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Warming impacts on early life stages increase the vulnerability and delay the population recovery of a long-lived habitat-forming macroalga

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Abstract

1. Understanding the combined effects of global and local stressors is crucial for conservation and management, yet challenging due to the different scales at which these stressors operate. Here we examine the effects of one of the most pervasive threats to marine biodiversity, ocean warming, on the early life stages of the habitat-forming macroalga *Cystoseira zosteroides*, its long-term consequences for population resilience and its combined effect with physical stressors.
2. First, we performed a controlled laboratory experiment exploring the impacts of warming on early life stages. Settlement and survival of germlings were measured at 16ºC (control), 20ºC and 24ºC and both processes were affected by increased temperatures. Then, we integrated this information into stochastic, density-dependent integral projection models (IPM).
3. Recovery time after a major disturbance significantly increased in warmer scenarios. The stochastic population growth rate (λ_s) was not strongly affected by warming alone, as high adult survival compensated for thermal-induced recruitment failure. Nevertheless, warming coupled with recurrent physical disturbances had a strong impact on λ_s and population viability.
4. *Synthesis:* The impact of warming effects on early stages may significantly decrease the natural ability of habitat-forming algae to rebound after major disturbances. These findings highlight that, in a global warming context, populations of deep-water macroalgae will become more vulnerable to further disturbances, and stress the need to incorporate abiotic interactions into demographic models.

Keywords: climate change, demography, human impacts, population ecology, quasi-extinction, recovery, seaweeds, stress interactions.

Introduction

Global change is predicted to modify the regime and intensity of disturbances in marine ecosystems worldwide (Easterling et al., 2000a; Jentsch, Kreyling, & Beierkuhnlein, 2007). Some chronic stressors, such as global warming (IPCC, 2013) or ocean acidification (Kroeker, Kordas, Crim, & Singh, 2010), are expected to increase in magnitude during the present century. Furthermore, acute, extreme events, such as El Niño (Yeh et al., 2009) and heatwaves (Déqué, 2007; Rose, Smale, & Botting, 2012), are expected to become more frequent and intense (IPCC, 2013; Kerr, 2011). All of these threats are unfolding in a background of human activities that can exacerbate their consequences (Hughes, Linares, Dakos, van de Leemput, & van Nes, 2013; Ling, Johnson, Frusher, & Ridgway, 2009). In order to predict the ecological responses of species to global change and design effective conservation actions, we need to understand not only the direct consequences of stressors

but also their combined long-term effects (Darling & Côté, 2008; Lindenmayer, Thorn, & Banks, 2017).

The highly idiosyncratic nature of ecosystems challenges our ability to comprehend the combined impacts of global change (Boyd, Lennartz, Glover, & Doney, 2014; Krumhansl et al., 2016). Experimental studies have provided crucial insight to understand the underlying (e.g. demographic or physiological) effects of warming or acidification (Kroeker, Gambi, & Micheli, 2013; Wernberg et al., 2010). On the other hand, modeling studies parameterized with field data provide valuable means to project and forecast the fate of populations under various scenarios (Linares & Doak, 2010; Madin, Hughes, & Connolly, 2012). Despite the recent progress in global change research, experimental and demographic modeling approaches have evolved as parallel disciplines, scarcely used together to predict long-term responses of marine species (Russell et al., 2012; Wernberg, Smale, & Thomsen, 2012). Most experimental marine studies have focused on a single life stage, yet marine species usually encompass multiple life stages with contrasting responses to threats (Caley et al., 1996; Harley et al., 2012). Because experimental manipulations of complete life cycles are not always feasible, exploring the response of key or elusive life stages in controlled conditions coupled with modeling approaches parameterized with field data can provide unique insights (Assis et al., 2017).

In this study, we explore the population-level consequences of warming (a chronic stressor) and its interaction with physical disturbances, such as storms and ghost fishing nets, on the Mediterranean habitat-forming macroalga, *Cystoseira zosteroides*. The Mediterranean Sea is a hot spot of biodiversity, but also of human impacts (Coll et al., 2010). Among these multiple stressors, warming is the most pervasive, impacting regional scales over the last decades (Lejeusne, Chevaldonné, Pergent-Martini, Boudouresque, & Pérez, 2010; Micheli et al., 2013; Somot, Sevault, Déqué, & Crépon, 2008). Heat waves in the Mediterranean can seriously affect marine invertebrates (Garrabou et al., 2009) and encrusting algae (Hereu & Kersting, 2016), but no studies have reported such evidence for brown macroalgae (Ballesteros et al., 2009). In contrast, physical disturbances, such as lost fishing gear (Thibaut, Pinedo, Torras, & Ballesteros, 2005) and low-frequency exceptional storms (Navarro, Ballesteros, Linares, & Hereu, 2011), can result in high mortality pulses, heavily impacting macroalgal populations. Furthermore, high temperatures are known to damage algal cells (Harley et al., 2012) which may lead to higher mortality rates or reduced growth rates and development, and ultimately impact population dynamics and species distribution (Assis et al., 2017; Harley et al., 2012; Wernberg et al., 2010). Early life stages of macroalgae are usually imperilled by warming (Andrews, Bennett, & Wernberg, 2014; Ladah & Zertuche-González, 2007), while adult individuals are more likely to physiologically compensate for high levels of thermal stress (Bennett, Wernberg, Arackal Joy, de Bettignies, & Campbell, 2015; Jueterbock et al., 2014). Thus, it is crucial to determine if the altered mortality of early life stages is important for overall population persistence.

Macroalgal forests dominated by *Cystoseira* species are heavily imperilled in the Mediterranean Sea, and have already experienced sharp declines and even local extinctions (Airoldi & Beck, 2007; Thibaut et al., 2005). Here we hypothesize that warming will seriously impact survival and settlement probabilities of the early life stages of *C. zosteroides*.

However, we anticipate that this effect will have little influence on the natural dynamics of its populations, given their low dependence on reproductive processes (Capdevila, Hereu, Riera, & Linares, 2016). We do expect important consequences of temperature for their recovery ability and long-term viability, based on the key role of recruitment for the recovery of *C. zosteroides* populations (Capdevila, Hereu, Riera, & Linares, 2016). To test these hypotheses, we first experimentally explored the consequences of warming on the survival and development of *C. zosteroides* early life stages, by culturing them under different temperature treatments. We then coupled these results with demographic data from five natural populations of *C. zosteroides*, to predict long-term effects of various thermal scenarios and its interactions with recurrent physical disturbances, such as storms and fishing nets. These two physical disturbances (storms and lost fishing nets) have been suggested to be among the main threats causing *Cystoseira* spp. decline in the Mediterranean Sea (Thibaut et al., 2005). The recurrence of mortality events from lost fishing gear is difficult to quantify, but there is evidence that such events are more important and more common than previously thought (Brown & Macfadyen, 2007). On the other hand, the frequency of storms impacting *C. zosteroides* populations is relatively low because only exceptional events reach such deep-water habitats (Navarro, Ballesteros, Linares, & Hereu, 2011), but these are predicted to increase in intensity and frequency in the coming decades (IPCC, 2013; Jentsch et al., 2007). With this study, we expect to provide useful information about how ocean warming will alter the response of these macroalgal forests to natural and anthropogenic disturbances.

Material and methods

Study species

Cystoseira zosteroides is an endemic alga from the Mediterranean Sea with a critical structural role (Ballesteros et al., 2009). *C. zosteroides* populations develop important forests on rocky bottoms at 15-50 m depth, mainly in the NW Mediterranean Sea, constituting highly diverse communities on relatively deep water sea beds (Ballesteros et al., 2009). This species typically has slow population dynamics, with low rates of somatic growth (0.5 cm $year^{-1}$) and long lifespan (~50 years; Capdevila, Hereu, Riera, & Linares, 2016). This species has a diplontic (*i.e.* only gametes are haploid) and iteroparous life cycle (*i.e.* multiple reproductive events during their lifetime; Fig. 1). Individuals can be either male or female, although hermaphrodites can occur. Adult individuals can be distinguished by their perennial thallus, except during their first year of life. The top of the thallus contains reservoir vesicles (tophules) from which primary branches emerge from February until October (Ballesteros, 1990). These primary branches contain receptacles, the reproductive structures of mature individuals. Maturity is typically attained at 3-4 years and reproduction starts between late March and early April and ends in June (P. Capdevila pers. obs.). Gametes are released and fertilization is external, forming a diploid zygote.

Temperature data

To describe the present thermal conditions where this species occurs, high-resolution hourly temperature recordings were obtained from the T-MedNet platform (http://www.t-mednet.org/). This temperature data is recorded using *in situ* Stowaway Tidbit and Hobo

Water Pro v2s autonomous sensors placed over different locations of the Mediterranean Sea. Here we used data from Cap de Creus Natural Park (42° 20' 0.456"N, 3° 17' 11.605"E), Montgrí, Medes Islands and Baix Ter Natural Park (42° 2' 58.920"N, 3° 13' 31.440"E) and Columbretes Islands Marine Reserve (39° 53' 30.112"N, 0° 40' 15.931"E), three locations where *C. zosteroides* populations are monitored (Appendix S1: Table S1.1and Fig. S1.1). Temperature recordings were only analyzed at a depth range of 20-35 m and from 2008 to 2015, corresponding to the depth range and period of our demographic study (see *Demographic modeling*, Appendix S1: Table S1.1 and Fig. S1.1). Note that at Columbretes Islands *C. zosteroides* does not develop populations at depths shallower than 25 m, so we limit the showed data for that location to the range of 25-35 m depth.

Experimental design

Early life stages of *C. zosteroides,* typical of any macroalgae, are very distinct from adult stages in terms of size and demography (Capdevila et al., 2015). Thus, to accurately measure the settlement rate and survival of early life stages, 27 branches from nine fertile individuals were collected by scuba diving from a well-developed *C. zosteroides* population between 20 and 25 m depth in Montgrí, Medes Islands and Baix Ter National Park (NW Mediterranean Sea, 42° 2' 34.026" N, 3° 13' 36.358" E) in April 2016. Fertile branches were transported in seawater containers (~3 h) to the Experimental Field Services at the University of Barcelona. Branches were then placed in small plastic bags with seawater inside fridges kept at 12ºC to promote the liberation of gametes (Susini, Mangialajo, Thibaut, & Meinesz, 2007). After 24 hours, three branches were placed in each of nine 12 L aquaria, where three Petri dishes were set at the bottom as a substrate for zygote settlement. Before exposure to the temperature treatments, we acclimatized the branches, by placing them at 16ºC for 24 hours, after which time temperatures were progressively increased in temperature treatments. Four 1 cm^2 quadrats were haphazardly marked on each Petri dish as a sampling surface (Appendix S2: Fig. S2.1). See Appendix S2 for further details about the experimental design.

To examine the effects of temperature on settlement and survival rates of early stages three temperature treatments were implemented. Each treatment was replicated within three separate aquaria (Appendix S2: Fig. S2.1). The chosen temperature levels were 16ºC, 20ºC, and 24ºC. During the reproductive season of *C. zosteroides* seawater temperature increases from ~14ºC to over 17ºC, with a mean value of ~16ºC, so here we used the 16ºC treatment as our control (Appendix S2: Fig. S2.2). The 20ºC treatment mimics the temperatures attained during previous warming years (see Results *Temperature data*) - temperatures that are becoming more frequent (Galli, Solidoro, & Lovato, 2017). The 24ºC simulates the increase of 3.5ºC scenario for the 21st century in the NW Mediterranean (IPCC, 2013; Somot et al., 2008). Indeed, during warm years, natural populations at present experience this temperature by the end of the reproductive season and mainly, between July and August during the recruits' development (see Results *Temperature data*).

A week after the branches were placed in the aquaria, once enough time had elapsed for the zygotes to settle and be distinct from non-fertilized eggs (Irving, Balata, Colosio, Ferrando, & Airoldi, 2009), branches were removed from the aquaria. Then, we estimated the number of zygotes per cm^2 inside the four quadrats marked on the Petri dishes by using a

stereomicroscope with a 4.5x magnification. Survival of zygotes (σ_s) was quantified weekly over a period of six weeks as the proportion of zygotes remaining from the previous week. The time of exposure represents the time span that these temperatures can take place in our studied localities (Fig. S2.2).

Settlement and survival statistical analysis

To quantify the effect of temperature on the settlement of *C. zosteroides* we used generalized linear mixed models (GLMM), with a Poisson error distribution and a logit link function. The independent variable was the number of zygotes, temperature was treated as a fixed variable and we used the ID of each quadrat of the Petri dishes as a random variable. Similarly, to test the effect of temperature and time (fixed factors) on germling survival (i.e. binary response), we used a GLMM with a binomial error distribution and a logit link function. Again, we used the ID of each quadrat of each Petri dish as a random variable to deal with the lack of independence between observations repeated at different times and a binomial error distribution was assumed to deal with the binary response variable (*survive vs*. *die*). For the two fitted models, we applied a Type II Wald χ^2 test to determine the effect of fixed variables. All analyses were performed using the statistical software R (R Development Core Team, 2014), models were fitted using the function "glmer" from the *lme4* package (Bates, Mächler, Bolker, & Walker, 2014), and the Wald χ^2 test was performed using the "Anova" function from the *car* package (Fox & Weisberg, 2011). For multiple comparisons, we applied the Tukey test using the "glht" function from the *multcomp* package (Hothorn, Bretz, & Westfall, 2008).

Demographic censuses

We estimated rates of survival (σ), growth (γ) and recruitment (Appendix S3: Table S3.2 and S3.3) by monitoring individuals along permanent transects at five *C. zosteroides* populations along the NW Mediterranean (one at Cap de Creus Natural Park, two at Montgrí, Medes Islands and Baix Ter Natural Park and, two populations at Columbretes Islands Marine Reserve; Appendix S1: Fig. S1.1), over the course of 3-4 years (see Appendix S1: Table S1.1). Each transect was 1 m wide and 3-10 m long, depending on the morphology of each sampling zone (see Appendix S1: Table S1.1 for details), and was partitioned using 50 × 50 cm^2 quadrats. We identified the individuals by mapping their position at each of the quadrats inside the permanent quadrat, and we measured the length of the main perennial axis using a caliper with 1 mm accuracy. Sampling was performed by scuba diving and transects were visited annually by experienced observers at the beginning of the summer (between July and August) when the deciduous branches are more developed and *C. zosteroides* individuals attain their highest seasonal biomass (Ballesteros, 1990). Vital rates were estimated according to the size of individuals, which typically spans from 0.5 cm to 16 cm, and has been demonstrated to be a good predictor of the demographic rates (Ballesteros et al., 2009; Capdevila, Hereu, Riera, & Linares, 2016). Transects were installed in the summer of 2008 at Montgrí, Medes Islands and Baix Ter Natural Park at ~20 m depth, where 209 and 181 individuals were identified respectively, while at Cap de Creus Natural Park and Columbretes Islands Marine Reserve transects were installed in May 2010 at 23, 28 and 24 m depth, 175, 124, and 130 individuals were identified, respectively.

Model parametrization

We used Integral Projection Models (IPMs; Easterling et al. 2000b) to examine the effects of projected increases in temperature on population performance, both alone and in combination with other physical disturbances (Fig. 1 and below). Because IPMs are based on regression models, they can easily estimate the variation of vital rates with continuous stages (Ellner & Rees, 2006), such as size in *C. zosteroides,* and they are robust when parametrizations are based on populations with few individuals (Ramula, Rees, & Buckley, 2009). We applied a density-dependent IPM, described further in Appendix S3.

We used data for each year and population to parameterize the vital rate functions that build the IPM. Medes and Montgrí coastal populations were both impacted by an extraordinary storm in 2008 and the Montgrí population also suffered a mortality event caused by a ghost fishing net in 2009 (Capdevila et al., 2015), so these two populations were not included in the survival and growth parameterization to avoid misleading estimates. Instead, they were used in our simulations to estimate storm and ghost fishing mortalities (see below). Thus, the IPM was built from the data obtained from each non-disturbed population and time interval (Columbretes I: from 2010-2012; Columbretes 2: from 2010-2012; Cap de Creus: from 2010-2012).

For each of the warming scenarios studied here (16, 20 and 24ºC) we measured the effects of temperature on the settlement (ε) and the survival of zygotes (σ_s), and these were incorporated into the full life cycle model (Fig. 1). Because during the earliest life stages of *C. zosteroides* are microscopic, field demographic censuses are not able to parametrize both settlement probability (ε) and zygote survival (σ_s), yet these parameters are intrinsic in recruitment measurements. For this reason, these two demographic processes (ε, σ_s) were estimated using our laboratory experiment data (see *Experimental design* section). Considering that our field recruitment data incorporated both processes, we decreased the zygote survival and settlement according to the attenuation levels measured in the experiment (see Appendix S3 for further details). We incorporated variation in these parameters in the model by means of sampling the mean coefficient of treatment and its confidence interval (95%CI) at each model iteration.

Demographic projections

We coupled continuous size-based vital rate estimates to build the IPM. The IPM's state variable for its continuous component was the size of the perennial thallus (in cm). To account for the variation between populations and years, we generated random transition kernels for each time step by sampling from the estimated distribution of population and year effects in survival and growth functions. That is, we incorporated the variation among years and populations in the slope of the survival and growth functions, by generating random numbers from survival and growth parameters' distribution and then constructing a kernel at each projection.

To estimate the effect of temperature on the ability of *C. zosteroides* populations to recover after disturbances, we simulated an 80% increase in mortality, based on empirical values obtained in a previous study from an extreme storm mortality event (Capdevila et al., 2015). The mortality impacted all the stages of *C. zosteroides* populations. Then, we projected it

100 years, 1000 times for each thermal scenario. To do so we multiplied the density-dependent kernel by a population density function $n_{(z,\ t)}$

$$n(z', t+1) = \int_L^U K(z', z,\ N) n(z, t) dz \qquad \text{(eq. 1)}$$

where $n_{(z',\ t+1)}$ and $n_{(z,\ t)}$ are the size distribution at time *t+1* and *t*, respectively. The parameters *L* and *U* in equation 1 are the minimum and maximum empirically observed states over which vital rates were modelled, respectively. In the case of *C. zosteroides* perennial thallus, *L* = 0.25 cm and *U* = 16 cm. $K_{(z',\ z,\ N)}$ is the density-dependent kernel, a function that describes the transition of individuals from size *z* at time *t*, to size *z'* and time *t+1*, and their descendants. Note that *N* accounts for the density dependence of the kernel. $K_{(z',\ z,\ N)}$ can be distilled into two sub-kernels representing the demographic processes of (i) survival and growth, $P_{(z',\ z)}$ and (ii) the per capita production of new recruits via reproduction, $F_{(z',\ z,\ N)}$. Thus, the density dependence of our IPM comes from the reproductive part of the model, because the number of recruits per adult is a decaying function of the density of adult individuals, independent of the adult size structure (Capdevila, Hereu, Riera, & Linares, 2016; Appendix S3). A detailed description of the model formulation is provided in Appendix S3.

The initial density function ($n_{(z,\ 0)}$) used to make the projections was taken from the stable size distribution obtained from the kernel at stationary equilibrium (λ=1). Because of their low variance in vital rates, natural and undisturbed *C. zosteroides* populations are commonly found close to the stationary equilibrium, with population growth rates close to 1 and population structure near to the stable stage distribution (Ballesteros et al., 2009; Capdevila, Hereu, Riera, & Linares, 2016). For this reason and given that choosing a population density function from the multiple years and populations that we studied would be a subjective decision, we decided to use a simulated well-preserved population structure (density function) instead of a "natural" one, in order to make fair comparisons between treatments (see below). At each time step, the kernel was updated to reflect density dependence and the impacts of temperature on recruitment, and to account for the variation in survival and growth rates.

To estimate population recovery ability, we simulated mortality events and then measured the minimum time required to achieve a minimum stable density of large individuals (>10 cm), defined here as 0.8 large individuals per m^2. This threshold (0.8 large individuals/m^2) was estimated according to the mean density of such mature individuals in both Columbretes populations, the best-preserved populations in our study. We accounted for the number of large individuals instead of total density to consider the structural complexity of the population (Ballesteros et al., 2009). We then calculated the minimum time required to reach the threshold for each thermal scenario and projection. The initial density function used to carry out the projections was a simulated mature population affected by an 80% mortality event. To calculate this initial density function, we first simulated the stable stage distribution of the population with a density of 3 individuals/m^2. This choice is in agreement with the characteristics of natural populations at equilibrium (Capdevila et al., 2015). Next, this population at its stable stage distribution was affected by a simulated mortality of 80% (all the stages were affected) and used as the initial density function for the projections.

Finally, we evaluated the consequences of interactive disturbances under the different thermal scenarios. To do so, we projected the simulated populations increasing the annual frequency of two relevant physical disturbances: extreme storms and fishing nets, each causing a mortality of 80% and 60% individuals respectively. We used these mortality levels for each disturbance based on empirical values obtained in a previous study (Capdevila et al., 2015). We do not have empirical evidence that vital rates variate in a predictable way following disturbance, so we did not change them after the simulated mortality events. The annual frequencies we examined included "Never", one disturbance every 75 years, every 50 years, every 25 years and every 5 years. For each of the aforementioned combinations, populations were projected for up to 100 years with 1,000 iterations.

For each of the projected populations and for each disturbance combination, we calculated the stochastic population growth rate (λ_s) as:

$$\log(\lambda_s) = \frac{\log(N_t) - \log(N_0)}{T} \qquad \text{(eq. 2)}$$

where N_0 is the mean population size at time t=0 and N_t the mean projected population size at time T. When $\log(\lambda_s)<0$ the population decreases, whereas $\log(\lambda_s)=0$ indicates a stable population and $\log(\lambda_s)>0$ indicates a growing population. To quantify the effect of these combined disturbances on the viability of *C. zosteroides* populations, we also obtained the probability of quasi-extinction at t=100 years. Quasi-extinction probability is the likelihood of a population falling below a minimum number of individuals below which the population is likely to be critically and immediately imperilled (Morris & Doak, 2002). For each simulation, we calculated the number of simulated populations that fell below a conservative extinction threshold, of 1% of the initial population size.

Results

Temperature data

The seawater temperature had a marked seasonality, with a summer maxima of 23, 24 to 27ºC and a winter minima of 10, 12 to 13ºC at the shallowest depth in Cap de Creus, Medes Islands and Columbretes Islands respectively (Fig. 2 and Appendix S2: Fig. S2.2). Thus, Cap de Creus and Medes Islands have a cooler thermal regime than the Columbretes Islands, which are located further south (Appendix S1: Fig. S1.1).

Considering the reproductive period of *C. zosteroides,* from April to July, there were similar thermal conditions at all studied sites (Fig. 2). Mean temperatures ranged between 15-17ºC with colder temperatures being at 35 m depth, and some years attaining values close to 20ºC at all sites (Fig. 2b). Maximum annual temperatures during the reproductive season, over the studied period, ranged from 17ºC in Medes Islands at 35 m depth to 25 ºC in Columbretes Islands at 25 m depth (Fig. 2c).

Effects of temperature on settlement and germling survival

Increasing temperatures caused a decline in zygotes settlement (χ^2_2=171.35, p-value<0.001).

Although settlement did not show significant differences between the 16ºC (control) and 20ºC treatment (Tukey test, z=0.30, p=0.951), we found a significant drop in zygote settlement when comparing the 24ºC treatment to the control (Tukey test, z=-12.22, p<0.001; Fig. 3a).

Germlings survivorship decreased gradually during the first six weeks of aquarium monitoring in all treatments (χ^2_4=17614336, p<0.001; Fig. 3b) but varied significantly among temperature treatments (χ^2_2=23254947, p<0.001). The survivorship of germlings remained almost constant during the six weeks of observation at 16ºC, attaining values close to 90% at the end of the experiment. However, survivorship was lower at 20ºC than in control conditions (z=-2635, p<0.001), with final values of ~50%, and even lower at 24ºC than at 20 ºC, falling to ~30% at week six (16-24: z=-4039, p<0.001; 20-24: z=-993, p<0.001; Fig. 3b). According to the fitted model, there was a reduction in survivorship of about 42% and 67% at the 20ºC and 24ºC treatments, respectively, compared to the control treatment.

Effects of temperature on populations' recovery ability

Warming reduces the resilience of *C. zosteroides* populations to small disturbances (Fig. 4). Using the stable population threshold of 0.8 large individuals/m^2, warming increased the recovery time following a high mortality event, with a mean recovery times of ~46 years (±20.06) at 16ºC, ~54 years (±21.29) at 20ºC and no recovery at 24ºC (Fig. 4). Among replicate projections, 92% and 69% reached the stable population threshold at 16ºC and 20ºC, respectively, whereas none of the projections at 24ºC reached the threshold (Appendix S4: Fig. S4.1).

Combined effects of temperature and recurrent impacts of two physical disturbances

When we simulated physical perturbations under different temperature regimes, we observed a general pattern: increasing temperatures decrease log(λ_s) (Fig. 5a,c) and raise the quasi-extinction probability (Fig. 5b,d). In the absence of further disturbances, there was little to no effect of temperature on long-term projections (Fig. 5a,c), nor on quasi-extinction probabilities (Fig. 5b,d). Under present conditions (16ºC), *C. zosteroides* populations had some ability to buffer the mortalities caused by a major storm. At a frequency of exceptional storms every 50 years, populations were displaced from stability (log(λ_s)=0) and resulted in quasi-extinction probabilities greater than 50% (Fig. 5a,b). Also in this control scenario, mortality caused by fishing nets had little effect on the population projections (Fig. 5c), with 0 probability of quasi-extinction at any frequency of fishing-net mortality event (Fig. 5d). Under the 20ºC scenario, populations maintained some degree of buffering to recurrent storms (Fig. 5a,b), and this buffering ability was greater in the case of fishing-induced mortalities (Fig. 5c,d), but always to a lesser degree than under the control scenario. Finally, under the 24ºC scenario, recurrent storm and fishing mortality events had the highest impact on stochastic population growth rate (Fig. 5a,c), and any nonzero frequency of storm or fishing mortality resulted in 100% probability of quasi-extinction (Fig. 5b,d).

Discussion

There is now much evidence that climate change affects the population dynamics of both marine and terrestrial species, ultimately resulting in changes to species distributions and persistence (Hoegh-Guldberg & Bruno, 2010; Parmesan, 2006; Pecl et al., 2017). Although recruitment plays a crucial role in ensuring the long-term population stability of macroalgae, few studies have explored whether recruitment is a bottleneck in a climate change scenario, and its consequences for their population resilience (but see Wernberg et al., 2010). In this study, we coupled laboratory experiments with full life-cycle models to examine how warming-related reductions in the growth and survival of early stages of macroalgae scale up to impact population growth and persistence. Our findings show that warming effects on early life stages have profound consequences for the recovery dynamics of the long-lived macroalgae *Cystoseira zosteroides*. Identifying and quantifying the impacts of temperature on these key demographic processes is a crucial step to understanding the consequences of climate change on macroalgae forests.

We found that increasing temperatures negatively affected key processes of early life stages. *Cystoseira zosteroides* zygotes settlement decreased and early mortality significantly increased in the temperature treatments of 20ºC and 24ºC. These are likely temperature scenarios in the Mediterranean Sea during the coming decades (Galli et al., 2017; Somot et al., 2008). In fact, during exceptionally hot years temperatures can exceed 25ºC in summer and 20ºC at the end of *C. zosteroides* reproductive season at 20 m depth (Fig. 2). This indicates that, in the absence of thermal adaptation, settlement and early survival will be seriously imperiled under a warming scenario. Thermal limits can be highly variable among macroalgae species (Harley et al., 2012), and some species display a wider range of thermal resistance than the early stages of *C. zosteroides* (e.g. *Ecklonia radiata*; Mohring, Wernberg, Wright, Connell, & Russell, 2014). This is likely because intertidal or shallow water species experience wider ranges of daily thermal fluctuations than deeper water species (Harley et al., 2012; Wernberg, de Bettignies, Joy, & Finnegan, 2016).

Impacts of temperature on early *C. zosteroides* stages do not imperil their populations *per se*. The detrimental effects caused by temperature on recruitment could be dampened by the high survival of adults. Undisturbed *C. zosteroides* populations hinge on adult stands (Ballesteros et al., 2009; Capdevila et al., 2015, 2016), so temperature-altered survival of the early life stages has a low impact on population maintenance (Appendix 4: Fig. S4.2). This is in line with life history theory, which predicts that increasing the variation in reproductive processes should have little effect on the population growth of long-lived organisms (Koons, Pavard, Baudisch, & Metcalf, 2009; Morris et al., 2008; Pfister, 1998). Furthermore, long-lived species, such as *C. zosteroides*, often allocate resources in structural biomass to maximize the survival of late stages, which are presumably more resistant to physiological stress (such as in trees; Kelly & Bowler, 2002). Accordingly, several studies provide evidence that adult individuals of brown macroalgae have physiological mechanisms to compensate temperature fluctuations (Graiff, Liesner, Karsten, & Bartsch, 2015; Jueterbock et al., 2014; Pearson et al., 2009). However, not including thermal impacts on adult survival in the modeling process may have made our results overly optimistic. Thermal compensation mechanisms are only effective for a limited range of temperature conditions, above which macroalgae cannot physiologically adjust (Graiff et al., 2015; Wernberg, de Bettignies, et al.,

2016), which may cause extensive canopy loss (Wernberg et al., 2016). The lack of field evidence for warming-related mortality in adult *C. zosteroides* populations suggests that this temperature threshold has not yet been surpassed, but we show that early stages do not have such thermal resistance. Still, we do not have data on the thermal effects on early stages for all the populations modeled here, so our results do not account for thermal adaptation and must be interpreted carefully.

In any case, warming effects on early stages lowered *C. zosteroides* recovery ability and rendered populations more vulnerable to further stressors. Some macroalgal populations are able to withstand mortality events by recruitment pulses as a consequence of relaxing negative density dependence (Dayton & Tegner, 1984; Navarro et al., 2011; Schiel & Foster, 2006), a widespread mechanism among sessile organisms (e.g. trees, Volkov, Banavar, He, Hubbell, & Maritan, 2005; corals, Vermeij & Sandin, 2008). Yet, the negative effects of temperature on reproduction and early life stage development exacerbate the cumulative effects of other disturbances. Similarly, many macroalgae species experience reduced reproductive outputs in populations located at warmer latitudes (Viejo, Martínez, Arrontes, Astudillo, & Hernández, 2011; Wernberg et al., 2010). Some studies have shown that these edge populations are sometimes able to persist through the remaining adults, but this always comes through a reduction of the population resilience (Pearson, Lago-Leston, & Mota, 2009; Wernberg et al., 2010). Given the probable scenario of multiple disturbances, our work illustrates that either directly or indirectly, increasing temperature will render macroalgal populations more vulnerable to further stressors.

Increasing the vulnerability of habitat-forming species in warmer waters can drive major shifts in ecological systems. For example, extreme heat waves have been reported to cause extensive loss of *Macrocystis pyrifera* in California, resulting in a reduction of the canopy cover up to 40 ha with the subsequent depletion of the associated community (Dayton & Tegner, 1984). However, following disturbance, the community experienced a rapid recovery, primarily, due to the long-range dispersal of propagules and adult fragments of *M. pyrifera* mediated by upstream currents (Dayton & Tegner, 1984). Our work illustrates that if temperature continue to rise at the current rate, the impact on early stage development may compromise the ability of macroalgal forests to deal with further disturbances, such as major storms. Indeed, a recent study showed that an extreme heat wave on the west coast of Australia catapulted the collapse of a kelp forest (Wernberg et al., 2016). The inhibition of recruitment, driven by several stressors such as competition with corals and herbivory by tropical fishes, prevented the recovery of kelp beds, which resulted in a completely changed community at the northern latitudes (Wernberg et al., 2016). This illustrates that the impacts of temperature on key demographic processes may have consequences for macroalgae populations functioning, with effects scaling up to the communities that they support.

Numerous reports agree on the projected losses of macroalgae in temperate seas worldwide (Airoldi & Beck, 2007; Assis et al., 2017; Krumhansl et al., 2016; Thibaut et al., 2005). Forecasting the consequences of increasing temperatures is challenging, as global change can have knock-on effects that may add additional layers of complication to such predictions (Vergés et al., 2014; Wernberg et al., 2016). Here we show that high temperatures have the

potential to impact the demographic structure of deep-water macroalgal populations; this, coupled with the predicted increase in the frequency of disturbances, may drive local extinctions (Airoldi & Beck, 2007; Thibaut et al., 2005) or even cause distributional range contractions (Assis et al., 2017; Smale & Wernberg, 2013). Anticipating the direction of change is crucial for the preservation of these habitat-forming organisms, but doing so often requires integrative approaches that can only be achieved by combining field data with laboratory manipulations, to identify key processes driving their population decline. Given our predictions, and those of others, about the increasing vulnerability of macroalgae (Mineur et al., 2014; Wernberg et al., 2010; Wernberg et al., 2016), reinforcing their protection against additional human disturbances might make the difference between local extinctions and demographic viability.

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Authors contributions

P.C., E.C., B.H. and C.L. conceived the idea and the experimental design. P.C., A.M. and G.R. carried out laboratory experiments. P.C., E.C., D.K., J.G., B.H. and C.L. designed and conducted the demographic fieldwork. P.C. and R.S-G. developed the demographic models and statistical analyses. P.C., B.H., R.S-G., and C.L. designed figures. P.C., B.H., R.S-G. and C.L. wrote the manuscript with contributions from all authors.

Data accessibility

The data and R code supporting the results of the study are available in Dryad Digital Repository: https://doi.org/10.5061/dryad.7n474b1 (Capdevila, 2018)

References

Airoldi, L., & Beck, M. W. (2007). Loss, status and trends for coastal marine habitats of Europe. *Oceanography and Marine Biology*, *45*, 345–405. doi:10.1201/9781420050943

Andrews, S., Bennett, S., & Wernberg, T. (2014). Reproductive seasonality and early life temperature sensitivity reflect vulnerability of a seaweed undergoing range reduction. *Marine Ecology Progress Series*, *495*, 119–129. doi:10.3354/meps10567

Assis, J., Berecibar, E., Claro, B., Alberto, F., Reed, D., Raimondi, P., & Serrão, E. A. (2017). Major shifts at the range edge of marine forests: the combined effects of climate changes and limited dispersal. *Scientific Reports*, *7*, 44348. doi:10.1038/srep44348

Ballesteros, E. (1990). Structure and dynamics of the community of *Cystoseira zosteroides* (Turner) C. Agardh (Fucales, Phaeophyceae) in the northwestern Mediterranean. *Scientia Marina*, *54*(3), 217–229.

Ballesteros, E., Garrabou, J., Hereu, B., Zabala, M., Cebrian, E., & Sala, E. (2009). Deep-water stands of *Cystoseira zosteroides* C. Agardh (Fucales, Ochrophyta) in the Northwestern Mediterranean: Insights into assemblage structure and population dynamics. *Estuarine Coastal and Shelf Science*, *82*(3), 477–484. doi:10.1016/j.ecss.2009.02.013

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting Linear Mixed-Effects Models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. doi:10.18637/jss.v067.i01

Bennett, S., Wernberg, T., Arackal Joy, B., de Bettignies, T., & Campbell, A. H. (2015). Central and rear-edge populations can be equally vulnerable to warming. *Nature Communications*, *6*, 10280. doi:10.1038/ncomms10280

Boyd, P. W., Lennartz, S. T., Glover, D. M., & Doney, S. C. (2014). Biological ramifications of climate-change-mediated oceanic multi-stressors. *Nature Climate Change*, *5*(1), 71–79. doi:10.1038/nclimate2441

Brown, J., & Macfadyen, G. (2007). Ghost fishing in European waters: Impacts and management responses. *Marine Policy*, *31*(4), 488-504. doi:10.1016/j.marpol.2006.10.007

Caley, M. J., Carr, M. H., Hixon, M. A., Hughes, T. P., Jones, G. P., & Menge, B. A. (1996). Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics*, *27*(1), 477–500. doi:10.1146/annurev.ecolsys.27.1.477

Capdevila, P., Hereu, B., Riera, J. L., & Linares, C. (2016). Unravelling the natural dynamics and resilience patterns of underwater Mediterranean forests: insights from the demography of the brown alga *Cystoseira zosteroides*. *Journal of Ecology*, *104*(6), 1799–1808. doi:10.1111/1365-2745.12625

Capdevila, P., Linares, C., Aspillaga, E., Navarro, L., Kersting, D. K., & Hereu, B. (2015). Recruitment patterns in the mediterranean deep-water alga *Cystoseira zosteroides*. *Marine Biology*, *162*(6), 1165–1174. doi:10.1007/s00227-015-2658-0

Capdevila, P. (2018). Data from: Warming impacts on early life stages increase the vulnerability and delay the population recovery of a long-lived habitat-forming macroalga. Dryad Digital Repository. doi:10.5061/dryad.7n474b1

Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Lasram, F. B. R., Aguzzi, J., … Voultsiadou, E. (2010). The biodiversity of the Mediterranean Sea: Estimates, patterns, and threats. *PLoS ONE*, *5*(8), e11842. doi:10.1371/journal.pone.0011842

Darling, E. S., & Côté, I. M. (2008). Quantifying the evidence for ecological synergies. *Ecology Letters*, *11*(12), 1278–1286. doi:10.1111/j.1461-0248.2008.01243.x

Dayton, P. K., & Tegner, M. J. (1984). Catastrophic Storms, El Niño, and Patch Stability in a Southern California Kelp Community. *Science*, *224*(4646), 283-285. doi:10.1126/science.224.4646.283

Déqué, M. (2007). Frequency of precipitation and temperature extremes over France in an anthropogenic scenario: Model results and statistical correction according to observed values. *Global and Planetary Change*, *57*(1–2), 16–26. doi:10.1016/j.gloplacha.2006.11.030

Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R., & Mearns, L. O. (2000). Climate Extremes: Observations, Modeling, and Impacts. *Science*, *289*(5487), 2068–2074. doi:10.2307/3078074

Easterling, M. R., Ellner, S. P., & Dixon, P. M. (2000). Size-specific sensitivity: Applying a new structured population model. *Ecology*, *81*(3), 694–708. doi:10.1890/0012-9658(2000)081[0694:SSSAAN]2.0.CO;2

Ellner, S. P., & Rees, M. (2006). Integral projection models for species with complex demography. *The American Naturalist*, *167*(3), 410–428. doi:10.1086/499438

Fox, J., & Weisberg, S. (2011). *An {R} Companion to Applied Regression Thousand* (Second). Oaks CA: SAGE Publications Inc.

Galli, G., Solidoro, C., & Lovato, T. (2017). Marine Heat Waves Hazard 3D Maps and the Risk for Low Motility Organisms in a Warming Mediterranean Sea. *Frontiers in Marine Science*, *4*, 1–14. doi:10.3389/fmars.2017.00136

Garrabou, J., Coma, R., Bensoussan, N., Bally, M., Chevaldonné, P., Cigliano, M., … Cerrano, C. (2009). Mass mortality in Northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. *Global Change Biology*, *15*(5), 1090–1103. doi:10.1111/j.1365-2486.2008.01823.x

Harley, C. D. G., Anderson, K. M., Demes, K. W., Jorve, J. P., Kordas, R. L., Coyle, T. A., & Graham, M. H. (2012). Effects of Climate Change on Global Seaweed Communities. *Journal of Phycology*, *48*(5), 1064–1078. doi:10.1111/j.1529-8817.2012.01224.x

Hereu, B., & Kersting, D. K. (2016). Diseases of coralline algae in the Mediterranean Sea. *Coral Reefs*, *35*(2), 713. doi:10.1007/s00338-016-1428-x

Hoegh-Guldberg, O., & Bruno, J. F. (2010). The Impact of Climate Change on the World's Marine Ecosystems. *Science*, *328*(5985), 1523–1528. doi: 10.1126/science.1189930

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, *50*(3), 346–363. doi:10.1002/bimj.200810425

Hughes, T. P., Linares, C., Dakos, V., van de Leemput, I. A., & van Nes, E. H. (2013). Living dangerously on borrowed time during slow, unrecognized regime shifts. *Trends in Ecology and Evolution*, *28*(3), 149–155. doi:10.1016/j.tree.2012.08.022

IPCC. (2013). Summary for Policymakers. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, 33. doi:10.1017/CBO9781107415324

Irving, A. D., Balata, D., Colosio, F., Ferrando, G. A., & Airoldi, L. (2009). Light, sediment, temperature, and the early life-history of the habitat-forming alga *Cystoseira barbata*. *Marine Biology*, *156*(6), 1223–1231. doi:10.1007/s00227-009-1164-7

Jentsch, A., Kreyling, J., & Beierkuhnlein, C. (2007). A new generation of climate change experiments : events, not trends. *Frontiers in Ecology and the Environment*, *5*(7), 365–374. doi:10.1890/1540-9295(2007)5[365:ANGOCE]2.0.CO;2

Jueterbock, A., Kollias, S., Smolina, I., Fernandes, J. M. O., Coyer, J. A., Olsen, J. L., & Hoarau, G. (2014). Thermal stress resistance of the brown alga *Fucus serratus* along the North-Atlantic coast: Acclimatization potential to climate change. *Marine Genomics*, *13*, 27–36. doi:10.1016/j.margen.2013.12.008

Kelly, C. K., & Bowler, M. G. (2002). Coexistence and relative abundance in forest trees. *Nature*, *417*(6887), 437–440. doi:10.1038/417437a

Kerr, R. A. (2011). Humans Are Driving Extreme Weather; Time to Prepare. *Science*, *334*(6059), 1040. doi:10.1126/science.334.6059.1040

Koons, D. N., Pavard, S., Baudisch, A., & Metcalf, C. J. E. (2009). Is life-history buffering or lability adaptive in stochastic environments? *Oikos*, *118*(7), 972–980. doi:10.1111/j.1600-0706.2009.16399.x

Kroeker, K. J., Gambi, M. C., & Micheli, F. (2013). Community dynamics and ecosystem simplification in a high-CO2 ocean. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(31), 12721–12726. doi:10.1073/pnas.1216464110

Kroeker, K. J., Kordas, R. L., Crim, R. N., & Singh, G. G. (2010). Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecology Letters*, *13*(11), 1419–1434. doi:10.1111/j.1461-0248.2010.01518.x

Krumhansl, K. A., Okamoto, D. K., Rassweiler, A., Novak, M., Bolton, J. J., Cavanaugh, K. C., … Byrnes, J. E. K. (2016). Global patterns of kelp forest change over the past half-century. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(48), 1–6. doi:10.1073/pnas.1606102113

Ladah, L. B., & Zertuche-González, J. A. (2007). Survival of microscopic stages of a perennial kelp (*Macrocystis pyrifera*) from the center and the southern extreme of its range in the Northern Hemisphere after exposure to simulated El Niño stress. *Marine Biology*, *152*(3), 677–686. doi:10.1007/s00227-007-0723-z

Lejeusne, C., Chevaldonné, P., Pergent-Martini, C., Boudouresque, C. F., & Pérez, T. (2010). Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. *Trends in Ecology and Evolution*, *25*(4), 250–260. doi:10.1016/j.tree.2009.10.009

Linares, C., & Doak, D. F. (2010). Forecasting the combined effects of disparate disturbances

on the persistence of long-lived gorgonians: A case study of *Paramuricea clavata*. *Marine Ecology Progress Series*, *402*, 59–68. doi:10.3354/meps08437

Lindenmayer, D., Thorn, S., & Banks, S. (2017). Please do not disturb ecosystems further. *Nature Ecology and Evolution*, *1*, 1–8. doi:10.1038/s41559-016-0031

Ling, S. D., Johnson, C. R., Frusher, S. D., & Ridgway, K. R. (2009). Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(52), 22341–22345. doi:10.1073/pnas.0907529106

Madin, J. S., Hughes, T. P., & Connolly, S. R. (2012). Calcification, Storm Damage and Population Resilience of Tabular Corals under Climate Change. *PLoS ONE*, *7*(10), 1–10. doi:10.1371/journal.pone.0046637

Micheli, F., Halpern, B. S., Walbridge, S., Ciriaco, S., Ferretti, F., Fraschetti, S., … Rosenberg, A. A. (2013). Cumulative human impacts on Mediterranean and Black Sea marine ecosystems: Assessing current pressures and opportunities. *PLoS ONE*, *8*(12), e79889. doi:10.1371/journal.pone.0079889

Mineur, F., Arenas, F., Assis, J., Davies, A. J., Engelen, A. H., Fernandes, F., … De Clerck, O. (2014). European seaweeds under pressure: Consequences for communities and ecosystem functioning. *Journal of Sea Research*, *98*, 91–108. doi:10.1016/j.seares.2014.11.004

Mohring, M. B., Wernberg, T., Wright, J. T., Connell, S. D., & Russell, B. D. (2014). Biogeographic variation in temperature drives performance of kelp gametophytes during warming. *Marine Ecology Progress Series*, *513*, 85–96. doi:10.3354/meps10916

Morris, W., & Doak, D. (2002). *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis.* Sunderland, MA: Sinauer Associates.

Morris, W. F., Pfister, C. A., Tuljapurkar, S., Haridas, C. V., Boggs, C. L., Boyce, M. ., … Menges, E. S. (2008). Longevity can buffer plant and animal populations against changing climate variability. *Ecology*, *89*(1), 19–25. doi:10.1890/07-0774.1

Navarro, L., Ballesteros, E., Linares, C., & Hereu, B. (2011). Spatial and temporal variability of deep-water algal assemblages in the Northwestern Mediterranean: The effects of an exceptional storm. *Estuarine, Coastal and Shelf Science*, *95*(1), 52–58.

doi:10.1016/j.ecss.2011.08.002

Parmesan, C. (2006). Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, *37*(1), 637–669. doi:10.1146/annurev.ecolsys.37.091305.110100

Pearson, G. A., Lago-Leston, A., & Mota, C. (2009). Frayed at the edges: Selective pressure and adaptive response to abiotic stressors are mismatched in low diversity edge populations. *Journal of Ecology*, *97*(3), 450–462. doi:10.1111/j.1365-2745.2009.01481.x

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., … Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*(6332), eaai9214. doi:10.1126/science.aai9214

Pfister, C. A. (1998). Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. *Proceedings of the National Academy of Sciences*, *95*(1), 213–218. doi:10.1073/pnas.95.1.213

R Development Core Team. (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramula, S., Rees, M., & Buckley, Y. M. (2009). Integral projection models perform better for small demographic data sets than matrix population models: A case study of two perennial herbs. *Journal of Applied Ecology*, *46*(5), 1048–1053. doi:10.1111/j.1365-2664.2009.01706.x

Rose, T. H., Smale, D. A., & Botting, G. (2012). The 2011 marine heat wave in Cockburn Sound, southwest Australia. *Ocean Science*, *8*(4), 545–550. doi:10.5194/os-8-545-2012

Russell, B. D., Harley, C. D. G., Wernberg, T., Mieszkowska, N., Widdicombe, S., Hall-Spencer, J. M., & Connell, S. D. (2012). Predicting ecosystem shifts requires new approaches that integrate the effects of climate change across entire systems. *Biology Letters*, *8*(2), 164–166. doi:10.1098/rsbl.2011.0779

Schiel, D. R., & Foster, M. S. (2006). The population biology of large brown seaweeds: Ecological consequences of multiphase life histories in dynamic coastal environments. *Annual Review of Ecology, Evolution, and Systematics*, *37*(1), 343–372. doi:10.1146/annurev.ecolsys.37.091305.110251

Smale, D. A., & Wernberg, T. (2013). Extreme climatic event drives range contraction of a

habitat-forming species. *Proceedings. Biological Sciences / The Royal Society*, *280*(1754), 20122829. doi:10.1098/rspb.2012.2829

Somot, S., Sevault, F., Déqué, M., & Crépon, M. (2008). 21st century climate change scenario for the Mediterranean using a coupled atmosphere-ocean regional climate model. *Global and Planetary Change*, *63*(2–3), 112–126. doi:10.1016/j.gloplacha.2007.10.003

Susini, M. L., Mangialajo, L., Thibaut, T., & Meinesz, A. (2007). Development of a transplantation technique of *Cystoseira amentacea* var. *stricta* and *Cystoseira compressa*. *Hydrobiologia*, *580*, 241–244. doi:10.1007/s10750-006-0449-9

Thibaut, T., Pinedo, S., Torras, X., & Ballesteros, E. (2005). Long-term decline of the populations of Fucales (*Cystoseira* spp. and *Sargassum* spp.) in the Albères coast (France, North-western Mediterranean). *Marine Pollution Bulletin*, *50*(12), 1472–1489. doi:10.1016/j.marpolbul.2005.06.014

Vergés, A., Tomas, F., Cebrian, E., Ballesteros, E., Kizilkaya, Z., Dendrinos, P., … Sala, E. (2014). Tropical rabbitfish and the deforestation of a warming temperate sea. *Journal of Ecology*, *102*(6), 1518–1527. doi:10.1111/1365-2745.12324

Vermeij, M. J. A., & Sandin, S. A. (2008). Density-dependent settlement and mortality structure the earliest life phases of a coral population. *Ecology*, *89*(7), 1994–2004. doi:10.1890/07-1296.1

Viejo, R. M., Martínez, B., Arrontes, J., Astudillo, C., & Hernández, L. (2011). Reproductive patterns in central and marginal populations of a large brown seaweed: Drastic changes at the southern range limit. *Ecography*, *34*(1), 75–84. doi:10.1111/j.1600-0587.2010.06365.x

Volkov, I., Banavar, J. R., He, F., Hubbell, S. P., & Maritan, A. (2005). Density dependence explains tree species abundance and diversity in tropical forests. *Nature*, *438*, 658–661. doi:10.1038/nature04030

Wernberg, T., Bennett, S., Babcock, R. C., Bettignies, T. De, Cure, K., Depczynski, M., … Wilson, S. (2016). Climate-driven regime shift of a temperate marine ecosystem. *Science*, *353*(6295), 169–172. doi:10.1126/science.aad8745

Wernberg, T., de Bettignies, T., Joy, B. A., & Finnegan, P. M. (2016). Physiological responses of habitat-forming seaweeds to increasing temperatures. *Limnology and*

Oceanography, *6*(6), 2180–2190. doi:10.1002/lno.10362

Wernberg, T., Smale, D. A., & Thomsen, M. S. (2012). A decade of climate change experiments on marine organisms: Procedures, patterns and problems. *Global Change Biology*, *18*(5), 1491–1498. doi:10.1111/j.1365-2486.2012.02656.x

Wernberg, T., Thomsen, M. S., Tuya, F., Kendrick, G. A., Staehr, P. A., & Toohey, B. D. (2010). Decreasing resilience of kelp beds along a latitudinal temperature gradient: Potential implications for a warmer future. *Ecology Letters*, *13*(6), 685–694. doi:10.1111/j.1461-0248.2010.01466.x

Yeh, S.-W., Kug, J.-S., Dewitte, B., Kwon, M.-H., Kirtman, B. P., & Jin, F.-F. (2009). El Niño in a changing climate. *Nature*, *461*(7263), 511–514. doi:10.1038/nature08316

Figure captions

Figure 1. Life cycle of *Cystoseira zosteroides.* Illustration of the possible fates of each of *C. zosteroides* life stages with special attention to the early phases. Once mature individuals reproduce (ϕ_i*δ), zygotes settle into the ground with a given probability (ε). Then these zygotes become germlings which must survive (σ_s), to become recruits. These two processes are colored in red because the effect of temperature has been quantified for both. Physical disturbances (here storms and ghost fishing nets) affect the survival of adult phases. Adult individual draw modified from Ballesteros (1990), lightning from de Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

Figure 2. Thermal regimes at the three locations where *Cystoseira zosteroides* populations were monitored at the depth range and years that were studied. Monthly mean temperature cycle (±SD) at 20 and 35 m depth for Cap de Creus Natural Park and Montgrí, Medes Islands, & Baix Ter Natural Park, and at 25 and 35 m depth in Columbretes Islands Marine Reserve (see map at Fig. S1). Vertical dotted lines indicate the reproductive period of *Cystoseira zosteroides*. Horizontal lines indicate the treatments used in our experiment. Boxplots of mean hourly temperature records (of all studied years) considering the April to July *Cystoseira zosteroides* reproductive period (b) and boxplots considering only the maximum annual temperature records (c). Cap 20 m and Cap 35 m: Cap de Creus Natural Park data at 20 and 35 m respectively. Mon 20 m and Mon 35 m: Montgrí, Medes Islands, & Baix Ter Natural Park data at 20 and 35 m respectively. Col 25 m and Col 35 m: Columbretes Islands Marine Reserve at 25 and 35 m.

Figure 3. Effects of temperature on settlement (a) and germling survivorship (b). (a) Density of recruits (individuals/cm^2) after one week of culturing fertile branches in the aquaria at the treatments of 16ºC, 20ºC, and 24ºC. Different letters indicate statistically significant different groups between treatments according to the Tukey test. Boxes represent the interquartile range, the horizontal line represents the median, vertical line represents the upper and lower extreme values, and dots are the outlier values. (b) Proportion of surviving

germlings at the different culturing temperatures during the 6 weeks of the experiment. Dots represent the mean survival, and error bars its standard error.

Figure 4. Violin plots representing the probability density data of the years needed to reach the threshold of 0.8 large individuals/m^2 for 1000 projected populations after an 80% increase of mortality at the different temperature scenarios. The horizontal line is the 50^{th} quantile, the point represents the mean and the vertical line shows the standard deviation.

Figure 5. Stochastic population rate of increase (λ_s; a, c) and quasi-extinction probability at 100 years (b, d) of 1000 simulated populations projected over 100 years at different yearly temperature scenarios and increasing physical disturbances, such as storm mortality recurrence (a, b) and fishing mortality recurrence (c,d). Boxes represent the interquartile range, the horizontal line represents the median, vertical line represents the upper and lower extreme values, and black dots represent outliers, defined as points out of the 95% of the interquartile range. The quasi-extinction probability was estimated over 1000 simulated populations. The extinction threshold was assumed to be 1% of the initial population.