

Forecasting fine-scale changes in the food-web structure of coastal marine communities under climate change

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Climate change is inducing deep modifications in local communities worldwide as a consequence of individualistic species range shifts. Understanding how complex interaction networks will be reorganized under climate change represents a major challenge in the fields of ecology and biogeography. However, forecasting the potential effects of climate change on local communities, and more particularly on food-web structure, requires the consideration of highly structuring processes, such as trophic interactions. A major breakthrough is therefore expected by combining predictive models integrating habitat selection processes, the physiological limits of marine species and their trophic interactions. In this study, we forecasted the potential impacts of climate change on the local food-web structure of the highly threatened Gulf of Gabes ecosystem located in the south of the Mediterranean Sea. We coupled the climatic envelope and habitat models to an allometric niche food web model, hence taking into account the different processes acting at regional (climate) and local scales (habitat selection and trophic interactions). Our projections under the A2 climate change scenario showed that future food webs would be composed of smaller species with fewer links, resulting in a decrease of connectance, generality, vulnerability and mean trophic level of communities and an increase of the average path length, which may have large consequences on ecosystem functioning. The unified framework presented here, by connecting food-web ecology, biogeography and seascape ecology, allows the exploration of spatial aspects of interspecific interactions under climate change and improves our current understanding of climate change impacts on local marine food webs.

Climate changes have significant impacts on the world's marine biodiversity (Barange et al. 2010) and exploited species (Hermant et al. 2010). The expected responses from marine biodiversity to global warming include a latitudinal shift in the distributions of a wide range of species as they track their climatic niches (Dulvy et al. 2008, Pinsky et al. 2013), local extinctions (Cheung et al. 2009) and a reorganization of local communities (Azzurro et al. 2011, Albouy et al. 2012). Sound predictions of the future composition and functioning of ecosystems are needed to inform stakeholders of potential climate change impacts (Mokany and Ferrier 2011, Nogués-Bravo and Rahbek 2011).

Species distribution models (SDM) are spatially explicit statistical models that can be used to describe biodiversity distribution and to make community-level forecasts. They commonly relate observations of species occurrence or

known environmental tolerance limits to abiotic variables (Araújo et al. 2011). By measuring the spatial translations of bioclimatic envelopes, SDMs allow the projection of species distribution shifts under different climate change scenarios (Cheung et al. 2009, Albouy et al. 2013 for marine fishes). Aggregating the results across species informs us of the future distribution of species richness (the 'predict first, assemble later' strategy; Ferrier and Guisan 2006). However, community structure is not only shaped by the abiotic environment but also by biotic interactions, such as competition, predation, parasitism, mutualism, or potential trophic cascade that rely on direct and indirect interactions (Gilman et al. 2010, Urban et al. 2012).

One challenge that marine ecologists are facing today is understanding how communities forming a complex interaction network will be reorganized following individual species responses to climate changes (Woodward et al. 2010). Spatial mismatch may separate previously interacting species (Schweiger et al. 2008), while novel interactions

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may appear due to new spatial co-occurrences (Gilman et al. 2010). Some species might migrate faster than others (Svenning et al. 2014), breaking the coherence of interaction networks. Consequently, understanding the food-web assembly remains crucial to predict the impacts of climate change on ecosystem functioning (Woodward et al. 2010). Nonetheless, only a few studies have considered the impact of climate change at the ecosystem-level (Woodward et al. 2010). Therefore, a major breakthrough is expected from the combination of predictive approaches expressing habitat selection processes and physiological limits of marine species and their trophic interactions.

Predicting which species will occur when and where and their potential interactions requires a priori knowledge of potential interactions among them (Morales-Castilla et al. 2015). Recently, Gravel et al. (2013) proposed a method to infer a 'metaweb', which represents potential interactions among all the taxa that are susceptible to co-occur in a given habitat. This method predicts the links between any pair of species with an allometric niche model based on the ubiquitous relationship between predator and prey body size (Brose et al. 2006). The rules are simple and drawn from the niche model of Williams and Martinez (2000). Each species has a niche position (the log of body size), an optimum (corresponding to the regression between log predator and prey size) and a feeding range around it. Such a model of the food web structure was found to closely match empirical data (Cattin et al. 2004, Dunne 2006, Allesina et al. 2008, Williams et al. 2010). The method has been applied at large spatial scales to infer a 'metaweb' describing potential trophic interactions among 256 fish species for the whole Mediterranean continental shelf (Albouy et al. 2014). Combined with SDMs, Albouy et al. (2014) investigated the potential effects of climate change on the fish food-web structure at a coarse spatial grain by calculating food-web descriptors under current and predicted climate conditions. They found that the number of feeding links between fish species and the generality (i.e. the mean number of prey species per predator species) was expected to decrease under climate change scenarios, and the connectance of the overall fish web would increase due to a differential loss rate of feeding links and species richness.

The next step in the development of such methods and scenarios is to downscale the analysis with the inclusion of local environmental constraints on species distribution (Hattab et al. 2014). This is particularly important in coastal areas where the species-habitat relationships are very structuring. For instance, habitat characteristics, such as seafloor type, strongly influence the distribution of marine species at small spatial scales (Moore et al. 2010, Hattab et al. 2013a). Therefore, because the local species diversity could vary in areas with high habitat heterogeneity, the integration of a habitat variable into SDM is crucial to provide a realistic prediction for conservation planning decisions when they are latterly used by environmental managers and stakeholders.

In this study, we forecasted the potential impacts of climate change on the food-web structure of local communities by coupling bioclimatic envelope and habitat models to an allometric niche food web model (Gravel et al. 2013). Our approach combines processes acting at regional (climate) and local scales (habitat selection and trophic interactions). We applied this approach to 60 exploited marine species of

the highly threatened Gulf of Gabes ecosystem located in the south of the Mediterranean Sea. Exploited species of this coastal region of Tunisia are strongly impacted by climate change, as previous studies showed that many species would experience a range shift (Albouy et al. 2013, Hattab et al. 2014). Our study highlights the potential impacts of climate change on the marine food-web structure at a fine spatial grain with potential deep consequences on ecosystem functioning.

Methods

Study area

The Gulf of Gabes, located in the southern Mediterranean Sea, covers the second-widest continental shelf area of this semi-enclosed sea. The Gulf is characterized by unique geomorphological, climatic, and oceanographic conditions that combine to support one of the most productive ecosystems in the Mediterranean Sea (Hattab et al. 2013b). The region has significant economic and ecological importance, supporting high fishery productivity and large *Posidonia oceanica* meadows. This particular ecosystem serves as a nursery, feeding site, and breeding ground for numerous fish and crustacean species. The fish production has gradually declined over the past 20 yr in the Gulf of Gabes, due to fishing pressure (Hattab et al. 2013b).

Actual and future species geographic distributions

Actual and future species distributions were generated using the multi-scale modeling approach proposed by Hattab et al. (2014). It is important to develop realistic SDMs across the range of climatic conditions in which a given species occurs (Thuiller et al. 2004). This is particularly critical for marine species, as climate is the main driver shaping their distributions at large spatial scales (Sunday et al. 2011, Jones et al. 2012). However, climate change effects on species' distributions are dependent on local-scale variables and, more particularly, those related to the habitat selection process (Heino et al. 2009), such as seafloor topography and seafloor type (Hattab et al. 2013a). Consequently, SDMs that do not account for species-habitat relationships may give unrealistic predictions at the local scale. Nevertheless, habitat variables are only well-described for small areas (Moore et al. 2010) and are generally not available over the full species range. The multi-scale modeling approach (Hattab et al. 2014) based on the concept of 'hierarchical filters' (Simpson 1953, Heino et al. 2009) was used to overcome these limitations. In this approach, SDMs were first built at a global extent to account for the full range of climatic conditions encountered by a given species. Second, habitat models were built using fine-grained habitat variables at a finer scale. Physical habitat (e.g. seafloor composition) represents the second filter for the studied species. We applied this modeling framework to the 60 most abundant and commercially exploited marine species of the Gulf of Gabes (fish, cephalopods and crustaceans; Supplementary material Appendix 1; Hattab et al. 2013b). The combined biomass of these species represents

86% of total biomass of surveyed species in the area (Hattab et al. 2013b).

Bioclimatic envelope modeling

The species presence data were obtained from global online databases: the Ocean Biogeographic Information System (OBIS; <www.iobis.org/>) and Global Biodiversity Information Facility (GBIF; <http://data.gbif.org>), all last accessed in 2013. Four derived metrics from sea surface temperature (SST) monthly climatologies (1982–2009) (annual maximum, minimum, mean and the annual range) and the sea surface salinity (SSS) climatologies (1961–2009) were used to model species bioclimatic envelopes (Supplementary material Appendix 2). Each variable was prepared on a 5 arc-min (ca 9.2 km) global grid. We used the regional oceanographic circulation model NEMOMED8 (Somot et al. 2006) to obtain the projected climatic data. This model predicted the SST and SSS based on water energy fluxes, river discharges and water exchanges with the surrounding seas (Beuvier et al. 2010). Based on the Intergovernmental Panel on Climate Change (IPCC) A2 scenario, NEMOMED8 predicted values for the SST and SSS anomalies until the end of the 21st century.

We modeled the species climatic envelope using an ensemble forecasting approach to account for uncertainty in the outcomes of different SDMs (Araújo and New 2007). Eight models, including generalized linear models (GLM), generalized additive models (GAM), general boosting method (GBM), classification tree analysis (CTA), artificial neural networks (ANN), flexible discriminant analysis (FDA), multivariate adaptive regression splines (MARS) and random forests (RF) were run individually. Analyses were implemented with the R BIOMOD package (Thuiller et al. 2009). The models integrated in BIOMOD required both presence and absence data. We generated pseudo absences to better characterize the set of environmental conditions that a species experiences within its current range (Barbet-Massin et al. 2012). We used the environmentally and geographically weighted methods based on both the suitability of area estimated using a presence-only model (Hirzel et al. 2002) and the distance from observations that were subsequently used as weights to allocate pseudo-absence points (see Hattab et al. 2013a for more details). The eight models were evaluated using a cross-validation procedure to avoid circularity when the same data were used to construct and evaluate the model. For each species, the models were calibrated using a random sample of the initial data (80%). Then, each model was evaluated on the remaining 20% of the dataset using the true skill statistic criterion (TSS; Allouche et al. 2006). This procedure was replicate 3 times (three-fold cross validation) and the contribution of each statistical model to the ensemble was based on the weighted average consensus (WAC) method to take into account model-based uncertainty (Marmion et al. 2009). We predicted the geographic location of the potential climatic niche for each species across the Gulf of Gabes using the projected temperatures and salinity for 2080–2099. Binary (presence/absence) outputs were generated from the current and projected probabilistic model outputs by selecting the threshold that maximized the TSS score (Thuiller et al. 2009).

Habitat modeling

Seafloor topography and seafloor type of the Gulf of Gabes were selected to develop habitat models for demersal and benthic species. These characteristics were captured by five habitat variables: seafloor type, depth, slope and aspect (describing two derived variables: the eastness and northness of the slope). Habitat data were obtained from the INSTM (National Inst. of Marine Sciences and Technologies, Tunisia) database (Supplementary material Appendix 2). Maps for each of the five variables were prepared using a 90-m grid resolution. The habitat models were built using the same methodology used for developing the SDMs (i.e. an ensemble forecasting approach using BIOMOD), an environmentally and geographically weighted method to simulate pseudo-absences, and a cross validation procedure and binary transformation using the TSS criterion.

Combining the models

Actual and future species geographic distributions at the scale of the Gulf of Gabes were derived by combining SDMs and habitat model predictions. To achieve this, the potential climatic niche maps were resampled to match the finer spatial resolution of the habitat models (i.e. a 90-m grid). A species was only considered present if, for any given cell, both the first filter (climate; SDM) and the second filter (seafloor type and topography; habitat model) predicted its presence (see Hattab et al. 2014 for more details).

Food-web modeling

Food-web data

A global interaction dataset was used to calibrate the allometric niche food web model (Barnes et al. 2008). This data set was composed of 34931 marine predator and prey interactions from 27 locations covering a wide range of environmental conditions from the tropics to the poles. The data set had 93 types of predators, with sizes ranging from 0.3 cm to over 309.69 cm, and 174 prey types, with sizes from 4.16 μm to over 122.66 cm. Each record included predator and prey scientific names, common names, taxa, life stages, sizes (length and mass with conversion details), and the type of feeding interaction. Interactions were compiled from published literature, and if the predator or prey length or mass were not measured in the original study, the length or mass was calculated using length–mass relationships (Barnes et al. 2008).

The allometric niche model was evaluated using an independent data set and conducted into a prey/predator matrix representing the trophic interaction between the set of 60 exploited marine species of the Gulf of Gabes (Hattab et al. 2013b). Feeding interactions between species indicated by either 1 or 0 (1 if species j eats species i and 0 if not) were mainly determined from the stomach contents where the input data originated from the Gulf of Gabes or adjacent areas. This validation dataset included 60 species, plus 2 compartments that represented the primary and secondary producers that contained 473 realized interactions among 3844 potential interactions (62×62).

Allometric niche modeling

We inferred interactions using the framework developed by Gravel et al. (2013) and applied at a Mediterranean scale by Albouy et al. (2014). This method was based on the niche model for food web structure (Williams and Martinez 2000). It considered that body size was the main niche axis structuring food webs and, therefore, the niche position n corresponded to the log of the body size (Colloca et al. 2010, Williams et al. 2010, Romanuk et al. 2011). The niche species-specific niche centroid 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 of the diet r was given by the 5 and 95% quantile regressions of this relationship. We calibrated the food-web model using the dataset from Barnes et al. (2008). The three parameters (n , c , r) were then interpolated for the 60 species of our study area. A species i fed on all prey species whose body size fell within the boundaries $c_i - r_i$ and $c_i + r_i$. Primary and secondary producers were assumed present at all locations and non-limiting on the whole Gulf of Gabes, and their parameters were fixed at $n = 0$, $c = 0$ and $r = 0$.

The model was subsequently evaluated by computing the TSS method using the expected metaweb and the validation dataset. We considered $TSS = (dg - ef) \times [(d + f) \times (e + g)]^{-1}$, where 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 links that were forbidden because of incompatible bathymetric constraints, and we re-computed the TSS.

Impact of climate change on food-web structure

We generated actual and future trophic networks for each of the 53 815 cells of the Gulf of Gabes based on actual and future species occurrences, respectively, and the metaweb describing potential trophic interactions among the 60 exploited species. A trophic interaction between species i and j was considered to happen locally if the two species were predicted to co-occur. We computed descriptors of the food-web structure for current and predicted fish communities: the number of species (S), the number of links (L), and the fraction of all that are realized in the network, called connectance ($C = L \times S^{-2}$), vulnerability (i.e. the mean number of consumer species per prey species), generality (i.e. the mean number of prey species per predator species) the averaged trophic level (Williams and Martinez 2004) and the average body size of assemblage. These indices were highlighted as important in terms of population stability and community structure (Petchey et al. 2010). Connectance is also known as a convenient summary metric because it strongly constrains several properties, such as modularity and nestedness (Poisot and Gravel 2014). The average path length was also computed to describe the number of interactions that an average unit of inflow passes before leaving the system (Finn 1976, Latham and Luke 2006). Thereafter, a mean trophic level was assigned to each cell of the grid. We classified all of the species into four

trophic guilds (Supplementary material Appendix 1) based on trophic levels and pathways: top predators (i.e. species having many prey and no predators), macro-carnivorous species (i.e. species that are prey for top predators and that feed mainly on macroscopic prey), forage species (i.e. species with trophic level lower than macro-carnivorous that are prey for a large number of species) and basal species (i.e. species feeding only on secondary producers). Finally, we computed and mapped the difference between the baseline and the future period 2080–2099 for each index of the food-web structure.

Results

Calibration of the metaweb

The relationship between predator and prey body sizes from the Gulf of Gabes was coherent with the relationship of the global dataset and occupied high positions on the niche axis (Fig. 1). This was due to the high trophic level of species considered in our study when compared with species from the global interaction dataset. Indeed, approximately 13% of the 60 exploited species fed directly on primary and secondary producers; the remaining 87% were forage species (33.36%), macro-carnivorous species (36.70%) and top predators (16.67%). We found a satisfying correspondence between the observed and modeled trophic interactions for the Gulf of Gabes ($TSS = 0.52$), indicating that our parameterization captured essential aspects of this food-web structure (Fig. 1, 2). The TSS increased to 0.63 once forbidden links due to bathymetric constraints were removed. This improvement was mainly due to the decrease of the e fraction (e reports predicted links with no observation) into the TSS calculation. The final metaweb has 929 links and a connectance of 0.24 (Table 1).

Mapping current food-web index

The indices of the food-web structure were mapped using the baseline climatic conditions (1982–2009) for each of the 53815 cells composing the Gulf of Gabes (Fig. 3). There were, on average, 34 species per cell ($SD = 11.43$) and 321 links ($SD = 184$). Not surprisingly, the spatial distribution of the link density closely followed the species richness (Fig. 3). On average, there were 11 predator species per prey species (vulnerability, $SD = 3.4$; Fig. 3) and 8 prey species per predator species (generality, $SD = 2.8$ Fig. 3). Within the community with the largest number of species and links, the vulnerability and generality reached maximum values. The mean connectance per community was 0.24 ($SD = 0.02$), with the highest values (0.28) for offshore communities (Fig. 3), where the trophic inflow passed through 2.7 compartments (i.e. the average path length) on average from primary producers to top predator (Fig. 3). The mean trophic level was 3.40 ($SD = 0.13$) and reached maximum values (3.62) for communities dominated by top predators and macro-carnivorous species, and where the percentage of basal species was low (Fig. 3).

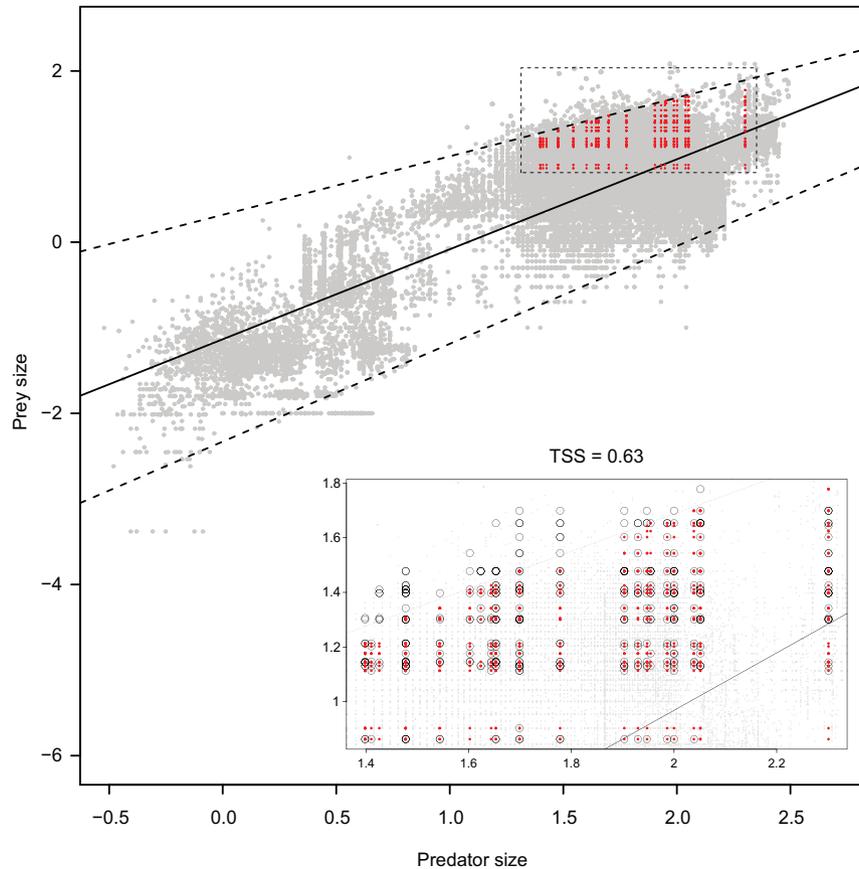


Figure 1. Relationship between prey and predator body size for the global interaction data set (Barnes et al. 2008). The black line represents the linear model between the log body size of predators and the log body size of prey. The two dotted lines represents the 5 and 95% quantile regressions of this relationship. The circles represent the observed links between the Gulf of Gabes prey and predator species, the red dots represent the links predicted by the allometric model. TSS represents the true skill statistic and assesses the proportion of prediction success relative to false predictions.

Projected changes in species composition and metaweb structure

According to NEMOMED8 model projections (using the IPCC A2 scenario), the mean SST was projected to be 2.42°C higher by the end of the century (2080–2099) in the Gulf of Gabes, while the mean SSS would increase by 0.7 practical salinity units (PSU; Supplementary material Appendix 3). Based on these future climate conditions, projections given by SDMs suggested that 34 of the 60 exploited coastal species would experience a range shift, and 14 species were projected to lose climatically suitable areas by the end of the 21st century in the Gulf of Gabes (Fig. 2). Therefore, 414 potential trophic links could be lost in the projected metaweb following the extinction of 14 species (Fig. 2, Table 1), resulting in a decrease of connectance, prey-averaged trophic level, vulnerability and generality and an increase in the average path length (Table 1).

Mapping projected food-web index

The SDMs predicted, on average, 13 species lost per cell (SD = 5.38; Fig. 4). The widespread decrease of local species richness would be followed by a decrease in the number

of links, with an average reduction of 210 links (SD = 123; Fig. 4) between the two time periods. The decreasing number of links would follow the same rate as the loss of species richness, resulting in an average decrease of connectance of only 0.01 (SD = 0.017; Fig. 4). The reduction in the number of link would be slower than species richness for 18% of the cells, corresponding to the ones where the connectance is expected to increase (Fig. 4). The decrease in species richness also resulted in a reduction of vulnerability and generality across the Gulf, where, on average, 5.3 (SD = 2.00) predator species per prey species and 3.6 (SD = 1.40) predator species per prey species would disappear (Fig. 4). The whole Gulf would experience a decrease in the mean trophic level of 0.19 (SD = 0.10; Fig. 4) and the average body size of assemblage of 4.8 cm (SD = 5.33; Fig. 4). This may result from the decrease of the percentage of top predator and forage species (by 6 and 10% on average, respectively) and the increase of the percentage of basal and macro-carnivorous species (by 8 and 6% on average, respectively) within communities (Fig. 4). The modification of the trophic guild structure would also result in an increase of the average path length for 96% of the communities, with an average increase of 0.1 (SD = 0.060; Fig. 4).

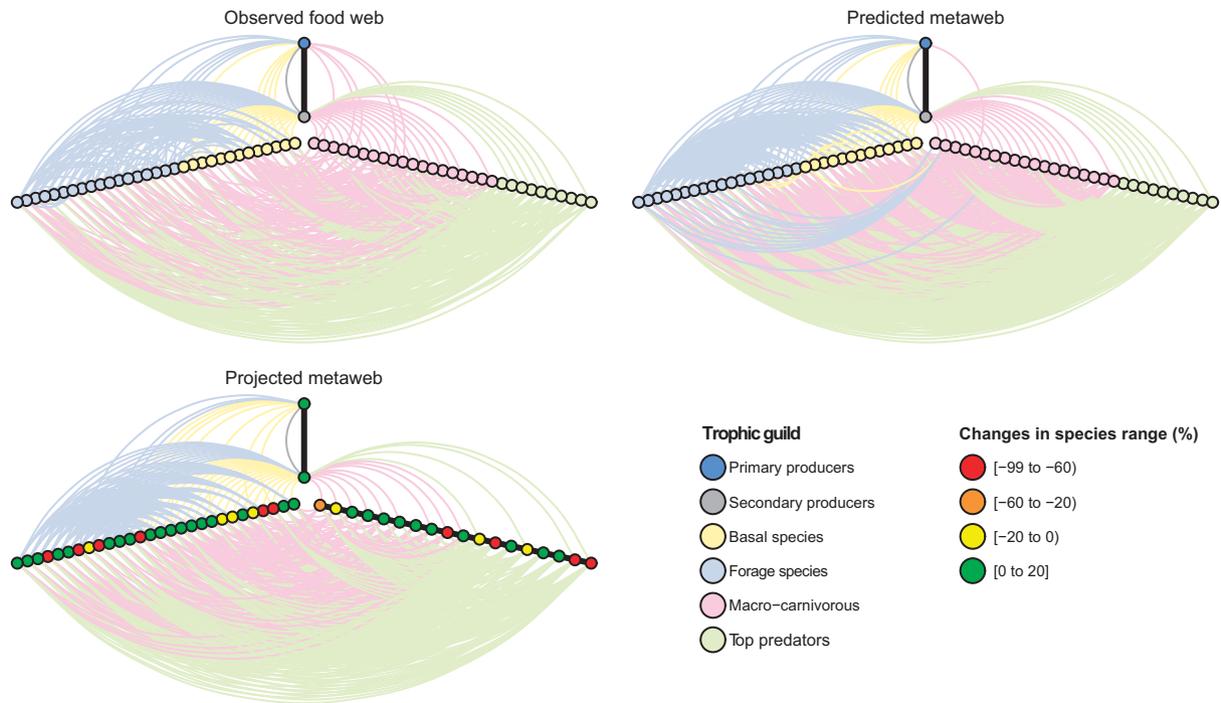


Figure 2. A hive plot representation of the observed food web in the Gulf of Gabes and the predicted and projected metabweb. In this network layout, the curved edges represent the feeding interactions. The 62 species (represented by nodes) were placed on radially oriented linear axes (representing 6 different trophic guilds) according to their prey-averaged trophic levels. Hive plots can be directly compared to demonstrate differences between networks because they have a fixed coordinate system (Krzywinski et al. 2012).

Discussion

The assumption that communities are a simple collection of independent species represents a major gap in the field of species distribution modeling (Wiszniewski et al. 2013). For instance, recent studies highlighted the need to incorporate biotic interactions when forecasting community changes under climate change (Pellissier et al. 2013, Albouy et al. 2014). In the present study, we tackled this issue by combining the hierarchical approach proposed by Hattab et al. (2014) and the one proposed by Gravel et al. (2013) in which body size is used to infer trophic interactions between species that had not previously co-occurred. Coupling these two approaches allowed assessing the potential impacts of climate on coastal marine communities at a fine spatial resolution (90 m), hence refining the projections of biodiversity modification under climate change (see Supplementary material Appendix 4 for comparison). Accomplishing this task has important implications since the field of species distribution modeling is used to support decision making for

conservation purposes (Guisan et al. 2013). For instance, the selection of sites to design a robust network of marine protected areas (MPAs) requests the inclusion of multiple source of knowledge at a local scale, and consequently coarse-scale projections of biodiversity change (Albouy et al. 2013) are not specific enough to be used by marine resource managers. By mapping projected food-web index at a fine spatial resolution, we were able to highlight some future areas that are likely to be robust to species loss and where the food-web index showed the lowest variation, such as the area located between the coastline and the 10 m isobaths (Fig. 4).

An allometric niche food web model was used in this study to predict a metabweb that describes potential trophic interactions on the entire study area. The diet of a given species at local scale (cell) was constrained by the expected actual and future community composition. Then, the model allowed predators to adapt their choice of prey in response to the changing population body size structure. Therefore, this model describes the opportunistic predation and the adaptive flexibility of the feeding behavior of marine species, which play an important role in defining the food web dynamics (Dill 1983, Trenkel et al. 2005). Predation by marine fish is often described as opportunistic, with constraints imposed by the local prey availability and predator-prey size ratios (Jennings et al. 2002, Woodward et al. 2005, Ménard et al. 2006) which explains the great diversity of prey species in the fish diet (Thompson et al. 2007). As a consequence, marine ecosystems will be characterized by highly connected food webs, with a multitude of weak predator-prey linkages and a great trophic omnivory (Trenkel et al. 2005, Thompson et al. 2007), as was the case of the Gulf of Gabes food web.

Table 1. Food web structural indicators calculated for the Gulf of Gabes observed food web and the predicted and projected metabweb. S is the number of species, L is the number of links, C is the connectance value, MTL is the mean trophic level at the community scale, APL is average path length, Gen is the generality value that represents the mean number of prey by predator, and Vul is the vulnerability that represents the mean number of predator by prey.

	S	L	C	MTL	APL	Vul	Gen
Observed	62	473	0.12	3.62	2.50	9.09	7.75
Predicted metabweb	62	929	0.24	3.53	2.46	18.58	15.22
Projected metabweb	48	515	0.22	3.44	2.50	12.87	10.95

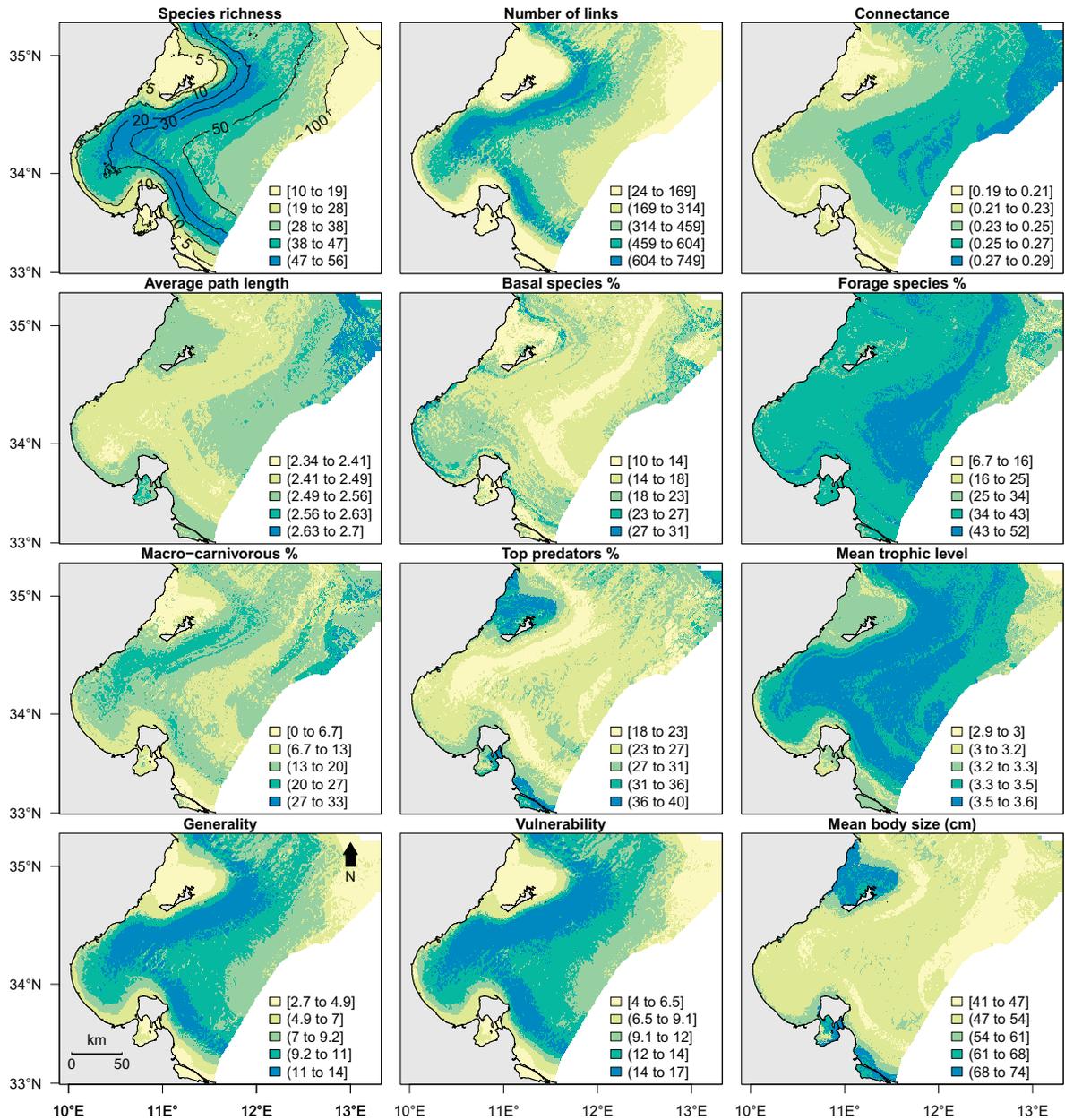


Figure 3. Maps of species richness, number of links, connectance, average path length, percentage of basal forage, macro-carnivorous and top predator species per community, mean trophic level generality vulnerability and the average body size of assemblage, values for the baseline scenario (1982–2009) in the Gulf of Gabes. Solid gray lines indicate the 5, 10, 20, 30, 50 and 100 m isobaths.

Our results suggested that the projected climate change under the A2 scenario would markedly modify the structure of local food webs in the Gulf of Gabes. By the end of the 21st century, the mean fish body size of communities and the number of links were projected to decrease, hence resulting in a decrease of connectance, generality, vulnerability and mean trophic level and an increase of the average path length. These results were broadly in accordance with those reported in a previous study considering the whole Mediterranean Sea (Albouy et al. 2013). The projected decrease of the mean trophic level at the community scale resulted from the decrease of number of top-predators and forage species (by 6 and 10% on average, respectively) and the increase of number of basal and macro-carnivorous

species within communities (by 8 and 6% on average, respectively). The projected increase of the average path length resulted from the loss of connections between top predators and forage species, which may cause a reduction in the possibilities of trophic flow transfer through short pathways. The Gulf of Gabes exploited assemblages may have less prey (generality) and less predator species (vulnerability) by the end of the 21st century, which may further enhance their extinction probability. Indeed, the loss of top predators and indirect effects of meso-predator release and trophic cascades have resulted in widespread trophic downgrading of ecosystems (Heupel et al. 2014). Lastly, the decrease of connectance may negatively affect the food webs' robustness to perturbation, which may lead to species extinction. The

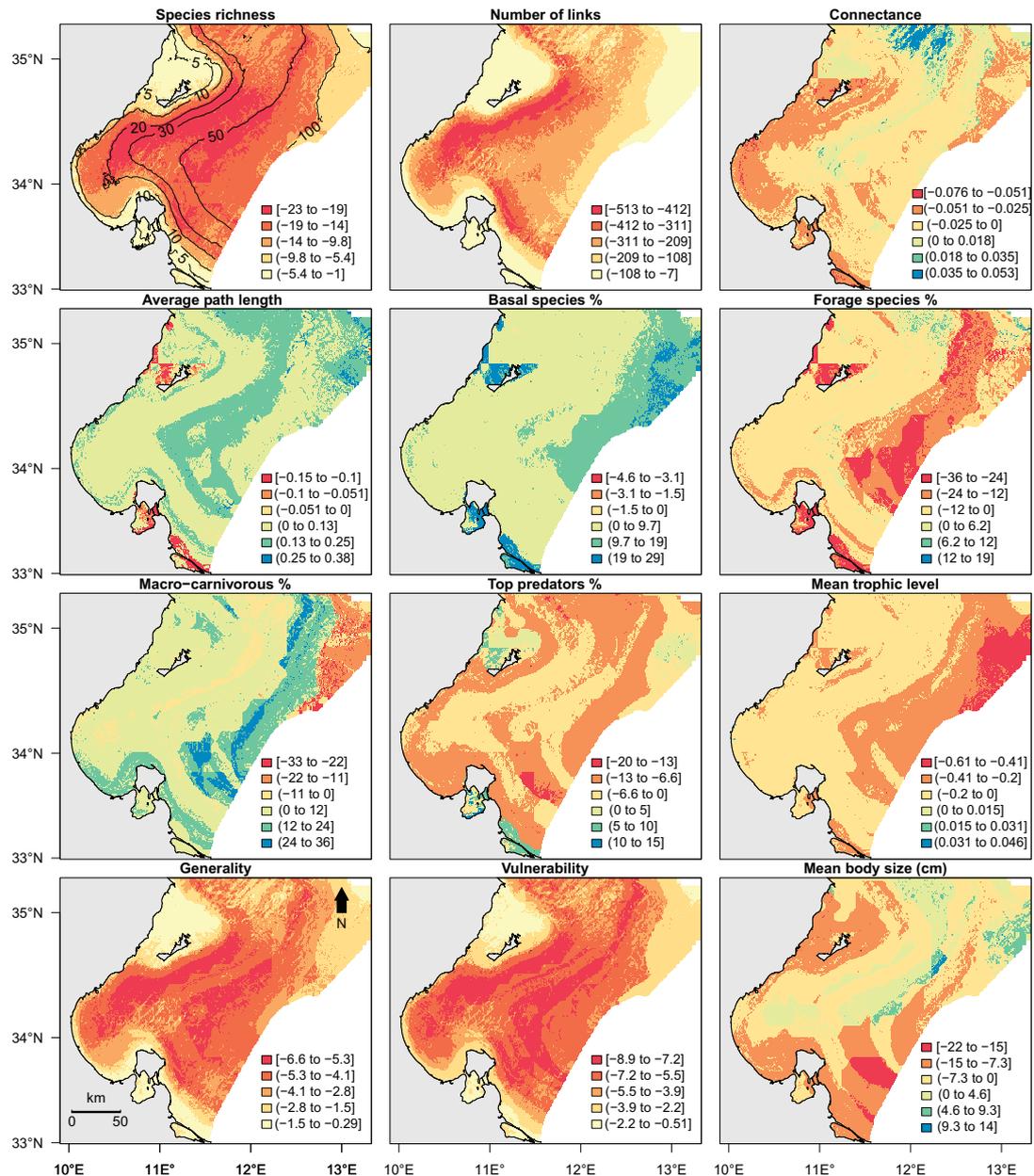


Figure 4. Differences in species richness, number of links, connectance, average path length, percentage of basal, forage, macro-carnivorous and top predator species per community, mean trophic level, generality, vulnerability and the average body size of assemblage, values in the Gulf of Gabes between the baseline scenario (1982–2009) and the end of the 21st century scenario (2080–2099). Solid gray lines indicate the 5, 10, 20, 30, 50 and 100 m isobaths.

connectance is indeed a global topological measure of the complexity of food webs that measures the ‘interaction richness’ of a network (Estrada 2007), and was positively related to food web robustness (Dunne et al. 2002, 2004). Food webs with high connectance would tend to be more robust to species loss than one with low connectance. In addition, a network quantified by high connectance and low path length may also rapidly disperse strong effects throughout marine food webs, thus decreasing the overall impact of any particular fluctuation (Dunne et al. 2004). Accordingly, the decrease of connectance and the increase of the average path length projected in the Gulf of Gabes may negatively influence the structural robustness of future networks. However, contrary to the general trend, some communities located in

the northern part of the Gulf of Gabes would experience an increase in connectance. This situation is expected to occur when the rate of realized species richness could decrease faster than feeding links. The increasing prevalence of forage species within these communities has resulted in a more important ratio between observed and projected species richness than the ratio between observed and projected number of links, thus producing more connected communities.

It is well known that the food-web structure can influence ecosystem functioning (Thompson et al. 2012, Saint-Béat et al. 2015) and, consequently, the predicted changes in food web structural components may have several implications. For instance, as top-down control should be weakened following the loss of top predator species, climate

change may induce trophic cascades where the loss of species (in particular, large ones) has alternating positive and negative effects on the trophic levels below (Estes et al. 2011). These trophic cascades generally structure biomass distributions across populations in different ecosystem types (Borer et al. 2005, Brose et al. 2012). Indeed, the loss of large-bodied species in food webs may cause secondary-extinction avalanches (Binzer et al. 2011, Curtsdotter et al. 2011, Brose et al. 2012). However, these implications should be viewed with caution. Here, we examined the food web as its structural components and we did not consider the strength of the interactions. It is now known that the strength of the interactions between predators and their prey may constrain the energy flow through the food webs (Thompson et al. 2012) and strongly determine the stability of ecological communities (Bascompte and Stouffer 2009).

Achieving a mechanistic understanding of how the location of species within a network relate to their functional role and how ecosystem structure relates to ecosystem functioning is necessary for estimating the impacts of species loss and invasion and for managing ecosystems for ecosystem services (Thompson et al. 2012). Investigating this relation requires the implementation of dynamic food-web models with fluxes of materials between species. Incorporating these complexities into food-web models will be challenging, but there are clear avenues for future research (Thompson et al. 2012). For instance, rates of energy flows can be predicted using allometric scaling relationships, such as metabolic and feeding rates with body sizes (Woodward et al. 2005). Extending these simple physiological relationships for individual animals to the community level can be achieved using a 'size spectrum' modeling framework (Hartvig et al. 2011, Brose et al. 2012). This framework allows food web models to integrate ontogenetic growth and life-history omnivory at the individual level (Hartvig et al. 2011, Thompson et al. 2012). The allometric niche model presented in this study could be used to specify the structure of food webs at the cell scale within a size spectrum modeling framework. Therefore, by integrating processes at the level of individuals, the interaction strengths among individuals can be predicted through the size-dependent food selection and the population dynamics. For instance, Fernandes et al. (2013) developed a modeling approach based on similar concepts by combining a species-based dynamic bioclimate envelope model (DBEM; Cheung et al. 2008a, b, 2009, 2011) and a size based trophic model. The DBEM projects changes in marine species distribution, abundance and body size with the explicit consideration of population dynamics, dispersal (larval and adult) and ecophysiology (Cheung et al. 2008a, b, 2009, 2011, 2013). The size spectrum was used to determine resource limits in a given geographical area, and these limits, along with habitat suitability for a given species, determine the biomass of that species that can be supported in this area. However, Fernandes et al. (2013) combined the DBEM with a size spectrum model to predict spatial and temporal changes in species' abundance and distribution in response to predicted future changes and not to investigate their impact on the structure and functioning of food webs.

Despite the challenge posed by the complexity of food webs in marine ecosystems, the allometric niche model captured a number of structural food web properties in the Gulf

of Gabes, and it was able to predict the independent validation data set as suggested by the TSS value of 0.63. However, although the TSS value reflected a good fit between the predictions and the independent validation data set (Landis and Koch 1977), the e component reporting predicted links with no observation was high. This can be explained by the fact that the diet composition derived from the stomach contents analysis may be affected by the sampling effort both in space and time in the local study (Bascompte and Stouffer 2009). As a result, the allometric niche model may make predictions that have not yet been confirmed by the stomach content analysis. To a lesser extent, the model may predict the absence of links while they are observed, and this can be explained by the fact that ecomorphological traits broadly predict the belonging of species to trophic guild, but fail to exactly reproduced fish diet due to potential versatility in the food acquisition (Albouy et al. 2011). Moreover with our approach we well predicted 83% of the observed feeding link but we probably miss some behavioural differences based on other life history traits like differences in activity periods (e.g. night active vs day active).

Despite the temptation to infer the structure of the entire food web, it is important to note that the change in the food web structure predicted in this study related to only an isolated block of the overall food web. Therefore, the next step to our approach will be to explicitly incorporate secondary producers and low trophic levels into the model by modeling their current and future geographical ranges. Moreover, it will be important to simulate the colonization of species coming from the Red Sea or from the Atlantic Ocean, given that species invasions may affect both the structure and the functioning of the ecosystem under climatic change (Edelist et al. 2013, Fanelli et al. 2015). For instance, Edelist et al. (2013) showed that the abundance and biomass of exotic fish in shallow waters of the Levantine have doubled in just two decades. However, as demonstrated by Libralato et al. (2015), in the north of the Mediterranean Sea, the consequences of invasion by exotic species on the structure or functioning of an ecosystem is not trivial and is difficult to forecast.

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Supplementary material (Appendix ECOG-01937 at <www.ecography.org/appendix/ecog-01937>). Appendix 1–4.