Climate change exacerbates interspecific interactions in sympatric coastal fishes

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Summary

1. Biological responses to warming are presently based on the assumption that species will remain within their bioclimatic envelope as environmental conditions change. As a result, changes in the relative abundance of several marine species have been documented over the last decades. This suggests that warming may drive novel interspecific interactions to occur (i.e. invasive vs. native species) or may intensify the strength of pre-existing ones (i.e. warm vs. cold adapted). For mobile species, habitat relocation is a viable solution to track tolerable conditions and reduce competitive costs, resulting in ‘winner’ species dominating the best quality habitat at the expense of ‘loser’ species.

2. Here, we focus on the importance of warming in exacerbating interspecific interactions between two sympatric fishes. We assessed the relocation response of the cool-water fish Coris julis (a potential ‘loser’ species in warming scenarios) at increasing relative dominance of the warm-water fish Thalassoma pavo (a ‘winner’ species). These wrasses are widespread in the Mediterranean nearshore waters. C. julis tolerates cooler waters and is found throughout the basin. T. pavo is common along southern coasts, although the species range is expanding northwards as the Mediterranean warms.

3. We surveyed habitat patterns along a thermo-latitudinal gradient in the Western Mediterranean Sea and manipulated seawater temperature under two scenarios (present day vs. projected) in outdoor arenas. Our results show that the cool-water species relocates to a less-preferred seagrass habitat and undergoes lower behavioural performance in warmer environments, provided the relative dominance of its warm-water antagonist is high.

4. The results suggest that expected warming will act synergistically with increased relative dominance of a warm-water species to cause a cool-water fish to relocate in a less-preferred habitat within the same thermal environment.

5. Our study highlights the complexity of climate change effects and has broad implications for predictive models of responses to warming. To achieve more accurate predictions, further consideration is needed of the pervasive importance of species interactions. We believe these fundamental issues to be addressed to understand the biotic consequences of climate change.

Key-words: behaviour, cold-adapted, competition, labrids, Mediterranean Sea, relocation, global warming

Introduction

Empirical evidence suggests that climate warming should favour warm-adapted species over cold-adapted species at the same site (Parmesan & Yohe 2003). In some marine regions, average sea surface temperatures (SST) have risen faster than the global average (Trenberth et al. 2007) and rapid poleward shifts of isotherms have been recorded (Burrows et al. 2011). Consequently, mass mortality events, depth/latitudinal shifts and relative dominance changes of several marine species have been well documented over the last decades (Perry et al. 2005; Sabatés et al. 2006; Dulvy et al. 2008; Coma et al. 2009; Lejeusne et al. 2009; Coll et al. 2010). Indeed, thermal sensitivity is a fundamental physiological attribute and one principal reason for climate-induced changes in natural communities (Pörtner & Farrell 2008). Species coexist where their thermal windows overlap, although thermal windows may be
not identical (Pörtner & Peck 2010). In turn, coexistence may increase inter-specific interactions under warming (Tylianakis et al. 2008) and these can modify the magnitude of species responses to climate change (Harborne & Mumby 2011).

Hence, attributes other than fundamental temperature-related physiological processes (Pörtner & Farrell 2008) may be evoked to further explain biotic changes (Gilman et al. 2010). Although (i) species interactions are among the most important forces structuring ecological communities; and (ii) information on how a changing climate affects the extent of density changes is considered central to building more accurate predictions, climate change impacts on species distribution, biodiversity and ecosystem functioning are probably underestimated by current forecasts mostly neglecting such processes (Harley et al. 2006; Tylianakis et al. 2008; Gilman et al. 2010).

At present, empirical evidence on the role of warming in modulating the strength of species interactions is still in its infancy (but see Helland et al. 2011; Harley 2011). Given likely stability in overall species composition, documented changes in the relative dominance of species along a thermal gradient (Simpson et al. 2011) are expected to have a much greater impact on the ecology and exploitation of fish assemblages than any range extensions or contractions (Harborne & Mumby 2011), for example, creating novel inter-specific interactions or exacerbating pre-existing antagonistic ones (Gilman et al. 2010). Under a warming scenario, local or regional relocations that track tolerable conditions (Parmesan & Yohe 2003) and reduce competitive costs (Parmesan 2006) are viable solutions for mobile species. This may result in ‘winner’ (i.e. warm-adapted) species dominating the best quality habitat at the expense of ‘loser’ (cold-adapted) species.

Here, we investigate (i) the thermo-latitudinal patterns of habitat selection of a warm-water and a cool-water species in several locations spanning 10° latitude in the Western Mediterranean Sea and analyse (ii) the effects of experimentally increasing the relative dominance of a potential ‘winner’ species on the relocation and behavioural responses of its ‘loser’ antagonist, under present day and projected SST by 2100 (Somot et al. 2008). We studied two ecologically and morphologically similar Atlantic–Mediterranean coastal wrasses (Ostistchthyes: Labridae). Specifically, we tested the hypothesis that projected warming combined with higher relative dominance of the warm-water fish will (i) displace the cool-water species from the preferred habitat and (ii) alter its behaviour.

Materials and methods

STUDY SPECIES AND HABITAT USE IN THE WILD

We selected two sympatric coastal fish as species model: the rainbow wrasse Coris julis Linnaeus, 1758 and the ornate wrasse Thalassoma pavo Linnaeus, 1758 (Fig. S1, Supporting information). These wrasses are among the most abundant and widespread species in the Eastern Atlantic and the Mediterranean Sea nearshore waters and have similar body size, habitat preference, feeding strategies and diets (Kabukkasal 2001). C. julis tolerates cooler waters and is found throughout the Mediterranean basin (Froese & Pauly 2011). T. pavo is more common in warmer southern coasts (Froese & Pauly 2011), although it is expanding northward as the Mediterranean warms (Lejeune et al. 2009; Coll et al. 2010) (Supporting Information).

To assess the thermo-latitudinal patterns of habitat selection of these wrasses, density of both species was estimated along replicated linear transects of 5 × 25 m (Harmelin-Vivien et al. 1985) positioned at 3–10 m depth in uniform algal (Cystoseira spp. forest) and seagrass habitats (Posidonia oceanica meadow). Sampling locations were located at four thermo-latitudinal levels crossing the 14 °C February isotherm (−40°N), a long recognized biogeographical divide that several warm-water species (including T. pavo) have crossed over the 25 years as the Mediterranean have warmed (Bianchi 2007). To avoid any confounding from other anthropogenic stressors (e.g. pollution and angling), within each latitude level, two locations were randomly selected among low-impacted, pristine and marine protected areas in the Sicily Strait (~35°N), Southern Tyrrhenian Sea (~38°N), Central Tyrrhenian Sea (~41°N) and Ligurian Sea (~44°N) (Fig. 1a). Two random areas within each location were selected, and replicated counts were performed in each site for the two species independently (see Experimental design section), and then standardized to 100 m².

MANIPULATIVE EXPERIMENTS IN OUTDOOR ARENAS

Individuals of both species were collected from three different locations along the northern coast of Sicily (e.g. Messina Strait, Ustica Island and Gulf of Carini). We choose to collect animals from southern Mediterranean locations, thus potential differences in the responses we searched for might be conservative, being animals adapted to a warmer average annual SST.

Hypotheses of habitat relocation and interspecific interactions between the two wrasses species under two thermal scenarios have been experimentally approached on a step-by-step base: 1. the ‘single species’ and 2. the ‘relative dominance’ experiments. All the individuals to be used for the manipulative experiments (a total of 1620 T. pavo and 990 C. julis) were selected according to their adult colour phases and total length (see Table S1, Supporting information).

Under present-day and projected SST, a choice of different artificial habitats was offered to independent groups of fifteen individuals of both species separately (the ‘single species’ experiment) and to fifteen Coris julis individuals at increasing levels of Thalassoma pavo relative dominance: 1X (fifteen T. pavo individuals, that is, both species in the same proportion), 2X (30 T. pavo ind.) and 3X (45 T. pavo ind.). Size structure of each group of fifteen fishes was: two terminal phase males (80–180 mm total length), eight intermediate initial phase females or sneaker males (81–140 mm TL) and five small initial phase females (50–80 mm TL) individuals for both species (Table S1, Supporting information). The ranges of abundance and size structure were based on own field data, and experimental densities were standardized to the arena surface. Before each experiment started, fish were acclimated to holding tanks under the same experimental conditions of the outdoor arenas for 20 days (Supporting information). The same individual was used only once within each thermal scenario,
whilst the same specimens were used for present-day and projected SST scenarios to avoid excessive collection of fish (Supporting information). Combinations of fish individuals of different sizes among different thermal scenarios were randomly chosen by capturing fishes from the holding tanks.

Average SST of the Mediterranean Sea have risen faster than the global average (Trenberth et al. 2007), increasing by 0.66°C in the Western part of the basin and by 1.1°C in the Levantine basin over the past 20 years (Nykjaer 2009). As the Mediterranean Sea is constrained to the north by the European landmass and its average SST are predicted to increase by a further 2°C/C1°C (Coll et al. 2010) by the end of this century, biological responses to warming may be dramatic in the near future. Therefore, rearing conditions in small tanks and test conditions in two large outdoor arenas (8 m diameter; 1.5 m depth; 50 m² surface) were based on present-day and on projected SST for 2100: a present-day scenario (Sa, 38.01°C), Tavolara (Ta, 40.55°C) and Ponza (Po, 40.55°C) (SSTw 13.6 ± 0.6°C and SSTs 25.1 ± 1.1°C) in the Tyrrhenian Sea; Gallinara (Ga, 44.01°C) and Palmaria (Pa, 44.14°C) (SSTw 14.0 ± 0.6°C and SSTs 23.6 ± 0.6°C). (b-c) Mean densities (±SE) of the two wrasse species and average summer SST (±SD) along the latitudinal gradient in the algal and the seagrass habitat, respectively. Note that the y-axis scale varies among plots.

Supporting information, and if values exceeded our desired ranges, the experiment trials were stopped.

Different artificial habitats were provided to animals for the choice experiments. The artificial macroalgae (Flowering Cabomba, AquaPlant® Penn-Plax®, Memphis, TN, USA) mimicked the size (~35 cm high) and shape of Cystoseira spp., the most common erect macroalgae in all study areas. The artificial seagrass habitat mimicked the P. oceanica seagrass (Scofield 2003), a Mediterranean endemic species considered a key ecosystem in the region (Hemminga & Duarte 2000); each shoot was made of green plastic raffia, forming eight leaves of ~60 cm height and 0.8 cm wide. Artificial macroalgae and seagrass shoots were placed ~25 cm apart, with approximately 500 mimics on a 25 m² surface of substrate. Bare plastic net substrate was also considered as artefact treatment (see experimental designs section and supplementary information).

**Density and Behavioural Estimates in the Arenas**

The density of C. julis was visually assessed and used as a proxy of habitat selection both for the ‘single species’ and the ‘relative dominance’ experiment. Observations occurred between 8:00 and 16:00 h, the peak activity period for wrasses (Willis, Badalamenti & Milazzo 2006). Direct observations were made from the arena border by a motionless operator, whose presence
did not appear to disturb the fish. To avoid the observer bias, three of us (M.M., S.M. and M.G.) haphazardly followed a single individual separately, repeating observations three times for each combination of treatments. A 3-min observation period was used for recording habitat permanence and the other behavioural activities only when the fish was inside the selected habitat in the pairwise choice (Supporting information). The following behaviours of C. julis were quantified: (i) searching (i.e. swimming close to and looking at the substrate); (ii) resting (i.e. remaining motionless over the substrate); (iii) interacting with conspecifics (swimming near conspecifics or exhibiting interactions with other C. julis individuals); and (iv) interacting with T. pavo (swimming near or exhibiting antagonist interactions with T. pavo individuals). Habitat permanence and behavioural activities were expressed as the percentage of time spent in the selected habitat upon the observation period.

Each trial consisted of a single replicate for density estimates (i.e. counts were repeated three times at randomly chosen 10-min intervals and their average was treated as a single replicate; a total of three replicates were considered for each combination) and three replicated habitat permanence and behavioural observations of C. julis individuals of different size classes. Individuals were haphazardly selected from each arena for observations: one terminal phase male, one intermediate initial phase and one small initial phase female for each trial. A total of nine replicates were considered for each combination. After the experiment, fish were removed from arenas using hand nets or traps and released in the holding tanks.

EXPERIMENTAL DESIGNS AND STATISTICAL ANALYSES

To assess patterns of habitat selection of the two wrasses in the wild, a five-way design was conducted including the following factors (and treatments): ‘Species’ (SP: C. julis and T. pavo), ‘Latitude’ (LA: 44°-41°-38°-35°N), ‘Habitat’ (HA: Algae vs. Posidonia seagrass), ‘Location’ (LO: two levels) and ‘Area’ (AR: two levels). Four random density replicates (individuals 100 m⁻²) were considered for each combination of the above treatments (N = 256) (Fig. S2, Supporting information).

A preliminary ‘single species’ experiment was performed to assess the most preferred artificial habitat by each fish species separately. Trials consisted of single species at 1X density (15 individuals) released within arenas. The factors involved were Habitat (HT: A×S, S×A), Thermal scenarios (TS: present day and projected) and Arena (A1 and A2). The number of individuals 25 m⁻² at each combination of treatments was visually assessed and used as surrogate of habitat selection for C. julis and T. pavo separately. A total of three density replicates were collected (N = 24) (Fig. S3, Supporting information).

To evaluate the relocation response of the cool-water fish to increasing relative dominance of the warm-water fish at two distinct temperature scenarios, a pairwise choice of combinations of two habitats (algae and seagrasses) and of an appropriate artefact control (i.e. the plastic net substrate) was provided to fish in large outdoor arenas. In this case, the experimental design consisted of three factors: ‘Temperature scenario’ (TS: C as Present day and W as Projected SST); ‘T. pavo density’ (DT: 1X, 2X, 3X of C. julis density); ‘Habitat’ (HT) with six levels resulting from independent combinations of Algae + Net (A), Seagrass + Net (S) and Net substrate (N): A×S, A×N, S×A, S×N, N×A, N×S. A total of three density replicates (no. of individuals ∙ 25 m⁻²) were collected (N = 108) to assess the relocation response of the cool-water C. julis, and a total of nine replicates were considered for each combination (N = 324) to assess its habitat permanence (Time%) and the behavioural responses (Time%) (Fig. S4, Supporting information).

To avoid pseudoreplication, observations were independently carried out on different combinations of pairwise choices of habitats provided to both species in the ‘single species’ experiment and to the cool-water fish in the ‘relative dominance’ experiment. The A×S treatment indicates that algae is the observed habitat in the pairwise choice algae vs. seagrass, whilst in the S×A treatment observations were conducted on the seagrass habitat. Each day, the combinations of factors’ treatments (Figs S3–S4, Supporting information) were randomly assigned to two arenas and each replicate of the same combination was collected on different days. Moreover, habitat substrates were randomly positioned/oriented within arenas (Fig. S5, Supporting information).

Linear regression analyses were used to assess the relationships between SST along the latitudinal gradient and the T. pavo and C. julis density in the two shallow habitats separately. Five- and three-way ANOVAs were used to test for species differences in the patterns of habitat selection along the thermo-latitudinal gradient, habitat preference in the ‘single species’ experiment and the habitat relocation, habitat permanence and behavioural activities of the cool-water species in the ‘relative dominance’ experiment. Cochran’s test was used to check for the homogeneity of variances. Significant interaction terms were examined individually using Student–Newman–Keuls (SNK) a posteriori pairwise tests to separate means at P = 0.05 (Underwood 1997).

Results

CORRELATIVE FIELD PATTERNS OF HABITAT SELECTION IN THE WESTERN MEDITERRANEAN SEA

From cooler to warmer locations (44°N-35°N), a shift in the dominance of species was observed in the preferred algal habitat (Fig. 1b; ANOVA: interaction term SP×LA×HA F₉,₂₅₅ = 29.18, P < 0.01; Table S2, Supporting information) with C. julis being more abundant than T. pavo at northern latitudes and the opposite occurring at southern latitudes (Table 1). As expected, the density of the cool-water C. julis in the algal habitat was negatively correlated to the summer (b = −11.6; r = −0.899, P < 0.01; n = 8) and the winter SST (b = −22.3; r = −0.931, P < 0.001; n = 8), whilst the warm-water T. pavo density was positively correlated to summer SST (b = 13.4; r = 0.837, P < 0.01) and winter SST (b = 28.4; r = 0.955, P < 0.001; n = 8). The shallow seagrass beds at 38° and 35°N were increasingly occupied by the cool-water wrasse (Fig. 1c; Table 1; Table S2, Supporting information), and despite its affinity to cooler temperatures, its density was positively correlated to summer SST (b = 1.4; r = 0.756, P < 0.05) and to winter SST (b = 2.6; r = 0.779, P < 0.05; n = 8). Few individuals of T. pavo were recorded in the seagrass habitat – even where its density on the preferred algal habitat was high (Fig. 1b,c; Table 1) – and no correlation with either
summer or winter SST was observed (summer SST: $b = 0.1$; $r = 0.612$, $P < 0.05$; winter SST: $b = 0.2$; $r = 0.450$, $P < 0.05$; $n = 8$).

**MANIPULATIVE EXPERIMENTS IN LARGE OUTDOOR ARENAS**

In the preliminary ‘single species’ experiment, the warm-water *Thalassoma pavo* and the cool-water *Coris julis* exhibited similar patterns of habitat selection, with a higher preference for the algal habitat than the seagrass one (*C. julis* $F_{1,24} = 23.01$, $P < 0.001$). *T. pavo* $F_{1,24} = 43.49$, $P < 0.001$; SNK test: Algae > Seagrass for both species at $P < 0.05$). This finding confirms the patterns observed in the field; however, the thermal scenario *per se* slightly affected the selection of *C. julis* ($F_{1,24} = 4.92$, $P < 0.05$; SNK test: Cool > Warm), and no differences were detected in the interaction Habitat x Thermal scenario (*C. julis* $F_{1,24} = 0.04$, $P > 0.05$, *T. pavo* $F_{1,24} = 2.32$, $P > 0.05$). Moreover, the single species experiments did not reveal any effect of the arena either in the *T. pavo* or in the *C. julis* trials ($F_{1,24} = 0.92$, $P > 0.05$, *T. pavo* $F_{1,24} = 0.06$, $P > 0.05$).

The potential interactions between the two wrasses were further examined in the ‘relative dominance’ experiment. If in these trials the cool-water *C. julis* retained the habitat preferences exhibited in the ‘single species’ experiment, the two species would largely overlap in habitat. This was not

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<tr>
<th>Table 1. Summary of the results of the Student–Newman–Keuls post hoc tests. Only significant interaction terms at ($P &lt; 0.05$) are reported</th>
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<tr>
<td>Habitat selection (n. ind. 100 m$^{-2}$) in the field patterns – Interaction term SP×LA×HA (Table S2, Supporting information)</td>
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<tr>
<td>44°: Algae (Cj &gt; Tp), 41°: Algae (Tp &gt; Cj), 38°: Algae (Tp &gt; Cj), Seagrass (Cj &gt; Tp), 35°: Algae (T &gt; Cj), Seagrass (Cj &gt; Tp)</td>
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<td>Seagrass: <em>C. julis</em> (35° = 38° = 41° &gt; 44°); Algae: <em>Thalassoma pavo</em> (35° = 38° = 41° &gt; 44°)</td>
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<td><em>C. julis</em>: 41° (Al &gt; Se), 44° (Al &gt; Se). <em>Thalassoma pavo</em>: 35° (Al &gt; Se), 38° (Al &gt; Se), 41° (Al &gt; Se)</td>
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<td>Habitat selection (n. ind. 25 m$^{-2}$) in the ‘relative dominance’ experiment – Interaction term TS×DT×HT (Table S3, Supporting information)</td>
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<td>1X: A×N (W &gt; C), S×N (W &gt; C), N×A (C &gt; W), N×S (C &gt; W). 2X: S×A (W &gt; C). 3X: S×A (C &gt; W)</td>
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<td>Projected: A×S (1X &gt; 2X = 3X), S×A (3X = 2X &gt; 1X), S×N (1X &gt; 2X = 3X)</td>
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<td>3X: Projected (S×A &gt; A×S = A×N = S×N = N×A = N×S)</td>
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<td>Habitat permanence (% time) in the ‘relative dominance’ experiment – Interaction term TS×DT×HT (Table S3, Supporting information)</td>
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<td>Searching (% time) in the ‘relative dominance’ experiment – Interaction terms TS×HT and TS×DT (Table S4, Supporting information)</td>
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<td>TS×HT interaction term N×A (C &gt; W)</td>
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<td>TS×DT interaction term 2X: (C &gt; W). 3X: (C &gt; W)</td>
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<td>Resting (% time) in the ‘relative dominance’ experiment – Interaction term TS×DT×HT (Table S4, Supporting information)</td>
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<td>1X: A×N (W &gt; C), N×S (W &gt; C). 2X: S×A (W &gt; C). 3X: A×N (W &gt; C), S×A (W &gt; C), S×N (W &gt; C)</td>
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<td>Present day: A×S (1X &gt; 2X = 3X). Projected: A×N (3X = 1X &gt; 2X &gt; 1X), S×A (3X = 2X &gt; 1X), S×N (3X = 2X &gt; 1X), N×A (3X = 2X &gt; 1X), N×S (1X &gt; 2X = 3X)</td>
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<td>Interacting with <em>C. julis</em> (% time) in the ‘relative dominance’ experiment – Interaction term TS×DT×HT (Table S4, Supporting information)</td>
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<td>2X: Projected (S×N &gt; A×S = S×A = A×N = N×A = N×S)</td>
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<td>Interacting with <em>T. pavo</em> (% time) in the ‘relative dominance’ experiment – Interaction term TS×HT and term DT (Table S4, Supporting information)</td>
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<td>TS×HT interaction term N×A (W &gt; C)</td>
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<td>DT term 3X &gt; 1X = 2X</td>
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*Cj* = *Coris julis*, Tp = *Thalassoma pavo*, Al = Algae; Se = Seagrass, Latitudes: 44°-41°-38°-35°N. 1X, 2X and 3X are the relative dominance treatments of the warm-water species, W = projected warming scenario, C = cooler present-day scenario, A = algae with net substrate, S = seagrass with net substrate, N = net substrate without algae or seagrass.

the case even in the present-day scenario, where the cool-water fish showed no selection of any habitat regardless of increasing relative dominance of the warm-water fish (Fig. 2a–c; Table 1; Table S3, Supporting information) and no differences were revealed in the habitat permanence (Fig. 3a–c; Table 1; Table S3, Supporting information). Searching over the substrate by the cool-water fish was the main behaviour under the present-day SST scenario, particularly at 2X and 3X relative dominance of the warm-water antagonist. Under this thermal scenario, resting activity of C. julis was higher at the lowest relative dominance level (1X) of T. pavo (Fig. 4a; Table 1; Table S4, Supporting information). Under projected warming, the cool-water wrasses shifted from algae to seagrass only when the relative dominance of the warm-water fish was 3X (Fig. 2c; Table 1; Table S3, Supporting information). Accordingly, C. julis spent a larger proportion of permanence time (%) in the less-preferred habitat (Fig. 3c; Table 1; Table S3, Supporting information), showing decreased searching activity and increased resting underneath seagrass leaves (Fig. 4a,c; Table 1; Table S4, Supporting information).

Searching activity was significantly lower in the projected than the present-day scenario, particularly at 2X and 3X relative dominance of the warm-water fish (Fig. 4a; Table 1; Table S4, Supporting information). No clear pattern was observed in the time (%) spent by C. julis interacting with conspecifics, although higher time (%) was recorded in the algal habitat only at 1X density of T. pavo (Fig. 4b; Table 1; Table S4, Supporting information). Interspecific interactions (time%) of the cool-water fish were significantly higher at 3X density of the warm-water wrasse, independently to the thermal scenario (Fig. 4d; Table 1; Table S4, Supporting information). The resting activity of the cool-water fish significantly differed under the present-day scenario only at 1X relative dominance of the warm-water T. pavo (Fig. 4c; Table 1; Table S4, Supporting information), whilst resting in the seagrass habitat was the dominant behaviour at 2X and 3X of T. pavo relative dominance in the projected SST condition (Fig. 4c; Table 1; Table S4, Supporting information).
Discussion

Here, we show the role of warming in exacerbating interspecific interactions between two ecological antagonists, suggesting that anthropogenic climate change can alter interspecific interactions and produce unexpected changes in species distributions among habitats, potentially affecting community structure and diversity. More broadly, our results on a two species model highlight the importance of incorporating interspecific interactions into projections regarding ecological responses to climate change.

Using correlative and experimental approaches, our results showed that higher temperatures and relative dominance increase of a warm-water species may act synergistically causing a cool-water species (i) to relocate to a less-preferred habitat within the same thermal environment; and (ii) to alter its behavioural activity. However, responses to seawater warming only took place when the dominance of the warm-water fish was high, both in the field study and in the experimental trials. In the most southern and warmer locations of the thermo-latitudinal gradient examined, we recorded the habitat relocation of the cool-water fish to the seagrass meadows when the density of its warm-water antagonist in the preferred algal habitat was from 5 to 7 times higher (particularly at 35°N).

Our manipulative experiments did support the observed field patterns, highlighting that the ecological and behavioural responses of the cool-water Coris julis are affected by projected warming, provided the relative dominance of its warm-water antagonist Thalassoma pavo was 3-fold higher. No such effects are recorded in the present-day scenario.

Habitat relocation is a viable solution for interacting species and often results in a characteristic distribution of individuals among habitats. This should result in 'winner' warm-adapted species dominating the best quality habitat with lots of individuals, whilst the 'loser' cold-adapted species maintains fewer individuals, if it is present at all (Tokeshi 1999). Indeed, the observed ability of C. julis to modify its habitat selection according to the increasing relative dominance of T. pavo is an important response, which reduces habitat overlap, related ecological costs and probably allows for coexistence in heterogeneous seabeds. Posidonia oceanica meadows might be regarded as a suboptimal habitat, underused by T. pavo and representing a 'refuge' for C. julis where this species can avoid potential detrimental inter-specific effects when its normally preferred habitat is occupied by the dominant antagonist T. pavo. Similarly, a marked vertical shift in sloping algal seabeds was recently observed, with C. julis expanding to deeper and cooler environments when the relative dominance of T. pavo was high in the warmer and shallow water algal habitat, and the two species coexisting in slowly sloping algal seabeds (Milazzo et al. 2011). Both species swim close to the substrate and are visual predators of invertebrates, and a strong association with rocky algal assemblages is likely due to foraging (Kabakasal 2001). Their small invertebrate preys live on or under the algal canopy in the Cystoseira forest (Chemello & Milazzo 2002), whilst in seagrasses, benthic preys are concentrated in rhizomes and matte layers, which are not easily accessible to these wrasses (Hemmings & Duarte 2000). Accordingly, previous studies...
showed that *T. pavo* is rare in seagrass beds whilst *C. julis* is more commonly associated with this habitat and detects prey along its edges particularly when the meadows are fragmented (Vega-Fernandez *et al.* 2005). If in one hand, the observed displacement of the cool-water species to the *Posidonia oceanica* habitat is a viable solution to reduce ecological costs, on the other an increasing habitat use of *C. julis* in the seagrass meadows may cascade on other community components (e.g. several other resident wrasse species) potentially causing a rearrangement of the entire community structure and functioning. However, projected trajectories of *P. oceanica* persistence under forecasted seawater warming in the Western Mediterranean demonstrate that the seagrass density may be affected by climate change in the near future, possibly reaching a density threshold below which meadow functionality is lost by year 2049 (Jordà, Marbà & Duarte 2012). Although the cool-water wrasse species may potentially benefit by a lower *P. oceanica* seagrass density (Vega-Fernandez *et al.* 2005), whether and how its ecological performance will be affected in the long term is presently unknown.

The cool-water fish showed decreased searching activity under projected warming and increased resting in the less-preferred seagrass habitat when its ecological antagonist was on patrol at 2X and 3X relative dominance. As expected, we also recorded increased interspecific interactions at 3X relative dominance of the warm-water fish, independently to the thermal scenario considered. When these interspecific interactions occurred under projected warming, they were likely to cause behavioural changes in the cool-water species. Interspecific behavioural interactions between wrasses, considered an essential part of their ability to coexist (Jones 2002), mainly consisted of the cool-water species readily forming hetero-specific groups with several warm-water individuals (i.e. the swimming with *T. pavo* behaviour). This kind of behavioural interaction was made up by individuals of *C. julis* starting to swim faster or to exhibiting antagonist interactions with *T. pavo* individuals. Although a low number of aggressive encounters between wrasses have been observed, we noticed this behaviour to cause evident alterations (i.e. decrease in searching activity and increase in resting activity in the less-preferred habitat at 2X and 3X density of *T. pavo*) to the cool-water fish under the projected scenario. We explain the observed lower performance of the cool-water wrasse as a result of these interspecific behavioural interactions. In general, animals can compete either by reducing the availability of a shared resource to other animals (exploitation competition) or by reducing the ability of other animals to make use of a shared resource through behavioural interactions (interference competition) (e.g. Tokeshi 1999). Therefore, our findings suggest that the habitat segregation between *T. pavo* and *C. julis* is essentially an interactive segregation with species showing behavioural interactions and warming playing a key role in the activity pattern and in the relocation response of the cool-water species to the less-preferred seagrass habitat. Temperature is known to be a fundamental factor in controlling fish metabolic scope (Fry 1971). Hence, the lower ecological and behavioural performance of the cool-water species at projected warming conditions may be due to a decrease in its metabolic capacity (aerobic scope, i.e. the metabolic confines within which any energy-demanding activity in excess of basal metabolic rate must be undertaken) (Fry 1971) that occurred when its ecological antagonist was highly dominant. Accordingly, it was recently demonstrated that competitive interactions between two salmonid fishes resulted in contrasting performance during simulated winter conditions of ice-covered lakes (higher darkness and lower temperatures), whilst a decreasing ice cover with warmer temperatures may reverse this situation (Helland *et al.* 2011).

Present predictions concerning biological responses to warming are largely based on the assumption that these species will remain within their bioclimatic envelope as environmental conditions change (Parmesan & Yohe 2003; Guisan & Thuiller 2005). Therefore, information on the direct effects of seawater warming on temperate cool-adapted species (i.e. species range contractions and deepening to track more favourable conditions) has increased over the last decades (e.g. Perry *et al.* 2005; Dulvy *et al.* 2008; Simpson *et al.* 2011). However, studies aimed at investigating the responses of cool-water species to novel inter specific interactions or to exacerbated pre-existing interactions with warm-water species are largely lacking or have been only hypothesized (Sabatés *et al.* 2006).

Our results provided insight into the importance of warming and interspecific interactions in affecting the patterns of distribution of species among shallow habitats, thus contributing to filling an information gap (Harley *et al.* 2006). Habitat suitability models (HSMs) applied to Mediterranean endemic fish assemblages demonstrated that by the end of the 21st century, the coldest areas of the Mediterranean Sea (the Adriatic Sea, the Ligurian Sea and the Gulf of Lion) are projected to become a geographical ‘trap’ that would drive cool-water endemic fish species towards extinction if projected warming occurs (Ben-Rais Lasram *et al.* 2010). These findings might even be conservative as models do not take into consideration that other forcing biotic factors can enhance direct warming effects (Ben-Rais Lasram *et al.* 2010). We suggest that the complex ecological consequences of climate change can only be accurately anticipated if we are able to understand the ways in which biotic and abiotic factors interact. This knowledge is critical to achieve more accurate predictions of responses to climate change (Gilman *et al.* 2010). Therefore, important future challenges in studies of climate-induced ecological responses should take into account the pervasive importance of interactions between ecologically similar species (i.e. cold vs. warm adapted, native vs. invasive) and increase our knowledge on food web
interactions and on the role of other drivers of density change (e.g. habitat degradation, overfishing, pollution, ocean acidification). We believe more detailed models may be needed to adequately account for the effects of interspecific interactions when predicting the distribution and abundance of species under warming, the related community- and ecosystem-level responses.

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References


Supporting Information

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

Fig. S1. The Two Wrasses Species. Terminal phase males of the warm-water *T. pavo* (a) and the cool-water *C. julis* (c). Initial phase individuals of *T. pavo* (b) and *C. julis* (d) respectively.

Fig. S2. Details of the experimental design adopted for the field patterns of habitat selection.

Fig. S3. Details of the experimental design adopted for the ‘single species’ experiment.

Fig. S4. Details of the experimental design adopted for the ‘relative dominance’ experiment.

Fig. S5. The two outdoor arenas (in black) used for the manipulative experiments at the IAMC-CNR, Messina (Italy). Both arenas have similar size: 8 m diameter, 1.5 m depth, and ~50 m² surface.

Table S1. Number of individuals of both species used in the ‘single species’ and the ‘relative dominance’ experiments divided according to colour phases and relative size structure. Note that the same individuals were used for the present-day and the projected SST treatments to avoid excessive collection of fish.

Table S2. ANOVA on the density of the wrasses in two shallow habitats (algae and seagrass) at four latitudes. ns not significant, *P < 0.05, **P < 0.01, ***P < 0.001. In bold the significant interaction further examined by post-hoc SNK test (Table 1).

Table S3. ANOVA on the habitat selection and habitat permanence of the cool-water fish in the relative dominance experiment. ns not significant, **P < 0.01, ***P < 0.001. In bold the significant interactions further examined by post-hoc SNK tests (Table 1).

Table S4. ANOVA on the searching, interacting with co-species (*Cj*), interacting with *T. pavo* (*Tp*) and resting activities of the cool-water fish in the relative dominance experiment. ns not significant, *P < 0.05, **P < 0.01, ***P < 0.001. In bold the significant interactions further examined by post-hoc SNK tests (Table 1).

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