Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

Note

Ecophysiological responses of three Mediterranean invasive seaweeds (*Acrothamnion preissii, Lophocladia lallemandii* and *Caulerpa cylindracea*) to experimental warming

Guillermo Samperio-Ramos [a,b], Ylva S. Olsen [c], Fiona Tomas [d,e], Núria Marbà [a,*]

[a] *Department of Global Change Research, IMEDEA (CSIC-UIB), Institut Mediterrani d'Estudis Avançats, Miquel Marquès 21, 07190 Esporles, Illes Balears, Spain*
[b] *Universidad de Las Palmas de Gran Canaria (ULPGC), Facultad de Ciencias del Mar, 35017 Las Palmas de Gran Canaria, Spain*
[c] *The UWA Oceans Institute and School of Plant Biology, The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia*
[d] *Department of Ecology and Marine Resources, IMEDEA (CSIC-UIB), Institut Mediterrani d'Estudis Avançats, Miquel Marquès 21, 07190 Esporles, Illes Balears, Spain*
[e] *Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis 97331, OR, USA*

ARTICLE INFO

ABSTRACT

The Mediterranean Sea is a hotspot for invasive species and projected Mediterranean warming might affect their future spreading. We experimentally examined ecophysiological responses to the temperature range 23–31 °C in three invasive seaweeds commonly found in the Mediterranean: *Acrothamnion preissii, Caulerpa cylindracea* and *Lophocladia lallemandii*. The warming range tested encompassed current and projected (for the end of 21st Century) maximum temperatures for the Mediterranean Sea. Optimal ecophysiological temperatures for *A. preissii, C. cylindracea* and *L. lallemandii* were 25 °C, 27 °C and 29 °C, respectively. Warming below the optimal temperatures enhanced RGR of all studied invasive seaweeds. Although sensitive, seaweed photosynthetic yield was less temperature-dependent than growth. Our results demonstrate that temperature is a key environmental parameter in regulating the ecophysiological performance of these invasive seaweeds and that Mediterranean warming conditions may affect their invasion trajectory.

© 2015 Elsevier Ltd. All rights reserved.

1. Introduction

Bioinvasions are increasing worldwide and rank among the most important threats to ocean biodiversity (e.g., Vitousek et al., 1996; Carlton and Geller, 1993; Worm et al., 2006). The increasing success of invasive species has been attributed to synergistic effects of Global Change affecting both the vectors of introduction and settlement and spreading processes (Sala et al., 2000). After the arrival of a non-indigenous species, its settlement and invasive success depend on the invasibility of the native community and the competitive ability of the non-indigenous species (Blossey and Nötzold, 1995; Kennedy et al., 2002; Inderjit et al., 2006). The environmental conditions at the site of arrival have been identified as key drivers of invasion and climate warming may facilitate the settlement of non-indigenous species that inhabit warmer regions. This highlights climatic warming may be an emerging component of global change contributing to trigger the occurrence

of marine bioinvasions (Stachowicz et al., 2002; Raitsos et al., 2010).

The Mediterranean Sea is a "hot spot" of marine species introductions (Gollach, 2006; Kaluza et al., 2010) and the number of arrivals of non-indigenous species has doubled every 20 years since the early 20th century (Streftaris et al., 2005). Seaweeds are an important component of marine non-indigenous species due to their physiological plasticity, high tolerance to environmental stress and vegetative reproduction (Boudouresque and Velarque, 2002). Non-indigenous seaweeds account for up to 5% of the total flora in some regions and 10–40% of globally introduced species (Johnson and Chapman, 2007). Currently, in the entire Mediterranean basin, at least nine non-indigenous seaweeds are considered to have an invasive behaviour (Ballesteros, 2007). The Mediterranean Sea is warming 3-fold faster than the global ocean (Burrows et al., 2011) and the occurrence and duration of extreme temperature events has increased over the past 50 years (e.g. Vargas-Yáñez et al., 2007). This may lead to a progressive "tropicalization" of Mediterranean ecosystems since species of tropical and subtropical origin may have a competitive advantage over native species in a warming Mediterranean (Bianchi, 2007).

---

* Corresponding author.
   E-mail address: nmarba@imedea.uib-csic.es (N. Marbà).

Temperature is a key factor regulating biological rates pivotal for dispersal and spread of invasive species (Brown et al., 2004; Tilman et al., 2004). The Boltzmann–Arrhenius model from chemical reaction kinetics, incorporated into the Metabolic Theory of Ecology (MTE), can be used to quantify the temperature-associated change of biological rates (Brown et al., 2004) before and beyond the optimal temperature, and to compare the thermal sensitivity across rates and species (Dell et al., 2011). Knowledge on the thermal ecophysiological responses of the invasive species can be used to predict invasive capacities of the species into the Mediterranean Sea. Identification of species optimal temperatures in combination with Mediterranean current temperature and warming projections (Jordà et al., 2012) may help to assess the time window when thermal conditions may enhance the invasion.

Here, we experimentally examine the ecophysiological (growth and photosynthetic yield) responses of three non-indigenous seaweeds *Acrothamnion preissii*, *Lophocladia lallemandii* and *Caulerpa cylindracea* with high rates of spread in the Mediterranean Sea (Piazzi and Balata, 2009; Mineur et al., 2010) to current and projected Mediterranean spring–summer temperatures (Jordà et al., 2012). We do so by culturing seaweeds in short-term mesocosms experiments at a temperature range of 23–31 °C. We compare the optimal temperature and activation energy (Brown et al., 2004) of ecophysiological rates across species and discuss the possible effect of projected Mediterranean warming, under IPCC scenarios of mild emissions, on the invasion of these species during the current Century.

2. Methods

Specimens of *A. preissii, L. lallemandii* and *C. cylindracea* were collected in May and June of 2011 from Dragonera, Balearic Islands, Spain (39°34′05″N; 002°18′06″E) at 4–10 m depth. The *in situ* seawater temperature at the time of seaweed collection ranged from 21 °C to 23 °C. Seawater temperature in the region ranges from 13.28 ± 0.20 °C in February–March (unpublished data) to 27.62 ± 0.55 °C in August (Marbà and Duarte, 2010). The seaweed fragments were transported to the laboratory where they were gently washed with filtered seawater (0.45 μm) and left to acclimatize at 23 °C for three days inside a temperature-controlled chamber.

After the acclimation period, 1 fragment of each species was introduced in a transparent plastic bag filled with 1 L of seawater. Seven replicate bags per macroalgal species were incubated in 150 L mesocosms filled with water at the following treatment temperatures: 23, 25, 27, 29 and 31 °C. We used a total of 5 mesocosms, one per treatment temperature, and each mesocosm contained incubation bags of all species. The temperature inside each mesocosm was regulated and recorded with an IKS-Aquastar system using IKS-Aquastar-winsoft software. This set up maintained target treatment temperatures constant ($SE_{target\ temperature}$ = 0.01) during the experiment. The bags were submerged in the mesocosms with the top of each bag sticking out above the surface and open to the atmosphere. This allowed for full gas exchange with the atmosphere while the water inside the bags was mixed by stirring of the mesocosms using aquarium pumps. Fluorescent aquarium growth lamps with neutral day-length (12 h) illuminated the mesocosms. Light intensity inside the plastic bags was measured with a HOBO light sensor and averaged 160 μmol m^{-2} s^{-1}. The seawater in the incubation bags was renewed every 3 days (2 times in total). Some bags were perforated during the experiment and algal material lost. These replicates were excluded from analysis and the number of replicate measurements used for the analysis therefore varied from 3 to 7. The experiment lasted for 8 days.

2.1. Growth rates

We estimated Relative Growth Rate (RGR, d^{-1}) for all 3 seaweed species. We blotted the surface of the experimental fragments dry and recorded wet weight at the beginning and end of each experiment. At the end of the experiment we dried the fragments at 60 °C for five days and obtained dry weights. We estimated initial dry weights from linear relationships between wet and dry weights of each species. The RGR (d^{-1}) was estimated as the exponential increase in biomass using the equation (Hunt, 1990):

$$RGR = (\ln DW_2 - \ln DW_1)/t \tag{1}$$

where DW_1 and DW_2 are the dry weights at the beginning and the end of the experiment, respectively, and t is the number of days in culture.

2.2. Photosynthetic yield

Using a pulse amplitude modulated (PAM) fluorometer (Waltz Diving-PAM) we determined the baseline photosynthetic yield and the effect of experimental warming on photosynthetic yield of the seaweeds by measuring optimal quantum yield on dark-adapted fragments immediately after collection in the field and at the end of the experimental period.

2.3. Temperature relationships and activation energy of biological rates

The sensitivity of biological activity of seaweeds to warming was characterised by quantifying the optimal temperature for growth and photosynthetic yield and the rate of change and activation energy of seaweed ecophysiological traits. The response of any biological rate to increasing temperature describes a bell shaped function along the thermal breadth it operates. We therefore estimated the rate of change and activation energy for the thermal ranges before (rise component) and after (fall component) the optimal temperature (i.e. temperature of maximum rate), both including the biological activity at optimal temperature.

The rate of change of seaweed growth and yield with increasing temperature was calculated as the slope of the fitted linear regression equation between seaweed traits and temperature when it included at least 3 subsequent temperature treatments. Otherwise, the rate of change of seaweed traits was calculated as the difference between the magnitude of responses at two consecutive temperature treatments divided by the difference in temperature.

We estimated the Activation Energy (E) using the MTE equation (Brown et al., 2004; Dell et al., 2011):

$$R = R_o\, e^{(-E/kT)} \tag{2}$$

where R is the biological parameter (i.e. RGR and yield), R_o is a scaling coefficient dependent on the organism, E is the activation energy, k is Boltzmann's constant (8.62 * 10^{-5} eV K^{-1}) and T is the temperature (in kelvin).

2.4. Data analysis

We used one-way analysis of variance (ANOVA) to test for significant effects of temperature on RGR and quantum yield in each of the three species for each experiment. The assumptions of normality and homoscedasticity were verified using the Shapiro–Wilk and Barlett tests, and data were transformed when necessary as indicated in the results section. The relationship between photosynthetic yield and relative growth was examined

with linear regression analysis. For all statistical analyses, a probability level of $\alpha = 0.05$ was considered.

3. Results

3.1. Growth

Average seaweed RGR across the experimental temperature range differed significantly between the species, *C. cylindracea* growing 1.8-fold and 2.9-fold faster than *L. lallemandii* and *A. preissii*, respectively (Fig. 1a). Temperature had a significant effect on the relative growth rate in all three seaweeds (ANOVA, $p < 0.05$), but the responses and optimum temperatures differed among species. The RGR of *A. preissii* increased between 23 °C and 25 °C where it reached its maximum of 0.034 ± 0.002 g dry wt d^{-1} (Fig. 1a, Tables 1 and 2). Above this temperature, growth of *A. preissii* steadily declined with warming and the lowest RGR of 0.006 ± 0.002 g dry wt d^{-1} was measured at 31 °C (Fig. 1a, Table 1). We also detected loss of turgidity and pigmentation in *A. preissii* (visual observations) at high temperatures (29 °C and 31 °C).

RGR of *L. lallemandi* exhibited the greatest variability out of the three seaweeds in response to warming RGR in *L. lallemandi* increased sharply with warming from 23 °C to 29 °C (Fig. 1a), reaching its peak rate of 0.064 ± 0.007 g dry wt d^{-1} (Fig. 1a, Tables 1 and 2). Warming exceeding 29 °C triggered a rapid decline in RGR suggesting this species has a relatively narrow range of optimum temperature for growth.

The response of *C. cylindracea* to temperature was moderate and RGR was significantly the highest at the intermediate temperatures tested (25–29 °C, Fig. 1a, Table 1). The lowest RGR of *C. cylindracea* was recorded at 23 °C (Fig. 1a).
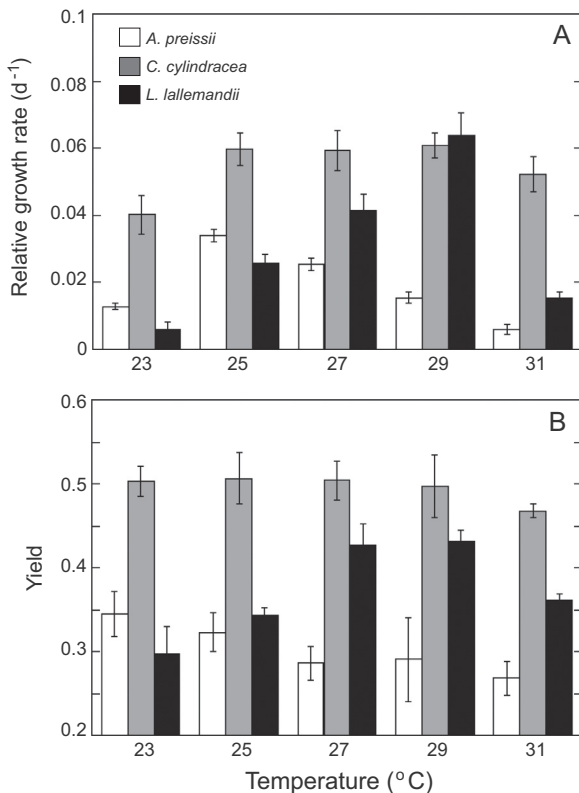

Fig. 1. Average relative growth rate (panel A) and quantum yield (panel B) of *Acrothamnion preissii*, *Caulerpa cylindracea* and *Lophocladia lallemandii* in response to experimental warming. Error bars indicate the standard error of the mean.

Table 1
Results (p-values) from TukeyHSD comparisons of relative growth rate (RGR, d^{-1}) for *Acrothamnion preissii*, *Caulerpa cylindracea* and *Lophocladia lallemandii* and optimum quantum yield (Y) for *Lophocladia lallemandii*. No significant differences were found for Y in *A. preissii* or *C. cylindracea*. Significant differences are highlighted in bold.

Variable		Temperature (°C)			
		25	27	29	31
A. preissii					
RGR	23	**<0.01**	**<0.01**	0.891	0.105
	25		**<0.01**	**<0.01**	**<0.01**
	27			**<0.01**	**<0.01**
	29				**<0.05**
C. cylindracea					
RGR	23	0.085	**<0.05**	0.083	0.428
	25		0.996	1	0.851
	27			1	0.639
	29				0.804
L. lallemandii					
RGR	23	**<0.01**	**<0.01**	**<0.01**	0.436
	25		**<0.05**	**<0.01**	0.377
	27			**<0.01**	**<0.01**
	29				**<0.01**
Y	23	0.855	**<0.05**	**<0.05**	0.443
	25		0.083	0.098	0.904
	27			0.994	0.587
	29				0.502

3.2. Photosynthetic yield

Photosynthetic quantum yields measured in the field immediately after collection were 0.646 ± 0.019 in *C. cylindracea*, 0.542 ± 0.016 in *A. preissii* and in *L. lallemandii* 0.429 ± 0.014. For *C. cylindracea* and *A. preissii* the average quantum yields measured in the field were higher than those measured in the experiment (Welch two sample *t*-test; $t = 8.66$, df $= 5.91$, $p < 0.001$ and $t = 12.01$, df $= 11.66$, $p < 0.001$ respectively.) In *L. lallemandii* quantum yield was slightly higher in the experiment compared to measurements made in the field (Welch two sample *t*-test; $t = -4.33$, df $= 5.82$, $p < 0.01$).

Quantum yield variability across the temperature range examined mirrored that of growth. *C. cylindracea* showed the least variation in yield, maintaining high yield values across the entire tested temperature range, whereas optimal temperatures for yield in *A. preisii* and *L. lallemandii* where similar to those for growth rates (Fig. 1b, Table 2).

Temperature had no significant effect on yield in *A. preissii* or *C. cylindracea* (ANOVA, $p > 0.05$). Quantum yield in *L. lallemandii* increased significantly with temperature from a minimum at 23 °C (0.297 ± 0.032) peaking at 29 °C (0.431 ± 0.013, Fig. 1b, Tables 1 and 2).

Variability in photosynthetic yield significantly correlated to that in RGR in *L. lallemandii* and *A. preissii* ($R^2 = 0.22$, $F = 11.74$, $p < 0.01$ and $R^2 = 0.55$, $F = 35.03$, $p < 0.0001$ respectively) (Fig. 2). No relationship was found between yield and RGR in *C. cylindracea* (Fig. 2).

3.3. Temperature relationships and activation energy

The biological activity of *A. preissii* and *L. lallemandii* was more dependent on thermal conditions within the range of 23–31 °C than that of *C. cylindracea*. Indeed, thermal conditions accounted for most (>80%) variability in RGR of *A. preissii* and *L. lallemandii* whereas they only explained 22% of RGR variability in *C. cylindracea* (Table 2). Similarly, for the thermal range tested, the rate of increase of RGR per degree Celsius in *A. preissii* and *L. lallemandii* was twice that in *C. cylindracea* (Table 2). The activation energy

Table 2
Optimal temperature, biological activity at optimal temperature (Optimal biological activity), and the rate of change and activation energy (E_{rise}, E_{fall}) of biological activity during the rise and fall component of the bell-shaped response to experimental warming (23–31 °C) of *Acrothamnion preissii*, *Caulerpa cylindracea* and *Lophocladia lallemandii*. See methods for calculation of the rates of rise and fall and the activation energies. When at least the rise or fall component spanned across 3 consecutive treatment temperatures the slope, standard error of the slope, coefficient of determination, significance of the fit and number of observations are provided inside brackets. Only average rates of change and activation energy of biological activity are provided when the rise or fall component spanned across 2 consecutive treatment temperatures and the biological activity were statistically different (TukeyHSD). ns: not significant.

| Species	Variable	T_{opt} (°C)	Optimal activity (Average ± SE)	Rate of rise (°C^{-1})	E_{rise} (eV)	Rate of fall (°C^{-1})	E_{fall} (eV)
A. preissii	RGR (d^{-1})	25	0.03 ± 0.00	0.010	3.22	−0.004 ± 0.000 ($R^2 = 0.88$; $p < 0.0001$; $N = 20$)	2.36 ± 0.32 ($R^2 = 0.76$; $p < 0.0001$; $N = 20$)
	Yield	23	0.35 ± 0.03			−0.009 ± 0.006 ($R^2 = 0.16$; $p < 0.05$; $N = 24$)	0.26 ± 012 ($R^2 = 0.17$; $p < 0.05$; $N = 24$)
C. cylindracea	RGR (d^{-1})	27	0.06 ± 0.00	0.005 ± 0.002 ($R^2 = 0.22$; $p < 0.05$; $N = 20$)	0.81 ± 0.32 ($R^2 = 0.26$; $p < 0.05$; $N = 20$)	ns	ns
	Yield	25	0.51 ± 0.06	ns	ns	ns	ns
L. lallemandii	RGR (d^{-1})	29	0.06 ± 0.01	0.009 ± 0.001 ($R^2 = 0.83$; $p < 0.0001$; $N = 19$)	3.31 ± 0.45 ($R^2 = 0.76$; $p < 0.0001$; $N = 19$)	−0.020	4.21
	Yield	29	0.43 ± 0.01	0.025 ± 0.006 ($R^2 = 0.45$; $p < 0.0005$; $N = 17$)	0.57 ± 0.13 ($R^2 = 0.55$; $p < 0.0005$; $N = 19$)	ns	ns
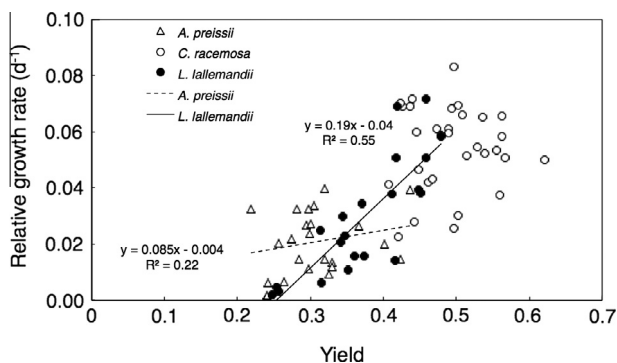
Fig. 2. Relative growth rate (d^{-1}) and quantum yield of *Acrothamnion preissii*, *Caulerpa cylindracea* and *Lophocladia lallemandii* during the experiments. Significant relationships between variables are indicated for *A. preissii* and *L. lallemandii*. No significant relationship was found for *C. cylindracea*.

during the rise and fall components of the growth response to warming in *A. preissii* and *L. lallemandii* were high (>2 eV) and more than twice those of *C. cylindracea* (Table 2). Although sensitive, seaweed photosynthetic yield was less temperature-dependent than growth as reflected by the lower coefficient of determination of temperature–yield relationships and lower activation energy when it significantly responded to temperature change (fall phase in *A. preissii*, rise phase in *L. lallemandii*, Table 2).

4. Discussion

Our results demonstrate that temperature is a key environmental parameter in regulating the ecophysiological performance of the studied invasive seaweeds. Yet, the three Mediterranean invasive species studied – *A. preissii*, *L. lallemandii* and *C. cylindracea* – exhibited notable differences in growth and photosynthetic rates along the temperature range tested. This reveals species-specific differences in ecophysiological rates, in optimal thermal ranges for population development as well as in sensitivity to warming.

Optimal temperatures for growth and photosynthetic yield of the three studied seaweeds are within the thermal range investigated. Yet, *A. preissii* has lower optimal temperature than *L. lallemandii* and *C. cylindracea*, and warming exceeding 23–25 °C would stress this species by suppressing its growth and photosynthetic yield. Both growth and photosynthetic yield of *L. lallemandii* increase with warming up to 29 °C. The very low values of

quantum yield of *L. lallemandii* measured at 23 °C may indicate photosynthetic stress at the lower range of temperatures tested. Despite *C. cylindracea* displays maximum growth rate and yield at 27 °C and 25 °C, respectively (Table 2), it maintains high ecophysiological rates between 25 °C and 29 °C (Fig. 1). Uniform growth and yield responses of *C. cylindracea* in the Mediterranean to the temperature range 22–30 °C have also been described in the past using specimens from a Gulf of Ischia population (Flagella et al., 2008) and an unknown donor population (Gattuso and Jaubert, 1985). Our yield values, however, are slightly lower than those (yield = 0.75 for temperature range 22–30 °C) measured by Flagella et al. (2008), reflecting differences between studied populations or suggesting that our procedure might have caused some stress to specimens.

A. preissii and *L. lallemandii* are more sensitive to warming within the thermal range 23–31 °C than *C. cylindracea*, as reflected by their faster rates of change of growth and yield per increasing degree Celsius, the coefficient of determination of ecophysiology–temperature relationships and the activation energy of biological rates (Table 2). The activation energy of *A. preissii* and *L. lallemandii* growth rate for the rise and fall components are more than 2-fold higher than average values reported for biological systems (i.e. $E_{rise} = 0.66 ± 0.05$ eV, $E_{fall} = 1.15 ± 0.39$ eV; Dell et al., 2011), revealing that thermal conditions within the studied range may play a key role triggering and regulating the abundance of these species in the Mediterranean. Conversely, the activation energy for the rise component of *C. cylindracea* growth is similar to the average value reported for biological systems (Dell et al., 2011). In addition, the sensitivities of the studied species to warming differ depending on whether they are exposed to thermal conditions below or above the optimal ecophysiological temperature.

The differences observed of the studied invasive species to temperature may reflect the thermal ranges their native populations are exposed to. *A. preissii*, the studied seaweed with the lowest optimal temperature and the most vulnerable one to the warming range tested, is native to South Australia (cf Verlaque, 1994; AlgaeBase, 2011). There, surface seawater temperature annually ranges from 15 °C to 22 °C, considerably lower than the range tested in our experiment. Native *L. lallemandii* populations, distributed along the Indian coastal ocean and the Red Sea (Verlaque, 1994; AlgaeBase, 2011), have evolved in a geographic range characterised by warm seawater (range 25–31 °C). For instance in the Red Sea and the Arabic Gulf, temperature rarely drops below 20 °C (Traoug et al., 1999; Abualnaja, 2009). The tropical origin of *L. lallemandii* could be reflected in the high optimal

temperature and the rapid acceleration of growth of this species observed in our study. Molecular markers and morphological traits identify that *C. cylindracea* invading the Mediterranean Sea originates from South Western Australia, where surface seawater temperature annually ranges between 15 °C and 24 °C (Verlaque et al., 2003). Yet, the invasive seaweeds *A. preissii* and *C. cylindracea* exhibit optimal responses at temperatures exceeding the upper temperature range inhabited by native populations. Similarly, a recent study (Zerebecki and Sorte, 2011) demonstrates that tunicates and briozoans growing beyond their native biogeographical boundaries have a broader range or higher limit of thermal tolerance than native ones.

The thermal ecophysiological responses of the invasive seaweeds observed in our study agree with the current thermal range encompassed by their growing season in Western Mediterranean shallow waters. Whereas populations of *A. preissii* are present during spring-early summer, those of *C. cylindracea* develop from August to December (Box et al., 2010) and those of *L. lallemandii* are almost confined to the month with the highest SST (September, Ballesteros et al., 2007). The thermal responses of invasive seaweeds we found suggest that the Mediterranean warming projected for the current century, under moderate scenarios of greenhouse gas emissions (SERES A1B; Jordà et al., 2012), is likely to drive their spread in the basin. An ensemble of 12 global and regional atmospheric–ocean circulation models project current Mediterranean summer temperature (27 °C in the Western basin) to increase by two degrees Celsius by year 2050 and by 3.4 °C by year 2100 (Jordà et al., 2012). Under these projected thermal conditions, our findings suggest *A. preissii* to shift its phenology towards early spring. We might expect *C. cylindracea* to continue increasing its presence and spread in summer as well as widen its growing season. Similarly, projected warming may facilitate the spread of *L. lallemandii* in the Mediterranean by enhancing growth rates and widening the growing season. However, projected maximum summer Mediterranean SST for the second half of the 21st Century (Jordà et al., 2012) would exceed optimal temperatures for growth of *C. cylindracea* and *L. lallemandii*, and trigger the decline of abundance and spread of these species during late summer. Although our study has not addressed the possible interactions between invasive seaweeds, Piazzi and Cinelli (2002) observed that turfs composed of the invasive seaweed *Womersleyella setacea* and *A. preissii* facilitated the spread of *C. cylindracea*. If so, warming could additionally accelerate the invasion of some species through changes in species interactions.

In conclusion, our results demonstrate that the Mediterranean invasive seaweeds *A. preissii*, *L. lallemandii* and *C. cylindracea* exhibit optimal growth and photosynthetic yield within the thermal range projected for the Mediterranean during the 21st Century. Mediterranean warming, however, is expected to affect the invasion trajectory of these three species differently given their thermal ecophysiological responses observed in our study. Our results suggest that the development and proliferation of populations of these invaders may be favoured by the temperature increase predicted for coming decades as their growing season is extended. In addition, the algae may accommodate periods where temperatures exceed their thermal optima by shifting phenology as already demonstrated for marine biota (Poloczanska et al., 2013). Hence, the Mediterranean seawater warming projected for the current century could trigger high abundances of the studied invasive seaweeds in the Mediterranean coastal areas and thus accelerate the decline of the already threaten native habitats. Particularly, given the vulnerability to warming of native critical habitat-forming species such as seagrasses (e.g. Marbà and Duarte, 2010) and gorgonians (e.g. Coma et al., 2009), the projected increase in temperatures may severely reduce biotic resistance of Mediterranean native communities to the invasion of these non-indigenous seaweeds. Global actions towards mitigation of climate warming would help preventing the rapid proliferation of invasive seaweeds.

References

Abualnaja, Y., 2009. Estimation of the net surface heat flux in the Arabian Gulf based on the equilibrium temperature. JKAU, Mar. Sci. 20, 21–29.

AlgaeBase, 2011. Department of Education & Science, Ireland.

Ballesteros, E., 2007. Invasive algae in Mediterranean benthic ecosystems: extent and evaluation of the problem. In: 7th MEDPAN Workshop.

Ballesteros, E., Cebrían, E., Alcoverro, T., 2007. Mortality of shorts of Posidonia oceanica following meadows invasions by the red alga *Lophocladia lallemandii*. Bot. Mar. 50, 8–13.

Bianchi, C.N., 2007. Biodiversity issues for the forthcoming tropical Mediterranean Sea. Hydrobiologia 580, 7–21.

Blossey, B., Nötzold, R., 1995. Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. Ecology 83, 887–889.

Boudouresque, C.F., Velarque, M., 2002. Biological pollution in the Mediterranean Sea: invasive versus introduced macrophytes. Mar. Pollut. Bull. 44, 32–38.

Box, A., Martín, D., Deudero, S., 2010. Changes in seagrass polychaete assemblages after invasión by *Caluerpa racemosa var. Cylindracea* (Chlorophyta: Caulerpales): community structure, trophic guilds and taxonomic distictness. Scientia 74 (2), 317–329.

Brown, J.H., Gilloly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. Ecology 85 (7), 1771–1789.

Burrows, M.T. et al., 2011. The pace of shifting climate in marine and terrestrial ecosystems. Science 334, 652–655.

Carlton, J.T., Geller, J.B., 1993. Ecological roulette: the global transport of nonindigenous marine organism. Science 261, 78–82.

Coma, R., Ribes, M., Serrano, E., Jiménez, E., Salat, J., Pascual, J., 2009. Global warming-enhanced stratification and mass mortality events in the Mediterranean. Proc. Natl. Acad. Sci. 106, 6176–6181.

Dell, A.I., Pawar, S., Savage, V.M., 2011. Systematic variation in the temperature dependence of physiological and ecological traits. Proc. Natl. Acad. Sci. 108, 10591–10596.

Flagella, M.M., Lorenti, M., Buia, M.C., 2008. Temperature response in a shallow-water Mediterranean population of Caulerpa racemosa var. cylindracea (Caulerpales, Chlorophyta), and a possible strategy of season anticipation. Bot. Mar. 51, 278–284.

Gattuso, J.P., Jaubert, J., 1985. Photosynthesis and respiration of *Caulerpa racemosa* (Chlorophyceae, Caulerpales) grown in aquaria: effects of light and temperature. Bot. Mar. 27, 327–332.

Gollach, S., 2006. Overview on introduced aquatic species in Europe navigational and adjacent waters. Helgol. Mar. Res. 60, 84–89.

Hunt, R., 1990. Basic Growth Analysis. Unwin Hyman Ltd., London, 112 pp..

Inderjit, A., Chapman, D., Ranelletti, M., Kaushik, S., 2006. Invasive marine algae: an ecological perspective. Bot. Rev. 72 (2), 153–178.

Johnson, C.R., Chapman, R.O., 2007. Seaweed invasions: introduction and scope. Bot. Mar. 50, 321–325.

Jordà, G., Marbà, N., Duarte, C.M., 2012. Mediterranean seagrass vulnerable to regional climate warming. Nat. Clim. Change 2, 821–824. http://dx.doi.org/10.1038/Nclimate1533.

Kaluza, P., Kölzsch, A., Gastner, M.T., Blasius, B., 2010. The complex network of Global cargo ships movements. J. Roy. Soc. 7, 1093–1103.

Kennedy, T.A., Naemm, S., Howe, K.M., Knops, J.M.H., Tilman, D., Reich, P., 2002. Biodiversity as a barrier to ecological invasion. Nature 417, 636–638.

Marbà, N., Duarte, C.M., 2010. Mediterranean warming triggers seagrass (*Posidonia oceanica*) shoot mortality. Glob. Change Biol. 16, 2366–2375.

Mineur, F., Davies, A.J., Maggs, C.A., Verlaque, M., Johnson, M.P., 2010. Fronts, jumps and secondary introductions suggested as different invasion patterns in marine species, with an increase in spread rates over time. Proc. Roy. Soc. B 277, 2693–2701.

Piazzi, L., Balata, D., 2009. Invasion of alien macroalgae in different Mediterranean habitats. Biol. Invasions 11, 193–204.

Piazzi, L., Cinelli, F., 2002. Effect of spread of introduced *Rhodophyceae Acrothamnion preissii* and *Wormersleyella sestacea* on the macroalgal community of Posidonia oceanica rhizomes in the Western Mediterranean Sea. Cryptogamie Algol. 21 (3), 291–300.

Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J., Brander, K., Bruno, J.F., Buckley, L.B., Burrows, M.T., Duarte, C.M., Halpern,

B.S., Holding, J., Kappel, C.V., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F., Thompson, S.A., Richardson, A.J., . Global imprint of climate change on marine life. Nat. Clim. Change 3 (10), 919–925.

Raitsos, D.E., Beaugrand, G., Georgopoulos, D., Zenetos, A., Pancucci-Papadopoulou, M., Theocharis, A., Pappathanassiou, E., 2010. Global Climate Change amplifies the entry of tropical species into the Eastern Mediterranean Sea. Limnol. Oceanogr. 55 (4), 1478–1484.

Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenekke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. Science 287, 1770–1774.

Stachowicz, J.J., Terwin, J.R., Whithlatch, R.B., Osman, R., 2002. Linking climate change and biological invasions: ocean warming facilitates non-indigenous species invasions. Proc. Nat. Acad. Sci. 99 (24), 15497–15500.

Streftaris, N., Zenetos, A., Papathanassiou, E., 2005. Globalisation in marine ecosystems: the story of non-indigenous marine species across European seas. Oceanogr. Mar. Biol. 43, 419–453.

Tilman, D., Hillerrislambers, J., Harpole, S., Dybzynski, R., Fargione, J., Clark, C., Lehman, C., 2004. Does metabolic theory apply to community ecology? It's a matter of scale. Ecology 85 (7), 1797–1799.

Traoug, E., Garrett, C., Outerbridge, R., Gilman, C., 1999. The heat and freshwater budgets of the Red Sea. J. Phys. Oceanogr. 29 (10), 2504–2522.

Vargas-Yáñez, M., García-Martínez, M.C., Moya-Ruiz, F., Tel, E., Parrilla, G., Plaza, F., Lavín, A., 2007. Cambio Climático en el Mediterráneo español. Instituto Español de Oceanografía (IEO). Ministerio de Educación y Ciencia, pp. 43–57.

Verlaque, M., 1994. Inventaire des plantes introduites en Méditerranée: origines et répercussions sur l'environnement et les activités humaines. Oceanol. Acta 17, 1–23.

Verlaque, M., Durand, C., Huisman, J.M., Boudouresque, C.F., Le Parco, Y., 2003. On the identity and origin of the Mediterranean invasive *Caulerpa racemosa* (*Caulerpales, Chlorophyta*). Eur. J. Phycol. 38 (4), 325–339.

Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Westbrooks, R., 1996. Biological invasions as global environmental change. Am. Sci. 84, 468–478.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., Watson, R., 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314, 787–790.

Zerebecki, R.A., Sorte, C.J.B., 2011. Temperature tolerance and stress proteins as mechanisms of invasive species success. PLoSOne 6 (4), e14806. http://dx.doi.org/10.1371/journal.pone.0014806.