes marins, ils maintiennent la productivité des niveaux supérieurs en fournissant des proies pour les prédateurs. En outre, la phylogénie est un déterminant important de la structure du réseau trophique puisque les espèces étroitement liées phylogénétiquement ont tendance à avoir les même prédateurs (Naisbit et al. 2012). Ainsi le rôle joué par les gobies risque de ne pas être remplacé par d'autres familles. La perte de diversité phylogénétique, au niveau des assemblages locaux, pourrait donc avoir des conséquences écosystémiques.

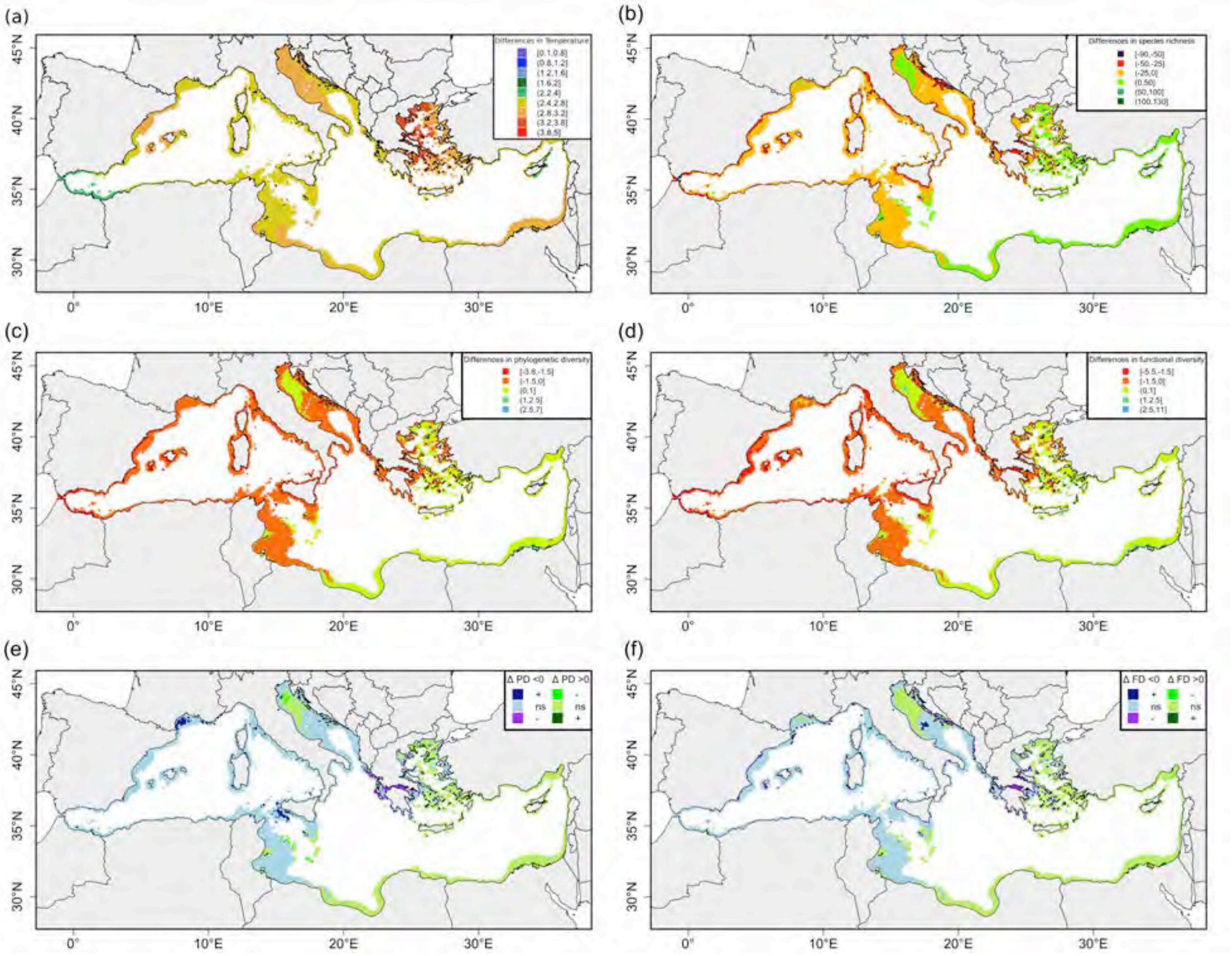


Figure 27 : Cartes représentant les différences entre la période 1961-1980 et la période future (2080-2099) pour (a) la température des eaux de surface (SST, °C); (b) la richesse spécifique; (c) la diversité phylogénétique; (d) la diversité fonctionnelle. Les cartes *e* et *c* représentent la significativité de la différence en diversité phylogénétique et fonctionnelle par rapport à un modèle nul. Ce modèle nul conserve l'identité des espèces ainsi que le nombre d'espèces gagnées ou perdues entre les deux périodes de modélisation. Le symbole + indique que le changement observé dans la différence phylogénétique ou fonctionnelle est plus élevé qu'espéré sous l'hypothèse du modèle nul, le symbole - représente le contraire. Le ns indique une différence est non significative.

Or, depuis les années 1960, les pêcheurs et les pouvoirs publics travaillent en collaboration pour mettre en place un réseau d'AMPs visant à limiter les effets de la pression anthropique. Cette étude souligne le besoin urgent d'intégrer l'effet du changement climatique sur l’ensemble des composantes de la biodiversité pour aboutir à un plan de conservation stratégique et raisonnée en Méditerranée. Des études en milieu terrestre portant sur les conséquences du changement climatique sur la diversité phylogénétique des assemblages de plantes, des oiseaux et des mammifères d’Europe (Thuiller et al. 2011) ou bien sur la diversité fonctionnelle des plantes (Thuiller et al. 2006) ont déjà été conduites mais de manière séparée. Ici nous les analysons conjointement à trois échelles spatiales. Connaître les effets de ces pertes de diversité sur le fonctionnement et la structure des écosystèmes est un challenge que l’expérimentation ne pourrait approcher que pour un petit nombre d’espèces. Il semble donc pertinent, pour prédire le fonctionnement futur d'un écosystème sous changement global avec un assemblage aussi riche et à large échelle, d’avoir recours à des outils de modélisation (Chapitre 4).

III.3 Une nouvelle méthodologie pour démêler les effets du changement climatique sur la diversité et la composition des assemblages

Cette partie est dédiée à la présentation d’une nouvelle méthodologie visant à améliorer l'interprétation des projections de changement de diversité taxinomique à l’échelle des assemblages. D’une part, nous suggérons d’analyser conjointement les changements temporels de richesse et de composition en espèces, ceci afin de mieux identifier les effets potentiels du changement climatique. Nous proposons ainsi une cartographie bidimensionnelle et spatio-temporelle qui représente à la fois le changement de richesse spécifique et le changement dans la composition en espèces. D’autre part, en s'appuyant sur des études antérieures portant sur l’analyse spatiale de la diversité β (Baselga, 2010, 2012), nous apportons des améliorations dans la façon d’évaluer les changements temporels dans la composition en espèces pouvant s'applique à tout type de système ou de taxa.

Dans les études prenant en compte les effets du changement climatique sur la distribution des espèces, les changements temporels d’assemblages sont mesurés en utilisant un indice de renouvellement, le STT (Peterson et al. 2002) qui est formulé comme suit :

$$\mathrm{STT} = \frac{G+L}{SR+G} \qquad \text{eq.(1)}$$

Où L est le nombre d'espèces disparues, G le nombre d'espèces acquises, et SR la richesse spécifique initiale. Par analogie avec l'équation 1 nous avons déterminé que le STT était équivalent à une version temporelle de l’indice de dissimilarité de Jaccard (Anderson et al. 2011). En effet si a est définie comme étant le nombre d'espèces communes aux deux périodes, b le nombre d'espèces présentes à la première période mais absentes à la seconde (équivalent à L), et c le nombre d'espèces présentes à la seconde période mais absentes à la première (équivalent à G), $a+b$ étant égal à SR, l’équation 1 peut être énoncée de la façon suivante :

$$\beta_{jac} = \frac{b+c}{a+b+c} \qquad \text{eq.(2)}$$

Le STT est donc équivalent à l’indice de dissimilarité de Jaccard. Nous avons appliqué les récents développements sur la partition de la biodiversité (Baselga 2010, 2012), en le partitionnant en deux composantes additives : (*i*) la composante de “remplacement” (β_{jtu}, équation 3) qui mesure le remplacement temporel d'espèces au sein d’un assemblage, indépendamment des changements de richesse spécifique, (*ii*) la composante d’emboîtement (β_{jne} ; équation *4*) qui mesure la différence temporelle de richesse spécifique au sein d’un assemblage dans lequel certaines espèces se maintiennent au cours du temps (a>0). Cette dernière composante est calculée en faisant la différence entre β_{jac} et β_{jtu} ($\beta_{jne} = \beta_{jac} - \beta_{jtu}$), puisque $\beta_{jac} = \beta_{jtu}$ lorsque a=0.

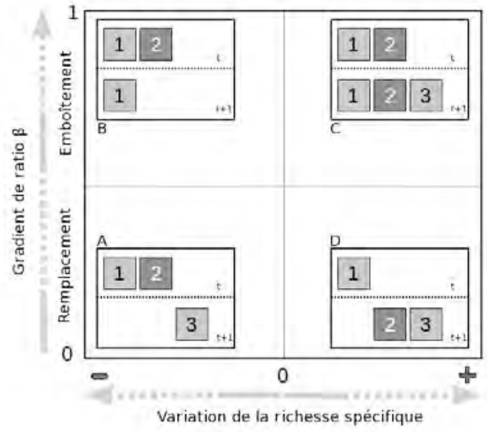
$$\beta_{jtu} = \frac{2 \times \min(b,c)}{a + 2 \times \min(b,c)} \qquad \text{eq.(3)}$$

$$\beta_{jne} = \frac{\max(b,c) - \min(b,c)}{a+b+c} \times \frac{a}{a + 2 \times \min(b,c)} \qquad \text{eq.(4)}$$

Afin de faciliter l’étude de la diversité β nous avons utilisé le rapport β_{ratio} entre β_{jne} et β_{jac} (Dobrovolski et al. 2011), qui donne la contribution relative de chaque composante. Des valeurs de ce rapport inférieures à 0,5 indiquent que le remplacement des espèces est le principal moteur du STT, alors que les valeurs supérieures à 0,5 indiquent que le STT est principalement dû à des modifications de richesse spécifique, donc à de l’emboîtement. Pour cartographier le continuum de situations entre les cas extrêmes illustrés dans l’Encart 3, nous proposons de représenter simultanément les valeurs de la diversité β (β_{jac} ou β_{ratio}) et les changements temporels de richesse spécifique sur la même carte. Nous avons appliqué cette méthodologie aux poissons côtiers méditerranéens.

Encart 3 : Pourquoi partitionner la β diversité ?

En utilisant des métriques qui reflètent à la fois les différences de richesse spécifique et les différences de composition en espèces (par exemple, l'indice de dissimilarité de Jaccard, voir Koleff et al. 2003), les utilisateurs peuvent confondre des situations attendues très différentes dans le cadre du changement climatique. Le changement climatique peut, par exemple, provoquer des remaniements importants au sein des assemblages (cas A et D). Cela peut être dû à une extinction des espèces sensibles aux variations de température (cas A, les espèces 1 et 2; cas D, espèce 1); qui seront à leur tour remplacées par moins (cas A) ou plus (cas D) de nouvelles espèces. Le réchauffement climatique pourrait également entraîner la disparition d'espèces, sans remplacement, si les nouvelles conditions environnementales sont trop contraignantes ou si l'isolement du lieu de disparition de ces espèces empêche l'arrivée de colonisateurs potentiels (Novak et al. 2011 ; cas B). On peut également observer un enrichissement en espèces dans un assemblage sans qu'il n'y ait d'altération de l'assemblage. Cela peut se produire si les espèces résidentes et entrantes sont adaptées aux nouvelles conditions environnementales (cas C).



Ce schéma conceptuel décrit les différents scénarios de modification de la composition des assemblages en fonction des modifications de richesse en espèces attendues sous les effets du changement climatique. L'axe horizontal représente la variation de la richesse spécifique et l'axe vertical représente le gradient du β_{ratio} (représentant la contribution relative de remplacement des espèces *versus* l'emboîtement). Chacune des boîtes (A, B, C, D) est divisée horizontalement en deux parties correspondant à deux périodes (t et t+1). Les cases numérotées représentent les différentes espèces. Le scénario A illustre une diminution de la richesse en espèces au cours du temps (t à t+1) couplée à un remplacement complet des espèces (espèces 1 et 2 sont remplacées par une nouvelle espèce 3) ce qui correspond à une faible valeur du β_{ratio}. Le scénario B présente également une diminution de la richesse spécifique entre les deux périodes, mais dans ce cas l'assemblage à t+1 est totalement imbriqué dans l'assemblage à l'instant t, ce qui entraîne une forte valeur du β_{ratio}. Les scénarios C et D représentent les mêmes processus (emboîtement comme dans B et remplacement comme dans A), mais avec une augmentation de la richesse spécifique entre les deux périodes.

Les résultats de notre cas d'étude montrent que le changement climatique pourrait entraîner différents types de modification de la composition des assemblages (remplacement d'espèces *vs* emboîtement temporel des assemblages causé par des gains ou des pertes d'espèces). Nos résultats montrent plus particulièrement que le remplacement d'espèces sera prépondérant dans certaines zones de la Méditerranée alors que pour d'autres, le changement de composition en espèces sera associé à des gains ou à des pertes d'espèces. Par exemple, les changements dans la composition des assemblages des poissons dans la partie nord de l'Adriatique sont principalement causés par du remplacement d'espèces (voir Fig. 28c), alors que ceux prévus dans le golfe de Gabès sont principalement causés par une disparition d'espèces (Fig. 28c).

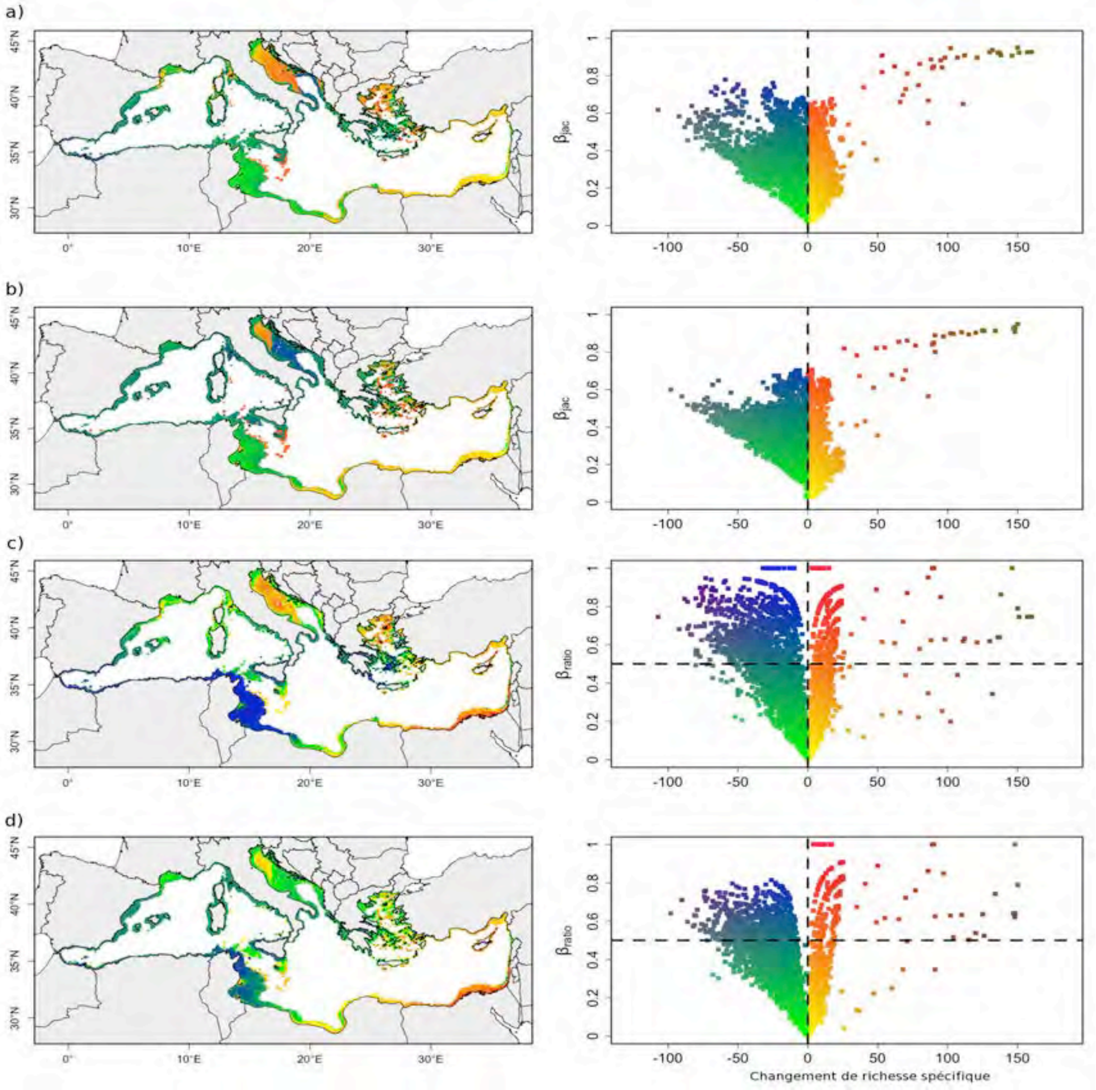


Figure 28: Variations de la richesse et de la composition en espèces entre la période de référence (1961-1980) et le futur (2040-2059 (a, c); 2080 -2099 (b, d)) pour les assemblages de poissons du plateau continental méditerranéen. Les changements dans la composition en espèces sont quantifiés en utilisant l'indice de dissimilarité de Jaccard β_{jac} (a, b) et l'indice β_{ratio} (c, d). La colonne de droite sert de légende à la cartographie. L'utilisation de deux gradients de couleur (jaune-marron ; vert-violet) illustre la dichotomie entre les cellules gagnant et les cellules perdant des espèces. Pour les figures a et b l'intensité du gradient montre les valeurs de β_{jac} , pour les figures c et d les couleurs jaune et verte indiquent le remplacement d'espèces et les couleurs bleue et rouge l'emboîtement d'espèces au sein des assemblages

L'exploration conjointe des changements de richesse spécifique et de composition en espèces montre également que l'ichtyofaune côtière de plusieurs régions de la Méditerranée pourrait subir un effet «cul-de-sac» face au réchauffement climatique (Ben Rais Lasram et al. 2010). En effet, au milieu du XXI^{ième} siècle, des niveaux élevés de remplacement d'espèces associés à une augmentation de la richesse spécifique pourraient se produire en mer Égée ainsi qu'en mer Adriatique (Fig. 28a). Cette augmentation de la richesse en espèces peut s’expliquer par le déplacement de nombreuses espèces de poissons côtiers vers le nord, lesquelles y trouveraient des conditions climatiques favorables. En revanche, à la fin du XXI$^{\text{ième}}$ siècle, le golfe du Lion, l'Adriatique et la mer Égée, devraient connaître une nette diminution de la richesse spécifique du fait de la perte de niche thermique pour de nombreux espèces (Fig. 28d), ces pertes n’étant pas compensées par l'arrivée de nouvelles espèces venant du sud. Globalement, la méthodologie mise en place dans le cadre de cette étude a permis d’identifier les différents types de modification de la composition des assemblages causés par le changement climatique. Ici, nous avons appliqué cette méthodologie aux changements de richesse spécifique, mais elle pourrait être appliquée aux changements de diversité phylogénétique et fonctionnelle temporelle ou de manière spatiale entre sites d’étude. Appliquée à la phylogénie les valeurs de a, b et c seraient les longueurs de branche de l’arbre phylogénétique (Leprieur et al. 2012), appliquée à la diversité fonctionnelle a, b et c seraient des volumes de l’espace décrivant le plus précisément l’ensemble des traits fonctionnels (Villéger et al. 2012). Nous avons établi une méthodologie très flexible permettant de quantifier et de visualsier les impacts du changement climatique sur l'ensemble des facettes de la biodiversité des assemblages. Afin que cette méthode puisse être utilisée globalement, le script R devrait être implémenté dans le package « Betapart ».

Chapitre 4 :

Inférence des réseaux trophiques pour une modélisation des impacts anthropiques et climatiques sur les écosystèmes marins

IV.1 Introduction

Pour étudier le fonctionnement des écosystèmes soumis aux influences anthropiques locales et aux changements globaux, il est important de déterminer les liens reliant les espèces entre elles et notamment les liens trophiques (Bracken & Low 2012) à partir des régimes alimentaires. En milieu aquatique, et plus particulièrement chez les poissons, une des manières de connaître les liens de prédation entre espèces est d'effectuer l'étude des contenus stomacaux (Kalogirou et al. 2012). Dans la pratique, l'identification de la composition du régime alimentaire des espèces est une tâche fastidieuse et exigeante avec de nombreux biais potentiels. En effet, il est très difficile d'identifier les proies ciblées par des espèces omnivores dans des communautés riches en proies (Araujo et al. 2008). La plupart des aliments ingérés par les poissons continuent à être digérés après la capture. Les contenus stomacaux sont influencés par des facteurs temporels (Horppila 1999, Lehikoinen 2005) et des facteurs spatiaux (Link & Garrison 2002) car les individus ne consomment pas la même proies aux différents moments de la journée et en différents endroits. Il en résulte que les régimes alimentaires évalués à partir des contenus stomacaux restent des "instantanés", une diversité de proies réalisée localement, mais ne peuvent refléter le régime complet ou potentiel d'une espèce ; sinon un effort d'échantillonnage conséquent serait requis.

Cependant la connaissance des régimes alimentaires des espèces est essentielle en écologie. Par exemple, le chevauchement dans la composition du régime alimentaire, qui détermine le partage des ressources entre les espèces, est un processus limitant la compétition interspécifique et qui permet la coexistence entre espèces (Sala & Ballesteros 1997, Colloca et al. 2010). Ainsi les espèces spécialistes, avec des régimes alimentaires peu diversifiés, pourraient constituer des assemblages plus riches en espèces (Belmaker et al. 2012). Les régimes alimentaires permettent également de déterminer les liens créées par une espèce exotique avec les espèces de son nouvel environnement et d'identifier la compétition avec des espèces natives de même niveau trophique (Kalogirou et al. 2012). Ils peuvent permettre de reconstituer les conditions environnementales rencontrées, à travers la diversité de proies, pour des espèces opportunistes terrestres (Bojarska & Selva 2012). Ils mettent aussi en évidence les capacités de résistance des espèces généralistes par rapport aux espèces spécialistes vis à vis des changements environnementaux (Terraube et al. 2011). Au vu de l'importance des régimes alimentaires en écologie et de la difficulté à les collecter pour un grand nombre d'espèces et à large échelle, nous avons cherché un ensemble de traits écomorphologiques permettant d'inférer les guildes trophiques des poissons et, plus finement, leurs différences de régime alimentaire. La connaissance des guildes reste notamment un prérequis lors de la mise en place de modèles écotrophiques qui simplifient et simulent les flux de matière entre compartiments dans les systèmes aquatiques (Christensen & Walters 2004).

Les réseaux trophiques sont au cœur du fonctionnement de l'écosystème puisque leur structure régit les flux d'énergies (Cardinale et al. 2006) et les processus clés tels que la productivité (Chassot et al. 2010) et la stabilité (Loreau 2010). La structure trophique d'un assemblage est cependant loin d'être une chaîne linéaire depuis les producteurs primaires jusqu'aux carnivores supérieurs (Beaugrand et al. 2003), avec le plus souvent de l'omnivorie (Thompson et al. 2007), des boucles de rétroactions, de la prédation intra-guilde et du cannibalisme (Polis & Strong 1996). Par conséquent, la compréhension des processus qui régissent les liens trophiques est cruciale afin de prédire la structure des réseaux trophiques à large échelle (spatiale ou temporelle) et donc les impacts anthropiques (comme la pêche) ou climatiques sur le fonctionnement des écosystèmes. Nous savons que le niveau trophique des poissons est principalement déterminé par la taille car le prédateur doit être capable de capturer puis d'ingérer sa proie (Stergiou & Karpouzi 2001, Romanuk et al. 2011). A partir de la relation positive entre la taille du prédateur et la taille de la proie, un motif récurrent dans la plupart des écosystèmes terrestres et marins (Brose et al. 2006), nous proposons, testons, et appliquons une nouvelle méthodologie pour inférer les liens trophiques entre espèces de poissons. Une telle règle avait déjà été largement utilisée pour reproduire des structures réalistes de réseaux trophiques (Shin & Cury 2001, Dunne 2006) et pour estimer les relations de prédation qui correspondent étroitement aux données empiriques (Cattin et al. 2004, Allesina et al. 2008, Woodward et al. 2010). L'originalité de notre travail est d'avoir formalisé un modèle inférentiel, proposé une estimation rapide des paramètres puis d'avoir testé la robustesse des prédictions sur 3 réseaux trophiques déjà résolus. Cette méthodologie a ensuite servi à prédire l'impact du changement global sur la structure trophique des assemblages de poissons en Méditerranée.

Les activités humaines sont à l'origine de changements sans précédent sur les systèmes marins côtiers, en partie à cause des effets directs et indirects de la pêche (Jackson et al. 2001). L'exploitation peut provoquer des changements majeurs dans les assemblages et induire une perte de biodiversité pouvant perturber le fonctionnement des écosystèmes et modifier la durabilité des biens et des services associés (Fig. 29 ; Lotze et al. 2006, Worm et al. 2006).

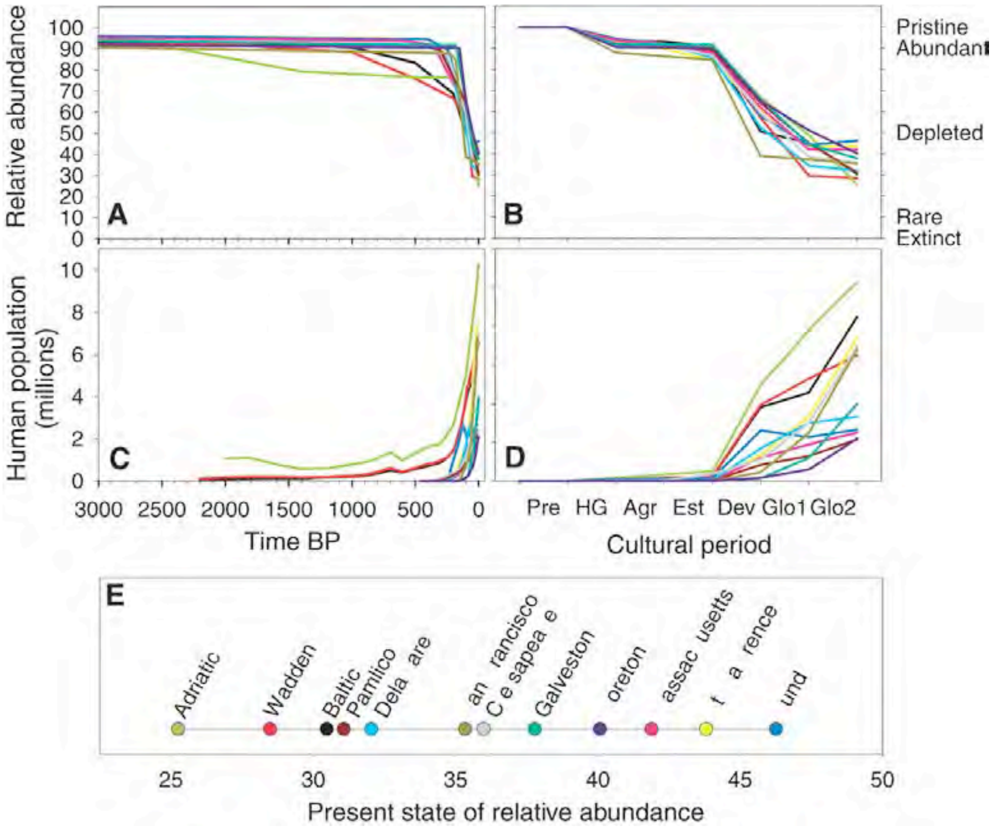


Figure 29 : Historique et état actuel de 12 écosystèmes côtiers et estuariens en Amérique du Nord, Europe et Australie. (A) Abondance relative de six groupes taxinomiques en en fonction du temps et (B) des périodes culturelles (Pré, pré-humain; HG, chasseur-cueilleur; Agr, agricole; Est, établissement du-marché-colonial; Dev, développement du-marché-colonial; Glo1, marché global (mondial) pour la période 1900-1950; et Glo2, marché global (mondial) pour la période 1950-2000). Les figure *C* et *D* illustrent la croissance démographique humaine en fonction du temps et des périodes culturelles. La figure *E* fait l'état des abondances relatives actuelles. Les codes couleurs dépeignent les systèmes d'étude comme indiqué dans *E*. (Lotze et al. 2006)

Il est par conséquent urgent d'évaluer l'impact potentiel que les différentes activités de pêche, seules ou combinées, peuvent avoir sur la durabilité des ressources et sur le fonctionnement général des écosystèmes côtiers. La Méditerranée occidentale est l'une des zones côtières les plus peuplées en Europe. L'augmentation de la population humaine entraîne une augmentation des activités de pêche récréative qui peuvent dans certains endroits dépasser, en terme d'effort, la pêche artisanale (Morales-Nin et al. 2005). Dans ce chapitre nous avons évalué l’impact de ces deux types de pêche sur le réseau trophique et le fonctionnement d’un écosystème côtier du nord de la Méditerranée, à l’aide d’une modélisation basée surles relations trophiques, le modèle Ecopath avec Ecosim (EwE; Christensen & Walters 2004). EwE intègre plusieurs niveaux d'analyses. Le premier niveau, Ecopath, est un bilan instantané (annuel) des flux trophiques dans un écosystème où l’élément clé de la modélisation est une matrice d’interactions entre compartiments trophiques où les espèces sont classées en fonction de leurs régimes alimentaires. Le second niveau, Ecosim, permet de simuler les tendances temporelles d’évolution du réseau trophique selon différents scénarios de pression de pêche (Christensen & Walters 2004).

Pour étudier les effets du changement climatique sur les réseaux trophiques nous avons suivi deux approches. Tout d'abord, nous avons utilisé un modèle OSMOSE (Object-oriented Simulator of Marine ecOSystems Exploitation ; Shin & Cury 2001), forcé par un modèle biogéochimique, dans lequel plusieurs scénarios de changement climatique ont été implémentés. Le modèle OSMOSE permet de représenter spatialement les cycles de vies de plusieurs espèces de poissons et d'analyser la dynamique des populations de poissons exploitées (Shin & Cury 2001, Travers & Shin 2010). Ce modèle intègre des processus tels que la croissance, la mortalité naturelle, la prédation, la reproduction, et la famine. L'hypothèse principale est la prédation opportuniste basée sur la taille entre un prédateur et sa proie. L'unité de base est un «super-individu» représentant une cohorte d'organismes de la même taille, vivant au même endroit et appartenant à la même espèce.

Cependant, même si ce type de modélisation peut fournir des informations très utiles au niveau local ou régional, il en ressort qu’il est très exigeant en terme de compilation de données, qu’il ne permet d’intégrer qu’un nombre limité d’espèces (20 maximum), et que le processus de calibration est long et complexe. Par conséquent cette modélisation est difficilement applicable à large échelle pour évaluer les conséquences trophiques du changement climatique sur une communauté riche en espèces. Dans notre cas d’étude nous avons recensé jusqu'à 212 espèces de poissons par cellule sur la côté méditerranéenne (Fig. 24a).

Afin d'intégrer ce grand nombre d'espèces pour inférer la structure des réseaux trophiques à large échelle, nous avons utilisé un modèle dont les hypothèses de base sont sensiblement identiques au modèle OSMOSE, mais notre nouvelle méthodologie est plus parcimonieuse : seulement trois paramètres on été utilisés par espèce alors qu'OSMOSE en nécessite plus de seize. En appliquant ce nouveau modèle, basé sur les relations de taille entre proie et prédateur, à trois réseaux trophiques méditerranéens résolus nous avons créé « un méta-réseau » qui comprend toutes les espèces de poissons qui pourraient coexister dans un même habitat ainsi que tous les liens trophiques possibles (Dunne 2006). À partir de ce « méta-réseau », les réseaux trophiques dans chaque cellule du plateau continental méditerranéen on été inférés, pour la période observée (1961-1980) ainsi que pour la période modélisées (2080-2099) en tenant compte des fluctuations des aires de répartition des espèces et donc de la composition spécifique de chaque cellule suite au changement climatique.

IV. 2 Inférence des guildes trophiques à partir des traits écomorphologiques

L'échantillonnage exhaustif des proies capturées par chaque espèce reste une tâche exigeante et fournit un résultat incomplet car la diversité du régime alimentaire est seulement "réalisé" dans un environnement donné. En cas de changement d'environnement et donc en présence de nouvelles proies potentielles tout l'enjeu est d'inférer de nouveaux liens de prédation sans que ceux ci n'aient jamais été observés. Il faut alors approcher le régime alimentaire "potentiel" des espèces en utilisant l'outil de modélisation. L'inférence des régimes alimentaires à partir d'autres variables, inhérentes à l'espèce et non à l'environnement, comme les traits fonctionnels, est la voie que nous avons explorée et approfondie.

Cette approche a été initiée en ichtyologie depuis les publications de Keast and Webb (1966) et Gatz (1979). Cependant, les preuves concernant une relation robuste entre les caractéristiques écomorphologiques des poissons et leurs régimes alimentaires restent rares. Ainsi, quelques études ont fait état de relations significatives entre les caractéristiques écomorphologiques et les régimes alimentaires des poissons (Norton 1991, Wainwright & Richard 1995, Ward-Campbell et al. 2005, Maldonado et al. 2009) alors que d'autres n'ont pas réussi à démontrer une telle relation (Labropoulou & Markakis 1998, Barnett et al. 2006). Au-delà de la significativité, le pouvoir explicatif des traits écomorphologiques sur le régime alimentaire doit être suffisamment élevé pour permettre des prédictions (Fig. 30). La force de notre étude par rapport à celles citées précédemment, réside dans le fait que nous avons pris en compte (*i*) un éventail d'espèces important issu de guildes trophiques très variées (des herbivores aux piscivores), (*ii*) plus de traits écomorphologiques, (*iii*) toutes les combinaisons possibles de traits facilement mesurables et (*iv*) nous avons utilisé deux méthodes de classification afin de prédire la prise alimentaire chez les poissons méditerranéens.

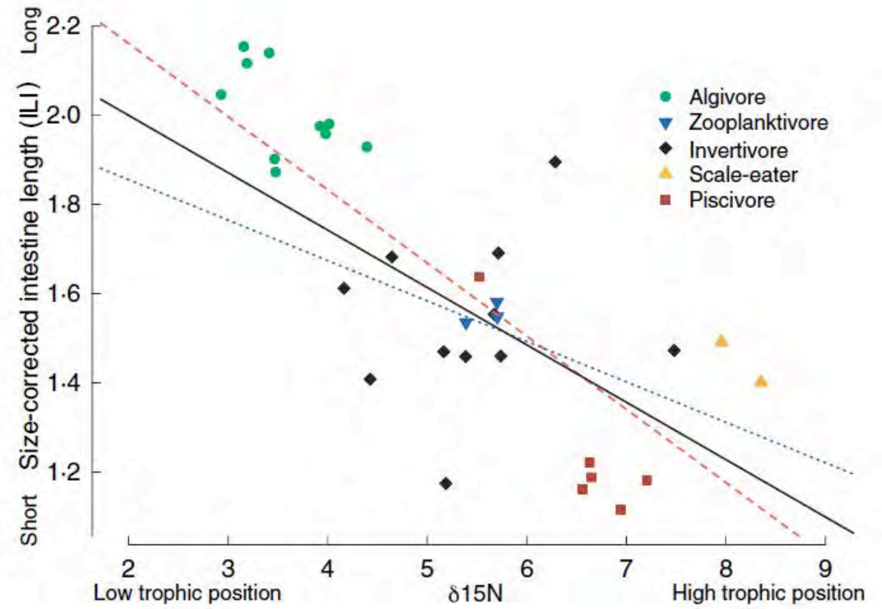


Figure 30 : Relation entre la taille des intestins et la position trophique pour 32 espèces de Cichlidés du lac Tanganyika regroupées en guilde trophique. Les guildes trophiques ont été définies sur la base des contenus stomacaux. Le pourcentage de variance expliqué par le modèle est de 50% (Wagner et al. 2009).

Nous avons tenté de prédire les guildes trophiques et le chevauchement des régimes alimentaires pour 35 espèces de poissons marins côtiers en utilisant 13 traits écomorphologiques liés à l'alimentation ainsi que toutes les combinaisons de traits. Les espèces de poissons ont été échantillonnées dans la Réserve Naturelle des Bouches de Bonifacio (RNBB, 80 000 ha, Fig. 36) en 2004 et 2005 (Mouillot et al. 2008). Cette AMP, créée en septembre 1999, est caractérisée par une prédominance de substrats rocheux et d'herbiers à *Posidonia oceanica*. Un maximum de dix spécimens adultes pour chacune des 35 espèces de poissons a été capturé par les pêcheurs artisanaux à l'intérieur ou aux alentours de la réserve (Mouillot et al. 2008). Les régimes alimentaires des poissons ont été obtenus à partir de données publiées. Treize traits fonctionnels ont ensuite été calculés à partir de 17 mesures morpho-anatomiques pour chaque individu puis moyennés pour obtenir des valeurs pour chaque espèce (Manuscrit G). Ces traits caractérisent la variété des stratégies utilisées par les poissons pour l'acquisition de nourriture. La classification des espèces en guildes trophiques reste controversée car le niveau de finesse pour définir des groupes peut être très subjective et variable. Deux méthodes statistiques ont été utilisées l'Analyse Linéaire Discriminante (LDA ; Fisher 1936) et le modèle « Random Forest » (RF ; Breiman 2001). Afin d'évaluer la capacité de ces modélisations prédictives à replacer correctement une espèce dans la bonne guilde à partir de ses traits écomorphologiques, une méthode de validation croisée a été utilisée. Les modèles ont été créés à partir de 30 espèces tirées de manière aléatoire puis évalués à l'aide des 5 espèces restantes. Cette méthode a été répétée dix fois, puis nous avons mesuré le pourcentage de bon réassignement (Fig. 31). Pour l'évaluation du chevauchement des régimes alimentaires, une méthode permettant d'exprimer la différence entre les régimes alimentaires et la différence entre des distances fonctionnelles entre paires d'espèces a été utilisée (GDM ; Generalized dissimilarity modeling ; Ferrier et al. 2007) ; pour plus de détails concernant le processus de modélisation voir l'annexe du Manuscrit G.

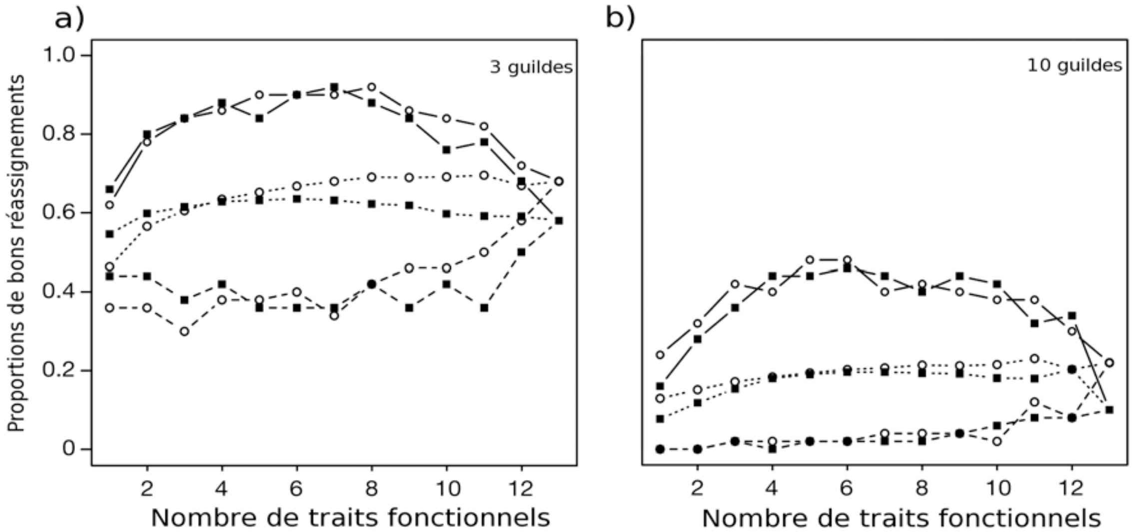


Figure 31 : Comparaison des performances entre l'analyse linéaire discriminante (LDA) et le modèle *Random Forest (RF)* pour 2 classifications, l'une avec trois guildes (a) et l'autre pour 10 guildes (b) pour chaque niveau de combinaison de traits. Maximum (ligne continue), minimum (ligne avec des tirets) et la moyenne (ligne pointillée) du pourcentage bon réassignement obtenu grâce à la méthode de validation croisée.

Pour contourner les limitations des études précédentes, à savoir un faible nombre de guildes et un faible nombre de traits et d'espèces prisent en compte, nous avons construit un large éventail de guildes et calculés le plus grand nombre de traits en relation avec la prise alimentaire. Les 35 espèces de poissons ont été classées afin de composer de deux à dix guildes grâce à l'algorithme k-means. Cet algorithme permet de regrouper les poissons de manière à ce qu'ils soient le plus semblables entre eux au sein de chaque guilde du point de vue de leurs régimes alimentaires (Legendre & Legendre 1998). Cette étude démontre que les guildes trophiques de poissons peuvent être prédites avec précision par les deux types de modélisations (LDA, RF) à partir d'un nombre limité de traits (Fig. 32). Par exemple avec la méthode RF pour 7 guildes un pourcentage de 74% de bon réassignement à été atteint avec une combinaison de 9 traits (B, Bsh, CPt, Eps, GRlst, Glst, Osf, Pfps, Pro; pour plus de détails voir Manuscrit G). Cependant les prédictions peuvent être considérées comme robustes jusqu'à une partition en sept guildes; au delà l'appartenance est difficile à prédire (avec seulement 60% de bon réassignement pour une combinaison de 8 traits).

Une prédiction robuste des guildes trophiques au sens large pourrait servir à composer les groupes pour les modèles trophiques à compartiment, mais également à identifier des convergences ou des divergences dans les structures trophiques des assemblages de poissons de différentes régions soumis à différents types d'impacts (Muñoz & Ojeda 1997, Garrison & Link 2000). En revanche, cette approche ne permet pas de prédire les régimes alimentaires précis en fonction des traits écomorphologiques.

Afin de modéliser la relation entre la différence des régimes alimentaires et la dissimilarité des traits écomorphologiques pour chaque paire d'espèces, nous avons utilisé l'extension multivariée du test de Mantel, le GDM (*General Dissimilarity Modelling*). Le meilleur compromis entre le nombre de traits et le pourcentage de déviance expliquée par le modèle GDM a été obtenu avec 6 traits. Néanmoins, seulement 24% de la déviance a été expliquée (Fig. 32). Cette faible relation indique que les traits écomorphologiques ne sont pas appropriés pour prédire le niveau des chevauchements entre les régimes alimentaires. Cette relation est triangulaire : elle montre également que des espèces ayant des traits fonctionnels très différents ne peuvent pas avoir le même régime alimentaire, mais que des espèces avec des traits identiques peuvent avoir des régimes alimentaires très différents. Les faibles relations entre traits et régimes alimentaires qui ont été trouvées (Bohning-Gaese & Oberrath 1999, Boyle & Horn 2006) indiquent généralement une capacité très limitée à prédire le régime alimentaire à cause, en partie, du degré d'opportunisme alimentaire (Bellwood et al. 2006). Plus généralement, cette étude propose un cadre statistique, qui peut être appliqué à tout type d'organisme pour lequel les stratégies d'alimentation doivent être déterminées à partir des traits. Pour les poissons marins côtiers il semble que la prédiction robuste se limitera à l'absence de chevauchement de régime alimentaire entre les espèces ayant des traits écomorphologiques très distincts ou à la prédiction de guildes trophiques grossières.

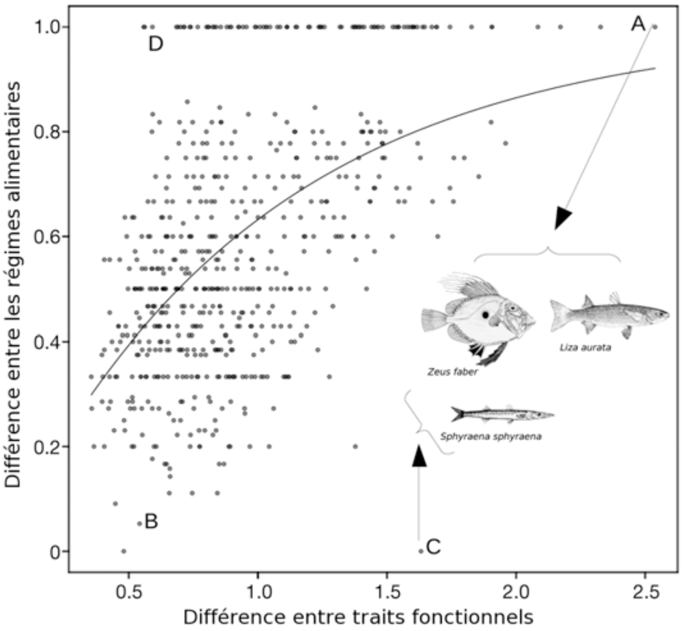


Figure 32 : Relation non linéaire croissante entre la différence de régime alimentaire et la différence de traits fonctionnel (6 traits considérés) pour 1190 paires d'espèces de poissons. La relation est triangulaire est pour une déviance expliquée de 24%. En effet, pratiquement aucune paire d'espèces avec des traits écomorphologiques très différents ont des régimes alimentaires identiques (C ; *Zeus faber*, *Sphyraena sphyraena*). *A contrario* des espèces avec des traits similaires peuvent avoir des régimes alimentaires identiques (B ; *Diplodus sargus*, *Diplodus vulgaris*) ou non (D ; *Symphodus tinca*, *Diplodus annularis*). Deux espèces peuvent avoir des traits et des régimes alimentaires très différents (A ; *Liza aurata*, *Zeus faber*).

IV.3 Inférence des relations trophiques entre espèces à partir de la taille du corps

Dans le chapitre précédent nous avons tenté de prédire les guildes trophiques et le chevauchement entre les régimes alimentaires à partir des traits écomorphologiques, mais pas les relations trophiques entre paires d'espèces qui restent très importantes à connaître pour approcher le fonctionnement des écosystèmes. De plus, mesurer une multitude de traits sur de nombreuses espèces peut être fastidieux et irréalisable sur les systèmes riches en espèces et à large échelle. Il est donc nécessaire de mettre au point une modélisation capable de prédire, à partir d'un minimum de traits et de règles d'assemblage simples, la structure d'un réseau trophique.

Dans cette étude, nous avons intégré les développements récents de la théorie des réseaux trophiques afin de déduire les interactions possibles entre toutes les paires espèces, même celles qui n'ont jamais coexisté. Le modèle est basé sur une relation positive entre la taille du prédateur et la taille de sa proie. En dépit de leur intérêt théorique, les méthodes développées récemment pour paramétrer les modèles trophiques offrent plusieurs inconvénients : elles sont difficiles à appliquer à grande échelle et la calibration des modèles est un défi sérieux pour les grands jeux de données car le nombre de paramètres à optimiser est très important ce qui nécessite de longs temps de calcul et exige des ressources informatiques coûteuses. Pour surmonter ces inconvénients nous proposons une méthode (Manuscrit H), conçue pour inférer, à partir de la taille des espèces, les réseaux trophiques. Dans le paragraphe suivant nous allons présenter cette méthode, sa calibration et sa validation.

IV.3.1 Description du modèle

Le modèle de niche développé ici, prédit la structure des réseaux trophiques à partir d'un ensemble de trois paramètres pour chaque espèce *i*: n_i la position sur l'axe de niche, c_i l'optimum alimentaire appelé aussi le centroïde, et r_i l'étendue du régime alimentaire (Fig. 28). Une espèce *i* peut consommer toutes les espèces *j* dont la position n_j est comprise dans l'intervalle $\left[c_i - r_i/2, c_i + r_i/2\right]$. En considérant que la taille des espèces est le trait principal déterminant les interactions trophiques, le paramètre n_i est directement déterminé par la taille.

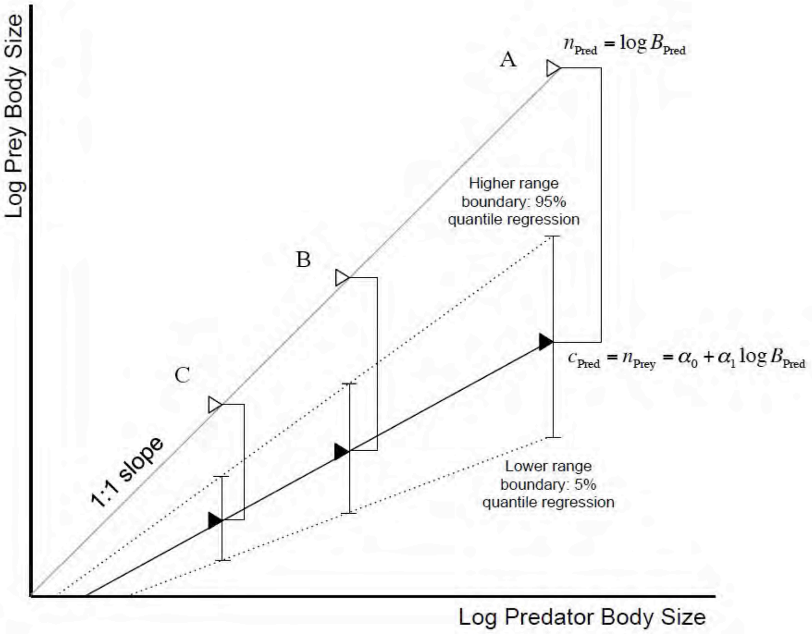


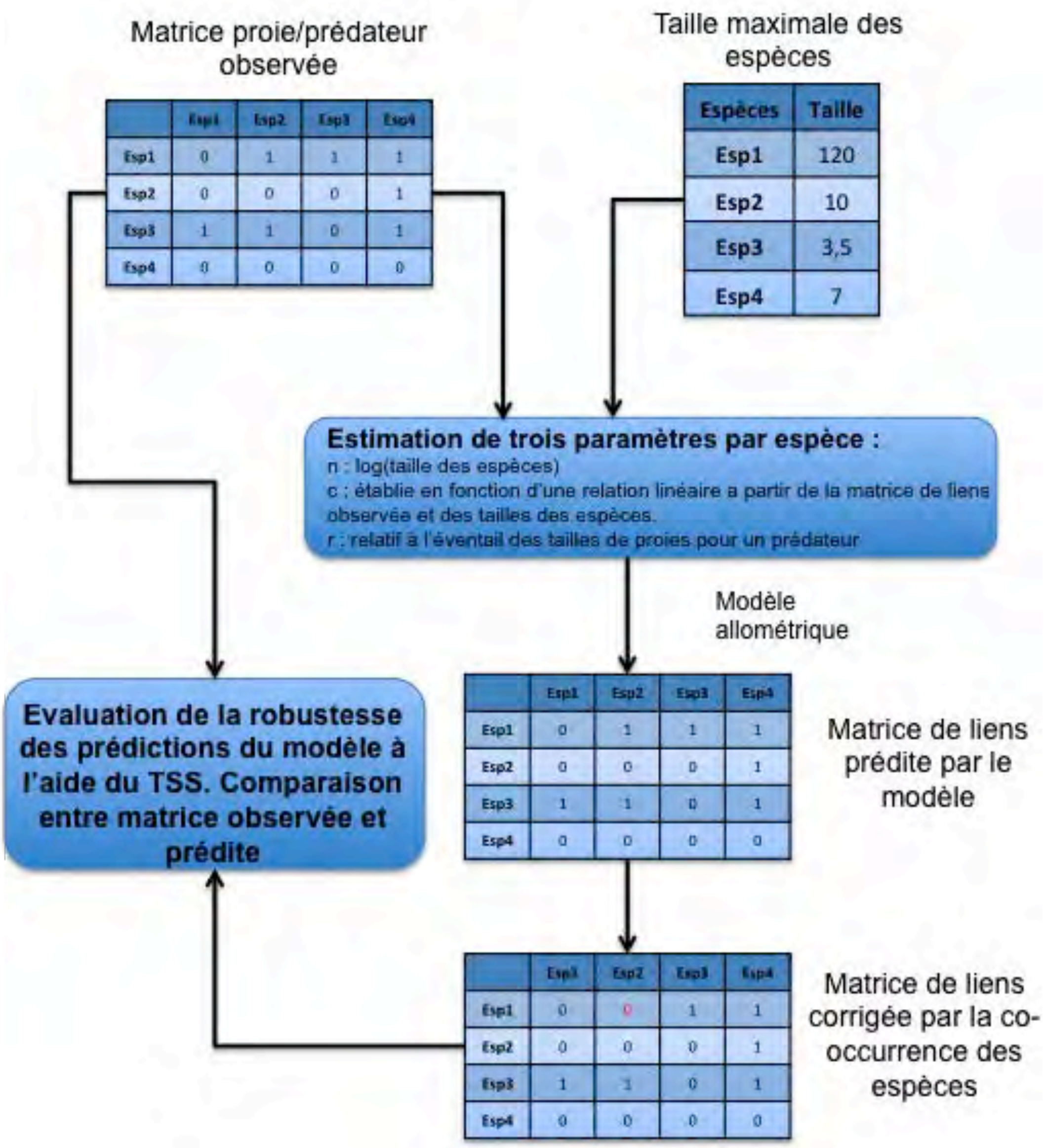
Figure 33 : Représentation schématique du modèle de niche et son application à la relation liant la taille du corps pour les couples prédateur-proie. Trois espèces de consommateurs sont représentées (A, B, C). Les triangles blancs correspondent à la position de niche des prédateurs (leur position sur l'axe X est transposée sur l'axe Y). Pour la plupart des cas, la taille des proies est plus petite que la taille du prédateur et donc tombe sous le rapport 1:1. Pour un prédateur donné, nous considérons que le centroïde de sa niche (c) est la taille de la proie moyenne, donnée par la relation linéaire entre la taille du prédateur et la taille des proies (ligne noire continue). Les limites de la gamme alimentaire (r) sont données par les régressions quantiles à 5% et 95%. Un prédateur (A) se nourrit de toutes les proies dont la taille se trouve entre ces limites. Dans cet exemple spécifique, le plus grand prédateur (A) se nourrit des deux plus petites espèces (B,C) et le prédateur intermédiaire se nourrit de la plus petite espèce (C).

Afin de déterminer le paramètre c_i, une relation linéaire entre le logarithme de la taille et le paramètre c a été obtenue en ajustant un modèle de type linéaire $c = \log_{10}(B_{prey}) = \alpha_0 + \alpha_1 \times \log_{10}(B_{pred})$ où B_{prey} et B_{pred} sont les tailles des proies et des prédateurs présents dans une matrice d'interaction observée. Les limites inférieures et supérieures pour l'étendue du régime alimentaire on été obtenues à partir de régressions quantiles pour 5% et 95% (Fig. 33).

IV.3.2.Calibration et validation du modèle

Pour calibrer un tel modèle il est important de disposer de réseaux trophiques résolus. Nous avons identifié puis compilé trois de ces réseaux en mer Méditerranée. Le premier réseau est celui de la RNBB, le second est le réseau trophique de la mer Catalane (Coll et al. 2006), et le troisième réseau vient de la mer Tyrrhénienne (Colloca et al. 2010). Ces trois réseaux ont été fusionnés dans une seule matrice d'interactions trophiques comportant 126 espèces de poissons (Fig. 34).

Dans le but d'évaluer la capacité de notre modélisation à prédire les liens trophiques, nous avons utilisé les tailles des espèces et les liens entre proie et prédateur référencés dans la matrice d'interactions pour calibrer le modèle allométrique et obtenir les paramètres n, c et r pour chaque espèce. Ces paramètres permettent de décrire la position de chaque espèce dans le réseau et de reproduire les interactions trophiques et par conséquent d'inférer la structure complète du réseau trophique. Afin d'améliorer la qualité de prédiction du modèle, les liens créées ont été corrigés par deux règles simples, (*i*) les espèces doivent cohabiter dans leur milieu (*ii*) et les espèces pélagiques ne peuvent pas consommer les espèces benthiques, toutes les autres interactions étant possibles (Fig. 29). Nous avons comparé le réseau obtenu avec la matrice d'interactions observées. La qualité du modèle a été mesurée à l'aide du TSS (voir Encart 2 Chapitre3).



Matrice proie/prédateur observée

	Esp1	Esp2	Esp3	Esp4
Esp1	0	1	1	1
Esp2	0	0	0	1
Esp3	1	1	0	1
Esp4	0	0	0	0

Taille maximale des espèces

Espèces	Taille
Esp1	120
Esp2	10
Esp3	3,5
Esp4	7

Matrice de liens prédite par le modèle

	Esp1	Esp2	Esp3	Esp4
Esp1	0	1	1	1
Esp2	0	0	0	1
Esp3	1	1	0	1
Esp4	0	0	0	0

Matrice de liens corrigée par la co-occurrence des espèces

	Esp1	Esp2	Esp3	Esp4
Esp1	0	0	1	1
Esp2	0	0	0	1
Esp3	1	1	0	1
Esp4	0	0	0	0

Figure 34 : Description du processus de calibration et d'évaluation du modèle

Le modèle de niche paramétré a tendance à surestimer le nombre de liens par rapport au réseau observé. Ce résultat n'est pas surprenant, étant donné que les ensembles de données observés ne contiennent pas forcément tous les liens (variabilité des régimes alimentaires, difficultés d'échantillonnage). Il est également bien connu que ce type de modèle prévoit un régime continu le long de l'axe de niche alors que les réseaux trophiques réels n'ont pas cette caractéristique. Nous avons donc, dans un premier temps, surestimé la densité des liens au sein de la niche d'une espèce donnée ; le TSS témoigne de ce résultat (TSS observé = 0,51). Des études antérieures (Allesina et al. 2008) montrent cependant que ce problème est facilement contourné quand un axe seconde niche tel que la co-occurrence des espèces entre en jeu. En appliquant cette règle simple, les espèces n'intergissent que si elles coexistent, la qualité du modèle prédisant les liens trophiques a été augmentée (Fig. 35) : la valeur du TSS est passée de 0,51 à 0,67 principalement en diminuant la part des liens prédits par le modèle mais non observés dans la matrice. Cette méthode permet par conséquent de prédire les interactions entre espèces et pourra être appliquée à large échelle afin d'étudier les effets de la pêche ou du changement climatique.

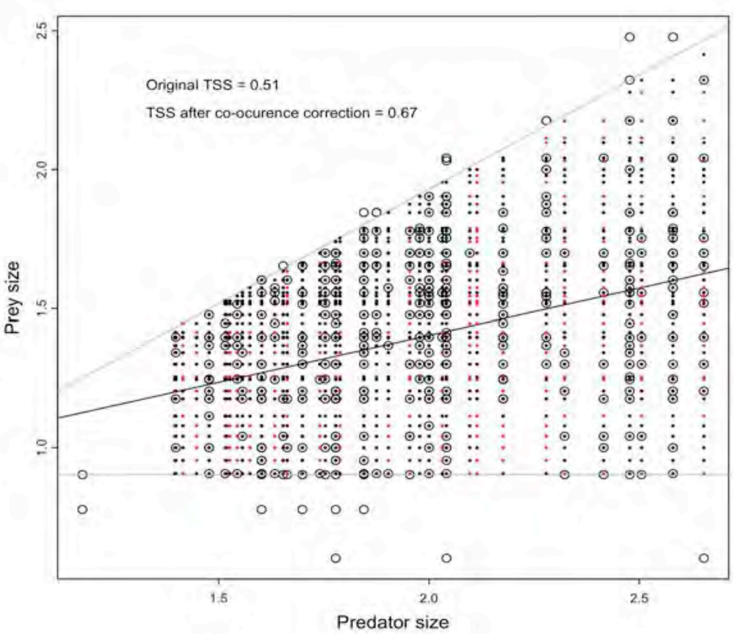


Figure 35 : Relation entre la taille des proies et celle des prédateurs pour la compilation des trois réseaux trophiques méditerranéens. Les cercles représentent les liens observés entre proie et prédateur, les points noirs représentent les liens prédits par le modèle et les points rouges représentent les liens supprimés pour des raisons de non co-occurrence entre espèces. On constate que 91% des liens observés sont bien prédit par le modèle.

IV.4 Impact de la pêche sur un écosystème côtier : la réserve naturelle des bouches de Bonifacio

Depuis les années 1960, une centaine d'AMP a été créée en mer Méditerranée pour répondre au défi de l'anthropisation croissante des systèmes marins. Leur rôle est d'assurer la protection de l'habitat et de la biodiversité mais aussi de contribuer à augmenter la biomasse disponible pour assurer une durabilité de la pêche artisanale. Ainsi, les AMP ne sont pas forcement des sanctuaires, elles peuvent présenter différents niveaux de protection et de restriction vis-à-vis de la pêche. Cependant, lors de la création des AMP, leur forte attractivité pour le tourisme ainsi que pour la pêche récréative a été sous estimée, à tel point que de nos jours la question d'une compétition entre pêche récréative et pêche artisanale se pose avec quelques questions cruciales. Quelle est la part de biomasse prélevée par la pêche récréative qui est confisquée à la pêche artisanale ? Quels sont les effets combinés de ces deux types de pêche sur les assemblages côtiers et leur fonctionnement ? Nous avons tenté d'apporter des éléments de réponse à ces enjeux en focalisant sur un cas d'étude qui combine étroitement ces deux types de pêche.

La réserve naturelle des bouches de Bonifacio (RNBB) a été choisie pour site d'étude car des données concernant les pêches artisanales et pour les densités d'espèces sont disponibles (Fig. 36). La RNBB présente une mosaïque de niveaux de protection vis-à-vis des

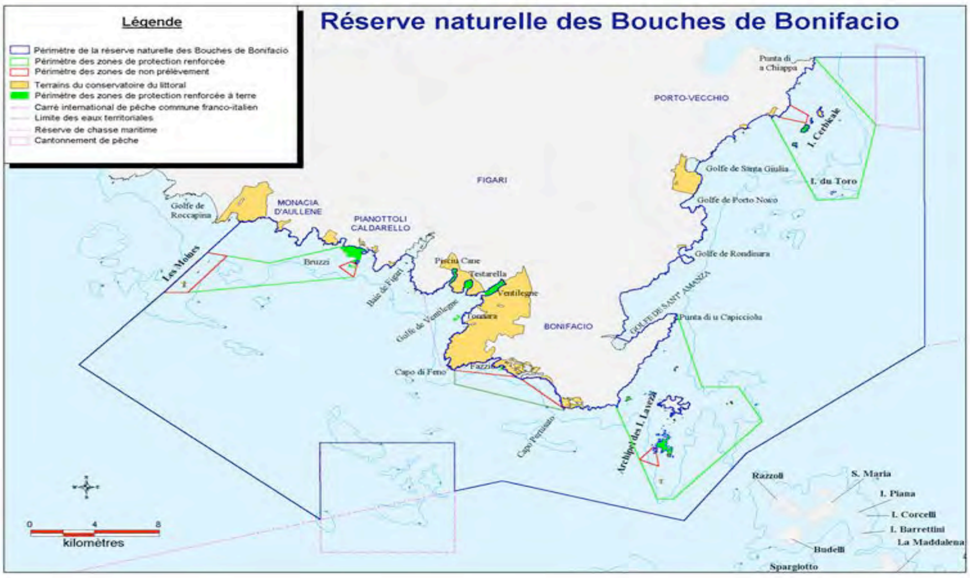


Figure 36 : Cartographie de la Réserve Naturelle des Bouches de Bonifacio (RNBB). En vert sont représentées les zones de protection renforcée où la chasse sous-marine est interdite, en rouge les zones de non prélèvement (pêche et plongée interdites), en bleu périmètre de la réserve.

activités nautiques allant des zones de non prélèvement (sanctuaire) au périmètre le plus externe de la réserve dans lequel le nombre de licences professionnelles est limité, mais qui autorise pêches artisanale et récréative.

A partir des régimes alimentaires des espèces, nous avons établi le réseau trophique complet de la RNBB à l'aide du logiciel Ecopath. Il s'agit d'un modèle à compartiments permettant de modéliser les flux de matière au sein des écosystèmes, en partant des bas niveaux trophiques (phytoplancton, zooplancton) vers les plus hauts (mammifères marins). Ecopath est composé de deux équations qui, à l'équilibre, nous renseignent sur des valeurs d'indices pour chaque compartiment mais aussi pour l'ensemble du système modélisé. Le modèle réalisé sur la RNBB comprend 32 groupes, 25 groupes d'espèces reliées

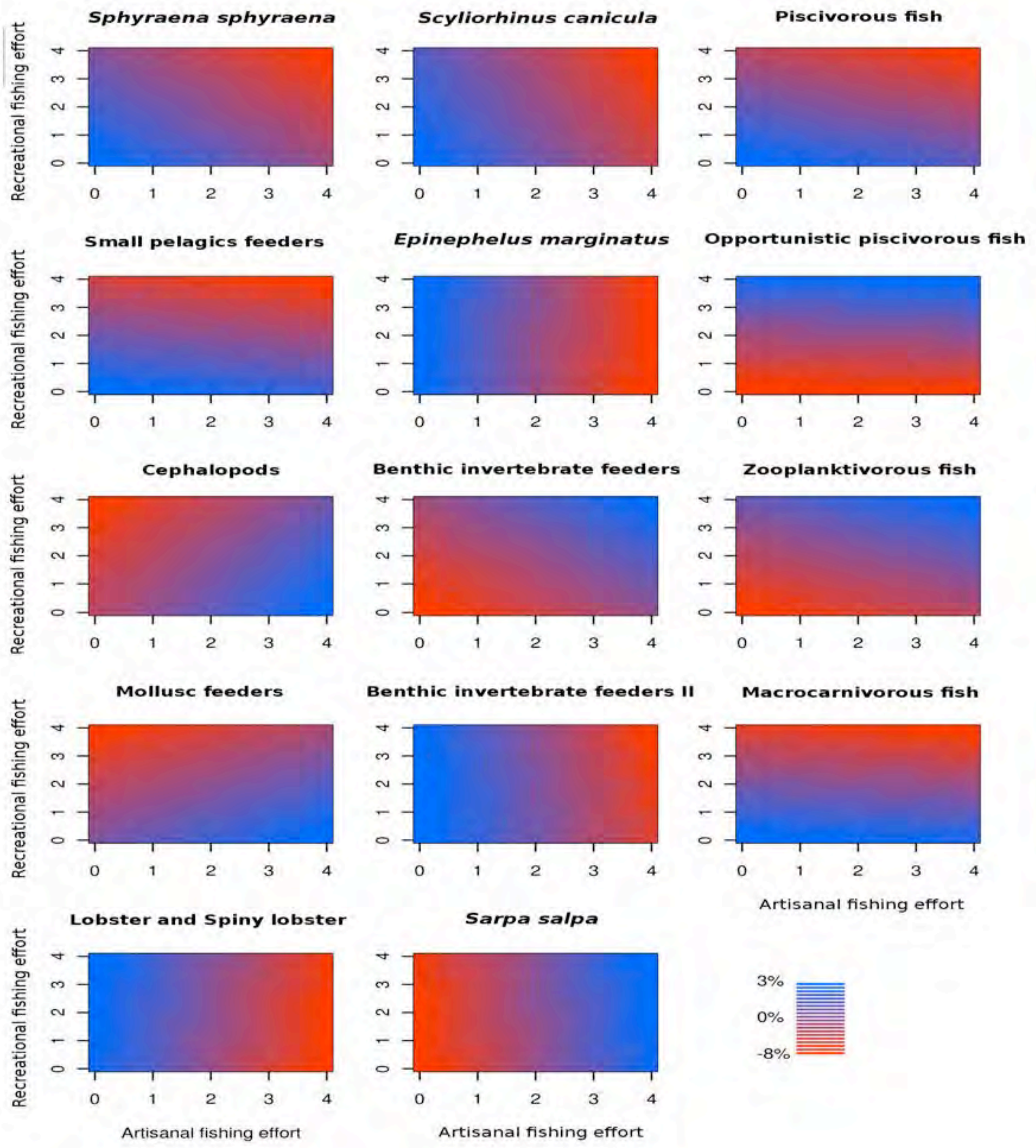


Figure 37 : Effets combinés des changements d'efforts pour les pêches artisanales et récréatives sur les biomasses des différents compartiments du réseau trophique de la réserve naturelle des Bouches de Bonifacio.

écologiquement et 6 groupes monospécifiques (Manuscrit I, Tableau 1). Par la suite, le modèle Ecosim qui permet de rendre dynamique dans le temps les équations du modèle Ecoptah a servi à réaliser 440 simulations de variation des efforts de pêche récréatives et artisanales qui correspondent à plusieurs scénarios (de 0 à 400% de l'effort actuel). Ces scénarios vont de l'arrêt total de ces deux types de pêche à leur augmentation conjointe d'un facteur 4.

En analysant les résultats des simulations utilisant Ecosim, trois catégories de réponse aux pressions exercées par la pêche récréative et commerciale ont été montrées (Fig. 37). Tout d'abord, nous nous sommes concentrés sur les groupes qui ont perdu de la biomasse en réponse à une augmentation de l'effort de pêche artisanale seulement. Pour ces groupes, une augmentation de l'effort de pêche récréative était sans influence. Par exemple pour le groupe des langoustes et homards, une interdiction totale de la pêche artisanale se traduirait par une augmentation de 2,7% de la biomasse au sein de la RNBB (soit une biomasse de 51 tonnes).

Certains groupes sont ciblés par les deux types de pêcheries, tels que les poissons piscivores, ou les petits pélagiques. Pour ces groupes, un effet cumulatif des deux types de pêche a été observé puisque leurs biomasses diminuent lorsque les efforts de pêche augmentent. Par exemple, lorsque les deux efforts de pêche sont au maximum (4 fois le niveau actuel), la biomasse des poissons piscivores a diminué de 4,7 % (soit 131 tonnes). Cependant si ces résultats semblent triviaux lorsque les deux types de pêche s'exercent il n'en n'est pas de même pour d'autres groupes trophiques (les consommateurs d'invertébrés benthiques, les consommateurs de mollusques et les céphalopodes). Ces groupes affichent des patrons non triviaux, qui sont reliés directement à des cascades trophiques. Par exemple pour les consommateurs d'invertébrés benthiques, lorsque les deux efforts de pêche augmentent, la biomasse de ce groupe augmente. Cette augmentation est liée à la diminution induite par les deux types de pêches sur les prédateurs (poissons piscivores) de ce groupe trophique.

Cette approche trophique révèle que certains groupes peuvent perdre de la biomasse lorsque les AMP sont mises en place ou renforcées, en raison des effets combinés de l'arrêt de la pêche artisanale et de la pêche récréative sur leurs prédateurs. Il est donc risqué de se fonder seulement sur une ou deux espèces présentant les mêmes caractéristiques pour évaluer l'état de santé d'une AMP. Dans l'ensemble, nos résultats illustrent l'intérêt de la modélisation pour interpréter les données et les indicateurs utilisés pour la gestion des AMP.

Les modèles offrent la possibilité d'anticiper les conséquences potentielles, au niveau des écosystèmes, des décisions socio-politiques qui visent à préserver les ressources côtières tout en gérant les pêcheries artisanales et récréatives. Cependant ce type de modélisation ne permet pas pour le moment de modéliser l'augmentation de la température et demanderait énormément de temps pour rassembler l'ensemble des paramètres nécessaires pour créer un modèle à l'échelle de la mer Méditerranée. Dans le but d'étudier de manière locale les effets du changement climatique au sein de trois réseaux trophiques connus, nous avons entrepris, en collaboration avec Marta Coll, d'intégrer les changements observés sur différents compartiments trophiques. Ces modifications seront intégrées à la version dynamique (Ecosim) de ces modèles locaux sous forme de fonction de forçage. Par exemple il a été rapporté que les cétacés pourraient être plus vulnérables aux maladies (Gambiani et al 2009), par conséquent nous forceront leur biomasse à diminuer dans les modèles afin d'observer les répercutions de ces modifications au sein des réseaux trophiques.

IV.5 Effet du changement climatique sur les réseaux trophiques en mer Méditerranée

IV.5.1 Modélisation Osmose

Le modèle Osmose (Object-oriented Simulator of Marine ecOSystems Exploitation) a été initialement développé pour simuler le fonctionnement des assemblages de poissons structurés en taille, interagissant via une prédation opportuniste prenant en compte la variabilité individuelle (Shin & Cury 2001, 2004). L'unité de base de ce modèle est une cohorte de poissons, s'apparentant à un banc, appartenant à la même espèce, ayant le même âge, la même taille et se trouvant au même endroit à un instant donné. Le pas de temps du modèle a été fixé à 15 jours et commence par la mise en place de la répartition spatiale des organismes. La mortalité naturelle est ensuite opérée avant le processus de prédation. De ce dernier découle le processus de croissance ou de mortalité lié au jeûne. Le pas de temps se termine par les processus de mortalité par pêche puis la reproduction (Fig. 38).

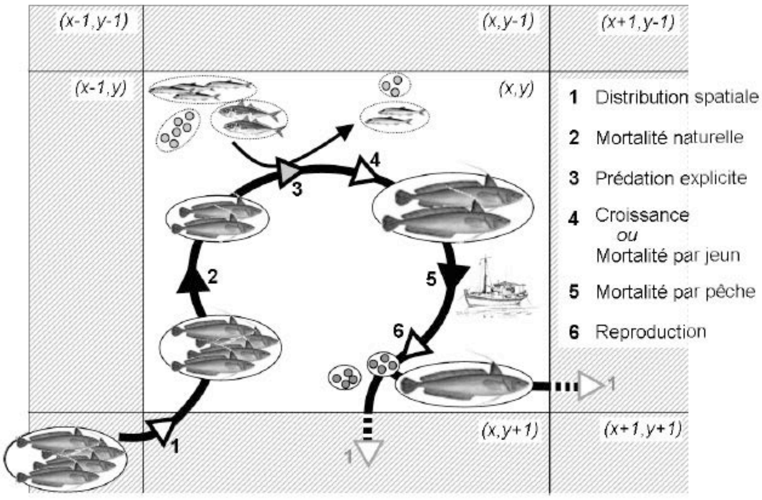


Figure 38 : Schéma de déroulement d'un pas de temps (15 jours) pour le modèle Osmose. Les deux processus de mortalité (naturelle, par pêche) sont représentés par les flèches noires. Du processus principal (la prédation en gris) découle les processus de croissance et indirectement de reproduction. Lors de ce dernier, les nouveaux individus créés subiront le pas de temps suivant comme des bancs indépendants (Travers & Shin 2010). Les *y* représentent la latitude et les *x* la longitude.

Le modèle osmose a été appliquée à la mer Adriatique et forcé par un modèle biogéographique constitué par le couplage du modèle océanique de Princeton (POM) et un modèle biogéochimique de flux (BFM). BFM est un modèle décrivant les processus biogéochimiques qui se produisent dans la colonne d'eau et dans les sédiments, ainsi que leurs interactions, en terme de cycle du carbone, de l'azote, du phosphore et du silicium dans l'écosystème marin.

Nous avons sélectionné 4 groupes planctoniques (diatomées, dinoflagellés, micro-zooplancton, méso-zooplancton) dont les tailles leur permettent d'être consommés par les larves de poissons. Les données en 3 dimensions de POM-BFM ont été interpolées pour ces 4 groupes le long de la colonne d'eau. La biomasse planctonique a été intégrée verticalement de 0 mètres à 100 mètres. Le modèle OSMOSE a été forcé de 1990 à 2000 en créant une climatologie annuelle. Les paramètres biologiques, de croissance, de reproduction, de survie et de prédation pour les poissons ont été collectés pour cette période. Nous avons sélectionné 11 espèces qui avaient un intérêt commercial ou un rôle clé dans la structure de l'écosystème (Tableau 4).

Tableau 4 : Paramètres biologiques pour les 11 espèces sélectionnées dans le modèle Osmose pour l'Adriatique. L_∞ K et t_0 sont les paramètres du modèle de croissance de Von Bertalanffy ; c est le facteur de condition de Fulton et b l'exposant de la relation allométrique taille poids ; φ est la fécondité relative et a_{mat} est lâge à maturité ; a_{max} la longévité ; M est la taux de mortalité ; F est le taux de mortalité par pêche ; a_{rec} est l'âge au recrutement ; Lthr est la taille pour laquelle une espèce change de régime alimentaire.

	Croissance					Reproduction		Survie				Predation				
Espèces	**L∞**	**K**	**t0**	**c**	**b**	**φ**	**a_mat**	**a_max**	**M**	**F**	**a_rec**	**L_thr**	**Min ratio**		**Max ratio**	
	cm (TL)	**y-1**	**y**	**g.cm3**		**eggs.g**	**Y**	**y**	**y-1**		**y**	**cm**	**Larv/ Juv**	**Adult**	**Larv /Juv**	**Adult**
Euphausiids	1,84	1,682	-0,1975	0,00738	3,16	42254	1,05	1	0.1	0	1	0,6	1000	1000	15	5
Sardina pilchardus	20,5	0,46	-0,5	0,004	3,22	156,25	1	10	0.5	0.24	1	10	100	400	10	10
Sardinella aurita	30	0,35	-0,42	0,0043	3,26	26,50	1	7	0.5	0.24	1	10	100	500	10	10
Engraulis encrasicolus	19,4	0,57	-0,5	0,0039	3,16	16,13	1	7	0.58	0.3	1	8	100	500	10	10
Trachurus trachurus	38,1	0,215	-0,39	0,0061	3,07	104,51	2,9	12	0.46	0.27	2	-	50		7	
Scomber scombrus	42	0,37	-0,5	0,0141	2,88	417,42	2	11	0.06	0.9	1	-	70		8	
Scomber japonicus	47,596	0,154	-2,177	0,0066	3,14	401,29	2,5	18	0.06	0.9	1	-	100		10	
Sarda sarda	80,6	0,36	-1,37	0,082	3,13	65,00	1,5	7	0.39	0.006	1	-	9		5	
Merluccius Merluccius	92,83	0,097	-0,629	0,00257	3,29	811,17	3	8	0.3	0.9	2	15	15	12	1,5	2
Sprattus sprattus	14,2	0,368	-2,3	0,0602	3,051	9,65	1	6	1,3	0.5	1	-	300		10	
Micromesistius poutassou	32,7	0,247	-0,35	0,006	3,029	30	2	20	0.62	0.14	1	-	50		5	

Les variations saisonnières et les migrations liées à la reproduction ont été prises en compte pour les anchois, la sardine et le merlu. Cependant, ce travail reste en cours de développement, suite à des contretemps lors des diverses phases de calibration du modèle. Tous les résultats ne sont pas encore disponibles. La suite de la modélisation consistera à forcer le modèle OSMOSE-Adriatique par trois scénarios de changement climatique issus du modèle POM-BFM. Il s'agira ensuite d'analyser les variations induites par le changement climatique sur la structure et le fonctionnement du réseau local.

Ce type de modélisation intégrant l'ensemble du cycle de vie des espèces n'est pas facile à calibrer et demande des ressources informatiques conséquentes. Même si l'intégralité de cette approche n'a pu être explorée faute de temps, il est évident que ce genre de modélisation ne pourra pas être appliqué à l'ensemble des poissons côtiers méditerranéens. Il ressort de cette expérience de modélisation que le modèle OSMOSE ne permettra pas d'étudier les effets du changement climatique sur le fonctionnement des écosystèmes côtiers méditerranéens mais sera limité à un nombre restreint d'espèces. Compte tenu de ces limitations, nous avons exploré en parallèle un autre type de modèle, plus parcimonieux, pouvant s'appliquer à large échelle et intégrant de nombreuses espèces tout en conservant les grandes hypothèses de la modélisation OSMOSE, à savoir la relation entre taille des proies et celle des prédateurs et la co-occurrence spatiale des espèces.

IV.5.2.Modélisation hybride intégrant niche climatique et niche trophique

Des progrès ont été réalisés en biogéographie au cours des quinze dernières années afin de prédire l'impact du changement climatique sur les modifications des aires de répartitions des espèces, les risques d'extinction, et les patrons de biodiversité (Thuiller 2004, Araújo & New 2007, Albouy et al. 2012a). Les nouveaux écosystèmes qui pourraient émerger comporteront des espèces qui n'ont jamais interagi auparavant. Un des défis majeurs auquel l'écologie et la biogéographie sont confrontées aujourd'hui est de comprendre comment les assemblages futurs seront réorganisés à la suite des réponses individuelles des espèces au changement climatique et comment ces écosystèmes émergents pourraient fonctionner (Montoya et al. 2009, Woodward et al. 2010).

Comme nous l'avons vu dans le chapitre 3, le changement climatique peut affecter les organismes individuellement, mais les effets peuvent également se propager au sein des populations et des écosystèmes. La forte association entre le climat et la distribution des espèces a conduit au développement de modèles basés sur les enveloppes bioclimatiques pour prédire les distributions futures des espèces (Buisson et al. 2008, Thuiller et al. 2009, Albouy et al. 2012b). Si la modélisation des aires de répartitions nous permet actuellement de mieux appréhender l'impact des changements globaux sur la biodiversité, nous en savons beaucoup moins sur le fonctionnement futur des assemblages d'espèces et sur les services rendus à l'homme. Il est un fait établi : les modèles prédisant les aires de répartition négligent les interactions entre espèces (Woodward et al. 2010). Or il est évident que la structure et la composition de ces réseaux d'interactions seront modifiées à la suite des changements globaux par l'arrivée et l'extinction d'espèces. Mais au delà de la modification de cette composante importante de la biodiversité qu'est la diversité des liens c'est l'ensemble des composantes qui vont être modifiées. La complexité des réseaux trophiques et les méthodes de modélisation n'ont pas permis de considérer jusqu'ici un grand nombre d'espèces comme des composants interagissant au sein d'un large réseau écologique empêchant ainsi d'explorer les impacts du changement climatique à large échelle sur le fonctionnement des écosystèmes (Woodward et al. 2010, Kissling et al. 2011).

La mer Méditerranée est exploitée de manière intensive (Coll et al. 2010) avec des impacts majeurs sur distribution en taille des peuplements de poissons ayant des conséquences écologiques sur la structure du réseau trophique et économiques pour la pêche

(Genner et al. 2010, Sumaila et al. 2011). La question n'est donc plus de savoir si les assemblages d'espèces marines seront modifiés avec le changement climatique, mais si de tels changements vont modifier le fonctionnement des écosystèmes et dans quelle mesure.

La taille maximale du corps a été utilisée pour prédire la structure trophique des futurs assemblages de poissons côtiers méditerranéens. Pour ce faire, un modèle de niche a été calibré en utilisant trois réseaux trophiques locaux méditerranéens. Le modèle a ensuite été utilisé pour inférer un « méta-réseau » décrivant les interactions trophiques potentielles parmi les 256 espèces de poissons, pour l'ensemble du plateau continental de la mer Méditerranée.

Cette étape de calibration effectuée, les tailles maximales de 256 espèces de poissons côtiers méditerranéens ont été utilisées pour créer une matrice d'interactions potentielles. Une fois ce « méta-réseau » établi, il a suffi de récupérer les compositions spécifiques observées et prédites grâce aux projections des aires de répartition de chaque cellule (Manuscrit J). Pour chacune des 8154 cellules et chacune des périodes projetées le réseau trophique potentiel en mer Méditerranée a été extrapolé. Différents indices tels que le nombre de liens, la connectance (nombres de liens réalisés en fonction des nombres de liens potentiels connaissant le nombre d'espèces), la vulnérabilité (nombre d'espèces de prédateurs par espèce de proies), la généralité (nombre d'espèces de proies par espèce de prédateurs) ou encore les niveaux trophiques ont été calculés entre les périodes observées et futures (Fig. 35). Pour le calcul des niveaux trophiques les liens entre chaque espèce présente dans l'étude et les producteurs primaires et secondaires ont été pris en compte en créant deux compartiments.

Nous avons constaté qu'une partie importante du plateau continental méditerranéen serait confronté à une diminution du nombre de liens trophiques, de la vulnérabilité et de généralité moyenne, tandis que la connectance et le niveau trophique dans les assemblages de poissons pourraient augmenter d'ici la fin du XXI$^{\text{ème}}$ siècle. Cette augmentation de la connectance est en majorité due à une perte plus lente des liens trophiques réalisés que de la richesse spécifique. En d'autres termes, malgré la perte d'espèces le nombre de liens reste relativement constant.

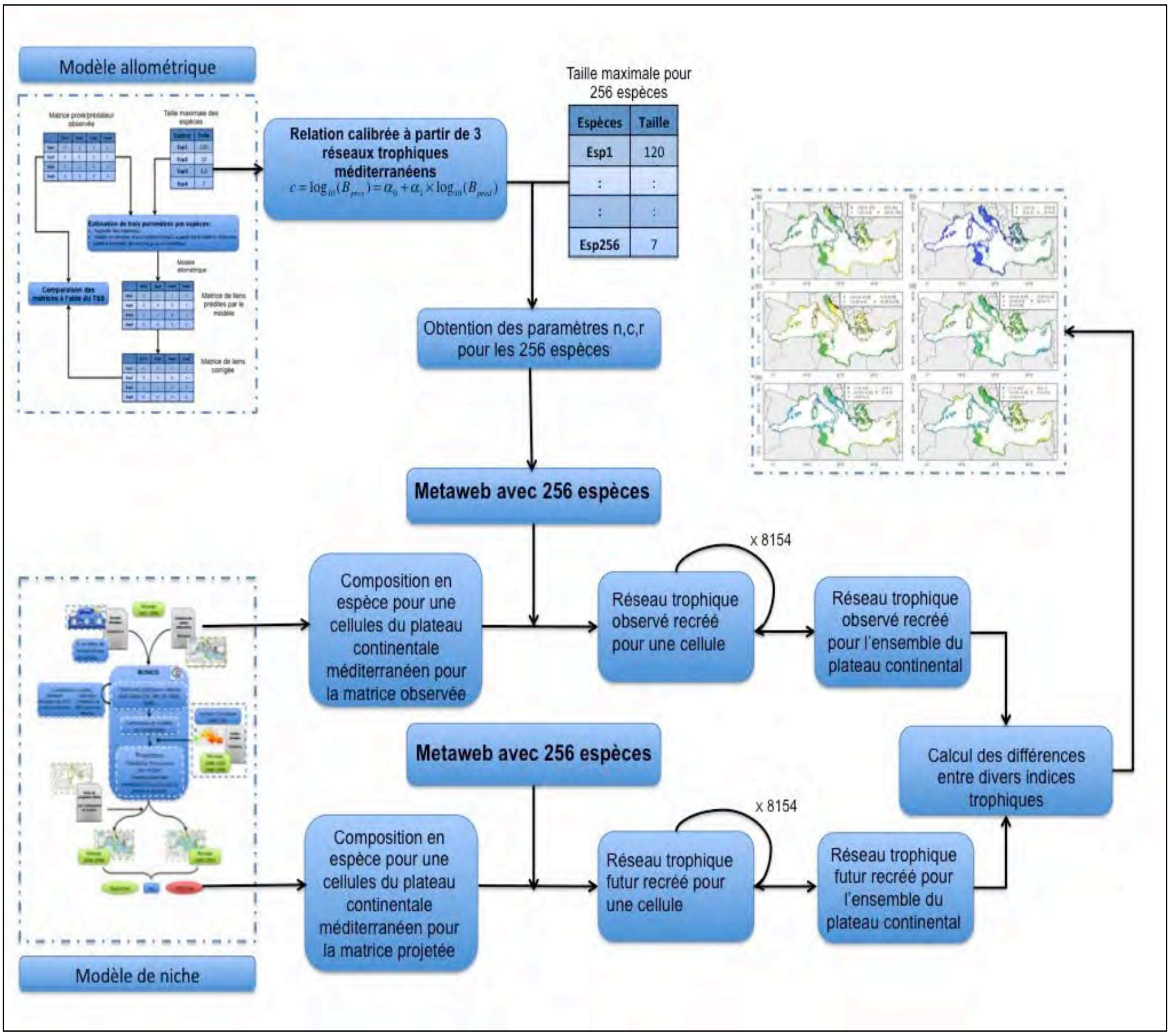


Figure 39 : Représentation schématique des différentes étapes de la modélisation permettant de coupler modèle de niche climatique et modèle de niche trophique en un modèle hybride.

Dans notre étude, le changement climatique conduirait à l'extinction potentielle de 54 espèces et 159 espèces pourraient subir une contraction de leur aire de distribution. Nous avons montré dans un travail précédent que les espèces basales pourraient être plus vulnérables au changement climatique, et pourraient perdre leur aire de répartition géographique plus rapidement que les autres espèces (Albouy et al. 2012b). En considérant ce fait, nous devrions observer une diminution de la connectance. Or ce n'est pas le cas, car cette baisse est pondérée par l'augmentation du nombre des espèces de niveau trophique intermédiaire et par les prédateurs supérieurs. C'est pourquoi une augmentation de connectance en particulier dans la mer Méditerranée occidentale est prédite (Fig. 40c). Selon ces observations, il est logique de prédire une augmentation du niveau trophique moyen parce que les espèces intermédiaires et les prédateurs supérieurs sont généralement de grande taille et que le niveau trophique est lié à la taille (Stergiou & Karpouzi 2001, Romanuk et al. 2011).

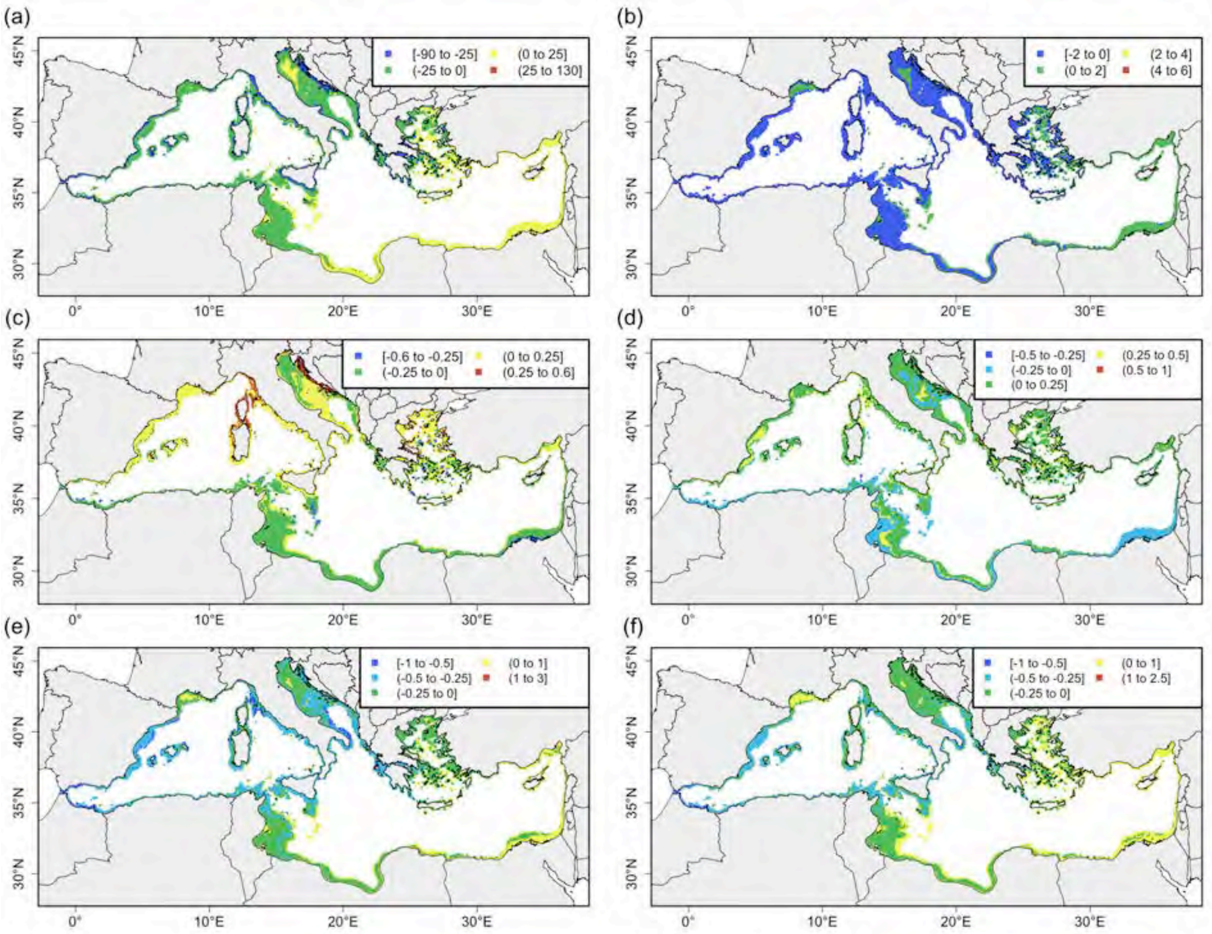


Figure 40 : Les différences de richesse en espèces (a), du nombre de liens (b), de connectance (c), de niveau trophique (d), de généralité (e) et de vulnérabilité (f), prévues sur le plateau continental de la mer Méditerranée pour les assemblages de poissons entre le scénario de référence (1961-1980) et la fin du 21e siècle (2080-2099). Pour une meilleure représentation, nous utilisons le logarithme plus 1 de la différence relative entre les périodes futures et observées.

Cependant, certaines zones de la mer Méditerranée où une augmentation de la richesse spécifique, de la vulnérabilité et de la généralité a été observée, pourraient perdre de la connectance. Cette situation peut se produire suivant deux scénarios possibles. Tout d'abord, les liens trophiques réalisés pourraient augmenter plus rapidement que la richesse spécifique (les nouvelles espèces créent beucoup de liens), comme par exemple dans le bassin Levantin et dans une petite zone de la mer Adriatique. Il est très probablement lié au fait que les grands prédateurs tels que le barracuda (*Sphyraeana viridensis*) ou le mérou d'Haïfa (*Epinephelus haifensis*) vont étendre leur aires de distributions sur la mer Méditerranée (Albouy et al. 2012a) et certaines espèces basales pourraient se déplacer vers le nord en passant par ces zones. Ou bien les liens trophiques réalisés pourraient diminuer plus vite que la richesse en espèces (il y a une arrivée nouvelle espèces mais qui créent moins de liens). Ce scénario est observé dans le golfe de Gabès. Dans ce cas, nous avons observé une augmentation des espèces de niveau trophique supérieur et une diminution des espèces de niveau trophique intermédiaire et basal.

Ce modèle permet donc d’inférer, pour un grand nombre d’espèces, les relations trophique observées et futures et permet d’explorer à large échelle les effets potentiels du changement climatique sur la structure des réseaux trophiques, composante de la biodiversité largement ignorée à ce jour. Cependant il ne permet pas d’inférer la force des liens car il ne prend pas en compte les biomasses des espèces contrairement au modèle OSMOSE. Il ne permet pas non plus d’intégrer certaines caractéristiques des cycles de vie des espèces telles que les migrations journalières ou la reproduction. Les points forts de ce modèle sont la possibilité de l’appliquer à large échelle et le peu de paramètres néccessaires, par conséquent nous envisageons de l’appliquer à l’échelle globale car les données concernant les aires de répartitions commencent à être disponibles.

Chapitre 5 :

Conclusions et perspectives

5.1 Conclusions générales

L'objectif de cette thèse était d'étudier les impacts potentiels du changement climatique sur les assemblages de poissons côtiers méditerranéens en utilisant une approche de modélisation basée sur les niches climatiques et trophiques des espèces (Fig. 41, 42). En préambule, une base de données intégrant des descripteurs de l'ensemble des composantes de la biodiversité a été mise en place. Elle sera mise à disposition de la communauté scientifique et des associations pour la préservation de la nature courant 2013.

Les premières études de ce travail de thèse ont permis de mettre en évidence l'état de la mer Méditerranée tant au niveau des menaces que de la biogéographie de sa biodiversité. Ensuite, les conséquences majeures du changement climatique futur sur les espèces de poissons méditerranéens côtiers ont été projetées grâce à l'implémentation d'un nouveau modèle climatique (NEMOMED8) et de modèles de niche basés sur les enveloppes climatiques. Nous avons mis en évidence l'effet « cul de sac » pour les poissons du nord de la Méditerranée. Les zones les plus froides pourraient dans un premier temps, servir de refuge pour les espèces d'eaux froides ou tempérées, puis avec l'intensification du réchauffement, ces zones pourraient devenir un piège d'où ces mêmes espèces ne pourraient s'échapper avec une disparition progressive de leur niche climatique. Ainsi, d'ici la fin du siècle (*i*) 54 espèces devraient perdre leur niche climatique et seraient en danger d'extinction, (*ii*) la richesse en espèces pourrait diminuer sur 70,4% du plateau continental en particulier en Méditerranée occidentale et en mer Égée, et (*iii*) la taille maximale moyenne des assemblages de poissons pourrait augmenter sur 74,8% du plateau continental. Ce sont en effet les espèces de petite taille, non ciblées par la pêche, qui sont les plus menacées par le changement climatique. D'autres composantes de la biodiversité pourraient aussi être fortement altérées comme la diversité phylogénétique qui diminuerait de 13,6% et la diversité fonctionnelle de 12,6% sur l'ensemble de la mer Méditerranée.

D'un point de vue méthodologie, pour améliorer l'interprétation des modifications de composition d'espèces au sein des assemblages suite au changement climatique nous recommandons de ne plus utiliser le STT, qui est équivalent dans sa formulation à l’indice de Jaccard (Anderson et al. 2011), utilisé en écologie pour quantifier la différence de composition en espèces dans l’espace. En alternative, nous suggérons de considérer les deux composantes complémentaires de l’indice de dissimilarité de Jaccard. La première composante reflète la perte (ou le gain d'espèces) entre deux pas de temps (composante emboîtée), alors que la deuxième composante reflète le remplacement d’espèces indépendamment des différences de richesse entre ces pas de temps (composante de remplacement). Nous suggérons d’analyser conjointement la dynamique en richesse spécifique et les changements dans la composition des assemblages suite aux perturbations et de représenter graphiquement ces deux composantes pour obtenir une vue complète des modifications observées ou attendues dans les assemblages d'espèces. Cette méthode nous a permis d’affiner les conclusions concernant les modifications d’assemblages et s’est avérée efficace pour étudier les processus sous-jacents à l’effet « cul-de-sac » projeté en mer Méditerranée.

Pour étudier la composante trophique de la biodiversité en fonction des pressions de pêche nous avons tout d’abord, au niveau local, modélisé le fonctionnement de l'écosystème de la Réserve Naturelle des Bouches de Bonifacio en établissant les flux entre différents compartiments trophiques (Ecopath) puis nous avons simulé sa dynamique sous différents niveaux de forçage à l’aide du modèle Ecosim. Au niveau régional nous avons établi puis simulé la dynamique des relations trophiques entre quelques espèces sous contrainte anthropique avec le modèle OSMOSE appliqué à l'Adriatique.

L’approche par compartiments trophiques du modèle Ecopath nous révèle, entre autres, que certains groupes peuvent perdre de la biomasse lorsque les AMP sont mises en place ou renforcées, en raison de l’arrêt de la pêche sur leurs prédateurs. Il est donc risqué de se fonder seulement sur une ou deux espèces présentant les mêmes caractéristiques pour évaluer l’état de santé d’une AMP car certains "signaux" peuvent se révéler contre-intuitifs. Malgré leur intérêt, ces deux approches se sont révélées difficilement applicables à large échelle pour étudier les effets du changement global sur un grand nombre d’espèces. Nous avons alors développé une nouvelle méthodologie plus parcimonieuse en paramètres mais reprenant les hypothèses de base du modèle OSMOSE. Au delà de la perte de biodiversité nous avons projeté les modifications attendues dans la structure des réseaux trophiques pour les assemblages de poissons côtiers méditerranéens. Nous avons constaté qu'une partie importante du plateau continental méditerranéen serait confrontée à une diminution du nombre de liens trophiques, de la vulnérabilité (nombre de prédateurs par proie) et de généralité (nombre de proies par prédateur) moyennes des espèces, tandis que la connectance et le niveau trophique dans les assemblages de poissons pourraient augmenter d'ici la fin du XXI^{ème} siècle. Cependant, les gains et les pertes pour ces différents indicateurs trophiques se produiraient de manière hétérogène sur l’ensemble du plateau continental méditerranéen.

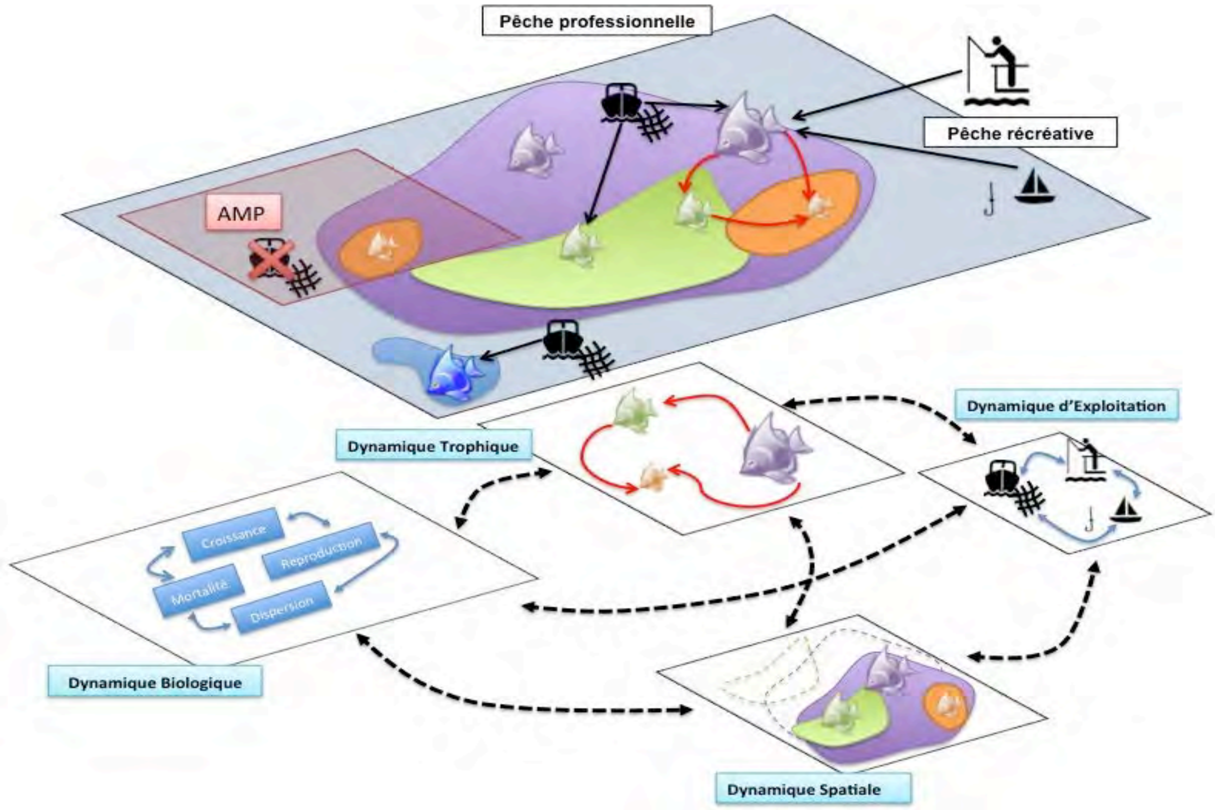


Figure 41 : Schéma représentant la dynamique de l'utilisation d’un littoral méditerranéen. Nous avons quatre espèces de poissons dont les aires de répartitions sont représentées par les surfaces colorées ; en violet une espèce de grande taille avec une aire de répartition importante ; en vert une espèce de taille intermédiaire avec une aire de répartition plus petite ; en orange une espèce de petite taille avec une petit aire de répartition fragmentée ; et en bleu une espèce thermophile de grande taille avec une petite aire de répartition. La pêche professionnelle et récréative sont représentées et ne ciblent pas la plus petite espèce. Une aire marine protégée est représentée en rouge, tout type de pêche y est interdit. Les dynamiques régissant cet écosystème sont représentées et regroupées en quatre types de processus, la dynamique trophique représentant les interactions structurées par la taille entre espèces, la dynamique spatiale prenant en compte les modifications des aires de répartition des espèces, la dynamique d’exploitation illustrant les efforts et les interactions entre les types de pêches et la dynamique biologique illustrant les étapes du cycle de vie des espèces ainsi que leur adaptation au milieu.

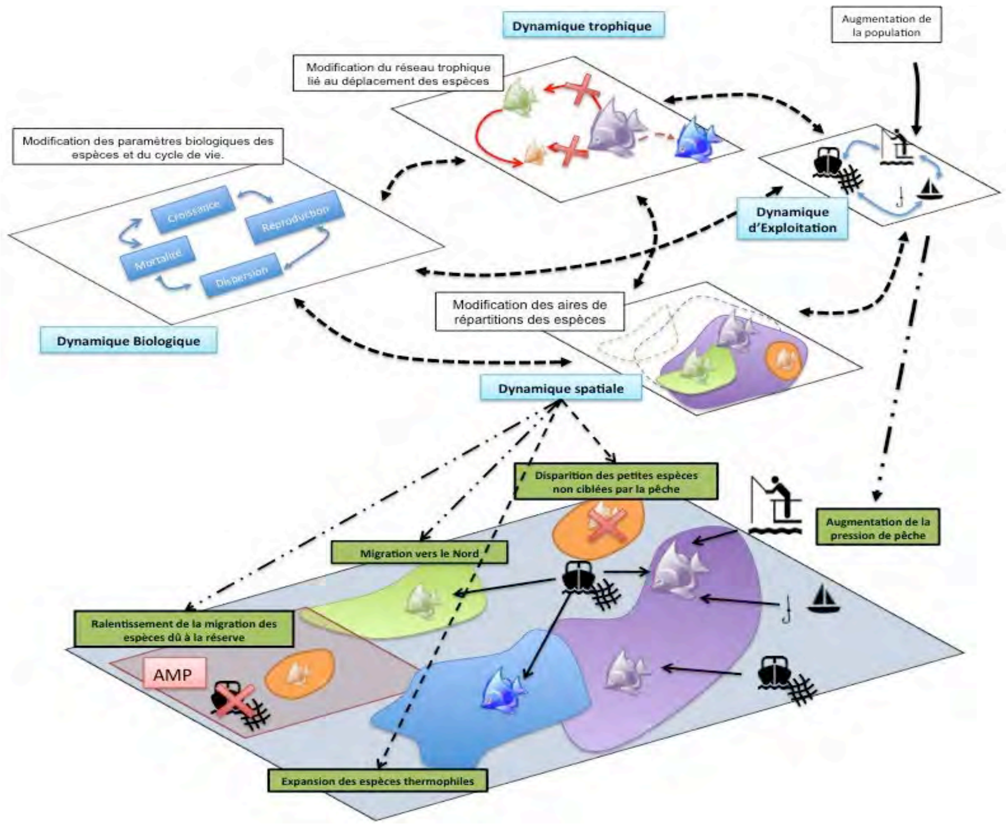


Figure 42 : Effet du changement climatique et de l'augmentation de la pêche sur ce même littoral méditerranéen. Le changement climatique pourrait induire une disparition des espèces non ciblées par la pêche (espèce orange), entraîner une migration des espèces vers le nord (espèce verte) et une expansion des espèces thermophiles (espèce bleue). Ces changements vont entraîner des modifications dans la structure du réseau trophique avec par exemple un nouveau lien créé entre l'espèce violette et bleue, et la disparition du lien entre l'espèce violette et orange. La pêche cible en milieu côtier les espèces de grande taille, le changement climatique les petites espèces. Pour contrebalancer ces effets, les AMP sont des outils de protection efficaces. Le changement climatique peut également agir sur le cycle de vie des espèces comme par exemple en diminuant la durée de vie larvaire, en augmentant le taux de mortalité ou en perturbant les événements de reproduction.

5.2 Perspectives

5.2.1 Intégration d'une troisième dimension : la bathymétrie

Par rapport aux études conduites en milieu continental, l'estimation des niches climatiques des espèces marines est un exercice beaucoup plus difficile car le domaine marin est un habitat tridimensionnel (comme la montagne) mais il est surtout fortement stratifié avec des discontinuités très marquées qui lui sont propres (plateau continental, zone aphotique, etc). La distribution bathymétrique est un élément à considérer lors de la modélisation de la distribution des espèces de poissons marins car différents facteurs environnementaux (température, oxygène) sont susceptibles d'influencer les caractéristiques du milieu à différentes profondeurs (Dambach & Roedder 2011). Cela implique que les espèces marines peuvent réagir au réchauffement de l'eau non seulement par un mouvement horizontal, mais aussi par un mouvement vertical. Cette hypothèse a déjà été vérifiée empiriquement pour les poissons de mer du Nord qui migrent en profondeur, à raison de 3,6 mètres par décade (Dulvy et al. 2008). Ces observations ne sont pas encore intégrées aux modèles car ces derniers ne permettent malheureusement pas de tenir compte de la migration en profondeur.

Comme cela a été récemment discuté par Dambach and Roedder (2011), un cadre de modélisation prometteur consisterait à mettre en place différents modèles d'enveloppes bioclimatiques pour différentes profondeurs, puis à combiner ces modèles afin de prédire la répartition des espèces sur les dimensions à la fois horizontales et verticales (Fig. 43) en combinant les prédictions pour chaque niveau.

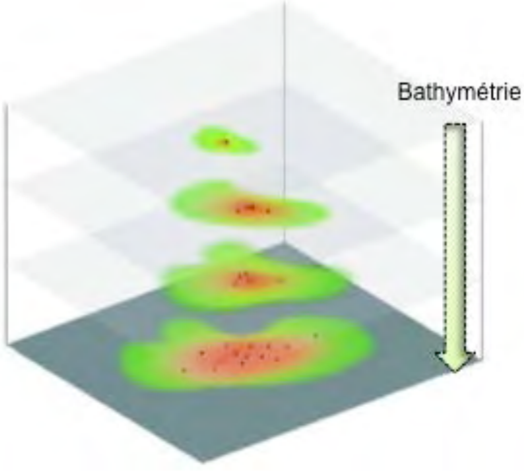


Figure 43 : Combinaison de différents modèles de niche développés pour différentes strates de profondeurs afin de prédire les migrations des espèces marines verticalement et horizontalement en fonction du changement global. Les points noirs représentent les occurrences d'une espèce théorique et les couleurs chaudes les environnements favorables à cette espèce.

Un tel cadre élargi permettra la modélisation des distributions actuelles et futures de l'enveloppe globale des espèces de poissons en Méditerranée, y compris les espèces peuplant le plateau continental (0-200 m), la pente continentale (200-800 m) ou les deux environnements, et celles qui sont confinées dans les habitats d'eau profonde (par exemple les bathypélagiques). Cependant, une telle approche nécessiterait une information de qualité sur les conditions thermiques et les présences des espèces en fonction du gradient de profondeur. Ces données ne sont pas disponibles pour la mer Méditerranée. Nous espérons que l'intérêt croissant pour le partage des données sur la biodiversité aidera au développement d'une modélisation tridimensionnelle pour le domaine marin en Méditerranée et ailleurs.

5.2.2. Intégrer l'incertitude des scénarios climatiques

Dans l'ensemble de cette thèse un seul scénario climatique a été pris en compte, (scénario SRES A2), car il était le seul disponible pour le modèle NEMOMED8 dédié à la mer Méditerranée. Néanmoins, dans un futur proche, S. Somot (URA CNRS & Météo-France) devrait nous fournir les différents scénarios SRES à savoir le B1, B2 et l'éventail des scénarios A1 (voir Encart 1 du Chapitre 1). Ces scénarios permettraient de prendre en compte l'incertitude liée aux scénarios climatiques dans les projections des aires de distributions des espèces et de la dynamique des différentes facettes de la biodiversité en intégrant différentes voies de développement en fonction d'un large éventail de facteurs démographiques.

De plus de nouvelles données climatiques provenant du projet CMPI5 (Coupled Model Intercomparison Project Phase 5) sont en train d'être mises à disposition de la communauté scientifique (Taylor et al. 2012) pour le rapport GIEC AR5 (http://cmip-pcmdi.llnl.gov/cmip5/).

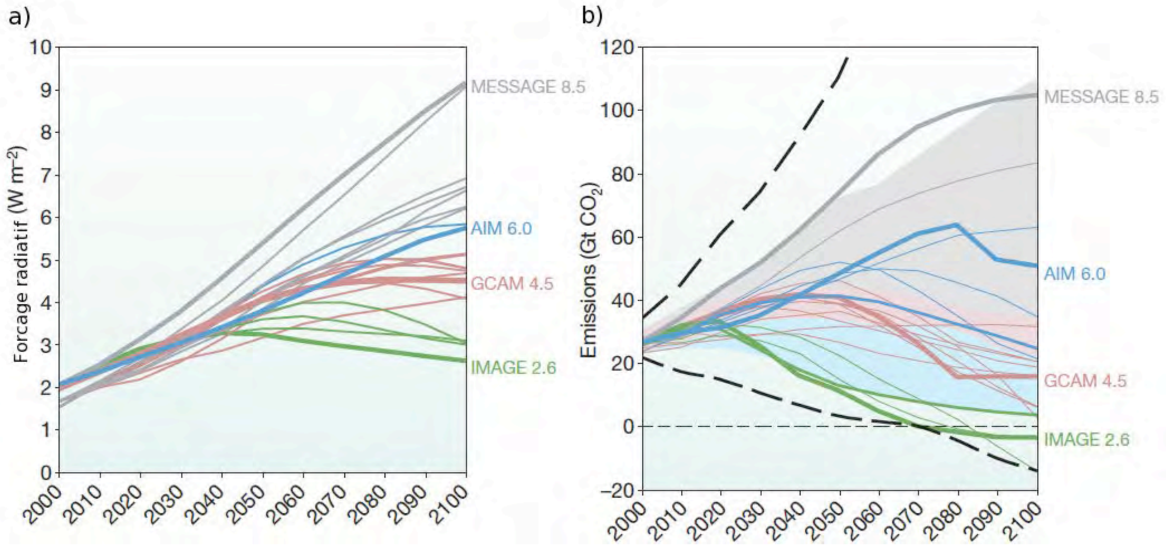


Figure 44 : Représentation des différents scénarios RCP (*Representative Concentration Pathways*), exprimée en forçage radiatif (a) ainsi qu'en émissions de CO_2 (b) en fonction du temps.

Le projet CMIP5 comprend différents types de simulations climatiques, certaines qualifient la capacité des modèles à reproduire le climat présent et passé, et d'autres fournissent des projections climatiques pour différents scénarios de forçage radiatif (Tableau 5, Fig. 44). Les nouveaux scénarios de forçage radiatif prennent en compte la modification de l'équilibre entre le rayonnement entrant et sortant dans l'atmosphère causée par la modification des constituants de l'atmosphère comme par exemple le dioxyde de carbone (Moss et al. 2010).

Tableau 5 : Résumé des caractéristiques des futurs scénarios de changement climatique

Nom du scénario	Forçage radiatif	Concentration en CO2 (p.p.m.)
RCP 8.5	> 8.5 Wm^{-2} en 2100	>1370
RCP 6.0	6 Wm^{-2} stabilisation après 2100	850
RCP 4.5	7.5 Wm^{-2} stabilisation après 2100	650
RCP 2.6	3 Wm^{-2} avant 2100 puis déclin	pic à 490 puis déclin après 2100

Pour ces derniers, le CMIP5 fournit des données de projection de température en fonction des concentrations de gaz à effet de serre, de l'irradiance solaire et d'émissions atmosphériques d'aérosols, répartis en quatre scénarios (RCP26, RCP45, RCP6 et RCP85).

5.2.3. Vers une intégration des processus physiologiques

Les méthodes actuelles de modélisation des aires de répartition des espèces de poissons marins, basées sur la niche thermique, sont généralement corrélatives, et mettent en relation la présence ou l'absence des espèces avec des données de température de surface en mer. L'approche "processus" ou "mécaniste" est encore largement ignorée en écologie marine alors qu'elle émerge fortement en milieu terrestre en intégrant notamment la dynamique des populations (Marion et al. 2012), l'adaptation (Schurr et al. 2012) et la physiologie (Higgins et al. 2012) dans la prédiction des aires de répartition des espèces.

Afin d'améliorer les prédictions des modèles d'enveloppes bioclimatiques, il apparaît pertinent d'intégrer des données physiologiques, obtenues à l'aide d'expérimentation, telles que les seuils de tolérance thermique ou le métabolisme aérobie. Néanmoins obtenir des informations valides et fiables sur la physiologie thermique des poissons serait un processus coûteux. Pour acquérir de tels paramètres, l'expérimentation serait nécessaire sur des populations de poissons sauvages capturés en Méditerranée. En utilisant des techniques de respirométrie (Killen et al. 2011), on pourrait mesurer les capacités maximales de dispersion, la tolérance thermique et le métabolisme aérobie pour différentes températures et concentrations en CO_2 ou bien en combinant les deux facteurs. Ces paramètres sont tous cruciaux pour appréhender la capacité des espèces à coloniser les habitats marins côtiers et pourrait compléter les modèles corrélatifs de niche climatique. En effet, les modèles d'enveloppe bioclimatique déterminent la niche réalisée des espèces, alors que la physiologie nous renseigne sur leur niche potentielle. Si la différence entre ces deux types de niche est très importante, à savoir que la niche potentielle est bien plus large que la niche réalisée, cela montrerait que des espèces pourraient encore s'étendre et s'adapter à des nouvelles conditions et qu'elles sont limitées par la dispersion. Ces données physiologiques pourraient nous fournir également de bons indicateurs de la résistance des espèces au changement climatique et nous permettre de corriger les projections des modèles de niches fondées sur la biogéographie. En somme, un enjeu majeur pour mieux prédire les futures aires de répartition des espèces marines est d'intégrer, dans une même approche, les relations corrélatives avec l'environnement et les processus démographiques, évolutifs et physiologiques (Dormann et al. 2012).

5.2.4. Changement climatique et emplacement des réserves en mer Méditerranée

La mise en place d'aires marines protégées (AMP) est l'un des outils de gestion disponible afin de lutter contre les impacts humains et environnementaux sur les écosystèmes marins côtiers, y compris le changement climatique. De récentes études ont démontré que les espèces sous l'influence du changement climatique vont se déplacer, et par conséquent les réserves actuelles risquent de ne plus être en adéquation avec les aires prioritaires de conservation comme les "points chauds" de biodiversité (Coetzee *et al.* 2009 ; Araujo *et al.* 2011). En effet Micheli et al. (2012) ont mis en évidence que les AMP permettraient d'accroître la résilience des populations marines à une mortalité massive causée par le climat. Ces résultats révèlent que les AMP peuvent ralentir les effets négatifs de changements environnementaux globaux en augmentant la résistance et le rétablissement des populations localement. *A contrario*, les zones fortement exploitées favoriseraient les effets du changement climatique en augmentant la sensibilité des populations de poissons (Hsieh et al. 2008). L'enjeu est donc d'optimiser l'emplacement des futurs AMP afin de contrer les effets du changement climatique sur le bouleversement des assemblages d'espèces.

Pour déterminer les zones présentant le taux de changement potentiel le plus important il est essentiel d'identifier les zones d'interface, correspondant souvent à des discontinuités de température (Ben Rais Lasram et al. 2009), où les assemblages sont les plus hétérogènes sur de faibles surfaces. En effet, les changements majeurs dus au réchauffement climatique devraient se concentrer dans ces zones de forte diversité β (McKnight et al. 2007). Il s'agirait donc de cartographier la diversité β en Méditerranée pour y favoriser la mise en place de protection renforcée car ce sont des zones sentinelles pour la modification des assemblages.

Plus globalement, à ce jour, aucune étude montrant l'efficacité du système d'AMP vis à vis des différentes composantes de la biodiversité n'a été entreprise. Dans un premier temps il s'agirait de réaliser une « gap analysis », méthode permettant de déterminer le degré de protection fourni par ces AMP vis-à-vis de l'ensemble de la biodiversité ichtyologique, c'est-à-dire le degré de couverture de l'ensemble des espèces. Dans le but de construire un réseau efficace répondant au critère de la CBD (10% de la mer Méditerranée protégée en 2020) et incluant les potentiels changements d'aires de répartitions des espèces nous proposons de réaliser une « gap analysis » pour les périodes 2050 et 2100 afin d'estimer l'efficacité futur du réseau d'AMP sous forçage du changement climatique sur la biodiversité. Une fois ce travail d'évaluation réalisé, il parait important de mettre en place une stratégie de « conservation planning » (planification de la conservation) pour identifier les zones candidates pour installer de nouvelles réserves en tenant compte de l'ensemble des composantes de la biodiversité, des activités humaines, et du changement climatique. Il serait important de prendre également en compte les zones où la diversité b est importante, mais aussi de considérer comment la connectivité entre les réserves pourrait être intégrée dans une approche multicritère pour hiérarchiser les zones à protéger en Méditerranée. Cette thématique est actuellement "portée" par François Guilhaumon, nouvellement recruté à l'IRD dans notre laboratoire, et j'espère y jouer un rôle important au même titre que nombreux chercheurs impliqués dans ECOSYM mais aussi à l'international à travers des projets ambitieux.

5.2.5. Limites et perspectives de la modélisation des relations trophiques

Au cours de cette thèse, en collaboration avec Dominique Gravel, nous avons développé un outil capable d'inférer les réseaux trophiques à partir de la taille des espèces et de simples règles d'interactions comme la co-occurrence des espèces. Nous avons appliqué cet outil à une base de données sur la mer Méditerranée (Albouy et al. 2012a) et recréé les réseaux trophiques actuels et futurs pour des cellules d'environ 100 km^2.

La principale limitation de notre approche est l'utilisation de la taille maximale pour estimer les interactions trophiques, sans tenir compte des changements de régime alimentaire au cours du développement ontogénique. Cela revient à ne considérer que les stades matures des individus dans l'écosystème alors que la prédation intervient aux différents stades de vie et influence largement la dynamique des populations. Par exemple, certaines relations proie-prédateur pourraient être inversées au cour du temps pour une espèce donnée. En mer Méditerranée, les adultes de *Merlangius merlangus* mesurant 75 cm consomment les juvéniles de *Merluccius merluccius* (Froese & Pauly 2012). A l'âge adulte, *Merluccius merluccius* (110 cm) se nourrit de jeunes *Merlangius merlangus*.

Afin de prendre en compte ces modifications ontogéniques nous pourrions introduire un nouveau paramètre dans le modèle de structure trophique basé sur la taille des individus. Pour ce faire, il faudrait considérer plusieurs compartiments pour les différents stades de vie d'une même espèce et ainsi augmenter la taille du « méta-réseau » dont les objets en interaction ne seraient plus simplement des espèces mais des stades de vie des espèces. Une autre limitation est l'intégration de la pression anthropique comme la pêche, qui a des impacts importants sur les réseaux trophiques (Lotze et al. 2011). La prochaine étape de notre approche serait l'intégration conjointe du changement climatique et de la pêche dans un modèle afin de déterminer la nature de l'interaction entre ces deux perturbations (effets additifs, synergiques ou antagonistes) et les conséquences sur la structure des réseaux trophiques. Ce type d'approche intégrée a déjà été conduite en mer du Nord (Kirby & Beaugrand 2009) et à l'échelle globale (Cheung et al. 2010) mais les prédictions à l'échelle globale ne sont pas encore faites pour simuler le fonctionnement des écosystèmes sous contraintes.

J'aimerais jouer un rôle dans ce nouveau champ d'investigation en analysant la réponse de la structure et le fonctionnement des assemblages de poissons pélagiques des grands biomes sous forçage climatique. Pour réaliser un tel objectif les étapes suivantes seraient nécessaires : (*i*) compiler des données de distribution (présence) et de taille corporelle des poissons à l'échelle globale à partir de bases de données publiques telles que Aquamap ou Fishbase; (*ii*) compiler des données climatiques fondées sur les prochaines prévisions du GIEC; (*iii*) prendre en compte de l'incertitude dans les projections en utilisant différents modèles climatiques implémentés avec des scénarios distincts; et (i*v*) développer d'une méthode pour lier le changement de structure au sein des réseaux trophiques au fonctionnement de l’écosystème. Cette dernière étape est la plus délicate et requiert un fort investissement en écologie théorique qui fera l'objet de mon post-doctorat.

L'approche que nous avons développée ici ne se limite pas aux poissons et pourrait être utile pour une variété d’écosystèmes où les relations interspécifiques sont structurées par la taille. Cette méthode est flexible et pourrait également être appliquée dans des contextes où les interactions peuvent être déduites à partir des traits fonctionnels individuels autres que la taille. Par exemple, la topologie des réseaux d'interactions complexes tels que les intéractions plantes-pollinisateurs peut être prédite à partir d'un petit ensemble de traits notamment les attributs permettant au pollinisateur d'atteindre le nectar des plantes (Santamaria & Rodriguez-Girones 2007).

5.2.6.Prise en compte des espèces envahissantes

Le dernier inconvénient de notre étude est la non-intégration des espèces envahissantes provenant de l'océan Atlantique et de la mer Rouge qui pourraient modifier les structures trophiques (Ben Rais Lasram et al. 2008). Il est très délicat de modéliser la distribution future pour ces espèces qui sont actuellement loin de l'équilibre, ce qui constitue une hypothèse fondatrice des modèles corrélatifs de distribution d'espèces (Thuiller 2004, Gallien et al. 2012). Il existe cependant des méthodes basées sur la présence actuelle des espèces telles que l’ENFA (Ecological-Niche Factor Analysis) ou Maxent (Maximum entropy modeling of species geographic distributions) permettant, à partir de variables abiotiques, de prédire les zones où ces espèces pourraient s’implanter. Cependant les données d’occurrences des espèces envahissantes dans leurs aires de répartition d’origine ne sont pas disponibles tandis que grâce au CIESM nous connaissons leurs évolutions en mer Méditerranée. Les aires des espèces dans leur milieu d’origine, mer Rouge ou Atlantique, pourrait permettre une meilleur anticipation de leur future évolution en mer Méditerranée mais les changements de niche à la faveur des introductions constitue encore un frein majeur aux prédictions (Broennimann et al. 2007).

Dans une seconde étape, le but serait d'anticiper le rôle de ces espèces envahissantes et les modifications qu'elles pourraient apporter dans le fonctionnement des écosystèmes côtiers. Notre approche de modélisation des interactions trophiques permettraient l'anticipation des liens trophiques potentiels que ces espèces pourraient effectuer en fonction de leur taille corporelle maximale, de leur probabilité d'occurrence, et leurs distributions bathymétriques.

Par conséquent, notre approche de modélisation trophique permettrait de tester l'impact potentiel d'une espèce ou un groupe d'espèces exotique et d'analyser leurs liens trophiques potentiels au sein d'assemblages d'espèces natives.

5.2.7. Prise en compte des abondances

Une étude récente fondée sur une série détaillée d'enquêtes biologiques comprenant plus de 100 millions de poissons de 177 espèces, et couvrant une superficie de plus d'un million de kilomètres carrés, démontre que lorsque les données sont réduites à la présence ou l'absence d'espèces, les modèles d'enveloppes climatiques pourraient masquer d'importants changements dans l'abondance sous l'influence du changement global (Simpson et al. 2011). Les prévisions de ces variations d'abondances futures ont une grande valeur écologique et économique. Néanmoins, obtenir des prédictions de biomasse fiables reste difficile à large échelle même en utilisant des données scientifiques. Une piste pour la mer Méditerranée est un programme européen regroupant plusieurs pays réalisant des pêches scientifiques dans le but d'estimer les abondances d'une trentaine d'espèces de poissons. Si les données brutes de ces campagnes scientifiques étaient facilement accessibles et utilisables, des modèles d'enveloppes bioclimatiques intégrant les abondances pourraient probablement être mis en place. Par conséquent le modèle trophique allométrique ne serait plus seulement basé sur les présences-absences des espèces mais sur les biomasses ce qui permettrait d'inférer les flux trophiques entre espèces. Il serait ainsi possible de tester l'influence du changement climatique sur la force des liens reliant les espèces. Cependant, ces propos doivent être modérés par le fait qu'il est difficile d'estimer à large échelle les biomasses des espèces à partir des campagnes scientifiques. Là encore, l'outil de modélisation sera nécessaire tout comme les théories de la macroécologie notamment celle couplant l'aire de répartition d'une espèce et son abondance locale ou les relations allométriques permettant d'inférer les productions de plusieurs niveaux trophiques à partir des flux. Par exemple Cheung et al. (2008) estiment de manière robuste la biomasse pêchée des espèces à partir de la production primaire dans leurs aires de répartition. Ils estiment aussi la diminution de taille des espèces suite au changement global à partir de relations allométriques et énergétiques (Cheung et al. 2012). Ce champ de recherche n'en est qu'à ses prémices et des verrous méthodologiques doivent encore être levés pour aboutir à une véritable biogéographie prédictive du fonctionnement des écosystèmes.

5.2.8 Vers l'utilisation de modèles hybrides en écologie prédictive

Fournir des modèles prédictifs fiables de la dynamique de la biodiversité face aux changements globaux est probablement l'un des plus grand défis auquel est confrontée la recherche en écologie. Pour cela il faut développer et intégrer dans un cadre de modélisation parcimonieux les processus démographiques de base, les interactions biotiques, le potentiel évolutif et adaptatif des espèces, les différents scénarios du réchauffement climatique et les conséquences humaines de l'exploitation de la nature. Pour atteindre de tels objectifs, l'acquisition de connaissances dans différentes disciplines telles que la biogéographie, la biologie évolutive, l'écologie des communautés, l'écologie trophique, la physique du climat, et les sciences sociales est nécessaire. Nous devons nous préparer, pour mieux inférer la dynamique de la biodiversité marine aux larges échelles, à la mise en place de modèles hybrides (Dullinger et al. 2012) intégrant, dans un même modèle ou dans une suite de modèles imbriqués, (*i*) la niche environnementale des espèces grâce aux modèles d'enveloppe bioclimatique, (*ii*) leurs capacités de dispersion à l'aide par exemple de modèles de dispersion larvaire issus de la biophysique ou de la génétique (*iii*) l'adaptation notamment physiologique à l'aide de modèles génétiques, (*iv*) la dynamique des populations en interactions à l'aide de modèles de type Lotka et Voltera, (*v*) les liens trophiques au sein des assemblages à partir de modèles trophiques comme celui développé dans cette thèse (Chapitre 4). Cette chaîne de modélisations devra être également intégrée dans un ensemble tridimensionnel caractérisant l'environnement marin.

L'enjeu reste aussi d'appliquer ces outils aux micro-organismes qui restent largement ignorés des prédictions à large échelle (mais voir ; Beaugrand et al. 2003). Malgré ses limites, cette deuxième génération de modèles de biodiversité devrait ouvrir la voie à une écologie prédictive plus intégrative des processus biologiques et donc capable de tenir compte des interactions entre les espèces et les réponses évolutives. C'est la voie que je vais tenter de suivre lors de mes prochaines années en recherche.

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Publications et manuscrits

Manuscrit A.

The Mediterranean Sea under siege: spatial overlap between marine biodiversity, cumulative threats and marine reserves

Manuscrit B.

Protected and threatened components of fish biodiversity in the Mediterranean Sea

Manuscrit C.

The Mediterranean Sea as a “cul-de-sac” for endemic fishes facing climate change

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Projected climate change and the changing biogeography of coastal Mediterranean fishes

Manuscrit E.

Beyond species loss: functional and phylogenetic diversity erosion under climate change in the Mediterranean Sea.

Manuscrit F.

Combining projected changes in species richness and composition reveals climate change impacts on coastal Mediterranean fish assemblages.

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Predicting trophic guild and diet overlap from traits: statistics, opportunities and limitations for marine ecology.

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Inferring food web structure from predator-prey body size relationships.

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From the spatial redistribution of species to changes in food web structure under climate change

Manuscrit A.

The Mediterranean Sea under siege: spatial overlap between marine biodiversity, cumulative threats and marine reserves.

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Global Ecology and Biogeography, (Global Ecol. Biogeogr.) (2012) **21**, 465–480

Global Ecology and Biogeography
A Journal of Macroecology

RESEARCH PAPER

The Mediterranean Sea under siege: spatial overlap between marine biodiversity, cumulative threats and marine reserves

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ABSTRACT

Aim A large body of knowledge exists on individual anthropogenic threats that have an impact on marine biodiversity in the Mediterranean Sea, although we know little about how these threats accumulate and interact to affect marine species and ecosystems. In this context, we aimed to identify the main areas where the interaction between marine biodiversity and threats is more pronounced and to assess their spatial overlap with current marine protected areas in the Mediterranean.

Location Mediterranean Sea.

Methods We first identified areas of high biodiversity of marine mammals, marine turtles, seabirds, fishes and commercial or well-documented invertebrates. We mapped potential areas of high threat where multiple threats are occurring simultaneously. Finally we quantified the areas of conservation concern for biodiversity by looking at the spatial overlap between high biodiversity and high cumulative threats, and we assessed the overlap with protected areas.

Results Our results show that areas with high marine biodiversity in the Mediterranean Sea are mainly located along the central and north shores, with lower values in the south-eastern regions. Areas of potential high cumulative threats are widespread in both the western and eastern basins, with fewer areas located in the south-eastern region. The interaction between areas of high biodiversity and threats for invertebrates, fishes and large animals in general (including large fishes, marine mammals, marine turtles and seabirds) is concentrated in the coastal areas of Spain, Gulf of Lions, north-eastern Ligurian Sea, Adriatic Sea, Aegean Sea, south-eastern Turkey and regions surrounding the Nile Delta and north-west African coasts. Areas of concern are larger for marine mammal and seabird species.

Main conclusions These areas may represent good candidates for further research, management and protection activities, since there is only a maximum 2% overlap between existing marine protected areas (which cover 5% of the Mediterranean Sea) and our predicted areas of conservation concern for biodiversity.

Keywords

Cumulative impacts, human threats, marine biodiversity, marine conservation, marine protected areas, Mediterranean Sea.

DOI: 10.1111/j.1466-8238.2011.00697.x
http://wileyonlinelibrary.com/journal/geb

INTRODUCTION

The Mediterranean Sea is the largest and deepest enclosed sea on earth. Located between Africa, Europe and Asia, it is a hotspot of terrestrial and marine biodiversity (Bianchi & Morri, 2000; Myers *et al.*, 2000; Coll *et al.*, 2010). Currently it is known to host more than 17,000 described marine species and contributes an estimated 7% to the world's marine biodiversity, including high percentages of endemic species (Coll *et al.*, 2010). Emblematic species of conservation concern, such as the bluefin tuna, *Thunnus thynnus*, and the Mediterranean monk seal, *Monachus monachus* (e.g. Groombridge, 1990; Reijnders *et al.*, 1997; Bearzi *et al.*, 2004; Mackenzie *et al.*, 2009), as well as several unique, endangered and sensitive habitats, such as the seagrass meadows of the endemic *Posidonia oceanica* (e.g. Blondel & Aronson, 2005; Ballesteros, 2006; IUCN-Med, 2009), occur in the basin.

This rich ecosystem has been altered in many ways throughout its history. Temporal trends indicate that overexploitation and habitat loss are the main human drivers of historical changes (Lotze *et al.*, 2011). However, since the Industrial Revolution and ensuing improvements in technology and a human population explosion, these pressures have grown exponentially (Coll *et al.*, 2010; Lotze *et al.*, 2011). At present, habitat loss and degradation, as well as extraction, pollution, eutrophication and the introduction of alien species, and recently climate change, are the most important threats that affect the greatest number of taxonomic groups occurring in the Mediterranean Sea (Coll *et al.*, 2010; Costello *et al.*, 2010).

Within the context of high biodiversity and high impacts of human activities, there is a need to move towards a fine-scale analysis of spatial congruencies between the cumulative impact of multiple threats and marine biodiversity across taxa in order to identify critical areas and thus future conservation needs. Anthropogenic pressures on marine ecosystems in the Mediterranean Sea are predicted to increase in the future (Coll *et al.*, 2010), especially those posed by climate change, habitat degradation and exploitation, as they may do world-wide (Butchart *et al.*, 2010). Though a large body of knowledge exists on these impacts on Mediterranean marine resources (e.g. Galil, 2000; Danovaro, 2003; Bianchi, 2007; Tsounis *et al.*, 2007; Abdulla & Linden, 2008; Stergiou *et al.*, 2009; Coll *et al.*, 2010; Lasram *et al.*, 2010, and references therein), little is known about their cumulative effects and their synergistic impact on marine species, communities and ecosystems. This limits environmental analyses, which usually consider few anthropogenic threats, and which may therefore lack realism, especially in highly affected areas such as the Mediterranean Sea (Costello *et al.*, 2010).

In the Mediterranean Sea, similarly to most of coastal ecosystems across the world, marine protected areas (MPAs) have become the primary tool for *in situ* habitat and biodiversity conservation with more than 100 MPAs that cover approximately 5% of the continental shelf (Abdulla *et al.*, 2008; MEDPAN, 2010). In addition, there is a growing consensus that MPAs protect the structure and function of ecosystems (Mouillot *et al.*, 2008; Libralato *et al.*, 2010) and rebuild and sustain fisheries (Russ *et al.*, 2004), particularly artisanal fisheries in the Mediterranean (Forcada *et al.*, 2009). However, Mediterranean MPAs have been set up following local sociopolitical decisions instead of ecological considerations (Francour *et al.*, 2001; García-Charton *et al.*, 2008) and the ability of this MPA network to protect most of the marine biodiversity from multiple threats is still unknown. A move towards sustainable management and planning requires spatial mapping of human impacts and protection efforts to assess their overlap with marine biodiversity. Similar initiatives have been developed in other regional seas (e.g. Selkoe *et al.*, 2009; Benn *et al.*, 2010) and at global scales (Halpern *et al.*, 2008) analysing the overlap between cumulative threats and marine ecosystems, or between MPA networks and marine biodiversity (Hamilton *et al.*, 2010).

Under an ecosystem-based approach, there is an increasing need to manage resources while ensuring their sustainable use. At the same time, regional, national and European agencies call for a better understanding of the impact of human activities on marine ecosystems. Therefore, quantifying biodiversity patterns in and threats to the biologically rich Mediterranean Sea is a major step forward in determining the possible responses of its ecosystems to anthropogenic impacts and global change.

In this context, our work had the aim of: (1) identifying the principal areas of conservation concern in the Mediterranean Sea, where interaction between marine biodiversity and threats may be more pronounced, and (2) quantifying the overlap between these areas and current protected sites. Firstly, we identified areas of high biodiversity in the Mediterranean Sea using available information on species distribution of marine mammals, marine turtles, seabirds, fishes and commercial or well-documented invertebrates (henceforth simply called 'invertebrates'). Secondly, we mapped potential areas of high anthropogenic threats where several such threats occur simultaneously. Finally, we quantified the areas of high conservation concern for biodiversity by looking at how biodiversity-rich areas spatially overlap with those of high cumulative threats, and with those currently protected.

MATERIALS AND METHODS

The Mediterranean Sea

The Mediterranean Sea has narrow continental shelves and a large area of open water (Fig. 1). It covers approximately 2,500,000 km^2 (excluding the Black Sea) with an average depth of 1460 m and a maximum of 5267 m. The Mediterranean Sea connects through the Strait of Gibraltar to the Atlantic Ocean in the west, and through the Strait of Bosphorus to the Sea of Marmara and the Black Sea in the north-east, while in the south-east the Suez Canal links the Mediterranean to the Red Sea and the Indian Ocean. The Strait of Sicily divides the sea into two distinct basins, the western (0.85 million km^2) and the eastern (1.65 million km^2).

General oceanographic conditions in the Mediterranean Basin have been previously described in detail (e.g. Hopkins,

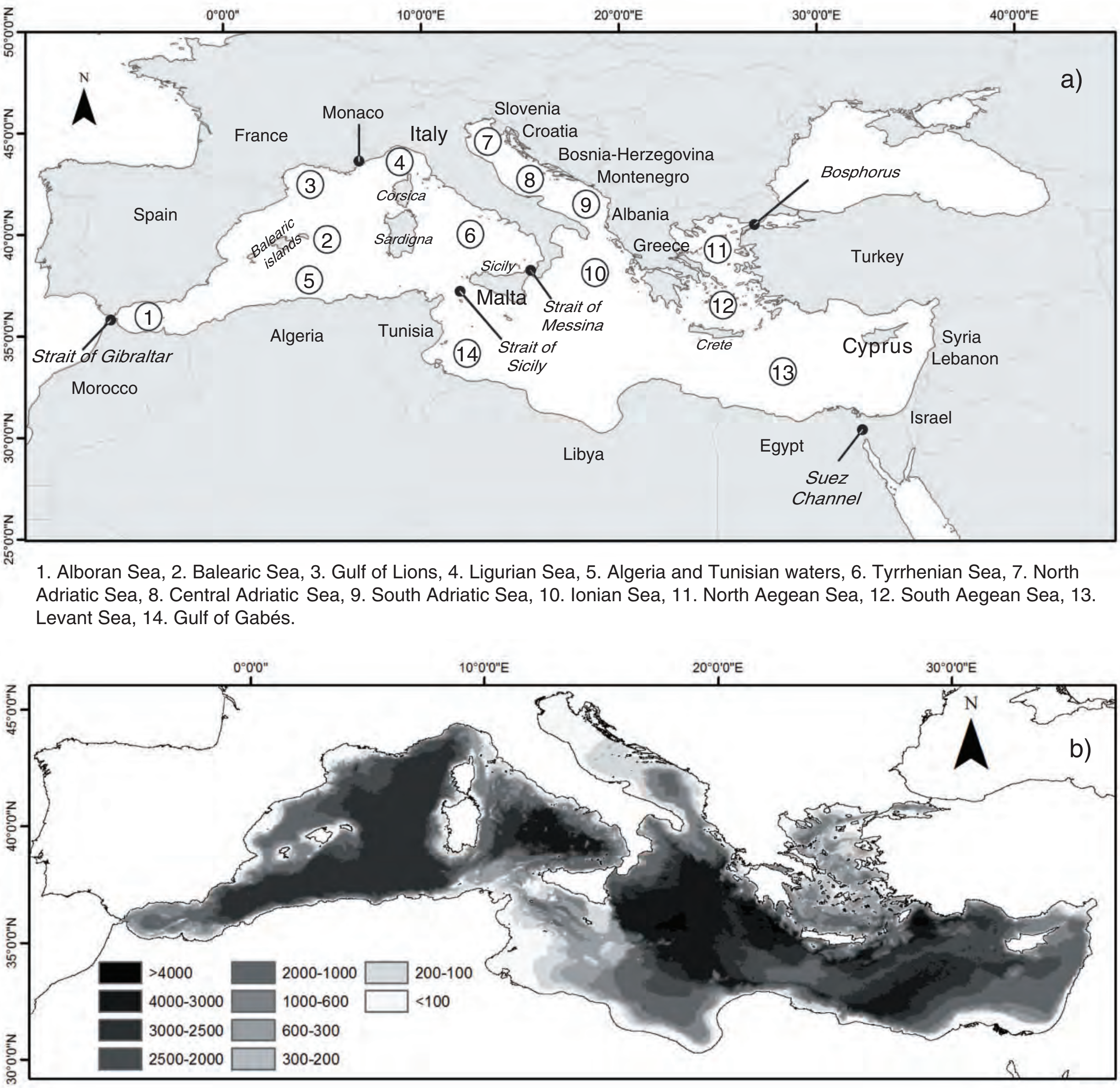

Figure 1 The Mediterranean Sea: (a) main biogeographic regions, basins and administrative divisions, and (b) maximum average depth (m).

1985; Pinardi *et al.*, 2006). The basin is characterized by strong environmental gradients making the eastern end more oligotrophic than the western end. Local features enrich coastal areas through changing wind conditions, temporal thermoclines, currents and river discharges and municipal sewage (Estrada, 1996; Bosc *et al.*, 2004). The annual mean sea surface temperature shows a high seasonality and important gradients from west to east and north to south (Hopkins, 1985). The biological production decreases from north to south and west to east and is inversely related to the increase in temperature and salinity (Danovaro *et al.*, 1999). This illustrates that the Mediterranean Sea is highly heterogeneous.

Mapping marine biodiversity

We collected available data on species diversity distribution of marine mammals, marine turtles, seabirds, fishes and invertebrates (data modified from Coll *et al.*, 2010) to identify areas of high species biodiversity (Table 1). Also, we mapped the distribution of large predators (species that are likely to have predator roles due to their body size and trophic behaviour) using the information from large fishes, marine mammals and turtles, and seabirds. Species included in the above-mentioned groupings and data sources are listed in Appendix S1 in the Supporting Information. This information is also now freely available

Table 1 Information used to map marine biodiversity in the Mediterranean Sea. The resolution of all data sets was 0.1° latitude by 0.1° longitude. Further information in Appendix S1.

Biodiversity	Number of species	Description	Time frame	Sources
Fish species	625	Main fish species	1990s	Lasram *et al.* (2009), Lasram & Mouillot (2009), Coll *et al.* (2010)
Marine mammals	9	Resident	1990s–2000s	Coll *et al.* (2010)
Marine turtles	3	Resident	1990s–2000s	Coll *et al.* (2010)
Seabirds	19	Breeding and non-breeding	1990s–2000s	Sea Around Us project database
Invertebrates	50	Commercial or well-studied	1950s–2000s	Sea Around Us project and FAO databases (Appendix S1)
Large predators	80	Predatory fish, marine mammals, turtles and seabirds	1990s–2000s	Lasram *et al.* (2009), Lasram & Mouillot (2009), Coll *et al.* (2010), Sea Around Us database

through SeaLifeBase (http://www.sealifebase.org; Palomares & Pauly, 2010), FishBase (http://www.fishbase.org; Froese & Pauly, 2010) and through the Sea Around Us project website (http://www.seaaroundus.org; Pauly, 2007)[1].

We used the above detailed spatial data, mostly available in the form of expert-drawn maps or sighting locations, to map spatial patterns of invertebrate and vertebrate species using geographical information system (GIS) software (ArcGIS v.9.3, Environmental Systems Research Institute). Following the methodology by Coll *et al.* (2010), we estimated species richness of different species groupings as the sum of the species co-occurring by overlapping distribution maps at fine-scale resolution (0.1° × 0.1° grid cells).

With the above information, we defined and mapped five species groupings: (1) invertebrates, (2) fishes, (3) marine mammals and marine turtles, (4) seabirds, and (5) large predators; we re-expressed known occurrences in relative terms between 0 (no species present) and 1 (100% of species present). Marine mammals and marine turtles were grouped together due to the low species diversity of marine turtles residing in the Mediterranean Sea (Groombridge, 1990).

Cumulative anthropogenic threats

We gathered from a variety of sources the available data on 18 direct and indirect anthropogenic threats in the Mediterranean Sea (Table 2). We considered all those human activities with available data documenting both direct and indirect impacts on marine species (Coll *et al.*, 2010). Specific information on sources and analysis for developing threat layers is provided in Appendix S2.

With the above data on threats, we created six layers of potential cumulative anthropogenic threats (Table 2):

1. Coastal-based impacts: cumulative effects from inorganic and organic coastal pollution, nutrient runoff and hypoxia, aquaculture activities and the presence of invasive species.

2. Trawling and dredging disturbance: cumulative (historical to present) high disturbance on the sea floor by bottom fishing gear operations (from 1950 to 2006).

3. Ocean-based pollution: cumulative effects from shipments of toxic substances (e.g. toxic waste, radioactive waste and fertilizers) and other ocean-based pollution from shipping traffic, deposition of heavy metals and inorganic nitrogen.

4. Exploitation of marine resources by fisheries: information relative to recent industrial or semi-industrial demersal and pelagic catches (both including low and high by-catch, and low or high habitat modification) and artisanal fisheries.

5. Maritime activities: cumulative effects from maritime traffic due to shipping and other transport and the presence of oil rigs.

6. Climate change: cumulative effects from changes in sea water temperature, in the intensity of ultraviolet radiation and in water acidification.

We used ArcGIS 9.3 software and a 0.1° × 0.1° grid cell resolution to map patterns of anthropogenic impacts and estimate the presence or absence of each threat to create cumulative threat layers (or threat models). Each continuous threat was first log(x + 1)-transformed and then normalized (expressed between 0 and 1) in order to compare the intensity of threats.

For each species biodiversity grouping, i.e. invertebrates, fishes, marine mammals and turtles, seabirds and large predators, we built a spatial cumulative threat model (equation 1 below) equal to a weighted sum of each of the six cumulative threat layers (Table 2). Vulnerability weights (Table 3) applied to each threat layer were estimated using published data on specific taxa and expert opinions (Coll *et al.*, 2010). Specifically, experts involved in the previous study were asked to rank main threats affecting the diversity of species groupings under their expertise using data available to them and personal experience. The threats were ranked from 0 to 5, taking into account the relative importance of each threat to biodiversity (i.e. 0 no importance, 5 highest in importance). The original scores are available elsewhere (Coll *et al.*, 2010) and Table 3 presents the relative weights of individual threats for different species groupings used in this study.

Each cumulative threat model (T_L) for each species biodiversity grouping (i) was expressed as a weighted average of individual threats ($T_{L,i}$):

$$T_{L,i} = \sum_{n=1}^{N} (L_n \cdot w_n) \qquad (1)$$

where L_n is the nth threat layer, w_n is the weight of layer L_n and $N = 6$ is the number of the threat layer (1, coastal-based impacts;

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[1] This information is available under Mediterranean LME: ecosystems information.

Table 2 Information used to map cumulative anthropogenic threats to marine biodiversity in the Mediterranean Sea.

Threat layers	Description & combined sub-layers	Resolution (degrees)	Time frame	Sources
1. Coastal-based impacts	Inorganic pollution (non-point, urban runoff)	0.5 × 0.5	2000–01	Halpern *et al.* (2008)
	Organic pollution (non-point, pesticides)	0.5 × 0.5	1992–2001	
	Nutrients (fertilizers)	0.5 × 0.5	1993–2002	
	Hypoxia sites	0.1 × 0.1	1990s–2000s	Diaz & Rosenberg (2008)
	Invasive species (fish species)	0.1 × 0.1	1990s	Lasram *et al.* (2009), Lasram & Mouillot (2009)
	Fish and shellfish aquaculture (location and nature of pens)	0.1 × 0.1	2004–06	P. Trujillo, *et al.*, submitted (Appendix S2)
2. Trawling and dredging disturbance	Benthic disturbance from fishing	0.5 × 0.5	1950–2006	Sea Around Us project database
3. Ocean-based pollution	Poison shipments	0.1 × 0.1	1979–2001	In.fondo.al.mar (2010)
	Ocean-based pollution (from shipping traffic and port data)	0.5 × 0.5	1999–2005	Halpern *et al.* (2008)
	Deposition of heavy metals (Cd, Pb, Hg)	0.1 × 0.1	2007	Ilyin *et al.* (2009)
	Inorganic nitrogen deposition	0.5 × 0.5	2000	Dentener *et al.* (2006)
4. Exploitation of marine resources by fisheries	Demersal and pelagic high and low by-catch and high and low habitat modification	0.5 × 0.5	2000–06	Watson *et al.* (2006a, b)
	Artisanal fishing	0.5 × 0.5	1999–2003	Sea Around Us project database
5. Maritime activities	Commercial shipping lanes	0.5 × 0.5	2004–05	Halpern *et al.* (2008)
	Benthic oil rig structures	0.5 × 0.5	2003	Halpern *et al.* (2008)
6. Impacts of climate change	Sea surface temperature anomalies	0.5 × 0.5	2000–05 vs. 1985–90	Halpern *et al.* (2008)
	UV increase	0.5 × 0.5	1996–2004	
	Ocean acidification	0.5 × 0.5	1870 vs. 2000–09	

Table 3 Weights of each threat layer by biodiversity grouping to create the threat models by group (the sum of the weights by biodiversity grouping is equal to 1).

	1. Coastal-based impacts	2. Trawling and dredging disturbance	3. Marine pollution	4. Exploitation of marine resources	5. Maritime activities	6. Climate change
Invertebrates	0.16	0.27	0.16	0.22	0.05	0.14
Fishes	0.11	0.28	0.17	0.28	0.06	0.11
Marine mammals and marine turtles	0.07	0.14	0.29	0.21	0.14	0.14
Seabirds	0.08	0.00	0.31	0.38	0.08	0.15
Large predators	0.09	0.16	0.24	0.29	0.09	0.13

2, trawling and dredging disturbance; 3, marine pollution; 4, exploitation of marine resources; 5, maritime activities; 6, climate change).

The total cumulative threat model was calculated as the sum of each cumulative threat model ($T_{L,i}$) for each biodiversity grouping i:

$$T_{L,total} = \sum_{i=1}^{I} (T_{L,i}) \qquad (2)$$

where $I = 4$ is the number of biodiversity groupings (1, invertebrates; 2, fishes; 3, marine mammals and turtles; 4, seabirds).

To explore how the weighting factors w_n of equation 1 could affect the overall results, we performed a sensitivity analysis and developed alternative results using (1) equal weighting and (2) randomly assigned weightings to threat layers. We compared these new results with results obtained using available weighting factors (Table 3).

Areas of conservation concern for biodiversity and overlap with MPAs

Spatial distributions of biodiversity by group and the cumulative threat models were used to identify important areas of conservation concern, i.e. areas where high biodiversity and high cumulative threats occurred simultaneously. We calculated a new index of overlap (OI) as follows:

$$OI_r = (BI_r + T_{L,\text{total},r})/2 \quad (3)$$

where *BI* is the biodiversity index (the sum of all the species or diversity by group normalized over space and scaled between 0 and 1), and $T_{L,\text{total}}$ is the threat index (equation 2 above, ranging between 0 and 1). *OI* values ranged from 1, indicating high concern, to 0, low or no concern using $r = 4$ intervals: < 25%, ≥ 25%, ≥ 50% and ≥ 75%. Therefore, the *OI* was calculated for areas where both species diversity and the intensity of cumulative threats were < 25%, ≥ 25%, ≥ 50% and ≥ 75% (thus, we calculated the $< OI_{25}$, OI_{25}, OI_{50} and OI_{75}, respectively). For example, OI_{25} identifies areas where diversity is equal to or higher than 25% and threat intensity is equal to or higher than 25%, and we excluded the cases where combinations of lower diversity and higher threats, or vice versa, would provide similar results.

We used the Spatial Analyst Toolbox of ArcGIS v.9.3 to calculate the total area of all regions that displayed a high degree of overlap between cumulative threat intensity and high species diversity. We expressed these areas as a percentage of the total surface of the Mediterranean Sea using the North Pole Lambert Azimuthal Equal Area Conic projection to minimize area distortions, and we plotted the maps using the World Geodetic 1984 coordinate system (WGS1984).

Furthermore, we compared how areas of high conservation concern overlapped with currently established MPAs. For this analysis we used data on existing national and international MPAs in the Mediterranean Sea (Abdulla *et al.*, 2008; MEDPAN, 2010) and complemented them with information from other Mediterranean institutions (see Appendix S3). We excluded from the analysis those sites that had only been formally declared as MPAs (e.g. those at present only proposed).

RESULTS

Areas of high marine biodiversity

High-biodiversity areas were primarily located in the coastal areas of Spain, France and Italy, including the Balearic Islands, Corsica, Sardinia and Sicily, the north-western coast of Africa, the eastern Adriatic Sea, and coastal regions of the Ionian and the Aegean Sea (Fig. 2).

Invertebrate species were of higher concentration in the coastal waters and over the continental shelf areas of the Mediterranean Sea, especially of the western area, the Adriatic and Aegean seas, and the coasts of Tunisia, Egypt and Israel (Fig. 2a). The Adriatic Sea exhibited the highest species richness of invertebrates (Fig. 2a). Fish were of highest species richness around Sicily, followed by the coastal and shelf areas of the western Mediterranean and the Ionian Sea (Fig. 2b).

Eight of the nine resident marine mammals were found in the western Mediterranean and were concentrated especially in the eastern Adriatic, in the waters of Alboran, Balearic, Ligurian, Aegean and Ionian seas, and along the coasts of western Africa and Israel (Fig. 2c). Seabird species distribution was concentrated over coastal areas throughout the Mediterranean region, especially around river deltas (Fig. 2d). Highest seabird species richness was found in the Ebro and Rhone deltas, southern Spain, southern Corsica and Sardinia and over coastal waters of the Aegean Sea. The diversity of large predators was higher in the western Mediterranean and in the Aegean Sea (Fig. 2e).

In general, species diversity declined from north to south and from west to east and was concentrated in coastal and shelf areas (Fig. 2f). This finding may highlight the heterogeneous nature of species distribution in the Mediterranean Sea, but it may also be a result of the lack of data from countries of the southern and eastern regions (Coll *et al.*, 2010).

Areas of cumulative threats

Coastal-based impacts were as expected most pronounced in parts of the Mediterranean Basin with the highest population densities (Fig. 3a). Trawling and dredging disturbance, ocean-based pollution and the exploitation of marine resources by fisheries extended to the shelves and slopes of the whole basin, and showed a tendency to concentrate in the north and western Mediterranean (Fig. 3b–d). The impact of shipping and maritime traffic was prevalent mainly in the open waters of the basin, especially along traffic routes, harbours and other important commercial coastal areas (Fig. 3e). Potential impacts of climate change were more pronounced in the southern and eastern regions (Fig. 3f).

The cumulative threat models for the five diversity groupings identified several areas of high potential risk for invertebrates, fishes, marine mammals and turtles, seabirds and large predators which were widespread throughout the western and eastern parts of the Mediterranean Basin (Fig. 4). Fewer areas were located in the south-eastern Mediterranean region. Areas where cumulative impacts on invertebrates, fishes and seabirds were greater were located along the coast and over the continental shelf (Fig. 4a, b, d). On the other hand, impacts on marine mammals were also pronounced in the open sea (Fig. 4c). These areas of high potential cumulative threat were largely similar between species groupings. This is due to the widespread potential impacts of cumulative threats on marine diversity in the Mediterranean Sea and a generally low sensitivity of the cumulative models to the different impact weights (Table 3) given to the threats for each biodiversity grouping (see sensitivity analysis results in Appendix S4a).

Areas of conservation concern for biodiversity

The main areas of conservation concern for biodiversity, i.e. where there was higher spatial overlap between areas of high biodiversity and threats, were notably different among species groupings (Fig. 5, Table 4).

For invertebrate and fish species, areas of OI_{50} were primarily located in coastal regions of Spain, France, Italy, the Aegean Sea, south-east of Turkey and regions surrounding the Nile Delta and north-west African coasts (Fig. 5a, b). These areas were relatively small and represented less than 3% of the total surface

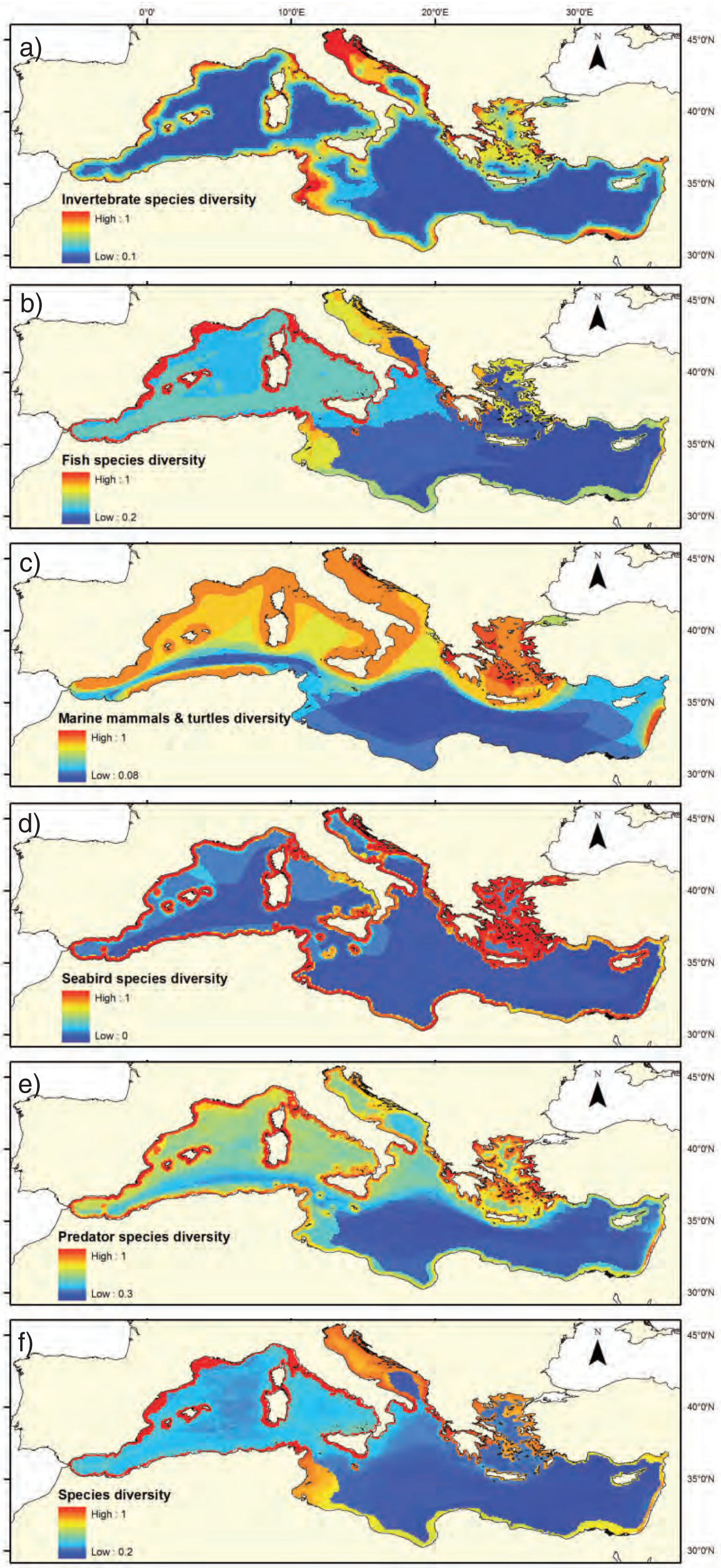

Figure 2 Species biodiversity in the Mediterranean Sea: (a) commercial or well-documented invertebrate species, (b) fish species, (c) marine mammals and turtles, (d) seabirds, (e) large predators (including large fishes, marine mammals, turtles and seabirds), and (f) all data combined. Richness is indicated as a relative amount (expressed between 0 and 1) of total species of group present.

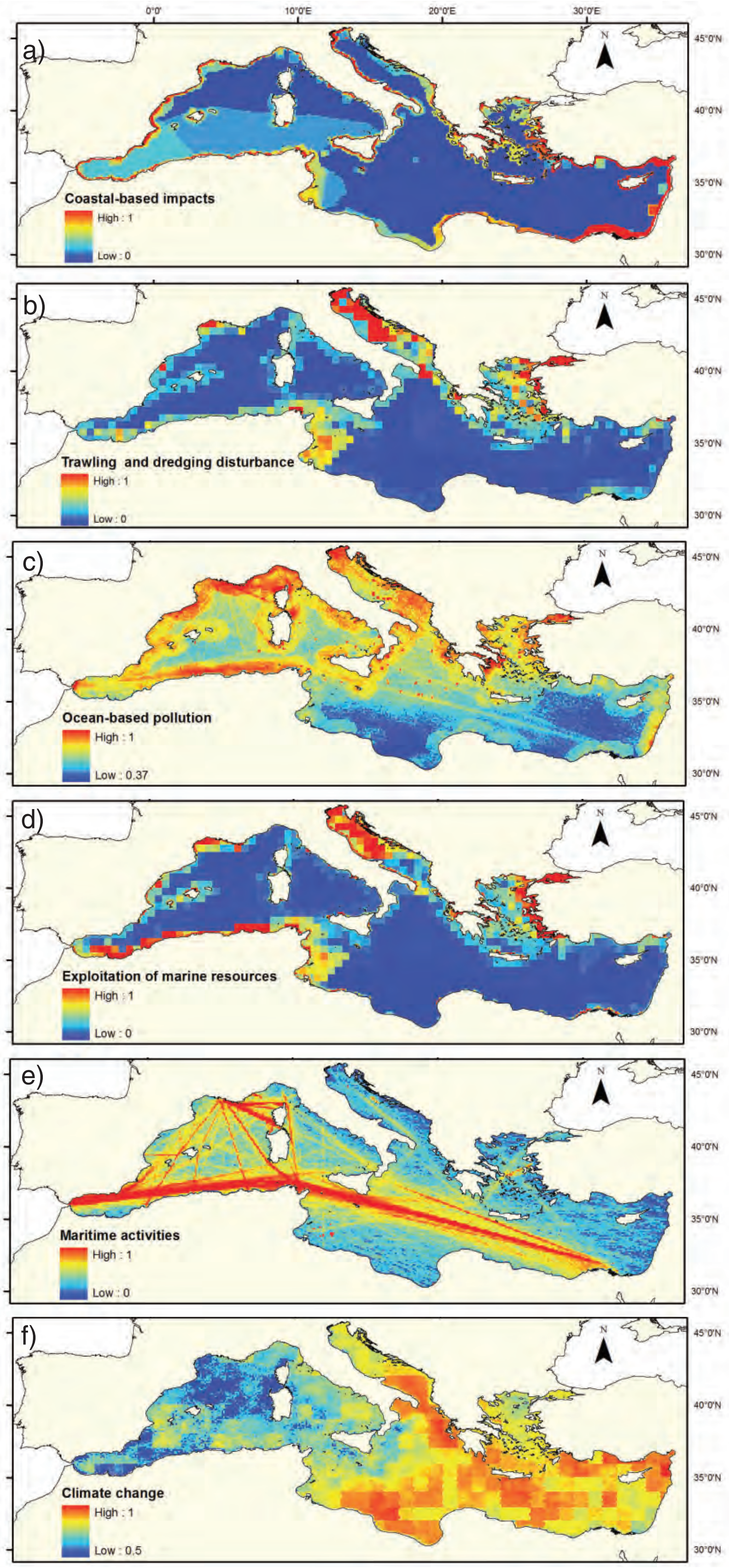

Figure 3 Human threats with potential impact on marine biodiversity in the Mediterranean Sea: (a) coastal-based impacts, (b) trawling and dredging disturbance, (c) ocean-based pollution, (d) exploitation of marine resources, (e) maritime activities, and (f) climate change impact. Each continuous threat was first log($x + 1$)-transformed and then normalized (expressed between 0 and 1) in order to compare the intensity of threats (see text for details).

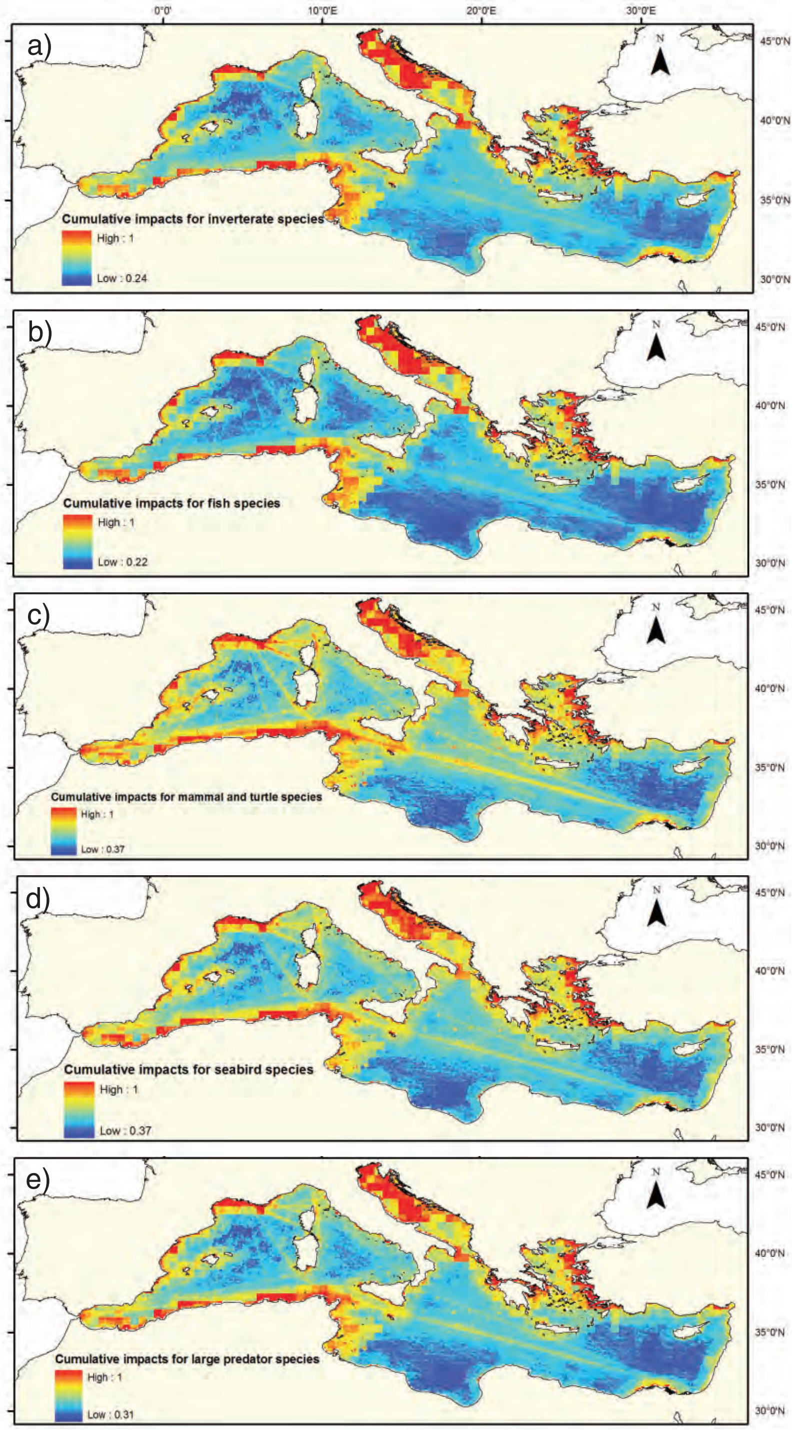

Figure 4 Areas of cumulative threats (expressed as relative values between 0 and 1) with potential impact on marine biodiversity in the Mediterranean Sea: (a) commercial or well-documented invertebrate species, (b) fish species, (c) marine mammals and turtles, (d) seabirds, and (e) large predators (including large fishes, mammals, turtles and seabirds). Cumulative threat (from equation 1) is equal to a weighted sum of each of the six cumulative threat layers (data sources from Fig. 3 and weighting factors on Table 3).

of the Mediterranean Sea (Table 4). Areas of OI_{50} for marine mammals were much larger (Fig. 5c) and represented 30% of the Mediterranean. OI_{50} areas for seabird species and large predators were located closer to coastal regions and showed intermediate extension (Fig. 5d, e, Table 4). OI_{75} areas were much smaller (Table 4) and primarily concentrated in the Gulf of Lions, the northern Adriatic Sea, the Aegean Sea and Tunisian waters, while areas with OI_{25} were large, especially for fishes and large predators (Fig. 5b, e), and were found over coastal waters, particularly for invertebrate species and seabirds (Fig. 5a, d). The identification of these areas showed low to moderate sensitivity to the impact weights given to the threats for each diversity group, especially for invertebrates, fishes and large predatory species (see sensitivity results in Appendix S4b). However, when using equal weighting and randomly assigned weighting, *OI* areas for marine mammal species and seabirds were smaller than *OI* areas calculated with weights assigned by experts (Appendix S4b).

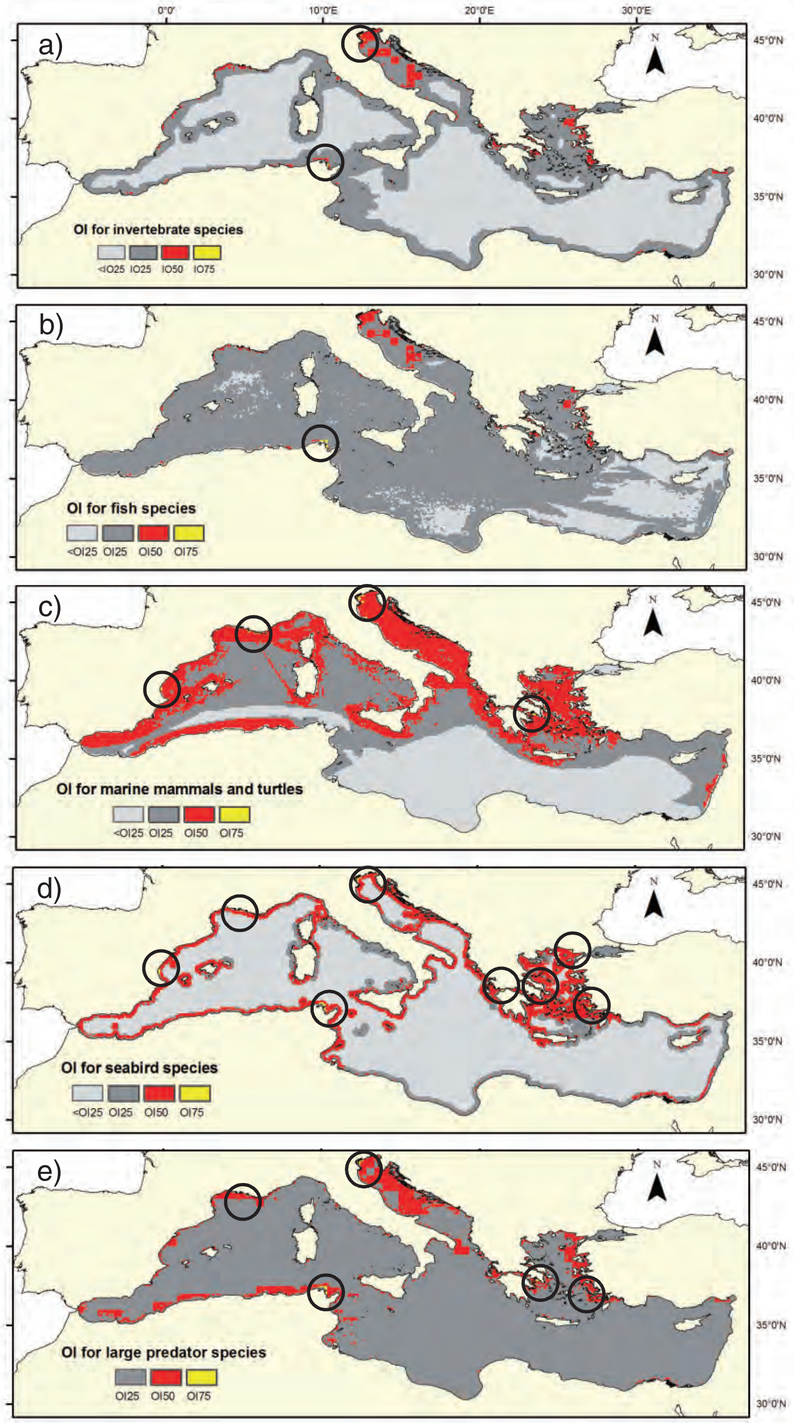

Figure 5 Identification of areas of conservation concern for biodiversity in the Mediterranean Sea, where high diversity and high threat overlap for: (a) commercial or well-documented invertebrate species, (b) fish species, (c) marine mammals and turtles, (d) seabirds, and (e) large predators (including large fish, marine mammals, turtles and seabirds). The overlap index (*OI*) indicates areas where both species diversity and intensity of cumulative threats were < 25% (< OI_{25}), ≥ 25% (OI_{25}), ≥ 50% (OI_{50}) and ≥ 75% (OI_{75}). Black circles indicate where values of OI_{75} occur.

For all species combined, total OI_{50} areas were identified over the Spanish Mediterranean shelf, the Gulf of Lions, the north-eastern Ligurian Sea, the north and central Adriatic Sea, the Aegean Sea, and regions of Tunisia and the western coast of Africa as areas of greatest conservation concern (Fig. 6b). These areas covered 1.3% of the Mediterranean Sea and were characterized by high species diversity as well as high cumulative threats. Threats were particularly high for four species groupings in this analysis (i.e. invertebrates, fishes, marine mammals and turtles, and seabirds; see Table 5). The OI_{50} areas for one or two biodiversity grouping out of the four groupings were larger (13–16%; Table 5). Areas of total OI_{25} were widespread along the coastal areas of the western Mediterranean, and the Adriatic and Aegean Seas, and the eastern coastal zone of Turkey, Syria, Lebanon, Israel and Egypt (Fig. 6a). They covered 13% to 32% of the Mediterranean Sea depending on how many groupings were included

Table 4 Quantification of areas of conservation concern for biodiversity in the Mediterranean Sea (results are expressed in % area). The overlap index (*OI*) indicates areas where both species diversity and intensity of cumulative threats were ≥ 25% (OI_{25}), ≥ 50% (OI_{50}) or ≥ 75% (OI_{75}). These areas are represented in Fig. 5.

OI_{25}: Areas of conservation concern with ≥ 25% diversity and ≥ 25% threats (%)	
Invertebrates	35.9
Fishes	82.8
Marine mammals and turtles	34.3
Seabirds	10.6
Large predators	90.8
OI_{50}: Areas of conservation concern with ≥ 50% diversity and ≥ 50% threats (%)	
Invertebrates	2.7
Fishes	1.9
Marine mammals and turtles	29.2
Seabirds	17.0
Large predators	9.1
OI_{75}: Areas of conservation concern with ≥ 75% diversity and ≥ 75% threats (%)	
Invertebrates	0.0
Fishes	0.0
Marine mammals and turtles	0.1
Seabirds	0.1
Large predators	0.1

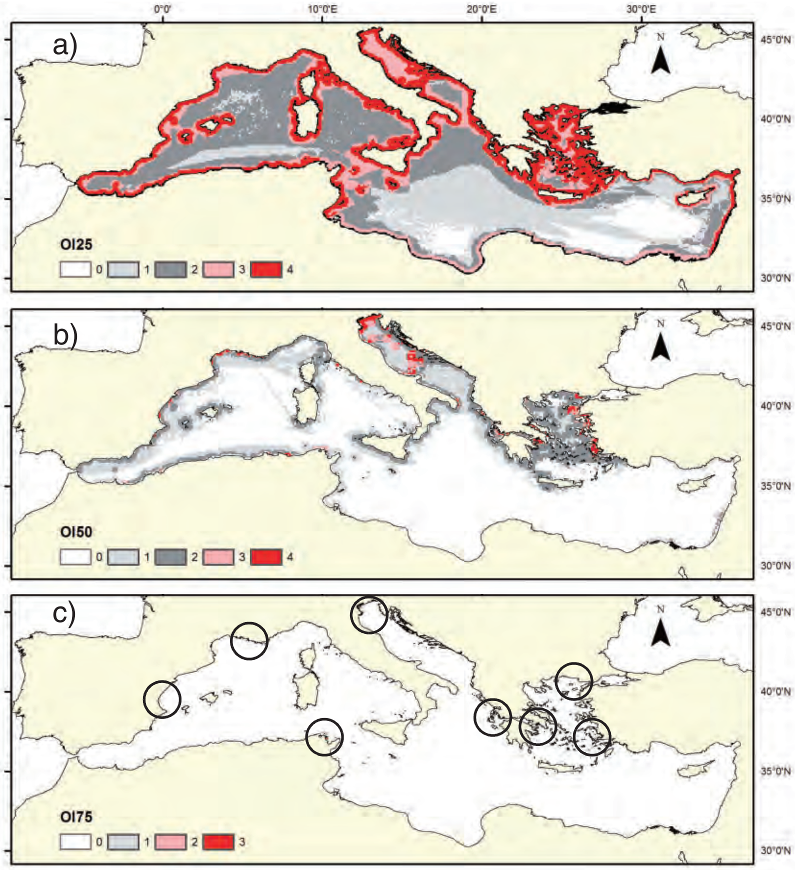

Figure 6 Global areas of conservation concern in the Mediterranean Sea where high biodiversity of invertebrates, fishes, marine mammals and turtles, and seabirds, and high threats overlap. The overlap index (*OI*) indicates areas where both species diversity and intensity of cumulative threats were: (a) ≥ 25% (OI_{25}), (b) ≥ 50% (OI_{50}) and (c) ≥ 75% (OI_{75}). 0 = no groups (of the four biodiversity groupings studied: invertebrates, fishes, marine mammals and turtles, and seabirds) show high diversity and high cumulative threats; 1 = only one group shows high diversity and high threats; 2 = two groups of the four show high diversity and high threats; 3 = three groups of the four show high diversity and high threats; and 4 = all groups show high diversity and high threats. Black circles indicate cells with data.

(Table 5). Areas of total OI_{75} were mainly confined to six coastal areas along the Mediterranean Sea (eastern coast of Spain, south coast of France, northern coast of Tunisia, northern Adriatic Sea, Ionian Sea, and coastal areas of the western, north-eastern and south-eastern Aegean Sea; Fig. 6c).

Overlap between protected areas and areas of conservation concern

Currently, MPAs cover less than 5% of the Mediterranean Sea when including the Pelagos Sanctuary in the Ligurian Sea, which

Table 5 Quantification of areas of conservation concern for biodiversity in the Mediterranean Sea that include high diversity and threats for one to four of the groupings studied (invertebrates, fishes, marine mammals and turtles, and seabirds) (results are expressed in % area). The overlap index (*OI*) indicates areas where both species diversity and intensity of cumulative threats were ≥ 25% (OI_{25}), ≥ 50% (OI_{50}) and ≥ 75% (OI_{75}). These areas are represented in Fig. 6.

OI_{25}: Areas of conservation concern with ≥ 25% diversity and ≥ 25% threats		OI_{50}: Areas of conservation concern with ≥ 50% diversity and ≥ 50% threats		OI_{75}: Areas of conservation concern with ≥ 75% diversity and ≥ 75% threats	
One grouping	23.8	One grouping	16.4	One grouping	0.1
Two groupings	32.1	Two groupings	12.9	Two groupings	0.1
Three groupings	12.9	Three groupings	1.3	Three groupings	0.0
Four groupings	22.0	Four groupings	1.3	Four groupings	0.0

Table 6 Overlap of marine protected areas (see Appendix S3) with areas of conservation concern for biodiversity in the Mediterranean Sea (from Fig. 6) for one to four of the groupings studied (invertebrates, fishes, marine mammals and turtles, and seabirds) (results are expressed in % of conservation concern areas in existing MPAs). The overlap index (*OI*) indicates areas where both species diversity and intensity of cumulative threats were ≥ 25% (OI_{25}), ≥ 50% (OI_{50}) and ≥ 75% (OI_{75}).

Total area (%) under protection*: 5%/0.45%[1];

Overlap of protected areas with areas of concern (*OI*):

≥ OI_{25}		≥ OI_{50}		≥ OI_{75}	
One grouping	0.0	One grouping	1.6	One grouping	0.0
Two groupings	1.6	Two groupings	1.1	Two groupings	0.0
Three groupings	0.6	Three groupings	0.0	Three groupings	0.0
Four groupings	2.0	Four groupings	0.1	Four groupings	–

*UNEP database, 1 without Pelagos Sanctuary.

is by far the largest protected area in the Mediterranean Sea (Abdulla *et al.*, 2008) and which is mainly dedicated to the conservation of marine mammals (Notarbartolo-Di-Sciara *et al.*, 2008). Without considering the Pelagos Sanctuary, the Mediterranean waters under protection are less than 0.5% (Appendix S3).

Less than 2% of the areas with OI_{25} coincide with existing protected areas (Table 6). Overlap with existing MPAs is lower (< 1.6%, Table 6) when considering areas of OI_{50} and OI_{75}. Areas of high conservation concern currently protected are mainly within the Pelagos Sanctuary. If we exclude the Pelagos Sanctuary, the overlap between protected and high conservation concern areas is lower than 0.2%.

DISCUSSION

The mapping of areas of high diversity is very important. Biodiversity is not just one element of natural ecosystems, but is of overarching importance both for science and society as a whole (McCann, 2007; Vira & Adams, 2009). Indeed, it is fundamental and critical for the understanding of biogeographic patterns and of evolutionary history; also it is linked to ecosystem functioning (e.g. Danovaro *et al.*, 2008; Duffy, 2009). Biodiversity is also related to ecosystem services and available resources for humans, to which we give monetary, recreational or other values (Pearce & Moran, 1994; Bengtsson *et al.*, 1997; Oksanen, 1997; Costanza *et al.*, 1998; Tilman, 2000).

Several threats that affect efforts to conserve biodiversity in the Mediterranean Sea were previously identified (Coll *et al.*, 2010). Our study expands on this issue by: (1) identifying the areas where these threats are more prevalent, and (2) quantifying the degree of overlap between anthropogenic threats and marine biodiversity, and the latter with MPAs. The quantification of overlap between cumulative threats and marine biodiversity is fundamental to understanding how biodiversity is affected by human activities and identifying future conservation needs. This is especially relevant in the Mediterranean Sea as a strongly impacted large marine ecosystem (Costello *et al.*, 2010).

Our results show a substantial overlap between regions with high biodiversity and high cumulative threats in the Mediterranean Sea, and are in line with other regional studies that investigated areas of ecological importance in the basin (e.g. Aguilar & De La Torriente, 2008). We show that anthropogenic threats to marine diversity in the Mediterranean Sea are diverse and extend from coastal areas to the open seas. The most important threats to diversity at present, i.e. pollution and eutrophication, habitat degradation and exploitation of marine resources (e.g. Danovaro, 2003; Tsounis *et al.*, 2007; Abdulla & Linden, 2008; Stergiou *et al.*, 2009), are mainly concentrated in the coastal and shelf areas; additional threats to diversity that are expected to substantially increase in the future and that are predicted to have an important effect on marine resources and fisheries in the Mediterranean Sea, such as climate change and invasive species (Galil, 2000; Bianchi, 2007; Cheung *et al.*, 2009, 2010; Lasram *et al.*, 2010), are widely distributed.

We evaluated alternative weighting formulations for threats and found that the areas of strong overlap between biodiversity and threats were robust to the weighting assumption (Appendix S4), indicating that the spatial patterns we identified are not an artefact of our methodology. Our results document the complex situation in the Mediterranean Sea, where both local and global stresses affect marine resources at a regional scale. These areas of conservation concern may be good candidates for future in-depth studies, and specific protection and management actions. They also represent important case studies for a further analysis of the impacts of cumulative anthropogenic threats on marine communities and food webs using a combination of advanced data analysis and modelling tools (e.g. Brown *et al*., 2010).

Our study also shows that cumulative threats to marine biodiversity in the Mediterranean Sea tend to be concentrated in coastal areas and on shelves, and are higher for seabirds, fishes and invertebrate species in coastal regions. Threats that occur in the open sea are especially important to the diversity of marine mammals, marine turtles and large predatory fish, which are under high pressure in the entire Mediterranean Basin (e.g. Bearzi *et al*., 2003; Abdulla, 2004). In our study, these organisms also scored highest regarding the area of high cumulative threats that overlapped with high-diversity areas (OI_{25}, OI_{50} and OI_{75}, Table 4).

We also show that the areas of highest concern are concentrated in the northern region of the Mediterranean Sea. This may reflect the higher impact that human populations pose in the northern parts of the basin, and the key role northern countries, most of them members of the European Community, have in the management and conservation of Mediterranean marine biodiversity as well as in policy initiatives. Since only a very small proportion of the areas of conservation concern for biodiversity are currently under protection (Table 6), this study illustrates that a significant amount of effort is still required to protect and manage marine biodiversity in the Mediterranean Sea.

This study is the first step towards a detailed analysis of biodiversity 'hot spots' in the Mediterranean Sea, and may also be relevant to map biodiversity 'cold spots' (Kareiva & Marvier, 2003). The comparison of our results with previously identified 'hot spots' for Mediterranean vertebrate species of special conservation concern (including critically endangered, endangered, vulnerable or near-threatened species of marine mammals, turtles and fishes) (Coll *et al*., 2010, Table 3) suggests that areas of conservation concern for biodiversity are complementary to those areas identified as biodiversity 'hot spots' for vertebrate species under threat. Thus, they should be considered together when directing conservation efforts towards the Mediterranean Sea. For example, the Alboran Sea, in the south-western part of the Mediterranean Sea, hosts a large concentration of listed vertebrate species, as well as some invertebrates, but may not be considered as an area of biodiversity concern in terms of maximizing the number of species per unit area. Therefore, other important criteria to take into account when identifying areas for the conservation of marine biodiversity in the Mediterranean Sea are the occurrence of rare, endemic and endangered species, non-resident species that may still require large areas, the preservation of functional and phylogenetic traits, the protection of species that require large areas to survive or areas that represent migratory paths, the consideration of important ecosystem services, and important socio-political and economical factors that play key roles in ensuring the maintenance of diversity (Kareiva & Marvier, 2003).

Our analysis of protected areas did not take into account the trawling ban below depths of 800–1000 m established by the General Fisheries Council for the Mediterranean (WWF/IUCN, 2004), since its establishment is limited to bottom trawling activities (and not to all fishing fleets) and its compliance is not assessed. Moreover, this work faced data limitations and uncertainties that need to be taken into account when interpreting results. As highlighted previously (Coll *et al*., 2010), the availability of biodiversity data from the Mediterranean Sea is highly heterogeneous and is limited in southern and eastern regions of the basin. This limitation may render conservative our identification of areas of conservation concern for biodiversity in the south-eastern regions of the basin. Moreover, available data regarding biodiversity of the Mediterranean Sea as well as threats were collected during an extended period of time (about 20 years) so they represent an average situation rather than the most up-to-date assessment. There is thus a need to revise the spatial distribution in these areas with data that are current. Data available on changes of species assemblages due to human activities are scarce, and this study assumes that changes have not occurred during the period from which most of our data originate (1980–2000). However, available analysis on the impacts of climate change on fish species distributions illustrates that climate change has already instigated some noticeable changes in species distributions (e.g. Sabatés *et al*., 2006) and is likely to have an important impact in the near future (Lasram *et al*., 2010). Therefore, the turnover rate of species assemblages may be important and may accelerate in the future due to cumulative human activities, which means that distribution changes should be included in future analysis of global change in the Mediterranean.

The availability of spatial data on anthropogenic threats has increased exponentially in the last decade and such data are abundant in the Mediterranean context. However, the resolution of these data precluded an analysis at finer scales than the large-regional focus adopted here. Detailed information on deep sea activities, such as submarine communication cables, marine research or historical dumping of radioactive waste, are difficult to access or are absent from the region, although a detailed study from the adjacent north-east Atlantic floor illustrated that these activities had moderate impacts compared to the impact of bottom trawling (included in our analysis), which was 'an order of magnitude greater than the total extent of all the other activities' (e.g. Benn *et al*., 2010). In addition, available data on other threats such as commercial shipping and fishing may be underestimated due to recreational activities and underreporting of commercial fishing. We assumed a linear relationship between driver magnitude and impact on marine biodiversity, which allowed for direct comparison between threats, but ignored the existence of thresholds that are likely conditioning the way anthropogenic impacts act in the ocean and the historical development of anthropogenic threats. This type of information is still extremely scarce. Finally, our analyses did not include dynamic changes in marine biodiversity such as annual variation in production and migration and of threats due to dispersion by oceanographic currents, and neither did they include the direct impact of environmental factors. These dynamics may be important in some cases and should be considered when future analyses are developed.

Despite these limitations, this study provides a first step towards the identification of important areas for conserving marine species biodiversity in the complex Mediterranean Sea, and should be seen as the best understanding of the situation with the current available data. Our results also set a baseline for the comparison of future projections, and are useful to identify actions of research and changes in the future. As new and more detailed data become available, these analyses will be hopefully refined and most certainly improved.

CONCLUSIONS

To move towards an ecosystem approach in the Mediterranean Sea we need to improve the available data on human activities and how they spatially accumulate and interact to have an impact on marine species, communities and ecosystems. In this paper we mapped for the first time how areas with high species diversity overlap with areas that suffer high anthropogenic threats in the Mediterranean Sea. These overlaps are widespread and can be used to identify priority areas for biodiversity protection. Since current MPAs hardly cover any of these priority areas, identified areas may be good candidates to consider during future research tasks, management activities and conservation plans. They should be considered in addition to areas that host high number of endangered, endemic or rare species, transient species, areas that represent biodiversity highways, and important areas to preserve functional or evolutionary traits and ecosystem services.

ACKNOWLEDGEMENTS

MC was funded by a European Community Marie-Curie postdoctoral Fellowship through the International Outgoing Fellowships (Call: FP7-PEOPLE-2007-4-1-IOF) to ECOFUN. DM was supported by a Marie Curie International Outgoing Fellowship (FISHECO) with agreement number IOF-GA-2009-236316. This work was partly funded by Fondation Total, Fondation pour la Recherche sur la Biodiversité (project BIODIVMED) and Centre National de la Recherche Scientifique throught program BiodivMEx. This work was supported by the Sea Around Us project, a scientific collaboration between the University of British Columbia and the Pew Environment Group. We are grateful to all those researchers who contributed to this analysis with their data.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 List of species included in each biodiversity layer and data sources.

Appendix S2 Description of threat layers used to document anthropogenic impacts on diversity.

Appendix S3 Marine protected areas existing in the Mediterranean Sea.

Appendix S4 Results of the sensitivity analysis on areas of cumulative threats and areas of conservation concern for biodiversity.

BIOSKETCH

Marta Coll is a post-doctoral fellow at the Institute of Marine Science (ICM-CSIC, Barcelona, Spain). She is currently working on her Marie Curie project 'ECOFUN: Analysis of biodiversity changes on structural and functional properties of marine ecosystems under cumulative human stressors'. Her interest focuses on understanding threats and changes to marine biodiversity and how they have been translated into changes of ecosystem structure and functioning, and services to humans, and how these changes may impact upon ecosystems in the future. She uses ecological modelling, spatial analysis tools and microcosm experiments.

Editor: Michael Rex

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Current Biology *21*, 1044–1050, June 21, 2011 ©2011 Elsevier Ltd All rights reserved DOI 10.1016/j.cub.2011.05.005

Report

Protected and Threatened Components of Fish Biodiversity in the Mediterranean Sea

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Summary

The Mediterranean Sea (0.82% of the global oceanic surface) holds 4%–18% of all known marine species (~17,000), with a high proportion of endemism [1, 2]. This exceptional biodiversity is under severe threats [1] but benefits from a system of 100 marine protected areas (MPAs). Surprisingly, the spatial congruence of fish biodiversity hot spots with this MPA system and the areas of high fishing pressure has not been assessed. Moreover, evolutionary and functional breadth of species assemblages [3] has been largely overlooked in marine systems. Here we adopted a multifaceted approach to biodiversity by considering the species richness of total, endemic, and threatened coastal fish assemblages as well as their functional and phylogenetic diversity. We show that these fish biodiversity components are spatially mismatched. The MPA system covers a small surface of the Mediterranean (0.4%) and is spatially congruent with the hot spots of all taxonomic components of fish diversity. However, it misses hot spots of functional and phylogenetic diversity. In addition, hot spots of endemic species richness and phylogenetic diversity are spatially congruent with hot spots of fishery impact. Our results highlight that future conservation strategies and assessment efficiency of current reserve systems will need to be revisited after deconstructing the different components of biodiversity.

Results

The geographic location of the Mediterranean Basin, at the margins of Africa, Europe, and West Asia (Figure 1A), provides a unique diversity of habitats, within which a succession of colonization events has shaped a remarkable diversity of species [4]. Indeed, the Mediterranean Sea may be seen as a marine biodiversity hot spot, exhibiting a singular mixture of endemics, species from the Atlantic, and others of tropical origins [1, 2]. Although it represents only 0.32% of the global oceanic volume and 0.82% of its surface area, the Mediterranean Sea holds 4%–18% of all known marine species (~17,000) and has a high level of endemism [1, 2].

Like most marine ecosystems worldwide, the Mediterranean Sea is highly impacted by several human-mediated threats [1], including intensification in the exploitation of resources from industrial, artisanal, and recreational fisheries, aquaculture, ever-increasing density of coastal populations, and pesticides and fertilizer runoff from agriculture. To counteract these increasing threats, about 100 marine protected areas (MPAs) have been established and reinforced in the Mediterranean Sea to conserve both species and habitats [5, 6]. However, these MPAs cover jointly 9910 km^2, i.e., only 0.4% of the surface area of the Mediterranean Sea [7]. Moreover, they have thus far been created as a result of national or even subnational initiatives, without regional consideration or management plans [8]. Hence, the spatial design of the realized MPA system in the Mediterranean Sea is mainly contingent on local socioeconomic and historical factors, rather than being based on large-scale scientific information, e.g., macroecological considerations [6]. For example, 73% of Mediterranean MPAs are located along its northern shores [7]. Surprisingly, the perceived efficiency of this existing MPA system, i.e., whether and how this system spatially matches with critical areas for conservation, has never been assessed.

In 2010, during the tenth meeting of the Conference of the Parties to the Convention on Biological Diversity (COP10), several headline targets were proposed toward a Strategic Plan for Biodiversity. Following target 11, at least 10% of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, would be conserved by 2020 through systems of protected areas and other effective area-based conservation measures. However, despite this decision, and the existence of approximately 100 MPAs, little attention has been devoted to the spatial overlap—if any—between the present system of Mediterranean MPAs, the hot spots of fish biodiversity (top sites ranked according to biodiversity level), and the hot spots of anthropogenic stresses (top sites ranked according to threat level). This oversight is particularly striking in comparison with the situation prevailing with terrestrial ecosystems [9]. Though delayed because of the lack of detailed and spatially explicit regional-scale data sets, such assessment is urgently needed if we are to achieve the targets of the COP10. Here, we present a fine-resolution mapping of spatial layers containing

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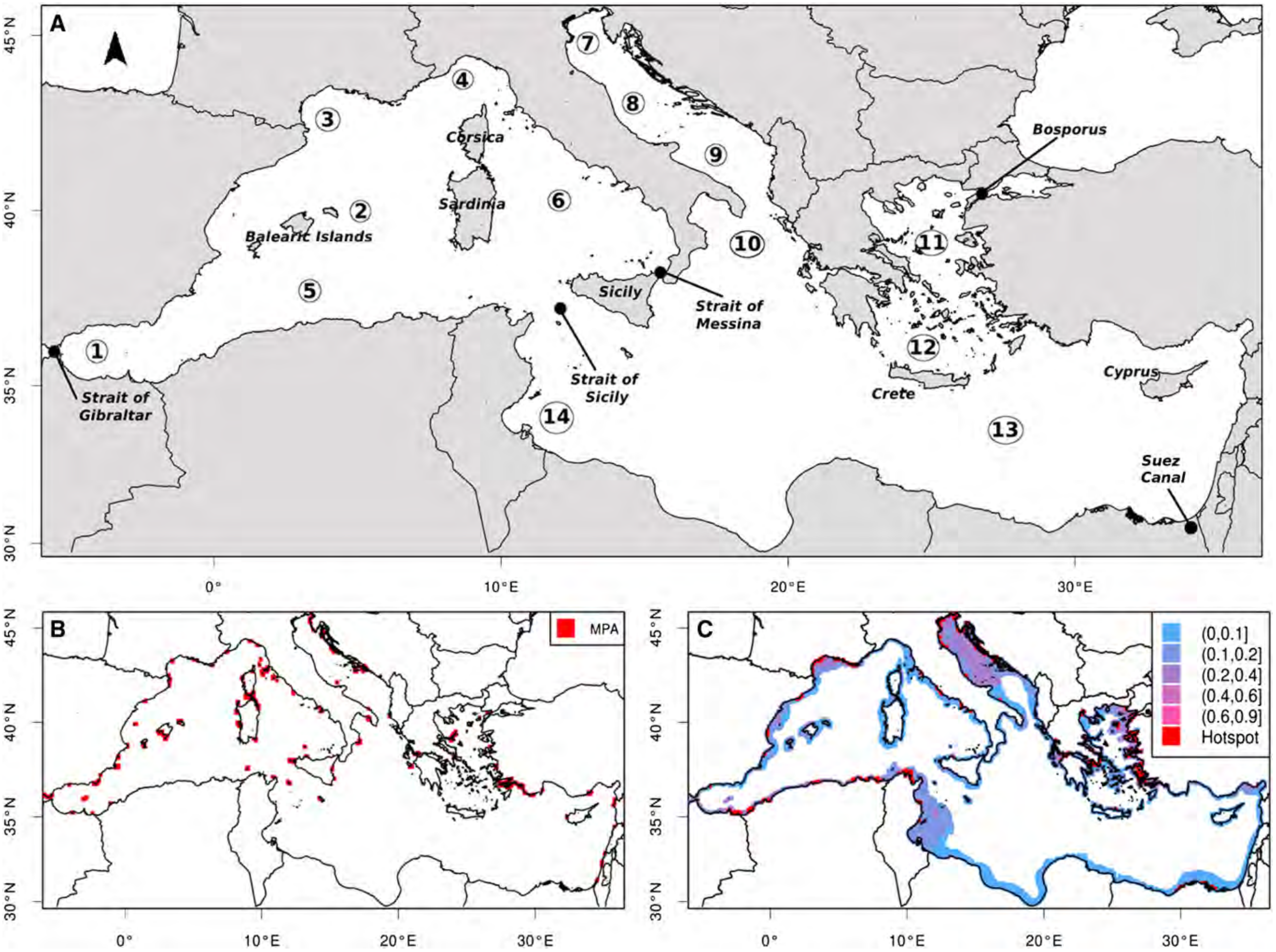

Figure 1. Regions, Basins, Marine Protected Areas, and Fishing Pressure in the Mediterranean Sea

(A) Main regions and basins in the Mediterranean: 1, Alboran Sea; 2, Balearic Sea; 3, Gulf of Lions; 4, Ligurian Sea; 5, Algerian and Tunisian waters; 6, Tyrrhenian Sea; 7, North Adriatic Sea; 8, Central Adriatic Sea; 9, South Adriatic Sea; 10, Ionian Sea; 11, North Aegean Sea; 12, South Aegean Sea; 13, Levant Sea; 14, Gulf of Gabès.

(B and C) Locations of the 100 marine protected areas (MPAs) (B) and gradient of fishing pressure (C). See Supplemental Experimental Procedures.

extensive information on fish species distributions, fishing pressure, and MPA location. We use this data set to evaluate how Mediterranean coastal fish biodiversity is protected by the extant MPA system and threatened by coastal fisheries.

The IUCN Red List rankings are largely based on criteria of rarity and range size, especially when population size and temporal trends are not available. However, the recent literature has highlighted the need to rely on other attributes that make species unique in terms of biological traits [10, 11] or genes [12, 13] for biodiversity conservation. More generally, the concept of biodiversity encompasses many components [3, 14], and total species richness, the most commonly used component of diversity in conservation, may remain silent on the number of threatened or endemic species [15] or on functional and phylogenetic differences among species [3]. We adopted a multifaceted view of Mediterranean fish biodiversity by considering, probably for the first time in aquatic systems, the species richness of total, endemic, and threatened (IUCN) fishes as well as the functional (traits) and phylogenetic (lineages) diversity of assemblages. The two last components have been largely ignored in conservation planning and reserve network assessment (but see [3, 16]), yet they both are key to the diversity of life on Earth [10, 12] and ecosystem functioning [17, 18].

We created a database gathering the geographical distribution of the 282 coastal and continental shelf teleost species using a grid cell at a resolution of 0.1° × 0.1° [19]. For those species, we built a dated phylogeny based on molecular data and a functional dendrogram based on 15 traits to estimate phylogenetic and functional diversity, respectively. We then mapped all the components of fish biodiversity that we overlaid with the geographic occurrence of MPAs and the spatial distribution of fishing intensity. We also identified hot spots of total, IUCN, and endemic species richness; hot spots of phylogenetic and functional diversity; and hot spots of threats corresponding to the cells with the highest 5% values (roughly the percentage of cells contained in the MPA system). Our study provides the first comprehensive assessment of the extent to which fish biodiversity components spatially match the current distribution of MPAs and fishing pressure.

We recorded a total of 100 MPAs in the Mediterranean Sea (Figure 1B). Among the 8186 spatial cells used in this analysis,

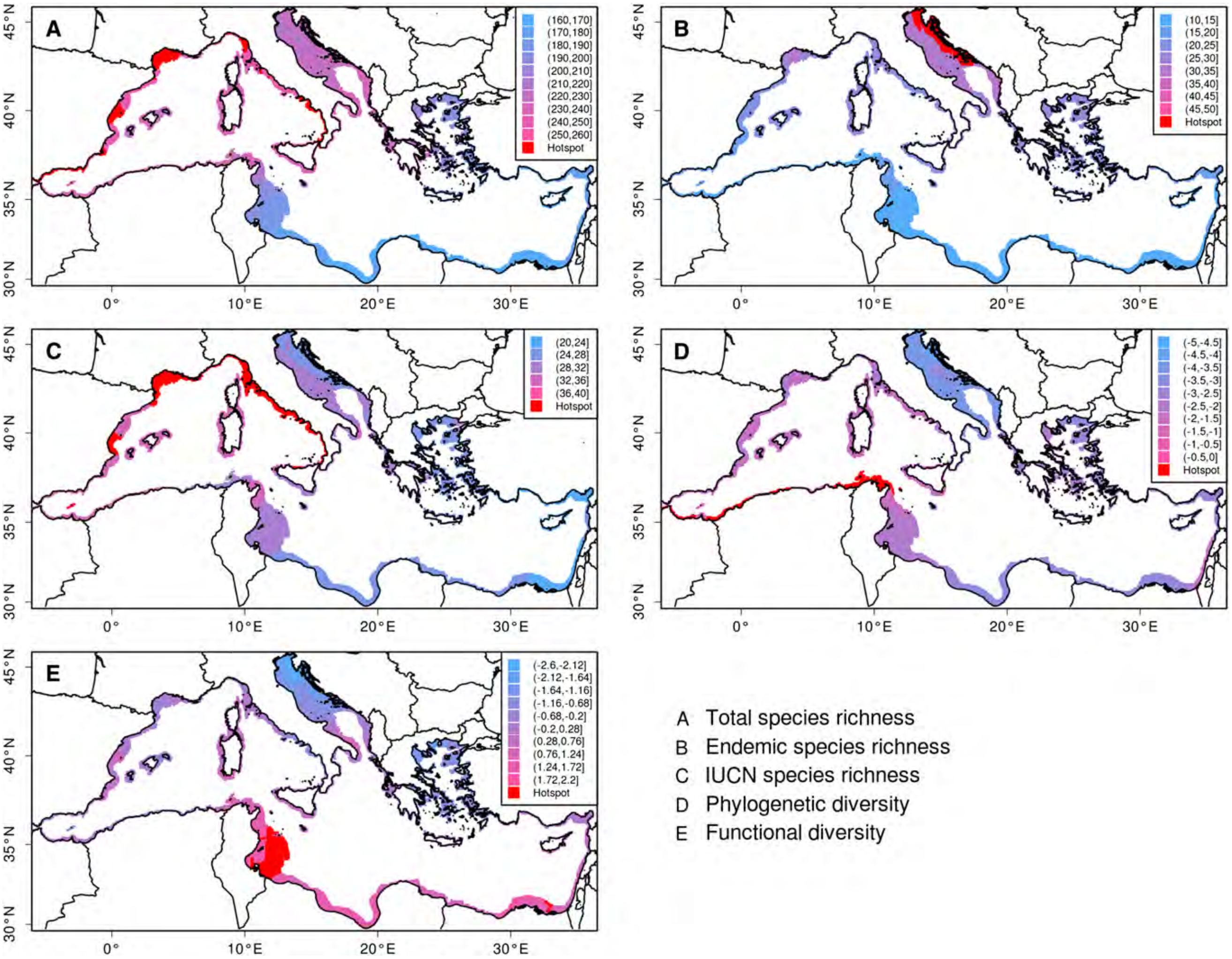

Figure 2. Observed Gradients for All Fish Biodiversity Components

Range maps for 282 coastal species, among which 81 are endemic and 45 are on the IUCN Red List, were digitalized on a regular grid (8186 cells) of 0.1° latitude × 0.1° longitude covering the continental shelf [19]. Nonnative, migratory large pelagic species as well as those mainly occurring beyond the continental shelf (60% or more of their total range) were also excluded because they do not benefit from MPAs situated on the continental shelf. From a dated phylogeny and a functional dendrogram built using 15 functional traits, phylogenetic and functional diversity of fish assemblages contained in each grid cell were respectively computed using a standardized effect size estimation to provide a diversity value independent of species richness (see Supplemental Experimental Procedures).

390 overlapped with an MPA, and about three-fourths of those were along the north coast of the Mediterranean. The coasts least impacted by fisheries were located in the southeast; hot spots of fishery impact were widespread in the rest of the Mediterranean (Figure 1C).

There was a decreasing gradient from west to east in total fish richness (Figure 2A). Sicily was the hot spot of richness, with up to 257 species per cell. The endemic richness gradient was more pronounced from north to south: the northern side exhibited a greater richness, and the Adriatic appeared as a hot spot of endemism, with 42 species per cell (Figure 2B), i.e., 18% of endemic fishes. Similar to the total fish richness gradient, the IUCN species richness gradient decreased from west to east, with up to 37 endangered species per cell, i.e., 15% of total fish richness in these cells, on the western Italian coast and along the French and Spanish coasts (Figure 2C). Similarly, phylogenetic diversity of fish assemblages showed a decreasing gradient from west to east, with hot spots mainly located along the western North African coast (Figure 2D). Finally, there was an increasing gradient of functional diversity from north to south, and almost all hot spots were in the Gulf of Gabès, Tunisia (Figure 2E).

Endemic and IUCN species richness were significantly and positively correlated with total species richness, functional diversity was negatively correlated with endemic species richness, and phylogenetic diversity was positively related with IUCN species richness (Table 1, top). Fishing pressure was positively correlated with total and endemic richness but negatively correlated with functional diversity ($r = -0.423$, $p < 0.05$).

Phylogenetic and functional diversity hot spots spatially mismatched with all other components of fish diversity, whereas total and IUCN richness hot spots were spatially congruent (Table 1, bottom). The system of MPAs was highly congruent with hot spots of total, endemic, and IUCN species richness components of fish diversity but missed the hot spots

Table 1. Spatial Congruence between Biodiversity Components, Fishing Pressure, and Marine Reserves

	End	IUCN	SES.FD	SES.PD	Press	Res
Rich	0.616*	0.839*	−0.413	0.290	0.268*	0.101
End		0.202	−0.800*	−0.413	0.330*	0.079
IUCN			0.010	0.557*	0.128	0.068
SES.FD				0.334	−0.423*	−0.078
SES.PD					−0.003	0.040
Press						0.028

	End	**IUCN**	**SES.FD**	**SES.PD**	**Press**	**Res**
Rich	0 (26.1)***	372 (52.6)***	0 (30.1)***	0 (26.0)***	33 (26.0)	44 (24.7)***
End		0 (41.8)***	0 (23.9)***	0 (20.6)***	64 (20.6)***	32 (19.6)**
IUCN			0 (48.2)***	0 (41.6)***	17 (41.6)**	60 (39.6)***
SES.FD				0 (23.7)***	1 (23.8)***	0 (22.6)***
SES.PD					81 (20.5)***	16 (19.5)
Press						20 (19.5)

Top: pairwise correlations between variables (Rich, fish richness; End, endemic fish richness; IUCN, IUCN threatened fish richness; SES.FD, standardized functional diversity [see Supplemental Experimental Procedures]; SES.PD, standardized phylogenetic diversity [see Supplemental Experimental Procedures]; Press, demersal fishing pressure; Res, presence of reserve) and their significance level after correction for autocorrelation (see Supplemental Experimental Procedures) (*$p < 0.05$).

Bottom: pairwise observed spatial overlaps between hot spots of variables (and expected value under independence: null hypothesis) and their significance level after permutation test (**$p < 0.01$, ***$p < 0.01$).

of functional diversity (Table 1, bottom). Endemic richness and phylogenetic diversity hot spots significantly matched hot spots of fishing pressure, whereas IUCN richness and functional diversity hot spots mismatched this pressure.

Because the above approach relies on an arbitrary hot-spot threshold criterion (5%), we also used an alternative tool that quantifies the percentage of protected sites (or alternatively, the percentage of hot spots of high fishery pressure) for any level of diversity. This approach provides a synthetic and continuous assessment of whether sites including a given diversity value are also protected or, on the contrary, exposed to high fishing pressure. This analysis revealed that, beyond only considering hot spots, cells with high functional diversity values and high numbers of endemic species (except the very first ranks) were not congruent with MPAs, whereas those including high species and IUCN richness values mostly belonged to the existing system of MPAs (Figure 3A). Also, cells with a high number of endemic species and a high phylogenetic diversity value spatially matched hot spots of fishery impact, whereas cells with a high number of IUCN-listed species and a high functional diversity value tended to have low congruence with the highest fishery impact (Figure 3B).

Discussion

Protected areas are indisputably the primary tool for in situ biodiversity conservation across the world, and 0.65% of the world's oceans were protected by the mid-2000s [20]—a low percentage, but one that has recently doubled through the creation of very large MPAs in the Pacific and Indian oceans. Currently, about 4% of global continental shelf areas are incorporated within MPAs, and protection is greater in tropical than in temperate realms [21]. For coastal ecosystems, MPAs have been shown, consistently over the world, to enhance the abundance, size, and diversity of sedentary species, with benefits for local fisheries [22, 23]; this also applies to the Mediterranean Sea [5].

Beyond these local benefits and to reach the COP10 target 11 of protecting at least 10% of coastal and marine areas by 2020, there is an urgent need to identify biodiversity hot spots and human-mediated threats at the fine spatial scale corresponding to MPA size. This is particularly critical in regions with low MPA coverage such as the Mediterranean Sea. Moreover, these MPAs have different status, with various impacts on fish recovery [5, 6]. Here we considered all MPAs as having the same impact on fish populations; thus, our study can be considered as a conservative "best-case scenario." This being said, we have addressed two largely overlooked issues in marine environments. First, we have studied the spatial congruence between the system of MPAs and biodiversity hot spots. Second, we have identified the components of biodiversity that are protected and those that are under threat.

These two goals have been achieved only recently for terrestrial networks of protected areas, and results generally indicate a failure of reserve networks to be representative of the entire biodiversity of a region [3, 24, 25]. Yet, no comparable integrative assessment has been carried for marine environments because, until now, they have relied only on species richness [26, 27]. Here we show that despite its relatively small size, the Mediterranean MPA system is spatially congruent with the hot spots of taxonomic fish diversity (total, endemic, and IUCN) even if cells with medium to high levels of endemism are underrepresented in the system (Figure 3A). However, this system completely misses hot spots of functional diversity and partly those of phylogenetic diversity.

Phylogenetically informed conservation research is not new [28]. Protecting phylogenetic diversity [3, 16, 29] would imply, for instance, prioritizing conservation efforts toward species that have a singular evolutionary history [28, 30]. The rationale of this approach is that the loss of the most phylogenetically distinct species would remove a greater proportion of the Tree of Life [31]. As a consequence, it would be likely to decrease the ability of nature to cope with environmental changes. Indeed, losing phylogenetic diversity at any scale can lead to a reduced potential for communities to respond to changing conditions [29] because climate tolerances are not randomly distributed across phylogenies [32, 33]. Phylogenetic diversity has also recently been proposed as a good proxy for ecosystem functioning [17]. Based on the assumption that fishes from different lineages are more likely to perform different functions [34], we may expect an impact of

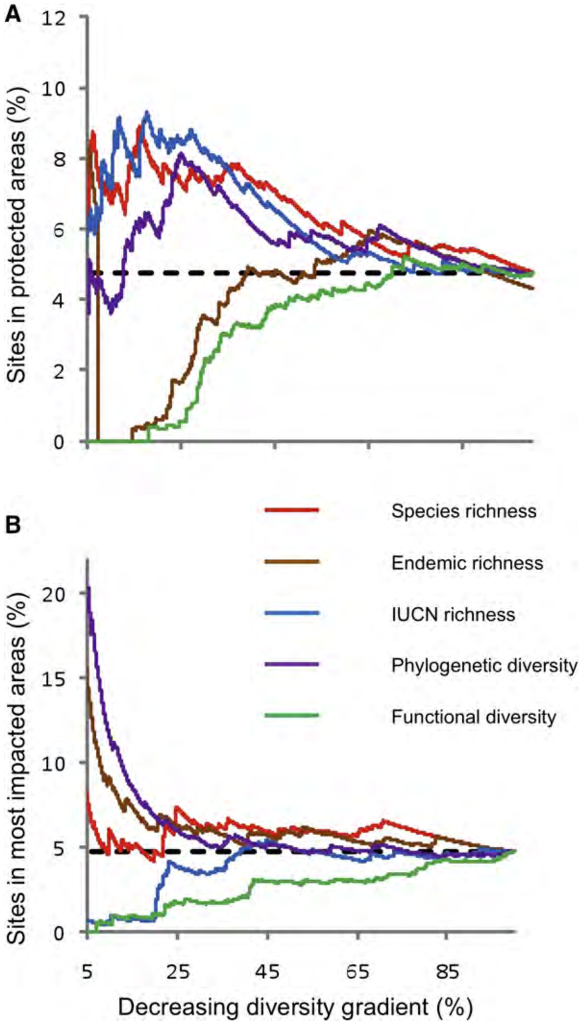

Figure 3. Proportion of Biodiversity Components Included in Marine Protected Areas and Hot Spots of Fishing Pressure

Cumulative proportion of total species richness, endemic richness, IUCN richness, phylogenetic diversity, and functional diversity included in marine protected areas (A) and hot spots of fishing pressure (B). For each diversity component, we ranked the 8186 cells from the most to the least diverse. Along this decreasing diversity gradient (x axis, expressed as a percentage), we calculated the cumulative percentage of protected cells (y axis). For any given value of the diversity gradient, if the MPA system is unbiased, one expects the proportion of protected cells to match the overall proportion of protected cells among all cells (i.e., 4.7%, dashed horizontal line). Therefore, proportions of protected cells located over and under the dashed line reveal the over- and underrepresentation, respectively, of cells located in protected areas or hot spots of fishing pressure.

the breath of evolutionary diversification on ecosystem functioning [35]. Our study has shown that the present Mediterranean MPA system does not protect fish phylogenetic diversity hot spots present along the southwestern coast. We also show that fishing pressure is highest in these ecosystems. These areas should thus be of primary conservation focus when establishing new MPAs, in order to protect the large amount of fish evolutionary history that they represent.

We highlighted that the hot spots of Mediterranean fish functional diversity are located in the Gulf of Gabès (Figure 2E) and, more generally, along the eastern North African coast, where few MPAs have been established (Figure 1B) but also where fishing pressure is low (Figure 1C). Experiments [36] and empirical studies carried out on the Mediterranean coast [18] have shown that fish functional diversity has a major influence on ecosystem functioning, and thus the conservation of this overlooked biodiversity component should be of main concern in aquatic systems. Recent studies suggest that human-mediated pressures decrease fish functional diversity [37], whereas MPAs successfully restore or maintain this critical component [11, 38]. However, the incorporation of functional diversity into conservation strategies is very recent and only limited to terrestrial cases [3, 39]. In the Mediterranean, hot spots of fish functional diversity are overlooked by the current Mediterranean system of MPAs. A new MPA establishment strategy would need to pay more attention to such areas, given their potential to be representative of overall coastal ecosystem functioning.

Conservation targets for systematic conservation planning, i.e., optimizing the combination of sites that either achieves conservation targets at minimum cost (the minimum set coverage problem) or satisfies the largest number of conservation targets given a budget constraint (the maximum coverage problem), are usually set at the level of individual species [9]. Previous studies attempting to incorporate phylogenetic diversity into the systematic conservation planning process have shown that considering the optimization of phylogenetic diversity would not fundamentally change the results of the planning effort except in very limited cases [16]. Our results suggest that phylogenetic and functional diversity do not always overlap with taxonomic diversity; this implies that conservation planning integrating all biodiversity components would be more useful than previously thought. Current strategies to incorporate phylogenetic (or functional) diversity into conservation planning involve the ranking of species according to their phylogenetic (or functional) originality, a combination of threat and originality [31], or the representation of phylogenetic (or functional) diversity without a minimum area requirement [16]. These strategies are not fully appropriate to represent these two crucial components of diversity because they still use a species-centered approach for optimization or ignore the basic principle of minimum area requirement. Thus, the spatial optimization of the Mediterranean MPA system, taking into account all biodiversity components and both political and social constraints (conflicts with fisheries, country policies, etc.), still requires conceptual developments and further data.

Given the exceptional biodiversity of the Mediterranean and the major threats that it faces, protecting the diversity of its biological traits as well as its evolutionary heritage should be viewed as a priority. To reach the COP10 target 11, we need to rapidly turn a much larger surface area into MPAs. To optimize future conservation efforts, i.e., number, size, and spacing of MPAs, we may rely on many criteria, among which connectivity and biodiversity patterns are essential. Connectivity among MPAs, the extent to which populations in different MPAs are linked by exchange of larvae, recruits, juveniles, or adults [40], may promote regional persistence particularly for exploited species within a context of global change [41]. By highlighting the spatial mismatching between the different components of fish biodiversity, our study poses new challenges for the design of a "true" MPA network in the Mediterranean Sea, i.e., a system of interconnected MPAs designed to protect all the components of fish biodiversity and integrating the potential impacts of climatic change [42] and connectivity among populations [22].

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.cub.2011.05.005.

Acknowledgments

This study was partly funded by Fondation Total, Fondation pour la Recherche sur la Biodiversité project BIODIVMED, Agence National de la Recherche project ANR-09-PEXT-01102 546 EVORANGE, and Centre National de la Recherche Scientifique program BIODIVMEX. D.M. was supported by Marie Curie International Outgoing Fellowship (FISHECO) IOF-GA-2009-236316. M.C. was funded by the European Commission through a Marie Curie International Outgoing Fellowship to the ECOFUN project (FP7-PEOPLE-2007-4-1-IOF). This publication is contribution number 2011-049 of the Institut des Sciences de l'Evolution de Montpellier (UMR CNRS-UM2 5554).

Received: March 14, 2011
Revised: April 20, 2011
Accepted: May 4, 2011

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Current Biology, Volume *21*

Supplemental Information

Protected and Threatened Components of Fish Biodiversity in the Mediterranean Sea

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Supplemental Experimental Procedures

Fish Species Distributions

We collected data, using a Geographical Information Systems (GIS) software (ArcGIS v.9.3 by Environmental Systems Research Institute), on fish species distributions, mostly available in the form of expert-drawn maps or sighting locations, to map spatial patterns of biodiversity components. Such data were available from the 'Fishes of the Northern Atlantic and Mediterranean' (FNAM atlas) [19]. We estimated species richness of different species groupings as the sum of the species co-occurring by overlapping distribution maps at fine-scale resolution (0.1 x 0.1 degree grid cell, i.e. approximately 11 km at this latitude).

MPA Locations

MPAs were digitized on the basis of MedPan data (http://www.medpan.org/) as well as from maps, polygons and GPS coordinates provided by managers of the Mediterranean MPAs. We overlaid MPAs polygons with the 0.1°x0.1° regular grid considering that even if a small part of a cell belongs to a protected area, the whole species occurring in that cell potentially benefit from the reserve effect. Since our inventory of 100 Mediterranean MPAs (the Pelagos sanctuary being excluded) are strictly coastal, we only considered the continental shelf in the analyses. We thus only considered a set of 8186 cells corresponding to the limit of 200m water depth from the 27078 cells constituting the entire Mediterranean Sea dataset.

The Pelagos Sanctuary is entirely dedicated to the protection of marine mammals and thus does not provide any level of protection for fish. Furthermore the major part of the Pelagos Sanctuary is located in non coastal waters. Thus we did not considered the Pelagos Sanctuary as a coastal MPA potentially beneficial to coastal fishes.

Mapping Fishing Pressure

To map fishing pressure we included the exploitation of marine resources by fisheries. We integrated information from industrial or semi-industrial demersal and pelagic fisheries, and from artisanal fisheries. We used the half-degree global database developed by the Sea Around Us project (www.seaaroundus.org) based on FAO and other datasets for commercial (both demersal and pelagic fisheries) and artisanal fisheries for the period 2000-2006 [43-44]. This dataset provided gear type and species caught for all reported fished species, which was used to calculate and average catch rate (in tonnes per km^2 per year) for each fishing category for each half-degree cell. A similar dataset was used by the “Global Map of Human Impacts to Marine Ecosystems” project, but there are limitations to the data [45]. Hotspots of high fishing pressure were defined as areas with the top 5% values.

Phylogenetic Tree for the 282 Fish Species

A first analysis of available sequences allowed to select genes with enough representation among species in order to be included in the analysis. Five genes were subsequently used to reconstruct Mediterranean teleost phylogeny, including four belonging to the mitochondrial genome (12S rRNA, 16S rRNA, cytochrome b, and cytochrome oxidase I), and one of nuclear origin (rhodopsin). After alignment of these individual genes, a 5-gene supermatrix was assembled, allowing the inclusion of 356 species (67% of the Mediterranean teleosts) and 17 extra-Mediterranean species. The least represented gene was the cytochrome oxidase I gene with 126 species (32 %), and the best represented one was 16S rRNA with 276 species (74 %). A total of 2,839 sites was subjected to a maximum likelihood (ML) analysis under PAUP*, version 4b10 [46]. Then, the highest-likelihood topology was used for a molecular dating procedure under a log-normal rate autocorrelated molecular clock under PhyloBayes [47], with paleontological calibrations on 23 nodes.

For the purposes of the present study we needed maximal representation of coastal species. Therefore, we eliminated non-coastal species from the resulting ultrametric tree, yielding a 203-taxon dated tree. To increase the taxonomic coverage, we grafted an additional 79 coastal species for which no sequence data was available, but for which congeneric species were already present in the ML topology. First, 30 species were attached to the backbone tree as polytomies at the most recent common ancestor (MRCA) of their congeneric species [48]. Second, when congeneric species were unavailable, the procedure was extended by using more distant taxonomic relatives: respectively 31 and 18 species were grafted to the MRCA of members of their families and orders. To ensure that this new tree remained ultrametric, branch lengths leading to each of the 79 grafted species were set to the age of the node where they had been attached. The final 282-taxon ultrametric tree of Mediterranean coastal species was used in all subsequent analyses.

Phylogenetic Diversity

A dated phylogeny for the 282 Mediterranean coastal teleost fish species was reconstructed from molecular data downloaded from GenBank (Supplemental Experimental Procedures).

We calculated the phylogenetic diversity (PD) of fish assemblages contained in each grid cell [30]. We used the standardized effect size PD (SES.PD), which is the difference between the observed phylogenetic diversity in an assemblage and the mean phylogenetic diversity obtained with null assemblages generated using a random choice of species from the regional pool, divided by the standard deviation of phylogenetic diversities in the null data [49-50]. Thus, positive SES.PD values indicate higher phylogenetic distances among co-occurring species, or higher phylogenetic diversity than expected regarding the number of species while negative SES.PD values indicate lower phylogenetic diversity than expected. These calculations were carried out using the R software and the picante 2.1 package [51].

Functional Diversity

We compiled information for the 282 species on the following 15 traits: depth at which species are encountered (minimum and maximum), mean length, maximum length, horizontal and vertical distribution, habitats, migration, reproduction, semelparity, sex shift, larvae types behavior, species origins, diets, based on different sources (fishbase.org). Since we had a mixture of quantitative and qualitative traits with some missing values (filling rate 97.1%) we computed a Gower distance between each pair of species [52-53]. This distance gives the same weight to each variable regardless of the number of missing values and the type of data. Then we built a functional dendrogram depicting the functional relationships among species using hierarchical classification. Because cophenetic distances estimated from hierarchical classification may depend on the clustering method, we used a consensus approach [54]. This method tests all combinations of clustering methods and then selects the most reliable dendrogram to estimate ultrametric functional distances between species pairs.

We used the FD index [55] to estimate functional diversity of fish assemblages. Since FD has a monotonic increase with species richness [55-56], we computed a standardized effect size FD (SES.FD) to provide an estimation of functional diversity independent from species richness.

Statistical Analyses

We implemented two different methods that are commonly used to assess spatial congruence: correlations and overlap between hotspots [15, 57]. First, we calculated coefficient of correlations between all pairs of variables. Significance levels were calculated using Dutilleul's degrees of freedom (a correction for spatial autocorrelation), implemented in the program SAM [58]. This correction was necessary because spatial autocorrelation in both of the variables under consideration can greatly inflate Type-I statistical error rates [59].

Second, we tested for congruence between the components of fish biodiversity, the reserve system, and the fishing pressure by measuring the extent of spatial overlap between hotspots. Since MPAs are present in 390 cells, which roughly represent 5% of the total number of cells on the continental shelf, we defined hotspots as the 5% of grid cells with the highest values for each variable. When two or several cells had the same number of species they were all considered as hotspots. To this aim, all pairs of variables were considered successively and the observed number of overlaps Oo (i.e. the number of cells for which we had a hotspot for both variables) was counted. The expected number of overlaps Oe, corresponding to the independence between the two hotspot ensembles, was calculated as Oe = Ni . Nj / NT, where Ni is the number of hotspots for the first variable i, Nj is the number of hotspots for the second variable and NT is the total number of grid cells. To assess whether the observed number of overlaps (Oo) is significantly different from that obtained by chance (Oe) we computed a randomization procedure. Values contained in cells of one of the two variables considered were randomly permuted 9999 times and the number of overlaps was estimated for each permutation. The observed numbers of overlaps (Oo) were then compared to their respective null distributions to calculate p-values [60].

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Manuscrit C.

The Mediterranean Sea as a "cul-de-sac" for endemic fishes facing climate change.

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Global Change Biology

Global Change Biology (2010) **16**, 3233–3245, doi: 10.1111/j.1365-2486.2010.02224.x

The Mediterranean Sea as a ‘cul-de-sac’ for endemic fishes facing climate change

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Abstract

The Mediterranean Sea is a hotspot of biodiversity, and climate warming is expected to have a significant influence on its endemic fish species. However, no previous studies have predicted whether fish species will experience geographic range extensions or contractions as a consequence of warming. Here, we projected the potential future climatic niches of 75 Mediterranean Sea endemic fish species based on a global warming scenario implemented with the Mediterranean model OPAMED8 and a multimodel inference, which included uncertainty. By 2070–2099, the average surface temperature of the Mediterranean Sea was projected to warm by 3.1 °C. Projections for 2041–2060 are that 25 species would qualify for the International Union for the Conservation of Nature and Natural Resources (IUCN) Red List, and six species would become extinct. By 2070–2099, 45 species were expected to qualify for the IUCN Red List whereas 14 were expected to become extinct. By the middle of the 21st century, the coldest areas of the Mediterranean Sea (Adriatic Sea and Gulf of Lion) would act as a refuge for cold-water species, but by the end of the century, those areas were projected to become a ‘cul-de-sac’ that would drive those species towards extinction. In addition, the range size of endemic species was projected to undergo extensive fragmentation, which is a potentially aggravating factor. Since a majority of endemic fishes are specialists, regarding substratum and diet, we may expect a reduced ability to track projected climatic niches. As a whole, 25% of the Mediterranean Sea continental shelf was predicted to experience a total modification of endemic species assemblages by the end of the 21st century. This expected turnover rate could be mitigated by marine protected areas or accelerated by fishing pressure or competition from exotic fishes. It remains a challenge to predict how these assemblage modifications might affect ecosystem function.

Keywords: BIOMOD, fragmentation, global warming, habitat suitability model (HSM), IUCN, species turnover, species vulnerability

Received 2 November 2009; revised version received 11 February 2010 and accepted 15 February 2010

Introduction

Over the past 100 years, the worldwide climate has warmed by 0.61 °C and, by the end of the 21st century, the Intergovernmental Panel on Climate Change (IPCC) has projected that air temperatures will increase by 1.4–5.8 °C (IPCC, 2007). Recent investigations have shown that, although ambitious mitigation efforts can be implemented to reduce global warming, the inertia in climate and human systems will lead to increasing temperatures worldwide, even above those previously estimated (Van Vuuren *et al.*, 2008).

A large body of evidence has accumulated that demonstrates the multiple impacts of climate warming on biodiversity. The expected responses to global warming include (i) a wide spectrum of taxa seeking cooler environments by shifting geographic distributions towards the poles or higher altitudes (Hickling *et al.*, 2005; Parmesan, 2006; Lenoir *et al.*, 2008), (ii) high global extinction rates (Thomas *et al.*, 2001; Cheung *et al.*, 2009), and (iii) marked reorganizations of local communities that have resulted, in some cases, from native population extinctions and the expansion of exotic thermophilic species (Mills *et al.*, 2004; Olden *et al.*, 2006). Moreover, global warming has a strong effect on the growth, survival, and reproduction rates of many species (e.g., Diaz Almela *et al.*, 2007; Foden *et al.*, 2007);

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this may, in turn, modify the size-based structures of communities (Blanchard *et al.*, 2005). The effects of these changes on the Earth's biota are currently under scrutiny; but 'winner' species that expand their geographical ranges can already be distinguished from 'loser' species that are subject to range contractions (Wilson *et al.*, 2004). Just as for their terrestrial counterparts, marine fish communities are changing markedly in response to climate changes (Attrill & Power, 2002; Genner *et al.*, 2004; Perry *et al.*, 2005; Hiddink & Hofstede, 2008). Indeed, southern fish species have shown increased abundance and a northward expansion of geographical ranges as a result of warming seas in the Northern hemisphere (e.g., Perry *et al.*, 2005; Hiddink & Hofstede, 2008; Cheung *et al.*, 2009).

The impacts of global warming are particularly critical in areas where range shifts are physically constrained, for example, in semienclosed areas (Pozdnyakov *et al.*, 2007) or polar regions (Cheung *et al.*, 2009). The Mediterranean Sea, an inland sea that comprises only 0.32% of the global oceanic volume, contains 4–18% of all known marine species (Bianchi & Morri, 2000), and nearly 10% of fishes are endemic to the Mediterranean Sea (Quignard & Tomasini, 2000). Over the past 30–40 years, water temperatures of the western Mediterranean Sea have been increasing at depth (Bethoux *et al.*, 1990; Rixen *et al.*, 2005) and at the surface (Diaz Almela *et al.*, 2007), and this reflects increased occurrences of thermophilic marine species (Goren & Galil, 2005) and shifts in fish geographic distributions (Sabates *et al.*, 2006; Ben Rais Lasram & Mouillot, 2009).

Fish geographic distributions are strongly clustered in the Mediterranean Sea: subtropical species occur in the south-eastern area, where water temperatures are higher than average (Theocharis *et al.*, 1993), whereas cold-adapted species inhabit northern areas (Bianchi & Morri, 2000). However, as a result of global warming, species that were typically found in the warm waters of the southern areas have been observed more frequently in the north, where waters are becoming warmer (Astraldi *et al.*, 1995; Bianchi & Morri, 2000; Sabatés *et al.*, 2006). In parallel, the abundance of some boreal species has markedly decreased since the 1980s (Quignard & Raibault, 1993).

Changes in thermal conditions have been documented to drive the reorganization of fish assemblages (Rahel & Hubert, 1991; Ben Rais Lasram & Mouillot, 2009). Thus, sea surface warming is expected to drive a general northward shift of fish ranges in the Mediterranean Sea leading to the gradual replacement of cold-temperate species by thermophilic species. Hence, the coldest parts of the Mediterranean Sea (Gulf of Lion and northern Adriatic, Fig. 1) could initially serve as a sanctuary for cold-temperate species; but, with intensified warming, those areas might become a 'cul-de-sac', from which cold-temperate species could not escape. This phenomenon would be critical to endemic species, because the trapping effect would lead to species extinction. The vulnerability of endemic Mediterranean Sea fishes is important because its surface waters are expected to warm by an average of 3.1 °C by the end of the 21st century (Somot *et al.*, 2006). Consequently, an assessment of future distributions of climatic niches for Mediterranean Sea endemic fishes is urgently needed to anticipate the potential biological response to the projected climate warming.

In addition to species geographic range shifts, climatic warming may also induce the fragmentation of suitable habitats. This issue has been largely neglected in studies that previously explored spatial responses to climate change. Indeed, there is a potential synergism

Fig. 1 Main geographical features of the Mediterranean Sea. The axes indicate degrees latitude (*x*-axis) and longitude (*y*-axis).

between climatic constraints and habitat fragmentation that may accelerate population decline and extinction rates (Opdam & Wascher, 2004). At the very least, habitat fragmentation can cause a loss of genetic diversity (Gibbs, 2001), and an increased population's vulnerability to extreme events and disturbances (Piessens *et al*., 2009). The northern coast of the Mediterranean Sea is the more sinuous; the semiisolated basins (e.g., Adriatic Sea) and islands (Fig. 1) may promote increasing fragmentation of the geographic distributions of species as they move northward to seek cooler temperatures. Thus, to understand the total potential risk that climate change poses to Mediterranean Sea endemic fishes, consideration also must be given to the spatial fragmentation of thermally suitable habitats.

The degree of specialization is thought also to contribute strongly to extinction risk following climate change because specialist species require particular resources or habitats in addition to suitable thermal conditions in order to survive (e.g., Biesmeijer *et al*., 2006). Here, we refer to the Grinnellian specialization, defined as the breadth of biotic and abiotic resources required for a species to survive (e.g., DeVictor *et al*., 2010). Mediterranean Sea endemic fishes are more or less specialized in these resource requirements. This information must be considered for a precise interpretation of the predicted geographic range shift in response to the projected climate warming. Indeed, the most specialized fishes will face constraints in addition to simply seeking suitable thermal conditions; these fish may be considered at greater risk of population decline and extinction compared with the generalist species that are able to exploit a wide range of resources.

Here, we assessed the potential impacts of climate change on the spatial distribution of Mediterranean Sea endemic fish species. More precisely, we investigated the vulnerability of species to climatic niche reductions that might result from sea temperature changes predicted to occur by 2041–2060 and 2070–2099. Because the temperature of air and water are roughly correlated (Caissie, 2006), most forecasts of aquatic species range shifts consider air temperature to be a proxy of water temperature (e.g., Buisson *et al*., 2008). This might be acceptable for inland water bodies, like rivers or lakes, but it is not appropriate for the marine habitat, where many forcing factors interact within a climate change context. For that reason, we calculated future sea surface temperatures (SST) using a Mediterranean Sea thermohaline circulation model that accounted for relevant forcing parameters, including river runoff, exchanges with connected water masses, and wind regimes (Somot *et al*., 2006). These climatic data were combined with habitat suitability models (HSM) to obtain consensus forecasts of potential future climatic niches (Araujo & New, 2007). For each species, we quantified the potential changes in geographic range and thermal habitat fragmentation. The potential effect of global change on Mediterranean Sea endemic fishes was summarized by assessing their potential endangerment according to their eligibility for Red Listing by the International Union for the Conservation of Nature and Natural Resources (IUCN). Finally, at the assemblage level, we mapped the expected temporal turnover in endemic species composition across the Mediterranean Sea and calculated a threat indicator based on the population status before and after climate warming.

Materials and methods

Species data

A database was generated for the geographic distributions of the 79 known endemic fish species in the Mediterranean Sea ('wide' and 'narrow' endemism, according to Quignard & Tomasini, 2000) using a Geographical Information System software package (ARCVIEW 3.3 by ESRI). Data were compiled from the atlas of Fishes of the Northern Atlantic and Mediterranean (FNAM; Whitehead *et al*., 1986). That atlas is based on regional data sets and expert knowledge; it provides the only available basin-wide information on the geographic ranges of all Mediterranean Sea fish species (Ben Rais Lasram *et al*., 2009). Four species were deleted from the dataset for the following reasons: *Tetrapturus belone*, because its presence throughout the Mediterranean Sea made discrimination between presence and absence impossible; *Gobius strictus*, *Microichthys sanzoi*, and *Nansenia iberica* because their extremely low prevalence might introduce bias in geographic range predictions (Stockwell & Peterson, 2002; Thuiller, 2004).

Over 93% of Mediterranean Sea endemic fish species are strictly confined to coastal waters; i.e., they do not live beyond the limits of the continental shelf. Thus, we restricted the dataset to the continental shelf (200 m depth limit). Our final dataset described the extent of occurrences for 75 endemic species on a 0.1° resolution grid covering the whole Mediterranean Sea continental shelf.

We collected ecological information for these 75 fish species to evaluate their degree of specialization in terms of habitat and feeding resources. First, we distinguished pelagic fish, with no substratum requirements, from benthic and demersal species, which require particular substrata (rocky shores, seagrasses). The former species were classified as habitat generalists (HG) while the latter were classified as habitat specialists (HS). Second, we classified fish species according to their feeding guild. Carnivorous fishes were considered to be diet specialists (DS) because they feed on particular prey while omnivorous and planktivorous fishes were considered diet generalists (DG) because they feed on a large range of resources. This information was obtained from FishBase (Froese & Pauly, 2009) and from the FNAM atlas (Whitehead *et al*., 1986).

Temperature data

In terrestrial ecosystems, numerous environmental variables (temperature, rainfall, soil structure, and geochemistry, etc.) are required to make satisfactory predictions of species occurrences (e.g., Beaumont *et al.*, 2007). In contrast, marine ecosystems are constrained by fewer limiting factors. The main driver of fish geographic ranges was demonstrated to be water temperature (Sabates *et al.*, 2006; Dulvy *et al.*, 2008; Hiddink & Hofstede, 2008; Cheung *et al.*, 2009). In addition, the gradients and thresholds of SST have been shown to shape fish distributions in the Mediterranean Sea (e.g., Ben Rais Lasram & Mouillot, 2009). Thus, SST was used as the sole predictor of fish distribution patterns in this study.

The FNAM atlas used to digitize the spatial distributions of species was edited between 1984 and 1986. Therefore, we used the SST values averaged from an early period as a baseline to calibrate the species distribution models: weekly SST values on a 1° grid were taken for the period 1981–1984 from the National Climatic Data Center (NCDC) National Operational Model Archive and Distribution System of Meteorological Data Server (NOMADS) of the US National Oceanic and Atmospheric Administration (NOAA) Satellite and Information Service (www.osdpd.noaa.gov/PSB/EPS/SST/al_climo_mon.html). 0.1° resolution needed for analysis were interpolated by means of ordinary kriging (Diggle & Ribeiro, 2007). Fourteen variables were obtained – 12 monthly SST means, the absolute minimum SST, and the absolute maximum SST. All these variables were considered because some studies have reported the influence of winter, but not summer, conditions on fish composition assemblages (Henriques *et al.*, 2007), whereas others have emphasized the importance of surface temperature during particular life stages to predict fish spatial boundaries. For example, Sabates *et al.* (2006) demonstrated that the abundance of round sardinella (*Sardinella aurita*), in some parts of the Mediterranean Sea, was significantly correlated with the SST of the previous year recorded at the start of gonad maturation (April). However, species distribution models with too many predictive (and covarying) variables may overfit the data and show reduced predictive ability. To mitigate this problem, we reduced the set of predictive variables on the basis of a correlation analysis (Pearson's coefficient).

Future SST values were obtained for the middle (2041–2060) and the end of the 21st century (2070–2099) from the Mediterranean model OPAMED8, based on the IPCC A2 scenario (Somot *et al.*, 2006). OPAMED is a regional model (the Atlantic Ocean is considered only as a buffer zone) that accounts for the main drivers of SST, including air–water energy fluxes, river discharges, and water exchanges with the surrounding seas. Although widely used for regional scenarios of climate change (Christensen *et al.*, 2002), the A2 scenario is considered a conservative, but not the worst, future prediction of global warming. It assumes a very heterogeneous world that preserves local identities, and which results from a continuously growing human population and atmospheric CO_2 concentrations of $\sim$815 ppm by 2099 (IPCC, 2007). The A2 scenario was chosen for OPAMED because it has become the standard for regional climate studies (Christensen *et al.*, 2002). Future climate data were averaged for the middle (2041–2060) and the end of the 21st century (2070–2099). Maps were interpolated at 0.1° resolution using ordinary kriging.

Model calibration and evaluation

Equilibrium is a required assumption for predicting and projecting species distribution areas (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005). Indeed, to be reliable, models must capture the fully realized niche in order to avoid spurious results due to truncated responses (Thuiller *et al.*, 2004). Because our analysis was restricted to endemic species at a basin-wide scale, we assumed that the equilibrium condition was not violated.

Since there is still uncertainty in the modeling of climatic habitats that determine species geographic distributions, we implemented an ensemble forecasting method (Thuiller, 2004; Araujo & New, 2007; Buisson *et al.*, 2009; Marmion *et al.*, 2009). The 75 fish species distributions were modeled using seven of the techniques available in the BIOMOD package for ensemble forecasting of species distributions (Thuiller *et al.*, 2009). These HSM were implemented in R (R Development Core Team, 2008): (1) Generalized Linear Models (GLM), (2) Generalized Additive Models (GAM), (3) Classification Tree Analysis (CTA), (4) Random Forest (RF), (5) Boosted Regression Trees (BRT), (6) Mixture Discriminant Analysis (MDA), (7) Surface Range Envelope (SRE).

We implemented a cross validation procedure to avoid circular reasoning when the same data were used to construct and evaluate the model (e.g., Kohavi, 1995). For each species, models were calibrated using a random sample of the initial data (80%). Then, each model was evaluated on the remaining 20% of the initial data set for each species with the True Skill Statistic (TSS) criterion. Because AUC (Swets, 1988) and Kappa (Cohen, 1960) methods have been severely criticized (Termansen *et al.*, 2006; Austin, 2007; Peterson *et al.*, 2007; Lobo *et al.*, 2008), we based our evaluation on TSS, as recommended by Allouche *et al.* (2006) and used in some recent studies (e.g., Allouche *et al.*, 2008; Boitani *et al.*, 2008; Freeman & Moisen, 2008; La Morgia *et al.*, 2008). TSS scores were interpreted with the same classification as was used for Kappa, according to the Landis & Koch (1977) accuracy classification scheme: $TSS > 0.8$, excellent; $0.6 > TSS < 0.8$, good; $0.4 > TSS < 0.6$, fair; $0.2 > TSS < 0.4$, poor; and $TSS < 0.2$, no predictive ability.

The predicted presence/absence of a species was derived from the predicted probability of occurrence using the threshold that maximized model accuracy; i.e., that maximized the percentage of presence and absence that could be correctly predicted (Thuiller, 2003).

Model projections

Alternative HSMs may provide markedly different projections for the same dataset, and model evaluations often cannot demonstrate which projection is superior (Araujo & New, 2007). To overcome these limitations, we used the Weighted Average Consensus (WAC) method (Marmion *et al.*, 2009; Thuiller *et al.*, 2009) that takes into account model-based uncertainty. Using the projected temperatures for 2041–2060 and 2070–2099, we projected the potential thermal habitat for each species according to each of the seven HSMs. We assumed no dispersal limitation towards new areas with suitable temperature conditions because recent invasions showed that Lessepsian fishes (exotic species from the Red Sea invading the Mediterranean Sea) reach a mean dispersal rate of $221 \pm 5.4\,\mathrm{km\,yr^{-1}}$ on the northern side of the Mediterranean Sea, given favorable climatic conditions, regardless of their biological traits (Ben Rais Lasram *et al.*, 2008). Then, for each grid cell, we calculated a probability of occurrence (W) according to the weight of each model, based on TSS values

$$W_i^{\mathrm{TSS}} = \frac{\sum_j (\mathrm{TSS}_j \times m_{ji})}{\sum_j \mathrm{TSS}_j}, \tag{1}$$

where i is a given grid cell, j is a given model, and m_{ji} is the projected probability of occurrence in cell i according to model j. The future weighted probabilities of occurrence were then transformed into presence/absence values according to the same threshold values as were used for the current predictions (Thuiller *et al.*, 2009).

Species vulnerability

First, patterns of fragmentation in current and projected spatial distributions were measured for the 75 species. Fragmentation was calculated using the Fragstats Spatial Pattern Analysis Program for Quantifying Landscape Structure, Version 3.1 (McGarigal *et al.*, 2002). The term 'fragmentation' was reserved for the breaking apart of a habitat, independent of habitat loss; thus, we measured fragmentation in terms of the number of patches (NP). A myriad of fragmentation metrics are available, but most are highly redundant and would lead to similar results (McGarigal & Marks, 1995).

Second, the shift in a species' geographic range was calculated by subtracting the projected suitable habitat from the currently used habitat. Then, the species' vulnerability was assessed by identifying its IUCN Red List category (version 3.1 criterion A3c IUCN, 2001, following Bomhard *et al.*, 2005; Thuiller *et al.*, 2005), which depended on the projected reductions of suitable habitat:

- Extinct (Ex): a projected reduction of 100%
- Critically endangered (CE): a projected reduction between 80% and 100%
- Endangered (En): a projected reduction between 50% and 80%
- Vulnerable (V): a projected reduction between 30% and 50%
- No concern (NC): below 30% or expansion

Third, a composite threat indicator at the level of the entire endemic fish assemblage was calculated to determine whether a trend in global biodiversity threat could be expected following a given climate change. This indicator, introduced by Dulvy *et al.* (2006), is based on fish population status according to the IUCN list decline criteria. In summary, the indicator is a weighted average of species threat scores at the assemblage level. Species threat scores (according to Butchart *et al.*, 2004) include: 0 (no concern), 1 (vulnerable), 2 (endangered), or 3 (critically endangered). This indicator was estimated for the present range sizes and IUCN classifications, and for their projected status both in 2041–2060 and 2070–2099.

Species turnover

Beyond the conservation of individual species, scientists are increasingly concerned with the conservation of ecological assemblages and ecosystems. Assemblage degradation comprises at least three components: change in species composition, change in structure, and disruption of the ecological processes (Franklin *et al.*, 2002). However, current methods for assemblage level projections require scrutiny, and they have not proven to improve the accuracy of predictions for species range shifts due to climate changes (Baselga & Araujo, 2009). Hence, we quantified the level of endemic assemblage degradation by evaluating the expected turnover in each cell

$$\mathrm{TO} = (P + G)/(\mathrm{SR} + G)100, \tag{2}$$

where TO is the turnover percentage, P is the number of species lost by a cell, G is the number of species gained per cell, and SR is the current species richness per cell (Peterson *et al.*, 2002; Thuiller *et al.*, 2006).

Results

Present and future climates

The map of the mean SSTs in the early 1980s (Fig. 2a) revealed that the warmest area of the Mediterranean Sea was the Levantine Basin, with a mean SST of 21.8 °C; the coolest areas were the Gulf of Lion and the Ligurian Sea, with a mean SST of 16.9 °C. By 2041–2060, the majority of the Mediterranean Sea is expected to become warmer, but the northern Adriatic is expected to become cooler; this is according to the OPAMED8 model, based on the A2 IPCC scenario (Fig. 2b). By 2070–2099, the Mediterranean Sea is projected to warm up by 3.1 °C (Fig. 2c); the last cool enclaves are expected to be the Gulf of Lion and the northern Adriatic, with a mean SST of around 18 °C.

Among the 14 SST values studied (one for each month, the maximum, and the minimum), there were very high correlations among the following groups: December, January, February, and March (all $r > 0.980$); July, August, and the absolute maximum (all $r > 0.980$); and September, October, and November (all $r > 0.989$). Accordingly, the number of predictor SST variables could be reduced to seven: April, May, June, the absolute minimum, the absolute maximum, the winter mean, and the autumn mean.

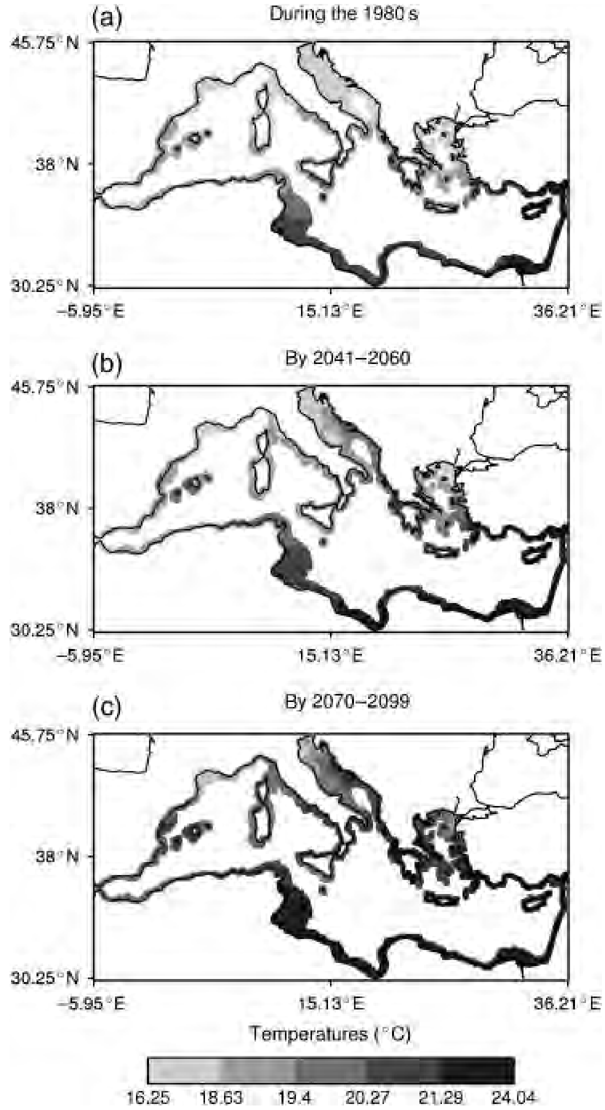

Fig. 2 Sea surface temperature (SST) changes predicted on the continental shelf of the Mediterranean Sea. (a) SST during the 1980s [according to NOAA data; (www.osdpd.noaa.gov/PSB/EPS/SST/al_climo_mon.html)]; (b) SST predicted for 2041–2060 and (c) SST predicted for 2070–2099 (according to the OPAMED8 based on the A2 IPCC scenario). The axes indicate degrees latitude (*x*-axis) and longitude (*y*-axis).

Model prediction accuracies

The climatic niches of the 75 fish species were based on the fish distributions and SSTs collected in the early 1980s. These were modeled according to seven classical techniques. The predictive accuracy over all seven HSMs was classified as 'excellent', with a mean TSS criterion of 0.89. The least accurate model was the SRE, with a TSS = 0.56 whereas the most accurate model was the RF, with a TSS = 0.98. The TSS was insensitive to prevalence since model accuracy was excellent even for species of low prevalence and fragmented habitats. However, no evidence of model superiority emerged; thus, we used the WAC method to project potential climatic niches.

Projected species vulnerability

According to the WAC method, by 2041–2060, 31 species (41%) were projected to gain geographic range (winners) whereas 44 species (59%) were projected to lose geographic range (losers) (Fig. 3a). Among the 44 loser species, 36 were expected to experience increased spatial fragmentation whereas six were projected to become extinct (Fig. 3a). The 31 winner species were predicted to experience higher fragmentation with more patches occupied (Fig. 3a). When species were classified into different specialization categories, the species classified as both habitat (pelagic) and diet (omnivorous or planktivorous) generalists were projected to become either more fragmented or extinct by 2041–2061 (Fig. 3b); those considered HG and DS were predicted to gain range size, but with more fragmentation (Fig. 3c); and those considered HS were projected to become either more fragmented or extinct (Fig. 3d and e).

By the end of the 21st century, only 25 species (33%) were projected to gain geographic range, and the remaining 50 endemic species (66%) were projected to lose geographic range (Fig. 3a). Among the 50 loser species, 23 were expected to become more fragmented and 14 were projected to become fully extinct (Fig. 3a). Among the 25 winner species, 23 were predicted to experience a more fragmented geographic distribution (Fig. 3a). As for the predictions for the middle of the century (2041–2060), by 2070–2099 all generalist species were predicted to become either more fragmented or extinct (Fig. 3b); those species considered to be HG and DS (Fig. 3c) were projected to gain range size compared with their present distributions. Only one benthic carnivorous species, *Solea aegyptiaca*, was predicted with a thermal suitable habitat spread almost all over the Mediterranean Sea continental shelf (Fig. 4a). Among the 14 species projected to become extinct (Fig 3a), 12 are HS. Of note, among the 49 species considered specialists in both HS and DS, only 14 were predicted to gain range size, and 13 of those would experience more fragmentation of suitable climate niches (Fig. 3e). For example, in the 1980s, the Scaldback (*Arnoglossus kessleri*) was continuously distributed throughout all Mediterranean Sea basins except the Alboran Sea; by the end of the 21st century, however, that species was expected to lose 90% of its potential suitable climatic habitat and its range would be restricted to the Gulf of

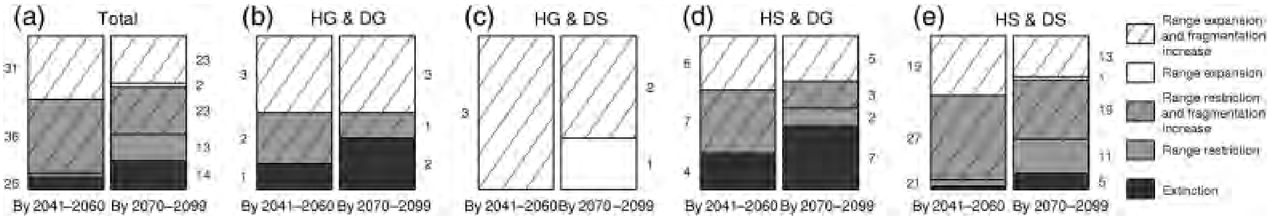

Fig. 3 Predicted changes in range size and habitat fragmentation of endemic fish species due to global warming at the middle (by 2041–2060) and end (by 2070–2099) of the 21st century. (a) Changes predicted for the entire assemblage of Mediterranean Sea fish species, and (b–e) for species categories: (b) Generalists in both habitat and diet (HG & DG); (c) generalists in habitat, but specialists in diet (HG & DS); (d) specialists in habitat, but generalists in diet (HS & DG); and (e) specialists in both habitat and diet (HS & DS). HG, habitat generalists (pelagic species); HS, habitat specialists (benthic and demersal species); DG, diet generalists (omnivorous and planktivorous species); DS, diet specialists (carnivorous species). The numbers on the *y*-axes indicate the numerators of the fraction of the given population that was predicted to undergo the indicated change.

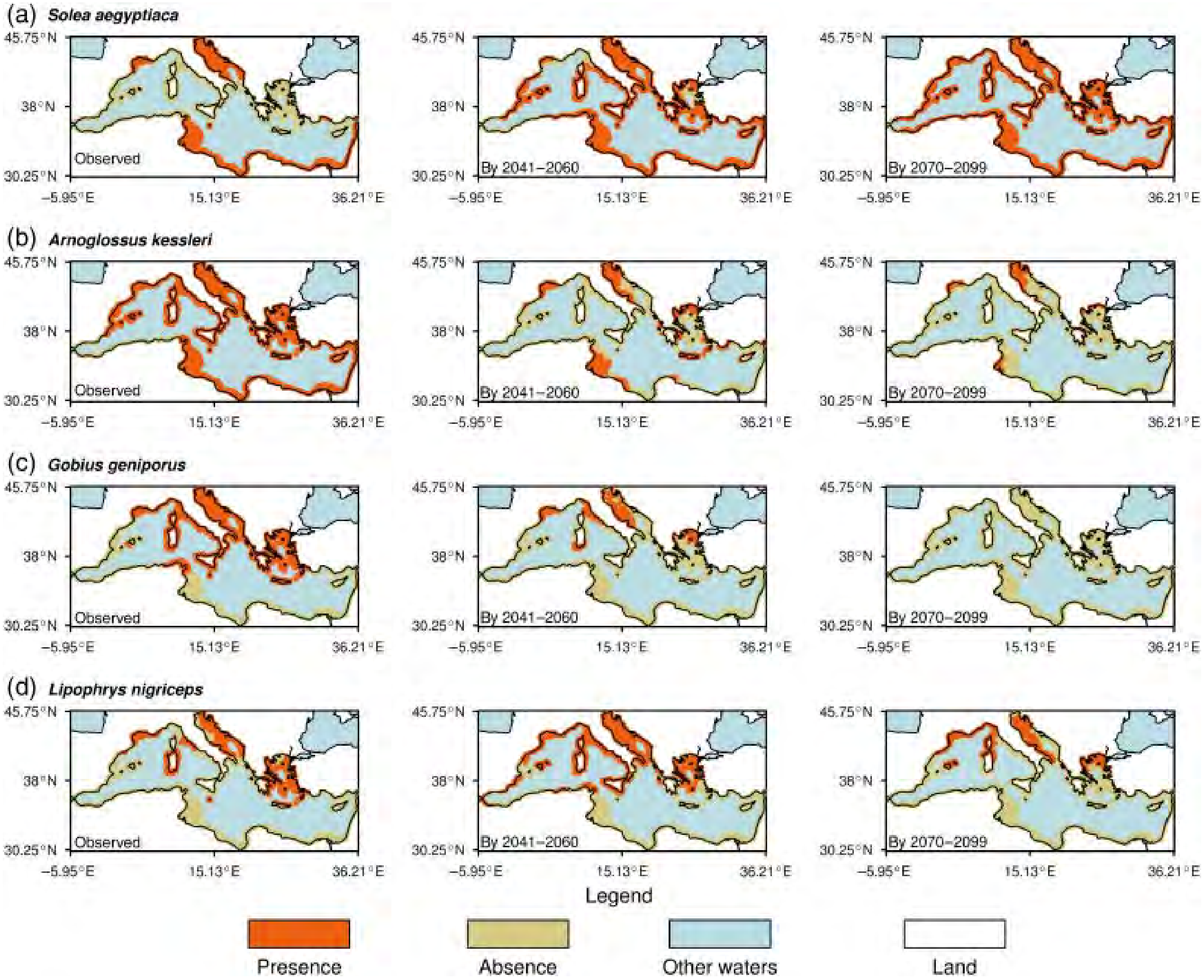

Fig. 4 Observed distribution areas of endemic Mediterranean Sea fish species (1980s) and projected potential future thermal habitats (by 2040–2060 and 2070–2099) with a model-averaging approach. The axes indicate degrees of latitude (*x*-axis) and longitude (*y*-axis).

Lion, the northern Adriatic, and the northern Aegean (Fig. 4b). For the Slender goby (*Gobius geniporus*) a range reduction of 80% by the middle of the century is predicted, and for this species to be restricted to the Gulf of Lion, south Sardinia, the northern Adriatic, and the northern Aegean. Extinction by the end of the century is predicted for this species (Fig. 4c).

Other patterns were less obvious. Indeed, some species expected to be winners at the middle of the century might lose the gained suitable climate niche 50 years later. For instance, *Lipophrys nigriceps* was expected to extend its potential suitable climatic space by 73% at the middle of the century, but then, would lose it at the end of the century (Fig. 4d).

Changes in IUCN status and threat indicator

According to the WAC method, by 2041–2060, 31 endemic fish species were expected to qualify for the IUCN Red List; currently, only five species are on the list, according to geographic range sizes observed in the 1980s (Table 1). By 2070–2099, 45 species were projected to qualify for the IUCN Red List, and 42 species (56% of the total) would qualify as at least endangered.

The threat indicator increased for the whole assemblage, but also for each specialization category, except species considered HG and DS (Fig. 5). The 1980 values of the threat indicator were close to zero because most species were not on the IUCN Red List. This indicator was predicted to reach a maximum of 2.18 by 2070–2099 for the subset of endemic fish considered HS and DG. For the whole assemblage, the threat indicator showed a 10-fold increase over the period of global warming.

Projected species turnover

By the middle of the 21st century, the Levantine Basin and the southern side of the eastern basin were expected to experience a turnover rate of 100% in species composition (Fig. 6a). That is, all endemic species in those areas would disappear (by extinction or migration) and would be replaced by different colonizing endemic species. By the end of the 21st century, 25% of the Mediterranean Sea continental shelf was predicted to experience a total modification of endemic species assemblages. At that point, global warming would be so marked that none of the endemic fish assemblages of the Mediterranean Sea would be identical to those of the 1980s (Fig. 6b).

Table 1 Number of endemic fish species that qualify for each IUCN status according to current geographic range sizes (current) and projected range sizes, following climate changes by the middle of the 21st century (2041–2060) and by the end of the 21st century (2070–2099)

IUCN status	Current	2041–2060	2070–2099
Extinct (Ex)	0	6	14
Critically endangered (CE)	1	7	12
Endangered (En)	3	11	16
Vulnerable (V)	1	7	3
No concern (NC)	70	44	30

IUCN, International Union for the Conservation of Nature and Natural Resources.

Discussion

Taken together, our results showed that the endemic fish assemblage of the Mediterranean Sea would be under increasing threat during the 21st century, because, with sea surface water warming, species that tracked suitable climatic habitats were expected to move into constrained areas that could support only reduced populations. This predicted loss of biodiversity in a hotspot of endemism has strong conservation implications. Indeed, Tortonese (1985) and Quignard & Tomasini (2000) distinguished two kinds of endemism: 'narrow' endemism, which included taxa found strictly in the Mediterranean Sea and 'wide' endemism, which included taxa that reached the neighboring Atlantic Ocean and Black Sea. Clearly, the threat of

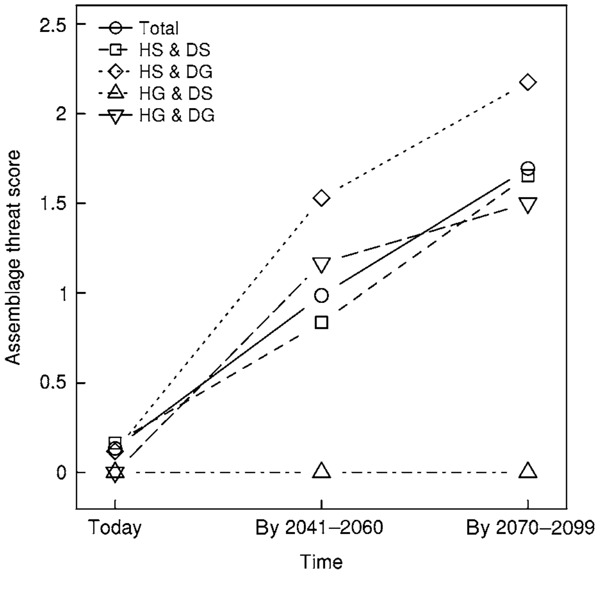

Fig. 5 Changes in IUCN endangerment qualification status based on threat indicator scores for the Mediterranean Sea endemic fish assemblage and for categories of species specialization from 1980 through the end of the 21st century. HG, habitat generalists (pelagic species); HS, habitat specialists (benthic and demersal species); DG, diet generalists (omnivorous and planktivorous species); DS, diet specialists (carnivorous species).

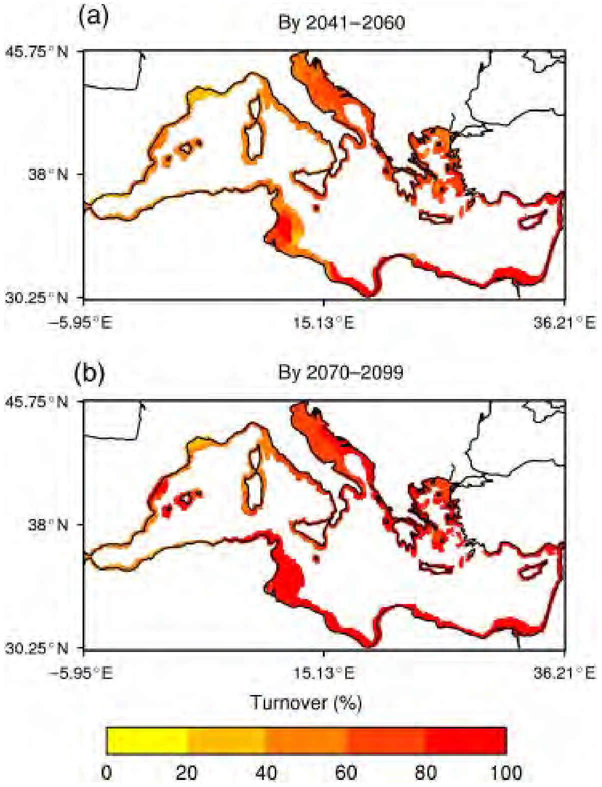

Fig. 6 Predicted percent turnover in endemic fish species of the Mediterranean Sea due to projected sea surface temperature. The percent of species replacement (turnover) predicted to occur by (a) 2040–2060 and (b) 2070–2099. The axes indicate degrees of latitude (*x*-axis) and longitude (*y*-axis). The color range legend indicates the percent of turnover of the assemblage of Mediterranean Sea fish species.

extinction is more critical for narrow than for wide endemic species. Indeed, in the event of extinction in the Mediterranean Sea, wide endemic species may continue to survive elsewhere; in contrast, narrow endemic species would face irreversible extinction. At the end of the 21st century, *Acipenser stellatus* and *Huso huso* are projected to be extinct in the Mediterranean Sea, but they could continue to survive in the Black Sea, where they are currently abundant (Froese & Pauly, 2009). Similarly, *Gobius fallax*, *Gymnammodytes cicerelus*, and *Lipophrys adriaticus* all are projected to be extinct in the Mediterranean Sea, though they may continue to survive around the Canary Islands, from coastal Morocco to Angola, and in the Black Sea; thus, they might avoid global extinction. Conversely, the extinction of *Acipenser naccarii*, *Buenia affinis*, *Corcyrogobius liechtensteini*, *Didogobius schlieweni*, *Gobius geniporus*, *Microichthys coccoi*, *Opeatogenys gracilis*, *Paralepis speciosa*, and *Speleogobius trigloides* in the Mediterranean Sea would represent irreversible extinction, because these species are strictly endemic.

We distinguished four scenarios for species predicted to lose part of their geographic range size and hence, qualify for the IUCN Red Listing: (i) a high probability of immediate extinction (e.g., *Corcyrogobius liechtensteini*), (ii) a high probability of extinction by the end of the 21st century, after severe climatic niche reduction (e.g., *Gymnammodytes cicerelus*), (iii) severe habitat fragmentation (e.g., *Arnoglossus kessleri*) (Fig. 4b), and (iv) migration to the coldest areas, associated with habitat reduction (e.g., *Cyclothone pygmaea*). In contrast, among the species projected to gain range, thermophilic species, such as *Solea aegyptiaca*, are predicted to experience the widest extensions, with up to 80% increases (Fig. 4a). Thus, by the middle of the 21st century, the coldest areas of the Mediterranean Sea (Adriatic Sea and Gulf of Lion) might serve as a sanctuary for cold-water species, but by the end of the century, they are likely to become 'cul-de-sacs', which would drive those species to extinction. This scenario is similar to that described as the upward altitudinal response of terrestrial organisms to global warming; initially, mountains might serve as refuges, but later, they are likely to become potential traps (e.g., Parmesan & Yohe, 2003; Chen *et al*., 2009). Considering all the Mediterranean Sea fish species of this study, over 19% (14 species) were predicted to completely lose their ranges by 2070–2099, independently of habitat and diet considerations. This is a high extinction rate compared with, for example, the <5% extinction expected for the endemic Namibian flora following similar climate change (Thuiller *et al*., 2006).

For many species, range size contraction may occur faster than predicted by models, because HSMs are likely to be too conservative (Lawler *et al*., 2009). For example, HSMs do not take into consideration the fact that warming can intensify the influence of other forcing factors, such as competition from exotic species. Indeed, flourishing thermophilic exotic species can directly compete with endemic species and thus accelerate their extinction (Olden *et al*., 2006). This competitive pressure from exotic species is likely to occur in the Mediterranean Sea, where an increasing spatial overlap between exotic and endemic ichthyofauna has been observed previously (Ben Rais Lasram & Mouillot, 2009). Endemic Mediterranean Sea species are thus likely to undergo both biotic and abiotic stress as a consequence of warming. Moreover, warming often is related to other changes; for example, acidification might affect the survival of many fish species by impacting the survival of invertebrate prey (Dupont *et al*., 2008), the quality of fish growth, and the ability of fish to reproduce (Ishimatsu *et al*., 2008). However, there is no consensus on these impacts, and the biological consequences remain challenging to predict (Bernhard *et al*., 2009).

Our models are likely also to be conservative in predicting the outcomes for species that were expected to track their climatic niche without other limitations and to colonize new areas in the Mediterranean Sea. Indeed, the main weakness of HSMs resides in the fact that they do not consider several biotic aspects (Heikkinen *et al.*, 2006). For example, in this study, we made the assumption that all species were able to migrate towards any suitable temperature condition; this may be an over-optimistic assumption. Migration is particularly important for low prevalence species, because they generally exhibit a lack of dispersion ability (Gaston, 1994); thus, they are unlikely to fill the entire potential niche projected by HSMs. Moreover, a species might become extinct because its migration rate is too slow to track the optimum temperature. Dispersion is very difficult to model, especially at the leading edge of a species range shift (Midgley *et al.*, 2006; Thuiller *et al.*, 2008). However, adequate dispersion is less difficult for marine fish than for other organisms, such as butterflies, which are also affected by global warming (Parmesan *et al.*, 1999). Indeed, butterflies are unable to cross physical barriers such as open seas or mountains to seek suitable habitats (Menendez *et al.*, 2006). Conversely, marine fishes are less restricted and can undertake long migrations without obstacles, due to the continental shelf providing a more or less continuous habitat (Hiddink & Hofstede, 2008). For example, Lessepsian fishes successfully dispersed in the Mediterranean Sea at a mean annual rate of $221 \pm 5.4\,\mathrm{km\,yr^{-1}}$ (Ben Rais Lasram *et al.*, 2008) which, at the temporal scale of our study, is fast enough to track potential changes in climatic habitats along the coast. Moreover, fish propagules (eggs and larvae) have the possibility to disperse with marine currents regardless of the depth and cross the barrier of the continental shelf (Gaston, 2003; Shanks *et al.*, 2003).

A species may also be limited by its degree of specialization in its ability to track a climatic niche. Indeed, the majority (49 out of 75 species) of endemic fishes are here considered specialists both in substratum (benthic and demersal species) and dietary (carnivorous) requirements whereas only six species were considered generalists for these two attributes (Fig. 3). Specialization may add constraints that accelerate range size decline and extinction; for example, in present terrestrial assemblages, specialist species are severely threatened (Biesmeijer *et al.*, 2006; DeVictor *et al.*, 2010). Although the Mediterranean Sea coast has highly patchy substrata (e.g., Garcia-Charton *et al.*, 2004), at the scale of observation used in this study ($0.1^\circ \times 0.1^\circ$), it was unlikely that a primary substratum (rock, seagrass, or sand-mud) would be absent in any cell or not within fish swimming distance. It was more likely that climate change and subsequent range shifts would induce a spatial mismatch between carnivorous fish species and their prey (Durant *et al.*, 2007); however, this is not possible to predict, because geographic distributions of small prey and trophic links are only partially known.

An issue that has been largely overlooked in studies that explored spatial responses to climate change is the potentially synergistic effect of climatic constraint and habitat fragmentation. Indeed, habitat fragmentation, through a loss of connectivity between local populations, is known to reduce genetic diversity (Gibbs, 2001) and lower resistance to extreme events and disturbances (Piessens *et al.*, 2009). Thus, thermal habitat fragmentation, which may lead to species range fragmentation, is an aggravating factor for species survival. Connectivity among local populations plays a key role in species persistence: recolonization by individuals from neighboring areas is enhanced by a continuous distribution area, but may be difficult between fragmented areas (e.g., Fagan *et al.*, 2005). In this study (Fig. 3), both loser and winner species were predicted to undergo increased fragmentation of their suitable climatic habitats, due to global warming and the sinuosity of the northern Mediterranean Sea coast (e.g., *Arnoglossus kessleri*, Fig. 4b; *Lipophrys nigriceps*, Fig. 4d). Hence, climate change and habitat fragmentation could be expected to have negative synergistic effects on species survival (Opdam & Wascher, 2004); however, this was not taken into account in the present study.

Other factors may accelerate species decline and loss of biodiversity. For example, human activities, like pollution and overfishing, can aggravate an already declining population. Because overfishing remains a common practice in the Mediterranean Sea (FAO, 2007), the extinction rates revealed by this study are likely to be underestimates. Indeed, Hsieh *et al.* (2008) demonstrated that exploited fish populations are more vulnerable to climate variability than unexploited fish populations. Accordingly, marine protected areas, in addition to their benefit to coastal ecosystems (Garia-Charton *et al.*, 2008), may also mitigate the effect of climate warming in the Mediterranean Sea. Finally, the combination of biotic interactions, abiotic constraints, and human pressures or protection can markedly impact the vulnerability of fish species to climate change; thus, more investigations are merited in this area, particularly in potential antagonistic or synergistic relationships. Unfortunately, the modeling of these relationships is still in its infancy and requires advancement to be able to provide a broader understanding of biodiversity threats in marine ecosystems.

Despite the potentially confounding effects of many biotic and abiotic factors and their interactions, our HSMs performed projections based only on temperature conditions, which were taken as proxies for all niche components (Lawler *et al.*, 2009). This simplification is acceptable only for species with ranges and shifts that are strongly determined by climatic constraints. This is certainly the case for many species at a coarse spatial scale, because environmental filters are assumed to overcome competitive interactions (Angermeier & Winston, 1998). In the case of fish species that invade the Mediterranean Sea, Ben Rais Lasram *et al.* (2008) have previously shown that the directions and rates of fish dispersal are primarily driven by thermal conditions. Sabates *et al.* (2006) also correlated the distribution of round sardinella to April temperatures, during the initiation of gonad maturation. The assumption was thus made that the thermal niche was the main driver of fish species distributions in the Mediterranean Sea. To reinforce this assumption, we showed that HSMs based only on SST could very accurately predict the geographic distribution of the current niches of Mediterranean Sea endemic species. Counter-intuitively, these models were accurate even for species of low prevalence and fragmented habitats; this result could be explained by the marked spatial heterogeneity of SST in the Mediterranean Sea (Ben Rais Lasram *et al.*, 2009).

There is accumulating evidence that many species expand or shift their distribution areas pole-ward rather than adapt to warmer temperatures (Hickling *et al.*, 2005; Perry *et al.*, 2005; Parmesan, 2006). Other terrestrial species undertake altitudinal migrations to reach suitable conditions (Parmesan & Yohe, 2003). Similarly, some marine species seek deeper water in response to climate warming. This hypothesis has been confirmed by Dulvy *et al.* (2008), who presented evidence for North Sea fish migrations to deeper water in response to climate change ($3.6\,\mathrm{m\,decade^{-1}}$). This issue was considered less critical in the present study because (i) deeper waters are limited in availability, and the focus is on the continental shelf, (ii) many species are unable to survive in deeper water (Dulvy *et al.*, 2008), and (iii) endemic species would have colonized other deeper habitats at equilibrium. Hence, although we cannot reject the issue of seeking deeper water in response to global change for Mediterranean Sea endemic fish, we are confident that northward migrations along the coast are more plausible, because adaptation to deeper water is usually detrimental to growth and survival rates (Sogard & Olla, 1996; Lloret *et al.*, 2005). In a similar vein, a number of researchers have argued for substantive roles of evolution to mitigate the influence of global warming and adaptation to buffer geographic range shifts (e.g., Rowan, 2004). However, both fossil records and contemporary data show little evidence for the evolution of novel phenotypes; instead they support shifts in geographical distributions after climate changes (Parmesan, 2006). Under that assumption, our study predicted that 14 endemic fish species would become extinct (19% of the total endemic assemblage), and over half of the endemic species would shift in their qualifications for IUCN status by the end of the 21st century. In addition, the average turnover rates in endemic fish assemblages could exceed 64% by 2041–2060 and 79% by 2070–2099. These rates are exceptionally high; they surpass the typical predicted turnover rates of terrestrial species (e.g., Peterson *et al.*, 2002; Thuiller *et al.*, 2005; Broennimann *et al.*, 2006) and other aquatic species (e.g., Buisson *et al.*, 2008). This implies that endemic assemblages would be markedly modified; in turn, these modifications could have consequences on ecosystem functioning. Indeed, we know that fish communities strongly shape trophic cascades in the Mediterranean Sea (Guidetti, 2006). Our results support the notion that the ecosystem-level impact of the predicted changes in species composition is indisputable and requires further investigation.

Acknowledgements

F. Ben Rais Lasram was partly funded by a PhD grant from the Cooperation and Cultural Action Services of the French Embassy in Tunisia. This project was also supported by the Total Foundation and the FRB 'Fondation pour la recherche sur la biodiversité'. W. Thuiller was partly funded by the FP6 EU Ecochange project (GOCE-CT-2007-036866).

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Projected climate change and the changing biogeography of coastal Mediterranean fishes.

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Journal of Biogeography (*J. Biogeogr.*) (2012)

ORIGINAL ARTICLE

Projected climate change and the changing biogeography of coastal Mediterranean fishes

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ABSTRACT

Aim To forecast the potential effects of climate change in the Mediterranean Sea on the species richness and mean body size of coastal fish assemblages.

Location The Mediterranean Sea.

Methods Using an ensemble forecasting approach, we used species distribution modelling to project the potential distribution of 288 coastal fish species by the middle and end of the 21st century based on the IPPC A2 scenario implemented with the Mediterranean climatic model NEOMED8.

Results A mean rise of 1.4 °C was projected for the Mediterranean Sea by the middle of the 21st century and 2.8 °C by the end of the 21st century. Projections for the end of the century suggest that: (1) 54 species are expected to lose their climatically suitable habitat, (2) species richness was predicted to decrease across 70.4% of the continental shelf area, especially in the western Mediterranean Sea and several parts of the Aegean Sea, and (3) mean fish body size would increase over 74.8% of the continental shelf area. Small-bodied species that are not targeted by either commercial or recreational fleets presented, on average, the highest predicted decrease in geographic range size.

Main conclusions Projected climate change in the Mediterranean Sea may have deleterious effects on coastal fish diversity, including a significant loss of climatically suitable habitat for endemic fish species. In addition, climate change may contribute to the loss of small and low trophic-level fishes, which may have ecosystem-wide impacts by reducing food supply to larger and higher trophic-level species. Fishing pressure is already selectively removing large-bodied species from marine ecosystems, and so fishing and climatic change might act in tandem to drive both direct and secondary extinctions.

Keywords

Body size, climate change, commercial fishing, Mediterranean fish, recreational fishing, species distribution modelling.

INTRODUCTION

The Mediterranean Sea, at the margins of three continents (Africa, Europe and Asia; Fig. 1), has remarkable habitat diversity and has experienced major colonization events, which together have shaped highly heterogeneous patterns of species diversity (Ben Rais Lasram *et al.*, 2009). The Mediterranean Sea is the largest (2.97 million km^2) and deepest (mean 1460 m, maximum 5267 m) enclosed sea on earth and is indubitably a marine biodiversity hotspot. Despite representing only 0.32% of the global oceanic volume, the Mediterranean also harbours an unusually high level of endemism of 20% (over 17,000 compiled marine species; Coll *et al.*, 2011).

Like all marine ecosystems, the Mediterranean Sea is highly affected by anthropogenic activity including intensification in the exploitation of fisheries, a high concentration of aquaculture and heavy deposition of pesticides and fertilizers from agriculture (Coll *et al.*, 2011). Beyond these local pressures, the Mediterranean Sea is also one of the most responsive regions to climate change (Giorgi, 2006). All these threats may act independently or in synergy towards the

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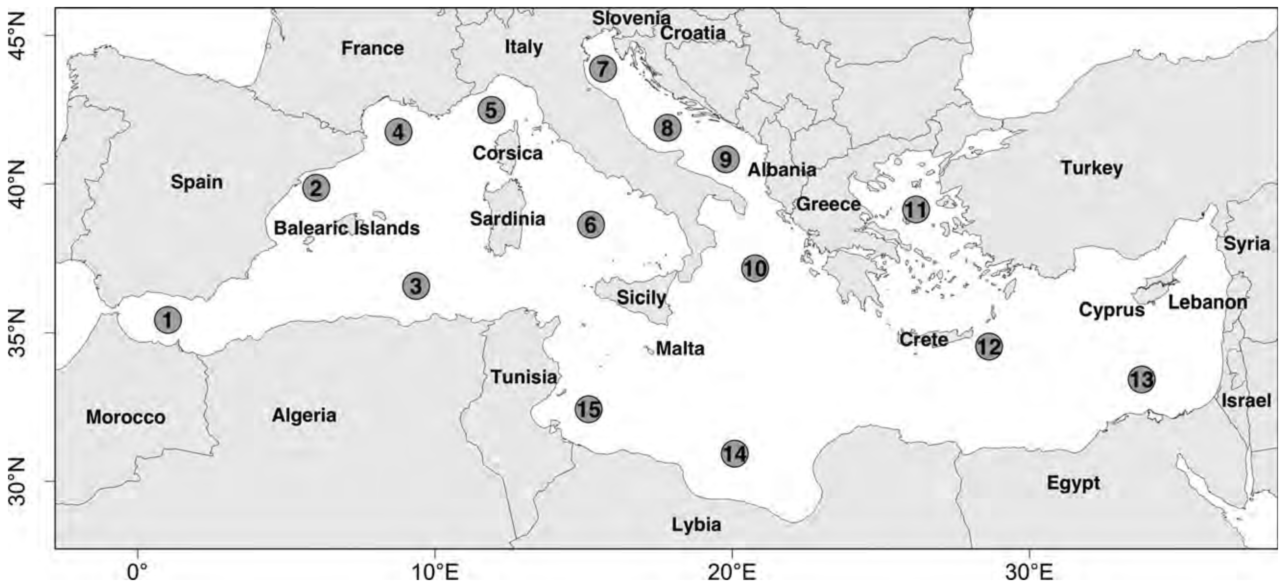

Figure 1 Main regions and basins in the Mediterranean Sea: 1, Alboran Sea; 2, Balearic Sea; 3, Algerian and Tunisian waters; 4, Gulf of Lion; 5, Ligurian Sea; 6, Tyrrhenian Sea; 7, north Adriatic Sea; 8, central Adriatic Sea; 9, south Adriatic Sea; 10, Ionian Sea; 11, north Aegean Sea; 12, south Aegean Sea; 13, Levant Sea; 14, Gulf of Sidra; 15, Gulf of Gabès.

decline or movement of coastal fish populations (Ben Rais Lasram *et al.*, 2010), upon which industrial, artisanal and recreational fisheries depend. For instance the total landing in 2008 for the Mediterranean Sea and the Black Sea was estimated at 1,686,351 tonnes (FAO, 2010). Thus, perhaps more than anywhere else in the world, the conservation of such a unique biota and the maintenance of declining coastal fisheries rely on predicting the combined impacts of local human pressures and global change on Mediterranean fish assemblages.

Species distribution models (SDMs) have commonly been used to evaluate potential impacts of climate change on biodiversity patterns such as net differences in species richness (Thuiller, 2004). This approach has received considerable attention from conservation biologists because climate change is thought to contribute to the ongoing sixth extinction crisis (Van Calster *et al.*, 2008). Species richness has been demonstrated to be a main driver of ecosystem functioning in a wide range of biomes (Balvanera *et al.*, 2006). However, in addition to species richness a number of recent studies have stressed the relevance of species traits to ecosystem functioning (e.g. Mouillot *et al.*, 2011). Thus the crucial question for the sustainability of ecosystem processes is no longer how many species will become extinct because of climate change but what roles are played by those species that will face extinction first and what are the expected changes in functional trait composition within assemblages.

Body size is an important functional trait influencing ecological interactions among animals (Hildrew & Townsend, 2007) and thus underlying the structure of food webs. In addition, body size is considered to be a 'synthetic' functional trait (Woodward *et al.*, 2005), i.e. it directly influences the physiology and ecology of organisms such as metabolic rate, growth and mortality, clutch size, egg mass, age at first maturity, survivorship (Hildrew & Townsend, 2007), population density (Blackburn *et al.*, 1993), spatial distribution (Brown & Maurer, 1989) and secondary production (Jennings *et al.*, 2002). Overall, there is now ample evidence that variation in body size can affect ecological processes at scales ranging from individuals to ecosystems (Woodward *et al.*, 2005). Consequently, fish body-size distribution determines, in combination with species richness, ecosystem functioning (Fisher *et al.*, 2010) and fishery yields (Pinsky *et al.*, 2011). The impacts of fishing constrain the body-size distributions of marine fish populations, as most fishing gear is size-selective and targets preferentially large-bodied organisms at the highest trophic levels (Myers & Worm, 2003). The effect of climate change on marine fish populations has been less studied than the effects of fishing, yet its impact on fish body size distributions may be significant (Genner *et al.*, 2010). Hence, in addition to the projected changes in fish species richness due to climate change, we need large-scale projections of climate-mediated changes in the among-species distribution of body size.

In the present study, we first assessed the potential impact of climate change on the species richness of coastal fish of the Mediterranean Sea. To do so we used an ensemble of SDMs (Thuiller *et al.*, 2009) to project the potential future distributions of 288 coastal fish species based on a SRES (Special Report on Emissions Scenarios) global warming scenario (A2; IPCC, 2007) implemented with the Mediterranean climatic model NEOMED8 (Beuvier *et al.*, 2010). We also investigated the change in body-size distributions at grid-cell scale for present-day and future time periods. Finally we discuss the ecosystem-wide impacts potentially induced by both fishing activities and climatic change by the end of the present century.

MATERIALS AND METHODS

Species data

The geographical distributions of 635 known Mediterranean fish species were compiled using the geographical information system (GIS) software ArcMap 9.3 (ESRI, http://www.esri.com). We distinguished between endemic, exotic and ubiquitous species. Species considered as ubiquitous are encountered in different seas and oceans around the world. Exotic species distributions (i.e. species originating from the Red Sea and the Atlantic Ocean) were gathered from the exotic fish species list of the CIESM atlas (Golani *et al.*, 2002) and the list provided in Quignard & Tomasini (2000). For other species, data were compiled from a published atlas of fishes of the northern Atlantic and the Mediterranean (FNAM; Whitehead *et al.*, 1986). This atlas is based on regional data sets and expert knowledge and was edited between 1984 and 1986. It currently provides the only available basin-wide information on the extent of occurrence of all fish species of the Mediterranean Sea.

The above-mentioned atlases do not account for the bathymetric distribution of Mediterranean fish species, yet bathymetry is considered as one of the main factors accounting for the distributions of marine fish (Louisy, 2005). We therefore refined the extent of occurrence maps by clipping off areas with depths that fall outside the minimum or maximum known for the species. Species bathymetric ranges were obtained from FishBase (Froese & Pauly, 2010) and from Louisy (2005). The bathymetry of the Mediterranean Sea was obtained from the ETOPO2v2 (ETOPO2v2, 2010) Global Gridded 2-minute Database (see Appendix S1 in Supporting Information).

We restricted our analyses to the continental shelf of the Mediterranean Sea (200 m depth limit) for two reasons. First, major threats such as fishing pressure are mainly concentrated on the coastline (Coll *et al.*, 2011). Second, climate change is more likely to affect coastal species (Lloyd *et al.*, 2012), which do not benefit from the temperature inertia of deep waters (Stefansdottir *et al.*, 2010). Exotic species were discarded from our analyses because the equilibrium with environmental conditions is a required assumption for predicting and projecting species distributions (Guisan & Thuiller, 2005). Overall, our final data set summarizes the occurrences of 288 strictly coastal fish species on a 0.1° resolution grid system covering the continental shelf of the Mediterranean Sea (8154 cells).

We qualitatively assessed the potential fishing pressure on these 288 fish species. As the ever-increasing recreational fishing effort may locally surpass that of artisanal fisheries in the Mediterranean (Morales-Nin *et al.*, 2005) we adopted a target-specific approach using two categories: (1) species targeted by commercial fisheries, and (2) species targeted by recreational fisheries. It is worth noting that several species belonged to both of these groups. The maximum body size of each species was gathered from different sources (Whitehead *et al.*, 1986; Louisy, 2005; Froese & Pauly, 2010). Finally we created four categories of fish species combining their fishing sector and body size: small or large species targeted by both commercial and recreational fisheries (SBTS, small-bodied targeted species; LBTS, large-bodied targeted species), and small or large species not targeted by fisheries (SBNTS, small-bodied non-targeted species; LBNTS, large-bodied non-targeted species). We defined large-bodied species as those with a maximum body size greater than 20 cm and small-bodied species as those with a maximum body size less than 20 cm.

Current and projected sea surface temperatures

We used a regional marine model of oceanographic circulation (NEMOMED8) that predicts sea surface temperature (SST) based on the following drivers: water energy fluxes, river discharges and water exchanges with the surrounding seas (Beuvier *et al.*, 2010). This model covers the whole Mediterranean Sea and a buffer zone including a part of the near Atlantic Ocean. The horizontal resolution of NEMOMED8 is 1/8° longitude, resulting in square grid cells of 9–12 km depending on the latitude (Appendix S2). NEMOMED8 is a Mediterranean configuration of the NEMO ocean model and can be seen as an improved version of the OPAMED8 model (Somot *et al.*, 2006) used in Ben Rais Lasram *et al.* (2010). Technical details about NEMOMED8 can be found in Beuvier *et al.* (2010) and are summarized in Appendix S2.

We used daily SST values predicted by NEMOMED8 from the period 1961–80 as a baseline to calibrate the SDMs (Beuvier *et al.*, 2010). The daily data were averaged to infer monthly data, leading to 15 variables: 12 monthly averaged SST values, the absolute minimum SST, the absolute maximum SST and the absolute range of SST (i.e. the difference between the absolute maximum and minimum SST). Several SST variables were considered because fish are ectothermic and thus highly dependent on the precise characteristics of their thermal environment for breeding and developmental success (Mann & Blackburn, 1991). For instance, larval and juvenile recruitment is strongly dependent on maximum temperatures (Burreson & Sypek, 1981).

However, to avoid model over-parameterization and reduce collinearity among predictor variables (Thuiller, 2004), we removed redundant temperature variables. To do so, we reduced the set of predictive variables on the basis of a *k*-means partitioning method. The optimal number of groups was determined according to the highest simple structure index (SSI), following Dolnicar *et al.* (1999). We obtained eight synthetic variables by averaging inside each group determined by the *k*-means clustering. Projected SST values were obtained from NEMOMED8 for the middle (2040–59) and the end (2080–99) of the 21st century according to the IPCC A2 scenario. This scenario was considered as conservative for future prediction of global warming (IPCC, 2007). It assumes a very heterogeneous world that preserves local identities, and which results from a continuously growing human population and an atmospheric CO_2 concentration of 815 p.p.m. by 2099 (IPCC, 2007). The A2 scenario is a standard for regional climate studies and it is the only available scenario implemented by NEMOMED8.

Large-scale patterns of fish species distributions in marine ecosystems are constrained by several limiting factors (Dambach & Rödder, 2011). Among them, water temperature is recognized as one of the main drivers shaping fish species distributions (Dulvy *et al.*, 2008). To investigate this assumption, we conducted an outlying mean index analysis (OMI; Doledec *et al.*, 2000), which identifies the main environmental variables separating species niches. The OMI analysis using eight variables related to SST and one variable related to salinity confirmed that the SST variables were most important for explaining fish species niche characteristics (Appendix S2). In addition, the ranges and thresholds of SST have been shown to explain endemic fish distributions in the Mediterranean Sea (Ben Rais Lasram *et al.*, 2009). SST variables were therefore used as the sole predictors of fish species distribution in the present study.

Species distribution modelling

We implemented an ensemble forecasting approach to account for uncertainty in the outcomes of different SDM methods (Araújo & New, 2007). Fish species distributions were therefore modelled using seven different SDM methods: (1) generalized linear models (GLMs), (2) generalized additive models (GAMs), (3) classification tree analysis (CTA), (4) random forests (RFs), (5) boosted regression trees (BRTs), (6) multivariate adaptive regression splines (MARS), and (7) surface range envelopes (SREs). Modelling was performed with the BIOMOD R-package (Thuiller *et al.*, 2009; R Development Core Team, 2010).

We applied a cross-validation procedure to avoid circularity when the same data are used to construct and evaluate the model. For each species, models were calibrated using a random sample of the initial data (80%). Then, each model was evaluated on the remaining 20% of the initial data set using the true skill statistic (TSS) criterion (three-fold cross validation). We based our evaluation on TSS, as recommended by Allouche *et al.* (2006). The TSS scores were interpreted following the Landis & Koch (1977) accuracy classification scheme. For a given species the predicted presences/absences were derived from the predicted probabilities of occurrence using the threshold that maximized the TSS (Thuiller *et al.*, 2009).

Alternative SDMs may provide markedly different projections for the same data set, and model evaluation often cannot demonstrate which projection is superior (Araújo & New, 2007). To overcome these limitations, we used the weighted average consensus (WAC) method to take into account model-based uncertainty (Ben Rais Lasram *et al.*, 2010).

Using the projected temperatures for 2040–59 and 2080–99, we predicted the geographic location of the potential climatic niche (as inferred by the WAC) for each species. We assumed no dispersal limitation towards new climatically suitable areas because recent invasions show that fish may reach a mean dispersal rate of 221 ± 5.4 km year^{-1} on the northern side of Mediterranean Sea (Ben Rais Lasram *et al.*, 2008). However, we imposed some bathymetric limitations by not allowing a species to be present in a cell if that cell's depth did not conform to the species' known bathymetric range.

For each time period, we inferred species richness and the mean body size of the fish assemblage in each cell. To limit the effect of extremely large body sizes and account for non-normal distributions we used the logarithm of body size and applied the geometric rather than the arithmetic mean (Fisher *et al.*, 2010). We then quantified the absolute change in species richness and mean body size between 1961 and 1980 and: (1) the middle of the 21st century (2040–59), and (2) the end of the 21st century (2080–99). We also assessed the difference in mean body size for species for which range size contractions are predicted and those for which expansions are predicted (Mann–Whitney *U*-test). We quantified the potential effect of climate change on species range sizes by calculating the relative loss or gain as a coefficient of variation

$$\Omega = \frac{r_{\text{future}} - r_{\text{baseline}}}{r_{\text{baseline}}}$$

where r is the distributional range size of species. We tested for differences in the potential effect of climate change across the four categories defined according to body size and fishing pressure (see above) using Kruskal–Wallis nonparametric tests.

RESULTS

Sea surface temperature

According to the predictions of the IPCC A2 scenario implemented in the NEMOMED8 model, mean SST showed a steady increase over the whole Mediterranean Sea during the 21st century (Fig. 2). The Mediterranean Sea was projected to warm by a mean of 1.4 °C for 2040–59 (Fig. 2a) and by 2.8 °C for 2080–99 (Fig. 2b). The projected increase in mean SST was highest in the Aegean Sea, for both periods, with a net mean increase in SST ranging from 1.6 to 2 °C and from 2.8 to 3.8 °C. For the second period other areas were also projected to experience marked increases in mean SST, namely the Adriatic Sea, the Catalan Sea (2.8–3.2 °C) and the Levantine Basin (2.4–3.2 °C).

Projected fish species distributions

Based on observed fish distributions ($n = 288$) and baseline SST predictor values, the predictive accuracy of the seven different SDM methods was classified as 'fair' to 'good' with a mean TSS

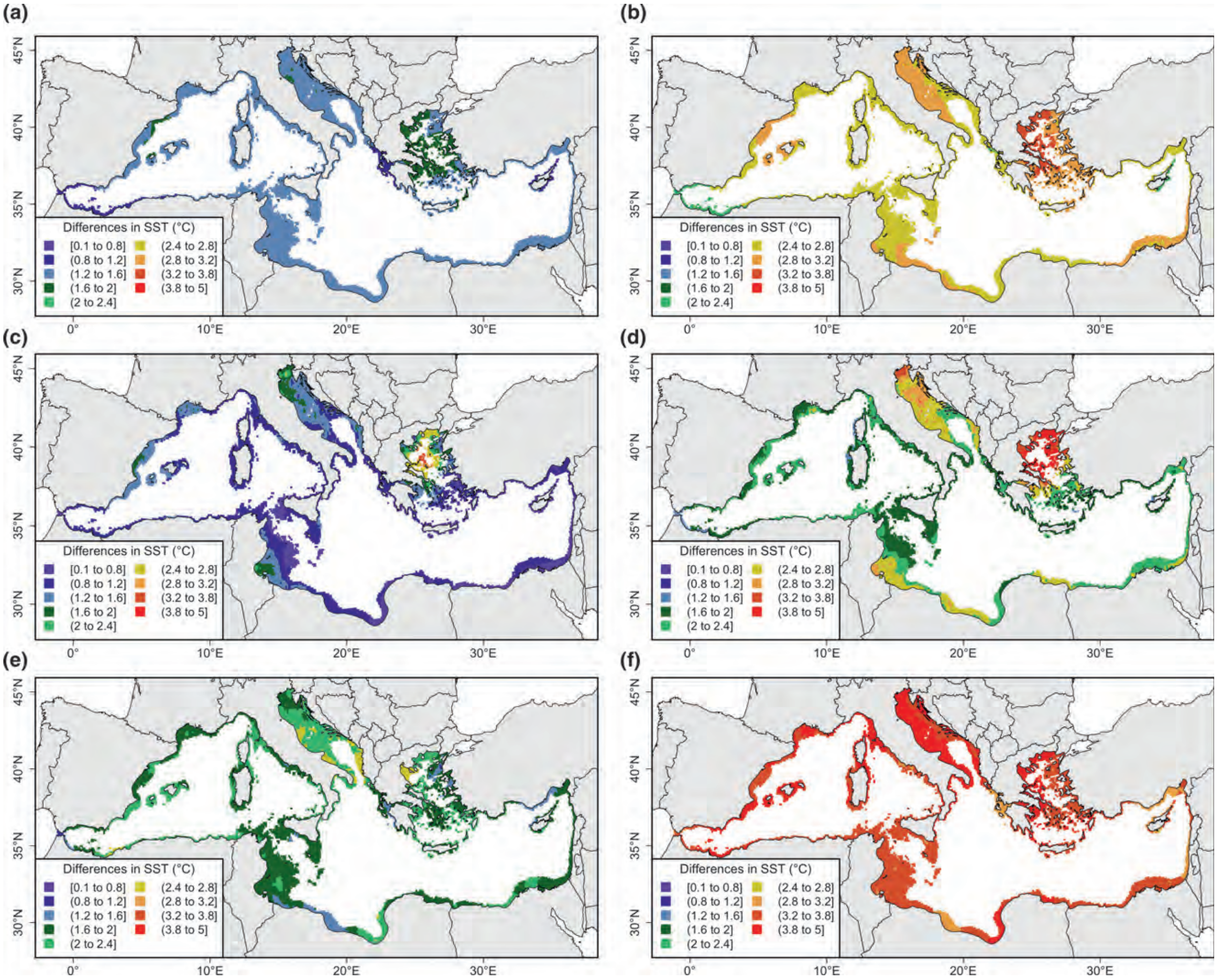

Figure 2 Net differences (°C) in sea surface temperature (SST) between the baseline scenario (1961–80) and two time periods (2040–59, left column; 2080–99, right column) predicted on the continental shelf of the Mediterranean Sea according to the A2 scenario implemented in the NEMOMED8 climatic model. Results are shown for mean SST (a, b), absolute minimum SST (c, d) and absolute maximum SST (e, f). The axes indicate degrees of latitude (*x*-axis) and longitude (*y*-axis).

of 0.61. The least accurate method was SRE with a mean TSS of 0.4, whereas the most accurate was CTA with a mean TSS of 0.71.

Model projections showed that 20 species might have no suitable thermal conditions remaining on the continental shelf by 2040–59. These included 50% of species endemic to the Mediterranean Sea, 22.2% currently of fishing interest and 60% listed on the IUCN Red List (http://www.iucnredlist.org/; see Table 1). Among the eight families containing fish species that were projected to lose all their climatically suitable areas, the Gobiidae family was predicted to be the most affected with 60% of the species potentially losing their climatically suitable areas by 2040–59.

By 2080–99, 54 species were projected to have no climatically suitable areas remaining. These included 40.7% of species endemic to the Mediterranean Sea, 42.3% currently harvested by fisheries and 81.5% included on the IUCN Red List (Table 1). Among the 25 families containing species that potentially lose their climatically suitable habitat in this time period, the Gobiidae was again the most affected family, totalling 37% of the species with no climatically suitable areas remaining. Species projected to lose all their climatically suitable conditions by 2080–99 were more commonly targeted by commercial fleets (18 species out of 54) than by recreational fleets (4 species out of 54).

Under the A2 climate change scenario, by 2040–59 geographic range sizes were projected to decrease for 158 species and increase for 130 species (Fig. 3a). By 2080–99, 172 and 116 species were respectively projected to lose and gain geographic range size (Fig. 3b). However, although similar proportions of ‘loser’ and ‘winner’ species were projected for both periods (2040–59 and 2080–99), the two time periods differed in terms of the amount of change in range size. We predicted, on average, a stronger decrease in the range sizes of loser species than the increase in the range sizes of winner species by 2080–99. Considering only species targeted by

Table 1 List of Mediterranean coastal species that would totally lose their suitable climatic habitat for the two modelled periods (2040–59, 2080–99) according to the A2 scenario implemented in the NEMOMED8 climatic model. Species are classified by family, IUCN Red List category and fishing interest.

Species that totally lose their suitable climatic habitat by the middle of 21st century				Species that totally lose their suitable climatic habitat species by the end of 21st century			
Family	Species	IUCN category	Fishing interest	Family	Species	IUCN category	Fishing interest
Acipenseridae	_Acipenser gueldenstaedtii_	CR	Com	Acipenseridae	_Acipenser stellatus_*	CR	Com
	Acipenser nudiventris	CR	Com	Alopiidae	_Alopias vulpinus_	VU	Com
Callionymidae	_Callionymus reticulatus_	DD		Ammodytidae	_Gymnammodytes cicerelus_*	DD	Com
Exocoetidae	_Exocoetus volitans_	DD	Com	Blenniidae	_Microlipophrys adriaticus_*	LC	
Gobiidae	_Corcyrogobius liechtensteini_*				_Microlipophrys canevai_	LC	
	_Didogobius splechtnai_*				_Microlipophrys dalmatinus_	DD	
	_Gammogobius steinitzi_*				_Parablennius tentacularis_	LC	
	_Gobius ater_*	DD		Callionymidae	_Callionymus fasciatus_	LC	
	_Gobius strictus_*	LC		Clupeidae	_Alosa alosa_	LC	Com/Rec
	_Pomatoschistus knerii_*	DD		Cottidae	_Taurulus bubalis_	DD	Com
	_Speleogobius trigloides_*	DD		Cyprinodontidae	_Aphanius iberus_*	EN	Com
	_Thorogobius macrolepis_*			Gadidae	_Gaidropsarus mediterraneus_	LC	Com
	Buenia jeffreysii				_Gaidropsarus vulgaris_	LC	Com
	Gobius luteus				_Phycis phycis_		Com
	Pomatoschistus microps	CR		Gobiesocidae	_Apletodon dentatus_	DD	
	Vanneaugobius pruvoti				_Lepadogaster purpurea_	LC	
Labridae	_Symphodus bailloni_	DD			_Opeatogenys gracilis_		
Rajidae	_Raja rondeleti_*			Gobiidae	_Buenia affinis_*	LC	Com
Syngnathidae	_Syngnathus taenionotus_*	EN			_Didogobius schlieweni_*	DD	
					_Gobius fallax_*	DD	
					_Odondebuenia balearica_*	LC	
					_Pomatoschistus bathi_*	DD	
					_Pomatoschistus canestrinii_*	LC	
					_Pomatoschistus pictus_*	DD	
					Pomatoschistus norvegicus	DD	
				Muraenesocidae	_Cynoponticus ferox_	DD	Com
				Odontaspididae	_Carcharias taurus_	CR	Com
				Pleuronectidae	_Platichthys flesus_	NT	Com/Rec
					Pleuronectes platessa	NT	Com/Rec
				Pristidae	_Pristis pristis_	CR	Com
				Sciaenidae	_Umbrina ronchus_	DD	Com/Rec
				Soleidae	_Microchirus azevia_	LC	Com
				Sphyrnidae	_Sphyrna tudes_	VU	Com
				Tripterygiidae	_Tripterygion melanurus_*	LC	

EN, endangered; VU, vulnerable; LC, least concern; DD, data deficient; NT, near threatened; CR, critically endangered; Com. commercial; Rec, recreatiional.
*Refers to endemic fish species.

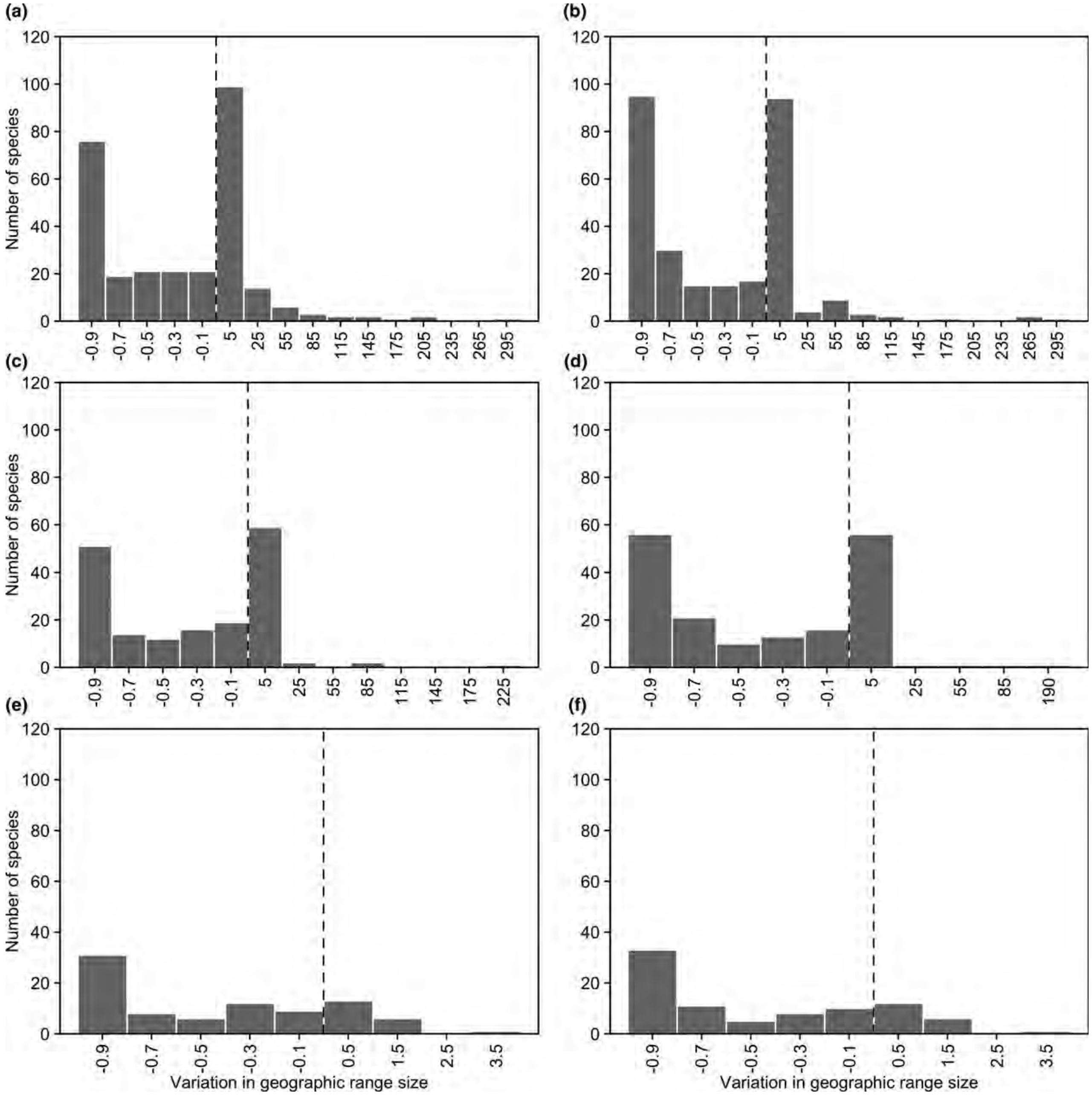

Figure 3 Species relative gain (positive value) or loss (negative value) of geographic range size (measured as the number of cells) between the baseline scenario (1961–80) and two time periods (2040–59, left column; 2080–99, right column) predicted for the continental shelf of the Mediterranean Sea according the A2 scenario implemented in the NEMOMED8 climatic model. Results are shown for all fish species (a, b), for species targeted by commercial activities (c, d) and for species targeted by recreational activities (e, f).

commercial fishing, by 2040–59 112 and 64 species were projected to lose and gain geographic range size, respectively (Fig. 3c). Similar results were found for 2080–99 with 116 and 60 targeted species projected to lose and gain geographic range size, respectively (Fig. 3d). However, the magnitude of loss of species range was more important in 2080–99 than in the earlier period. Considering species targeted by recreational fishing, we found that 67 and 19 species were projected to lose and gain geographic range, respectively, for both 2040–59 and 2080–99 (Fig. 4e,f).

Projected changes in species richness

By 2040–59, model projections showed that 61.4% of the continental shelf area would experience a reduction in species richness whereas the remaining area would gain species (Fig. 4a). The highest predicted levels of species loss were observed in the western half of the Mediterranean Sea (i.e. in the western basin, the Tyrrhenian Sea, the Gulf of Gabès and the Peloponnese; Fig. 1). By 2080–99, 70.4% of cells were predicted to lose species and 26.8% of cells to gain species

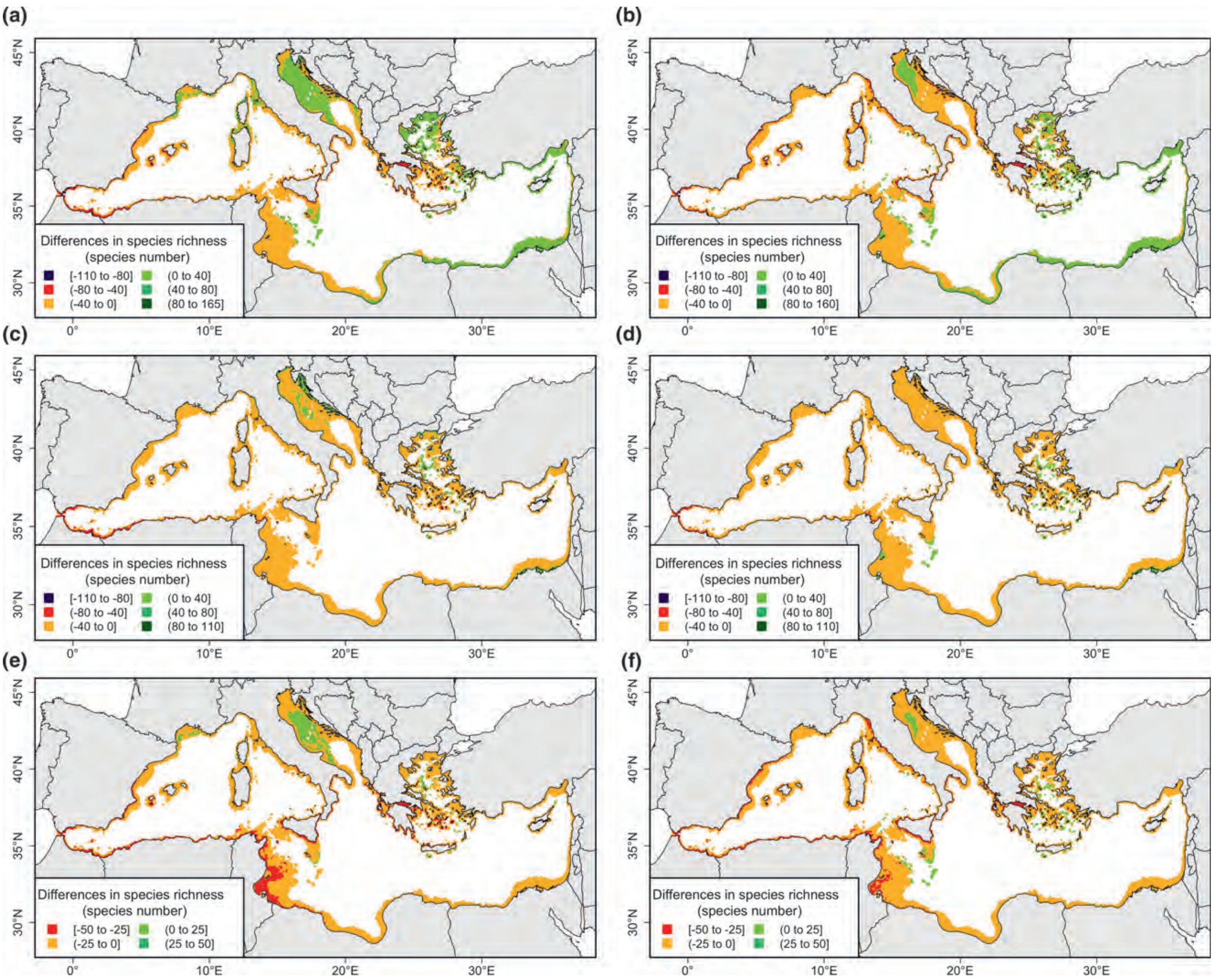

Figure 4 Net differences in fish species richness between the baseline scenario (1961–80) and two time periods (2040–59, left column; 2080–99, right column) predicted for the continental shelf of the Mediterranean Sea according the A2 scenario implemented in the NEMOMED8 climatic model. Results are shown for all fish species (a, b), for species targeted by commercial activities (c, d) and for species targeted by recreational activities (e, f).

(Fig. 4b). For this period, the greatest loss of species richness was predicted in the western Mediterranean Sea and in several parts of the Aegean and Adriatic seas. The highest levels of gains in species richness were predicted in the Levantine Basin and in small areas of the North Adriatic Sea (see Fig. 1).

Predictions of richness loss for species targeted by commercial and recreational fleets were similar to predictions for overall species richness. By 2040–59, 87.2% of the continental shelf area was predicted to represent suitable thermal habitat for commercial fish species and 92.7% for recreational fish species (Fig. 4c,d). Several areas of the Adriatic and Aegean seas were predicted to accumulate species targeted by both commercial and recreational fisheries without any increase in overall species richness (Fig. 4e,f). By 2080–99, 91.0 and 94.9% of the continental shelf area was predicted to lose species targeted by commercial and recreational fisheries, respectively (Fig. 4d,f). In contrast to the period 2040–59, only small areas of the Adriatic and Aegean seas were likely to gain species targeted by commercial and recreational fisheries (Fig. 4d,f).

Projected changes in body-size distributions

By 2040–59 SDMs projected a decrease in (geometric) mean body size for 25.7% of the continental shelf area and an increase over 74.3% of its area. The greatest decrease in mean body size was predicted in the Adriatic Sea, the Alboran Sea and the Levantine Basin, i.e. between 0 and −0.15 log(cm) (Fig. 5a). Similar trends were found when analysing the period 2080–99: mean body size was predicted to decrease over 25.2% of the continental shelf area whereas an increase was predicted over the remaining 74.8% (Fig. 5b). The southern part of the Levantine Basin and the Alboran Sea showed the highest decrease in mean body size by the end of the 21st century, i.e. between 0 and −0.15 log(cm) (Fig. 5b).

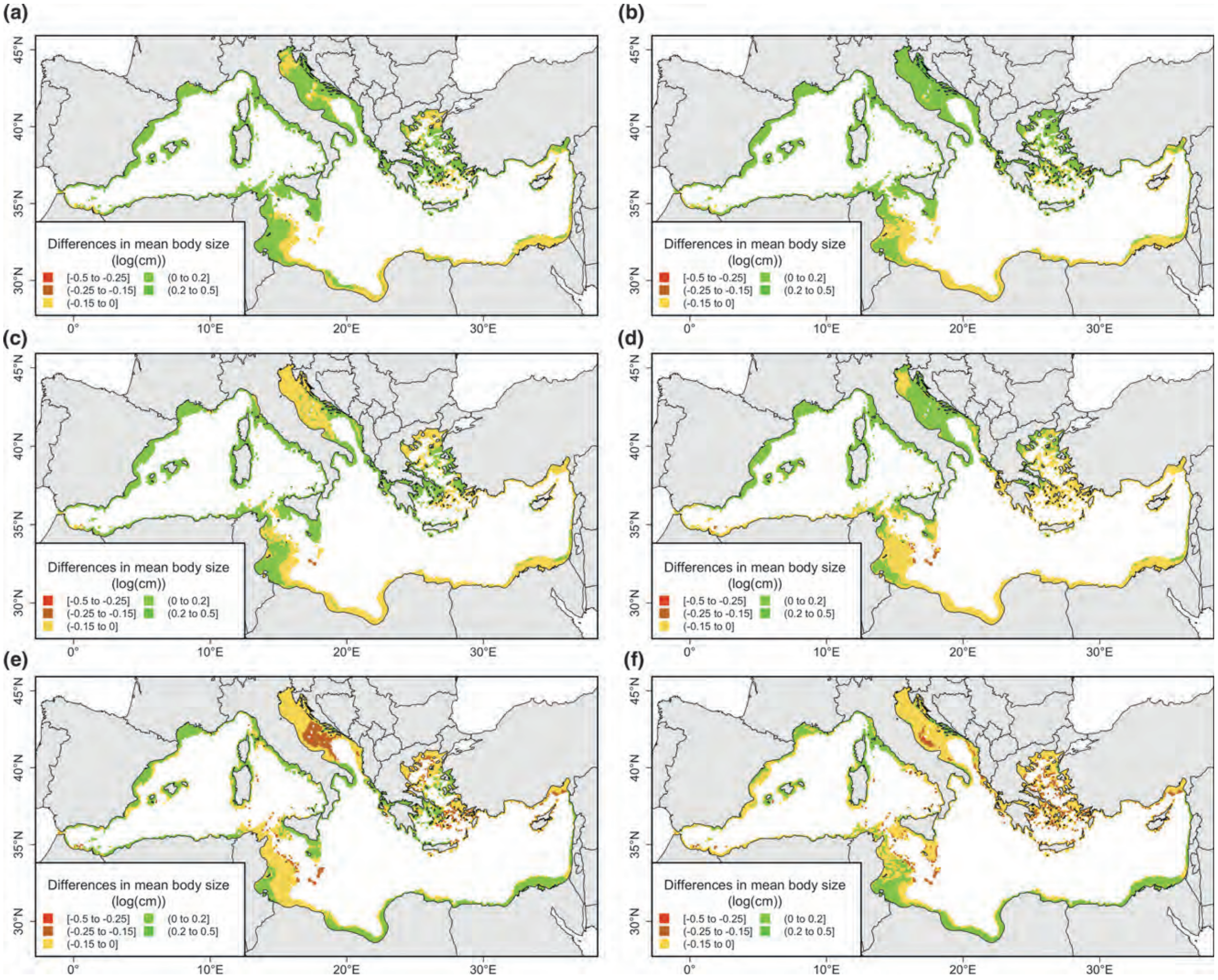

Figure 5 Net differences in geometric mean body size between the baseline scenario (1961–80) and two time periods (2040–59, left column; 2080–99, right column) predicted on the continental shelf of the Mediterranean Sea according the A2 scenario implemented in the NEMOMED8 climatic model. Results are shown for all fish species (a, b), for species targeted by commercial activities (c, d) and for species targeted by recreational activities (e, f).

Focusing on species targeted by commercial and recreational fleets provided similar results, especially for the mid-21st century. By 2040–59, roughly half of the continental shelf area (56.2%) showed a projected increase in geometric mean body size for commercial fish species (Fig. 5c). Similarly, 53.9% of the continental shelf area showed a decrease in geometric mean body size for recreational fish species (Fig. 5d). The Gulf of Lion and the Adriatic and Aegean seas showed the greatest decrease [between −0.15 and −0.25 log (cm)]. A markedly different trend was found when analysing the period 2080–99: around half of the continental shelf area (50.8%) showed a decrease in geometric mean body size for commercial fish species (Fig. 5d), with the Levantine Basin, the Adriatic and the Aegean seas showing the greatest decrease [between −0.15 and −0.25 log(cm)]. In contrast, for recreational fish species, 65.6% of the continental shelf cells were predicted to experience a decrease in geometric mean body size (Fig. 5e), with the Adriatic Sea, the Aegean Sea and the Gulf of Lion (between −0.15 and −0.25, Fig. 5e, f) again showing the greatest decrease.

Distinguishing between small- and large-bodied species with or without fishing interest provided more detailed results (Fig. 6). The Kruskal–Wallis test revealed significant differences in range size modifications among the four groups for both the 2040–59 (Kruskal–Wallis rank sum statistic = 20.98, d.f. = 3, $P < 0.0001$) and 2080–99 periods (Kruskal–Wallis rank sum statistic = 28.37, d.f. = 3, $P < 0.0001$). Small-bodied species, mainly belonging to the Gobiidae family, that are not targeted by either commercial or recreational fisheries (SBNTS category), showed the highest loss of range size by both 2040–59 and 2080–99. By 2040–59 SBNTS presented a net decrease in their geographical range size (416 cells on average), which corresponds roughly to 4×10^5 km² (Fig. 6a). This trend was even more pronounced when considering the end of the 21st century with an average loss for SBNTS of 600 cells (i.e. *c.* 6×10^5 km², Fig. 6b). In contrast, for SBTS and LBTS and

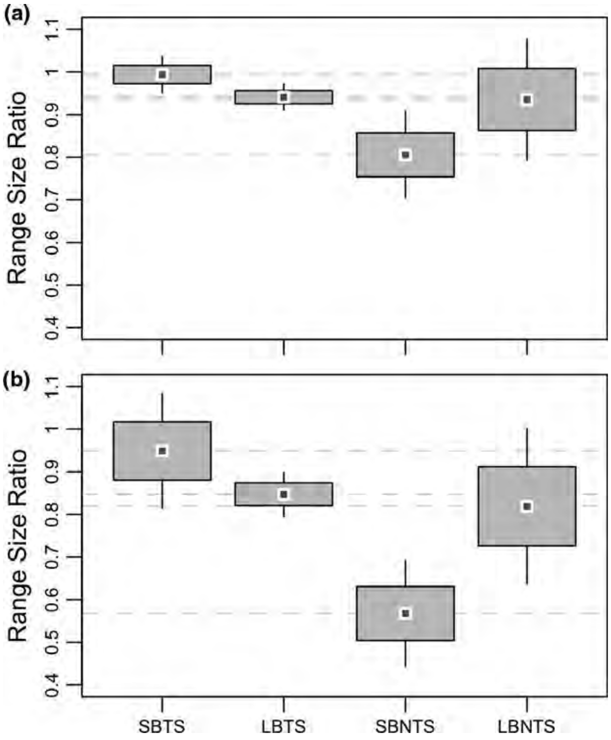

Figure 6 The relationship between the ratio of range size (logarithm) modelled under the baseline scenario and the predicted for two periods: (a) first period 2040–59, (b) second period 2080–99. Fish body size (logarithm) is grouped into four classes: small-bodied targeted species (SBTS, body size < 20 cm), large-bodied targeted species (LBTS, body size > 20 cm), small-bodied non-targeted species (SBNTS), large-bodied non-targeted species (LBNTS). Squares represent the mean value, box brackets the standard error of the mean (± SE) and whiskers represent 95% confidence intervals (± 1.96 SE).

LBNTS there were no significant changes in geographic range size for both periods (Wilcoxon rank test for SBTS $V = 24.5$, $P > 0.05$; for LBTS $V = 179$, $P > 0.05$; for LBNTS $V = 4375$, $P > 0.05$).

DISCUSSION

Our results predict that by the end of the 21st century most of the coastal area of the Mediterranean Sea will experience a decrease in native fish species richness. This decrease is due to (1) the potential loss of entire climatically suitable areas for 54 species, (2) a reduction in range size for 169 out of the 288 modelled species, and (3) species range-shifts that track climate niches towards northern latitudes. Our projections provide a preliminary attempt to forecast the strength of temporal changes in coastal fish assemblages facing climate changes and should be interpreted cautiously as our modelling framework does not provide a holistic view of processes affecting fish species distributions (Dambach & Rödder, 2011). For instance, we did not take into account species interactions or environmental stressors such as water eutrophication and fisheries overexploitation that may amplify or mitigate the projected changes in species distribution at large spatial scales (Coll *et al.*, 2011). In addition, we used presence/absence data instead of abundance because the abundance of almost all of the species studied is currently not available over the whole continental shelf of the Mediterranean Sea. Finally we did not consider fish species potentially arriving from the Atlantic Ocean or the Red Sea, because these species clearly break the assumption of equilibrium being reached with climatic conditions (Guisan & Thuiller, 2005). In comparison to Ben Rais Lasram *et al.* (2010), who predicted the potential extinction of 14 endemic fish species by the end of the 21st century, here using a refined climatic model (NEMODED8) and bathymetric constraints, we predict that 24 endemic fish species will entirely lose their climatically suitable areas on the Mediterranean continental shelf. Overall, by the middle of the 21st century, the coldest areas of the continental shelf of the Mediterranean Sea might serve as a sanctuary for cold-water species, but by the end of the century, these areas are likely to become a trap. Here we extended the prediction of this trap effect not only for endemic species (Ben Rais Lasram *et al.*, 2010) but for the whole coastal fish assemblage. As an illustration of this effect, the Adriatic Sea, the Aegean Sea and the Gulf of Lion would gain species during the first period while they would lose species during the second period (Fig. 4). This pattern is similar to the upward elevational response to climate change by terrestrial organisms: initially mountains might serve as refuges, but later, when species are confined to mountaintops, elevational upward shifts are no longer possible, inducing a trap effect (e.g. Parmesan & Yohe, 2003). This effect has also been demonstrated for endemic stream fishes that are constrained within hydrographical networks experiencing climate change (Bond *et al.*, 2011).

Consequences of climate change for species richness are likely to be different among fish categories based on their sensitivity to fishing activities. At the end of the 21st century, the diversity of fish species targeted by both commercial and recreational fleets may decrease markedly. This may induce several modifications in fishing habits, especially in the western part of the Mediterranean Basin. The challenge is thus to know whether fishermen will be able to exploit and sell alternative fish species. Fisheries might increasingly exploit deep-sea stocks (deeper than 400 m). Global landings of demersal marine fishes have shifted to deeper-water species over the last 50 years. Morato *et al.* (2006) suggest that this trend may cause deep-water fish stocks to be at serious risk of depletion, as the life histories of these species make them highly vulnerable to overfishing. Deep-sea fisheries are already exploiting the last refuges for commercial fish species and should therefore not be seen as a sustainable replacement for declining resources in shallower waters.

Fishing activities have a strong impact on fish abundance and can drive coastal species to extinction (Pinsky *et al.*, 2011). The status of most European commercial fish stocks is currently at its lowest known level (Gascuel *et al.*, 2011); the proportion of overfished stocks, depleted or recovering from depletion, has increased from 10% in 1974 to 32% in 2008 (FAO, 2010). In the Mediterranean Sea the overall situation has been stable but critical since the last assessment. For instance all stocks of hake (*Merluccius merluccius*) and mullet (*Mullus barbatus*) are overexploited, and this may also apply to the main stocks of soleids (Soleidae) and most stocks of *Dentex* spp. (FAO, 2010). The main stocks of small pelagics, e.g. the European pilchard (*Sardina pilchardus*) and the European anchovy (*Engraulis encrasicolus*), are fully exploited or overexploited (FAO, 2010). Our projections for the end of the 21st century show that one small pelagic species (the allis shad, *Alosa alosa*) and one Soleidae (*Microchirus azevia*) might vanish. For these two species, extinction predictions based on climate change predictions are enforced by the deleterious effect of anthropogenic exploitation. Indeed, Hsieh *et al.* (2008) demonstrate that exploited species are more vulnerable to climate variability. They argue that the response of these species might be a consequence of reduced spatial heterogeneity caused by fishery-induced age (size) truncation and the constriction of geographic ranges that accompanies fishing pressure.

We point out also that other species of fishing interest, such as the starry sturgeon (*Acipenser stellatus*), the Danube sturgeon (*Acipenser gueldenstaedtii*), the allis shad (*Alosa alosa*) and the European flounder (*Platichthys flesus*) are likely to be affected by climatic change. Moreover, for these diadromous species (i.e. using both marine and freshwater habitats during their life cycle) geographic range modifications may occur simultaneously in their freshwater and marine habitats. For instance, the allis shad may disappear from the southern part of its present freshwater distribution and the European flounder may disappear from all freshwaters around the Mediterranean Basin (Lassalle & Rochard, 2009).

Beyond changes in fish species richness, we predict that under climate change the mean maximum body size of fish assemblages will increase for both periods with an increase in mean body size over 56.2 and 74.8% of the continental shelf area for the periods 2040–59 and 2080–99, respectively (Fig. 5). This may be due to the range expansion of southern large-bodied species such as the yellowmouth barracuda (*Sphyraena viridensis*), the Haifa grouper (*Epinephelus haifensis*) or the round stingray (*Taeniura grabata*) (for more details see Appendix S3). More generally, the global increase in mean body size of Mediterranean fish species at the end of the 21st century can be explained by the fact that species predicted to expand their range are significantly larger than species predicted to contract their range (72.4 vs. 69.8 cm, Mann–Whitney *U*-test, $P < 0.05$).

Overall, Mediterranean fish could be caught in a vice between two principal threats: fishing and climatic change. Climate change seems to affect smaller-bodied, non-fishery-targeted species by reducing their geographic range size. This trend is marked for both modelled periods and may have ecosystem-wide impacts by reducing food supply to larger fish, seabirds and marine mammals (Pinsky *et al.*, 2011; Cury *et al.*, 2011). Further, fisheries act as a selective pressure, decreasing mean body size in exploited assemblages by removing top predators (Kuparinen & Merila, 2007). This may affect the population dynamics of lower trophic levels and eventually disrupt ecosystem functioning. Hence, climate change and fishing may act in combination, antagonistically or synergistically, and may lead to direct or indirect extinctions, the latter remaining challenging to predict.

Beyond the study of changes in biodiversity patterns mediated by climate change, the disruption of ecosystem functioning induced by changes in food web structure has largely been overlooked. The bulk of studies on the effect of global change on biodiversity rely mainly on species biogeography and focus on population distribution and phenology, while very little is known about the changes in the properties of species interaction networks (Guisan & Thuiller, 2005). Projections based on SDMs neglect species interactions, while a myriad of ecological interactions are potentially sensitive to environmental changes. Predicting shifts in the mean body size of fish assemblages is only a first step toward the assessment of major disruptions induced by climate change on ecosystem functioning and associated services. Yet body size is a very important trait affecting physiological and ecological characteristics such as metabolic rates and interactions with other species (Fisher *et al.*, 2010). We thus believe that the integration of SDMs and trophic modelling within the same framework will become a valuable tool for the investigation of the impacts of climate change on ecosystems.

Perspectives in modelling fish species distribution in the marine realm

In the present study, we only considered fish species distributions over the continental shelf to overcome the problem of high temperature variability across depth layers that characterize the open oceanic environment (Dambach & Rödder, 2011). Arguably, compared with their terrestrial counterparts, estimating the climatic niches of marine species is a much more difficult exercise because the marine realm is a three-dimensional habitat. The bathymetric distribution is a third component to consider when modelling the distributions of marine fish species as different environmental factors (e.g. temperature, oxygen) are likely to influence habitat suitability at different depth ranges (Dambach & Rödder, 2011). This implies that marine species may respond to water warming not only with a horizontal movement but also with a vertical shift (Dulvy *et al.*, 2008).

As recently discussed by Dambach & Rödder (2011), a promising modelling framework would be to compute SDMs for different depth ranges and then to combine these models to predict species distributions over both horizontal and vertical dimensions. Such an extended framework would allow modelling of the current and future distributions of the overall pool of Mediterranean fish species, including species inhabiting either the continental shelf (0–200 m), the continental slope (200–800 m) or both environments, and those that are confined to the deep-sea habitats. However, such an approach would require high-quality information on both thermal conditions and species occurrences across the depth gradient. These data are currently not available for the Mediterranean Sea. We hope that the increasing interest in the sharing of biodiversity data within publicly available platforms (see the OBIS Project; Vanden Berghe, 2007) will help the development of three-dimensional-based SDMs in the marine realm.

ACKNOWLEDGEMENTS

We thank Regan Early for her constructive comments on the manuscript and language editing. We are grateful to the three anonymous referees for all the remarks and suggestions that improved the manuscript. This work was partly funded by the Total Foundation, the 'Fondation pour la Recherche sur la Biodiversité' (project BIODIVMED). D.M. was supported by a Marie Curie International Outgoing Fellowship (FISHECO) with agreement number IOF-GA-2009-236316. F.G. was supported by the 'Range Shift' project (PTDC/AAC-AMB/098163/2008) from Fundação para a Ciência e a Tecnologia (Portugal), co-financed by the European Social Fund. The 'Rui Nabeiro' Biodiversity Chair is financed by Delta Cafés.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Bathymetric correction of species ranges.
Appendix S2 Temperature and salinity variables: acquisition and importance.
Appendix S3 List of modelled species, maximum length, range modifications and centroid shift direction.

BIOSKETCH

Camille Albouy is a PhD student in ecology at the University of Montpellier 2. His research is focused on large-scale patterns and processes of marine fish biodiversity. He is particularly interested in forecasting the changes in marine fish biodiversity as a result of climate change using both correlative and mechanistic modelling approaches.

Editor: Peter Pearman

SUPPORTING INFORMATION

Projected climate change and the changing biogeography of coastal Mediterranean fishes

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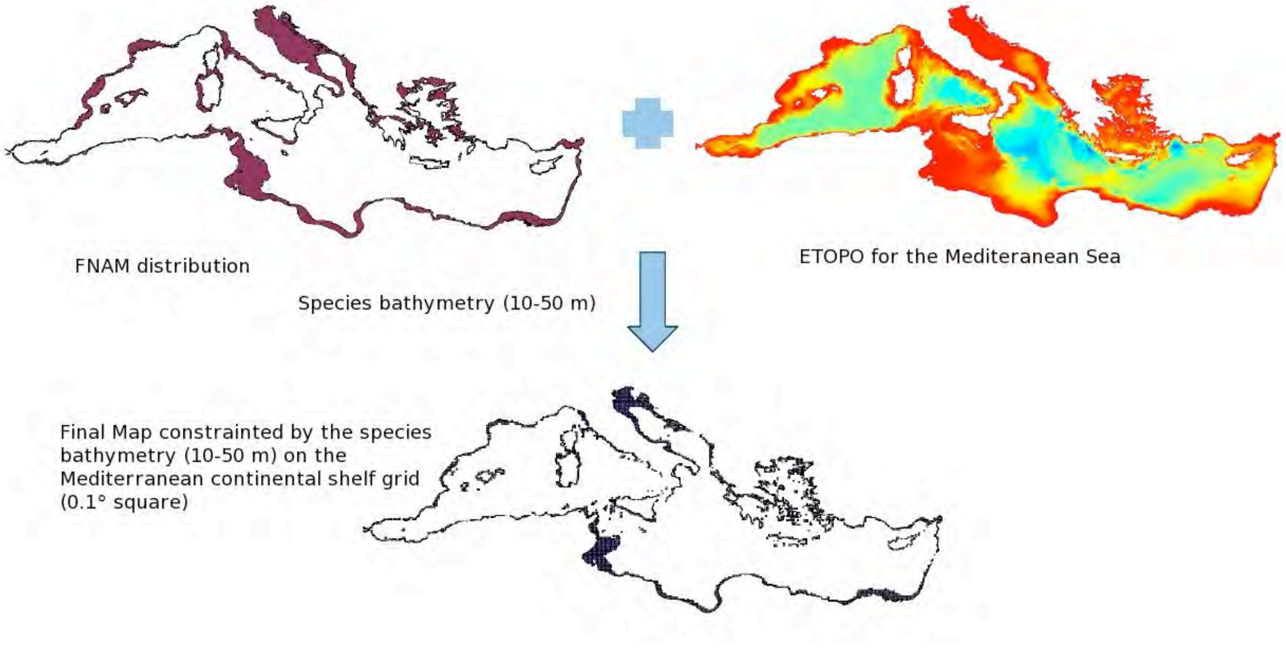
Roland Aznar, Laure Velez, François Le Loc'h and David Mouillot

Journal of Biogeography

Appendix S1: Bathymetric correction of species ranges

This figure depicts the bathymetric correction process we used in this study for a species with an extent of occurrence all over the Mediterranean continental shelf but known to be restricted to a depth range of 10–50 m.



Appendix S2: Temperature and salinity variables: acquisition and importance

Modelling sea surface temperature

The NEMOMED8 model is a regional barotropic ocean model that predicts sea surface temperature (SST) based on the following drivers: heat and water air-sea fluxes (radiative and turbulent), river discharges including a simple description for the Black Sea and finally heat and water exchanges with the near Atlantic ocean (Beuvier *et al*., 2010). NEMOMED8 covers the whole Mediterranean Sea plus a buffer zone including a part of the near Atlantic Ocean. It does not cover the Black Sea. The horizontal resolution of NEMOMED8 is 1/8° in longitude with square grid-cells. The resolution of a grid-cell thus depends on its latitude and varies between 9 and 12 km from the north to the south of the Mediterranean domain. It is a Mediterranean configuration of the NEMO ocean model and can be seen as an updated version of the OPAMED8 model (Somot *et al*., 2006) already used in Ben Rais Lasram *et al*. (2010). Indeed these models share the same area, the same grid and the same forcing variables. However, NEMOMED8 has been improved with, for instance, the filtered free surface scheme (Roullet & Madec, 2000) and the partial cell parameterization (the local deepest level in the model is included in order to fit the real bathymetry).

The NEMOMED8 grid is tilted and stretched at the Gibraltar Strait in order to better follow the SW–NE axis of the real strait and to increase the local resolution up to 6 km. NEMOMED8 is three dimensional and has 43 vertical layers with thickness varying from 6m at the surface to 200m at the bottom with 25 levels in the first 1000 m. A time step of 20 minutes was applied.

Various forcing factors can be applied to NEMOMED8 depending on the scientific goals of the simulations. Recently, dynamical downscaling of the ERA40 data set reanalysis (Herrmann & Somot, 2008) was applied for realistic hindcast simulations of the period 1960–2001 (Beuvier *et al*., 2010) and of the ECMWF analyses for the period 2001–2007. Driven by realistic forcing factors, NEMOMED8 has been proved to accurately simulate the temporal variability of the Mediterranean Sea water mass and spread over the last decades (Beuvier *et al*., 2010; Herrmann *et al*., 2010). However these forcing factors rely on a past reanalysis and do not allow simulation of the 21st century. In the current study, NEMOMED8 was instead forced by data from a high-resolution climate change scenario obtained from an atmospheric regional climate model called ARPEGE-

Climate developed at Meteo-France/CNRM (Déqué & Piedelievre, 1995). The atmospheric model follows the observed greenhouse gas and aerosol concentrations up to the year 2000 and the SRES-A2 scenario between 2001 and 2099. The forcing is the same as in Somot *et al.* (2006). This scenario is homogeneous in time throughout the time period from 1960 to 2099. This atmospheric model provided daily data at 50 km spatial resolution. This level of detail has been found to be sufficiently accurate to model Mediterranean Sea SST elsewhere (Somot *et al.*, 2006; Beuvier *et al.*, 2010).

Other second-order forcing factors were also applied to the NEMOMED8 model, namely river discharges, Black Sea freshwater input and near-Atlantic ocean characteristics. These forcing factors were dealt with following an anomaly approach as described in Somot *et al.* (2006). During the 1960–2000 period, observed climatological seasonal cycles were used for these forcing factors. Between 2001 and 2099 climatological values from 1901–1999 were used for these forcing factors, with the addition of decadal anomalies computed from SRES-A2 scenarios. In order to ensure consistency between the SST computed by NEMOMED8 and the heat flux generated by the ARPEGE-Climate model, the NEMOMED8 SST was relaxed towards the daily SST used by the ARPEGE-Climate model, with an 8-day equivalent restoring timescale (Barnier *et al.*, 1995). For the present climate, the RivDis data set (Vörösmarty *et al.*, 1996) provided the monthly runoff of 33 Mediterranean rivers and the Stanev *et al.* (2000) data provided the monthly mean values of the freshwater exchange between the Black Sea and the Aegean Sea. Reynaud *et al.* (1998) provided data to assess the Atlantic water characteristics in the buffer zone, with a restoring term that became gradually weaker from western limit of the buffer zone towards the Gibraltar Strait. The freshwater fluxes over the sea (precipitation, evaporation, inflow from rivers) are poorly known from observations and are not perfectly simulated by ARPEGE-Climate. Consequently, in order to avoid errors in surface salinity in NEMOMED8, we added a spatially homogeneous correction of the water flux for each month; the 12 values obtained were applied every year to conform to the classical hypothesis that model bias is constant through time. This correction is relatively weak with a yearly-mean value of -0.2 mm day−1, reducing the net surface evaporation by about 10%. It allows the Mediterranean salt content to stabilize during the control run without altering the spatial and temporal variation of the freshwater flux and of the sea surface salinity (SSS). As the correction acts as an additive constant, it has no impact on the long-term trend of both variables that can evolve freely.

Before the start of the scenario run (1960–2099), we first carried out a fifteen-year spin-up. The initial state was given by the MEDATLAS-II climatology for the Mediterranean part of the model (MEDAR, MEDATLAS-Group (2002)), and by the climatology for the Atlantic buffer zone (Reynaud *et al.*, 1998). The aim of the spin-up period was to provide sufficiently stable initial conditions for the scenario run, limiting non-physical temperature or salinity drifts after the end of the spin-up period. Starting at the end of the spin-up, we ran NEMOMED8 between August 1960 and December 2099. Daily mean outputs of the surface fields and monthly-mean outputs of the 3D fields can be used for analysis.

In the current study, the impact of the climate change during the 21st century is measured as the difference in SST between a future period (2070–2099) and a control period serving as reference for the present climate (1961–1990).

The outlying mean index (OMI) analysis

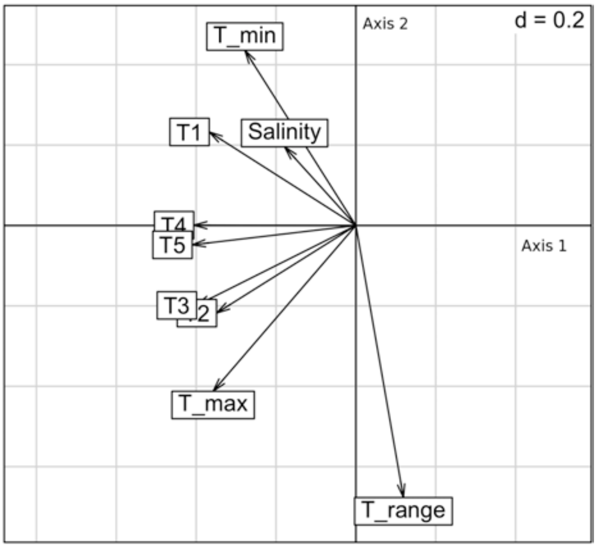
To identify the main environmental variables separating fish species niches and structuring fish assemblages, we first used a multivariate approach, the outlying mean index analysis. The OMI analysis aims at separating species niches and at measuring two niche descriptors: niche position (i.e. marginality) and niche breadth (i.e. tolerance). The marginality of species habitat distribution measures the distance between the mean habitat conditions used by a species and the mean habitat conditions across the 8154 cells of the Mediterranean continental shelf. Niche breadth measures the amplitude in the distribution of each species along the sampled environmental gradients.

We applied the OMI analysis using several variables related to salinity and sea surface temperature (SST; see the main text for more details about SST variables). Salinity data were extracted from the World Ocean database on the NOAA web site for the period 1961–1980. These data were then interpolated on our continental shelf grid. Last, the average salinity across depths (0–200 m) was quantified for each grid cell of the continental shelf.

The first two axes of the OMI analysis accounted for 97.2% of the explained variability in species niche separation. The first axis explained 84.5% of the variability. The OMI analysis showed that the main variables that constrained the fish species niche were related to SST (Fig. S1).

The salinity played a minor role as this variable displayed the lowest canonical weights with the first and second axes of the OMI analysis. To avoid over parameterization, SST variables were therefore used as the sole predictors of fish species distribution in the present study.

Figure S1 Results of the OMI analysis showing the canonical weights of the environmental variables on the two first axes of the OMI analysis. The length of the arrows describes the relative importance of each variable in explaining fish species niche characteristics (T1: average SST from January to April; T2: average SST from July to September; T3 average SST for October and June, T4 average SST for December and May; T5 average SST for November; T_min absolute minimum SST; T_max absolute maximum SST: T_range difference between the absolute maximum and minimum SST).



Appendix S3: List of the 288 modelled species with corresponding maximum length, range modifications, and centroid shift direction. (SE: South East, SW: South West; NE: North East; NW: North West; NA: Not Applicable). The first and the second periods correspond to 2040-2059 and 2080-2099, respectively.

Species	Maximum length (cm)	Observed range	Modelled range for the first period	Modelled range for the second period	Centroid shift direction for the first period	Centroid shift direction for the second period
Acipenser_gueldenstaedtii	230	28	0	0	NA	NA
Acipenser_naccarii	200	231	176	70	NE	SE
Acipenser_nudiventris	200	28	0	0	NA	NA
Acipenser_stellatus	190	623	169	0	SE	NA
Acipenser_sturio	300	1463	568	97	SE	SE
Aidablennius_sphynx	8	1555	1303	625	NW	NW
Alectis_alexandrinus	100	1340	3691	4261	SE	SE
Alopias_vulpinus	760	4707	639	0	SE	NA
Alosa_alosa	70	2540	1279	0	NE	NA
Anthias_anthias	27	4180	4102	4142	NE	NE
Aphanius_fasciatus	9	1453	1705	1823	SW	SE
Aphanius_iberus	5	49	102	0	NE	NA
Aphia_minuta	6	4269	2040	3190	NW	NW
Apletodon_dentatus	5.1	300	68	0	NE	NA
Apogon_imberbis	15	4271	4299	4299	NW	NW
Apterichtus_anguiformis	60	1530	756	90	NE	NE
Apterichtus_caecus	60	1292	935	276	NE	NE
Argentina_sphyraena	45	4094	3649	1655	NE	NE
Argyrosomus_regius	200	5401	5227	5306	NE	NE
Ariosoma_balearicum	50	5203	5061	5129	NE	NE
Arnoglossus_imperialis	25	1986	1251	192	NE	SE
Arnoglossus_kessleri	13	6891	7329	7414	SW	SW
Arnoglossus_thori	25	1632	816	102	NE	NE
Aspitrigla_cuculus	50	6730	6736	6736	NW	NW
Aspitrigla_obscura	40	5238	5141	5220	NE	NE
Atherina_boyeri	13	7592	6146	7068	NW	NW
Atherina_hepsetus	20	7589	5605	7109	NW	NW
Atherina_presbyter	20	387	495	179	NE	NE
Balistes_carolinensis	45	3540	3441	3483	NE	NE
Belone_gracilis	95	6548	3565	1237	SE	SE
Belone_svetovidovi	57	139	2691	2314	NE	NE
Blennius_ocellaris	20	1515	653	733	NW	NW
Boops_boops	36	3268	3251	3305	NE	NE
Bothus_podas	45	3543	3425	3506	NE	NE
Buenia_affinis	3.2	21	1	0	SE	NA
Buglossidium_luteum	16	3140	3153	3156	NE	NE

Callionymus_fasciatus	12	429	167	0	SE	NA
Callionymus_pusillus	14	1472	1122	718	NW	NW
Callionymus_reticulatus	11	180	0	0	NA	NA
Callionymus_risso	8	4127	4137	3678	NW	NW
Campogramma_glaycos	75	4216	5130	2823	NE	NE
Caranx_rhonchus	60	2340	5117	5583	NE	NE
Carapus_acus	20	3203	3201	3211	NE	NE
Carcharhinus_brevipinna	325	7591	6227	7045	NW	NW
Carcharhinus_limbatus	340	4427	5908	7349	NE	NE
Carcharhinus_melanopterus	200	2311	6691	7981	SE	SE
Carcharhinus_plumbeus	300	6233	5662	6228	NE	NE
Carcharias_taurus	320	491	4	0	SW	NA
Cepola_macrophthalma	70	4492	4391	4461	NE	NE
Chaetodon_hoefleri	27	534	525	25	SE	NE
Cheilopogon_heterurus	40	2315	1812	39	NE	SE
Chelon_labrosus	90	7592	5746	7056	NW	NW
Chromis_chromis	15	2491	2516	2516	SW	SW
Chromogobius_quadrivittatus	6.6	1292	573	30	SE	SE
Citharus_linguatula	30	2800	2762	2793	NE	NE
Clinitrachus_argentatus	10	1459	1184	829	NW	NW
Conger_conger	300	6271	6297	6297	NW	NW
Corcyrogobius_liechtensteini	3	23	0	0	NA	NA
Coris_julis	28	4828	4855	4855	NW	NW
Coryphoblennius_galerita	10	1408	844	67	SE	SE
Ctenolabrus_rupestris	18	2761	2787	2778	NW	NE
Cynoponticus_ferox	200	234	1	0	SE	NA
Dactylopterus_volitans	55	3401	3415	3415	SW	SW
Dalophis_imberbis	150	4510	4403	4502	NE	NE
Dasyatis_centroura	220	4271	4299	4299	NW	NW
Dasyatis_tortonesei	80	8128	8154	8154	NW	NW
Dasyatis_violacea	90	1581	4702	1761	NE	NE
Deltentosteus_collonianus	7	2505	1803	360	NE	NE
Deltentosteus_quadrimaculatus	9	2454	728	294	SW	SW
Dentex_dentex	100	3401	3402	3412	NE	NE
Dentex_gibbosus	100	4295	5245	5261	SE	SE
Dentex_macrophthalmus	65	3891	4956	5292	SE	SE
Dentex_maroccanus	45	2501	3861	4158	SE	SE
Dicentrarchus_labrax	110	3322	3325	3317	SE	NE
Dicentrarchus_punctatus	70	1167	2085	2126	SE	SE
Dicologlossa_cuneata	30	1276	1626	542	NE	SE
Didogobius_bentuvii	3.84	18	472	986	SW	SE
Didogobius_schlieweni	5	11	10	0	SW	NA
Didogobius_splechtnai	3.5	5	0	0	NA	NA
Diplecogaster_bimaculata	6	1728	1063	366	NE	NE
Diplodus_annularis	25	2761	2787	2787	NW	NW
Diplodus_cervinus_cervinus	55	2737	3044	3552	SE	SE
Diplodus_puntazzo	60	3543	3500	3528	NE	NE
Diplodus_sargus	45	3867	3816	3889	NE	NE

Diplodus_vulgaris	45	4271	4299	4299	NW	NW
Echelus_myrus	100	6577	6363	6468	NE	NE
Echeneis_naucrates	110	1521	7033	7827	NE	NE
Echiichthys_vipera	16	2091	2126	2126	NW	NW
Epinephelus_aeneus	130	2617	4778	5165	SE	SE
Epinephelus_alexandrinus	140	4375	5295	5557	SE	SE
Epinephelus_caninus	160	2193	3469	2488	NE	NE
Epinephelus_haifensis	110	59	288	736	SE	SE
Epinephelus_marginatus	150	3539	3453	3514	NE	NE
Eutrigla_gurnardus	60	6339	6135	6312	NE	NE
Exocoetus_volitans	30	45	0	0	NA	NA
Gaidropsarus_mediterraneus	45	1975	499	0	SE	NA
Gaidropsarus_vulgaris	60	1687	199	0	NE	NA
Gammogobius_steinitzi	4.3	11	0	0	NA	NA
Gobius_ater	7	39	0	0	NA	NA
Gobius_auratus	10	1654	421	26	SE	SE
Gobius_bucchichi	10	1789	1808	1823	NE	NW
Gobius_cobitis	30	1789	1811	1794	SW	NE
Gobius_cruentatus	18	1936	398	36	SW	SE
Gobius_fallax	9	50	3	0	SW	NA
Gobius_geniporus	16	1666	595	54	SE	SE
Gobius_luteus	10	119	0	0	NA	NA
Gobius_niger	15	2090	2126	2126	NW	NW
Gobius_paganellus	15	1789	1807	1804	SE	NE
Gobius_strictus	6.5	21	0	0	NA	NA
Gobius_vittatus	6	114	411	851	NW	NW
Gobius_xanthocephalus	10	1769	573	61	SE	SE
Gouania_willdenowi	6	1726	471	39	SE	SE
Gymnammodytes_cicerelus	18	4501	998	0	SE	NA
Gymnothorax_unicolor	110	5576	5604	5604	NW	NW
Gymnura_altavela	400	4825	4855	4855	NW	NW
Halobatrachus_didactylus	50	2443	2064	1436	NE	SE
Hippocampus_hippocampus	15	2090	2126	2126	NW	NW
Hippocampus_ramulosus	16	2090	2126	2126	NW	NW
Huso_huso	400	1122	155	2	SE	SE
Hypleurochilus_bananensis	12	45	460	963	NW	SW
Hyporhamphus_picarti	18	520	2653	6043	SW	SE
Knipowitschia_panizzae	4	329	356	46	SE	SE
Kyphosus_sectator	76	71	64	95	NE	NE
Labrus_bimaculatus	40	2674	709	404	SW	SW
Labrus_merula	50	2674	356	33	SW	SW
Labrus_viridis	50	3132	2438	2344	SW	SE
Lampetra_fluviatilis	50	3960	1323	702	NE	NW
Lappanella_fasciata	15	5877	3394	1783	SE	SE
Lebetus_guilleti	2.5	2768	433	34	NE	NE
Lepadogaster_candollei	8	1607	535	36	NE	SE
Lepadogaster_lepadogaster	8	1015	205	41	NW	SE
Lepadogaster_purpurea	7.5	188	58	0	NE	NA

Lesueurigobius_friesii	10	4392	1415	94	SE	SE
Lesueurigobius_suerii	8	3551	1001	11	SE	SW
Leucoraja_naevus	72	4033	2240	356	NE	NE
Lipophrys_adriaticus	5.5	146	10	0	SW	NA
Lipophrys_basiliscus	18	347	79	23	NW	SW
Lipophrys_canevai	8	1444	142	0	SW	NA
Lipophrys_dalmatinus	4.5	322	9	0	SW	NA
Lipophrys_nigriceps	4.5	670	73	15	SW	SW
Lipophrys_pavo	13	1452	1043	536	NW	NW
Lipophrys_trigloides	13	1412	583	528	NW	NW
Lithognathus_mormyrus	50	4269	4299	4299	NW	NW
Liza_ramada	70	7591	5826	7046	NW	NW
Liza_saliens	40	7592	5603	7071	NW	NW
Merlangius_merlangus	75	2347	452	54	SW	SE
Microchirus_azevia	40	823	572	0	NE	NA
Microchirus_ocellatus	22	6521	1690	391	SE	SE
Millerigobius_macrocephalus	5	81	186	271	NW	NW
Mobula_mobular	550	7591	5536	7115	NW	NW
Mugil_cephalus	120	7592	5553	7061	NW	NW
Mullus_surmuletus	45	5571	5385	5500	NE	NE
Muraena_helena	150	4269	4205	4243	NE	NE
Mustelus_asterias	150	7399	7141	7284	NE	NE
Mustelus_mustelus	160	4100	3992	4040	NE	NE
Mycteroperca_rubra	80	3399	3415	3415	NW	NW
Myliobatis_aquila	180	4100	3964	4045	NE	NE
Nerophis_maculatus	30	58	532	949	NW	SW
Nerophis_ophidion	30	2092	2092	2095	NE	NE
Oblada_melanura	30	2062	2086	2104	NE	NE
Odondebuenia_balearica	3.9	79	104	0	SE	NA
Oedalechilus_labeo	25	2060	2082	2103	NE	NE
Oligopus_ater	12	1055	644	186	SE	SE
Opeatogenys_gracilis	3	662	73	0	SE	NA
Ophidion_barbatum	30	2725	1495	91	NE	NE
Ophidion_rochei	30	1839	1059	113	NE	SE
Orcynopsis_unicolor	130	3305	7655	8100	NE	NE
Pagellus_acarne	36	4135	3405	2221	NE	SE
Pagellus_erythrinus	60	5204	5063	5145	NE	NE
Pagrus_auriga	80	3124	3860	4717	SE	SE
Pagrus_caeruleostictus	90	3468	4210	4518	SE	SE
Pagrus_pagrus	80	5402	5227	5337	NE	NE
Panturichthys_fowleri	70	35	633	1561	SW	SW
Parablennius_gattorugine	30	1984	1304	1243	NW	NW
Parablennius_incognitus	8	1426	733	63	SE	SE
Parablennius_rouxi	8	2137	582	31	SE	SE
Parablennius_sanguinolentus	22	1417	845	626	NW	NW
Parablennius_tentacularis	15	1807	843	0	SE	NA
Parablennius_zvonimiri	8	612	545	770	NW	NW
Parophidion_vassali	26	1512	1476	294	NE	SE

Petromyzon_marinus	120	2252	1894	1187	SE	SE
Phycis_phycis	60	2652	1045	0	NE	NA
Platichthys_flesus	60	562	6	0	NE	NA
Platichthys_luscus	55	1013	67	16	SE	SE
Plectorhinchus_mediterraneus	80	274	414	89	NE	NE
Pleuronectes_platessa	100	855	15	0	NW	NA
Pomadasys_incisus	50	1690	2846	3037	SE	SE
Pomatomus_saltator	120	7398	6772	7888	SW	NW
Pomatoschistus_bathi	3.5	78	37	0	SE	NA
Pomatoschistus_canestrinii	6.7	67	82	0	SE	NA
Pomatoschistus_knerii	4	35	0	0	NA	NA
Pomatoschistus_marmoratus	6.5	2759	2787	2787	NW	NW
Pomatoschistus_microps	7	50	0	0	NA	NA
Pomatoschistus_minutus	9,5	2761	2787	2787	NW	NW
Pomatoschistus_pictus	6	133	20	0	SW	NA
Pomatoschistus_quagga	5	1429	527	33	SE	SE
Pomatoschistus_tortonesei	3.7	28	244	216	NE	NE
Pristis_pristis	500	125	13	0	SW	NA
Psetta_maxima	110	5238	5263	5263	NW	NW
Pseudaphya_ferreri	3.5	959	445	42	SE	SE
Pteromylaeus_bovinus	150	6269	6060	6193	NE	NE
Raja_asterias	75	4510	4411	4485	NE	NE
Raja_miraletus	60	5627	5504	5625	NE	NW
Raja_montagui	100	1217	717	18	SE	SE
Raja_rondeleti	50	244	0	0	NA	NA
Rhinobatos_cemiculus	200	4270	4299	4299	NW	NW
Rhinobatos_rhinobatos	100	6269	6124	6297	NE	NW
Rhinoptera_marginata	200	4826	4773	4824	NE	NE
Rostroraja_alba	200	5447	4357	1792	SE	SE
Sarda_sarda	95	8042	8042	8042	NA	NA
Sardina_pilchardus	25	5828	2583	564	SE	SE
Sardinella_maderensis	30	3207	7154	8019	NE	NE
Sarpa_salpa	50	2488	2516	2516	NW	NW
Scartella_cristata	10	208	517	836	NW	SW
Sciaena_umbra	55	2602	2548	2566	NE	NE
Scophthalmus_rhombus	100	2719	2022	889	NE	NE
Scorpaena_loppei	15	1604	992	94	NE	SE
Scorpaena_maderensis	15	220	178	184	SW	SE
Scorpaena_notata	20	3543	3478	3498	NE	NE
Scorpaena_porcus	30	2758	2762	2765	NE	NE
Scorpaena_scrofa	50	5204	5030	5160	NE	NE
Scorpaenodes_arenai	11	53	218	14	NE	SE
Scyliorhinus_canicula	100	5203	5041	5159	NE	NE
Scyliorhinus_stellaris	190	4100	4012	4108	NE	NE
Serranus_cabrilla	40	8125	8154	8154	NW	NW
Serranus_hepatus	25	6730	6561	6736	NE	NW
Serranus_scriba	36	3327	3358	3358	NW	NW
Solea_aegyptiaca	30	1053	3727	4299	NE	SE

Solea_impar	35	4110	4533	4605	NE	NE
Solea_kleinii	40	5142	2918	712	SE	SE
Solea_lascaris	40	1862	1062	339	NE	NE
Solea_nasuta	40	2437	588	1	SE	SE
Solea_vulgaris	70	5250	5061	3985	NE	NE
Sparisoma_cretense	50	2315	2772	2787	SE	SE
Sparus_aurata	70	2601	2606	2611	SE	NE
Speleogobius_trigloides	2.3	29	0	0	NA	NA
Sphyraena_sphyraena	165	8128	7915	8004	NE	NE
Sphyraena_viridensis	165	166	1305	2720	SE	SE
Sphyrna_tudes	150	1136	402	0	SE	NA
Sphyrna_zygaena	420	8023	8154	8154	NW	NW
Spicara_flexuosa	22	4270	4299	4299	NW	NW
Spicara_maena	26	4270	4299	4299	NW	NW
Spicara_smaris	22	6137	7734	7968	NE	NE
Spondyliosoma_cantharus	70	4101	3933	4023	NE	NE
Squatina_oculata	200	2178	1980	697	NE	NE
Squatina_squatina	250	6269	6297	6297	NW	NW
Stromateus_fiatola	55	6268	8024	8154	NE	NE
Symphodus_bailloni	20	12	0	0	NA	NA
Symphodus_cinereus	12	2761	2787	2787	NW	NW
Symphodus_doderleini	10	3274	3358	3358	SE	SE
Symphodus_melanocercus	14	2168	2514	2516	SE	SE
Symphodus_melops	25	1412	453	40	NE	SE
Symphodus_ocellatus	12	2487	2516	2516	NW	NW
Symphodus_roissali	17	2091	2126	2126	NW	NW
Symphodus_rostratus	13	2757	2787	2787	NW	NW
Symphodus_tinca	35	2758	2760	2755	NE	NE
Syngnathus_abaster	21	1789	1813	1811	SW	NE
Syngnathus_acus	46	2488	2516	2516	NW	NW
Syngnathus_phlegon	20	6474	6080	7545	NE	NE
Syngnathus_taenionotus	25	71	0	0	NA	NA
Syngnathus_tenuirostris	39	54	3	7	SE	SE
Syngnathus_typhle	35	2758	2787	2787	NW	NW
Synodus_saurus	43	4268	4299	4299	NW	NW
Taurulus_bubalis	20	382	81	0	NE	NA
Thalassoma_pavo	25	3327	3268	3326	NE	NE
Thorogobius_ephippiatus	13	1667	404	33	SE	SE
Thorogobius_macrolepis	6.5	37	0	0	NA	NA
Torpedo_marmorata	100	5543	5364	5486	NE	NE
Torpedo_torpedo	80	6269	6098	6247	NE	NE
Trachinus_araneus	50	6270	6207	6284	NE	NE
Trachinus_draco	40	2758	2787	2787	NW	NW
Trachinus_radiatus	50	3430	3374	3437	NE	NW
Trigla_lucerna	75	6337	6146	6322	NE	NE
Trigloporus_lastoviza	40	5203	5058	5149	NE	NE
Tripterygion_delaisi	9	1236	890	1135	NW	NW
Tripterygion_melanurus	5.3	827	49	0	SE	NA

Tripterygion_tripteronotus	8	1284	194	28	SW	SW
Trisopterus_luscus	45	1623	1365	357	NE	SE
Trisopterus_minutus	40	2589	1321	13	NE	NE
Tylosurus_acus	135	1059	2370	4722	NW	SW
Umbrina_cirrosa	100	4269	4299	4299	NW	NW
Umbrina_ronchus	80	931	264	0	NE	NA
Uranoscopus_scaber	35	5401	5212	5292	NE	NE
Vanneaugobius_pruvoti	3.9	28	0	0	NA	NA
Xyrichthys_novacula	50	2611	2787	2787	SE	SE
Zebrus_zebrus	6.5	1389	623	616	NW	NW
Zeus_faber	70	5289	5201	5284	NE	NW
Zosterisessor_ophiocephalus	25	69	43	8	SE	SE

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Beyond species loss: functional and phylogenetic diversity erosion under climate change in the Mediterranean Sea.

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Soumis à Nature climate change

Beyond species loss: projected functional and phylogenetic diversity erosion under climate change

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Abstract

Climate change is known to have drastic effects on biodiversity distribution across all ecosystems but beyond changes in species composition the impact on the phylogenetic (PD) and functional (FD) diversity of assemblages is still overlooked particularly in the marine realm. Here we modelled the effect of climate change on the amount of evolutionary history and on the diversity of functional traits in Mediterranean fish assemblages across scales. We projected an erosion of PD and FD (13.6% and 12.6%, respectively) at the Mediterranean scale between the actual period and the end of 21st century following species loss. At a smaller scale we found areas where fish assemblages would lose more PD and FD than predicted given the decrease in species richness. Those areas, located in the Western basin, are heavily exploited with few marine protected areas. Since the erosion of PD and FD is not proportional to species diversity loss there is an urgent need to mitigate the effect of climate change on the different facets of biodiversity to preserve ecosystem's long-term viability.

Keywords: Mediterranean Sea, Phylogenetic erosion, Functional erosion, Bioclimatic envelop model, ensemble forecasting, Mediterranean Coastal fish.

Introduction

In the past 540 millions years five major extinction crises have happened resulting, at each period (Ordovician, Devonian, Permian, Triassic and Cretaceous), in the loss of more than three quarters of the Earth biodiversity[1]. There is a large consensus among scientists that we are living the sixth extinction crisis that is mainly due to human-mediated activities on ecosystems such as habitats fragmentation, introduction of non-native species, harvesting of natural resources and climate change[1-4]. Beyond the accumulated evidence that ecosystems are rapidly losing species diversity worldwide, the amount of phylogenetic (lineages) and functional (traits) diversity being lost is still under scrutiny. While it may deeply imperil the conservation of evolutionary history[4] and the provision of ecosystem services[5], respectively.

If some studies have focused on the effect of climate change on the erosion on the tree of life[4] or on the breadth of functional roles played by species assemblages[5], marine organisms have been largely ignored. Our understanding of the effect of climate change on marine ecosystems is still far lagging behind that of terrestrial ecosystems. Hoegh-Guldberg and Bruno [6] argue that this lag is partly due to the size and the complexity of oceans but also to the relative difficulty of obtaining measurements in marine environments and sampling their diversity. However, thanks to the emergence of regional oceanographic models, niche modeling approaches are providing a first step towards the assessment of climate change impacts on marine assemblages and ecosystem functioning[7-9]. However, this framework has never been used to investigate the expected changes in marine phylogenetic and functional diversity under climate change. Here, we fill this gap of knowledge using coastal fish of an archetypal region where climate change is expected to deeply modify both species richness and biological structure of assemblages: the Mediterranean Sea[10,11].

To estimate the projected changes in phylogenetic (PD) and functional (FD) diversity of coastal fish assemblages in the Mediterranean Sea under climate change, we first digitalized the geographical distributions of 230 teleost species of the Mediterranean continental shelf using a grid cell at a resolution of 0.1° by 0.1° [9] (for more details see methods). For those species, we extracted a dated phylogeny based on molecular data [12] and we built a functional dendrogram based on 15 functional traits to estimate actual and future patterns of phylogenetic and functional diversity of teleost assemblages, respectively. We used classical measures to explore both phylogenetic and functional diversity, namely the PD index[13] that only relies on the amount of evolutionary history (i.e. based on branch length on a phylogenetic tree) and the FD index that represents the extent of the functional differences among species based on the distinction of their morphological, physiological and ecological traits [14].

We then used a regional marine model of oceanographic circulation (NEMOMED8) based on a SRES (Special Report on Emissions Scenarios) A2 global warming scenario to predict sea surface temperatures (SST) at the end of the 21st century. According to this climate-warming scenario, we forecasted the geographic distributions of the 230 coastal Mediterranean teleostean fish species using an ensemble forecasting of niche models[15]. We finally estimated changes in PD and FD between present-day and the end of the 21st century at multiple spatial scales: (*i*) the whole Mediterranean Sea, (*ii*) the Mediterranean marine ecoregions and (*iii*) the 8154 cells (0.1° by 0.1°) of the Mediterranean continental shelf. The extent to which changes in PD and FD were independent of species richness changes was tested using null models, which consists in randomizing species on phylogenetic and functional trees while maintaining species richness constant in assemblages.

Results

Among the 230-modeled species, projections predicted that 40 species might have no suitable thermal conditions remaining on the continental shelf by 2080-2099 (Fig. 1a). These included 50% of species endemic to the Mediterranean Sea, and 85.5% listed on the IUCN Red List. The most represented family for extinct species was the Gobiidae. PD would decrease by 13.6% between the actual period and the end of the present century, i.e. that 13.6% of the phylogenetic tree for coastal Mediterranean fish, in terms of branch length that would be eroded. This amount of PD erosion was higher than expected by chance (13.1%), albeit not significant (p-value=0.39). FD would decrease by 12.8% between the observed period and the end of the present century but this amount of erosion is lower than expected by chance (13.8%, p-value = 0.17), albeit not significantly. Indeed the group represented by extinct species (in red, Fig. 1a, b, c) fills an amount of functional space, using three dimensions only, significantly lower than that filled by the other species groups (Permanova test: F.model = 7.52, DF = 229, p.value < 0.01). More precisely the group of species that would expand their range under climate change (in green) fills almost the whole functional space. Thus functional diversity loss would be restrained to the part of the functional space since it corresponds to the volume filled by extinct species (red) which is not embedded in the volume filled by non extinct species (green and blue).

When we focused on the Mediterranean ecoregions, the most important decrease in species richness would be observed in the Ionian (-25.5%) and Adriatic (-21.8%) following by the western Mediterranean (-17.51%) ecoregions. The PD of fish assemblages would be eroded at the end of the actual century under climate change excepted for the Aegean Sea (Fig. 2). The most important decrease in PD would be observed in the Ionian (-18.2%) and Adriatic Sea (-15.4%). Using null models we found that, given the loss of species, the level of PD erosion is higher than expected by chance, albeit only marginally significant, in the Alboran (p-value =

0.076), Western Mediterranean (p-value = 0.067) and the Levantine Sea (p-value = 0.062). FD would also decrease the end of the actual century under climate change for all ecoregions but the Aegean Sea (Fig. 2). The most important decrease in FD is expected in the Ionian (-16.9%) and in the western Mediterranean Sea (-12.1%). This decrease is significant, i.e. more marked than expected given species loss, in the Adriatic (p-value = 0.017), the Levantine (p-value = 0.019) and the western Mediterranean Sea (p-value = 0.045).

According to the predictions of the IPCC A2 scenario implemented in the climatic model, mean SST showed a steady increase of 2.8 °C over the whole Mediterranean Sea during for the end of 21st century (Fig. 3a). Among the 230-modelled species 40 species were projected to have no climatically suitable areas remaining. By 2080–99, 70.4% of cells were predicted to lose species and 26.8% of cells to gain species suitable areas remaining. For this period, the greatest loss of species richness was predicted in the western Mediterranean Sea and in several parts of the Aegean and Adriatic seas. The highest levels of gains in species richness were predicted in the Levantine Basin and in small areas of the North Adriatic Sea (Fig. 3b). At local scale, by 2080–2099, 74.6 % and 72.8 % of the continental shelf would experience a decrease in PD and FD of fish assemblages, respectively (Fig. 3c, d). These decreases are more marked in the western part of the Mediterranean Sea where the expected loss of species richness is the highest (Fig. 3b). Independently of species loss, we found that PD and FD erosion would be more pronounced than expected in the Western part of the Mediterranean while the Eastern part would loss less PD than expected (Fig. 3e). We identified two areas of significant PD erosion: in the Gulf of Lion and the South Sicilia. Beyond species loss, the found two areas of significant FD loss under climate change in the Gulf of Lion and the Adriatic Sea (Fig. 3f).

Discussion

Even if studying the modification in species richness under climate change is a logical starting point, it may hide other aspects of biodiversity loss. Our result highlights the importance of investigating changes in the structure of assemblages with different angles, beyond simple metrics ignoring biological differences between species related to their evolution or their function. The projected decrease of fish species richness at all scales induces a trivial decrease of PD and FD but in some areas fish assemblages are losing more diversity of lineages and traits than predicted simply as a result of species richness erosion. It means that, beyond losing species with an aesthetic or ethical value, those assemblages are losing species carrying a large amount of evolutionary history (long branches on the phylogenetic tree) and unique combinations of traits (extreme species in the functional space). Our study is the first one to put in light the potential effect of climate change on a combined loss of phylogenetic and functional diversity in assemblages across scales. Overall these two facets of the biodiversity have been largely ignored in climate change impact assessment and conservation planning yet they both are key to the diversity of life on Earth [16,17] and ecosystem functioning[18,19].

Indeed, ecosystem functioning and associated services depends on the maintenance of multiple processes across time and environmental change scenarios[20]. This requires species with complementary functions[21] however, we are far from being able to assess the roles played by individual species, especially in highly diverse regions where data are lacking even for common species. Instead we might resort to indirect measurements of ecological roles based on either functional traits or lineages that may embrace, thanks to phylogenetic conservatism[22], species potential functions. The loss of species with distinctive traits or lineages, i.e. those that overwhelmingly contribute to FD and PD respectively, may thus markedly affect ecosystem functioning[23,24], especially when multiple functions are considered [25]. This assumption is based on experiments showing that species with unique combination of traits can regulate ecosystem processes[23,26] and that trait dissimilarity within species assemblages increases ecological process rates[27,28]. Since the diversity of roles played by species is not fully understood across a suite of traits, the amount of phylogenetic diversity within an assemblage has been shown to explain ecosystem productivity[18] and stability[29]. It is therefore critical to know the degree to which PD and FD are eroded beyond species loss.

In the Mediterranean it has been already demonstrated that small species non-targeted by fishing may disappear first following climate change[9]. Here we show that the probable loss of suitable climatic niche was grouped across the phylogenetic tree particularly on the Gobiidae family. Those species are poorly known and not protected because they have no commercial interest. However, as most of small species in marine ecosystems, they sustain the productivity of higher trophic levels by providing food supply to larger fish, seabirds, and marine mammals. Furthermore phylogeny is a crucial determinants of food web structure since closely related species tend to overlap in their set of consumers[30], thus the role played by gobies is likely to be irreplaceable by other families[31].

At a smaller scale, i.e. ecoregions or local assemblages, the patterns of PD and FD erosion show a high heterogeneity with some areas of the Mediterranean continental shelf, notably the Western basin, losing a high proportion of evolutionary history or functional space. This disproportional PD and FD erosion compared to species loss would occur where resource overexploitation is marked and where few marine protected areas (MPA) are established like in the Alboran Sea and along the Algerian and Tunisian coasts[32]. This spatial congruence may even increase the impact of climate change on Mediterranean biodiversity since MPA enhance the resilience of marine populations to disturbances[33] while fishing enhances the climatic sensitivity of fish by reducing geographic distribution and population abundance and truncating individual age and size distribution[34].

Since the amount of evolutionary history and the diversity of roles in a species assemblage do not decrease systematically with decreasing species diversity there is an urgent need to integrate the effect of climate change on the different facets of biodiversity. This means that actions that focus on maintaining the level of species richness may not be sufficient to preserve an ecosystem's long-term viability. The conservation of fish PD and FD, that would be more eroded than suggested by species richness loss in the Mediterranean, can be considered as a priority within a climate change context coupled to overexploitation.

Methods

The phylogenetic information for the 230 Mediterranean teleost species were extracted from a dated phylogeny constructed from a DNA supermatrix composed of four mitochondrial genes 12S ribosomal DNA, 16S ribosomal DNA, cytochrome c oxidase subunit I and cytochrome.

We compiled information for the 230 species on the following 15 traits: depth at which species are encountered (minimum and maximum), mean length, maximum length, horizontal and vertical distribution, habitats, migration, reproduction, semelparity, sex shift, larvae types behaviour, species origins, diets, based on different sources (fishbase.org). We computed a functional dendrogram by using a gower distance between each pair of species[17,35]. The phylogenetic and functional diversity were evaluated by the use of the two well-know metrics, the phylogenetic diversity (PD) measures (Faith, 1992) and is functional homologous (FD; Petchey & Gaston 2006).

To infer global and ecoregional pattern of diversity loss we measured phylogenetic and functional diversity using classical[13,14] measures. We implemented a null model, corresponding to a simulation of 9999 null assemblages using a random choice of species from the regional pool by reshuffling species positions among the tips of the phylogenetic and functional tree for the second period.

To infer local patterns of both functional and phylogenetic diversity modification we calculated the difference in FD and PD measures between each time periods. We implemented a null model on the difference in FD and PD, we kept the identity of common species constant. We also respected the number of species lost or win through time periods but their identities were shuffled.

Based on ensemble forecasting approach, we used species distribution modelling to project the potential distribution of 230 coastal fish species by the middle and end of the 21st century based on the IPPC A2 scenario. This scenario was implemented with a Mediterranean climatic model NEOMED8. In order to account for unsuitable habitats, observed species occurrences were corrected by clipping off the bathymetry outside the minimum and maximum observed values for each species from the extent of occurrence maps (Froese *et al.*, 2010).

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Acknowledgments

We are grateful to the XXX anonymous referees for all the remarks and suggestions that improved the manuscript. This work was partly funded by the Total Foundation, the ‘Fondation pour la Recherche sur la Biodiversité’ (project BIODIVMED). D.M. was supported by a Marie Curie International Outgoing Fellowship (FISHECO) with agreement number IOF-GA-2009-236316.

Figure captions

Figure 1: Changes in suitable climate (A2 scenario for 2080-2099) mapped onto the phylogeny of coastal Mediterranean fish (a). Green edges indicate positive a range expansion, other colours indicate range contraction: blue for a decrease and red for extinction. Changes in suitable climate (A2 scenario for 2080-2099) mapped onto the functional space of coastal Mediterranean fish (b). Polygons indicate the functional space occupied by (*i*) in green, species that expand their range (*ii*) in blue, species that contract their range and in red, species that lost their range. The 3D functional space was represented in (b) with the first and the second PCOA axes, in (c) with the first and the third PCOA axes, in (d) with the second and the third axes.

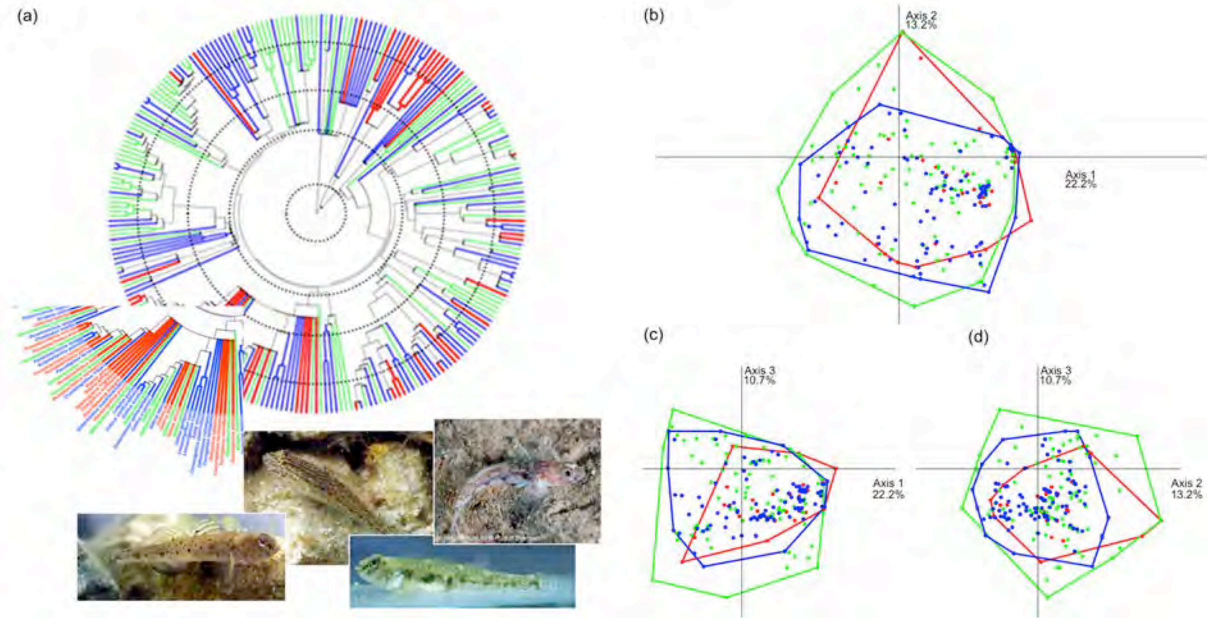
Figure 2: Difference in species richness, phylogenetic and functional diversity of coastal fish assemblages between the baseline (1961-1980) and the modelled period (2080-2099) for the seven Mediterranean ecoregions. When the difference in phylogenetic (**Δ** PD) or functional (**Δ** FD) diversity is significant given the change in species number and using a null model generating a random choice of species from the regional pool, the stars indicate the p-value level (* 0.1>p-value> 0.05, ** p-value >0.05) and the signs, + or -, indicate whether the difference is more or less pronounced than expected, respectively.

Figure 3:

Mediterranean maps showing the net differences in: (a) mean sea surface temperature (SST, °C) ; (b) fish species richness ; (c) fish phylogenetic diversity; (d) fish functional diversity between the baseline scenario (1961–1980) and future time periods (2080–2099) predicted for the continental shelf of the Mediterranean Sea according the A2 scenario implemented in the

NEMOMED8 climatic model. Significance of the difference in phylogenetic (e) or functional diversity (f) against a null model. This null model of the difference in FD and PD, kept the identity of common species constant, and respected the number of species lost or win through time periods. The “+” symbol indicates that the changes observed in differences in phylogenetic or functional diversity are significantly greater than expected under the null hypothesis ($P > 0.975$), whereas the **“–”** symbol indicates that the changes observed in differences in phylogenetic or functional diversity significantly lower than expected under the null hypothesis ($P < 0.025$). ns indicates that the in differences in phylogenetic or functional diversity are not significantly different from the values expected under the null hypothesis.

Figure 1


(a)
(b)
Axis 2
13.2%
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(c)
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10.7%
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(d)
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Axis 2
13.2%

Figure 2:

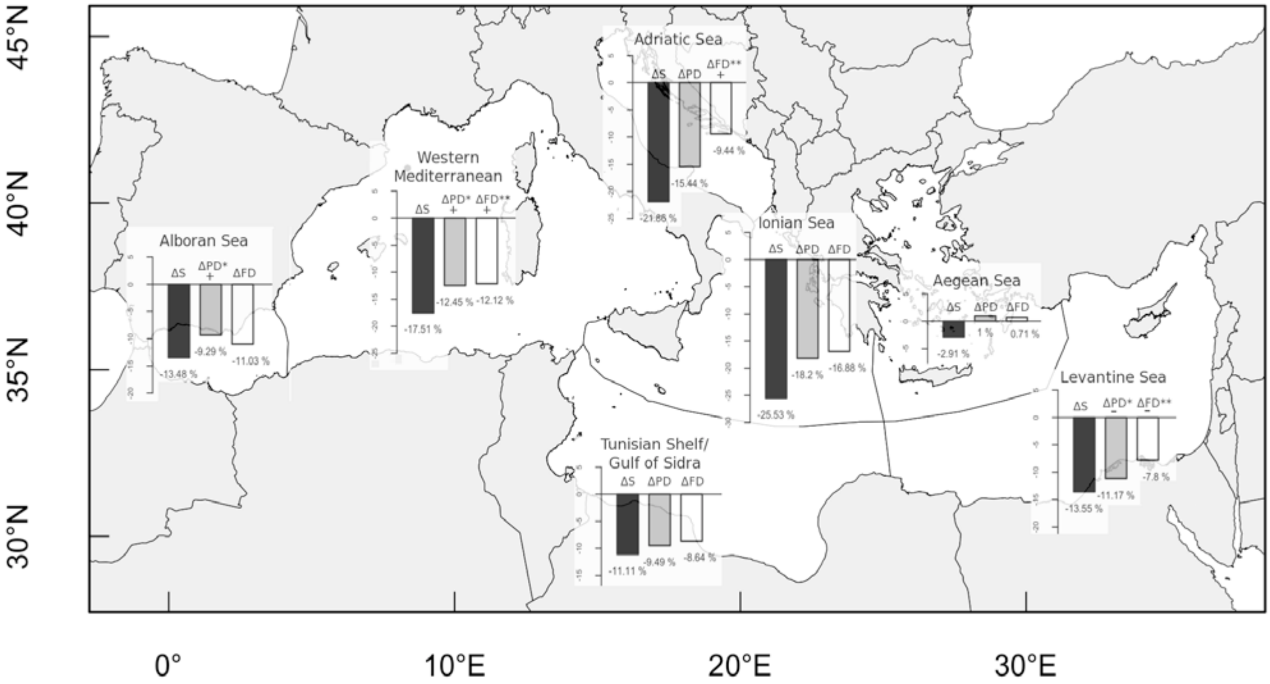
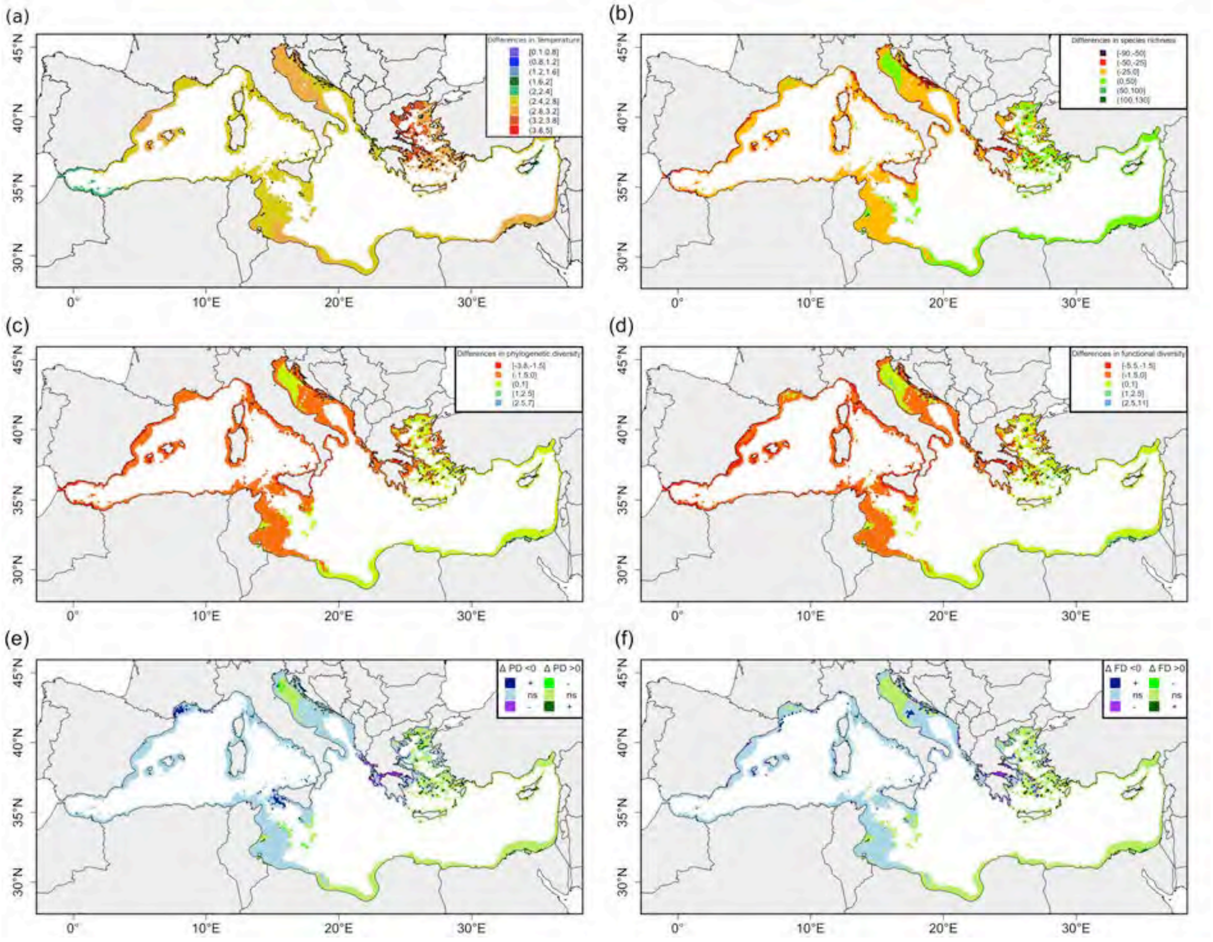

45°N
40°N
35°N
30°N
0°
10°E
20°E
30°E
Alboran Sea
ΔS
ΔPD*
+
ΔFD
-13.48 %
-9.29 %
-11.03 %
Western Mediterranean
ΔS
ΔPD*
+
ΔFD**
+
-17.51 %
-12.45 %
-12.12 %
Adriatic Sea
ΔS
ΔPD
ΔFD**
+
-21.66 %
-15.44 %
-9.44 %
Ionian Sea
ΔS
ΔPD
ΔFD
-25.53 %
-18.2 %
-16.88 %
Aegean Sea
ΔS
ΔPD
ΔFD
-2.91 %
1 %
0.71 %
Levantine Sea
ΔS
ΔPD*
−
ΔFD**
−
-13.55 %
-11.17 %
-7.8 %
Tunisian Shelf/ Gulf of Sidra
ΔS
ΔPD
ΔFD
-11.11 %
-9.49 %
-8.64 %

Figure 3:


(a)
Differences in Temperature
[0.1,0.8]
(0.8,1.2]
(1.2,1.6]
(1.6,2]
(2,2.4]
(2.4,2.8]
(2.8,3.2]
(3.2,3.8]
(3.8,5]
(b)
Differences in species richness
[-90,-50]
[-50,-25]
(-25,0]
(0,50]
(50,100]
(100,130]
(c)
Differences in phylogenetic diversity
[-3.8,-1.5]
(-1.5,0]
(0,1]
[1,2.5]
(2.5,7]
(d)
Differences in functional diversity
[-5.5,-1.5]
[-1.5,0]
(0,1]
[1,2.5]
[2.5,11]
(e)
Δ PD <0
Δ PD >0
+
ns
-
-
ns
+
(f)
Δ FD <0
Δ FD >0
+
ns
-
-
ns
+
45°N
40°N
35°N
30°N
0°
10°E
20°E
30°E

Manuscrit F.

Combining projected changes in species richness and composition reveals climate change impacts on coastal Mediterranean fish assemblages.

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Global Change Biology

Global Change Biology (2012), doi: 10.1111/j.1365-2486.2012.02772.x

Combining projected changes in species richness and composition reveals climate change impacts on coastal Mediterranean fish assemblages

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Abstract

Species Temporal Turnover (STT) is one of the most familiar metrics to assess changes in assemblage composition as a consequence of climate change. However, STT mixes two components in one metric, changes in assemblage composition caused by a process of species loss or gain (i.e. the nestedness component) and changes in assemblage composition caused by a process of species replacement (i.e. the species replacement component). Drawing on previous studies investigating spatial patterns of beta diversity, we propose measures of STT that allow analysing each component (species replacement vs. nestedness), separately. We also present a mapping strategy to simultaneously visualize changes in species richness and assemblage composition. To illustrate our approach, we used the Mediterranean coastal fish fauna as a case study. Using Bioclimatic Envelope Models (BEMs) we first projected the potential future climatic niches of 288 coastal Mediterranean fish species based on a global warming scenario. We then aggregated geographically the species-level projections to analyse the projected changes in species richness and composition. Our results show that projected changes in assemblage composition are caused by different processes (species replacement vs. nestedness) in several areas of the Mediterranean Sea. In addition, our mapping strategy highlights that the coastal fish fauna in several regions of the Mediterranean Sea could experience a 'cul-de-sac' effect if exposed to climate warming. Overall, the joint exploration of changes in species richness and composition coupled with the distinction between species replacement and nestedness bears important information for understanding the nature of climate change impacts on biodiversity. These methodological advances should help decision-makers in prioritizing action in the areas facing the greatest vulnerability to climate.

Keywords: beta diversity, Bioclimatic Envelop Model, Mediterranean coastal fish, Mediterranean Sea, nestedness, Nestedness, Species Temporal Turnover, turnover, Turnover

Received 21 February 2012; revised version received 12 June 2012 and accepted 15 June 2012

Introduction

Climate change is already affecting species distributions and species composition within assemblages (Tingley *et al*., 2009; Hillebrand *et al*., 2010), and deeper changes are expected during the 21st century (Hoegh-Guldberg & Bruno, 2010; Thuiller *et al*., 2011). The most commonly used method to forecast climate change impacts on biodiversity is bioclimatic envelope models (BEMs, Araújo & Peterson, 2012). BEMs describe associations between current species distribution and climate, and use these associations to forecast changes in species distribution under climate change scenarios. The structure and composition of local assemblages are then inferred by geographically aggregating the results of species-level projections (the 'predict first, assemble later' strategy from Ferrier & Guisan, 2006).

How can such changes in biodiversity be measured? The most familiar metric of compositional change is species temporal turnover (STT, Peterson *et al*., 2002; Thuiller *et al*., 2005). STT counts the numbers of species gained and lost within each geographical unit and

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compares them with the total number of species recorded in the baseline period (Peterson *et al.*, 2002; Thuiller *et al.*, 2005; Buisson *et al.*, 2008). Both conceptually and numerically, STT is a metric of temporal beta diversity equivalent in its formulation to the Jaccard's dissimilarity index (see methods; Anderson *et al.*, 2011).

As with several measures of beta diversity (Baselga, 2010, 2012), STT (or the Jaccard's dissimilarity index) mixes two components that are relevant to understand climate change impacts on biodiversity at a given location: (i) changes in assemblage composition caused by the loss or gain of species (i.e. the nestedness component of beta diversity); and (ii) changes in assemblage composition caused by a process of species replacement (i.e. the species replacement component of beta diversity). Consequently, using broad-sense measures of STT that account for differences in both species richness and species identities (e.g. the Jaccard's dissimilarity index, see Koleff *et al.*, 2003) may confound very different situations that can be expected under climate change (see Fig. 1). For instance climate warming may induce large reshufflings of local communities (e.g. cases A and D, Fig. 1). This may be due to a total extinction of the local pool of warm-sensitive species (case A, species 1 and 2; case D, species 1); those species being in turn replaced by either less (case A, Fig. 1) or more (case D, Fig. 1) warm-tolerant species tracking their climatic niches and not limited in their dispersion (Somero, 2012). In contrast, climate warming may cause the loss of species without replacement if the new environmental conditions are too harsh or if the location is too isolated for the establishment of potential colonizers (Novak *et al.*, 2011). This scenario implies a nested subset pattern in species composition over time (case B, Fig. 1). Nested patterns of species composition over time can also result from species gains in localities (or regions) where the future environmental conditions are suitable to both resident and incoming species not limited in their dispersion (case C, Fig. 1).

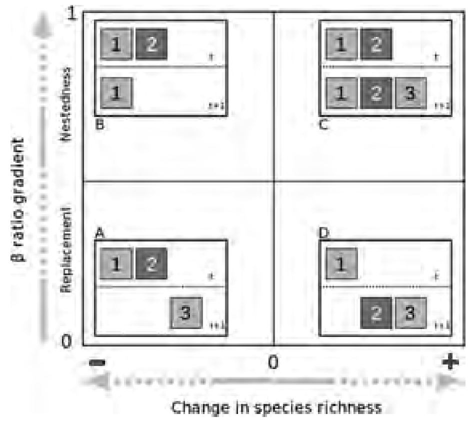

Fig. 1 Conceptual diagram describing the different scenarios of change in species richness and assemblage composition expected under global change. The horizontal axis represents the change in species richness and the vertical axis represents the gradient of β_{ratio} (representing the relative contribution of species replacement vs. nestedness in explaining species temporal turnover STT, see main text). Boxes (A, B, C, D) are divided into two parts that represent two time periods (t and $t + 1$). Numbered squares represent different species. Scenario A illustrates a decrease in species richness over time (t to $t + 1$) coupled to a full species replacement (species 1 and 2 are replaced by a new species 3) thus corresponding to a low value of β_{ratio}. Scenario B also represents a decrease in species richness between the two time periods, but in this scenario the assemblage at $t + 1$ is completely nested in the assemblage at t, resulting in a high value of β_{ratio}. Scenarios C and D depict the same processes responsible for assemblage turnover as in B (nestedness) and A (replacement), but with an increase in species richness between the two time periods.

These four extreme scenarios also show that beyond change in species composition, the amount of temporal change in species richness is a crucial and complementary facet to fully investigate biodiversity changes caused by climate change (Thuiller *et al.*, 2005). Yet, previous BEM-based studies commonly analysed separately the projected changes in species richness and composition (e.g. Peterson *et al.*, 2002; Thuiller *et al.*, 2005; Buisson & Grenouillet, 2009), although they are clearly not trivially independent patterns. For instance, changes in species composition due to full species replacement can be coupled with either a decrease or increase of species richness over time (cases A and D respectively, Fig. 1). Similarly, changes in species composition due to nestedness can be coupled with either a decrease or increase of species richness over time (cases B and C respectively, Fig. 1).

In the present study, we present a strategy to improve the interpretation of BEMs forecasts by two means. First, we propose that changes in species richness and changes in species composition are being analysed together to fully apprehend the potential effects of climate change on species assemblages, and highlight a bivariate mapping strategy to picture simultaneously the spatio-temporal trend of both processes. Second, drawing on previous studies investigating spatial patterns of beta diversity (Baselga, 2010, 2012), we propose modifications in the usually used metric of temporal beta diversity (STT). We exemplify this strategy using coastal fish assemblages in the Mediterranean Sea as a case study. The region accounts for just 0.32% of the global oceanic volume, but it hosts high densities of species and endemism (Coll *et al.*, 2010). Fish assemblages are also expected to be deeply modified as a result of climate change (Giorgi, 2006; Ben Rais Lasram *et al.*, 2010; Azzurro *et al.*, 2011). For these reasons, the Mediterranean Sea provides a good template to investigate

21st century impacts of climate change on spatial and temporal components of coastal fish diversity.

Material and methods

Methodological developments

Equivalence between the species temporal turnover index and the Jaccard's dissimilarity index. In studies assessing climate change effects on species distributions, temporal modifications of species assemblages are measured using the species temporal turnover index (STT, Peterson *et al*., 2002) as follows:

$$\mathrm{STT} = \frac{G+L}{SR+G}. \tag{1}$$

where L is the number of species lost, G is the number of species gained, and SR is the baseline species richness. Rearranging eqn (1) leads to a temporal version of the long known pairwise Jaccard's dissimilarity index (Anderson *et al*., 2011):

$$\beta_{jac} = \frac{b+c}{a+b+c}. \tag{2}$$

where a is the number of species present at both time steps, b is the number of species present in time step one but not in time step two (equivalent to L in eqn 1), and c is the number of species present at time step two but not at time step one (equivalent to G in eqn 1) with a+b being equal to SR in eqn 1. β_{jac} ranges from 0 (species composition does not change between time periods) to 1 (species composition completely changes between time periods).

Decoupling the species replacement and nestedness components of species temporal turnover. To distinguish between the species replacement and nestedness components of STT, we apply the partitioning framework proposed by Baselga (2010, 2012), which consists in decomposing the pair-wise Jaccard's dissimilarity index (β_{jac}, eqn 2) into two additive components. The species replacement component of the Jaccard's dissimilarity index (β_{jtu}, eqn 3) describes species replacement without the influence of richness difference between time periods. This index is formulated as follows:

$$\beta_{jtu} = \frac{2\min(b,c)}{a+2\min(b,c)} \tag{3}$$

where a, b and c are like in eqn 2.

Baselga (2012) showed that β_{jac} is equal to β_{jtu} in the absence of nestedness (i.e. a = 0). The nestedness component of the Jaccard's dissimilarity index (β_{jne}, eqn 4) is therefore simply the difference between β_{jac} and β_{jtu} ($\beta_{jne} = \beta_{jac} - \beta_{jtu}$). This index that accounts for the fraction of dissimilarity due to richness difference is formulated as follows:

$$\beta_{jne} = \frac{\max(b,c)-\min(b,c)}{a+b+c} \times \frac{a}{a+2\min(b,c)}. \tag{4}$$

where a, b and c are like in eqn 2. In eqn 4 the first term expresses a measure of richness difference, whereas the second part corresponds to the similarity version of β_{jtu} that is independent of richness difference ($1-\beta_{jtu}$; Baselga, 2010). β_{jac}, β_{jtu} and β_{jne} can be studied separately, however, the ratio between β_{jne} and β_{jac} ($\beta_{ratio} = \beta_{jne}/\beta_{jac}$; Dobrovolski *et al*., 2011) is useful to describe the relative contribution of each component (species replacement vs. nestedness) in explaining the overall amount of STT. Values smaller than 0.5 indicate that species replacement is the main driver of STT, whereas values greater than 0.5 indicate that STT is mostly caused by nestedness. For a β_{ratio} value equal to 1, the nestedness component is the sole driver of STT. When β_{ratio} equals 0 this indicates that the species replacement component is the sole driver of STT. β_{jac} equals 0 when b and c are both null in eqn 2, which means that no change in species composition occurred between time periods (implying no change in species richness, thus a null β_{jne}), in this rare case β_{ratio} is not defined.

Mapping changes in species richness and assemblage composition. To map the continuum of situations bracketed by the extreme cases illustrated in Fig. 1, we propose to picture simultaneously the β-values (β_{jac} or β_{ratio}) and the temporal changes in species richness on the same map. To do so, two different 3-colour linear ramps describing the gradients in β-values for positive vs. negative changes in species richness are required. In this article we used a green to blue to purple colour ramp matching, respectively, the 0, 0.5 and 1 β-values for cells showing a decrease in species richness and a yellow to red to brown colour ramp (matching the 0, 0.5 and 1 β-values) for cells showing an increase in species richness.

The R functions required to calculate β_{jac}, β_{jtu}, β_{jne} and β_{ratio} values as well as to map simultaneously β-values and changes in species richness are available in the 'betapart' package for the R (R 2.13.0, R Development Core Team, 2011) statistical and programming environment (http://CRAN.R-project.org/package=betapart).

Case study: the future of the Mediterranean coastal fish fauna

We exemplify the approach by exploring the potential effects of climate change on Mediterranean coastal fish assemblages for the mid and late 21st century. Using BEMs we projected the potential future climatic niches of 288 coastal Mediterranean fish species based on a global warming scenario implemented with the Mediterranean model NEMOMED8. We then aggregated geographically the species-level projections to analyse the projected changes in species richness and assemblage composition. We used eqns 3 and 4 to characterize the two components (species replacement vs. nestedness) of expected species temporal turnover. Using the strategy highlighted above we mapped simultaneously changes in species richness and β_{ratio} values to discuss the changing biogeography of coastal Mediterranean fishes. In addition, we analysed patterns of STT (species replacement vs. nestedness) at a finer spatial scale using the marine ecoregions defined by Spalding *et al.* (2007).

Species Data. We used the geographical distributions (extent of occurrence maps) of 288 endemic and native coastal fish species on the continental shelf of the Mediterranean Sea (Ben Rais Lasram *et al*., 2009, 2010; Coll *et al*., 2010). Data were compiled from the atlas of fishes of the Northern Atlantic and Mediterranean (FNAM; Whitehead *et al.*, 1986). This atlas is based on regional data sets and expert knowledge and was edited between 1984 and 1986. It currently provides the only available basin-wide information on the geographical ranges of all Mediterranean Sea fish species (Ben Rais Lasram *et al.*, 2009).

The above-mentioned atlas does not account for the bathymetric distribution of Mediterranean fish species, yet bathymetry is considered as one of the main factors accounting for marine fish distributions (Louisy, 2005). We therefore refined the extent of occurrence maps by clipping off areas with depths that fall outside the range (minimum–maximum) known for the species (Froese & Pauly, 2010). Species' bathymetric ranges were obtained from fishbase and Louisy (2005). The bathymetry of the Mediterranean Sea was obtained from the ETOPO2v2 (ETOPO2v2, 2010) Global Gridded 2-min Database. Exotic species were discarded from our analyses since the equilibrium with environmental conditions is a required assumption for predicting and projecting species distributions (Guisan & Thuiller, 2005). In addition, we did not consider potential colonizations of fish species from neighbouring regions (i.e. the Atlantic ocean and the Red Sea). We therefore explored a scenario of climate change impact on the native coastal Mediterranean fish fauna only. We acknowledge that this scenario is restrictive but most of range maps of Lessepsian and Atlantic fish species are currently not available. Overall, our final data set contained the occurrences of 288 strictly coastal fish species on a 0.1° resolution grid system covering the whole continental shelf of the Mediterranean Sea (8154 cells).

Current and projected Sea Surface Temperatures (SST). Water temperature is one of the main drivers shaping marine fish species distributions and thus the composition of local assemblages (Dulvy *et al.*, 2008; ter Hofstede & Rijnsdorp, 2011), especially in the Mediterranean (Raitsos *et al.*, 2010; Azzurro *et al.*, 2011). We used a Mediterranean regional marine model (NEMOMED8) that predicts SST based on the following drivers: water energy fluxes, river discharges and water exchanges with the surrounding seas (Beuvier *et al.*, 2010). We used daily SST values predicted by NEMOMED8 for the period 1961–1980 as a baseline to calibrate the species distribution models (Beuvier *et al.*, 2010). The daily data were averaged to infer monthly data, leading to 15 variables: 12 monthly averaged SST values, the absolute minimum SST, the absolute maximum SST and the absolute range of SST (i.e. the difference between the absolute maximum and minimum SST). Several SST variables were considered because fish are ectothermic and thus highly dependent on their thermal environment for critical life-history steps such as breeding and developmental success (Mann & Blackburn, 1991). For instance, larvae and juvenile recruitment is strongly dependent on maximum temperatures (Burreson & Sypek, 1981) while growth rate may be limited by increased metabolic costs above a certain SST (Neuheimer *et al.*, 2011).

However, to avoid model over-parameterization and strong collinearity among predictor variables (Thuiller *et al.*, 2005), we aggregated redundant temperature variables. To do so, we reduced the set of predictive variables on the basis of a k-means partitioning method (Legendre & Legendre, 1998). The optimal number of groups was determined according to the highest Simple Structure Index (SSI) following Dolnicar *et al.* (1999). We obtained eight synthetic variables by averaging inside each group determined by the k-means clustering. Projected SST values were extracted for the middle (2040–2059) and end of the 21st century (2080–2099) from NEMOMED8 outputs, based on the IPCC A2 scenario (the only scenario implemented in NEMOMED8); this scenario is conservative and not the most pessimistic regarding future prediction of global warming (IPCC, 2007).

Bioclimatic envelope modelling. To account for model-based uncertainties in the modelling process, we applied an ensemble forecasting approach (Araújo & New, 2007) based on seven statistical algorithms: (1) Generalized Linear Models, (2) Generalized Additive Models, (3) Classification Tree Analysis, (4) Random Forests, (5) Boosted Regression Trees, (6) Multivariate Adaptive Regression Splines and (7) Surface Range Envelope. Analyses were implemented with the BIOMOD package (Thuiller *et al.*, 2009) for the R statistical and programming environment (R Development Core Team, 2011). Each model in the ensemble was weighted according to the True Skill Statistic (TSS) criterion (Allouche *et al.*, 2006). Species presences/absences were derived from probabilistic model outputs using the threshold that maximized the TSS (Thuiller *et al.*, 2009). The predictive accuracy was classified as 'fair' to 'good' for the seven BEMs, with a mean TSS of 0.61. However, overall no clear evidence of model superiority emerged. We therefore implemented ensemble forecasts (Weighted Average Consensus) to project potential thermal niches in the future.

Using the projected temperatures for 2040–2059 and 2080–2099, we predicted the geographical location of the potential climatic niche (as inferred by the WAC) for each species. We assumed no dispersal limitation towards new climatically suitable areas because recent invasions show that fish may reach a mean dispersal rate of 221 ± 5.4 km yr^{-1} on the northern side of Mediterranean Sea (Ben Rais Lasram *et al.*, 2008). However, we imposed some bathymetric limitations by not allowing a species to be present in a cell if that cell's depth did not fall inside the species' known bathymetric range (Froese & Pauly, 2010). In addition, we estimated the potential dispersal distances travelled by species under climate warming by measuring changes in the geographical position of species range centroids (Tingley *et al.*, 2009).

Results

When considering the whole continental shelf of the Mediterranean Sea, species replacement contributes more than nestedness in explaining the temporal pattern of coastal fish turnover (2040–2059: mean $\beta_{\text{ratio}} = 0.36$; 2080–2099: mean $\beta_{\text{ratio}} = 0.315$). Indeed, nestedness contributes more than 75% to the total amount of STT in only 1053 cells (12.9%) and 184 cells (2.3%) of the continental shelf for the first and the second modelled periods respectively.

When analysing patterns of STT at a finer spatial scale (i.e. marine ecoregions, see Fig. 2 for more details), the relative contribution of species replacement vs. nestedness differs markedly among marine ecoregions. For instance, STT in the Alboran Sea for both the first (2040–2059: mean $\beta_{jac} = 0.498$) and second (2080–2099: mean $\beta_{jac} = 0.417$) periods is mostly caused by nestedness ($\beta_{ratio} > 0.5$) (see Table 1 and Fig. 2) with a clear decrease in species richness (the case B in Fig. 1). In contrast, the low levels of STT in the Adriatic (mean $\beta_{jac} = 0.356$) and Aegean Seas (mean $\beta_{jac} = 0.322$) for the first modelled period are associated with species replacement ($\beta_{ratio} < 0.5$). This replacement of species is accompanied by an overall increase in species richness (the case D in Fig. 1), more particularly in the northern and central parts of the Adriatic and Aegean Seas (Fig. 2c). For the second modelled period, similar patterns emerge in these two regions (Table 1), except that patterns of species replacement are associated to a net decrease in species richness (the case A in Fig. 1) on almost all the continental shelf of the Adriatic Sea (Fig. 2b, d).

The other marine ecoregions of the Mediterranean Sea also provided contrasting results. The low levels of STT observed in the Levantine basin ($\beta_{jac} = 0.158$) are equally explained by both species replacement and nestedness ($\beta_{ratio} \sim 0.5$ for both the first and second modelled periods, see Table 1, Fig. 2). The Levantine

Table 1 Values of the Jaccard index (β_{jac}) measuring temporal turnover and the β_{ratio} index measuring the relative contribution of species replacement vs. richness difference to the total turnover in seven Mediterranean marine ecoregions (Fig. 2) calculated between the baseline time period (1961–1980) and two future periods (2040–2059; 2080–2099); n is the number of grid cells in each marine ecoregion

		2040–2059		2080–2099	
Ecoregion	n	β_{jac}	β_{ratio}	β_{jac}	β_{ratio}
Alboran Sea	250	0.498 ± 0.135	0.659 ± 0.156	0.417 ± 0.10	0.530 ± 0.157
Western Mediterranean	1958	0.345 ± 0.104	0.322 ± 0.236	0.411 ± 0.09	0.400 ± 0.146
Tunisian Plateau/Gulf of Sidra	1359	0.199 ± 0.09	0.55 ± 0.321	0.232 ± 0.09	0.353 ± 0.226
Ionian Sea	770	0.376 ± 0.09	0.435 ± 0.181	0.407 ± 0.08	0.339 ± 0.179
Adriatic Sea	1373	0.356 ± 0.120	0.179 ± 0.130	0.462 ± 0.106	0.187 ± 0.109
Aegean Sea	1481	0.322 ± 0.117	0.282 ± 0.188	0.351 ± 0.105	0.172 ± 0.137
Levantine Sea	944	0.158 ± 0.09	0.396 ± 0.259	0.167 ± 0.09	0.415 ± 0.248

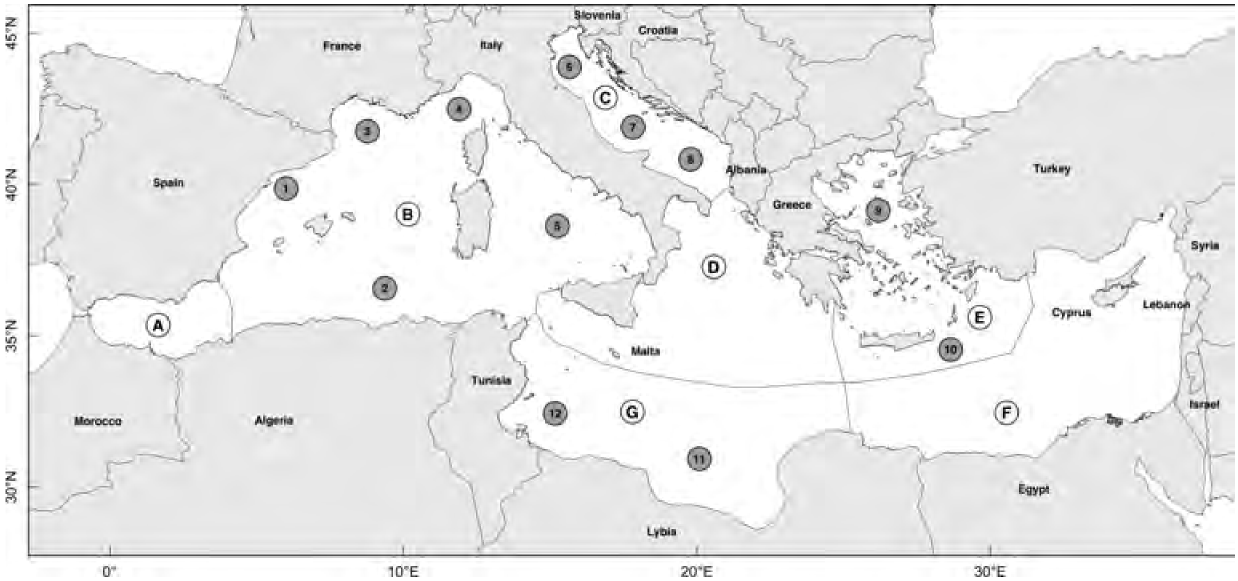

Fig. 2 Main marine ecoregions (Spalding *et al.*, 2007) and basins in the Mediterranean Sea. Ecoregions: A, Alboran Sea; B, Western Mediterranean; C, Adriatic Sea; D, Ionian Sea; E, Aegean Sea; F, Levantine Sea; G, Tunisian shelf/Gulf of Sidra. Basins: 1, Balearic Sea; 2, Algerian and Tunisian waters; 3, Gulf of Lions; 4, Ligurian Sea; 5, Tyrrhenian Sea; 6, North Adriatic Sea; 7, Central Adriatic Sea; 8, South Adriatic Sea; 9, North Aegean Sea; 10, South Aegean Sea; 11 Gulf of Sidra; 12, Gulf of Gabès.

basin also shows a net increase in species richness, in contrast to the Algerian and Tunisian coasts and the Gulf of Gabès (see Fig. 1 for localization) that experience similar levels of STT but mainly caused by nestedness ($\beta_{\text{ratio}} \sim 0.75$, see Fig. 2c, d).

Finally, 61.11% of the 288-modelled fish species are predicted to experience a shift towards the northern part of the Mediterranean Sea during the first period (Fig. 4). On average, for the first period, the overall fish assemblage moves to *c.* 70 km northwards and 30 km eastwards. More particularly, species range centroids move to north-eastwards for 37.85% of the modelled species. A similar trend emerges when considering the second period: 53.82% of the species shift in their geographical ranges towards the northern part of the Mediterranean Sea. On average, for the second period, the overall fish assemblage moves to *c.* 140 km westwards and 90 km northwards.

Discussion

Previous studies assessing climate change impacts on species assemblages typically measured changes in species richness, STT, or both (Peterson *et al.*, 2002; Thuiller *et al.*, 2005; Araújo *et al.*, 2006; Ben Rais Lasram *et al.*, 2010; Garcia *et al.*, 2011). Here we showed that changes in assemblage composition over time can be caused by either species replacement or nestedness or combinations of both, which may hence reflect different impacts impinging on local assemblages when they are exposed to climate change (Fig. 1). Recent works highlighting the effect of past glaciations on large-scale biodiversity patterns have successfully demonstrated that disentangling the species replacement and nestedness components of beta diversity improves understanding of past environmental changes on species assemblages (Baselga, 2010; Dobrovolski *et al.*, 2011; Leprieur *et al.*, 2011). The same may apply for biodiversity forecast. Yet, those advances have not been incorporated into climate change impact assessments on species assemblages. Here, we illustrate how such developments in macroecology can offer insights for understanding impacts of climate change on local species assemblages.

The results related to our case study demonstrate that temporal turnover in projected coastal fish assemblages are caused by different processes (species replacement vs. nestedness related to species loss or gain), with different relative magnitudes in several areas of the Mediterranean Sea. For instance, the Jaccard's dissimilarity index, usually used to measure species temporal turnover in climate change studies (Peterson *et al.*, 2002), shows that the extreme north of the Adriatic Sea and the Gulf of Gabès would display similar turnover levels (Fig. 3a, b). However, changes in fish fauna composition on the northern part of the Adriatic Sea are almost entirely driven by species replacement (see Figure S1), whereas those projected in the Gulf of Gabès are mainly caused by species loss (Fig. 2c, d). We thus suggest that a measure of STT emphasizing species replacement (e.g. β_{jtu}) is more suitable for the identification of areas that would gain and lose species as a result of climate change than the traditional Jaccard's dissimilarity index.

A complementary approach is to map changes in species richness and assemblage composition altogether (e.g. Williams *et al.*, 1999). Using a mapping tool allowing the joint exploration of changes in richness and assemblage composition, we show that the coastal fish fauna in several regions of the Mediterranean Sea could experience a 'cul-de-sac' effect if exposed to climate warming (see also Ben Rais Lasram *et al.*, 2010). By the mid-21st century, high levels of species replacement associated to an increase in species richness are projected in most of the Aegean and Adriatic Seas (see Fig. 3c). This increase in species richness can be explained by the immigration of many coastal fish species that track their climate niches from the different parts of the Mediterranean Sea (Azzurro *et al.*, 2011), including the Gulf of Gabès that would experience a net loss of species (Fig. 3c). Our results (see Fig. 4) demonstrate that species ranges are expected to move northwards and eastwards, i.e., in direction of the Aegean and Adriatic Seas. In contrast, by the end of 21st century, most of the Gulf of Lion as well as the Adriatic and Aegean Seas are projected to experience a net decrease in species richness resulting from a loss of thermal niche for numerous fish that are not balanced by the arrival of other species from the south (Fig. 3d). Such a 'cul-de-sac' effect has been already described as the upward altitudinal response of terrestrial organisms to climate change (Tingley *et al.*, 2009); initially mountains might act as refugia for species, but as temperature increases, species have nowhere to migrate being trapped in the mountain tops and tends to disappear (Parmesan & Yohe, 2003).

These results have important fundamental and applied implications. For instance, the very high STT predicted in the Adriatic and Aegean Seas during the 21st century may have marked consequences on ecosystem functioning (Hillebrand *et al.*, 2010; Wardle *et al.*, 2011). However, previous studies have mostly focused on ecosystem impacts of species gain and loss in isolation from each other (see Vaughn, 2010; Wardle *et al.*, 2011). Yet, both species gain and loss are frequently encountered simultaneously in ecological communities (Jackson & Sax, 2010). Empirical approaches evaluating the functional roles of species

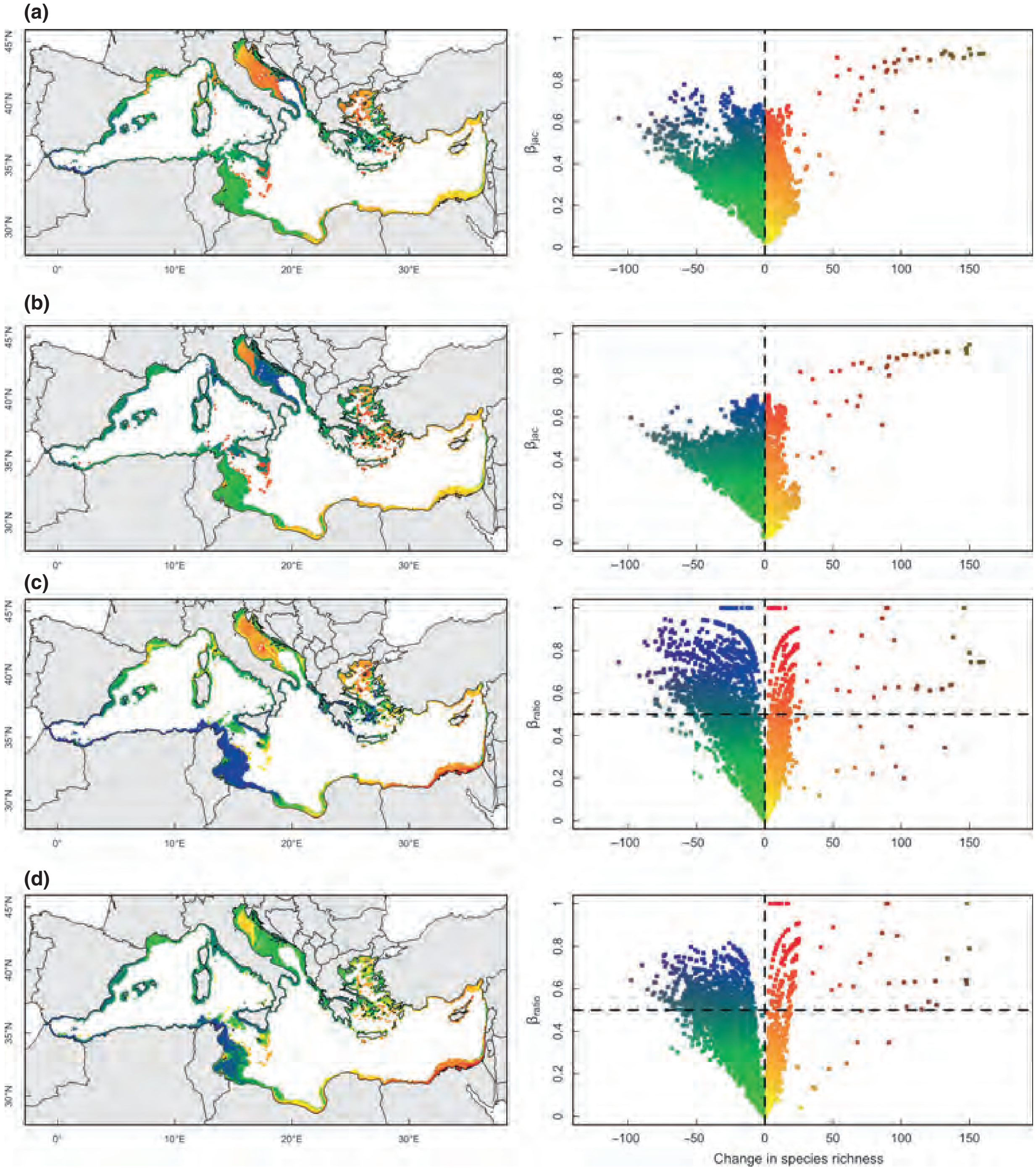

Fig. 3 Changes in species richness and composition between the baseline time period (1961–1980) and the future (2040–2059 (a, c); 2080–2099 (b, d)) for the fish assemblages of the Mediterranean continental shelf. Changes in species composition are quantified using the Jaccard's dissimilarity index β_{jac} (a, b) and the β_{ratio} index (c, d).

that are both lost and gained are therefore urgently needed (Suding *et al.*, 2008). For instance, the degree of functional redundancy between loser and winner species is a key issue for understanding the consequences of high STT on ecosystem properties and functioning. In the best-case scenario, remaining or arriving species in local assemblages after global change impact would share combinations of functional traits with lost species, thereby maintaining ecosystem functioning. In the worst-case scenario, lost species would have functional traits distinct from those of remaining or arriving species, hence the functions they

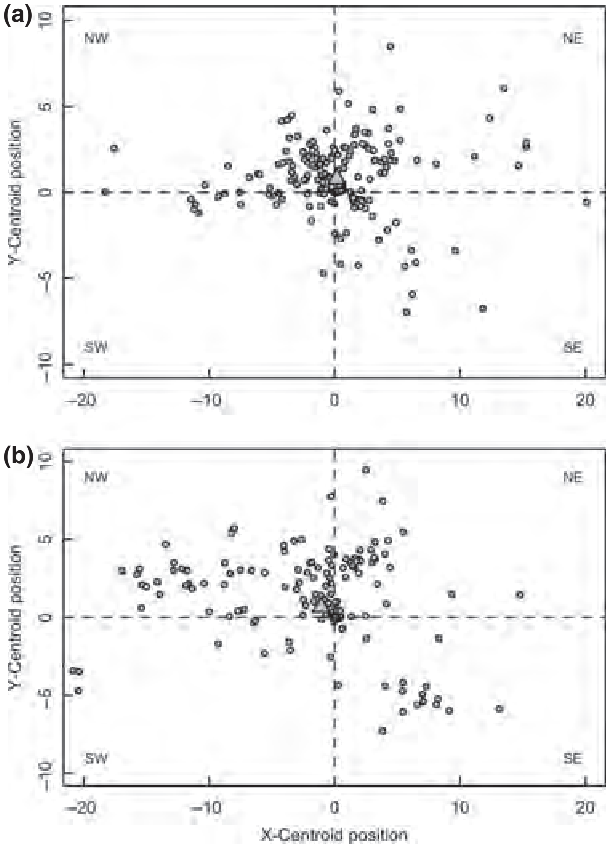

Fig. 4 Expected geographical species shifts for the 288 coastal Mediterranean fish species for both periods (a: 2040–2059; b: 2080–2099). Shifts were calculated from geographic range centroids and are expressed in degrees (NW: North West, NE: North East, SE: South East, SW: South West). Triangles represent the overall displacement of the fish assemblage calculated as the average centroid geographical shift.

support would go extinct and would imperil ecosystem functioning. Functional redundancy is also recognized as an important feature of communities insuring ecosystem resilience (Rosenfeld, 2002). This is particularly important since coastal ecosystems are facing multiple anthropogenic perturbations (e.g. habitat loss due to urbanization, overexploitation, human-mediated species invasion and toxic pollution) that may act in synergy with climate change towards local extinctions (Crain *et al*., 2009).

From a conservation perspective, distinguishing between the different scenarios that can be expected under climate change (Fig. 1) may reveal further challenges for the evaluation and the optimal design of protected areas network in a changing world. For example, a recent macroecological evaluation of the Mediterranean system of protected areas investigated the overlap of protected areas with hotspots (areas of exceptionally high diversity) of total, endemic, threatened coastal fish species richness as well as with hotspots of functional and phylogenetic diversity (Mouillot *et al*., 2011). They showed that the fish biodiversity components are spatially mismatched and that protected areas, mainly situated along the north coast, are spatially congruent with the hotspots of all taxonomic components of fish diversity but misses hotspots of functional and phylogenetic diversity. Our results suggest that the composition of coastal fish assemblages in the Mediterranean Sea will be deeply modified during the 21st century, more particularly in the current areas of high fish species richness (Ben Rais Lasram *et al*., 2009). The high projected level of species replacement in these regions, coupled with species richness decline, may therefore make current assessment of protected area networks obsolete in the future, challenging the future extension of the Mediterranean system of protected areas.

Acknowledgements

We are grateful to the editor and the three anonymous referees for all the remarks and suggestions that improved the manuscript. This study was partly funded by Fondation Total, Fondation pour la Recherche sur la Biodiversité (BIODIVMED), and Centre National de la Recherche Scientifique program BIODIVMEX. MBA acknowledges the Spanish Research Council (CSIC), the 'Rui Nabeiro' Biodiversity Chair, and the Danish NSF for support of his research. D.M. was supported by Marie Curie International Outgoing Fellowship (FISHECO) IOF-GA-2009-236316. F.G. was supported by the 'Range Shift' project (PTDC/AAC-AMB/098163/2008) from Fundação para a Ciência e a Tecnologia (Portugal), co-financed by the European Social Fund. The 'Rui Nabeiro' Biodiversity Chair is financed by Delta Cafés.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Representation of the species replacement component (β_{jtu}) of STT between the baseline time period (1961–1980) and the future (2040–2059 (a); 2080–2099 (b)) for the fish assemblages of the Mediterranean continental shelf.

Manuscrit G.

Predicting trophic guild and diet overlap from traits: statistics, opportunities and limitations for marine ecology.

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Vol. 436: 17–28, 2011
doi: 10.3354/meps09240

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published August 31

Predicting trophic guild and diet overlap from functional traits: statistics, opportunities and limitations for marine ecology

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ABSTRACT: Fish diets provide information that can be used to explore and model complex ecosystems, and infer resource partitioning among species. The exhaustive sampling of prey items captured by each species remains, however, a demanding task. Therefore, predicting diets from other variables, such as functional traits, may be a valuable method. Here, we attempted to predict trophic guild and diet overlap for 35 fish species using 13 ecomorphological traits related to feeding ecology. We compared linear discriminant analysis and random forest (RF) classifiers in their ability to predict trophic guild. We used generalized dissimilarity modelling to predict diet overlap from functional distances between species pairs. All models were evaluated using the same cross-validation procedure. We found that fish trophic guilds were accurately predicted by an RF classifier, even with a limited number of traits, when no more than 7 guilds were defined. Prediction was no longer accurate when finer trophic guilds were created (8 or more guilds), whatever the combination of traits. Furthermore, predicting the degree of diet dissimilarity between species pairs, based on their ecomorphological traits dissimilarities, was profoundly unreliable (at least 76% of unexplained variation). These results suggest that we can predict fish trophic guilds accurately from ecomorphological traits, but not diet overlap and resource partitioning because of inherent versatility in fish diets. More generally, our statistical framework may be applied to any kind of marine organism for which feeding strategies need to be determined from traits.

KEY WORDS: Generalized dissimilarity modeling · Mediterranean · Fish · Non-linear model · Random forest · Versatility

INTRODUCTION

Knowledge of species' diets is a core issue in both fundamental and applied ecology. Indeed, most ecosystem modelling approaches, such as Ecopath with Ecosim (Pauly et al. 2000, Christensen & Walters 2004) or Loops (Levins 1975, Bodini 1998), require integration of the trophic links in food webs. Other quantitative approaches rely on knowledge of the trophic level of species, which necessitates investigation of their diet composition (e.g. Cortes 1999). More generally, gathering species into guilds or functional groups according to their prey items has been recognized as useful in simplifying and modelling highly complex ecosystems (Garrison & Link 2000, Vander Zanden & Vadeboncoeur 2002, Coll et al. 2006) and in develop-

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ing biotic indicators relevant to human impacts (Sosa-Lopez et al. 2005). In addition, overlap in diet composition and resource partitioning between species is a key element of interspecific competition that can determine stable coexistence (Sala & Ballesteros 1997, Colloca et al. 2010). Determining the level of diet overlap among species is, therefore, also a major tool in predicting extirpations of species as a result of competitive interactions with invasive species (Karlson et al. 2007, Glen & Dickman 2008, Arismendi et al. 2009, Gregory & Macdonald 2009, Zeug et al. 2009).

In practice, identifying the diet composition of species is a very time-consuming and demanding task with many potential biases. Indeed, a complete knowledge of prey items targeted by omnivorous species is unrealistic in prey-rich communities (Araújo et al. 2008). Diet composition is often assessed using stomach contents, which are influenced by many temporal (Lehikoinen 2005, Horppila 2009) and spatial factors (e.g. opportunistic behaviors; Link & Garrison 2002). Hence stomach content analysis is a time-consuming method that can only provide a fragmentary image of a species' diet.

An alternative approach to investigate dissimilarity in diet composition among species is to study ecomorphological traits used for feeding. This approach has been particularly favoured in fish ecology since the seminal papers of Keast & Webb (1966) and Gatz (1979) but also in the study of benthic invertebrates (Bremner et al. 2003, Danovaro et al. 2008). Reliable morphological indicators of food consumption have been gathered in both empirical (e.g. Ibanez et al. 2007) and laboratory studies (e.g. Winemiller & Taylor 1987). For example, intestine lengths and gill raker morphology are known to be discriminant features among herbivorous, carnivorous and omnivorous fishes (Gatz 1981, Bowen 1983, Castillo-Rivera et al. 1996). Apart from these classical examples, however, evidence of a clear relationship between ecomorphological characteristics and fish diets has been mixed, and even when statistically significant, is often rather weak and of questionable biological importance (Ibanez et al. 2007). Thus, previous studies have reported significant relationships between ecomorphological characteristics and fish diets (Norton 1991, Wainwright & Richard 1995, Ward-Campbell et al. 2005, Maldonado et al. 2009) whereas others have failed to find such relationships (Labropoulou & Markakis 1998, Barnett et al. 2006, Bellwood et al. 2006).

The accuracy of diet prediction from ecomorphological traits is of crucial importance in fish ecology because it determines the extent to which unknown diets of some fishes can be predicted from known diets of functionally similar species. Most of these studies used linear discriminant analyses (LDA) and retained only one set of ecomorphological traits to predict diets, i.e. the set including all of the traits considered *a priori* relevant to the analysis. Such analyses are likely to reveal only a limited proportion of the explanatory power because particular combinations or subsets of traits may determine fish diets, and most ecomorphological traits will not relate linearly with prey item characteristics (Kramer & Bryant 1995). However, the relevance of many ecomorphological traits in diet assessment, such as gill raker morphology, is still debated (Tanaka et al. 2006), and particular subsets of traits may perform better than extensive collections in predicting diets. Moreover, because no universal ecomorphological trait has yet been shown to explain fish diet, the overlooked question of what represents the best combination of traits is still open.

Here, we present a statistical framework to study the links between species diet and functional traits. Through an extensive analysis including all possible combinations among 13 ecomorphological traits, used as predictors for linear as well as non-linear models, we tested the predictability of trophic guild and diet overlap for 35 Mediterranean fish species. We discuss the opportunities and the limitations of the approach but also the broader perspectives that this framework could offer to marine ecology.

MATERIALS AND METHODS

Data. ***Fish collection:*** The fish species were sampled in the Bonifacio Strait Natural Reserve (80 000 ha; Corsica Island, France, Mediterranean Sea) in 2004 and 2005 (Mouillot et al. 2008). This marine protected area, created in September 1999, is characterized by a predominantly rocky substrate and *Posidonia oceanica* seagrass beds at shallow depths (~35 m). Adult specimens were captured by artisanal fishermen within or near the marine protected area (Mouillot et al. 2008). Sampling was organized to collect 10 individuals (on average) of 35 fish species belonging to 17 families and 6 orders (1 Anguilliformes, 1 Clupeiformes, 2 Gadiformes, 11 Perciformes, 1 Pleuronectiformes and 1 Zeiformes). Those species cover the full range of trophic guilds: piscivores (e.g. *Sphyraena sphyraena* and *Scorpaena scrofa*), planktivores (e.g. *Boops boops*), herbivores (e.g. *Sarpa salpa*) and benthic invertebrate feeders (e.g. *Mullus surmuletus*). The full list of species is provided in Table S1 in the supplement at www.int-res.com/articles/suppl/m436p017_supp.pdf.

Diet data and ecomorphological traits: Fish diets were obtained from published data based on stomach contents of adult individuals (see Table S1 in the supplement). We obtained quantitative data, i.e. the percentage of each item in each fish diet. When the literature provided un-defined dietary categories, such as ‘other’ or ‘unidentified’, data were re-expressed (out of 100 %). Unidentified items were always negligible (generally less than 1 %) compared with other categories.

Thirteen ecomorphomogical traits were estimated for each individual (see Table S2 in the supplement at www.int-res.com/articles/suppl/m436p017_supp.pdf), encompassing a variety of strategies used by fishes for food acquisition (Table 1). As a first step, 17 morpho-anatomical measures (Fig. 1) were estimated for each individual. The 13 functional traits (Table 1) were then derived from these morpho-anatomical measures. The second step was to calculate mean trait values for each species from the individual measurements.

These continuous traits are the most commonly used in ecomorphological studies on fishes (Sibbing & Nagelkerke 2001, Dumay et al. 2004, Mason et al. 2007, Villeger et al. 2010). Moreover, our set of traits was not designed for a restricted family or morphology, so it could potentially be applied in any study of fish communities (Mouillot et al. 2007, Mason et al. 2008). We acknowledge that the list of traits is not exhaustive and that some more sophisticated traits were not included (Bellwood et al. 2006). We focused, however, on traits that were both easily measurable and commonly used as proxies of diets.

Statistical analyses. *Trophic guild classification:* Classifying species into trophic guilds remains controversial because the level of similarity/dissimilarity used for defining groups can be very subjective. To overcome this limitation, we first calculated pairwise Bray-Curtis dissimilarities between species based on quantitative diets. Then we used the k-means algorithm to create k guilds such that the fishes within each guild were more similar to one another than to fishes in other guilds with respect to their quantitative diets (Legendre & Legendre 1998). Nine gradually more precise trophic classifications were tested for the 35 fish species, comprising from 2 to 10 trophic guilds.

Trophic guild prediction: We tested the ability of 2 multivariate classification methods, LDA and random forest (RF), to predict the partitioning of fish species into trophic guilds according to their functional traits.

The purpose of LDA is to predict the membership of statistical units (here fish species) to predefined classes (here trophic guilds) by building discriminant axes that

Table 1. List of 13 functional traits derived from 17 morphological measures (see Fig. 1 for definitions) with abbreviations and calculations

Functional trait	Abbreviation	Calculation	Ecological meaning
Oral gape surface	Osf	$\frac{\mathrm{Mw} \times \mathrm{Md}}{\mathrm{Bw} \times \mathrm{Bd}}$	Nature/size of items captured (adapted from Karpouzi & Stergiou 2003)
Oral gape shape	Osh	$\frac{\mathrm{Md}}{\mathrm{Mw}}$	Method to capture food items (Karpouzi & Stergiou 2003)
Oral gape position	Ops	$\frac{\mathrm{Mo}}{\mathrm{Hd}}$	Feeding position in the water column (adapted from Sibbing & Nagelkerke 2001)
Protrusion	Pro	Pro	Relative to capacity and efficiency of the capture (Sibbing & Nagelkerke 2001)
Gill raker length	GRlst	$\frac{\mathrm{GRl}}{\mathrm{Hd}}$	Filter feeding ability or gill protection (adapted from Sibbing & Nagelkerke 2001)
Eye size	Edst	$\frac{\mathrm{Ed}}{\mathrm{Hd}}$	Prey detection (adapted from Boyle & Horn 2006)
Eye position	Eps	$\frac{\mathrm{Eh}}{\mathrm{Hd}}$	Vertical position in the water column (Gatz 1979)
Body transversal shape	Bsh	$\frac{\mathrm{Bd}}{\mathrm{Bw}}$	Vertical position in the water column and hydrodynamism (Sibbing & Nagelkerke 2001)
Body transversal surface	Bsf	$\frac{\ln\left(\left(\frac{\pi}{4} \times \mathrm{Bw} \times \mathrm{Bd}\right)+1\right)}{\ln(\mathrm{B}+1)}$	Hydrodynamism (mass distribution along the body)
Pectoral fin position	PFps[a]	$\frac{\mathrm{PFi}}{\mathrm{PFb}}$	Pectoral fin use for maneuverability (Dumay et al. 2004)
Caudal peduncle throttling	CPt	$\frac{\mathrm{CFd}}{\mathrm{CPd}}$	Caudal propulsion efficiency through reduction of drag (Webb 1984)
Gut length	Glst	$\frac{\mathrm{Gl}}{\mathrm{Bl}}$	Processing of energy poor resources such as vegetation and detritus (residence time of food) (Kramer & Bryant 1995)
Biomass	B	B	Contribution to environment via metabolism

[a] Flatfishes were considered without functional pectoral fins, so PFps was fixed to 0 for these species

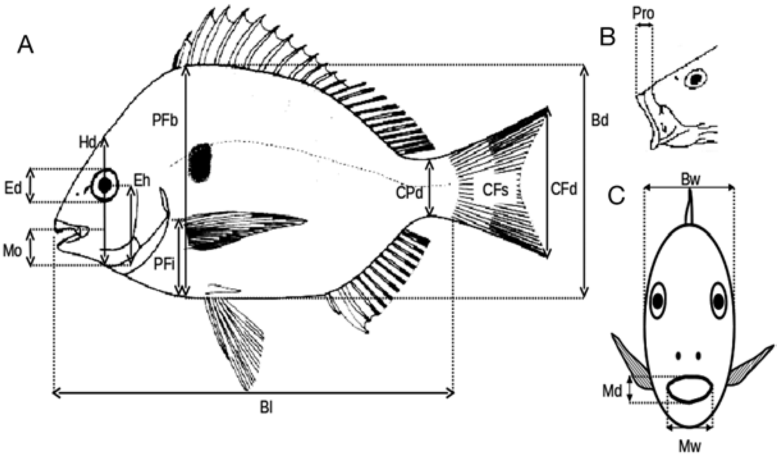

Fig. 1. Morphological traits were measured on fish using electronic calipers. (A) Side view. (B) Mouth gape. (C) Front view. Bd: body depth; Bl: body standard length; Bw: body width; CFd: caudal fin depth; CPd: caudal peduncle minimal depth; Ed: eye diameter; Eh: distance between the bottom of the head and the eye center along the head depth axis; Hd: head depth along the vertical axis of the eye; Md: mouth depth; Mw: mouth width; PFb: body depth at the level of the pectoral fin insertion; PFi: distance between the insertion of pectoral fin and the bottom of the body; Pro: stretched protrusion length. Also measured, but not shown in diagrams — GRl: gill raker length; Gl: gut length

are linear combinations of the predictor variables (here functional traits), maximizing the standard deviation of between-class dispersion and minimizing within-class dispersion by projection (Fisher 1936). LDA is an efficient method when assumptions for linear discrimination are met (i.e. classes can be separated by lines in 2 dimensions, by planes in 3 dimensions and by hyperplanes in higher dimensional spaces). Potential drawbacks to LDA include weak performance when groups are strongly nested and a tendency towards overfitting (Dixon & Brereton 2009).

As an alternative to LDA, we implemented RF classifiers, which represent a powerful tool (Biau et al. 2008), free of any assumption on data distribution, that has been applied in various different ecological fields (Perdiguero-Alonso et al. 2008, Oppel et al. 2009, Catherine et al. 2010, Mercier et al. 2011). No application to trophic guild discrimination has, however, been performed using this method. Classification with RF is based on the averaging of a large number of classification trees (Breiman 2001). Each classification tree recursively split a bootstrap data set into binary groups until the terminal nodes of the tree contain only a unique species. Group splitting at each node is carried out by searching among a random subset of predictors (here functional traits), the one that maximizes homogeneity within each of the 2 groups defined by each node. Five hundred trees were built, each using a different data set obtained by bootstrap re-sampling with replacement in the original data set. Thus, 2 levels of randomisation occurred in the building of the RF classifier: one in the initial selection of individuals (here fish species) for the building of each tree, and one in the selection of the ecomorphological trait used for group splitting at each node. A final guild prediction for a given species is obtained by running that species down the 500 trees of the classifier (i.e. the forest) and using a majority rule to average this 'forest' of votes.

LDA and RF models were constructed using standardized data (see Fig. S1 in the supplement at www.int-res.com/articles/suppl/m436p017_supp.pdf) in order to assign equal weights to each functional trait. All possible combinations of traits were created (for trait numbers ranging from 1 to 13) in order to investigate both the influence of the number of traits and the identity of traits on LDA and RF predictive accuracy.

For comparative purposes, LDA and RF models were both evaluated using the same cross-validation procedure. For each combination of traits, the data set was split into 2 parts: 30 randomly chosen species were used to calibrate the models whereas the 5 remaining species were used for model evaluation. Model accuracies were obtained from confusion matrices with the mean percentage of correct assignments as a criterion (Kohavi & Provost 1998). The procedure was repeated 10 times for each model, to account for the stochastic aspect of the algorithm and thus obtain robust estimates of model accuracy.

Diet overlap modeling: We used generalized dissimilarity modeling (GDM) to investigate the relationship between fish diet dissimilarities (Bray-Curtis distance) and ecomorphological traits dissimilarities (Euclidean distance). GDM is a multivariate extension of the popular Mantel approach (Legendre 1993), and was initially developed to model patterns of differentiation in community composition in relation to differentiation in environmental data (Ferrier et al. 2007). Nevertheless, GDM is a flexible method that can be adapted to accommodate a variety of ecological data (Ferrier et al. 2007).

Particularly suitable for ecological studies (Ferrier et al. 2007), GDM is able to accommodate 2 types of recurrent non-linearity. First, GDM can take into account the predicted curvilinear and asymptotic relationship between fish dietary dissimilarities, measured with the Bray-Curtis index, and their functional distances. Indeed, as the functional difference between 2 species increases, these species may feed on progressively fewer common prey until they exhibit totally different diets; the Bray-Curtis index then reaches an asymptotic value of 1 that will remain unchanged regardless of any further increment in the functional distance. GDM takes into account this non-linear relationship by using a link function (Eq. 1) to model the asymptotic relationship between the predicted response (diet dissimilarity between fish species), δ and the 'multi-predictor combination' (multivariate functional distance between fish species, ζ:

$$\delta = 1 - e^{-\zeta} \tag{1}$$

GDM also considers a second type of non-linearity related to the increasing rate of dietary turnover along functional trait ranges. This non-linearity is accounted for by fitting flexible functions (*I*-spline combinations, *f*) to the functional variables, then using distances between fish species, measured from these functions *f*, as predictors of the link-transformed dietary dissimilarity. The general form of the model is therefore (see Ferrier et al. 2007 for more details):

$$\zeta = \alpha + \sum_{p=1}^{P} |f_p(x_{pi}) - f_p(x_{pj})| \tag{2}$$

where P is the number of predictors (functional traits). α (the intercept) is the estimated value of the link function for 2 species i and j that have identical values for all explanatory variables and when back-transformed with the inverse link function, it gives an estimate of the expected compositional dissimilarity for 2 species that do not differ in their functional traits (Overton et al. 2009). Each of the P functions is defined as a linear combination of *I*-splines:

$$f_p(x_p) = \sum_{k=1}^{K} a_{pk} I_{pk}(x_p) \tag{3}$$

where K is the number of *I*-splines estimated for each functional trait, I_{pk} is the kth *I*-spline for functional trait x_p and a_{pk} is the fitted coefficient for I_{pk}, subject to the constraint $a_{pk} \geq 0$

The modelling approach was similar to the one applied for the trophic guild prediction procedure (exhaustive comparison of models constructed with all combinations of traits) with the percentage of explanation (deviance) as a criterion (for more details see Fig. S2 in the supplement at www.int-res.com/articles/suppl/m436p017_supp.pdf).

Software: LDA and RF model were implemented using the MASS and RandomForest packages, respectively, in the R statistical environment (R Development Core Team 2008). The PCA was performed using the PCA function in the FactoMineR package. For GDM, we used a package which has been proposed by Ferrier et al. (2007) and modified to account for non-integer abundance data (S. Ferrier et al. pers. comm.).

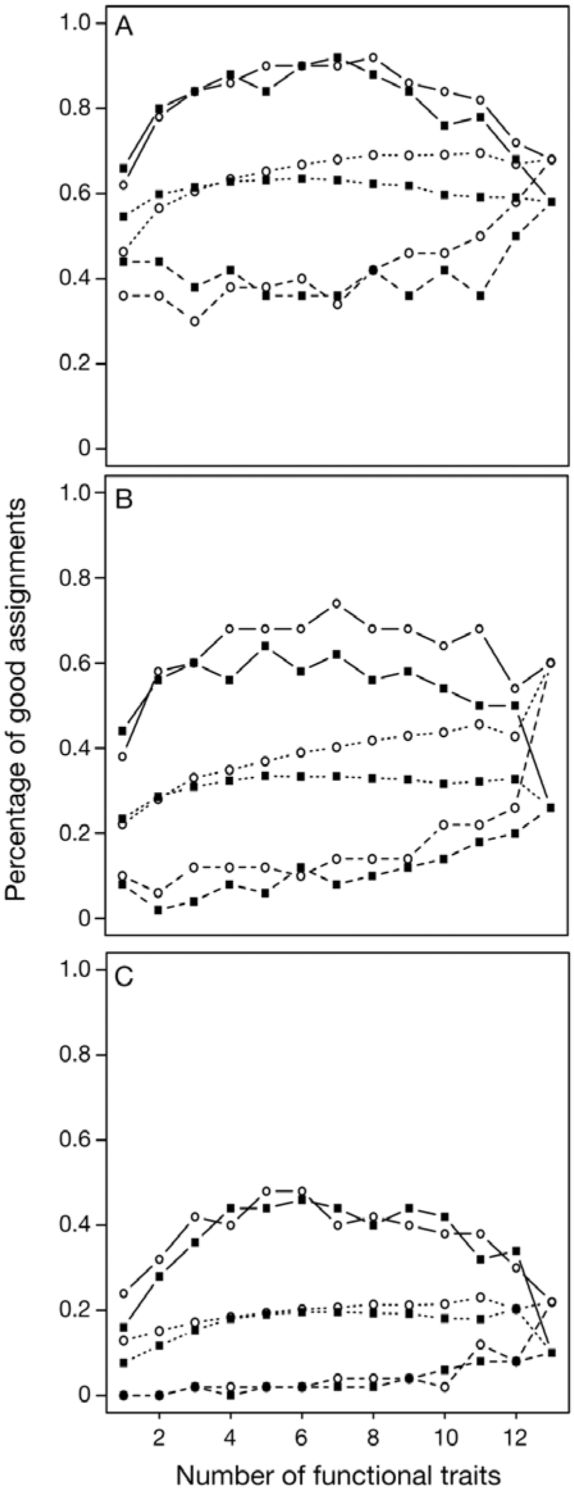

Fig. 2. Comparison of performance between linear discriminant analyses (LDA) and random forest (RF) models, for 3 classifications — (A) 3 guilds, (B) 6 guilds and (C) 10 guilds — and each combination of traits. RF and LDA are represented by circles and squares, respectively. Maximum (continuous line), minimum (dashed line) and mean (dotted line) percentage of correct fish assignment are provided for each level of combination of traits

Table 2. Mean (±SD) maximum percentage of correctly classified fish species into trophic guilds for 2 discriminant methods and different numbers of trophic guilds. Only the best combination of traits is provided. Trait abbreviations are given in Table 1. The trait with the highest occurrence in best combinations is in **bold,** whereas the one with the lowest occurrence is in *italic*

Method	No. of trophic guilds	Correct guild assignment (%)	No. of traits	Traits
Random forest	2	0.98 ± 0.06	7	B **Bsh** CPt Edst Ops Osf Osh
	3	0.92 ± 0.1	8	Bsf **Bsh** Eps GRlst Pro Ops Osf Osh
	4	0.90 ± 0.11	4	**Bsh** CPt GRlst Osf
	5	0.70 ± 0.24	6	Bsf **Bsh** Eps Glst Grlst Ops
	6	0.74 ± 0.16	7	B **Bsh** CPt Edst Eps Glst Pro
	7	0.74 ± 0.19	9	B **Bsh** CPt Eps GRlst Glst Osf *Pfps* Pro
	8	0.60 ± 0.25	8	B **Bsh** Edst CPt GRlst Glst Eps Pro
	9	0.56 ± 0.18	6	Bsf Edst Ops Osf *Pfps* Pro
	10	0.48 ± 0.14	6	Bsf Edst Eps Glst Ops Pro
LDA	2	0.96 ± 0.08	3	Bsf Cpt Eps
	3	0.92 ± 0.14	7	B Bsf **Bsh** Cpt Glst Ops Osh
	4	0.80 ± 0.19	5	Bsf Edst Ops Osf Osh
	5	0.62 ± 0.15	8	B **Bsh** CPt Eps Glst Ops Pro Bsf
	6	0.64 ± 0.21	5	**Bsh** GRlst Eps Pro Osf
	7	0.66 ± 0.16	4	**Bsh** GRlst Ops Pro
	8	0.58 ± 0.18	7	Bsf Edst Eps Ops Osf *PFps* Pro
	9	0.54 ± 0.25	8	B **Bsh** Edst GRlst Osf Osh Ops *PFps*
	10	0.46 ± 0.19	6	**Bsh** Edst Eps GRlst Osf Pro

RESULTS

Prediction of trophic guild

The *k*-means classifications yielded clustering that corresponded to well-identified trophic guilds such as piscivores, planktivores and benthic invertebrate feeders (for more details on guild compositions see Table S3 in the supplement at www.int-res.com/articles/suppl/m436p017_supp.pdf). The mean percentage of correct assignments decreased with increasing number of guilds (Fig. 2, Table 2): almost all species were correctly classified into 2 trophic guilds whereas less than half of species were correctly assigned to 10 trophic guilds.

We evaluated the relative predictive ability of RF and LDA by comparing their minimum, mean and maximum rates of correct assignments along the gradient of the number of traits used as predictors. We exemplify 3 classifications out of 9 representing increasing degrees of precision in the trophic classification (3, 6 and 10 trophic guilds; Fig. 2). For a low number of trophic guilds (3; Fig. 2A) and 8 traits, the maximum percentage of correct assignments was 92% for LDA and RF. For an intermediate number of trophic guilds (6; Fig. 2B), the percentage of correct assignments decreased to 74% for RF and 64% for LDA. Considering a larger number of trophic guilds (10; Fig. 2C) and 6 traits, the maximum percentage of correct assignments fell below 50% for both modelling methods. On average, RF predicted trophic guild slightly more accurately than LDA. Comparing the maximum percentages of correct assignments between RF and LDA for each classification (from 2 to 10 guilds), we obtained higher percentage values for RF than for LDA (Table 2).

The best predictive accuracy for trophic guild was not obtained with the full collection of traits (Fig. 2). For example, the maximum percentage of species correctly classified into 4 trophic guilds was obtained with only 4 traits (body transversal shape, caudal peduncle throttling, gill raker length and oral gape surface) for the RF model. Some traits, such as body transversal surface, were more often present (13 times among 20) in the best combinations than others, for example pectoral fin position (4 times among 20; Table 2).

Prediction of diet dissimilarity

Overall, the percentage of explained deviance in diet dissimilarity increased as the number of functional traits considered increased. However, for a given size of the predictors set, there was a substantial variability in the explained deviance in Bray-Curtis dissimilari-

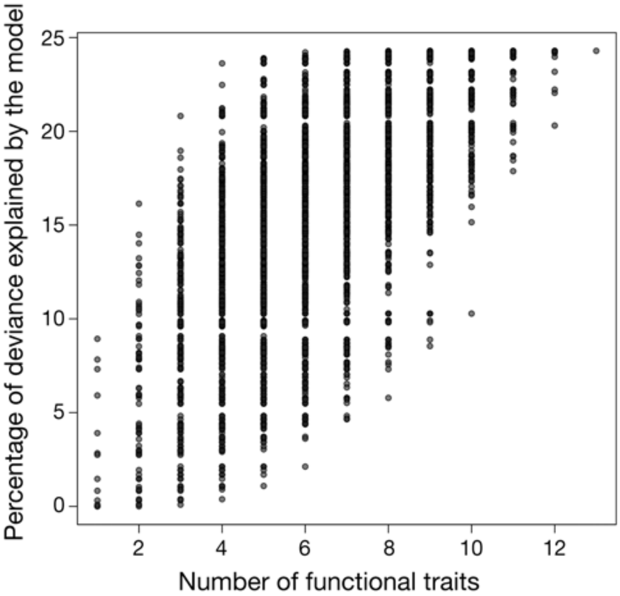

Fig. 3. Percentage of deviance explained by all generalized dissimilarity modelling models for all combinations of traits

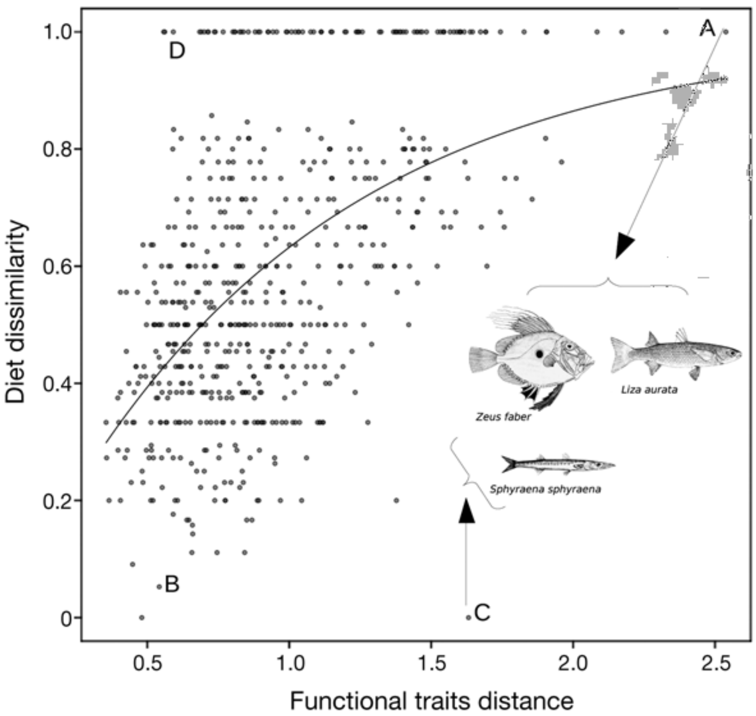

Fig. 4. GDM model output summarizing the relationship between diet dissimilarity and trait dissimilarity (6 traits considered, see 'Discussion') for all pairs of fish species. A (*Liza aurata*, *Zeus faber*), B (*Diplodus sargus*, *Diplodus vulgaris*), C (*Zeus faber*, *Sphyraena sphyraena*) and D (*Symphodus tinca*, *Diplodus annularis*) represent remarkable examples of species couples (see 'Discussion: Prediction of diet overlap')

ties. For instance, the explained deviance had a minimum of 2.4% for 6 traits but reached a maximum of 24% (Fig. 3) for the combination including the following traits: oral gape position, eye position, biomass, protrusion, gut length and oral gape shape.

This GDM model with 6 traits shows an asymmetric relation between functional and trophic dissimilarities (Fig. 4). Two species whose functional attributes were highly dissimilar (between 1.7 and 2.5) could not have the same diet (the empty bottom right triangle of Fig. 4). More generally, most of the species pairs with highly dissimilar traits, such as *Zeus faber* and *Liza aurata* (point A in Fig. 4), also had highly dissimilar diets. Conversely, species with small functional differences in traits (from 0.5 to 1) may have either very similar (point B in Fig. 4) or totally different diets (point C in Fig. 4; observed dissimilarity of 1).

PCA analysis

To illustrate the relationships between ecomorphological traits and trophic guild, we mapped 2 *k*-means trophic classifications (3 and 6 guilds; Fig. 5B,C) on the first plane of a PCA of ecomorphological traits (45.24% of inertia; Fig. 5A).

For the classification into 3 trophic guilds (Fig. 5B), planktivorous fishes such as *Sardinella pilchardus*, *Atherina* sp. and *Boops boops* and piscivorous fishes such as *Dentex dentex*, *Zeus faber* and *Conger conger* were clearly discriminated. For the classification into 6 trophic guilds (Fig. 5C), species belonging to different trophic guilds were not clearly discriminated except the planktivorous, piscivorous or benthic invertebrate feeders, for which functional traits were relatively similar within the trophic guild.

DISCUSSION

Prediction of trophic guild

The results reveal that both LDA and RF could discriminate the principal fish trophic guilds on the basis of functional traits but only to a certain extent. With a fine classification (10 groups), the model predictions were not accurate, regardless of the combination of traits (Fig. 2). The ecomorphological traits used in this study (in any combination) were not effective in predicting finely defined trophic guilds, mainly because fishes sharing similar traits may have very different diets (Figs. 4 & 5). Nevertheless, with a trophic classification based on 3 guilds (piscivores, planktivores and others), LDA and RF models correctly assigned 92% of species when using the optimal combination of traits (Table 2). Some combinations accurately predicted wide trophic guilds, suggesting a link (albeit weak) between diet and morphology. Interestingly, 90% of correct assignments were reached when fishes were divided into 4 trophic guilds (to piscivores, planktivores, benthic invertebrate feeders and others) using only 4 traits (Bsh, Cpt, Grlst and Osf; see Table 1) and the RF model.

This result has important implications because it indicates that we can accurately predict fish trophic guilds from a few suitable ecomorphological traits in a model that accounts for complex interaction structures in the data. Thus, for example, in species-rich assemblages where the description of diet items for all the species is highly demanding, the measurement of a short set of suitable morpholological traits would allow an investigator to assign fish species to major trophic guilds.

The study of trophic guilds may identify convergence in the trophic structure of fish communities from different regions (Mathieson et al. 2000, Boyle & Horn

2006, Irz et al. 2007) and thus identify commonalities in the response of fish communities to various impacts (Munoz & Ojeda 1997, Garrison & Link 2000). The prediction of trophic guilds could also be very useful for the creation of trophic groups to be used in ecosystem modelling approaches. Models such as Loops (Levins 1975) are based on a qualitative approach, whereby interactions between species are represented by the nature of predation without a requirement to quantify the prey ingested. In this context, species could be assigned to broad trophic guilds without knowing their precise diets, just by measuring a relevant combination of easily measurable functional traits.

Our results are in accordance with previous studies that demonstrated weak relationships between diet and functional traits in birds (Hormada et al. 2003) and fish (Wainwright et al. 2002, Boyle & Horn 2006, Ibanez et al. 2007), and more precisely for apogonid (Bellwood et al. 2006), chaetodontid (Motta 1988) and cichlid fishes (Barel 1982).

In the present study, this weak link is illustrated by members of the *Diplodus* genus (*D. vulgaris* and *D. annularis*) which have common morphological attributes (highly oval body, laterally flat body, similar fins; Miniconi 1994) but are widely divergent in their diet (Rosecchi 1983, Sala & Ballesteros 1997). Similarly, Fig. 5 shows that the herbivorous *Sarpa salpa* is grouped with other species that are detritivorous (e.g. *Mullus surmuletus*).

Prediction of diet overlap

The best compromise between the number of traits and the percentage of explained deviance by a GDM model was obtained with 6 traits, which explained up to 24 % of the deviance. This weak relationship tells us that we cannot rely on ecomorphological traits to predict the level of competitive interactions driven by diet overlap, for which the study of fish stomach and gut contents therefore remains a necessity (Declerck et al. 2002, Mookerji et al. 2004).

Despite the low ability of GDM to predict diet overlap, we obtained a clear pattern that revealed the triangular relationship between diet and traits dissimilarities: species with very different ecomorphological

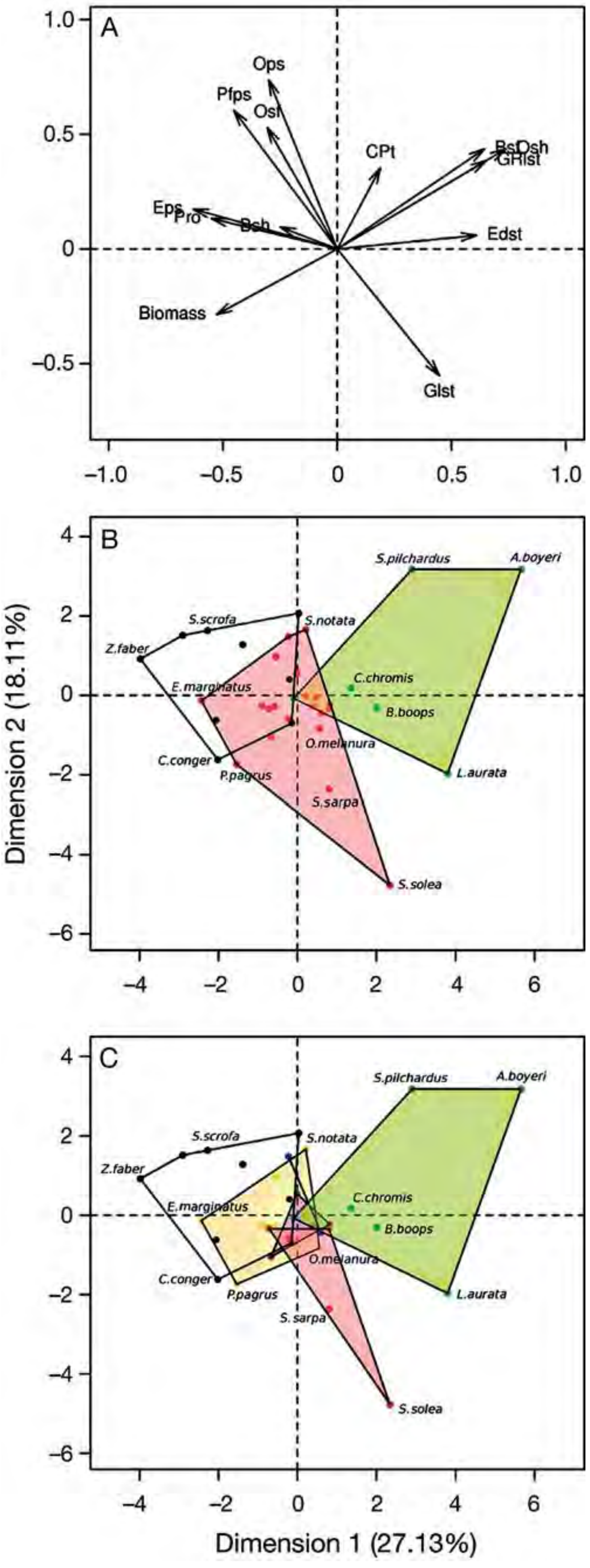

Fig. 5. PCA of 13 traits measured in 35 Mediterranean fish species. Coloured polygons illustrate the output of *k*-means partitioning carried out on diets. (A) Correlation circle of traits; (B) *k*-means partitioning into 3 trophic guilds (black: piscivorous; green: planktivorous; red: others); (C) *k*-means partitioning into 6 trophic guilds (black: piscivorous; green: planktivorous; red: benthic invertebrate feeders; purple: benthic invertebrate feeders; blue: macrocarnivorous; yellow: other. For trait abbreviations see Table 1

traits (functional distance > 2) could not have a similar diet. For instance, *Zeus faber*, a demersal piscivorous fish with a very laterally compressed body and rudimentary gill rakers, has a totally different diet from *Liza aurata*, a benthic detritivorous fish with an elongated fusiform body (point A in Fig. 4). These 2 fish species are not in competition for food resources, as revealed by the high trait dissimilarity linked to a high diet dissimilarity. By contrast, *Diplodus sargus* and *D. vulgaris* (point B in Fig. 4) are very similar species in terms of both diet and traits. They share 9 prey items: gastropods, molluscs, decapods, amphipods/isopods, polychaetes, echinoderms, cnidarians/sponges, plants and macroalgae (Rosecchi & Nouaze 1987, Sala & Ballasteros 1997). The strong diet overlap (diet dissimilarity = 0.005) between these 2 species and their potential competitive interaction for resources (if limiting) can, therefore, be predicted from their ecomorphological traits.

We found an overall weak relationship between diet dissimilarity and trait dissimilarity, which can be illustrated with many examples. For instance, *Symphodus tinca* and *Diplodus annularis* have strong morphological similarity but rather different diets (point D in Fig. 4). Indeed, although they share some common prey items (polychaetes, decapods and molluscs), they show marked differences for others: *S. tinca* feeds on macrophytes whereas *D. annularis* feeds on small fish and eggs. Thus, although traits may provide a false signal of intense competition for resources, diet overlap may reveal the opposite, with clear partitioning. The relationship between diet dissimilarity and trait dissimilarity is asymmetric (Fig. 4), and caution is therefore required in predicting diet dissimilarity from trait dissimilarity because species with similar traits may have either none or all of their prey items in common.

Sources of unexplained variation

The relative lack of explanatory power in the present study may derive in part from our collection of traits. Although the list is widely used in the literature, it may need to be extended to include other traits that are more directly related to food acquisition. This issue of trait choice has been debated by ecomorphologists for many decades, particularly for birds (James 1982) and fishes (e.g. Gatz 1979), without reaching a consensus. Barnett et al. (2006) and Bellwood et al. (2006) proposed more sophisticated ecomophological traits such as the lower jaw length and head length (tip of premaxilla to posterior margin), but were nonetheless unable to find a clear match between these traits and diet. Qualitative traits, such as the structure of the teeth (Portz & Tyus 2004), could also be used to increase the ability to discern diet overlap. Even with these 'simple' traits, we obtain similar levels of prediction to those found in previous studies that included more sophisticated traits.

The limited success of models in correctly assigning fish species to the correct guild, when these are more finely defined and their number increases, could be due to at least 3 sources of variation that were untestable in our study. Firstly, the boundaries between guilds are less clear (Table S2 in the supplement) and the uncertainty in associating fishes to guilds increases as guild number increases. Secondly, fewer species can be assigned to each guild and the sampling for traits associated with each diet category is therefore less effective. Thirdly, our study ignores potential variation in diets caused by differences in foraging patterns, habitat partitioning and other behavioural factors (Wainwright & Reilly 1994, Luczkovich et al. 1995).

CONCLUSIONS

Many studies have tried to predict species' diets from functional traits or phylogeny, for both applied and theoretical objectives. The weak relationships that have typically been found (e.g. Bohning-Gaese & Oberrath 1999, Boyle & Horn 2006) indicate an intrinsic unpredictability of diets caused by a degree of versatility (Bellwood et al. 2006) that cannot be modelled and/or suffers from methodological limitations, including non-linear effects and large numbers of trait combinations. The present study on 35 species comprised much of the dietary diversity among Western Mediterranean fishes, for which precise diets and ecomorphological traits related to food acquisition were known. We showed that the RF modelling technique, which can account for complex interaction structures in the data, can accurately predict fish trophic guilds when these are quite general (up to 7 groups), even with a limited number of traits. The accurate prediction of fine trophic guilds (8 groups and more) cannot, however, be achieved, regardless of the combination of traits considered. In a similar manner, we were not able to predict the level of diet overlap between fish species pairs based upon similarity in ecomorphological traits. Therefore, our study reinforces the versatility hypothesis of Bellwood et al. (2006), but also reveals that general trophic guilds can be predicted from just a few functional traits, which may be very useful in simplifying the modelling of complex aquatic systems.

Beyond the scope of fish ecology, our study exemplifies a statistical framework that may be relevant for other marine organisms. For example, the functional diversity of benthic invertebrate fauna, which is important for both coastal and deep-sea ecosystem functioning, can be measured as the number of different trophic roles played by the benthic species and can be inferred from the diversity in morphofunctional traits (Danovaro et al. 2008). Furthermore, the recovery of benthic communities from trawling or pollution could also be investigated through a guild approach (Colvard & Edmunds 2011, Rimet & Bouchez 2011), where the assignment of individuals to feeding guilds, using functional traits, may be less time-consuming and financially costly than individual species identification. One might also be able to monitor the temporal recovery of a damaged benthic community by looking at changes in the types or guilds of fish that feed in the area. For instance, some fish species might feed on the normal, undamaged, surface deposit-feeding worm community. If these fish species are absent for a period of time that coincides with the time period over which the benthic community was damaged and then later reappear, it might be because the surface deposit-feeding worms have returned to the benthic community that has recovered from its damaged state.

Acknowledgements. We thank the staff of the Bonifacio Strait Natural Reserve for collecting the data. We thank S. Ferrier and G. Manion for programming and modifing the GDM function. We thank D. Mckenzie for his constructive comments on the manuscript and language editing. This work was partly funded by the Total Foundation, the 'Fondation pour la Recherche sur la Biodiversité' (project BIODIVMED) and the ANR project AMPHORE. We also thank anonymous referees for helpful comments on the manuscript.

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Editorial responsibility: Hans Heinrich Janssen,
Oldendorf/Luhe, Germany

Submitted: May 26, 2010; Accepted: June 6, 2011
Proofs received from author(s): August 24, 2011

The following supplement accompanies the article

Predicting trophic guild and diet overlap from functional traits: statistics, opportunities and limitations for marine ecology

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Marine Ecology Progress Series 436:17–28 (2011)

Supplement. Data sources for diet, the averaged functional traits values, the classification of species into guilds for 35 Mediterranean fish and the conceptual framework of the present study

Table S1. Species and their associated data sources for diet

Order	Family	Species	Source
Anguilliformes	Congridae	*Conger conger*	Cau & Manconi 1984
Cupleiformes	Cupleidae	*Sardinella aurita*	Moreno & Castro 1995
Gadiformes	Gadidae	*Phycis phycis*	Papaconstantinou & Caragitsou 1989
	Merlucciidae	*Merlicius merlicius*	Le Loc'h 2004
Perciformes	Atherinidae	*Atherina* sp.	Pinnegar & Polunin 2000
	Centracanthidae	*Spicara maena*	Khoury 1987
	Labridae	*Coris julis*	Bell & Harmelin-Vivien 1983
		Labrus merula	Bell & Harmelin-Vivien 1983
		Labrus viridis	Bell & Harmelin-Vivien 1983
		Symphodus tinca	Khoury 1987
	Mugilidae	*Liza aurata*	Blaber 1976
	Mullidae	*Mullus surmuletus*	Pinnegar & Polunin 2000
	Pomacentridae	*Chromis chromis*	Bell & Harmelin-Vivien 1983
	Scorpaenidae	*Scorpaena notata*	Bell & Harmelin-Vivien 1983
		Scorpaena porcus	Bell & Harmelin-Vivien 1983
		Scorpaena scrofa	Bell & Harmelin-Vivien 1983
	Serranidae	*Serranus cabrilla*	Bell & Harmelin-Vivien 1983
		Serranus scriba	Arculeo et al. 1993
		Epinephelus marginatus	Reñones et al. 2002
	Sparidae	*Boops boops*	Bell & Harmelin-Vivien 1983
		Dentex dentex	Morales-Nin & Moranta 1996
		Diplodus annularis	Rosecchi & Nouaze 1987
		Diplodus puntazzo	Sala & Ballasteros 1997
		Diplodus sargus	Rosecchi & Nouaze 1987
		Diplodus vulgaris	Sala & Ballasteros 1997
		Oblada melanura	Moreno & Castro 1995
		Pagellus acarne	Morato et al. 2001
		Pagellus erythrinus	Rosecchi 1983
		Pagrus pagrus	Papaconstantinou & Caragitsou 1989
		Sarpa salpa	Havelange et al. 1997
		Spondyliosoma cantharus	Bell & Harmelin-Vivien 1983
	Sphyraenidae	*Sphyraena* sp.	Barreiros et al. 2002
	Uranoscopidae	*Uranoscopus scaber*	Sanz 1985
Pleuronectiformes	Soleidae	*Solea solea*	Darnaude 2005
Zeiformes	Zeidae	*Zeus faber*	Bell & Harmelin-Vivien 1983

Table S2. Averaged values and standard deviation of traits on 35 Mediterranean fish

	Biomass	Biomass SD	Ops	Ops SD	Osh	Osh SD	Osf	Osf SD	Edst	Edst SD	Eps	Eps SD	Grlst	Grlst SD	Glst	Glst SD	Pro	Pro SD	Pfps	Pfps SD	Cpt	Cpt sd	Bsh	Bsh SD	Bsf	Bsf SD
Atherina sp	3.63	0.58	0.59	0.06	2.21	0.26	0.35	0.06	0.61	0.02	0.61	0.02	0.28	0.02	0.56	0.06	2.97	0.41	0.46	0.02	4.88	0.43	1.52	0.07	2.89	0.17
boops boops	116.39	39.80	0.54	0.09	1.59	0.25	0.12	0.02	0.56	0.05	0.60	0.05	0.04	0.02	1.92	0.73	3.92	0.51	0.73	0.08	4.56	0.49	1.55	0.14	1.44	0.06
Chromis chromis	21.50	9.63	0.49	0.14	1.43	0.19	0.11	0.00	0.42	0.08	0.65	0.06	0.03	0.01	0.85	0.07	2.86	1.05	0.70	0.18	2.65	0.18	2.29	0.06	1.96	0.13
Conger conger	1350.00	130.00	0.59	0.14	0.67	0.04	0.31	0.09	0.60	0.02	0.91	0.03	0.00	0.00	0.51	0.01	0.00	0.00	0.71	0.05	0.00	0.00	0.87	0.10	1.10	0.04
Coris julis	21.00	-	0.66	-	1.42	-	0.16	-	0.36	-	0.75	-	0.00	-	0.23	-	1.00	-	0.77	-	0.00	-	1.93	-	1.78	-
Dentex dentex	1060.00	1145.51	0.40	0.11	1.02	0.06	0.26	0.04	0.28	0.04	0.84	0.02	0.03	0.02	0.76	0.03	9.25	3.80	0.78	0.05	4.34	0.72	2.34	0.07	1.26	0.12
Diplodus annularis	60.18	18.27	0.39	0.08	1.41	0.28	0.02	0.02	0.39	0.04	0.72	0.06	0.03	0.01	1.49	0.43	3.36	0.65	0.76	0.03	3.65	1.39	3.25	0.28	1.60	0.09
Diplodus puntazzo	200.00	-	0.48	-	1.53	-	0.07	-	0.33	-	0.65	-	0.03	-	1.55	-	2.00	-	0.76	-	5.64	-	2.88	-	1.38	-
Diplodus sargus	460.29	334.97	0.42	0.07	0.95	0.24	0.11	0.04	0.28	0.06	0.72	0.03	0.02	0.01	1.46	0.42	4.74	0.96	0.76	0.04	4.16	0.44	2.89	0.27	1.40	0.22
Diplodus vulgaris	99.08	72.01	0.36	0.08	1.28	0.52	0.11	0.04	0.39	0.04	0.70	0.05	0.03	0.02	1.03	0.46	5.39	2.06	0.76	0.03	4.19	1.94	3.17	0.21	1.55	0.08
Labrus merula	230.88	165.60	0.50	0.08	1.24	0.14	0.14	0.02	0.36	0.07	0.82	0.06	0.05	0.01	0.95	0.38	7.19	2.67	0.77	0.04	2.15	1.13	1.96	0.30	1.37	0.08
Labrus viridis	185.29	70.84	0.49	0.10	1.18	0.20	0.17	0.07	0.35	0.04	0.84	0.07	0.03	0.02	0.72	0.32	7.39	1.57	0.76	0.04	2.09	0.83	2.07	0.16	1.36	0.07
Merlicius merlicius	151.60	87.23	0.72	0.07	1.28	0.10	1.41	0.41	0.60	0.08	0.74	0.11	0.03	0.01	0.67	0.13	0.00	0.00	0.80	0.14	4.14	0.49	1.19	0.13	1.36	0.07
Liza aurata	48.67	6.89	0.35	0.04	1.15	0.07	0.16	0.01	0.50	0.04	0.51	0.03	0.25	0.03	3.25	0.61	4.68	0.37	0.48	0.03	3.01	0.29	1.32	0.09	1.62	0.03
Mullus surmuletus	107.63	77.13	0.24	0.10	1.11	0.15	0.31	0.04	0.38	0.03	0.81	0.06	0.03	0.01	0.69	0.12	4.31	1.29	0.78	0.03	3.07	0.44	1.76	0.08	1.47	0.07
Oblada melanura	150.00	-	0.34	-	1.27	-	0.15	-	0.38	-	0.74	-	0.04	-	1.59	-	6.41	-	0.69	-	4.85	-	2.16	-	1.44	-
Pagellus acarne	104.80	34.48	0.48	0.04	1.13	0.21	0.20	0.02	0.58	0.15	0.80	0.15	0.04	0.01	0.67	0.32	6.93	1.34	0.71	0.04	3.18	0.39	1.81	0.10	1.49	0.05
Pagellus erythrinus	170.46	191.28	0.33	0.07	1.42	0.21	0.19	0.04	0.43	0.05	0.69	0.02	0.03	0.01	0.84	0.30	7.17	1.58	0.79	0.03	4.59	0.55	2.29	0.38	1.48	0.13
Pagrus pagrus	1549.60	2027.08	0.27	0.05	1.03	0.20	0.16	0.03	0.31	0.11	0.71	0.05	0.02	0.01	0.99	0.25	8.01	2.95	0.74	0.04	3.96	0.70	2.29	0.14	1.30	0.14
Phycis phycis	540.00	409.88	0.54	0.16	1.03	0.10	0.49	0.08	0.49	0.07	0.76	0.06	0.03	0.02	0.89	0.19	0.00	0.00	0.62	0.16	2.55	0.14	1.52	0.27	1.29	0.07
Sardina pilchardus	33.50	5.73	0.70	0.06	2.22	0.31	0.33	0.06	0.53	0.03	0.73	0.07	0.26	0.03	0.95	0.15	0.00	0.00	0.97	0.02	4.48	0.79	1.89	0.19	1.62	0.05
Sarpa salpa	486.10	72.64	0.39	0.07	0.84	0.09	0.06	0.01	0.32	0.02	0.62	0.06	0.07	0.00	2.58	0.58	0.00	0.00	0.65	0.03	4.29	1.19	2.00	0.12	1.29	0.02
Scorpaena notata	23.00	5.66	0.50	0.07	1.18	0.23	0.71	0.01	0.53	0.17	0.93	0.09	0.07	0.03	0.80	0.34	4.84	0.97	0.86	0.05	3.83	0.20	1.78	0.12	1.92	0.09
Scorpaena porcus	109.52	70.81	0.64	0.11	0.86	0.07	0.65	0.08	0.45	0.05	1.00	0.00	0.07	0.01	0.69	0.14	6.97	1.32	0.87	0.05	2.30	0.75	1.60	0.13	1.58	0.13
Scorpaena scrofa	409.08	498.37	0.74	0.13	0.97	0.15	0.77	0.21	0.30	0.04	1.00	0.00	0.06	0.01	0.75	0.26	8.78	3.09	0.90	0.14	3.31	0.32	1.47	0.13	1.47	0.19
Serranus cabrilla	83.60	23.45	0.67	0.22	1.10	0.12	0.79	0.14	0.44	0.07	0.84	0.08	0.10	0.04	0.84	0.28	4.66	0.59	0.73	0.12	4.20	0.65	1.92	0.13	1.50	0.05
Serranus scriba	90.63	35.82	0.64	0.21	1.09	0.16	0.63	0.11	0.40	0.10	0.87	0.20	0.09	0.03	0.76	0.32	4.99	1.18	0.74	0.04	2.41	0.68	2.01	0.19	1.51	0.08
Solea solea	88.70	18.30	0.00	0.00	1.18	0.17	0.11	0.02	0.58	0.09	0.88	0.06	0.00	0.00	1.93	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.01	1.46	0.03
Spicara maena	90.28	26.82	0.54	0.15	1.03	0.50	0.14	0.03	0.42	0.05	0.66	0.07	0.03	0.01	1.00	0.29	8.64	1.44	0.78	0.03	3.59	1.22	2.18	0.21	1.49	0.05
Spondyliosoma cantharus	169.67	78.68	0.40	0.06	1.37	0.31	0.10	0.03	0.39	0.03	0.63	0.05	0.04	0.01	1.18	0.08	6.17	0.76	0.78	0.03	3.49	1.05	2.38	0.36	1.46	0.07
Symphodus tinca	88.20	47.89	0.53	0.16	1.03	0.31	0.16	0.07	0.28	0.03	0.79	0.04	0.02	0.01	0.79	0.42	4.01	2.10	0.72	0.07	2.16	0.69	2.44	0.30	1.53	0.09
Uranoscopus scaber	306.00	137.90	0.94	0.04	0.99	0.43	0.37	0.13	0.15	0.02	1.00	0.00	0.00	0.00	0.87	0.13	8.44	1.10	0.96	0.01	3.39	0.78	0.70	0.05	1.35	0.04
Zeus faber	560.00	643.38	0.51	0.04	0.93	0.09	1.01	0.19	0.23	0.03	0.88	0.03	0.01	0.00	0.65	0.10	27.02	10.46	0.68	0.04	3.93	1.01	5.13	0.75	1.31	0.11
Epinephelus marginatus	1160.00	84.85	0.72	0.02	0.86	0.25	0.34	0.12	0.29	0.03	0.78	0.01	0.06	0.02	0.66	0.07	10.50	2.12	0.75	0.00	2.47	0.27	1.79	0.14	1.24	0.01
Sphyraena sphyraena	710.00	70.71	0.56	0.10	1.21	0.11	0.96	0.16	0.54	0.01	0.58	0.06	0.00	0.00	0.54	0.17	0.00	0.00	0.78	0.03	4.25	0.03	1.13	0.16	1.15	0.02

Table S3. Classification of species into trophic guilds according to their diets and the *k*-means partitioning method

k-means partition into 3 guilds

Piscivorous	**Planktivorous**	**Others**	
Conger conger	*Atherina* sp.	*Labrus viridis*	*Oblada melanura*
Dentex dentex	*Boops boops*	*Coris julis*	*Pagellus acarne*
Merlicius merlicius	*Chromis chromis*	*Diplodus puntazzo*	*Pagellus erythrinus*
Phycis phycis	*Liza aurata*	*Diplodus sargus*	*Pagrus pagrus*
Scorpaena porcus	*Sardina pilchardus*	*Diplodus vulgaris*	*Sarpa salpa*
Scorpaena scrofa	*Spicara maena*	*Diplodus annularis*	*Scorpaena notata*

Uranoscopus scaber		*Labrus merula*	*Serranus cabrilla*	
Zeus faber		*Mullus surmuletus*	*Serranus scriba*	
Sphyraena sphyraena		*Symphodus tinca*	*Solea solea*	
		Epinephelus marginatus	*Spondyliosoma cantharus*	

k-means partition into 6 guilds

Piscivorous	**Planktivorous**	**Benthic invertebrate feeders**	**Macrocarnivorous**	**Others**
Conger conger	*Atherina* sp.	*Coris julis*	*Spondyliosoma cantharus*	*Epinephelus marginatus*
Dentex dentex	*Boops boops*	*Diplodus puntazzo*	*Serranus cabrilla*	*Serranus scriba*
Merlicius merlicius	*Chromis chromis*	*Diplodus sargus*		*Scorpaena notata*
Phycis phycis	*Liza aurata*	*Diplodus vulgaris*		*Pagrus pagrus*
Scorpaena porcus	*Sardina pilchardus*			*Oblada melanura*
Scorpaena scrofa	*Spicara maena*	**Benthic invertebrate feeders II**		*Pagellus acarne*
Uranoscopus scaber		*Symphodus tinca*		*Pagellus erythrinus*
Zeus faber		*Solea solea*		*Labrus merula*
Sphyraena sphyraena		*Sarpa salpa*		*Labrus viridis*
		Mullus surmuletus		
		Diplodus annularis		

k-means partition into 10 guilds

Piscivorous	**Planktivorous**	**Benthic invertebrate feeders**	**Macrocarnivorous**	**Herbivorous**
Conger conger	*Atherina* sp.	*Coris julis*	*Serranus cabrilla*	*Sarpa salpa*
Dentex dentex	*Sardina pilchardus*	*Diplodus puntazzo*	*Spondyliosoma cantharus*	
Merlicius merlicius	*Spicara maena*	*Diplodus sargus*		
Zeus faber	*Chromis chromis*	*Diplodus vulgaris*		
Sphyraena sphyraena				
Piscivorous II	**Planktivorous II**	**Benthic invertebrate feeders II**		
Phycis phycis	*Boops boops*	*Diplodus annularis*		
Scorpaena porcus	*Liza aurata*	*Mullus surmuletus*		
Scorpaena scrofa		*Solea solea*		
Uranoscopus scaber	**Planktivorous III**	*Symphodus tinca*		
Labrus viridis	*Oblada melanura*			
	Pagellus acarne	**Benthic invertebrate feeders III**		
	Pagrus pagrus	*Labrus merula*		
	Serranus scriba	*Pagellus erythrinus*		
	Epinephelus marginatus	*Scorpaena notata*		

Fig. S1. Schema of the modeling methodology applied to diet and ecomorphological data using discriminant models (LDA and RF)

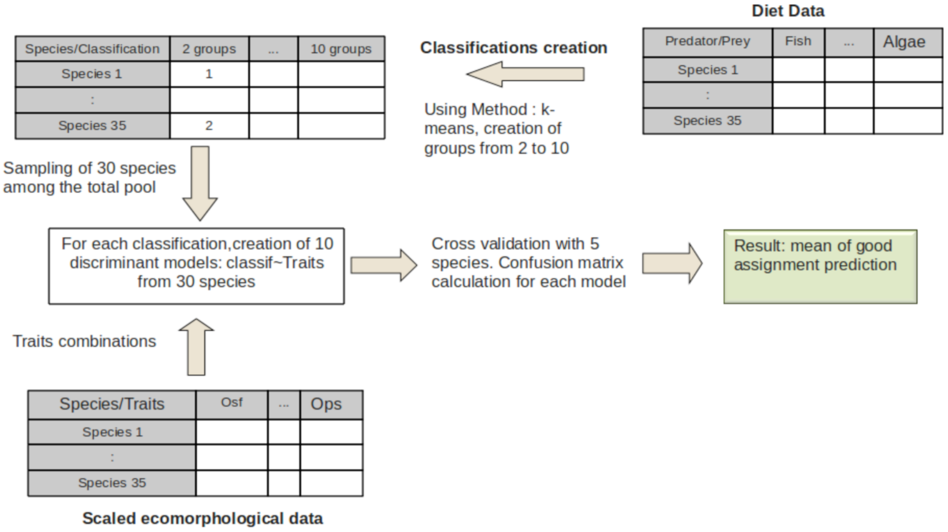
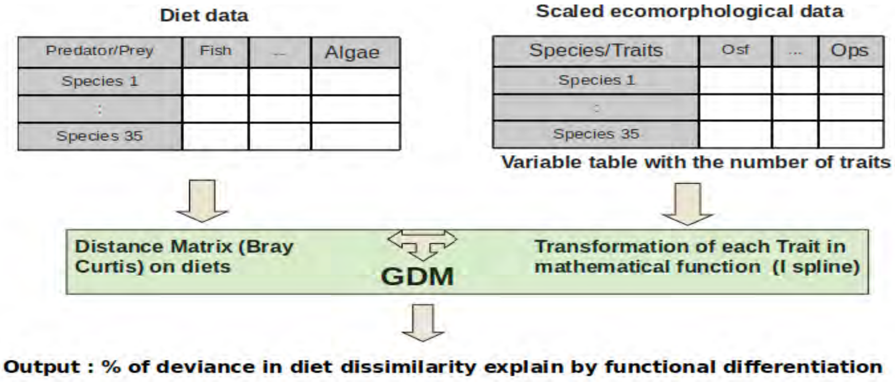


Fig. S2. Schema of the modeling methodology applied to diet and ecomorphological data using GDM models



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Manuscrit H.

Inferring food web structure from predator-prey body size relationships

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Soumis à Methods in Ecology and Evolution

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Keywords: Metaweb, Body size, Niche model, Food web

Words in the abstract: 179
Words in the main text: 2819
Words in the legends: 423
References: 45
Figures: 6
Table: 0

Abstract

Current ecological chaqnges makes it important to be able to predict how interactions will occur in emerging ecosystems. Most of the current methods to predict the existence of interactions between two species require a good knowledge of their traits, or rely on previous observations. In this paper, we overcome these limitations by developing a method, inspired from the niche model of food wrebs, which uses the statistical relationships between species trophic properties to infer a set of potential interactions. Our method works with a reduced set of information, namely the body size or body mass of species for which we want to estimate the interactions, and enough observations of interactions between these species to have a robust allometric scaling. We find that this method gives robust predictions of the structure of food webs, and that its efficiency is increased when the strength of the body- size relationship between predators and preys increases. We illutrate its ability to forecast the impact of global changes on ecosystem by predicting the properties of the mediterranean fishes metaweb under different fishing pressure scenarios.

1 Introduction

One of ecology's current challenges is to understand how communities will re-assemble following independent species responses to global changes. Understanding this is made all the more important as these emergent ecosystems will be more common with increasing human pressure. We know that species invasions, biomass harvesting, ranges shifts, disturbances and changes in land use are important drivers of biodiversity turnover. How they affect species composition is now well described (Pereira et al. 2010), but forecasting their impact on community structure and functioning requires *a priori* knowledge of potential interactions among species. Predicting interactions among species that never co-occurred proves challenging, as traditional empirical methods of food web sampling such as stomacal content analysis cannot be applied. While this task could be achieved using predictive modeling based on functional traits (Albouy et al. 2010; McGill et al. 2006) or phylogeny (Cavender-Bares et al. 2009; Mouquet et al. 2012) for competitive communities, it is much more difficult to forecast trophic interactions in a food web (Ings et al. 2009; Montoya & Raffaelli 2010; Tylianakis et al. 2008).

Inferring potential interactions among species of an arbitrary defined pool is a major step to predict the structure of emergent communities and their functioning. We call these potential interactions among species from a regional pool the *metaweb* (Poisot et al. 2012). A metaweb takes the form of an adjacency matrix $\mathbf{M}$, of size $s \times s$ for a pool of s species, and in which $\mathbf{M_{ij}} = 1$ if species i can consume species j, and 0 otherwise. This matrix aggregates the trophic interactions among all species from the pool that are susceptible to both co-occur and interact at the regional scale (Dunne 2006). With a metaweb in hands, one could analyze the impacts of global changes, such as range shifts or species invasions, on the potential community structure, by extracting the relevant species and examining the properties of the community they define. While this concept is progressively finding its way through theoretical spatial food web ecology (Gravel et al. 2011a,b; Lafferty & Dunne

2010; Pillai et al. 2009; Poisot et al. 2012), it is still limited by data availability and predictive accuracy. Published metaweb data rely on literature surveys (Baiser et al. 2012; Havens 1992; Piechnik et al. 2008), or a compilation of several local food webs (Canard 2011; "Mammal density and patterns of ectoparasite species richness and abundance"), making them resolved only for species that co-occurred a large enough number of times.

Development of predictive models of species trophic interactions could greatly improve our understanding of large scale food web structure and our capacity to anticipate major changes in ecosystem functionnig. Theory should provide some guidance about the general rules underpinning interactions among a set of species and thus help us to infer the metaweb. The actual food web theory is largely derived from the niche model (Williams & Martinez 2000). This model simply and intuitively poses that each species in a food web has a niche position n_i, a feeding niche optimum c_i and a range r_i of suitable preys around that optimum (Fig. 1). These simples rules are sufficient to generate realistic food web structures that fit most documented food webs (Dunne 2006). The niche model was a substantial improvement of the previous cascade model (Cohen1990) and subsequent models (e.g. the nested hierachy - (Cattin et al. 2004), the minimum potential model, (Allesina et al. 2008), the probabilistic niche model, (Williams et al. 2010) are somehow derived from these rules (Stouffer et al. 2005). Although it is based on different assumptions, the adaptive foraging theory of food web structure (Petchey et al. 2008) provides comparable predictions (Williams et al. 2010). The major recent breakthrough in food web theory have been the attempts to parameterize the niche model and other food web models from field data and to compare their fit through likelihood methods (Allesina et al. 2008; Williams 2011; Williams et al. 2010). The methods developed in these studies provide, for each species of the food web, the optimal parameters to fit the empirical web structures, given the hypothesized underlying rules. Despite their theoretical interest, these methods however come with several drawbacks at the time to perform biodiversity scenarios: i) they are difficult to apply at large scale because of the technical and logistical requirements of metaweb data collection; ii) once the model is parameterized, it could only be used to infer feeding interactions between species with already documented interactions (i.e. impossible to infer potential interactions among species that do never co-occurred) and iii) the model optimization is a serious challenge for large datasets with rough likelihood surfaces. There is consequently an urgent need for a method that could rapidly and easily provide an estimate of potential interactions in a metaweb based on incomplete data.

In this paper, we present a method designed to infer the metaweb from incomplete data on species interactions. We do so by a parameterization of the niche model, based on the well-known allometric scaling relationship between predator and prey (Brose et al. 2006; Cohen et al. 2003; Riede et al. 2010). We first develop the method and apply it to food webs from various environments. We find the method accurately predicts the interactions (and lack thereof), and that the accuracy increases with the strength of the predator-prey body size relationship. We then analyze the sensitivity of the method to incomplete data (missing links) and find that it is robust to sampling effort. We finally illustrate the potential of the method to infer the metaweb structure of pelagic fishes of the Meditarrannean sea and the consequences of alteration of body size distribution by global changes or anthropic forcings.

2 Model description

2.1 Inferring parameters from the niche model

The niche model predicts the food web structure from a set of three species-specific parameters: the niche position n_i, the feeding niche optimum c_i (called the centroid), and the feeding range r_i. A species i will predate all species j whose niche position n_j lies within the interval $[c_i - r_i/2, c_i + r_i/2]$ (Fig. 1). We evaluate these parameters from the predator-prey body size relationship, enabling us to parameterize the metaweb from *observed* interactions only. The parameterization is robust to the sampling effort, as it is much easier to document interactions than their absence (Martinez et al. 1999). Our approach is however mostly limited to predatory interactions since the body size relationship between herbivores and primary producers is not as general (Riede et al. 2010), and obviously do not hold for parasitic, mutualistic, or competitive networks.

Assuming that body size is the main niche axis responsible for trophic interactions, the parameter n_i corresponds simply to the log of body size of species i. Though only the relative position of all species along the body size gradient needs be respected, we suggest to standardize log body size values between 0 (minimum size in the regional species pool) and 1 (maximal size). We then consider a linear relationship between the decimal logarithm of body size and the centroid of the niche (the dark line at Fig. 1). This relationship is obtained by fitting the linear model $c = \log_{10}(B_{prey}) = \alpha_0 + \alpha_1 \times \log_{10}(B_{pred})$ to the data, where B_{prey} and B_{pred} are the prey and predator body size respectively. The lower and upper boundaries of the feeding range are easily obtained by fitting the 5% and 95% quantile regressions between $\log_{10}(B_{prey})$ and $\log_{10}(B_{pred})$ (the grey lines at Fig. 1, see the example at Fig. 2). In sum, the parameter n_i for any species of the metaweb is given by the standardized value of the log body size B_i, c_i is estimated from the linear regression between predator and prey log body size and r_i from the quantile regressions. Once these parameters are calculated from field data, even with a subsample of species from the regional pool, it is straightforward to obtain estimates of the parameters for all species and thus to reconstruct the metaweb.

3 Method accuracy

3.1 Predictive performance

We illustrate the method with the food web datasets of Brose et al. (Brose et al. 2005). The meta-analysis of Brose (Brose et al. 2006) was conducted on this dataset to test the generality of the predator-prey body size relationship across different systems (terrestrial, aquatic and marine). The relationship was found to be very strong across systems, but also to vary from one to another. Each web has between 26 and 380 species and 18 and 1466 feeding links. Several of these webs are repetitions over time at a single location and we thus regrouped the data for each of the 15 different locations to calculate the predator-prey body size relationship. We removed 4 datasets that had a non-significant predator-prey relationship and were thus useless with our approach. The links are not systematically sampled, meaning that any absence of a link between two species for a given dataset could either be a real absence or due to insufficient sampling or lack of information. While the predator-prey body size relationship is very strong over all datasets (Brose2006), there is quite substantial variation among them, enabling us to assess the sensitivity of the method to the strength of this relationship.

We assessed the performance of our method using the True Skill Statistic (TSS). The TSS is based on the partition of events (the prediction of a trophic interaction) between four components: the component a reports the number of links that are both predicted and observed, b reports predicted links with no corresponding observation, c reports the number of observed links that are predicted absent, and d reports the number of predicted and observed absences of links. The TSS is then calculated as $TSS = (ad-bc)/[(a+c)(b+d)]$. The TSS quantifies the proportion of prediction success relative to false predictions and returns values ranging between 1 (perfect predictions) and -1 (inverted forecast) (Allouche et al. 2006).

We calculated the TSS for each of the 11 different webs and related it to the strength of the predator-prey body size relationship, measured by the R^2 of the linear model. We find that the TSS is positive for all webs, ranging from 0.13 to 0.76 (Fig. 3A). We find a positive relationship between the R^2 of the linear model and the TSS ($R^2 = 0.50$, $p = 0.016$). When we decompose the different components of predictions and observations, we find that the fraction of prediction match is high, with an average of $(\overline{a} + \overline{d})/S^2 = 0.58$, Fig. 3B). The fraction of wrong predictions is lower, at $\overline{b+c}/S^2 = 0.40$, and decreases with the R^2 of the predator-prey body size relationship.

The parameterized niche model tends to overestimate the number of links in a web (see the example at Fig. 2). This result is significant but not surprising, given that these datasets do not necessarily contain all links, as they were not designed with this purpose, and thus some of the links might have been missed. It is also well known that the niche model predicts a continuous diet along the niche axis (the webs are said to be interval (Cohen et al. 1990; Stouffer et al. 2006)) while real food webs do not have this characteristic. We thus might over predict link density within the niche of a given species. Previous studies (Allesina et al. 2008) and the Application 1 however show this problem is easily circumvented when a second niche axis, *e.g.* an environmental niche, comes into play.

3.2 Sensitivity to sampling effort

We subsequently explored the impact of sampling effort on the accuracy of the model predictions. To do so, we selected a species rich food web ($S = 67$), with 601 observed feeding links and a good TSS (0.51). We randomly removed from 0 to 90% of the observed links when parameterizing the niche model and then calculated the TSS for the full web with these parameters (100 randomizations per removal category). This numerical simulation reproduces incomplete sampling in the process of building the food web. We find that the TSS remains constant up until 80% of the observed links are removed (Fig. 4). At this level, the TSS starts to decline drastically and its variance increases. This result shows that our parameterization of the niche model is robust to the sampling effort.

4 Application: Mediterranean food web structure under fishing pressure

4.1 Dataset

We now present an application of the method to infer the metaweb of interactions among fishes of the Mediterranean sea. The Mediterranean is known as a hotspot of fish diversity that is severely threaten by climate change and overfishing (Mouillot et al. 2011).There are 557 fish species in the regional pool, with a maximum body size ranging from 2.3 cm to 1100 cm (Froese & Pauly 2011; Louisy 2005; Whithead et al. 1986). Chondrichthyans, mammals and turtles were under represented in the two trophic networks and were removed from the analyses. We parameterized the niche model with a subset of species, from two different highly resolved food webs from the Catalan area (Coll et al. 2006) (82 species) and Corsica (Albouy et al. 2010) (58 species).

4.2 Inferring the metaweb for Mediterrannean fishes

We estimated parameters n, c and r for each of the 557 species and inferred the potential interactions among all of them. The metaweb has a total of 126 501 links, for a connectance of 0.41 (Fig. 5A). The metaweb is also highly nested (specialist species feed on a subset of prey of the most generalist species. Fig. 5A). We also considered a second niche axis related to species spatial distribution. Most fish species have restricted geographic range within the Mediterranean sea because of specific response to temperature and other environmental variables (Albouy et al. 2012). We therefore removed from the metaweb all links between species having no range overlap. Data on the extent of occurrence of fish species were compiled from a published atlas of fishes of the northern Atlantic and the Mediterranean (Whitehead & Unesco 1986). This atlas is based on regional data sets and expert knowledge and was edited between 1984 and 1986. It currently provides the only available basin-wide information on the extent of occurrence of all Mediterranean Sea fish species. The above mentioned atlas do not account for the bathymetric distribution of Mediterranean fish species, yet bathymetry is considered as one of the main factors accounting for marine fish distributions (Louisy 2005). We therefore refined the extent of occurrence maps by clipping off areas with depths that fall outside the minimum or maximum known for the species. Species' bathymetric ranges were obtained from FishBase (Froese 2010; Louisy 2005). The resulting metaweb has a total of 95 989 links, for a connectance of $C = 0.31$. This metaweb is less interval and there are modules (groups of species sharing similar interactions) emerging (Fig. 5B).

4.3 Impact of fishing pressure

Our method to parameterize the niche model has a unique feature relative to the original niche model (Williams & Martinez 2000): the network properties of the original model, such as the number of links, food chain length and degree distribution (the number of in and out feeding links per species), are controlled by the input parameters (species richness and connectance), while the properties of our parameterized niche model are emergent features of the predator-prey body size relationship and the frequency distribution of body size. This feature is particularly important when comes the time to understand global change impacts on community structure. For instance, a common prediction of the impact of fisheries on the body size distribution is reduction in the average and variance of body size (Jackson et al. 2001). We explored by simulations the impact of these changes on the degree distribution of the Mediterranean metaweb. Results are illustrated at Fig. 6. Even if the simulated scenarios are crude representations of the predicted alterations of community structure, they both show that fisheries impacts on body size will substantially alter the network properties. It is obvious from Fig. 6 that reduction in the average body size will decrease the average number of preys per predator. The two scenarios consequently increases substantially the relative abundance of species with a smaller degree, even for the average size reduction scenario where the total number of species is held constant. The change in the degree distribution has considerable impacts on the expected persistence of these species (Gravel et al. 2011a,b).

5 Discussion

In this paper, we presented a method to infer potential interactions among an arbitrary pool of species. The data required to perform this methodology are simple to obtain, as body size of a large number of species are available, or easy to measure. Because we rely on a robust allometric relationship, applying this method requires neither complex statistical techniques, nor an exhaustive knowledge of the realized interactions within the metaweb of interest. In addition to the conservation opportunity, our method can also help generating baseline expectations about the food web structure for environments which are notoriously difficult to sample, such as soils, deep-sea environments, or fossil records. However, because this allometric relationship is characteristic of predatory interactions, our method will likely not hold for other types of non-body-size structured interactions such as herbivory and parasitism.

The method should be completed with other sources of informations to better understand holes in the interaction matrix. The original niche model was definitely inspired by the predator-prey body size relationship, but was intented to be more general and eventually deal with several niche axis (Williams & Martinez 2000). Allesina et al. (Allesina et al.

2008) indeed found that adding a second axis, creating holes into the first axis interaction matrix, increases the fit of the model to real data. It also makes the network less interval, a structural issue of the niche model that was reported by Cattin et al (Cattin et al. 2004) and Bersier et al. (Bersier et al. 2006). There are numerous sources of information that could be used to improve the model, such as co-occurrence and functional traits. Our application with the Mediterannean pelagic fish food web provides a great example of how easily additional information could be added to the parameterization. A similar approach such as the one we described could also build on the comptability of other traits such as phenology, location in the water column or hunting modes. While the approach we describe here is based on very simple statistics, the next methodological efforts will also have to take into account more various and heterogeneous sources of data such as phylogeny (Eklöf et al. 2012) and expert knowledge. Bayesian inference appears a good candidate to achieve this goal with the possibility to constrain the prior distribution of parameters for each species.

Adding this method to the ecologist's toolbox is a timely issue. There has been impressive progress in biogeography over the last fifteen years to predict the impact of global changes on range shifts, extinction risks, and the future distribution of biodiversity, but we now face the realization that emerging ecosystems are unlikely to be a spatial displacement of the ones we currently know. This method will help assessing global change impacts of community structure, moving the field of biogeography closer to ecosystem functioning.

6 Acknowledgements

We thank I. Gounand for preparing the food web data. DG received financial support from NSERC and Canada Research Chair program. TP is funded by a MELS-FQRNT postdoctoral fellowship.

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Figure legends

Figure 1

Schematic representation of the niche model and its application to the predator-prey body size relationship. Three consumer species are represented. The white triangles correspond to the niche position of predators (their position on the X axis is transposed along the Y axis). For most cases, prey size is smaller that the predator size and thus fall under the 1:1 relationship. In some occasions, however, the feeding range can overlay the 1:1 relationship. For a given predator, we consider that the niche centroid (c) is the average prey size, given by the linear relationship between predator and prey size (black line). The boundaries of the feeding range (r) are given by the 5% and 95% quantile regression lines (dotted lines). A predator feeds on all prey species which their niche lies between these boundaries. In this specific example, the largest predator feeds on the two smaller species (the white triangles depicting the niche lies between range boundaries) and the intermediate size predator feeds on the smallest species.

Figure 2

Example of predator-prey body size relationship and predictions from the parameterized niche model. Black dots represent observed links while open dots are predicted interactions based on the parameterization of the niche model. The bullseye symbols thus correspond to a match between predicted occurrence of a link and the real data (the ”a” classification in the calculation of the TSS, see main text), a black dot a predicted link with not pbservation (”b”) and an open circle a non-predicted and observed link (”c”). Data from a creek bed located in Australia (Brose et al. 2005).

Figure 3

Performance of the parameterized niche model to predict food web structure for the 11 food webs. A) Relationship between the TSS and the R^2 of the predator-prey body size relationship. B) Partitionning of the different components of the TSS.

Figure 4

Effect of the sampling effort on the accuracy of the parameterized niche model to predict food web structure. The simulation was conducted with the same data as Fig. 2.

Figure 5

Illustration of the metaweb of the Mediterannean pelagic fishes. Panel A) represents the full metaweb and B) the same metaweb for which links between species not co-occuring together were removed (their range overlap for less than 0.1% of the Mediterannean sea).

Figure 6

Impacts of altering the body size distribution of Meditarrennean fishers on the degree distribution of the metaweb. The black line corresponds to the original metaweb degree distribution. For the first scenario, we simulated a 40% reduction in body size and recalculated the metaweb properties, keeping the predator-prey body size relationship constant (dotted line). For the second scenario we eliminated the top 40% largest species and recalculated the metaweb properties (dashed line).

Figures

Figure 1

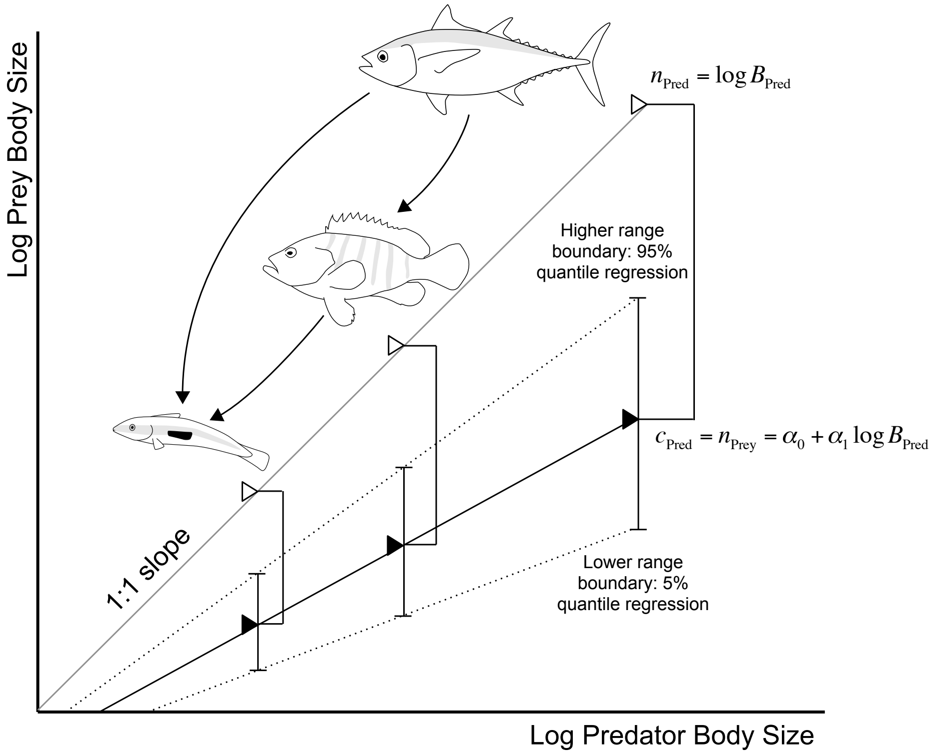


Figure 2

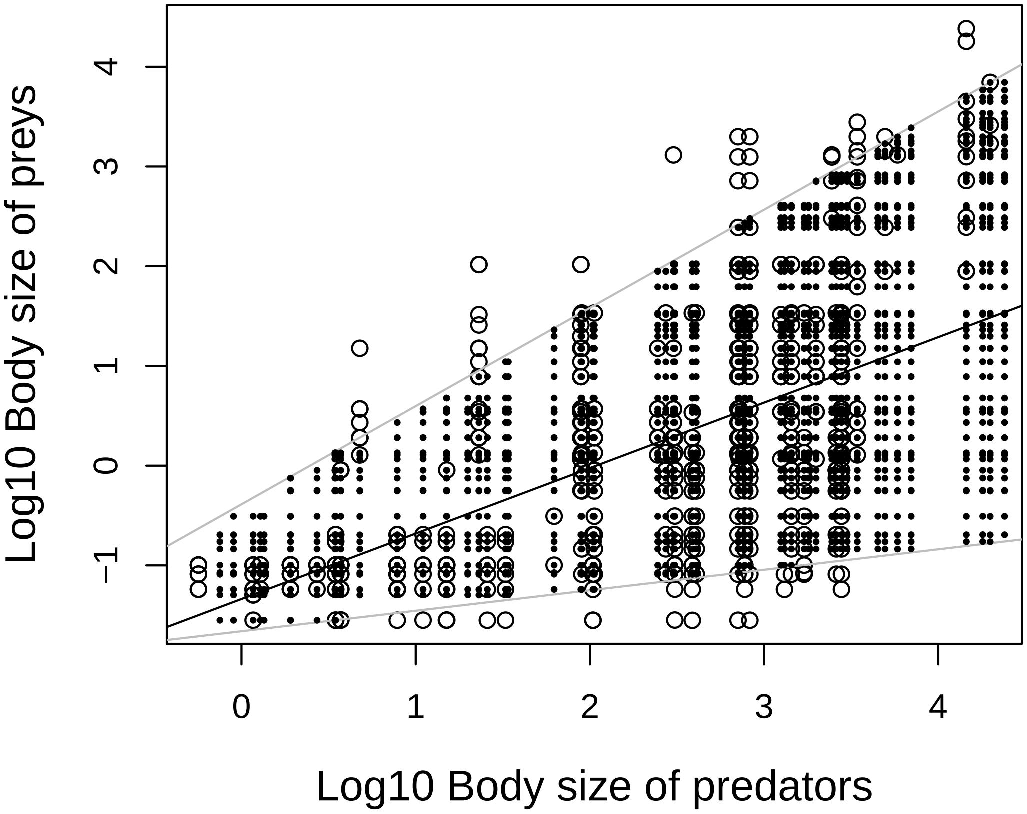

Log10 Body size of preys
Log10 Body size of predators
−1
0
1
2
3
4
0
1
2
3
4

Figure 3

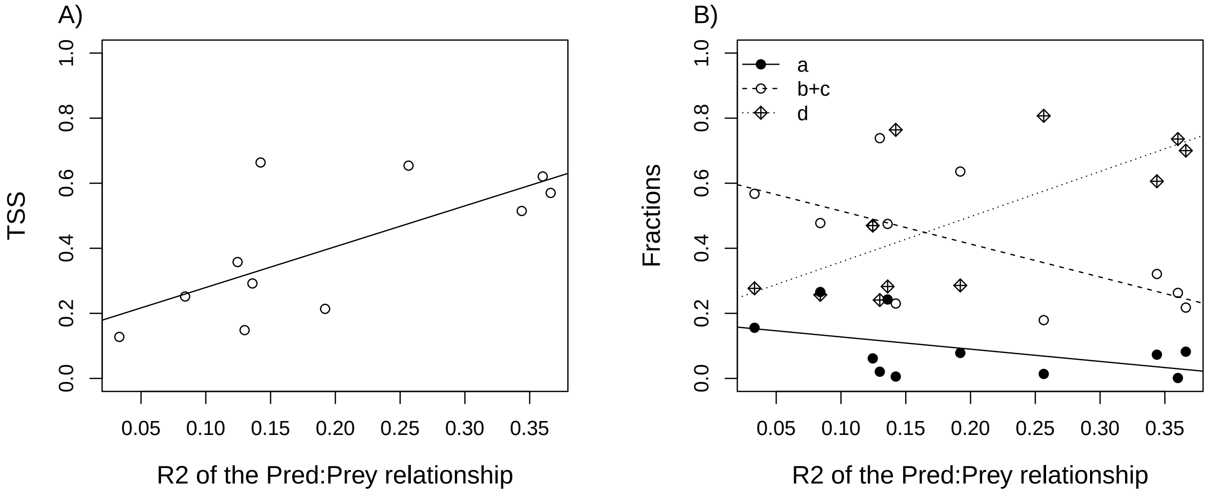
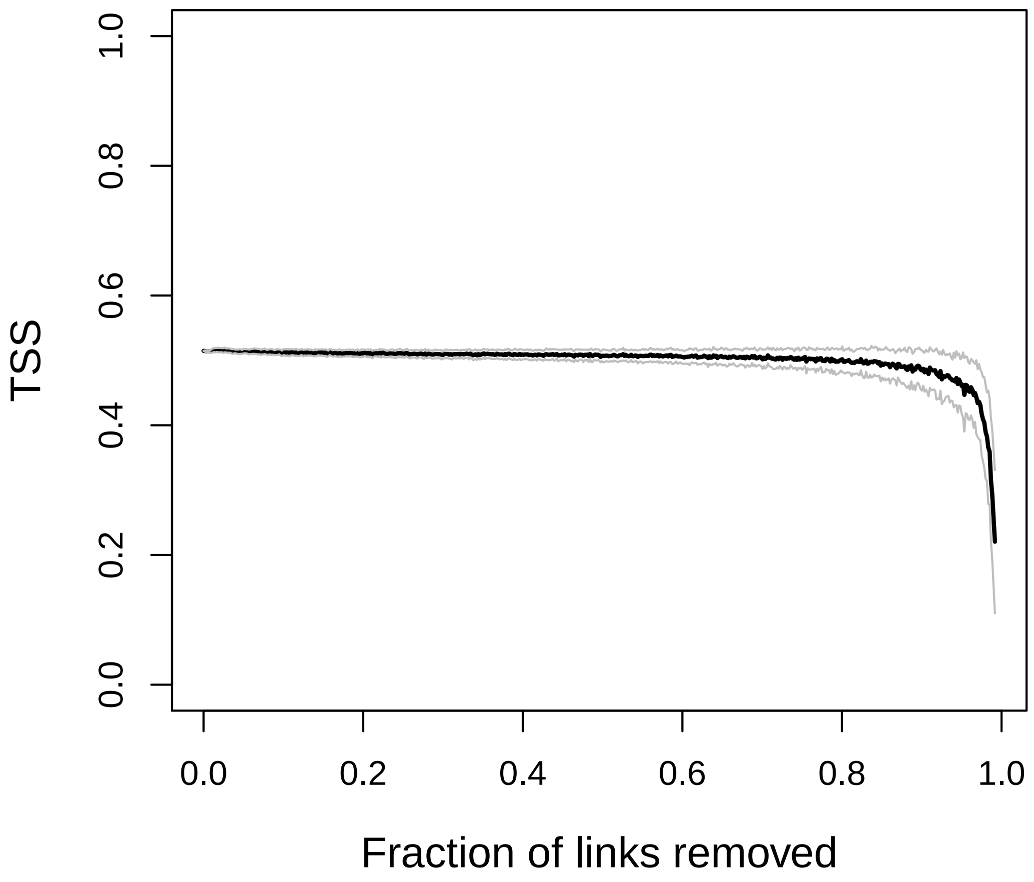
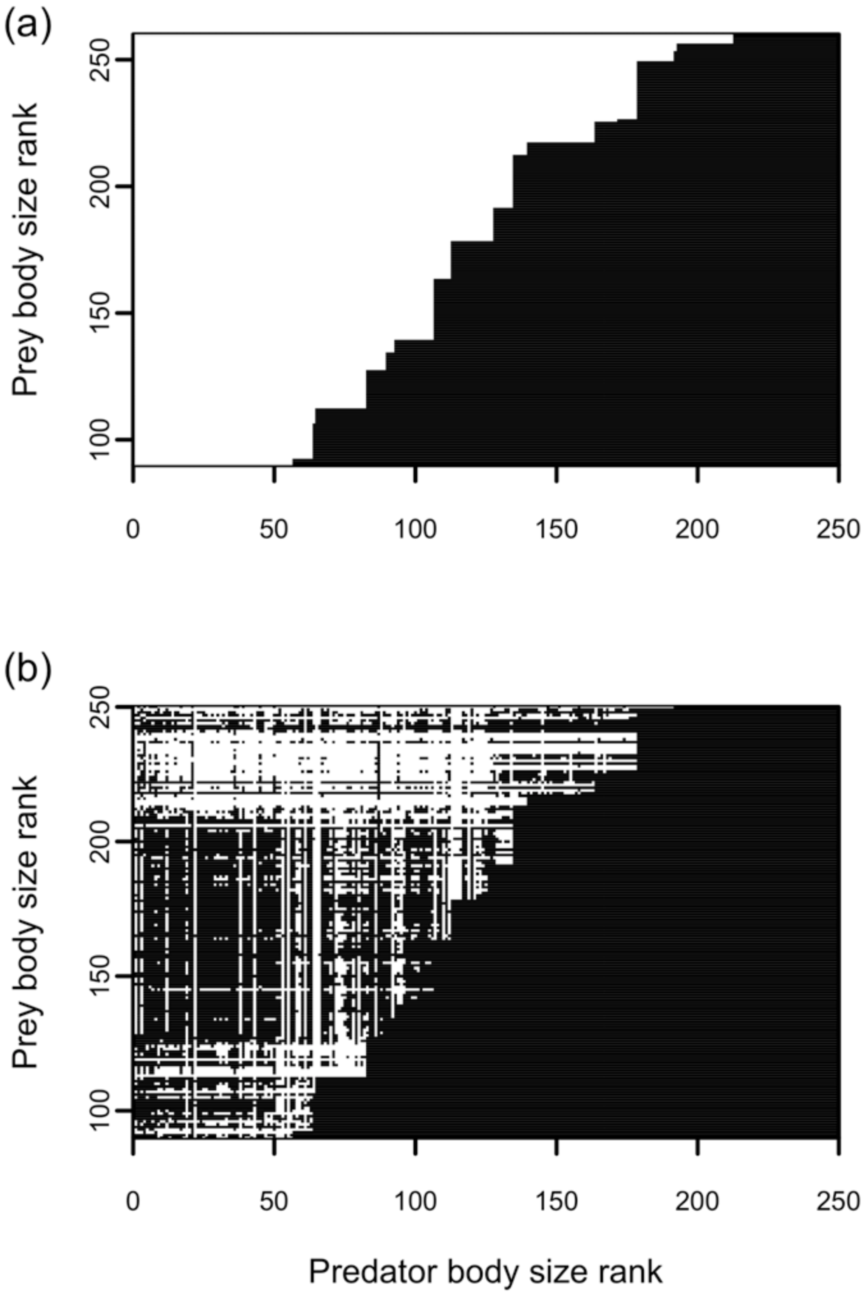
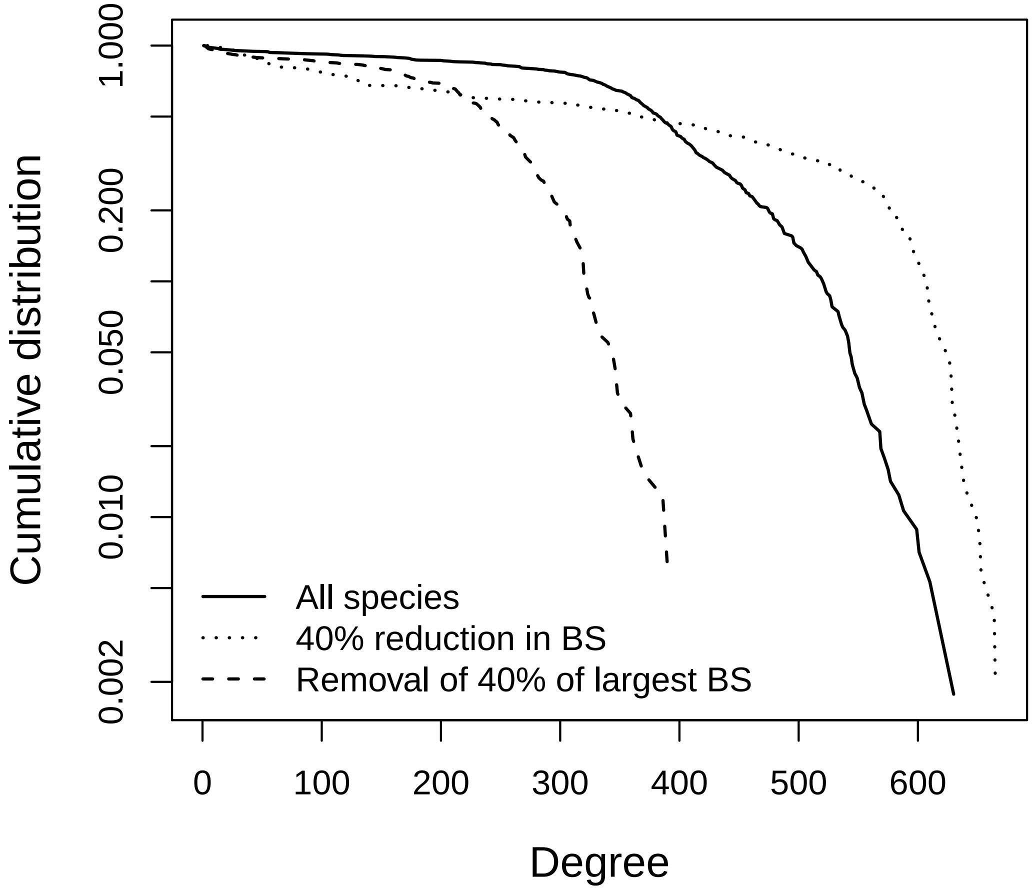

A)
TSS
1.0
0.8
0.6
0.4
0.2
0.0
0.05
0.10
0.15
0.20
0.25
0.30
0.35
R2 of the Pred:Prey relationship
B)
Fractions
1.0
0.8
0.6
0.4
0.2
0.0
a
b+c
d
0.05
0.10
0.15
0.20
0.25
0.30
0.35
R2 of the Pred:Prey relationship

Figure 4




(a)
Prey body size rank
100
150
200
250
0
50
100
150
200
250
(b)
Prey body size rank
100
150
200
250
0
50
100
150
200
250
Predator body size rank

429 **Figure 6**


Cumulative distribution
1.000
0.200
0.050
0.010
0.002
0
100
200
300
400
500
600
Degree
All species
40% reduction in BS
Removal of 40% of largest BS

Manuscrit I.

Simulation of the combined effects of artisanal and recreational fisheries on a Mediterranean MPA ecosystem using a trophic model.

Camille Albouy, David Mouillot, Delphine Rocklin, Jean M. Culioli and
François Le Loc'h

Vol. 412: 207–221, 2010
doi: 10.3354/meps08679

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published August 18

Simulation of the combined effects of artisanal and recreational fisheries on a Mediterranean MPA ecosystem using a trophic model

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ABSTRACT: Marine protected areas (MPAs) have the potential to enhance the long-term sustainability of coastal resources, and the artisanal fisheries which depend on them. However, recreational fisheries, which are increasing their impacts on coastal resources worldwide, may reduce the benefits that MPAs provide to declining artisanal fisheries. Here we used the Bonifacio Straits Natural Reserve (BSNR) Corsica as a study case to simulate the combined effects on coastal resources of artisanal and recreational fishing efforts. The BSNR ecosystem was modelled using mass-balance modelling of trophic interactions. This model was compared to another built on a non-protected area from the same region. We aggregated fishing fleets into artisanal and recreational categories, and we simulated various combinations of fishing effort over a 20 yr dynamic simulation using Ecosim. We showed that fishing activities have an additional top-down effect on the food web and that they decrease the targeted group's biomass, such as piscivorous species. We found, for some trophic groups, non-trivial patterns of biomass variation through trophic cascades. Our trophic approach revealed that some groups may suffer a biomass decrease when MPAs are set or enforced, due to the combined effect of artisanal and recreational fisheries. Overall, our results illustrate the value of modelling to manage MPAs, as a complementary tool to surveys. Models provide the opportunity to anticipate the potential consequences, at the ecosystem level, of socio-political decisions that aim to sustain coastal resources while managing artisanal and recreational fisheries.

KEY WORDS: Ecopath with Ecosim · *Epinephelus marginatus* · MPA · Trophic cascades · Artisanal fisheries · Recreational activities · Mediterranean Sea

INTRODUCTION

Human activities are causing unprecedented changes to coastal marine systems, partly through direct and indirect fishing effects (Jackson et al. 2001). Exploitation can cause major changes in biological assemblages and, ultimately, biodiversity loss that may disrupt the way the ecosystem functions and alter the sustainability of the goods and services provided by marine ecosystems (Lotze et al. 2006, Worm et al. 2006).

There is an urgent need, therefore, to evaluate the potential impact that the different types of fishing activities, alone and in combination, can have on the sustainability of coastal resources and on the general function of coastal ecosystems. The western Mediterranean Sea is one of the most overpopulated coastal areas in Europe, and the increasing size of the human population may bring an increase in recreational fishing activities. This has been recognized as one of the most common leisure activities in coastal zones, involv-

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ing several methods (boat-fishing, spearfishing, shore fishing). Moreover, it has been observed that the ever increasing recreational fishing effort (Cooke & Cowx 2004, Lloret et al. 2008a) may locally surpass that of artisanal fisheries (Morales-Nin et al. 2005), although discards are usually less important in recreational fisheries. Commercial and recreational activities have similar demographic and ecological effects on fish populations and may provoke serious ecological and economic damage (e.g. Coleman et al. 2004). For instance, spearfishing can affect benthic communities inhabiting shallow rocky bottoms (Dulvy & Polunin 2004, Meyer 2007). Over the last 20 yr, catches of several commercial stocks have been in decline in the western Mediterranean Sea while, in parallel, the recreational fishing effort has increased (Morales-Nin et al. 2005). Several policies have been applied to protect coastal ecosystems, biodiversity and artisanal fisheries, in response to the symptoms of overexploitation. To reduce such negative impacts, marine protected areas (MPAs) have been implemented worldwide as part of an ecosystem-based approach to coastal management (e.g. Lubchenco et al. 2003). However, the term MPA encompasses a large range of protection levels, from partially protected to entirely no-take areas. These restriction levels are often a result of a compromise between conservationists and extractive user groups (professional and recreational). However, positive reserve effects such as the spillover of biomass to professional fisheries (Forcada et al. 2009) have not reversed a decline in some Mediterranean artisanal fisheries (Gómez et al. 2006). Thus, the sustainability of artisanal fisheries on Mediterranean coasts is becoming ever more challenging, and there is increasing pressure from recreational fisheries which may further weaken such traditional socio-economic activities.

The study of interactions between species, and not just a mono-specific approach to a fish stock, is necessary to understand the whole dynamics of assemblages targeted by fishing activities, and the consequences for ecosystems (Gascuel 2005). Therefore, a consensus has emerged in fishery science to complement the 'single species' approach with an ecosystem approach to fisheries (Walters et al. 1997, Cury et al. 2005, 2008). This modern approach explicitly considers direct and indirect ecological interactions, particularly trophic links between ecosystem components, and allows simulations of the impacts of different fishing activities at the level of whole species assemblages. MPAs offer unique opportunities to study the behavior of species assemblages that are either facing disturbances or benefitting from restrictive policies. In addition, they have the advantage of being carefully monitored, and data sets are usually available over several years (e.g. Claudet et al. 2006, Guidetti et al. 2008).

The Bonifacio Straits Natural Reserve (BSNR), a multiple-use Mediterranean MPA, provides an opportunity to study the combined effects of artisanal and recreational fisheries on a Mediterranean ecosystem, within a multi-specific context. We built an Ecopath model with Ecosim (EwE) for this particular ecosystem. The BSNR is characterized by a predominantly rocky substrate, an ecosystem which is generally considered as one of the most impacted by human activities (Halpern et al. 2008). Moreover, the BSNR has a high touristic value, and attracts a large number of recreational anglers, particularly in the summer. This pressure, combined with the local small-scale artisanal fishery, may cause intense fishing effort on the unprotected parts of this ecosystem (Mouillot et al. 2008). Given the declining artisanal fisheries in the Mediterranean (Gomez et al. 2006), it is crucial to study interactions between commercial and recreational fishing in order to promote conservation measures that are (1) beneficial to the artisanal activity and (2) able to sustain the function of coastal ecosystems.

MPA managers are searching for tools to help them understand how ecosystems function and to evaluate policy effects. They need to assess the effects of their decisions in order to formulate new measures for protection. The evaluation of reserve effects usually relies on empirical results showing the gradients of species biomasses or catches (e.g. Russ & Alcala 1996, Stobart et al. 2009). Such observations, although necessary, do not allow predictions for different scenarios and cannot provide insight into the mechanisms which cause the observed patterns. To overcome these limitations, there is an urgent need to develop the modelling of MPA functions (e.g. Gardmark et al. 2006, Pérez Ruzafa et al. 2008).

EwE tools allow users to model exploited ecosystems. They integrate several levels of analysis: Ecopath is a snapshot of annual trophic flows within an ecosystem, while Ecosim is able to simulate temporal trends of food web properties under different scenarios of fishing pressure (Christensen & Walters 2004).

Here, using such trophic modelling tools, we studied the combined effects of artisanal and recreational fisheries on BSNR resources. To achieve this, we simulated scenarios with various combinations of commercial versus recreational fishing pressures.

MATERIALS AND METHODS

Study site and fishery fleets. The BSNR is located in southern Corsica (France; Mediterranean Sea, Fig. 1). Its surface area is approximately 800 km^2 and the maximum depth is 158 m. The BSNR is characterized by a predominantly rocky substrate and *Posidonia*

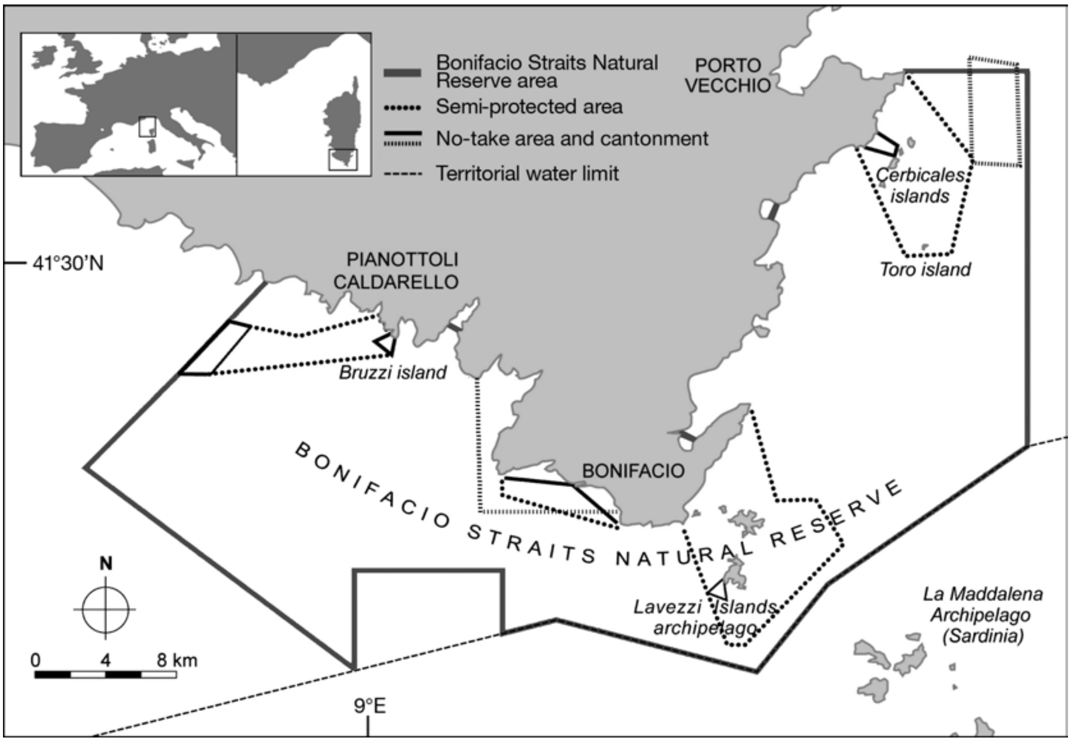


Fig. 1. Bonifacio Strait Natural Reserve (BNSR) study area. In semi-protected areas spearfishing is prohibited. The perimeter of the reserve is also the limit of the Ecosim (EwE) model

oceanica seagrass beds at shallow depths (Pluquet 2006). It was created in September 1999 and encompasses the Lavezzi Islands Reserve (LIR) created in 1982 (Mouillot et al. 2002). The LIR has been partially protected from spearfishing and other recreational fishing activities whereas traditional fisheries, using trammel nets, are permitted. In 1999, protection was strengthened (1) at the local level with the prohibition of longlines for recreational activities and with an additional 0.9 km^2 no-take area for a total of 50.5 km^2 in the LIR, and (2) at the regional level with the creation of the BSNR (Fig. 1); 5 no-take areas and 2 'cantonments' (voluntary no-fishing zones) (12 km^2), where all fishing activities and scuba-diving are forbidden, were created. Moreover, the limitation of recreational fishing activities was extended through partially protected areas (120 km^2), where spearfishing is forbidden while professional fishing is allowed (Mouillot et al. 2002). The aim of this MPA is to ensure protection of the ecological heritage while taking various economic factors into account, including the sustainability of the local small-scale artisanal fishery.

The BSNR artisanal fleet is composed of small boats (average length 7.7 m) fishing on the continental shelf (Mouillot et al. 2008). Generally, trammel nets are set for 24 h at depths ranging from 20 to 60 m. The minimum mesh size used for fish is 62.5 mm.

Ecopath and Ecosim models. ***Ecopath:*** Ecopath and Ecosim (version 6.0.7.114) models (Pauly et al. 2000, Christensen & Walters 2004) were employed to ensure energy balance and to quantify trophic flows in aquatic ecosystems. Basically, implementation of Ecopath is based on 2 master equations, one describing the production term and the other the energy balance for each group.

The first equation (Eq. 1) describes how the production term for each group *i* can be split into several components of the system.

$$P_i = \sum_{j=1} B_j \times M2_{ij} + P_i \times (1 - EE_i) + Y_i + E_i + BA_i \qquad (1)$$

The production (P) of each group (i) is divided into predation mortality ($M2_{ij}$) caused by the biomass of predators (B_j), exports from the system both from fishing activity (Y_i) and other emigration (E_i), the biomass accumulation rate (BA_i), and other mortality ($1 - EE_i$). The other mortality term includes natural mortality due to diseases, old age, starvation, etc. This term is constructed using an ecotrophic efficiency term (EE_i), which represents the proportion of production (P_i) that is exported out of the ecosystem or consumed by predators within it.

The second equation (Eq. 2) expresses the principle of conservation within a group: Consumption = Production + Respiration + Unassimilated food.

$$Q_i = P_i + R_i + U_i \qquad (2)$$

Eqs. (1) & (2) can be re-expressed as:

$$(P/B)_i \times B_i = \sum_{j=1} (B_j \times (Q/B)_j \times DC_{ji}) + (P/B)_i \times B_i \times (1 - EE_i) + Y_i + E_i + BA_i \qquad (3)$$

and

$$(Q/B)_i \times B_i = B_i \times (P/B)_i + R_i + U_i \qquad (4)$$

where $(P/B)_i$ represents the production of group (i) per unit of biomass; $(Q/B)_i$ is the consumption rate of group (i) per unit of biomass, DC_{ji} is the diet composition that indicates the proportion of (i) that is in the diet of predator (j), R_i is for respiration and U represents the unassimilated food rate of group (i).

For parameterization, EwE sets up a system with as many linear equations as there are groups in a system where, for each equation, 3 of the basic parameters, i.e. B_i, $(P/B)_i$, $(Q/B)_i$, and EE_i, have to be known for each group (i). If, and only if, all 4 of these parameters are entered, the program will prompt you during basic parameterization. If only 3 of the basic parameters are entered, other parameters such as the following must be implemented: catch rates, net migration rates, biomass accumulation rates, assimilation rates and diet compositions.

***Ecosim*:** Ecosim provides a dynamic simulation capability at the ecosystem level, with key initial parameters inherited from the Ecopath model (Christensen & Walters 2004). Ecosim uses a system of differential equations that derive from the Ecopath master equation (Eq. 3). The set of equations is solved in Ecosim using an Adams-Bashford or a Runge-Kutta 4th order integration routine (Christensen et al. 2005).

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = (P/Q)_i \times \sum_{j=1} Q_{ji} - \sum_{j=1} Q_{ij} + I_i - (M_i + F_i + e_i) \times B_i \qquad (5)$$

where $\mathrm{d}B_i/\mathrm{d}t$ is the biomass growth rate of group (i) during the time interval $\mathrm{d}t$, $(P/Q)_i$ is the net growth efficiency, M_i the non-predation natural mortality rate, F_i is the fishing mortality rate, e_i the emigration rate, I_i the immigration rate, and $I_i - e_iB_i$ the net migration rate. Calculations of the consumption rate (Q_{ji}) are based upon the 'foraging arena' theory, where the biomass of i is divided between available prey (vulnerable, V_i) and unavailable prey (non-vulnerable fraction, $B_i - V_i$).

Ecopath model parameters. The system modelled in this study represented an annual average of trophic flows on the whole BSNR area in 2000 to 2001. The model included 32 biological groups depicting the main trophic components of the studied ecosystem. It includes 12 fish groups (targeted and non-targeted fish; Table 1). Groups can correspond to single species or trophic aggregation, based on diet in our case. All details describing the parameter estimations and species grouping are presented in Supplement 1A at www.int-res.com/articles/suppl/m412p207_supp.pdf.

Fish groups based on diet composition: In order to create homogeneous fish groups according to their trophic role in the ecosystem, a preliminary diet matrix was gathered from published gut content items (54 species present in the BSNR). The diet matrix (Supplement 1B) was constructed preferentially using data from local studies (Supplement 1C), and from the Mediterranean Sea when necessary. We then calculated a Bray-Curtis distance matrix between species pairs. A *k*-means partitioning method was performed to determine the optimal composition of each group (Legendre & Legendre 1998). The optimal number of fish groups was selected using the highest SSI (simple tructure ndex) according to Dolnicar et al. (1999). Since the groups were based on diet, the aggregation should not hinder our ability to detect trophic cascades. Some species of particular ecological interest were excluded from fish trophic groups to constitute their own group: among these were the dusky grouper *Epinephelus marginatus*, a protected top-predator, the European barracuda *Sphyraena sphyraena*, the small-spotted catshark *Scyliorhinus canicula* and the salema *Sarpa salpa*, which is the only herbivorous fish in the BSNR.

Biomasses and catches: Biomass estimations of fish groups were based on a visual count method, using a circular fixed point (Bohnsack & Bannerot 1986, Samoilys & Carlos 2000). The underwater visual census (UVC) method is commonly employed for fish counts in Mediterranean marine environments (Guidetti et al. 2003, Claudet et al. 2006, Harmelin-Vivien et al. 2008).

UVCs were carried out monthly by scuba-diving from 2000 to 2001 in the BSNR. Observed fish were classified into 3 size classes (based on length), and the abundance of each species per length class was estimated. Length–weight relationships between size class and fish weight were estimated using the literature (Bauchot & Pras 1980, Froese & Pauly 2010). For species not observed in UVCs, biomass values were collected from the literature from other Mediterranean trophic models (Pinnegar & Polunin 2004, Coll et al. 2006). All details are given in Supplement 1A.

A second data source for estimating biomass of fish groups was based on catches of the BSNR artisanal fishery. Data were collected during the warm season (between April and September) just after the implementation of the MPA. Fish landings were randomly sampled from fishing boats in the BSNR. All caught species were measured and their total weight was also estimated using size–weight class correspondences. Overall, 65 species were sampled including teleosts and elasmobranchs. This pool of species included most species known to live in the BSNR, excluding very

Table 1. Input and output (values in italics) parameters used to model the Bonifacio Strait Natural Reserve ecosystem groups. *B*: biomass (t km^{-2}); *P/B*: production/biomass ratio (yr^{-1}); *Q/B*: consumption/biomass ratio (yr^{-1}); *EE*: ecotrophic efficiency; *U/Q*: unassimilated food. Landing and discards are expressed in t km^{-2} yr^{-1}; TL: trophic level; art: artisanal fishing; rec: recreational fishing

	Groups	*B*	*P/B*	*Q/B*	*EE*	*U/Q*	Landings art. fleet	Landings rec. fleet	Discards art. fleet	TL
1	*Tursiops truncatus*	0.007	0.01	13.49	0.00	0.2	–	–	–	5.22
2	*Sphyraena sphyraena*	0.253	0.60	5.00	0.02	0.2	0.0005	0.0021	0.0001	4.96
3	*Scyliorhinus canicula*	0.06	1.32	4.06	0.01	0.2	0.0007	–	–	4.6
4	Piscivorous fish	3.48	0.89	3.56	0.39	0.2	0.0194	0.0277	0.0004	4.45
5	Small pelagic feeders	1.15	0.93	4.47	0.93	0.2	0.0067	0.0144	0.0001	4.52
6	*Epinephelus marginatus*	0.874	0.28	2.74	0.00	0.2	0.0006	–	0.0003	4.30
7	Opportunistic piscivorous fish	7.56	0.64	4.83	0.96	0.2	0.0248	0.0160	0.0005	4.13
8	Cephalopods	3.42	2.12	5.27	0.97	0.4	0.0037	0.0002	–	3.94
9	Birds	0.001	5.74	85.03	0.03	0.2	–	–	–	4.43
10	Benthic invertebrate feeders	2.84	1.06	4.05	0.93	0.2	0.0065	0.0174	0.0004	3.65
11	Zooplanktivorous fish	13.30	0.44	9.42	0.95	0.2	0.0002	0.0001	0.0001	3.39
12	Mollusc feeders	10.08	0.75	6.60	0.90	0.2	0.0021	0.0084	0.0001	3.31
13	Benthic invertebrate feeders 2	8.00	1.03	6.40	0.96	0.2	0.0055	0.0035	0.0002	3.3
14	Shrimp	*5.86*	3.08	7.20	0.95	0.2	–	–	–	2.73
15	Macrocarnivorous fish	1.15	0.93	4.47	0.99	0.2	0.0030	0.0087	0.0001	2.91
16	Decapods	29.28	3.11	15.39	0.99	0.2	–	–	–	2.96
17	Lobster & spiny lobster	2.43	0.45	7.50	0.73	0.2	0.0197	–	–	2.83
18	Gastropods	*29.32*	1.94	10.89	0.95	0.2	–	–	–	2.45
19	Zooplankton	*4.11*	50.86	172.92	0.95	0.2	–	–	–	2.45
20	Polychaetes	49.87	3.42	19.57	0.99	0.6	–	–	–	2.44
21	Suspension feeders	*47.87*	1.52	6.78	0.95	0.4	–	–	–	2.28
22	Echinoderms	11.20	0.51	2.82	0.94	0.6	–	–	–	2.12
23	Protozoan plankton	*44.18*	90.00	305.16	0.95	0.4	–	–	–	2.11
24	*Sarpa salpa*	0.30	0.58	9.24	0.22	0.2	0.0004	–	0.0002	2.07
25	Other crustaceans	10.02	20.54	94.00	0.99	0.2	–	–	–	2.05
26	Amphipods	*22.86*	9.15	22.09	0.95	0.4	–	–	–	2.09
27	Bivalves	*12.19*	2.10	8.95	0.99	0.4	–	–	–	2.11
28	Macroplankton	*43.41*	25.43	71.20	0.95	0.4	–	–	–	1.68
29	Phytoplankton	*4.18*	114.00	–	0.99	–	–	–	–	1
30	Macro-algae	*150.62*	13.30	–	0.95	–	–	–	–	1
31	*Posidonia oceanica*	357.79	14.92	–	0.002	–	–	–	–	1
32	Detritus	230.85	–	–	0.37	–	–	–	–	1

small fish species (adult size <10 cm) such as Gobiidae and Blenniidae and very large transient species such as tunas. Discards data were also available from 2004 to 2006 (Rocklin et al. 2009).

The exploited biomass of some fish species (Supplement 1A) was inferred from artisanal fishing effort during the fishing season (2000 to 2001). It was then divided by the fishing mortality rate (*F*) and compared to other available data estimated for a similar ecosystem (Calvi Bay, Corsica, France; Pinnegar & Polunin 2004).

Recreational fishing activities were divided into spearfishing, on the one hand, and boat fishing and shore fishing activities, on the other hand. No data on recreational fishing catches were available for the study area. We used a list of species targeted by spearfishing provided by BSNR managers and a ratio from a study carried out in a Mediterranean MPA displaying similar habitats and similar species (Cap Creus, Spain, Lloret et al. 2008b). This study estimated that the biomass caught by spearfishers was equivalent to 40% of the total biomass extracted annually by the artisanal fleet. Similarly, following Morales-Nin et al. (2005), we made the assumption that the level of exploitation by boat and shore fishing is common to north-shore Mediterranean countries.

Target fish species were different depending on fishing gears, and this was determined based on information from the literature and expert opinions (Supplement 1C). Such differences were taken into account and re-expressed proportionate to the biomass of each species. In order to create one fleet representing all recreational fishing activities, the biomass of each target group was added to different fleets (boat-fishing, spearfishing, shore fishing).

Estimation of fish Q/B and P/B: Consumption/biomass (*Q*/*B*) ratios were then calculated according to the empirical regression of Pauly (1989) and Christensen & Pauly (1993):

$$\log Q/B = 7.964 - 0.204 \log W_\infty - 1.965T' + 0.083A + 0.532h + 0.398d \quad (6)$$

where W_∞ (or asymptotic weight) is the mean weight that a population would reach if it were to grow indefinitely, T' is the mean environmental temperature (for the BSNR 18.6°C for 2000 to 2001; see Supplement 1D for estimation) expressed as 1000/(°C + 273.15), A is the aspect ratio of the caudal fin indicative of metabolic activity and expressed as the ratio of the square of the height of the caudal fin and its surface area, h and d are dummy variables indicating herbivores ($h = 1$, $d = 0$), detritivores ($h = 0$, $d = 1$) and carnivores ($h = 0$, $d = 0$). Usually W_∞ was calculated from L_∞, using published length/weight parameters a and b. However, where asymptotic length (L_∞) was not available, we used estimated maximum lengths for Corsican species based on Miniconi (1994) and we assumed that $L_{max}/0.95 \approx L_\infty$ (Pauly 1984).

The P/B ratio was given by Beverton & Holt (1956), demonstrating that total mortality ($Z = P/B$) of a fish population, from which individuals grow according to the Von Bertalanffy Growth Function (VBGF), can be expressed by:

$$Z = P/B = \frac{K \times (L_\infty - L_\mu)}{L_\mu - L'} \quad (7)$$

where L_∞ is the asymptotic length, i.e. the mean size that individuals would reach if they could live and grow indefinitely, K is the VBGF curvature parameter (expressing the rate at which L_∞ is reached), L_μ the mean length of the population, computed from L' upward. Here, L' represents the mean length at recruitment to the fishery, assuming knife-edge selection.

Total Q/B, P/B, and diets for each fish group were calculated taking the relative biomass of each species in their trophic group into account.

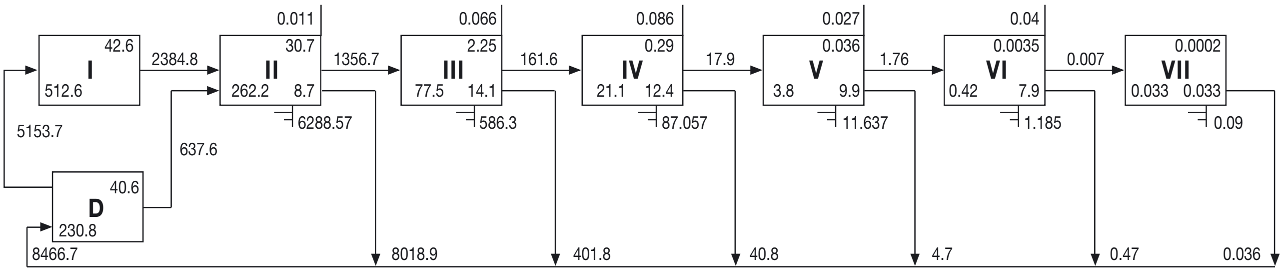
Balancing the Ecopath model. To balance our Ecopath model we did not use the Automatic Mass Balance Procedure proposed by Kavanagh et al. (2004). Instead, an ecological step-by-step approach was employed to find a more realistic equilibrium (Christensen et al. 2005). First, a model with all parameters available was created and basic outputs estimated. Three fish groups (macro-carnivorous fish, small pelagic feeders and benthic invertebrate feeders), a lobster/spiny lobster group and echinoderms presented an ecotrophic efficiency higher than 1, revealing an overpredation on these groups. The model was therefore balanced by reducing the predation on those 5 groups and by reallocating the consumption to other prey groups.

Ecological indicators from Ecopath. To interpret the Ecopath model, the software EwE includes a large number of ecological indicators based on trophic flows, thermodynamic concepts, information theory and network analysis (Christensen & Walters 2004, Coll et al. 2006). To calculate trophic levels, a value of 1 was assigned to primary producers and detritus. For consumers, a trophic level of 1 plus the weighted average of the prey's trophic level was assigned. Other indicators were provided at the system scale. For instance the ratio of system primary productivity over biomass (P/B) varies with the development status of the system (Christensen & Pauly 1993). Developing systems tend to have a high P/B, due to low biomass and high production values, while developed systems tend to have high biomass and low production rate values. Odum (1971) described the primary production over respiration ratio (P_p/R) as an important descriptor of ecosystem maturity. For immature systems, it is assumed that P_p exceeds total R, whilst for mature systems the ratio would tend to unity ($P_p/R = 1$). The Finn's cycling index expresses the percentage of total throughput (sum of all flows in a system) that is actually recycled (Finn 1976), and can be related to ecosystem maturity (Christensen & Pauly 1993). In order to represent transfer efficiencies, i.e. the energy transferred from a trophic level to the next trophic level through consumption, 'Lindeman spine' (Fig. 2) analysis synthesizes the trophic structure of 32 groups into a simple linear food-chain (Odum 1969, Christensen & Pauly 1993).

The mixed trophic impact routine derived from economic theory (Ulanowicz & Puccia 1990), shows direct and indirect impacts that a very small increase in the biomass of a group has on other groups of the system. All these indicators were analyzed and compared to other models (Christensen & Pauly 1993) in order to replace the BSNR trophic model within a wider context.

Building and simulating the Ecosim model. The Ecosim model was built from the BSNR Ecopath model and simulations were then run considering 2 assumptions. Firstly, over recent years (2000 to 2008), the number of active professional fishing boats has remained constant. Secondly, no major environmental disturbance (pollution, etc.) has impacted the ecosystem over that period. Variability in phytoplankton and zooplankton production, due to climatic factors, was modelled by generating a proportional environmental seasonal forcing function (Supplement 1E). Data related to variability in phytoplankton production were extracted from Bosc et al. (2004) for the period 2000 to 2001. For zooplankton, data were extrapolated from phytoplankton (Supplement 1E) to infer monthly values after a lag of 1 mo (Jamet et al. 2005).

One key feature of Ecosim is its ability to explore how the biomasses of different groups were controlled, with the implications for system dynamics. The 2 ex-



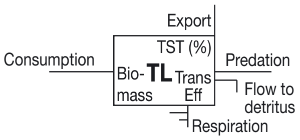


Fig. 2. Bonifacio Strait Natural Reserve (BNSR) ecosystem flow diagram organized by integer trophic levels (TL) in the form of a Lindeman spine. Primary producer (I) and detritus (D) are separated to clarify the representation. TST: total system throughput; Trans Eff: transfer efficiency

treme views were top-down and bottom-up controls (Christensen et al. 2005). This was modelled using vulnerability (*V*), expressing the maximum increase in predation mortality under conditions of high predator/prey abundance. Low vulnerability (close to 1) indicates that an increase in predator biomass will not result in any substantial increase in predation mortality, and can be related to bottom-up effects. High vulnerability indicates that if the predator biomass is doubled, it will result in an increase of the predation mortality for a given prey species, and can be related to top-down effects (Christensen et al. 2005).

Default values of vulnerabilities ($V = 2$) were used to represent mixed flow control, while values of $V = 1$ were set to describe vulnerability of zooplankton to 2 of its predators (zooplanktivorous fish and polychaetes) to match with a bottom-up flow control (Cury et al. 2000). Impact of mollusc feeders on bivalves and polychaetes was modified to be top-down controlled ($V = 10$), the same for vulnerability of zooplankton and suspension feeders on phytoplankton. Due to lack of data, this Ecosim model was not fit to time series.

In order to study the combined influences of recreational and artisanal fishing activities on the food web and on available resources, simulations of variations in fishing efforts were carried out over 20 yr. The initial value of fishing effort was set to 1 for both fishing types (the effort measured in 2000 to 2001) and varied from 0 to 4 by steps of 0.2 (a total of 440 simulations). In other words, we simulated a total prohibition of the artisanal fishery, a total prohibition of recreational activities, a 4-fold increase of these 2 fishing activities, and all combinations between these extreme possibilities. Even if our study could not rely on a rigorous estimation of recreational catches, which would be challenging to carry out in such a large MPA, the expert knowledge of BSNR managers and the data from comparable studies (Morales-Nin et al. 2005, Lloret et al. 2008a) suggest that recreational activities may extract between 40 and 100% of the artisanal fishery production. Such values were contained in the range of simulated fishing efforts (0 to 400%), which thus embrace realistic scenarios. After each simulation, the biomass ratio of each targeted fish group (end value /start value) was determined and compared to the initial value, and expressed as a percentage of variation.

RESULTS

Ecopath model

Based on available literature on fish diets, 8 groups were created using the SSI index and a *k*-means partitioning algorithm. The diet matrix and the composition of fish groups are available in Supplements 1B and 1C, respectively, at www.int-res.com/articles/suppl/m412p207_supp.pdf. Biomasses of fish groups, invertebrate groups and primary producer groups represented 4.4, 28.5 and 46.2% of the total biomass, respectively. Biomass extracted by fishing activities represented 0.4% of the total fish and lobster biomasses in the BSNR ecosystem, which is equivalent to a global biomass extraction of 152 t for the whole BSNR annually. The production of artisanal and recreational fishing activities (boat and spearfishing combined together) was estimated at ca. 65 and 87 t yr^{-1}, respectively. By comparison, dolphins consume a biomass of 0.094 t km^{-2} yr^{-1} (equivalent to 75 t on the BSNR), which is very close to the biomass exploited by the professional fleet (0.092 t km^{-2}).

Input parameters and basic estimate parameters of the Ecopath model are presented in Table 1. Ecotrophic efficiencies were close to 1 for many groups, while for others, such as the bottlenose dolphin *Tursiops truncatus*, birds, European barracuda *Sphyraena sphyraena*, and small-spotted catshark *Scyliorhinus canicula*, *EE* was very low (<0.05), indicating that the consumption of these groups is minimal. The pedigree index of the model was 0.61 (Table 2), suggesting the relative high quality of the data used.

Results of the BSNR model (Table 1) revealed that groups were organized into 5 trophic levels (TL). The highest TLs corresponded to top predators such as bottlenose dolphin, piscivorous fishes, *Sphyraenasphyraena*, *Scyliorhinus canicula,* and birds.

Table 2 comprises summary statistics computed by Ecopath. These statistics allowed comparisons with other ecosystems (protected Mediterranean rocky littoral system versus non-protected) and were useful attributes for assessing ecosystem development and maturity. For instance, the total primary production/ total respiration ratio (P_p/R) was equal to 1.12, the total primary production/total biomass (P/B) was equal to 8.91, and the Finn's cycling index was 10.71%.

The 'mixed trophic impact analysis' (MTI, Fig. 3) routine can be seen as a sensitivity analysis and was used to reveal the influence, through trophic cascades, of one group on the others. Here we used this routine to evaluate both direct and indirect impacts of all groups on the system. One of these direct impacts is illustrated by the decrease in the salema *Sarpa salpa* induced by a small increase in the dusky grouper *Epinephelus marginatu*, its main predator. An indirect impact is illustrated by the group of small pelagic feeders. A small increase in this group had a negative impact on European barracuda and a positive impact on the bottlenose dolphin and small-spotted catshark, due to trophic cascade by predation. Moreover, numerous groups in the model were impacted by groups situated at the base of the food web, such as macroalgae, amphipods and macroplankton. Some groups can have a negative impact on themselves, such as zooplankton and protozoan plankton. Several groups such as opportunistic piscivorous fish, zooplanktivorous fish and decapods had a large impact throughout the entire food web (Fig. 3).

Table 2. Ecological indicators related to the food web structure of the Bonifacio Strait Natural Reserve (BSNR) and Calvi model, statistics, and network flow parameters. The first (BSNR model) displays protection measures, contrary to the second (Calvi) model (Pinnegar & Polunin 2002). TL: trophic levels

(a) Model statistics

Parameter	BSNR	Calvi	Unit
Statistics and flows			
Sum of all consumption	21339.91	7130.626	t km^{-2} yr^{-1}
Sum of exports	569.7	751.724	t km^{-2} yr^{-1}
Sum of respiratory flows	15151.36	2424.958	t km^{-2} yr^{-1}
Sum of all flows into detritus	5723.24	3227.519	t km^{-2} yr^{-1}
Total system throughput	42784	13535	t km^{-2} yr^{-1}
Sum of all production	14006	3670	t km^{-2} yr^{-1}
Mean trophic level of catch	3.936	3.77	
Total catch	0.19	1.939	t km^{-2} yr^{-1}
Network flow indices			
Calculated total net primary production	7818.15	1929.396	t km^{-2} yr^{-1}
Total primary production/total respiration (P_p/R)	1.12	0.796	
Total primary production/total biomass (P/B)	8.91	1.503	
Total biomass/total throughput	0.017	0.095	
Total biomass (excluding detritus)	877.68	1284.056	t km^{-2}
System omnivory index	0.26	0.344	
Finn's mean path length	2.72	4.26	
Finn's cycling index	10.71	21.69	% of total throughput

(b) Transfer efficiency for BSNR model

	TL								
	II	III	IV	V	VI	VII	VIII	IX	X
Producers	12.7	12.6	13.2	9.2	6.7	5.4	4		
Detritus	6.4	15.2	11.7	10.6	8.7	6.4	4.8		
All flows	8.7	14.1	12.4	9.9	7.9	6	4.6	3.7	3

Proportion of total flow originating from detritus: 0.54

Average transfer efficiencies (calc. as geometric mean for TL II–IV)
From primary producers: 12.8%
From detritus: 10.4%
Total: 11.5%

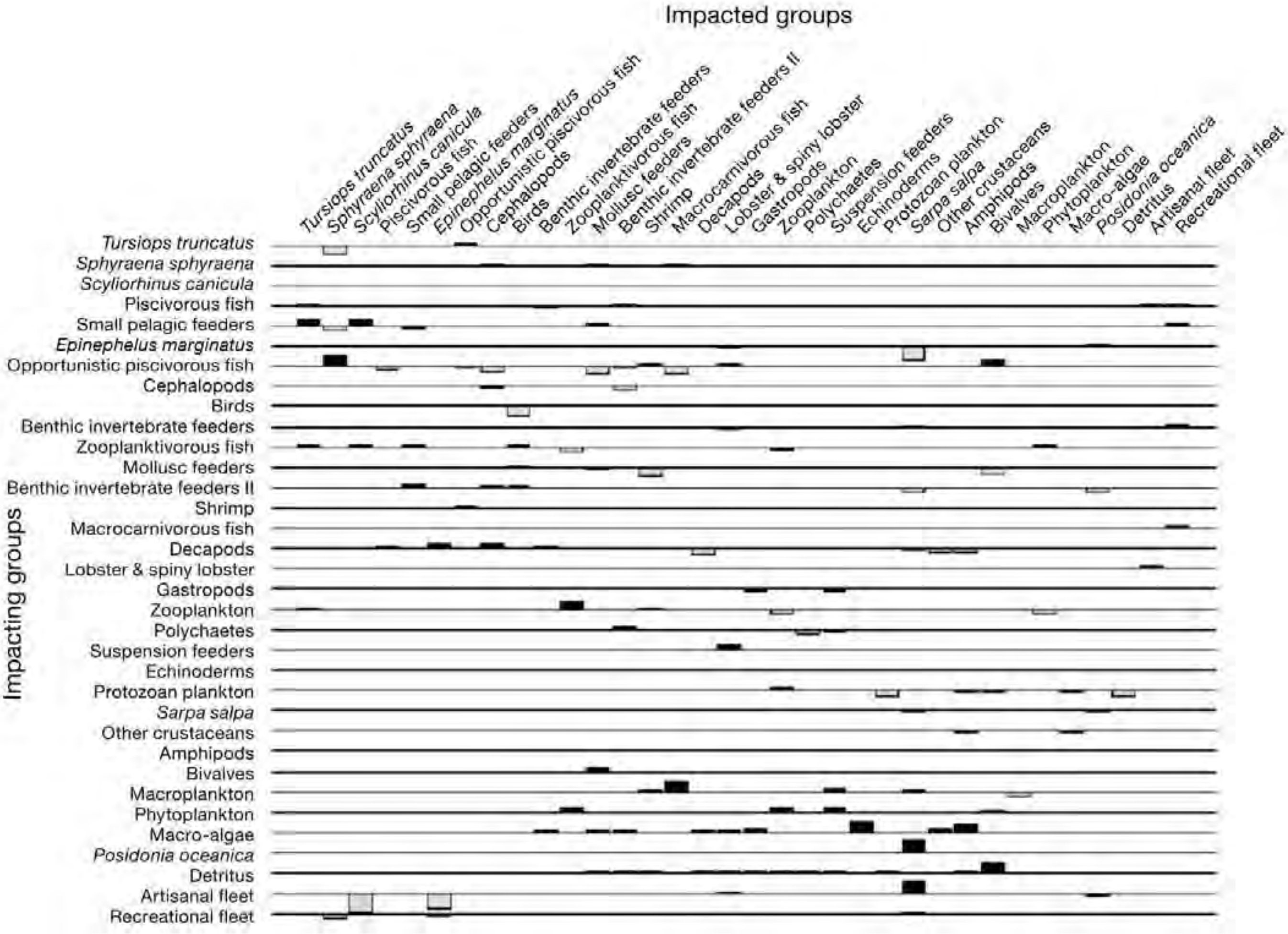


Fig. 3. Mixed trophic impacts analysis from the Bonifacio Strait Natural Reserve (BNSR) model showing the combined direct and indirect trophic impacts that an infinitesimal increase in impacting groups (vertical axis) is predicted to have on impacted groups (horizontal axis). Black bars: positive impacts (between 0 and 1); grey bars: negative impact (between 0 and –1)

Ecosim simulations

Results from simulations using Ecosim showed different response patterns when we simulated variations of both artisanal and recreational fishing efforts (Fig. 4), and we identified 3 categories of response.

Firstly, we focused on groups impacted exclusively by the artisanal fishery, meaning those losing biomass in response to an increase of the artisanal fishery effort. For instance, an increase in this effort induced a decrease in catches for *Epinephelus marginatus*, benthic invertebrate feeders II and of lobsters/spiny lobsters. For these groups, an increase in recreational fishing effort was without influence. In the case of the lobsters/spiny lobsters group, a total prohibition of the artisanal fishery effort (set to $F = 0$) would result in an increase in 2.7% of the system biomass. This amount corresponds to 51 t for the whole area of the BSNR.

Secondly, some groups were impacted by both fisheries, such as piscivorous fish, *Sphyraena sphyraena*, small pelagic feeders and *Scyliorhinus canicula*. For these groups there is an additional effect since their biomasses decreased in catches when both fishing efforts rose. For instance, when both fishing efforts were at the maximum in our simulations (4 times the actual level), piscivorous fish and the European barracuda biomasses decreased by 4.7 and 5.4%, respectively. These percentages corresponded to a loss of 131 t for piscivorous fish and of 10 t for *S. sphyraena*.

Thirdly, other groups (zooplanktivorous fish, benthic invertebrate feeders, mollusc feeders and cephalopods) displayed various non-trivial patterns, which were largely due to trophic cascades. For mollusc feeders and cephalopods, an increase in artisanal fishing effort induced an increase in their biomass, but coupled with an increase in recreational fishing effort, this

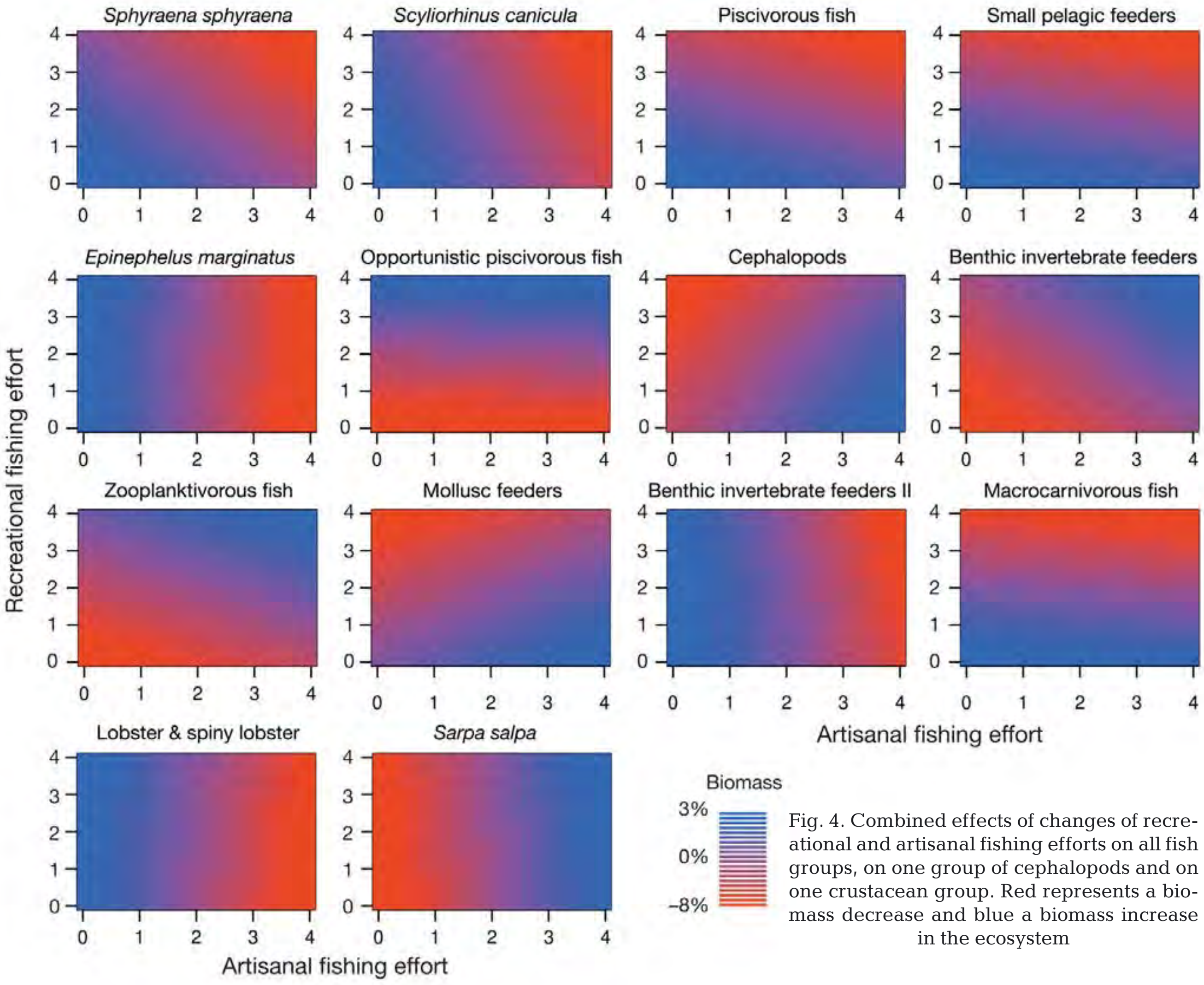


Fig. 4. Combined effects of changes of recreational and artisanal fishing efforts on all fish groups, on one group of cephalopods and on one crustacean group. Red represents a biomass decrease and blue a biomass increase in the ecosystem

biomass eventually decreased. For zooplanktivorous fish and benthic invertebrate feeders, an increase in artisanal fishing effort provoked a decrease in biomass in the system, but, coupled with an increase in recreational fishing effort, this biomass increased.

DISCUSSION

Ecopath results

Trophic levels, matter flows and summary statistics

Overall, ecological indicators related to community energetics, community structure, cycling of nutrients, and the comparison with other modelled ecosystems, suggest that the BSNR is a mature ecosystem, similar to most coastal ecosystems. The pedigree index (0.61) representing the model quality is within the range (0.164 to 0.676) of the 50 previously constructed models reported in Morissette (2007). TLs of fish species are in accordance with the range of previous results for the Mediterranean (Stergiou & Karpouzi 2001) as well as with TLs of another Corsican rocky littoral system models with similar attributes (Pinnegar & Polunin 2004). TLs obtained for bottlenose dolphins (5.22) and for *Sphyraena sphyraena* (4.96) are higher than TLs recorded by Pauly et al. (1998b) for dolphins (TL = 4.2) and by Ben-Tuvia (1986) for *S. sphyraena* (TL = 4.04). These differences are due to the diet of these 2 groups, which feed on predators, especially on fish species with a TL higher than 3.39, and could be due to MPA effects. Indeed, MPAs are known to promote biomass of large species and top predators (Claudet et al. 2006, Guidetti et al. 2008) increasing, by cascade, the TL of species feeding on them. Conversely, Pauly et al. (1998b) found that the diet of *Tursiops truncatus* (worldwide) is not exclusively composed of predator fishes, but of other items with lower TLs (large squid, small squid, small pelagics and miscellaneous fish) whereas Blanco et al. (2001) found that *T. truncatus* of the western Mediterranean Sea feeds partly on *Phycis* sp. and *Conger conger*. Therefore, it seems realistic that our TL for bottlenose dolphins is higher than that of Pauly et al. (1998b).

Tursiops truncatus is known to use fishing nets as an easily accessible feeding source, damaging or depredating fish caught in the nets (Reeves et al. 2001, Lauriano et al. 2004, Díaz-Lopez 2006). This species attacked, on average, 12.4% of the nets and, when they attacked, they damaged 8.3% of individuals caught in nets (Rocklin et al. 2009). Our data show that the fish biomass extracted by dolphins and by the artisanal fishery are similar in the BSNR. Moreover, the bottlenose dolphin and the artisanal fishery target the same groups of species (small pelagic feeders, piscivorous fish, cephalopods, benthic invertebrate feeders) according to Blanco et al. (2001). However, indirect negative interactions between dolphins and fisheries were not demonstrated (Rocklin et al. 2009), and the low level of exploitation (compared to the biomass available in the BSNR) induced by both artisanal fishery and dolphins suggest non-limiting resources and weak competitive interactions.

According to Odum (1969) and Christensen & Pauly (1993), a low ratio between system primary productivity and biomass (P/B) indicates a developed system, due to high biomasses and low production rates. This ratio ranges from 0 to 200 for 41 Ecopath models. Here the value of P/B (8.91) is low and equivalent to those reported for other coastal areas (Christensen & Pauly 1993), indicating great abundance of slow-growing individuals.

Odum (1971) explained that the ratio between total primary production and total system respiration (P_p/R) moves towards unity ($P_p/R = 1$) for mature systems. For the 41 Ecopath models that were mentioned above, P_p/R values range from 0.8 to 3.2. Our value of 1.12 is close to 1, i.e. the lowest boundary of that range, and indicates a very mature system.

The capacity of an ecosystem to entrap and cycle nutrients increases with maturity (Odum 1969) and can be estimated using the Finn's cycling index (Finn 1976). Christensen & Pauly (1993) found a relation between this index and maturity ranking across the 41 Ecopath models. In the BSNR Ecopath model, the value of Finn's cycling index was 10.71%. This moderate value is in accordance with values found in other coastal areas (Christensen & Pauly 1993) and once again suggests that our system is mature.

Transfer efficiencies (TE) represent the energy transferred from a trophic level to the next trophic level, through consumption. Since Lindeman (1942), it has often been assumed that TE varies around 10%. Our result (11.5%) is in accordance with the range (10 to 15%) of values reported in the literature (Christensen & Pauly 1993). Furthermore, for comparison, TEs are 12.62 and 10% for the Catalan and Adriatic Sea, respectively (Coll et al. 2006, 2007). To sum up, all these indicators of ecosystem maturity show that the BSNR model is in accordance with other Ecopath coastal models and with theory of trophic flows, suggesting that the model has realistic features despite some uncertainties.

In the mixed trophic impact analysis (Fig. 3) numerous groups at the base of the food web, such as *Posidonia oceanica*, macroalgae, phytoplankton, macroplankton, and zooplankton, have an impact on higher rank trophic groups by bottom-up predator–prey interactions occurring in the system (Hunter & Price 1992, Coll et al. 2006). On the other hand, some groups such as zooplanktivorous fishes (*Boops boops*, *Chromis chromis*, *Atherina* sp.) have a strong impact on numerous groups of both higher and lower trophic levels. This zooplanktivorous fish group has a top-down effect on zooplankton and a bottom-up control on predators. These results underline the importance of this key group in the ecosystem and possible wasp-waist predator–prey interactions (Cury et al. 2000, Coll et al. 2006). Opportunistic piscivorous fish species (*Pagellus acarne, Apongon imberbis*, *Scorpaena porcus*, etc.) occupy an intermediate trophic position (TL = 4.2) within the fish community and have a large number of trophic interactions with a wide variety of other groups. Changes in their biomass may induce simultaneous positive and negative effects on other groups, which can be interpreted as a wasp-waist effect (Cury et al. 2000).

A weak increase in *Epinephelus marginatus* leads to a decrease in *Sarpa salpa* and to an increase in *Posidonia oceanica* biomass. This food chain was created in accordance with data available in FishBase (Froese & Pauly 2010), identifying *E. marginatus* as the unique predator of *S. salpa* and *S. salpa* as the main consumer of *P. oceanica*. The protection of the dusky grouper, an emblematic fish species in the Mediterranean, may have a positive impact on *P. oceanica* meadows by means of a top-down effect. Since *P. oceanica* meadows constitute crucial habitats for nurseries (e.g. Gobert 2002), the management of top predators such as groupers is critical. In the same vein, a recent study showed that protection of large individuals of *S. salpa* may alter seagrass ecosystems (Prado et al. 2008). This type of investigation is possible in Ecosim through the use of mediation effects (Christensen et al. 2005), but here we only considered food web effects.

Through interaction analyses of the BSNR model, we were able to reproduce complex cascades of trophic interactions observed on Mediterranean coasts and in MPAs. One step further than observing cascades, we used such complex interactions to predict the status of the system according to scenarios involving non-trivial combined effects between fishing fleets.

Comparing two neighbour Mediterranean ecosystems: protected vs. non-protected areas

In order to understand the particularity of our system, we carried out a comparison with a non-protected area presenting similar sea surface temperature, habitats and species composition. This comparative analysis was established between 2 Ecopath models on rocky littoral ecosystems (Table 2), one protected (BSNR) and the other in a non-protected neighbour area (Calvi, Corsica; Pinnegar & Polunin 2004). There are great similarities in the model construction (target fish, invertebrate groups) allowing comparisons of these model outputs. Both ecosystems are mature (with higher values of P_p/R for the BSNR model); the fishing pressure is less and the mean trophic level of catches is higher in the BSNR than in the Calvi ecosystem (for values see Table 2).

The biomass extracted by artisanal fishing in the BSNR (0.09 t km^{-2} yr^{-1}) is very low compared to that at Calvi's (1.94 t km^{-2} yr^{-1}). The BSNR artisanal fleet is small (40 boats) and the fishing period extends over only 5 to 6 mo yr^{-1}. Bonifacio is the windiest area in Corsica with 328 d of wind per year (171 d with wind speed above 58 km h^{-1}). In the BSNR, a restrictive policy has been enforced on fishing activities since the creation of the MPA (in 1999): the number of professional licenses and the minimum mesh size were controlled and various protected perimeters were delimited. These restrictions tend to decrease the fishing pressure on the protected parts and to increase catches in terms of capture per unit of effort (CPUE) as demonstrated in Mouillot et al. (2008).

Pauly et al. (1998a) established that, with an increasing fishing pressure, the mean TL of catches decreases since fishes with high TLs are primarily targeted (generally benthic and demersal piscivorous). Top predators are thus progressively replaced by fishes with lower TLs , such as invertebrate feeders and planktivorous species. This index (mean TL of catches) is able to reveal the major difference in protection between these 2 ecosystems. The Calvi ecosystem is indeed more exploited than the BSNR, and its mean TL of catches is lower than for the BSNR model (3.77 vs. 3.94, respectively). An alternative explanation of this difference may come from the absence of *Epinephelus marginatus* (TL = 4.31) and the small pelagic feeder groups (TL = 4.54) in Calvi catches. Their presence in the BNSR data could be related to a higher conservation status. *E. marginatus* was usually targeted by spearfishing and is a relevant indicator species of this activity (Mouillot et al. 2002, Lloret et al. 2008b).

Simulated combined effects of artisanal and recreational fleets

Within the BSNR, artisanal and recreational fishing activities create a combined pressure on the ecosystem, although this pressure is low compared to the Bay of Calvi. Additional effects were observed when these 2 pressures increased in magnitude. The first level of interpretation was to distinguish which groups were particularly affected by either one or both types of fishing activity. The second level of interpretation was to understand the main trophic links between groups and to predict the combined effects of fishing pressure variations on the food web.

No group of fish represented in Fig. 4 is targeted exclusively by recreational activities. The nature of relations between the 2 types of fisheries is therefore limited to an additional effect or a lack of recreational fishing effect for remarkable groups having a protected status, and for which recreational catches are forbidden (*Epinephelus marginatus*, lobsters/spiny lobsters).

In the case of *Epinephelus marginatus*, protected since 1980, recreational fishing has no influence on its stock. However, *E. marginatus* is occasionally caught by the artisanal fishery. As pointed out above with MTI analysis (Fig. 3), several groups are connected to *E. marginatus* such as *Sarpa alpa*, which is itself connected to *Posidonia oceanica*. So an increase in catches of *E. marginatus* by artisanal fishing results in an overgrazing of *P. oceanica* by *S. salpa* (Fig. 4).

Mollusc feeders such as sparids (*Diplodus sargus sargus*, *D. vulgaris*, and *D. puntazzo*) showed a remarkable pattern (Fig. 4). Indeed, when artisanal fishing effort increases while recreational fishing effort is still limited, the biomass of this group increases. A possible interpretation of this result can be given by observing the position of this group in the network (Fig. 3). The trophic pressure exerted on mollusc feeders by top predators, such as *Sphyraena sphyraena* and opportunistic piscivorous fish, actually decreases when the fishing effort of the 2 fleets increases. Hence, this latter group of fish may be promoted by overfishing and may provide an erroneous signal of protection efficiency. If all species of *Diplodus* are present at high biomass, we may conclude that the ecosystem is well protected against fishing pressure, while an intensive artisanal activity may promote the diversity and biomass of such groups while recreational pressure is limited.

The opposite effect can be observed for zooplanktivorous fish, which are less targeted by both fisheries than other groups, due to policy protection regulations (mesh size authorized: 62.5 mm in length). A reduction in artisanal and recreational fishing efforts leads to the decrease in this group biomass in the system. When their predators are less exploited, predation on zooplanktivorous fish (forage fish) increases, leading to a decrease in their biomasses.

Based on these results, and the study of Christensen & Walters (2004), we suggest that recreational and artisanal fleets, by removing predators with high trophic levels, could cause top-down effects and thereby blur the classical patterns which are supposed to emerge when protection is enforced, i.e. an increase in fish biomasses. Hence, going one step further than highlighted by Tetreault & Ambrose (2007), we suggest that some species groups may provide negative signals (meaning a biomass decrease) when MPAs are set or enforced and such potential patterns are revealed by a trophic modelling approach and mechanistic relationships.

Limitations

Although this paper deals partly with recreational fisheries, we lack data on recreational catches. As an alternative, we assumed that the percentage of spearfishing represents 40 % of the artisanal production (Lloret et al. 2008b). In addition, we made the assumption that the level of exploitation by boat and shore fishing is common to north-shore Mediterranean countries and we used values proposed by Morales-Nin et al. (2005). However, recreational fishing pressure can be very different between sites as a function of human population density, tourist activity, cultural traditions, legislation and management policies. Thus, the chosen production for BSNR recreational fisheries is arbitrary and this choice may influence our results. To overcome this limitation we implemented simulations with a large range of recreational fishing effort (0 to 400 %) including realistic scenarios ranging from a total prohibition of such recreational activities to a strong increase (4-fold the value of artisanal production). The actual production lies between these 2 extremes, but further field investigations are needed to estimate this crucial variable.

Another limitation is the fact that the population dynamics of pelagic species and their home ranges exceed the borders of our area, while our model considers trophic transfer within this area with no external exchanges. This limitation is common to all EwE models which are not designed to include spatial dynamics. One solution would be to increase the model area to capture a larger fraction of their range or to drive their population as an input. However, 85 % of the total number of fish species and 90 % of fish biomass are benthic or demersal with few opportunities to disperse in such rocky Mediterranean habitats (Supplement 1C). The dolphins are also assumed to be sedentary to the BSNR throughout the year (WWF 2007). Thus, we suggest that our results are robust, even if they do not include migrations of pelagic species, since the main biomasses belong to sedentary species.

Our model cannot take spillover into account, an essential process by which MPAs sustain fishing activity in their neighboring areas (Pérez-Ruzafa et al. 2008, Forcada et al. 2009). However, all fishing activities tend to concentrate in the vicinity of no-take areas, which may lessen the spillover effect at a regional scale (Goni et al. 2008, Stelzenmüller et al. 2008). The amount of biomass exported from no-take areas towards exploited areas within and around the BSNR is of great interest to assess fully the benefit of protection. Using appropriate spatial data, an Ecospace approach would be useful to assess the function of such complex multiple-use and partial MPAs.

CONCLUSIONS

Overall, our results illustrate the utility of systemic approaches and the value of modelling tools in managing MPAs and predicting the ecosystem level consequences of socio-political conservation decisions. The BSNR model is a preliminary assessment of the combined effect of different types of fleets on a protected area, which takes into account the overall trophic links from the bottom to the top of the food web. After comparison with another Mediterranean coastal model, it appears that protection measures may have an impact on the mean trophic level of catches. Managers of the BNSR predict an increase in recreational fishing activities while the fishing effort from the artisanal fishery may stabilize. Considering the effect of recreational fishing on coastal ecosystems, and the predictions made by managers, it seems important to create new regulation policies for recreational activities.

This would necessitate the delimitation of more areas restricted to recreational activities but open to threatened artisanal fisheries. The effects of fishery interactions on food webs would then deserve to be studied using a spatial approach that takes into account dispersal rate, preferred habitats of species and variation in the size of protected areas (Pérez-Ruzafa et al. 2008). The BSNR Ecopath model can also be used to interpret how other threats, such as global change, species invasion and habitat destruction, can affect the trophic web and the sustainability of coastal fisheries.

Acknowledgements. We thank the staff of the Bonifacio Strait Natural Reserve for collecting the data. The study was partially funded by the PAMPA project through the LITEAU III program (French Ministry of Ecology and Sustainable Development). The authors are grateful to Pierre Lopez for drawing the map of the Bonifacio Straits Natural Reserve. Our research also benefited from 2 ANR projects (AMPHORE, GAIUS) which examined the effect of marine protected areas. We also thank the 4 anonymous referees for helpful comments on the manuscript.

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Editorial responsibility: Konstantinos Stergiou, Thessaloniki, Greece

Submitted: October 20, 2009; Accepted: May 27, 2010
Proofs received from author(s): August 11, 2010

The following supplement accompanies the article

Simulation of the combined effects of artisanal and recreational fisheries on a Mediterranean MPA ecosystem using a trophic model

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Marine Ecology Progress Series: 412: 207–221 (2010)

Supplement 1. Additional data

Supplement 1A. Input data and references by biotic group for the Bonifacio Straits Natural Reserve (BSNR) model. *B*: biomas; *P*/*B*: production per unit of biomass; *Q*/*B*: consumption rate per unit of biomass: *EE*: ecotrophic efficiency; *Z*: total mortality: *F*: fishing mortality rate; *M*: non-predation natural mortality rate

	Group	*B*	*P*/*B*	*Q*/*B*	*EE*	Diets
1	*Tursiops truncatus*	Life Linda 2000 to 2001 data from visual survey units of individuals has been transformed to t km^{-2} with the mean body weight per species	Data from Coll et al. (2006) corrected to consider differences of temperature with the equation of Opitz (Opitz 1996)			Blanco et al. (2001)
2	*Sphyraena sphyraena*	Unpublished BSNR data \ estimates from fishing data	$Z = F + M$; M = empiral equation from Pauly (1980)	Empirical relationship from Pauly et al. (1990)		See Supplement 1C
3	*Scyliorhinus canicula*	Unpublished BSNR data \ estimates from fishing data	$Z = F + M$; M = empiral equation from Pauly (1980)	Empirical relationship from Pauly et al. (1990)		See Supplement 1C

4	Piscivorous fish	Unpublished BSNR data \ estimates from fishing data and visual census	$Z = F + M$; M = empiral equation from Pauly (1980)	Empirical relationship from Pauly et al. (1990)	See Supplement 1C
5	Small pelagic feeders	Unpublished BSNR data \ estimates from fishing data	$Z = F + M$; M = empiral equation from Pauly (1980)	Empirical relationship from Pauly et al. (1990)	See Supplement 1C
6	*Epinephelus marginatus*	Unpublished BSNR data \ visual census data	$Z = F + M$; M = empiral equation from Pauly (1980)	Empirical relationship from Pauly et al. (1990)	Renones et al. (2002)
7	Opportunist piscivrous fish	Unpublished BSNR data \ estimates from fishing data and visual census	$Z = F + M$; M = empiral equation from Pauly (1980)	Empirical relationship from Pauly et al. (1990)	See Supplement 1C
8	Cephalopods	Unpublished BSNR data \ estimates from fishing data	Data from Opitz (1996) corrected to consider differences of temperature between areas with the Opitz equation		Ambrose & Nelson (1983)
9	Birds	Unpublished data from visual survey units of individuals has been transformed to t km^{-2} with the mean body weight per species	Data from Pinnegar & Polunin (2004) corrected to consider differences of temperature between areas with the Opitz equation		Hickling (1983)
10	Benthic invertebrate feeders	Unpublished BSNR data \ estimates from fishing data and visual census	$Z = F + M$; M = empiral equation from Pauly (1980)	Empirical relationship from Pauly et al. (1990)	See Supplement 1C
11	Zooplanktivorous fish	Data from the Pinnegar & Polunin (2004) model\ unpublished fishing data	$Z = F + M$; M = empiral equation from Pauly (1980)	Empirical relationship from Pauly et al. (1990)	See Supplement 1C
12	Mollusc feeders	Unpublished BSNR data \ estimates from fishing data and visual census	$Z = F + M$; M = empiral equation from Pauly (1980)	Empirical relationship from Pauly et al. (1990)	See Supplement 1C

13	Benthic invertebrate feeders 2	Unpublished BSNR data \ estimates from fishing data and visual census	$Z = F + M$; M = empiral equation from Pauly (1980)	Empirical relationship from Pauly et al. (1990)		See Supplement 1C
14	Shrimp		Data from Coll et al. (2006), corrected to consider differences of temperature between areas with the Opitz equation (Opitz 1996)		Fixed to current values	Opitz 1996
15	Macroplanktivorous fish	Unpublished BSNR data \ estimates from fishing data and visual census	$Z = F + M$; M = empiral equation from Pauly (1980)	Empirical relationship from Pauly et al. (1990)		See Supplement 1C
16	Decapods	Data from Sala (1997)	Data from Opitz (1996) corrected to consider differences in temperature between areas with the Opitz equation (Opitz 1996)	Data from Arias-Gonzales (1994) corrected to consider differences in temperature between areas with the Opitz equation (Opitz 1996)		Pinnegar & Polunin (2004)
17	Lobster & spiny lobster	Unpublished BSNR data \ estimates from fishing and sampling data	Data from Marin (1987) and Opitz (1996) corrected to consider differences in temperature between areas with the Opitz equation (Opitz 1996)			Opitz (1996)
18	Gastropods		Data from Opitz (1996) corrected to consider differences of temperature between areas with the Opitz equation (Opitz 1996)		Fixed to current values	Opitz (1996), Pearson & Gage (1984)
19	Zooplankton		Data from Pinnegar & Polunin (2004) corrected to consider differences of temperature between areas with the Opitz equation (Opitz 1996)		Fixed to current values	Kleppel (1993), Kleppel et al. (1996)
20	Polychaetes	Data from Sala (1997)	Data from Pinnegar & Polunin (2004) corrected to consider differences of temperature between areas with the Opitz equation (Opitz 1996)			Opitz (1996), Fauchald & Jumars (1979)

21	Suspension feeders		Data from Opitz (1996) corrected to consider differences in temperature between areas with the Opitz equation (Opitz 1996)		Fixed to current values	Chintiroglou & Koukouras (1992), Arias-Gonzales (1994), Coma et al. (1995), Ribes et al. (1999)
22	Echinoderms	Data from the Pinnegar & Polunin (2004) model	Data from Opitz (1996) and Pauly et al. (1993) corrected to consider differences in temperature between areas with the Opitz equation (Opitz 1996)			Arias-Gonzales (1994), Frantzis et al. (1988), Pearson & Gage (1984), Verlaque & Nedelec (1983)
23	Protozoan plankton		Data from Pinnegar & Polunin (2004) corrected to consider differences of temperature between areas with the Opitz equation (Opitz 1996)	Data from Sanchez & Olaso (2004) corrected to consider differences of temperature between areas with the Opitz equation (Opitz 1996)	Fixed to current values	Olivieri et al. (1993)
24	*Sarpa salpa*	Unpublished BSNR data \ estimates from fishing data	$Z = F + M$; M = empiral equation from Pauly (1980)	Empirical relationship from Pauly et al. (1990)		Havelange et al. (1997)
25	Other crustaceans	Data from the Pinnegar & Polunin (2004) model	Data from Pinnegar & Polunin (2004) corrected to consider differences of temperature between areas with the Opitz equation (Opitz 1996)			Arias-Gonzales (1994), Caine (1977), Vannier et al. (1998), Viejo & Arrontes (1996)
26	Amphipods		Data from Vetter (1996) and Schwinghamer et al. (1986) and corrected using the Opitz equation (Opitz 1996)	Data from Opitz (1996) corrected to consider differences in temperature between areas with the Opitz equation (Opitz 1996)	Fixed to current values	Greze (1968)
27	Bivalves		Data from Opitz (1996) corrected to consider differences in temperature between areas with the Opitz equation (Opitz 1996)		Fixed to current values	Opitz (1996)

28	Macroplankton		Data from Pinnegar & Polunin (2004) modified to consider area's temperature (Opitz 1996)		Fixed to current values	Dauby (1980), Hobson & Chess (1976), Kinsey & Hopkins (1994), Purcell (1981), Sullivan et al. (1994)
29	Phytoplankton		Data from Pinnegar & Polunin (2004) and modified to consider area's temperature (Opitz 1996)		Fixed to current values	
30	Macro-algae		Data from Opitz (1996) corrected to consider differences in temperature between areas with the Opitz equation (Opitz 1996)		Fixed to current values	
31	*Posidonia oceanica*	Data from Gobert (2002) modified to include the meadow surface	Data from Opitz (1996) corrected to consider differences in temperature between areas with the Opitz equation (Opitz 1996)			
32	Detritus	Data from the Pinnegar & Polunin (2004) model				

Supplement 1B. Final diet matrix of the Bonifacio Straits Natural Reserve (BSNR) model. BIF: benthic invertebrate feeders

	Prey\predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1	*Tursiops truncatus*																												
2	*Sphyraena sphyraena*																												
3	*Scyliorhinus canicula*																												
4	Piscivorous fish	0.200	0.025		0.070		0.022		0.01																				
5	Small pelagic feeders	0.528		0.460	0.022	0.050		0.008																					
6	*Epinephelus marginatus*																												
7	Opportunist piscivrous fish		0.715		0.109	0.263	0.103	0.020		0.106																			
8	Cephalopods	0.032		0.090	0.099	0.010	0.213	0.125	0.030	0.005	0.010																		
9	Birds																												
10	BIF	0.034	0.101		0.090	0.108		0.027			0.000																		
11	Zooplanktivorous fish	0.202		0.090	0.114	0.220	0.011	0.042	0.001	0.366	0.001	0.009																	
12	Mollusc feeders		0.125		0.073			0.155		0.275	0.005																		
13	BIF2		0.034		0.011	0.257	0.101	0.090	0.150	0.246	0.017			0.000															
14	Shrimp				0.006	0.009	0.013	0.153	0.035		0.057		0.163		0.002	0.113													
15	Macrocarnivorous fish				0.020			0.022																					
16	Decapods				0.365		0.418	0.276	0.636		0.489		0.127	0.179		0.036	0.083		0.008										
17	Superior crustaceans	0.004		0.160	0.004		0.057	0.001			0.024																		
18	Gastropods						0.020	0.007	0.041		0.004		0.178	0.037	0.070	0.001	0.030	0.218	0.042		0.005		0.009						
19	Zooplankton					0.007						0.773		0.028	0.113	0.001	0.063			0.006	0.042		0.001			0.009	0.027		
20	Polychaetes				0.005			0.012			0.109	0.084	0.034	0.406	0.050	0.001	0.012		0.125		0.089		0.001						
21	Suspensivors				0.005			0.003			0.001		0.009				0.010	0.375	0.090		0.027		0.073						
22	Echinoderms							0.013			0.098		0.008	0.012	0.016		0.001	0.032	0.001		0.001								
23	Protozoan plankton																0.050			0.394	0.050	0.063		0.247		0.009	0.050	0.100	0.010
24	*Sarpa salpa*						0.016																						
25	Other crustaceans			0.160	0.004		0.026	0.029	0.011		0.063	0.022	0.067	0.019	0.055		0.254		0.066		0.056		0.003						
26	Amphipods			0.040	0.001	0.009		0.007	0.049		0.114	0.074	0.067	0.214	0.087	0.150	0.262		0.006		0.048								
27	Bivalves							0.003	0.038				0.272		0.060	0.004	0.009												
28	Macroplankton					0.065		0.007				0.014			0.210	0.692	0.020				0.059	0.313	0.011		0.110				0.280
29	Phytoplankton											0.006								0.400	0.074	0.250			0.000	0.018		0.150	
30	Macro-algae				0.002							0.009	0.069	0.011	0.097	0.001	0.070	0.225	0.441		0.160		0.781	0.050		0.444	0.561		0.050
31	*Posidonia oceanica*													0.091									0.078		0.890				
32	Detritus														0.237		0.136	0.150	0.221	0.200	0.390	0.375	0.043	0.303		0.021	0.362	0.750	
33	Import																							0.400		0.499			0.660

Supplement 1C. Composition of fish groups and their associated references for diets. Asterisks show groups targeted by artisanal fishing, boat and shore fishing, or spearfishing

Group	Species	Artisanal fishing	Boat and shore fishing	Spear fishing	Source
Piscivorous	*Conger conger*	*		*	Cau& Manconi (1984)
	Dentex dentex	*	*	*	Morales-Nin & Moranta (1997)
	Lophius piscatorius	*			Macpherson (1981)
	Muraena helena	*		*	Cau & Manconi (1984)
	Phycis phycis	*		*	Papaconstantinou & Caragitsou (1989)
	Synodus saurus	*			Golani (1993)
Opportunist piscivorous fish	*Apogon imberbis*				Pinnegar & Polunin (2000)
	Labrus viridis	*		*	Bell & Harmelin-Vivien (1983)
	Pagellus acarne	*	*	*	Morato et al. (2001)
	Pagrus pagrus	*	*	*	Papaconstantinou & Caragitsou (1989)
	Scomber sp.	*		*	Cabral & Murta (2002)
	Scorpaena porcus	*		*	Arculeo et al. (1993)
	Scorpaena scrofa	*		*	Bell & Harmelin-Vivien (1983)
	Serranus scriba	*		*	Bell & Harmelin-Vivien (1983)
	Uranoscopus scaber	*			Sanz (1985)
Benthic invertebrate feeders	*Labrus merula*	*		*	Bell & Harmelin-Vivien (1983)
	Pagellus erythrinus	*	*	*	Rosecchi (1983)
	Sciaena umbra	*		*	Derbal & Kara (2007)
	Scorpaena notata	*		*	Bell & Harmelin-Vivien (1983)
	Thalassoma pavo				Bell & Harmelin-Vivien (1983)
Macroplanktivorous fish	*Serranus cabrilla*	*	*	*	Bell & Harmelin-Vivien (1983)
	Spondyliosoma cantharus	*	*		Bell & Harmelin-Vivien (1983)
	Trachinus draco/araneus	*			Morte et al. (1999)
	Trisopterus minutus	*			Le Loc'h (2004)

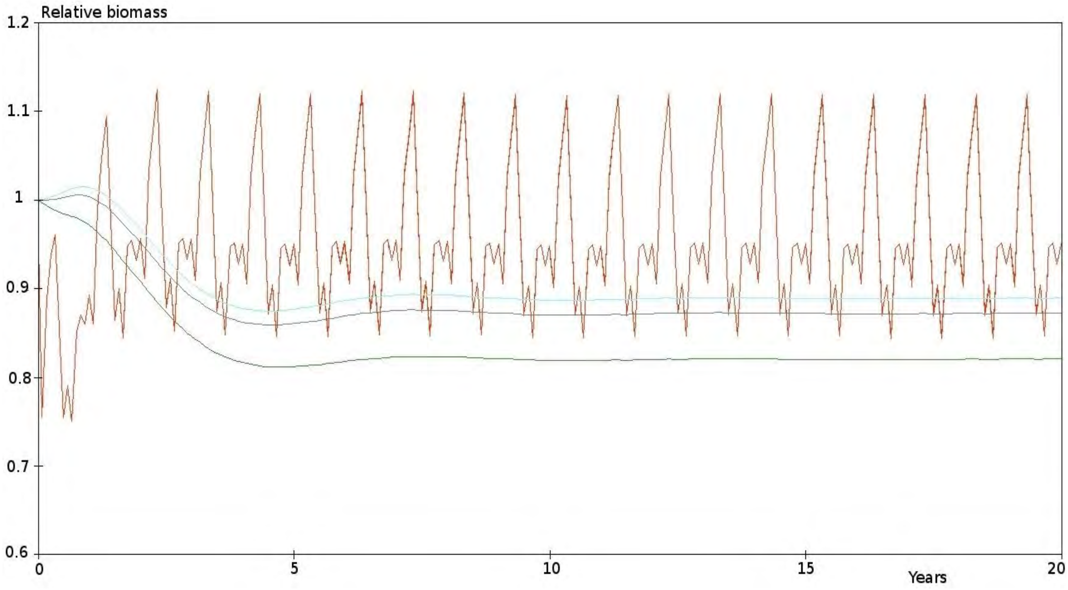
Small pelagic feeders	*Merluccius merluccius*	*			Le Loc'h (2004)
	Sarda sarda	*		*	Campo et al. (2006)
	Seriola dumerilii	*	*	*	Mazzola et al. (2000)
	Trachurus mediterraneus	*			Ben Salem (1988)
	Zeus faber	*			Bell & Harmelin-Vivien (1983)
Mollusc feeders	*Coris julis*		*		Bell & Harmelin-Vivien (1983)
	Diplodus puntazzo	*		*	Sala & Ballesteros (1997)
	Diplodus sargus	*	*		Sala & Ballesteros (1997)
	Diplodus vulgaris	*	*	*	Sala & Ballesteros (1997)
	Symphodus sp.	*			Bell & Harmelin-Vivien (1983)
	Trigla lucerna	*			Macpherson (1981)
Zooplanktivorous fish	*Atherina boyeri*				Pinnegar & Polunin (2000)
	Boops boops				Bell & Harmelin-Vivien (1983)
	Chromis chromis				Bell & Harmelin-Vivien (1983)
	Engraulis encrasicolus				Tudela & Palomera (1997)
	Mugilidés				Blaber (1976)
	Oblada melanura	*	*		Moreno & Castro (1995)
	Spicara maena	*			Khoury (1987)
Benthic invertebrate feeders 2	*Diplodus annularis*	*	*		Rossechi & Nouaze (1989)
	Gobius sp.				Dierter Zander & Berg (1984)
	Lipophrys pavo				Dierter Zander & Berg (1984)
	Mullus surmuletus	*		*	Pinnegar & Polunin (2000)
	Parablennius rouxi				Pinnegar & Polunin (2000)
	Solea sp.	*		*	Bell & Harmelin-Vivien (1983)
	Symphodus tinca	*		*	Khoury (1987)
	Tripterygion sp.				Bell & Harmelin-Vivien (1983)
Single species groups	*Epinephelis marginatus*	*			Renones et al. (2002)
	Sarpa salpa				Havelange et al. (1997)
	Sphyraena sphyraena	*	*	*	Barreiros et al. (2002)

Supplement 1D. Temperature assessment

An average temperature for the modelled area is primordial for assessing the consumption biomass ratio for fish (Eq. 6), and production per unit of biomass (*P*/*B*) and consumption rate per unit of biomass (*Q*/*B*) (for other groups). Values for other groups were taken from the worldwide literature and adapted to our system using the Opitz equation (Opitz 1996).

To estimate an annual average sea urface temperature (SST) of the Bonifacio Straits Natural Reserve (BSNR) we collected a grid (resolution of 1° of weekly SST values from the National Climatic Data Center (NCDC) National Operational Model Archive and Distribution System Meteorological Data Server (NOMADS) of the US National Oceanic and Atmospheric Administration (NOAA) Satellite and Information Service (www.osdpd.noaa.gov/PSB/EPS/SST/al_climo_mon.html). Then, maps were interpolated at the 0.1° resolution needed for our analyses via ordinary kriging. Weekly SST values were averaged over the 2000 to 2001 period to provide 14 SST variables for each 0.1° grid cell. Twelve monthly means were used to calculate the mean annual SST then an average SST was extracted. The mean annual temperature for the BSNR was 18.6°C for the 2000 to 2001 period.

Supplement 1E. Ecosim output, with the variation of relative biomass for phytoplankton (red line), the variation of relative biomass for piscivorous fish in the absence of fishing effort ($F = 0$) (light blue line), the variation of relative biomass for piscivorous fish and actual fishing effort ($F = 1$) (dark blue line), and the variation of relative biomass for piscivorous fish and a 4-fold increase in fishing effort ($F = 4$) (green line)



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Manuscrit J.

From the spatial redistribution of species to changes in food web structure under climate change

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Soumis à Ecology Letters

From the spatial redistribution of species to changes in food web structure under climate change

Running title: Consequences of climate change on food web structure

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Abstract

Climate change is inducing deep modifications in species geographic ranges worldwide. However, the consequences of such changes on community structure are still poorly understood, particularly the impacts on food web properties. Here we propose a new framework, coupling species distribution and trophic models, to predict climate change impacts on food web structure across the Mediterranean Sea. Sea surface temperature determined fish climate niches and their future distributions. Body size was used to infer trophic interactions between fish species. Our projections revealed that 54 fish species out of 256 would disappear by 2080-2099 on the Mediterranean continental shelf. The number of feeding links between fish species would decrease on 73.4% of the continental shelf but the connectance will increase on average from 0.26 to 0.29. This result masks a systematic decrease in predator generality, estimated as the number of prey species, from 30.0 to 25.4. Our study highlights large-scale impacts of climate change on food web structure with potential deep consequences on ecosystem functioning.

Keywords: Fish body size, Food webs, Niche model, Mediterranean Sea, Connectance, Vulnerability, Generality, Climate change, Metaweb.

Introduction

There has been impressive progress in biogeography over the last fifteen years to predict the impact of climate change on species geographic range shifts, extinction risks, and biodiversity patterns (Thuiller 2004; Araújo & New 2007; Albouy *et al.* 2012b). Future ecosystems are however unlikely to be a simple collection of independent species that will co-occur according to their future geographic distributions. Indeed, novel ecosystems will emerge with assemblages that have never been observed before and, most likely, with species that have not interacted yet. One of the greatest challenges that ecology and biogeography are facing today is thus to understand how those assemblages, forming complex interaction networks, will be reorganized following individual species responses to climate change and how these emergent ecosystems will function (Montoya *et al.* 2009; Woodward *et al.* 2010).

Food webs are central to ecosystem functioning since their structure governs fluxes of energy (Cardinale *et al.* 2006) and underpins key processes such as productivity (Chassot *et al.* 2010) and resilience (Loreau & Behera 1999). The biomass produced by basal species is distributed across the food web via trophic interactions towards apical species (Cury *et al.* 2003; Allesina & Bodini 2004; Colloca *et al.* 2010). This flux of matter is however far from a linear chain from primary producers to top carnivores, with most often omnivory, feeding loops, intra-guild predation and cannibalism (Polis & Strong 1996; Thompson *et al.* 2007). Network-level responses to climate change are thus likely to be more than simply the aggregate sum of all species-level responses. Spatial mismatch may separate previously interacting species (Schweiger *et al.* 2008), while novel interactions may appear thanks to new spatial co-occurrences (Gilman *et al.* 2010). Consequently, understanding the patterns and processes that govern food web assembly remains crucial to predict the impacts of climate change on ecosystem functioning (Woodward *et al.* 2010; Kissling *et al.* 2011). To this aim new modelling frameworks need to consider species as potential interacting components of a wider ecological network. We thus integrated recent developments from food web theory to infer potential interactions among species and predict large-scale alterations of food web structure under climate change. The model simply and intuitively assumes a positive relationship between predator and prey body size, an ubiquitous pattern found in most terrestrial and marine ecosystems (Brose et al. 2006). Such a simple rule has been largely employed to infer realistic food web structures (Shin & Cury 2001; Dunne 2006) and to predict trophic relationships that closely match to empirical data (Cattin *et al.* 2004; Allesina *et al.* 2008; Williams *et al.* 2010).

The general objective of this study is to assess the impact of climate change on the food web structure of coastal Mediterranean fish assemblages. The Mediterranean Sea is one of the most responsive regions to climate change (Giorgi 2006), with a Sea Surface Temperature (SST) expected to warm with an average of 2.8°C by 2070-2099 under the SRES A2 IPCC scenario (Somot *et al.* 2006). Marine species may respond to this modification by shifting their geographic range (Cheung *et al.* 2009; Albouy *et al.* 2012b). The question is therefore no longer whether marine species assemblages will be modified under increasing climate change, but whether such expected changes may modify ecosystem functioning and to which extent. We therefore use body size distribution within coastal Mediterranean fish assemblages to predict and map the structure of future food webs following climate change. To do so, we calibrate a niche model using three well-studied local trophic networks of the Mediterranean Sea. The model is then use to infer a "metaweb", describing potential trophic interactions among the 256 fish species, for the whole Mediterranean continental shelf. Finally, we estimate the potential effects of climate change on the trophic structure of fish assemblages by calculating food web descriptors under current and predicted climate conditions across the whole Mediterranean continental shelf.

Materials and methods

Food web data

The interaction dataset was composed of three finely resolved food webs from different regions of the Mediterranean Sea: the Bonifacio Strait Natural Reserve (Albouy *et al.* 2010), the Catalan Sea (Coll *et al.* 2006) and the Tyrrhenian Sea (Colloca *et al.* 2010). Feeding interactions were determined from stomach contents and completed by information from FishBase (Froese & Pauly 2009). For each studied site x, we obtained a prey/predator interaction matrix M_x of dimension S_x X S_x, with S_x being the total number of species. Trophic interactions m_{ijx} between species i and j are indicated by either 1 or 0 (1 if species j eats species i and 0 if not). The Bonifacio Strait Natural Reserve, the Catalan Sea and the Tyrrhenian Sea datasets were composed of 58, 82 and 35 species, respectively. Among the pool of species, 2 were mammals, 1 was a turtle and the others were fish. We focused on the fish/fish interactions; there were 185, 264 and 82 in the Bonifacio Strait Natural Reserve, the Catalan Sea and the Tyrrhenian Sea matrix, respectively. All these interactions were aggregated in a single matrix M_A, that contains a final dataset of 128 species and 635 realized interactions among 16384 potential.

Actual and future species geographic distributions

We collected actual geographical distributions (extent of occurrence maps) for 256 endemic and native coastal fish species on a 0.1° resolution grid system covering the whole continental shelf of the Mediterranean Sea (Albouy *et al.* 2012a). We restricted our analyses to the continental shelf of the Mediterranean Sea (200 m depth limit) because climate change is more likely to affect coastal species that are not benefiting from the temperature inertia of deep waters (Lloyd *et al.* 2012). For instance, (Stefansdottir *et al.* 2010) show that fish assemblages in hydrographically stable deep waters have not changed substantially over the last decade whereas assemblages in more variable shallow waters underwent a clear shift towards species representative of warmer temperatures.

To model future fish species distributions under climate change, we used sea surface water temperature (SST) as the main forcing variable (Azzurro *et al.* 2011; Albouy *et al.* 2012b). We employed a Mediterranean regional marine model (NEMOMED8) that predicts observed and future SST based on the following drivers: water energy fluxes, river discharges and water exchanges with the surrounding seas (Beuvier *et al.* 2010). Observed SST values were extracted for the period 1961-1980 and projected SST values were extracted for the end of the 21st century (2080-2099) from NEMOMED8 outputs, based on the SERS IPCC A2 scenario; this scenario is conservative but not the most pessimistic (IPCC 2007). The daily data were averaged to infer monthly data, leading to fifteen variables: 12 monthly averaged SST values, the absolute minimum SST, the absolute maximum SST and the absolute range of SST. The set of predictive variables was reduced to height on the basis of a k-means partitioning method in order to avoid model over parameterization (for more details see Albouy *et al.* 2012b).

An ensemble forecasting approach was applied (Araújo & New 2007) to account for model-based uncertainty in the modelling process, based on seven statistical algorithms (Generalized Linear models, Generalized Additive models, Classification Tree Analysis, Random Forests, Boosted Regression Trees, Multivariate Adaptive Regression Splines and Surface Range Envelope). Analyses were implemented using the BIOMOD package (Thuiller *et al.* 2009) from the R statistical and programming environment (R Development Core Team, 2010). Each model in the ensemble was weighted according to the TSS criterion (Allouche *et al.* 2006). Species presences/absences were derived from probabilistic model outputs using the threshold that maximized the TSS (Thuiller *et al.* 2009).

Food web modelling

Despite their theoretical interest, the recently developed methods to parameterize food web models offer several drawbacks to implement robust biodiversity scenarios at large scales since the model optimization remains challenging with rough likelihood surfaces and the optimization is time consuming. To overcome these drawbacks (Gravel *et al.* in revision), proposed a method to infer a master web that includes all the taxa that would potentially co-occur in a single habitat as well as all their possible feeding links, coined as the metaweb (Dunne 2006). This method predicts the links between species that have not interacted previously by parameterizing the niche model based on observed relationships between predator and prey body size.

First, we calibrated this model using the three resolved Mediterranean food webs pooled into the matrix M_A (for more details see supporting information). The TSS is then calculated as $TSS = (dg - ef) \times \left[(d+f) \times (e+g)\right]^{-1}$ to quantify the proportion of prediction success relative to false predictions and returns values ranging between 1 (perfect predictions) and -1 (inverted forecast; Allouche *et al.* 2006). The TSS is based on the partition of events (the prediction of a trophic interaction) between four components: the component d reports the number of links that are both predicted and observed, e reports predicted links with no observation, f reports predicted absences of links while observed, and g reports the number of predicted and observed absences of links. We removed the impossible predicted links where species do not co-occur in the field (bathymetric and spatial constraints were taken into account) and we recalculated the TSS to increase the realism of our niche model. Finally, we inferred potential trophic interactions for all local fish assemblages (cells of 0.1° by 0.1°)

using the calibrated allometric niche model (Gravel *et al.* in revision).

Impact of climate change on food web structure

We generated actual and future trophic networks for each of the 8154 cells of the Mediterranean coast based on actual and future fish occurrences, respectively, and the metaweb describing potential trophic interactions among the 256 fish species. A local (cell) trophic interaction between species i and j was considered to occur if the two species are predicted to co-occur, considering their observed bathymetry and their habitat, and if they are potentially interacting in the metaweb. We calculated descriptors of local food web structure for current and predicted fish assemblages (Williams & Martinez 2000; Bersier *et al.* 2002; Dunne *et al.* 2002). To assess the food web structure at cells scale we used, the number of species (S), the number of actual links (L) and finally the fraction of all possible links (S^2) that are realized in the network called connectance (L/S^2). These indices appeared to be the primary determinants of population stability and community structure (Petchey *et al.* 2010). To assess the modification of trophic network at species level we calculated the vulnerability, i.e. the mean number of consumer species per prey species and the generality, i.e. the mean number of prey species per predator species. We calculated and mapped the difference between the baseline period1961-1980 and the future period 2080-2099 for each index of food web structure.

Results

Calibration of the metaweb

We calibrated a metaweb for 256 fish species of the continental shelf of the Mediterranean Sea using three empirical food webs pooled into the matrix M_A and the allometric niche model. Approximately half of the 256 fish species (52.37%) are feeding on primary and secondary producers and do not have fish prey. One third of the species (33.50%) are top predators (not consumed by other fish species) and the remaining 14.13% are intermediate consumer species.

The comparison between observed and modelled trophic links for the three empirical food webs shows a TSS value of 0.51. After removing the links between species that cannot co-occur, the TSS reached a higher value of 0.67. This improvement was mainly due to the decrease of the f fraction into the TSS calculation, which reports the predicted absences of links while observed. The inferred corrected metaweb yields a realistic relationship between predator and prey body sizes, indicating that our parameterization captures some essential aspects of this food web structure (Fig.1). The Mediterranean metaweb constrained by bathymetric and spatial mismatch between species pairs contained 11 055 potential interactions and the directed connectance (number of links divided by the number of potential links; S^2) had a value of 0.17. On average, species had 76.7 potential predator species and 54.7 potential prey species, respectively regional vulnerability and generality values (Table 1).

Mapping current food web structure

Food web descriptors for the baseline period (1960-1980) were calculated and mapped at the cell scale (Fig. 2). On average, there were 79 species per cell (sd = 41.12) with the highest value (181 species) in the Tyrrhenian Sea and the lowest (8 species) in the Levantine basin (Fig. 2a). There were on average 2128 feeding links between fish species (sd =1891) per cell with the highest density (7158 links) in the Tyrrhenian Sea and the lowest (22 links) in the Levantine basin (Fig. 2b). The mean connectance per fish assemblage was 0.26 (sd = 0.048) with highest values (0.43) in the western basin, the Tyrrhenian Sea, the Adriatic Sea, the gulf of Gabès and in the Aegean Sea (Fig. 2c). The lowest connectance values (lower than 0.15) were inferred in the Levantine basin. On average, there were 24 predator species per prey species (vulnerability, sd = 12.9; Fig. 2d) and 30 prey species per predator species (generality, sd = 17.8 Fig. 3e). The highest values for both generality (67) and vulnerability (48) were observed in the Adriatic Sea. The lowest values for both generality (2.75) and vulnerability (2.75) were observed in the northern part of the Levantine basin.

Projected changes in food web structure

The projected species distributions according to climate change revealed that 54 species out of 256 would disappear by 2080-2099 from the Mediterranean continental shelf with a widespread decrease of local species richness (Fig. 3a). The number of feeding links would correspondingly decrease on 73.39% of the continental shelf (Fig. 3b). The number of links would only increase in the Gulf of Lion, the Adriatic Sea, the Aegean Sea and the Levantine basin. By 2080-2099, the decrease in species richness would be faster than decrease in link density for the 44.0% of fish assemblages which will have higher connectance than current values, like the North western part of the Mediterranean Sea, the south of the Adriatic Sea, a large part of the Aegean Sea and the northern part of the Levantine basin (Fig. 3c). On average the connectance between the two time periods would increase by 0.037. The generality of predator species is expected to decrease between the two periods, from 30 to 25.4 prey species by predator in each local assemblage on average. Consequently, 82.8% of fish would have a lower value of predator generality in the future than currently observed (Fig. 3d). Overall, 73.9% fish assemblages of the continental shelf would experience a decreasing vulnerability in the future, particularly the western basin, the Gulf of Gabès, the Peloponnese and the Tyrrhenian Sea, and a large part of the Adriatic Sea (Fig. 3e). On average, vulnerability values would decrease by 10.7% (from 24 to 21.1) over all fish assemblages between 1961-1980 and 2080-2099.

Co-variation between species generality, vulnerability and range size

Beyond changes of generality and vulnerability, we also need to investigate the relationship of these two food web components with the change in range size. We should be concerned by scenarios such as a joint reduction in generality and range size, or an increase in vulnerability and a decrease of generality. We first assessed the co-variation in vulnerability and generality to determine whether some species would be under both stresses, i.e. expected to have less prey and more predator species in the future (Fig. 4). The majority of species (113 out of 256) would have less prey at the end of the 21st century than in the baseline period (1960-1980), while a low number of species (11 out of 256) would have more prey. In parallel, 50 species would have more predators while 65 would have less predators. There was no relation between generality and vulnerability (Spearman correlation test; $\rho = -0.106$, p-value = 0.16). We also investigated the relationship between the change in range size due to climate change and the modification of generality and vulnerability experienced by species. We found no link between the change in range size and the variation in both vulnerability (Spearman correlation test; $\rho = -0.06$, p-value = 0.43) and generality (Spearman correlation test; $\rho = 0.0046$, p-value = 0.95).

Discussion

Climate change will impose modifications of species composition and trophic structure for almost all ecosystems on Earth (Tingley *et al.* 2009; Petchey *et al.* 2010; Thuiller *et al.* 2011). If changes in species composition have been widely investigated and modelled, we still lack a framework to assess changes in trophic structure. In this study, we developed such a flexible framework, based on an hybrid model mixing climatic and trophic niches, and we predicted future fish food webs in the Mediterranean Sea. The maps of food web descriptors as well as their projections under climate change revealed potential changes of interactions in Mediterranean fish assemblages with a high spatial heterogeneity. Indeed, we found that an important part of the Mediterranean continental shelf would face a decrease in the number of links, vulnerability and generality, while the connectance within fish assemblages would increase by the end of the 21st century. This increase in connectance is mainly due to a differential loss rate of realized feeding links and species richness. Indeed, climate change would drive 54 species towards potential extinction and 159 species toward a geographic range contraction. Among those loser species most are basal species which are only linked to fish predators in our network (Albouy *et al.* 2012b). In parallel we observed an increase of intermediate and top predator fish species, which make many trophic links.

Increasing number of links, vulnerability and generality are also predicted while connectance could decrease in some regions such as the Levantine basin. This situation is expected to occur due to two possible scenarios. First, realized feeding links could increase faster than species richness. The first scenario is observed in the Levantine basin and in a small area of the Adriatic Sea, and most likely because few top predator species with many links such as Yellowmouth barracuda (*Sphyraeana viridensis*) or Haifa grouper (*Epinephelus haifensis*), would appear tracking their climate niche across the Mediterranean Sea (Araújo & New 2007; Albouy *et al.* 2012b). Alternatively, realized feeding links could also decrease faster than species richness. Under this second scenario (decrease in both connectance and species richness), observed in the Gulf of Gabès, we observed an increase of top species and a decrease in intermediate and basal species.

The analysis of the biogeography of food web descriptors is the first step to understand the consequences of climate change impact on ecosystem functioning. Food webs descriptors such as connectance, link density, vulnerability and generality are related to well known properties of ecosystems, such as their stability (May 1972), persistence (Dunne *et al.* 2002; Gravel *et al.* 2011) and productivity (Thebault & Loreau 2003). Montoya *et al.* (2009) suggested that generalist and vulnerable species (i.e. with many connections) have a lower influence than specialist species at the assemblage level since their impact is diffused among a larger diversity of species forming a network of weak links. They also keep the network together, preventing secondary extinctions and network collapse (see also Dunne *et al.* 2002). In our case, the number of links per species is expected to decrease with climate change. Based on food web theory, we presume that the altered structure may make fish assemblages more sensitive to disturbances. Mediterranean fish species may have less prey and less predator species by the end of the 21st century, which may enhance further their extinction probability (Petchey *et al.* 2010).

The modification of trophic structure has also some impact on ecosystem functioning. Even if primary production is ultimately driving fishery yields (Chassot *et al.* 2010). This relationship is however not consistent when global patterns are examined across 52 large marine ecosystems (Friedland *et al.* 2012). Indeed, the relationship between net primary productivity and upper trophic levels is strongly influenced by processes determining movement of energy towards high trophic levels (Friedland *et al.* 2012). It is however impossible at this stage to infer the direction of the change in functioning from the alteration of food web structure we documented. There is not yet a predictive theory linking network structure and ecosystem functioning (Thompson *et al.* 2012). The current theory on biodiversity and ecosystem functioning in food webs revealed all the complexity of the problem (Duffy *et al.* 2007) and the inexistence of any general mechanism linking the structure to functioning. There are nonetheless some findings that could potentially guide intuitions. In small food webs with low trophic redundancy, the impact of species loss is highly variable because of the unique contribution of each species to the topological structure (Harvey et al. in press). There is however considerable predictability in larger networks, attributable to considerable distance-decay of the interaction strength between pairs of species (Berlow *et al.* 2009). Because most biological rates scale with body size (Brown *et al.* 2004) and because also of its important structuring role, this functional trait appears as a potentially very powerful variable to develop general predictions on ecosystem functioning. This is particularly relevant given the well-established relationship between climate and ecosystem fluxes in size-structured communities (Brose *et al.* 2012). A recent modelling study indeed revealed that climate change would cause a decline of primary and fish production in many areas via an effect on body-size distribution (Blanchard *et al.* 2012).

The approach we developed here is not limited to fish and will be useful for a variety of size-structured ecosystems. But this framework may also be applied in contexts where interactions can be confidently inferred from individual traits or other biological features. For instance the topology of complex interaction networks such as plant-pollinator can be predicted from a small set of traits (Santamaria & Rodriguez-Girones 2007). Mouillot *et al.* (2008) also show that phylogenetic constraints on host–parasite links produced webs very similar to empirical, and more generally every trait related to the niche of a species could be used to reconstruct realistic food web. To improve our modelling approach and underlined the fact that shifts in diet during ontogenic development can occurred in fish assemblage, we proposed to consider different life stages as different entities in the metaweb. Then ontogenic shifts in diet could be modelled along the trophic niche axis to infer unobserved interactions. This ontogenetic shift was observed for example for *Merlangius merlangus* and *Merluccius merluccius.*

The next step to our approach would be the integration of climate change in conjunction with fisheries to determine the nature of interaction between these two perturbations (additive, synergetic or antagonist effects) and the consequence on food web structure. Invasive species coming from the Atlantic Ocean and the Red Sea should also be integrated because they are susceptible to modify trophic structures (Ben Rais Lasram *et al.* 2008). The modelling approach for trophic interactions nonetheless allow the exploration of the possible feeding links that these species could done based on their body size, probability of occurrence, and their bathymetric ranges. Consequently, our approach allows testing the potential introduction of a species or a pool of species and analysing the potential feeding links that these species could create within local assemblages.

Global changes first influence demography of individuals, then species ranges and eventually the interactions within assemblages. Ecologists are urged to develop general methods flexible enough to be applied across ecosystems and able to better predict global change impacts on ecosystem functioning. Knowledge of individual species traits and life history is necessary to drive conservation practices, but we also need integrative tools at the ecosystem scale. Our study is an important step to that end. We proposed a novel methodology accounting for both climatic and trophic niches. We used knowledge of local food web structure to recreate the potential interactions among all Mediterranean fishes. This procedure could be highly useful to any other ecosystem where interactions are also constrained by species traits or phylogeny and facing perturbations such as climate change. The next step of analysis will be to identify species that are the most vulnerable to global change based on their trophic interactions. Our results suggest that traits such as diet generality, vulnerability and body size are good indicators of this vulnerability. Similar methods approximating potential interactions and their sensitivity to global changes should be developed for other systems, such as host-parasite and plant-pollinator systems. Our approach provides a parsimonious explanation to species distributions and open new perspectives to integrate the complexity of ecological interactions into simple species distribution models. We first predicted the future species distribution and then we constructed the trophic network, in a certain way we forced our projection model by a trophic model. The future challenge that can occupy ecologist will be to realize a coupled modelling framework in order to constraint the projection by the potential species interactions.

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Fig.1: Relation between prey and predator body size for the compilation of the three observed Mediterranean food-webs (Bonifacio Strait Natural Reserve, the Catalan Sea and the Tyrrhenian Sea). The circles represent the observed links between prey and predator species, the black dots represent the link predicted by the allometric model and the red dots represent the removed links due to absence of co-occurrence between species pairs due to either habitat or bathymetric mismatch. TSS represents the True Skill Statistic and assesses the proportion of prediction success relative to false predictions.

Fig.2: Maps of species richness (a), number of links (b), connectance (c), trophic level (d), generality (e) and vulnerability (f) values for the period 1961-1980 on the continental shelf of the Mediterranean Sea.

Fig.3: Differences in species richness (a), number of links (b), connectance (c), trophic level (d), generality (e) and vulnerability (f), predicted on the continental shelf of the Mediterranean Sea considering all fish species between the baseline scenario (1961-1980) and the end of the 21st century (2080-2099). For a better representation we represent the logarithm plus one of the relative difference between the future and observed periods.

Fig.4: Relation for each modelled species (excepted each that had no link into the created food-web), between the variation in generality, vulnerability and range shift. The colour gradient for points (red to blue) represents the variation (loss, gain) in range between the baseline scenario (1961-1980) and the end of the 21st century (2080-2099).

Table caption

Table 1: Indicators values calculated for the Bonifacio Strait Natural Reserve, the Catalan Sea, the Tyrrhenian Sea and for the Metaweb for the Mediterranean Sea. S is the number of species, L the link between two species, C is the connectance value (L/S^2), Gen the generality value that represent the mean number of prey by predator and Vul the vulnerability that represent the mean number of predator by prey.

	S	S^2	L	C	Gen	Vul
Bonifacio	58	3364	185	0.05	7.1	4.1
Catalan Sea	82	6724	295	0.04	6.8	4.9
Tyrrhenian Sea	35	1225	82	0.07	5.9	2.9
Metaweb	256	65536	18968	0.29	93.4	131.7
Metaweb corrected by bathymetry	256	65536	12961	0.20	64.1	90
Metaweb corrected by preferred habitats	256	65536	11055	0.17	54.7	76.7

Fig.1:

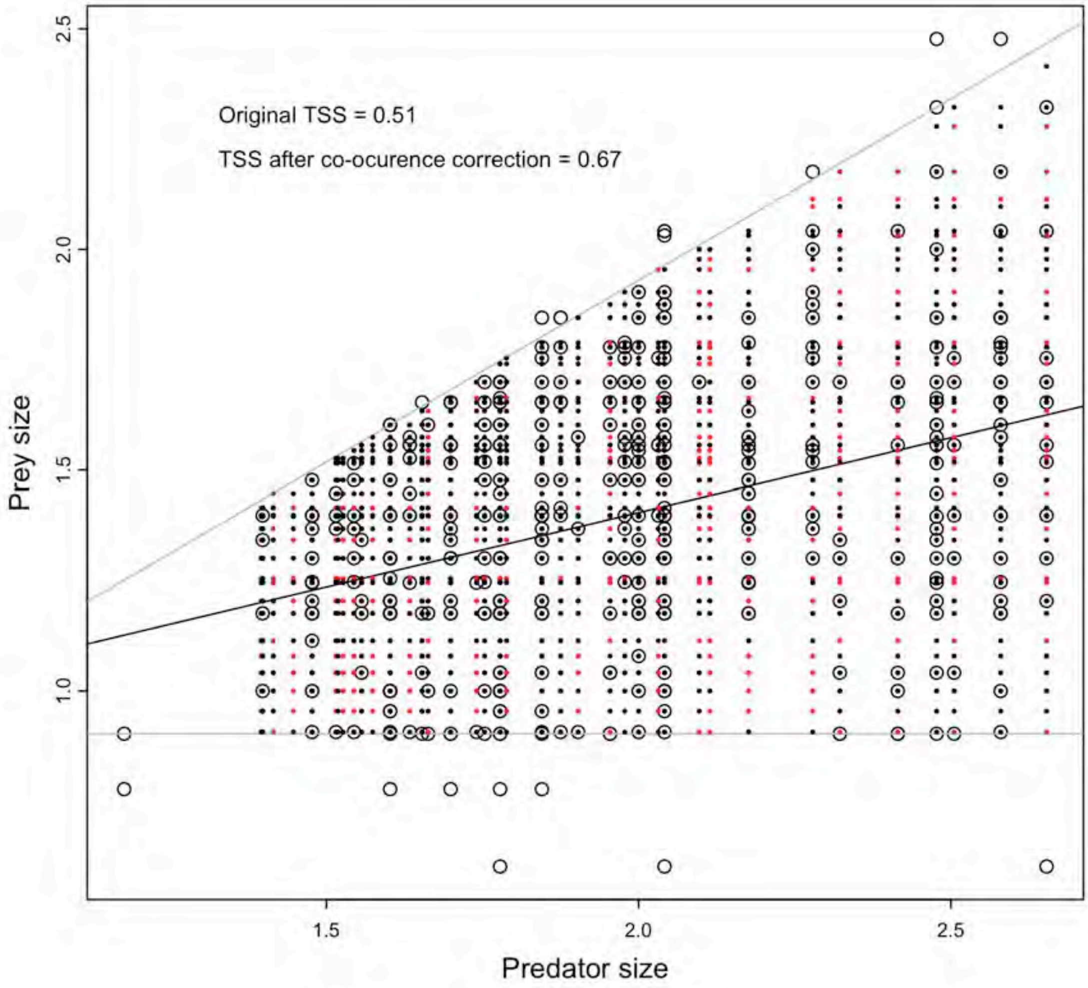

Original TSS = 0.51
TSS after co-ocurence correction = 0.67
Prey size
Predator size
2.5
2.0
1.5
1.0
1.5
2.0
2.5

Fig. 2:

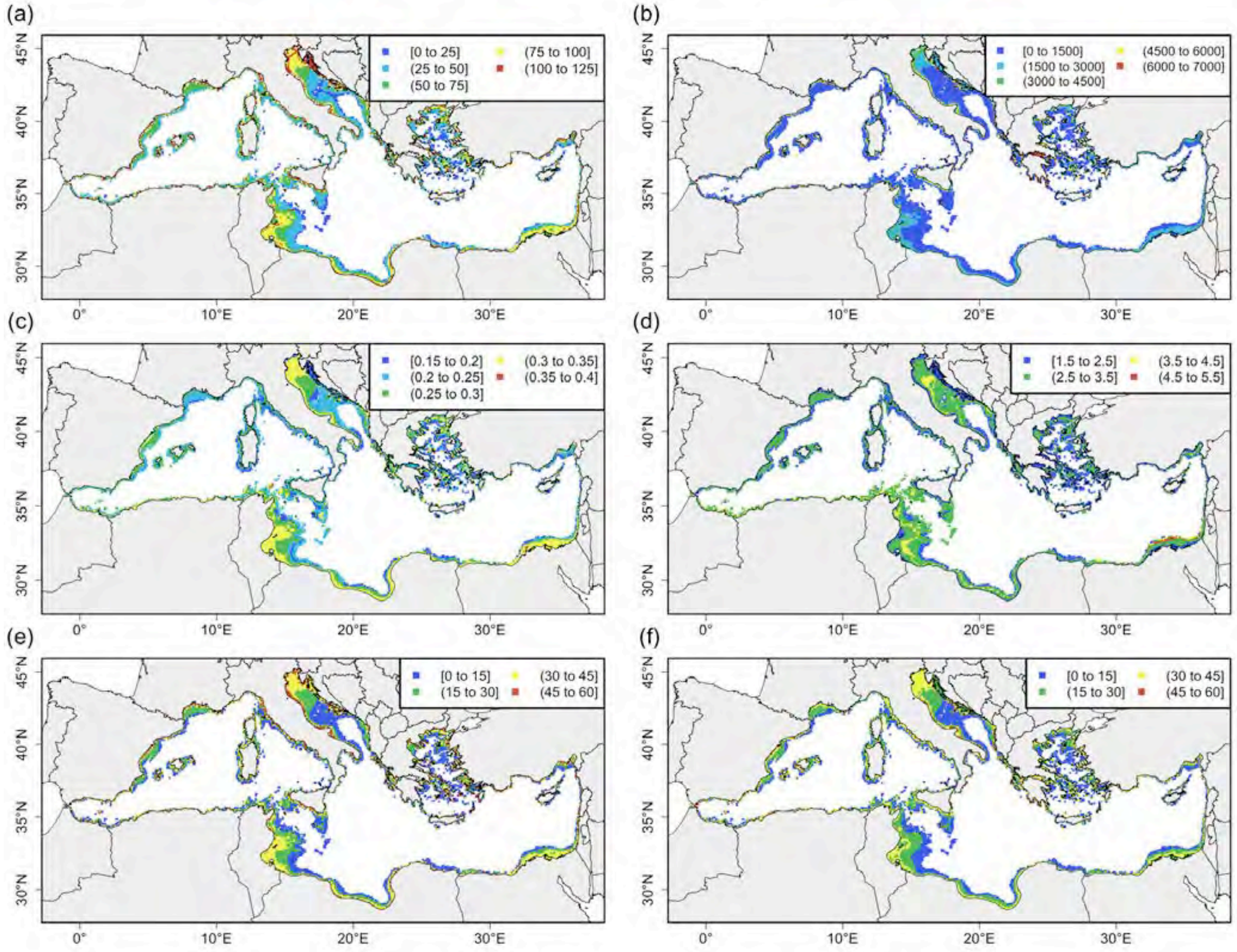

(a)
[0 to 25]
(25 to 50]
(50 to 75]
(75 to 100]
(100 to 125]
(b)
[0 to 1500]
(1500 to 3000]
(3000 to 4500]
(4500 to 6000]
(6000 to 7000]
(c)
[0.15 to 0.2]
(0.2 to 0.25]
(0.25 to 0.3]
(0.3 to 0.35]
(0.35 to 0.4]
(d)
[1.5 to 2.5]
(2.5 to 3.5]
(3.5 to 4.5]
(4.5 to 5.5]
(e)
[0 to 15]
(15 to 30]
(30 to 45]
(45 to 60]
(f)
[0 to 15]
(15 to 30]
(30 to 45]
(45 to 60]
45°N
40°N
35°N
30°N
0°
10°E
20°E
30°E

Fig. 3:

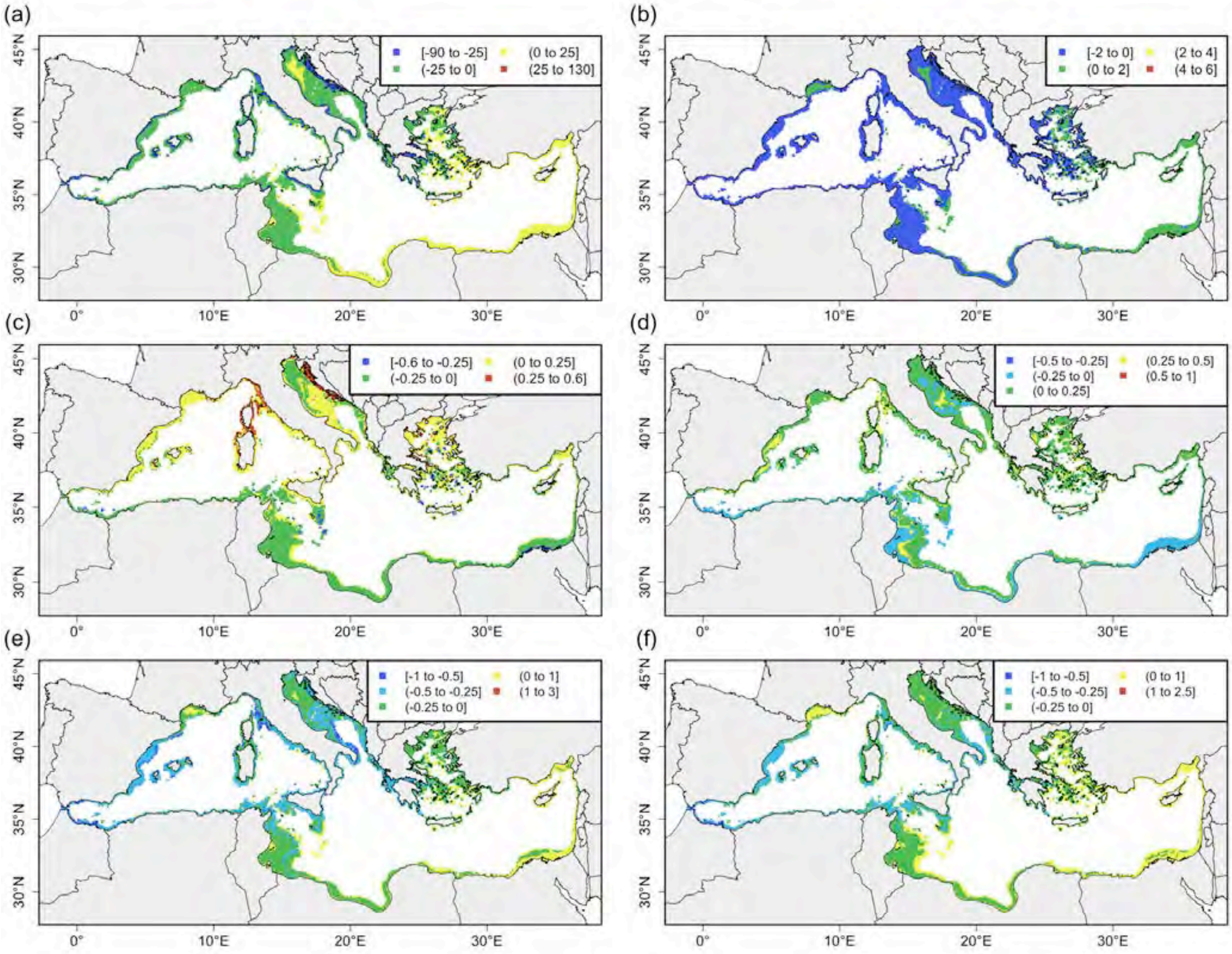
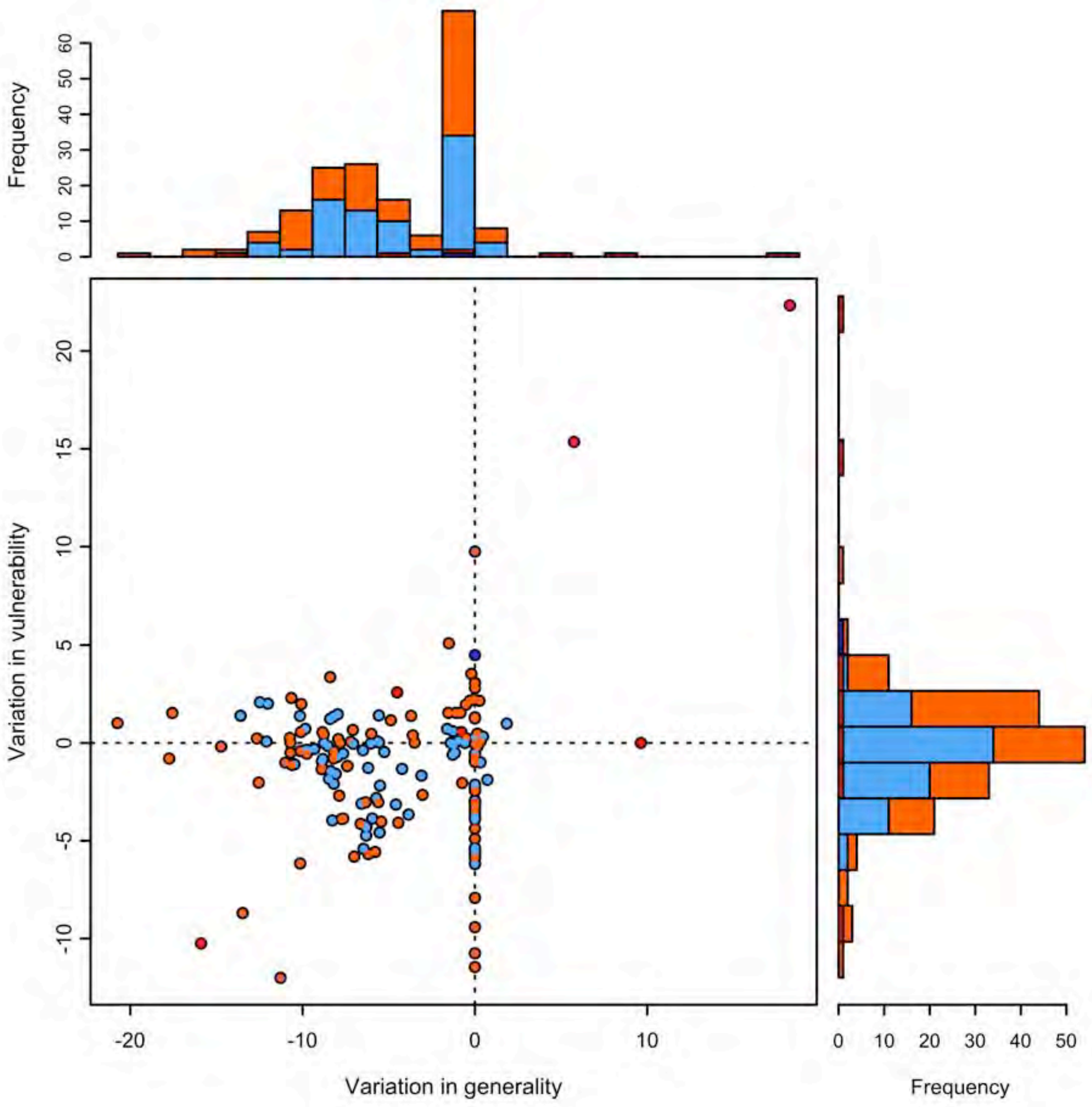

(a)
[-90 to -25]
(-25 to 0]
(0 to 25]
(25 to 130]
(b)
[-2 to 0]
(0 to 2]
(2 to 4]
(4 to 6]
(c)
[-0.6 to -0.25]
(-0.25 to 0]
(0 to 0.25]
(0.25 to 0.6]
(d)
[-0.5 to -0.25]
(-0.25 to 0]
(0 to 0.25]
(0.25 to 0.5]
(0.5 to 1]
(e)
[-1 to -0.5]
(-0.5 to -0.25]
(-0.25 to 0]
(0 to 1]
(1 to 3]
(f)
[-1 to -0.5]
(-0.5 to -0.25]
(-0.25 to 0]
(0 to 1]
(1 to 2.5]
45°N
40°N
35°N
30°N
0°
10°E
20°E
30°E

Fig. 4:


Frequency
0
10
20
30
40
50
60
Variation in vulnerability
-10
-5
0
5
10
15
20
-20
-10
0
10
Variation in generality
0
10
20
30
40
50
Frequency

Supporting information: The allometric niche model

The niche model (Williams & Martinez 200) predicts the food web structure from a set of three species-specific parameters: the niche position *n*, the feeding niche centroid *c* (the niche optimum) and a range of suitable prey *r*. Gravel *et al.* (in revision) assumed that body size is the main niche axis responsible for trophic interactions with a linear relationship between the niche position *n* and the log of body size. This assumption was confirmed by recent studies that have suggested a determinant role of body size in determining the structure of food webs (Allesina *et al.* 2008; Coloca *et al.* 2010; Williams *et al.* 2010; Riede *et al.* 2011). Some other traits that potentially shape species interactions such as mobility, home range or metabolism, are often highly correlated to body size (Williams *et al.* 2010). The species-specific parameter c was estimated for each species by fitting a linear model between the log body size of predators and the log body size of prey. The range r was obtained by the difference between the 5% and 95% quantile regressions between the log of predator body size and the log of prey body size. The three parameters (*n*, *c*, *r*) were evaluated for the 256 fish species. Primary and secondary producers were assumed present at all locations and non-limiting on the whole Mediterranean Sea, and their parameters fixed at $n = 0$, $c = 0$ and $r = 0$.

The evaluation of these three coefficients (*n*, *c*, *r*) was used to infer the feeding niche of each the 256 coastal osteichthyan species of the Mediterranean Sea. Chondrichthyans, mammals and turtles were under-represented in the three trophic networks and were removed from the analyses. Exotic species were discarded as well because they are not at equilibrium with environmental conditions, an assumption required for species distribution models (Guisan & Zimmermann; Guisan & Thuiller 2005). All potential trophic interactions between all coastal fish species of the Mediterranean Sea were calculated. We called the matrix of potential interactions M'_w the metaweb (Dunne 2006). The metaweb was corrected by two ways. Firstly, we removed links corresponding to species pairs that cannot co-occurred according to their bathymetry. Secondly, we removed links by applying a habitat constraint, we made the logical assumption that pelagic species cannot eat benthic species and reciprocally.

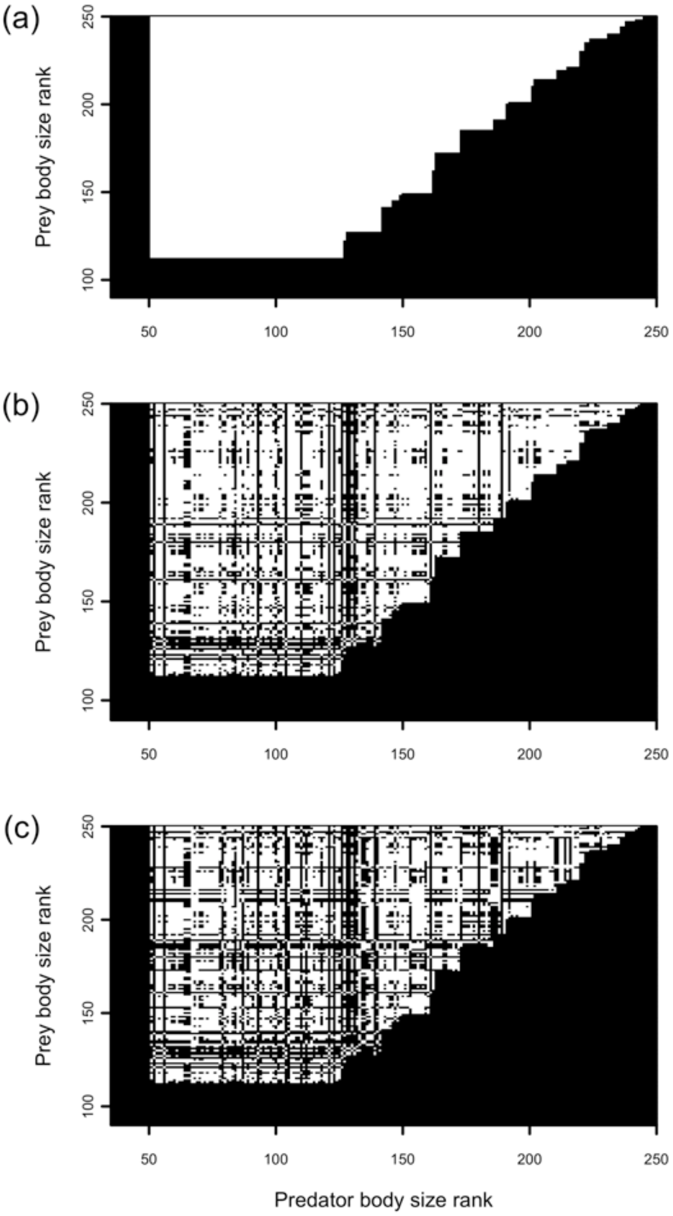


Fig.1: Relation between prey and predator body size for the Mediterranean metaweb (a), after bathymetric correction (b), and after both bathymetric and habitat correction (c).

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