

# Tropical rabbitfish and the deforestation of a warming temperate sea

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## Summary

1. A striking example of climate-mediated range shifts in marine systems is the intrusion of tropical species into temperate areas world-wide, but we know very little about the ecological consequences of these range expansions.

2. In the Mediterranean Sea, the range expansion of tropical rabbitfishes that first entered the basin via the Suez Canal provides a good example of how tropical herbivorous fish can impact the structure of rocky bottoms in temperate seas. Two species of rabbitfishes have now become a dominant component of total fish biomass in the southernmost part of the eastern Mediterranean. Experimental evidence shows these species can profoundly transform benthic communities, turning algal forests into 'barrens', but the specific mechanisms that facilitate this shift have not been established.

3. We surveyed ~1000 km of coastline in the eastern Mediterranean and identified two clearly distinct areas, a warmer group of regions with abundant tropical rabbitfish and a colder group of regions where these consumers were absent/ extremely rare. In regions with abundant rabbitfish, canopy algae were 65% less abundant, and there was a 60% reduction of overall benthic biomass (algae and invertebrates) and a 40% decrease in total species richness.

4. Video-recorded feeding experiments showed that the extensive barrens characteristic of regions with abundant rabbitfish were not due to greater rates of herbivory by these tropical consumers, but rather by functional differences among the herbivores. Temperate herbivorous fish displayed the greatest macroalgae consumption rates overall, but they fed exclusively on established adult macroalgae. In contrast, in regions with abundant rabbitfishes, these consumers fed complementarily on both established macroalgae and on the epilithic algal matrix, which typically contains macroalgal recruits.

5. *Synthesis.* Range-shifting tropical rabbitfish can severely reduce the biomass and biodiversity of temperate reefs at a scale of hundreds of kilometres. A shift from macroalgal dominance to barrens is mediated by the addition of functionally diverse herbivores that characterize tropical reefs. This work highlights the importance of assessing the functional traits of range-shifting species to determine potential mechanisms of impact on ecological communities.

**Key-words:** climate change, eastern Mediterranean, functional diversity, marine herbivory, phase shift, plant–herbivore interactions, tropicalization

## Introduction

As climate change forces the movement of isotherms over space and seasons (Burrows *et al.* 2011; Sen Gupta *et al.*

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2014), species are responding by shifting their phenology and distributions and these are now two of the most widely documented biological responses to a changing climate (Parmesan 2006; Poloczanska *et al.* 2013). Despite widespread shifts in the distribution of species, we know little about the ecological impacts of these movements (Gilman *et al.* 2010; Bates *et al.* 2014).

A changing climate can extensively shift ecological communities by altering the strength and stability of trophic interactions (Gilbert *et al.* 2014). Climate-mediated changes in the distribution of species can facilitate new species interactions, which can in turn alter ecosystem structure (Vergés *et al.* 2014). In particular, climate-driven changes in trophic interactions can severely impact entire communities when consumers are affected, as communities do not respond to climatic changes as discrete entities, and higher trophic levels tend to be more sensitive to climatic change (Voigt *et al.* 2003). Effects on one trophic level can thus trigger knock-on effects on other levels and act as ‘biotic multipliers of climate change’ (Zarnetske, Skelly & Urban 2012).

Marine communities are likely to be especially vulnerable to the effects of climate-driven shifts in species ranges. Rates of spread are over a magnitude greater in the sea than on land (Sorte, Williams & Carlton 2010; Poloczanska *et al.* 2013), and marine communities are also thought to be more strongly regulated by consumers – that is by top down forces – than terrestrial communities (Shurin *et al.* 2002). Plant–herbivore interactions in particular are remarkably intense in marine environments, with roughly 70% of primary production being consumed by herbivores (Poore *et al.* 2012), compared to only ca. 20% in terrestrial systems (Cyr & Pace 1993). Given the importance of plant–herbivore interactions in structuring marine systems, range shifts of marine herbivores are of particular concern as these may severely impact ecosystems (Vergés *et al.* 2014). For instance, the climate-driven expansion of the herbivorous sea urchin *Centrostephanus rodgersii* from mainland Australia into Tasmanian waters has led to catastrophic overgrazing of large areas of kelp forests and the loss of ~150 taxa associated with these seaweeds (Ling 2008). However, such range expansions may have even greater consequences if (i) they involve vertebrate consumers such as fishes, since they typically have higher consumption rates and greater mobility than invertebrates (Bruno *et al.* 2005), and (ii) species move between tropical and temperate systems, because of the potential disparity in the ecological and evolutionary processes that have shaped interactions in these different regions (Vergés *et al.* 2014).

Here, we quantify the spatial extent and ecological impacts of the expansion of tropical herbivorous fishes into a temperate sea. The climate-mediated intrusion of tropical fishes into temperate areas is now occurring in several places globally where ocean currents push tropical warm water into temperate regions (Vergés *et al.* 2014). This includes southern Japan (Yamaguchi 2010), eastern and western Australia (Figueira & Booth 2010; Wernberg *et al.* 2013), the Atlantic coast of North America (Fodrie *et al.* 2010), and south-eastern Africa (Lloyd *et al.* 2012). In most of these systems, only the first signs of a

‘tropicalization’ of fish communities have been observed, as indicated by the presence of adults and/or successful overwintering of tropical recruits (Figueira & Booth 2010). However, in the eastern Mediterranean, two species of tropical herbivorous rabbitfish (*Siganus luridus* and *S. rivulatus*) already make up a substantial proportion of fish abundance in some areas (between 5% and 45%; Harmelin-Vivien *et al.* 2005). Moreover, experimental evidence using fish exclusion cages demonstrates that these herbivorous fishes can shift structurally complex benthic communities dominated by canopy-forming macroalgae into barrens (Sala *et al.* 2011). The most common canopy-forming algae in the Mediterranean Sea are members of the order Fucales (*Cystoseira* spp., *Sargassum* spp.). While being small in size (length usually shorter than 0.4 metres), canopies of these species provide a complex biological structure that favours the development of other functional groups of algae and invertebrates. They are also critical for settlement and the juvenile stages of a wide array of fish (Cheminée *et al.* 2013).

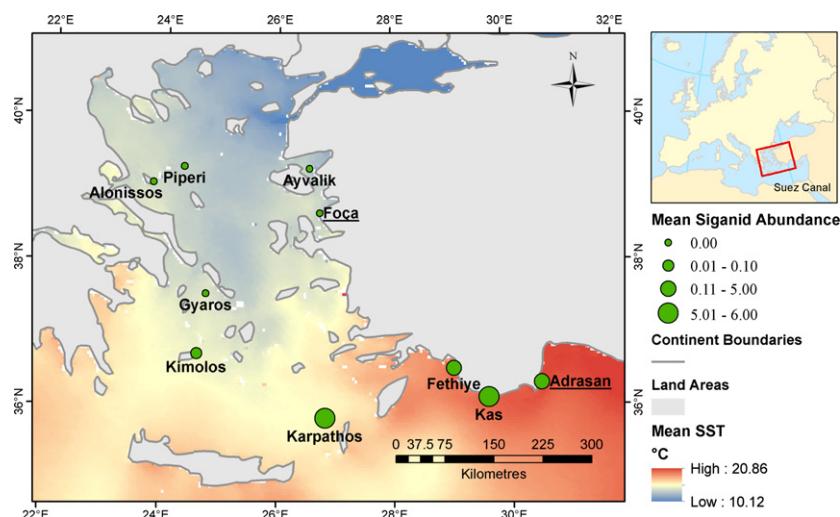
The range expansion of tropical fish into the Mediterranean was initially facilitated by the opening of the Suez Canal in 1869, enabling a process largely driven by ocean currents elsewhere and providing an exceptional opportunity to assess the ecological impacts of the range expansion of tropical consumers into a temperate system. *Siganus rivulatus* was first reported in the eastern Mediterranean in 1927, while *S. luridus* appeared in 1956. Since their initial introduction, the distribution of both species has expanded westwards (Azzurro & Andaloro 2004; Daniel *et al.* 2009), with temperature widely considered the main factor facilitating the spread of these species (Rilov & Galil 2009; Golani 2010; Bianchi *et al.* In press).

In this study, we measured spatial changes in the community composition and structure of eastern Mediterranean temperate rocky reefs along 1000 km of coastline that encompass major changes in the relative abundance of tropical herbivorous rabbitfish. Further, we obtained sea surface temperature (SST) measurements from these regions using satellite data and related it to rabbitfish abundance. Finally, we used underwater video assays to determine whether higher rates of herbivory or differences in feeding choices by tropical rabbitfishes are behind the creation of barrens as identified by Sala *et al.* (2011). Specifically, we asked: (i) How is rabbitfish abundance related to SST? (ii) How do regions with/without tropical rabbitfishes compare in community structure, benthic biomass and species richness? (iii) Is the overall consumption rate and feeding efficiency of tropical rabbitfish higher than that of temperate herbivorous fishes? (iv) Do tropical rabbitfish and temperate herbivorous fish differ in their feeding choices?

## Materials and methods

### SPATIAL VARIATION IN SST, RABBITFISH ABUNDANCE AND BENTHIC COMMUNITY COMPOSITION

This study took place across nine regions covering ~1000 km of coastline along the coasts of Turkey and Greece (Fig. 1). Regions



**Fig. 1.** Map of the regions studied displaying regional patterns in SST and abundance of tropical rabbitfish. We sampled six sites spaced at least 1 km from each other within each region (except in the small island of Piperi, where sites were spaced at least 0.8 km). Green bubble symbols correspond to biomass of *Siganus luridus* and *S. rivulatus*, red and blue colours represent warmer and colder water, respectively, as per Figure legend. Feeding experiments were undertaken in the regions that are underlined (Adrasan and Foça). For interpretation of the references to colour in this Figure legend, the reader is referred to the web version of this article.

were between 100 and 300 km apart. Within each region, six sites spaced at least 1 km from each other were sampled (except in the small island of Piperi, where sites were spaced at least 0.8 km). SCUBA surveys were conducted in May–June 2008 on shallow rocky reefs of similar slope and exposure between 8 and 12 m depth.

Measurements of mean sea surface temperature (SST) were taken from satellite data. Mean values for each region were obtained from an 8-year time series [from July 2002 to June 2010; as per (Sala *et al.* 2012)]. SST was derived from the Pathfinder Version 5 Advanced Very High Resolution Radiometer (AVHRR) data set provided by the Moderate-resolution Imaging Spectrometer (MODIS) carried aboard NASA's Aqua spacecraft.

Fish communities were sampled using underwater visual censuses. At each site, we conducted 3  $25 \times 5 \text{ m}^2$  transects measuring the size (in 2 cm increments of total length, TL) and abundance of all fish. Surveys were conducted between ~10 and 15 h at all sites. Fish biomass ( $\text{g wet mass m}^{-2}$ ) was estimated from size data using length–weight relationships from available literature and data bases, and each taxon was assigned to one of five trophic groups: herbivores, detritivores, planktivores, carnivores and top predators (full list of species detailed in Table S1).

Biomass of benthic algae and sessile invertebrates were sampled using 4 replicate  $20 \times 20 \text{ cm}^2$  quadrats at each locality (full list of species detailed in Table S1). Non-encrusting algae and invertebrates were scraped off and placed in an individual bag, and cover of encrusting algae (as % of the quadrat) was then estimated. Erect macroalgae and invertebrates were sorted to species in the laboratory and weighed ( $\pm 0.1 \text{ g}$ ). Turf algae were identified and weighed as individual species when possible, or they were weighed as a group. Biomass of encrusting algae and invertebrates were estimated by transforming cover data using conversion rates from the literature (see Table S1). Benthic biomass was estimated for each locality as the sum of the four quadrats (i.e.  $1600 \text{ cm}^2$ ), was expressed as g wet mass and was grouped into the following categories: erect algae (e.g. Fucales, Dictyotales), turf algae, encrusting algae (e.g. *Neogoniolithon*, *Hildenbrandia*) and invertebrates (see Table S1). The abundance of sea urchins was estimated from thirty haphazardly placed  $50 \times 50 \text{ cm}^2$  quadrats at each locality.

We used the mapping software ArcGIS to display spatial patterns in SST and rabbitfish abundance (Fig. 1). Differences in SST along the nine studied regions were tested using a one-way ANOVA with the mean SST values for each year between 2002 and 2010 as replicates.

Linear regressions were conducted to examine the relationship between the abundance of range-shifting tropical herbivorous fish (mean value per study region) and SST.

We quantified differences in the abundance of tropical rabbitfishes (*Siganus* spp.) along the nine studied regions using one-way ANOVAS, with the six sites within each region (fixed factor) used as replicates. Post hoc pairwise comparisons identified two distinct groups of regions regarding rabbitfish abundance, one where they were absent or extremely rare (mean biomass: 0 and  $0.06 \text{ g m}^{-2}$ ) and another where they were very abundant (mean biomass: 1.6 and  $2.8 \text{ g m}^{-2}$ ; see Results). Differences in benthic biomass, abundance of different fish trophic groups and taxon richness were subsequently analysed in relation to these two levels of rabbitfish abundance using two-factor nested ANOVAS (fixed factor 'Rabbitfish abundance', and Region (random factor) nested within 'Rabbitfish abundance', sites were replicates).

## FEEDING ASSAYS

To quantify feeding habits of temperate and tropical herbivorous fishes, in May 2011, we conducted feeding preference and tethering experiments *in situ* in two regions, one characterized by great densities of rabbitfishes (Adrasan) and the other where rabbitfishes were absent (Foça) (underlined regions in Fig. 1). Abundance of herbivorous fish and benthic community composition in Foça was very similar to that of Ayvalik (results not shown).

In the feeding preference assays, we offered a choice between four dominant canopy-forming macrophytes: three brown algae *Cystoseira barbatula* Kützinger, *Cystoseira compressa* (Esper) Gerloff & Nizamuddin var. *compressa* [hereafter referred to as *C. compressa*], *Sargassum vulgare* C. Agardh and the seagrass *Posidonia oceanica* (L.) Delile. These taxa were selected because they represent dominant macrophytes and constitute habitat-forming species in the eastern Mediterranean (Den Hartog 1970; Haritonidis & Tsekos 1974; Tsekos & Haritonidis 1974; Montesanto & Panayotidis 2011). The distribution of the three brown algae is mostly restricted to shallow waters (0–2 m depth), whereas the seagrass *P. oceanica* is found between 1 and 45 m. Seagrass shoots used in the assays were collected from shallow (8–15 m) meadows. We set up the experiments in shallow (~5–10 m depth) patches naturally clear of dominant macrophytes and characterized by a cover of EAM (epilithic algal matrix, sensu Wilson *et al.* 2003), and feeding on this surrounding EAM was also quantified.

We tied individuals of the four macrophytes to a rope that was weighed down at either end using lead pieces. In each replicate assay, we offered a choice of individual thalli (algae) or a shoot (seagrass) of similar initial biomass (3–12 g). At each region, we deployed five to eight replicate assays over four consecutive days ( $n_{\text{Temperate}} = 29$ ;  $n_{\text{Tropicalized}} = 32$ ). To maximize independence among replicates, we separated individual replicate assays by at least 5 m, and we positioned replicates in a different location every day within a large area encompassing approximately 2500 m<sup>2</sup>. Each replicate assay consisted of the weighted rope with the four tethered macrophyte species freely available to consumers and a paired assay that was similar in every respect except that it was protected from herbivores in triangular prism-shaped cages (8000 cm<sup>3</sup>; 2.25 cm<sup>2</sup> mesh size), to control for any biomass changes not due to herbivory [e.g. handling losses and algal detachment due to water movement, (Prince, LeBlanc & Maciá 2004)]. We deployed assays over 5–8 h, between 9 am and 6 pm, recording exact deployment time to calculate consumption per hour. We pad-dried macrophytes of excess water and measured fresh weight (to the nearest 0.1 g) before and after deployment. For each species, we calculated biomass loss due to herbivory by pairing individual treatment and control specimens (Prince, LeBlanc & Maciá 2004) and subtracting the change in biomass of the treatment specimen from the change in biomass of the control specimen (uncaged–caged). Average biomass changes in control specimens of each species were always < 2% of initial weight. Video footage verified that only fish accessed the macrophyte assays. We added up the biomass loss of the four different taxa in each replicate to compare total macrophyte consumption between the region with/ without rabbitfish (Adrasan and Foça, respectively). We analysed patterns in total consumption of macrophytes (combined biomass consumed of all four species offered in the bioassays) using a two-factor nested ANOVA with ‘Rabbitfish abundance’ as a fixed factor and Days as a random factor nested within ‘Rabbitfish abundance’ (four levels). Differences in biomass consumed of the four macrophytes within each region were analysed separately using Hotelling’s multivariate  $T^2$  test as outlined by Manly (1993), incorporating the suggestions by Prince, LeBlanc & Maciá (2004) of pairing treatment and control replicates in close proximity.

To examine spatial variation in fish feeding patterns within each region, we set up additional feeding assays (tethering experiments) in three different sites within each region (Fig. S1). Sites were chosen haphazardly on the basis of similar wave exposure and slope. Individual thalli (algae) and shoots (seagrass) of each species ( $n = 20$ ) were tied to metal pegs and deployed on the rocky seabed (between 5 and 10 m depth). All individuals used in the assays had no obvious signs of herbivory initially (i.e. no bite marks), and we used individuals of roughly the same size for each species, avoiding particularly small or large individuals. Individual macrophytes were deployed independently and haphazardly on the seabed, that is specimens were not deployed in groups of four species as in the previous assays. A minimum distance of at least 3 m was kept between individual thalli/shoots. At the end of the deployment, thalli/shoots were classified into five categories according to how much consumption was apparent: 0% consumed (no obvious bite marks), 25%, 50%, 75% and 100% consumed (latter category used when only a cable tie and a minimum amount of alga/ seagrass remained). In Foça, all individual macrophytes were collected and transported back to the laboratory after 6 h, as a visual inspection of the tethers indicated that substantial consumption had occurred by then and we wanted to avoid consumption of all available material (as that would not give us an indication of what species were consumed first). In contrast, in Adrasan, very little herbivory was observed after 6 h, and assays were

instead left out for 24 h, when overall total levels consumption were roughly similar to those observed in Foça. To compare consumption rates across regions, consumption data (% consumed) was standardized per hour. In these assays, some of the original replicate pegs were lost, leading to an unbalanced data set (final  $n$  ranged from 15 to 20, depending on species and site). These data were analysed using a three-way univariate ANOVA with Region as a fixed factor, Site as a random factor nested within Region and Macrophyte species as a fixed orthogonal factor.

In addition, we used underwater video cameras to film four of the feeding preference assays deployed each day to quantify macrophyte consumption patterns of individual fish species. On each filmed replicate, we counted the total number of bites taken by individual fish species on each macrophyte and on the EAM immediately surrounding the assays. Forays, where rapid consecutive bites by an individual fish took place without a discernable pause, were conservatively classed as a single bite (Bellwood & Choat 1990). We used bite rate data obtained from the video footage to analyse the feeding preferences of individual fish species. For each herbivorous fish species, we analysed differences in bite rates on the four macrophytes using Hotelling’s multivariate  $T^2$  test following the methods outlined by Prince, LeBlanc & Maciá (2004). Replicates where a given fish species was not observed feeding were excluded from the analysis. When an overall significant result was found using Hotelling’s test, we used post hoc pairwise comparisons by constructing confidence intervals as outlined in Roa (Roa 1992). Where necessary, data were log-transformed to comply with parametric test assumptions. Hotelling’s  $T^2$  test and post hoc tests were performed using R 2.9.0 software (R\_Development\_Core\_Team 2009).

We used replicates where a single fish species was responsible for all consumption of a given macrophyte to determine the macrophyte biomass consumed per bite of individual fish species (biomass loss/ number of bites, hereafter referred to as ‘bite impact’). From the data collected, we were able to analyse (i) differences among the temperate *Sarpa salpa* and the tropical *Siganus luridus* in their bite impact on *Cystoseira barbatula*, *C. compressa* and *Sargassum vulgare* and (ii) differences among *Sarpa salpa* and *Sparisoma cretense* in their bite impact on the seagrass *Posidonia oceanica*. All bite impact analyses were analysed with a one-way fixed factor ANOVA.

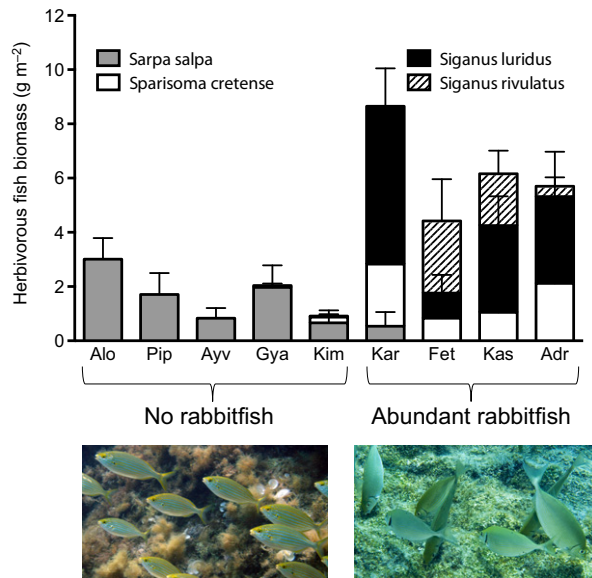
## Results

### SPATIAL VARIATION IN HERBIVORE ABUNDANCE AND TEMPERATURE

We found strong regional differences in yearly mean SST ( $F_{8,72} = 10.52$ ,  $P < 0.001$ , Fig. 1), with the three easternmost regions (Adrasan, Kas, Fethiye) being 2 °C warmer (mean  $\pm$  SE =  $16.74 \pm 0.2$ ) than the north-western regions (Alonissos, Piperi, Ayvalik, Gyaros, Kimolos; mean  $\pm$  SE =  $14.77 \pm 0.1$ ), and Karpathos displaying intermediate SST values (mean  $\pm$  SE =  $15.38 \pm 0.3$ ). The abundance of tropical rabbitfish (*Siganus rivulatus* and *S. luridus*) was positively correlated with mean SST ( $R^2 = 0.59$ ,  $P = 0.02$  on log-transformed rabbitfish abundance data). Sea urchin abundance was low throughout the study regions (mean  $0.50 \pm$  SE  $0.13$  ind m<sup>-2</sup>) and was therefore not considered in analyses beyond this point.

Regions strongly differed in the abundance of rabbitfish (i.e. *Siganus luridus* and *S. rivulatus*; Figs 1 and 2;





**Fig. 2.** Abundance of herbivorous fishes in regions with/ without rabbitfish. Data in all Figures represent means  $\pm$  SE. Bottom left-hand side photograph shows the temperate fish salema (*Sarpa salpa*), dominant in regions without rabbitfish. Bottom right-hand side photograph shows a group of marbled spinefoot (*Siganus rivulatus*) grazing on shallow rocky bottoms. Photograph credits: A. Vergés and Z. Kizilkaya. Alonissos = Alo, Piperi = Pip, Ayvalik = Ayv, Gyaros = Gya, Kimolos = Kim, Karpathos = Kar, Fethiye = Fet, Kas = Kas and Adrasan = ADR.

$F_{8,45} = 18.27$ ,  $P < 0.001$ ). Post hoc pairwise comparisons identified two distinct groups: one characterized by high abundance of tropical rabbitfish (with mean biomass of *Siganus* spp. between 1.6 and 2.8 g m<sup>-2</sup>) consisting of the warmer eastern regions (Adrasan, Kas, Fethiye and Karpathos;

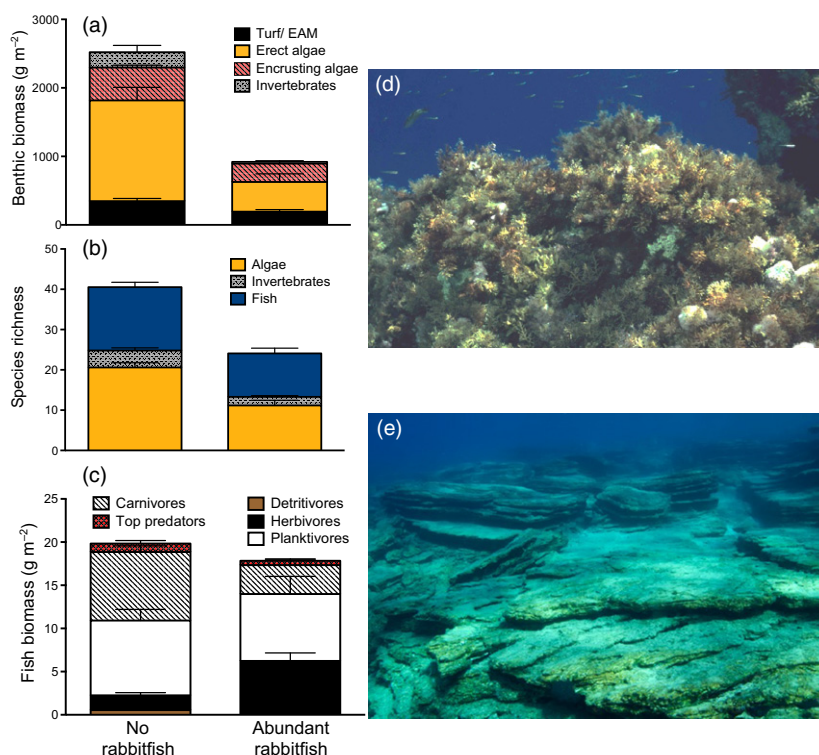
Figs 1 and 2) and a second group of regions encompassing the colder north-western regions (Alonissos, Piperi, Ayvalik, Gyaros, Kimolos; Figs 1 and 2), where rabbitfishes *S. luridus* and *S. rivulatus* were either absent or present in very low abundances (mean biomass between 0 and 0.06 g m<sup>-2</sup>). In regions with no rabbitfish, the native sparid *Sarpa salpa* was the main herbivorous fish recorded (Fig. 2).

#### PATTERNS IN BENTHIC AND FISH BIOMASS AND SPECIES RICHNESS AMONG REGIONS WITH/ WITHOUT RABBITFISH

Total benthic biomass was dramatically lower in the regions where rabbitfish were abundant (Fig. 3a; Table 1a). Regions with no rabbitfish were characterized by three times more biomass of canopy algae (Fig. 3d) than regions with abundant rabbitfish, which were generally barrens with low standing biomass dominated by EAM and encrusting algae (Fig. 3e). Species richness was also significantly lower ( $\sim$  half) in the regions with rabbitfish (Fig. 3b), irrespective of whether we considered species richness of fish or of benthic organisms (Table 1b). Total fish biomass was similar between regions with/ without rabbitfish, but there was an important shift in the biomass distribution among functional groups, with a strong decrease of  $\sim$ 50% in biomass and species richness of carnivores and a marked increase in herbivore abundance and richness in the regions with rabbitfish (Fig 3c and Table 1a).

#### FEEDING ASSAYS

Surprisingly, feeding assays revealed that total consumption of macrophytes (four species combined) was two times



**Fig. 3.** Benthic biomass and species richness patterns in regions with/ without rabbitfish. (a) Total biomass of dominant benthic organisms, (b) Total species richness of algae, invertebrates and fish, (c) Fish biomass of major trophic groups, (d) Photograph showing typical miniature forests of *Cystoseira* spp., representative of Mediterranean diverse shallow rocky bottoms, where tropical rabbitfishes are absent. (e) Barren area typical of eastern Mediterranean sites where range-shifting tropical rabbitfishes are abundant. EAM = epilithic algal matrix. Values are means  $\pm$  SE. Photograph credits: E. Ballesteros and Z. Kizilkaya.

**Table 1.** Results of nested anovas comparing biomass and species richness of benthic and fish communities in groups of regions with/ without abundant rabbitfish and regions within these areas

		Total benthic			Total fish			Detritivorous fish			Herbivorous fish		
Source of variation	d.f.	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
(a) Biomass													
Rabbitfish abundance	1	903874	9.94	<b>0.016</b>	52.93	0.22	0.65	4.04	0.86	0.38	274.5	25.18	<b>0.002</b>
Region (Rabbitfish abund.)	7	90933	5.18	<b>&lt;0.001</b>	235.42	2.43	<b>0.034</b>	4.7	1.01	0.44	10.90	1.02	0.43
Error	45	17568			96.88			4.66			10.73		
		Planktivorous fish			Carnivorous fish			Top predatory fish					
Source of variation	d.f.	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>			
Rabbitfish abundance	1	10.82	0.13	0.73	282.34	7.85	<b>0.027</b>	3.03	1.49	0.26			
Region (Rabbitfish abund.)	7	83.62	1.18	0.35	35.94	3.31	<b>0.006</b>	2.04	0.81	0.56			
Error	45	70.93			10.85			2.50					
		Total benthic			Total fish			Detritivorous fish			Herbivorous fish		
Source of variation	d.f.	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
(b) Species richness													
Rabbitfish abundance	1	1765.9	10.0	<b>0.016</b>	325.6	11.34	<b>0.012</b>	0.06	3	0.13	32.03	114.39	<b>&lt;0.001</b>
Region (Rabbitfish abund.)	7	176.23	8.95	<b>&lt;0.001</b>	28.71	4.27	<b>0.001</b>	0.02	0.5	0.83	0.28	0.82	0.58
Error	45	19.69			6.73			0.04			0.34		
		Planktivorous fish			Carnivorous fish			Top predatory fish					
Source of variation	d.f.	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>			
Rabbitfish abundance	1	3.12	1.45	0.26	455	19.43	<b>0.003</b>	0.13	0.12	0.74			
Region (Rabbitfish abund.)	7	2.15	3.71	<b>0.003</b>	23.42	4.97	<b>&lt;0.001</b>	1.08	2.25	<b>0.047</b>			
Error	45	0.58			4.71			0.48					

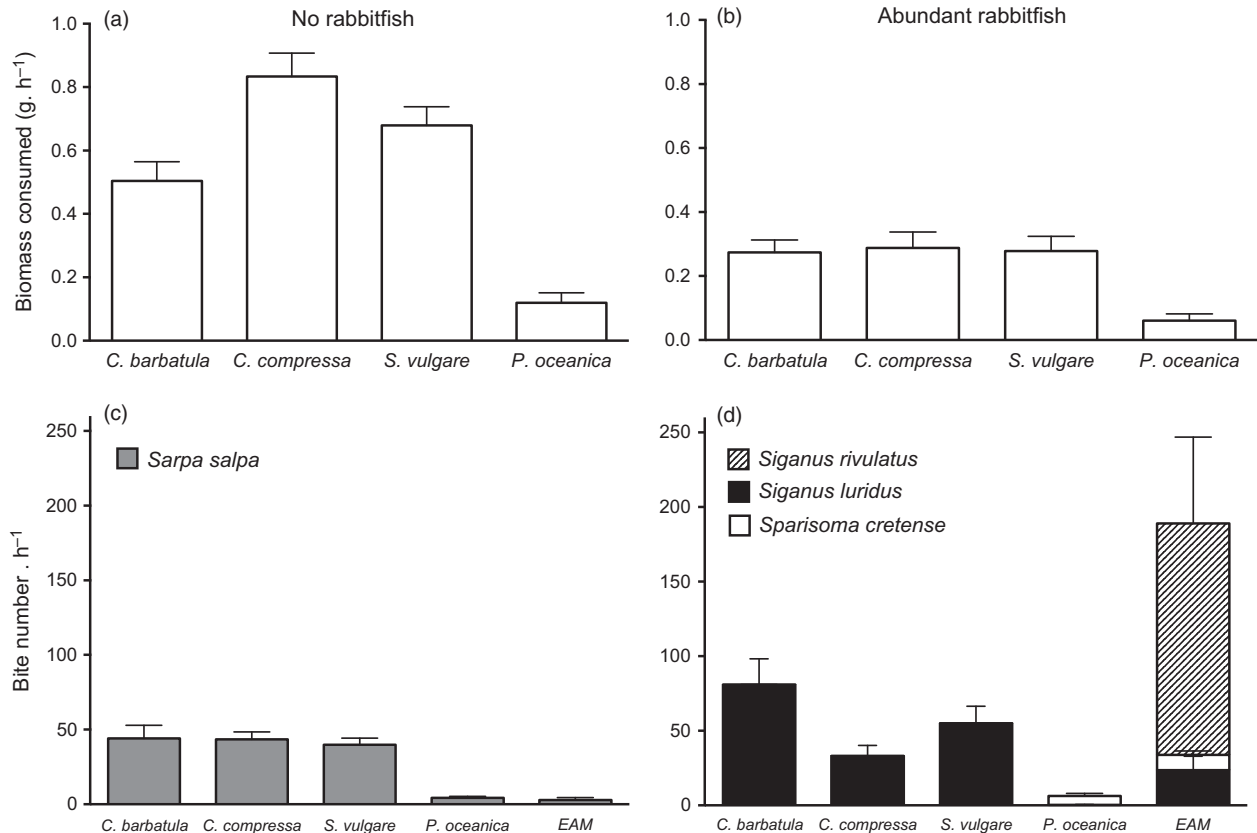
Significant effects are highlighted in bold.

greater in the region with no rabbitfish (Fig. 4a,b; region no rabbitfish =  $2.13 \pm 0.18 \text{ g h}^{-1}$ , region with rabbitfish =  $0.89 \pm 0.13 \text{ g h}^{-1}$ ;  $F_{1,6} = 17.55$ ,  $P = 0.005$ ). There were no differences in the total biomass consumed among days. The four macrophytes were consumed at different rates in both regions (Fig. 4a,b; Hotelling's multivariate test: no rabbitfish region:  $T^2 = 118.01$ ,  $F_{3,26} = 36.53$ ,  $P < 0.001$  and Rabbitfish abundant region:  $T^2 = 37.08$ ,  $F_{3,29} = 11.56$ ,  $P < 0.001$ ). Post hoc pairwise comparisons showed that brown algae were consumed at a greater rate, while seagrass was consumed at a much lower rate in both regions (Fig. 4a,b).

Similarly, in the unfilmed tethering experiments, the consumption rates of the four macrophytes varied significantly among both regions and sites (Table S2). All macrophytes were generally consumed at higher rates in the region with no rabbitfish (Fig. S2), but significant regional differences were only detected for *Cystoseira compressa*, with losses being two times higher in the region with no rabbitfish (pairwise comparison  $P = 0.03$ ). Other species were consumed at varying rates in the different sites within each region (significant

Site (Rabbitfish abundance)  $\times$  Species interaction; Table S2). In the region with no rabbitfish, *Cystoseira compressa* was consumed at higher rates than the other macrophytes at two out of three sites (pairwise comparisons  $P < 0.05$ ). Consumption rates were always lowest on the seagrass *Posidonia oceanica* in all sites within both regions ( $P \leq 0.05$  for all pairwise comparisons).

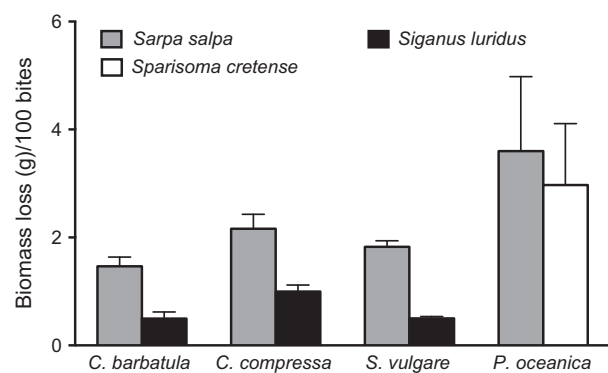
Video footage revealed that the region with no rabbitfish feeding was exclusively restricted to one herbivorous species, the temperate sparid *Sarpa salpa*, except for only one bite taken by the warm-temperate parrotfish *Sparisoma cretense* (both species are native to the Mediterranean; Fig. 4c). In the 92 h of footage viewed in this region, we counted a total of 689 feeding observations by *S. salpa* and no tropical rabbitfish were observed. In contrast, over the 104.3 h of video footage viewed in the region with rabbitfish, the most numerous fish observed feeding on our assays was *Siganus luridus* (753 feeding observations), followed by *Sparisoma cretense* (174 feeding observations) and *Siganus rivulatus* (89 feeding observations; Fig. 4d). No *Sarpa salpa* individuals were observed in the video footage in the region with rabbitfish.



**Fig. 4.** Macrophyte consumption patterns and bite rates of all herbivorous fishes on four dominant macrophytes and the surrounding epilithic algal matrix (EAM). Macrophyte biomass consumed per hour: (a) in Foça where rabbitfish were absent and (b) in Adrasan, where rabbitfish were abundant. (c) Bite rates taken by herbivorous fish in Foça. (d) Bite rates taken by herbivorous fish in Adrasan. Bars under continuous lines in panels denote non-significant differences between groups. The four macrophytes offered in the feeding assays were: the brown algae *Cystoseira barbatula*, *Cystoseira compressa*, *Sargassum vulgare*, and the seagrass *Posidonia oceanica*.

Species-specific analyses of the four herbivorous fishes observed feeding revealed strong feeding selectivity for all species. In the region with no rabbitfish, *Sarpa salpa* fed mostly on brown algae (all three species consumed at similar rates), whereas bite rates on the seagrass *Posidonia oceanica* or the EAM were an order of magnitude lower (Fig. 4c;  $T^2 = 168.07$ ,  $F_{3,9} = 30.56$ ,  $P < 0.001$ ). In contrast, rabbitfish exhibited strong complementarity (Fig. 4d). *Siganus rivulatus* fed exclusively on the EAM (i.e. consumed no macrophytes) and was responsible for > 80% of all bites taken on this substrate. *Siganus luridus* and *Sparisoma cretense* fed in a highly selective and complementary manner (Fig. 4d; respectively:  $T^2 = 27.28$ ,  $F_{3,12} = 5.36$ ,  $P = 0.01$  and  $T^2 = 23.46$ ,  $F_{3,13} = 4.69$ ,  $P = 0.02$  on log-transformed data). *Siganus luridus* exhibited the highest bite rates on the three brown algae, whereas seagrass consumption rates were an order of magnitude lower, and EAM consumption rates fell between brown algae and EAM (Fig. 4d). In contrast, the consumption rates of *Sparisoma cretense* were higher for the EAM and seagrass than for the three brown algae, which were hardly consumed (Fig. 4d).

The bite impact of *Sarpa salpa* (biomass consumed per bite) was significantly higher than that of *Siganus luridus* for all species of brown algae (Fig. 5; *C. barbatula*:



**Fig. 5.** Comparison of the bite impact of temperate and tropical herbivorous fishes on four dominant macrophytes. Data derived from a subset of filmed feeding assays where a single fish species was observed consuming a given macrophyte over the entire deployment period. Data represent means ± SE. Algae species are as per Fig. 4.

$F_{1,23} = 21.65$ ,  $P < 0.001$ ; *C. compressa*:  $F_{1,23} = 16.77$ ,  $P < 0.001$ ; *S. vulgare*:  $F_{1,23} = 130.4$ ,  $P < 0.001$ ). In contrast, *Sarpa salpa* and *Sparisoma cretense* had a similar bite impact on the seagrass *Posidonia oceanica* (Fig. 5;  $F_{1,20} = 0.12$ ,  $P = 0.73$ ).

## Discussion

In this study, we show that the range expansion of tropical herbivorous rabbitfishes is accompanied by a shift from diverse and productive Mediterranean algal forests to deforested, depauperate barrens, with a threefold reduction of benthic biomass and a 40% decrease in species richness. Interestingly, our results show that the observed community shift is not driven by greater consumption of macrophytes by tropical rabbitfish, as compared to native temperate herbivores. Instead, this shift appears to be mediated by differences in the functional diversity of the temperate and tropical herbivores. In regions with no rabbitfish, the temperate fish *Sarpa salpa* was the only species observed feeding, targeting exclusively adult macrophytes at comparatively higher rates than the rabbitfish. In contrast, in regions where rabbitfish are abundant, there was a mix of functionally distinct species that fed complementarily targeting both the adult macrophytes (*Siganus luridus*) and the earlier life-history stages through consumption of the EAM (*Siganus rivulatus* and *Sparisoma cretense*).

Algal forests and seagrass meadows are among the most productive and diverse communities of temperate coasts world-wide, providing resources such as food and habitat for a large number of fish, invertebrates and algae (Steneck *et al.* 2002; Waycott *et al.* 2009). The removal of algae by range-shifting tropical fish documented here not only causes a direct loss of algal abundance and diversity but also a loss of biogenic structure that, in turn, implies a loss of critical habitat for understory algae and many invertebrates that live in the algal canopies. These invertebrates are the main prey items for the majority of carnivorous fishes in the area (e.g. Labridae, Sparidae and Serranidae; Sala & Ballesteros 1997). The marked decline we observed in terms of both biomass and species richness of carnivorous fishes in the barren rabbitfish-occupied regions may thus be at least partly influenced by a lack of prey for this trophic group. In addition, it is likely that the loss of algal forests has also decreased fish recruitment rates, as numerous reef-associated fishes use algal forests as obligate settlement habitats (Ellison *et al.* 2005).

The results from the video-recorded feeding experiments provide two important novel insights. Firstly, they show that the full suppression of seaweed cover only occurs when a bio-diverse mix of herbivores feed complementarily and therefore provide an explanatory mechanism for the shift in community composition observed in the region with abundant rabbitfish. Here, one rabbitfish species (*Siganus luridus*) targeted adult macroalgae, while the other species (*Siganus rivulatus*) targeted the epilithic algal matrix, which contains early life-history stages of algae, therefore preventing macroalgae from becoming established. Moreover, warmer regions were also characterized by greater abundance of the parrotfish *Sparisoma cretense* (an EAM consumer) which has a distribution largely restricted to the warmest eastern and southern parts of the Mediterranean basin (Bernardi *et al.* 2000). Indeed, adult algae in regions dominated by rabbitfish were only present out of the reach from herbivorous fishes, either hidden within cre-

vices or at 0 m in wave-washed regions (Vergés *et al.* 2009). These findings are consistent with studies from healthy coral reef ecosystems that are also devoid of macroalgae, showing that functional diversity and feeding complementarity among herbivores is necessary to fully suppress seaweed abundance (Rasher, Hoey & Hay 2013). Secondly, our results show that temperate herbivorous fishes can consume macrophytes at a much greater rate than their tropical counterparts, both in terms of their bite impact (biomass consumed per bite) and in terms of the total algal biomass removed. This challenges some widely accepted views about temperate herbivorous fishes, which are often considered as consumers of minor importance when compared to tropical herbivorous fishes (Meekan & Choat 1997) or to other temperate herbivores such as urchins (Jones & Andrew 1990). However, high consumption rates of established macrophytes such as those displayed by *Sarpa salpa* in this study were not sufficient to denude the substrate of algae more generally, as illustrated by the fact that benthic communities dominated by this voracious consumer were nevertheless dominated by abundant canopy algae.

Our results suggest that the continued range expansion of tropical rabbitfishes poses a major threat to Mediterranean biodiversity and ecosystem services. We found a clear relationship between temperature and the abundance of rabbitfish, and a growing number of studies have linked the westwards expansion of tropical species originating from the Red Sea to distinct warming in the eastern Mediterranean (Raitso *et al.* 2010; Pancucci-Papadopoulou, Raitso & Corsini-Foka 2012; Zenetos *et al.* 2013). Indeed, warming of the Mediterranean is occurring at a particularly fast rate in the eastern part of the basin (Nykjaer 2009), and the occurrence of rabbitfish has now been reported as far west as Croatia (Dulcic *et al.* 2011) and the south of France (Daniel *et al.* 2009).

An increasing number of studies indicate that warming *per se* can strongly impact algal physiology and recruitment (Harley *et al.* 2012) and may therefore also be contributing to the observed deforestation in the eastern Mediterranean. However, caging experiments show that canopy algae habitats can be restored when herbivorous fishes are excluded (Sala *et al.* 2011), demonstrating that algal forests would still be present in this region in the absence of consumers. Another alternative hypothesis to the observed patterns is that chronic overfishing in the eastern Mediterranean may have released predation pressure on juvenile and adult rabbitfish and facilitated their survival in the eastern part of the basin. However, adult *Siganus* are consumed by large groupers that were missing equally in regions with/ without rabbitfish (Sala *et al.* 2012). Similarly, we found no significant differences between regions in the biomass of piscivores capable of eating juvenile rabbitfishes (Sala *et al.* 2012). Our results therefore reinforce the idea that the major factor that is facilitating the expansion of rabbitfishes is seawater temperature.

The herbivore-mediated community shift we describe here has implications for temperate macroalgal forests globally, as a poleward shift into temperate regions has already been documented for over 80 species of tropical herbivorous fishes belonging to 9 genera and representing functionally diverse



consumers such as grazers, scrapers, detritivores and browsers (Vergés *et al.* 2014; Feary *et al.* 2013). While temperate macroalgae may be able to mitigate climate change effects by metabolic adjustments or range shifts (Wernberg *et al.* 2010, 2011; Smale & Wernberg 2013), fish species tend to spread particularly fast (Poloczanska *et al.* 2013) and are thus likely to represent an important biotic pressure operating simultaneously to the direct impacts of climate change on macroalgae. Indeed, ocean warming by 1–2 °C in the last 20 years in southern Japan has been linked to increased feeding by tropical herbivorous fishes, contributing to so-called localized isoyake or barren, and leading to an overall decline of algal forests (Yamaguchi 2010). Similarly, an increase in water temperature of 3 °C in the northern Gulf of Mexico (USA) over the last three decades has also been associated with a 22-fold increase in the abundance of the parrotfish *Nicholsina usta* (Fodrie *et al.* 2010), a tropical species that consumes ca. five times more seagrass than the main native grazers in the area (Prado & Heck 2011).

Emerging evidence indicates that the incursion of functionally diverse tropical herbivores into temperate systems is a phenomenon of global importance that has the potential to profoundly transform temperate marine ecosystems (Vergés *et al.* 2014a). In this study, we show that the deforestation of algal forests in areas dominated by range-expanding tropical fishes in the eastern Mediterranean is not mediated by greater rates of herbivory *per se*, but is instead facilitated by an increase in herbivore functional diversity and the introduction of consumers capable of both browsing on adult seaweeds and grazing on epilithic algae. This work highlights the overall importance of understanding how species interactions may change in a warming ocean and emphasizes the importance of assessing the functional traits of range-shifting species to determine potential mechanisms of impact on ecological communities.

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## Data accessibility

Data available from the Dryad Digital Repository (Vergés *et al.* 2014b).

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## Supporting Information

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

**Table S1.** List of taxa (fish, alga and invertebrates) and their assigned trophic level or functional group encountered throughout the 54 sampling localities.

**Table S2.** PERMANOVA results of the tethering experiment to assess differences in consumption rates among regions with/ without abundant rabbitfish, among macrophyte species and among sites within regions.