Seasonal variations in photosynthetic irradiance response curves of macrophytes from a Mediterranean coastal lagoon

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Abstract:

The main photosynthesis and respiration parameters (dark respiration rate, light saturated production rate, saturation irradiance, photosynthetic efficiency) were measured on a total of 23 macrophytes of the Thau lagoon (2 Phanerogams, 5 Chlorophyceae, 10 Rhodophyceae and 6 Phaeophyceae). Those measurements were performed in vitro under controlled conditions, close to the natural ones, and at several seasons. Concomitantly, measurements of pigment concentrations, carbon, phosphorous and nitrogen contents in tissues were performed. Seasonal intra-specific variability of photosynthetic parameters was found very high, enlightening an important acclimatation capacity. The highest photosynthetic capacities were found for Chlorophyceae (e.g. *Monostroma obscurum* thalli at 17 °C, 982 µmol O_2 g^{-1} dw h^{-1} and 9.1 µmol O_2 g^{-1} dw h^{-1}/µmol photons m^{-2} s^{-1}, respectively for light saturated net production rate and photosynthetic efficiency) and Phanerogams (e.g. *Nanozostera noltii* leaves at 25 °C, 583 µmol O_2 g^{-1} dw h^{-1} and 2.6 µmol O_2 g^{-1} dw h^{-1}/µmol photons m^{-2} s^{-1} respectively for light saturated net production rate and photosynthetic efficiency). As expected, species with a high surface/volume ratio were found to be more productive than coarsely branched thalli and thick blades shaped species. Contrary to R_d (ranging 6.7–794 µmol O_2 g^{-1} dw h^{-1}, respectively for *Rytiphlaea tinctoria* at 7 °C and for *Dasya sessilis* at 25 °C) for which a positive relationship with water temperature was found whatever the species studied, the evolution of P/I curves with temperature exhibited different responses amongst the species. The results allowed to show summer nitrogen limitation for some species (*Gracilaria bursa-pastoris* and *Ulva* spp.) and to propose temperature preferences based on the photosynthetic parameters for some others (*N. noltii*, *Zostera marina*, *Chaetomorpha linum*).

Keywords: Photosynthesis; Light response curve; Macrophytes; Oxygen method; Seasonal variations; Seagrasses; Chlorophyceae; Rhodophyceae; Phaeophyceae; Thau lagoon

1. INTRODUCTION

From bibliographic analysis and new collections, a total of 196 taxa and stadia (life-history phases) of macroalgae were numbered in Thau Lagoon (Mediterranean Sea, France, 43°24'N and 3°32'E) far above the other Mediterranean lagoons (Verlaque, 2001). This lagoon is the seat of an important marine species introduction (45 recently introduced macroalgae), with shellfish cultivation activity recognised as the main vector of introduction (Verlaque, 2001). The success of these exotic species is probably due to their physiological plasticity as well as to the Thau lagoon hydrological characteristics. The lagoon (surface 75 km^2, mean depth 4 m) is a semi-closed marine ecosystem, communicating with the Mediterranean Sea through two narrow openings (mean water residence time, 3.8 months) and showing wide variations in water temperature and salinity (5-29°C and 27-40 PSU, respectively). The annual global solar radiations is 5483 ± 135 MJ.m^{-2} (mean value and standard deviation for years 1994 to 1999, data from Météo-France) and the mean water extinction coefficient is 0.4 m^{-1}.

Studies on photosynthetic light-response curves are widely reported for macrophytes (King and Schramm, 1976; Jiménez et al., 1987, Henley, 1993; Pérez-Lloréns et al., 1996; Rodrigues et al., 2000). These studies developed the measurement techniques, under controlled conditions, of the photosynthesis and dark respiration parameters, which then can be compared among species or varying environmental conditions (temperature, light, salinity, nutrients, inorganic carbon, etc.). Furthermore, the parameters obtained in this way are very useful for modelling purposes, and macrophyte production calculations. However, these studies usually focus on a limited number of species.

Within the framework of the pluridisciplinary French National Program on Coastal Ecology (PNEC), the aim of this study was to determine, for all the most common

macrophytes of the Thau lagoon, the photosynthesis parameters at several seasons, as well as their pigment and elemental contents, in order to relate to habitat conditions and to serve as a basis for the modelling of such macrophyte populations (Plus et al., 2003).

2. MATERIAL AND METHODS

Study site

In spring 1998, the distribution and biomasses of macrophytes in the Thau lagoon was studied (Plus et al., 2003). Fifty-seven stations distributed all over the lagoon were sampled and conducted to a total biomass estimation of about 12 000 tons dry weight. The total number of reported taxa was huge (196) but the elaboration of a simplified macrophyte map was possible since only ten species accounted for 93 % of total biomass. Then, seven zones with characteristic communities could be identified by means of a correspondence analysis (Fig. 1). Even if the macrophyte biomass decreases notably in winter (to about 50% of maximum summer biomass), a comparison with Gerbal & Verlaque (1995) survey carried out in November 1994, as well as with personal observations, seems to prove that this macrophyte communities representation remains valid all over the year. There is however an exception, since one of the characteristic species reported on the map, *Monostroma obscurum*, is absent from the lagoon during summer.

Collection

Plant material was collected by SCUBA diving at a depth varying from 0.5 to 2 m, in perpetually submerged areas. Four 4-day samplings were conducted in May 1998 (water temperature 17°C and salinity 36.4 PSU), July 1998 (25°C, 38.5 PSU), December 1998

(13°C, 40 PSU) and February 1999 (7°C, 39 PSU) and all the material was placed in tanks filled with natural seawater and brought back to the laboratory for analysis.

Approximately 2 cm^2 of apparently healthy thalli (or leaves in the case of seagrasses) fragments, below apical parts and free of macroscopic epiphytes, were sampled and kept in the dark in natural seawater at the temperature of experiment (the same temperature as the natural medium) during one night in order to reduce stress before analysis. All analyses were conducted the day after collection and some thalli were kept in buffered 4% formaldehyde-seawater for species determination.

Studied species

A total of 23 species were analysed: two Phanerogams, five Chlorophyceae, ten Rhodophyceae and six Phaeophyceae. In order to simplify, the general term of 'groups' will be used hereafter to describe the different above-mentioned categories. All species were not found at every seasons, but the absence of some species does not necessarily mean that those species were absent from the Thau lagoon at that particular season. Thus, the seasonal variations of photosynthetic parameters have been studied only for the six species collected at every season, i. e. *Zostera marina*, *Nanozostera noltii*, *Chaetomorpha linum*, *Ulva* spp., *Gracilaria bursa-pastoris* and S*argassum muticum*.

Oxygen production and respiration

Photosynthesis and respiration rates were measured using the Henley et al. method (1991 b), and a small incubation chamber (volume 20 mL) connected to a thermostatic water bath, and a computerized polarographic oxygen electrode (Hansatech Instruments, England). Before each experiment the incubation medium (natural sea-water, *p*H 8.2, 2.2

mM of inorganic carbon concentration) was vigorously stirred in order to reach saturation, and the oxymeter was calibrated using the oxygen solubility in sea water (Riley and Skirrow, 1975). In order to avoid an eventual disruption of the oxygen probe due to super-saturation, at the beginning of each experiment, the seawater inside the chamber was bubbled with nitrogen in order to lower the oxygen concentration to about 50% of the saturation. A fragment of alga or seagrass leaf was inserted in the chamber, perpendicularly to the irradiance, before it was hermetically closed. A magnetic stirrer insured homogenisation inside the vessel. Then, the plant material was submitted to increasing photon flux densities (PFDs, ranging from 0 for dark respiration measurement to 1670 µmol photons m^{-2} s^{-1}) provided by a 36 red light emitting diodes (photosynthetically active radiations, peak output above 635 nm, model LS3/LH36U, Hansatech Ltd, Kings Lynn, Norfolk, UK). At each PFD, oxygen concentration was measured during five minutes (except for the dark respiration measurement, 15 min), and the rate calculations were made after a few minutes, when the slope was stabilized. Total experiment duration never exceeded 45 min. With the same experimental system, Henley et al. (1991 b) measured that, for a 18 mL chamber, less than 10 % of the total DIC was depleted during a 35 min experiment with *Ulva* sp. We thus assumed that our experiments were short enough to avoid carbon limitation. At the end of the experiment the plant material was rinsed and dried for 48 hours at 80°C for dry weight (dw) determination. This protocol was repeated for three replicates.

PI parameters were calculated by fitting the data to the following photosynthetic light response model (Jassby and Platt, 1976):

$$P_n = P_{max}^b \times \tanh(\frac{I}{I_k}) - R_d \tag{1}$$

$$\text{and } I_k = \frac{P_{\max}^b}{\alpha} \tag{2}$$

with P_n, the net production rate (µmol O_2 g^{-1} dw h^{-1}), $P_{\max}^b$, the gross maximal

photosynthetic rate (µmol O_2 g^{-1} dw h^{-1}), I the PFD (µmol photons m^{-2} s^{-1}), I_k, the onset of

light saturation (µmol photons m^{-2} s^{-1}), R_d, the dark respiration rate (µmol O_2 g^{-1} dw h^{-1})

and α, the initial slope of the light saturation curve or photosynthetic efficiency (µmol O_2

g^{-1} dw h^{-1} / µmol photons m^{-2} s^{-1}).

An additional experiment was conducted on the belowground organs of the

phanerogams. Living rhizomes and roots, identified by their white brown colour, were

sampled and placed in the incubation chamber in order to measure their respiration in the

dark. The same general protocol as leaves was followed.

Chlorophyll and elemental contents

Concomitant to photosynthetic measurements, plant material was kept for

chlorophyll, carbon, nitrogen and phosphorus contents determination.

Pigment extraction was done by grinding the thalli or leaves together with 90%

acetone and Fontainebleau sand, in a mortar kept in the dark and in the cold. After

extraction for 24 h at 2 to 5°C, the extracts were centrifuged (at 1500 rpm for 5 min) and

the pigments assayed on the supernatant using absorption spectrophotometry and the

equations from Jeffrey and Humphrey (1975).

Carbon and nitrogen contents were measured on lyophilised plant material using a

Perkin-Elmer CHNSO thermo analyser. Phosphorus contents were determined following

the method from Aspila et al. (1976) after extraction with sulphuric acid of previously

ashed (2 h at 550°C) 40-80 mg plant samples.

3. RESULTS

Chlorophyll contents

Chlorophyll content ([Chl]) was highly variable, ranging between 8.8 mg g^{-1} dw (*Zostera marina* in May 1998) and 0.1 mg g^{-1} dw (*Halopitys incurva* in July 1998), with no clear seasonal pattern. A high seasonal variability was found for the two seagrass species whereas for *Gracilaria bursa-pastoris* and *Sargassum muticum* the [Chl] was almost constant over the study period. Rhodophyceae exhibited [Chl *a*] contents significantly lower than all the other groups (Tukey multiple comparison, $p<0.05$), whereas differences between Phanerogams, Chlorophyceae and Phaeophyceae were not significant.

Elemental contents

Carbon contents ranged between 38.9 % dw (*Zostera marina*, in February 1999) and 18.28 % dw (*Gracilaria bursa-pastoris*, in July 1998) (Table 1). Due to their higher cellulose content and the higher salt content in macroalgae, the two seagrasses exhibit higher carbon contents than all the other groups (Tukey multiple comparison, $p<0.05$). Nitrogen contents varied respectively between 4.32 % dw (*Dasya sessilis*, July 1998) and 0.37 % dw (*Chorda filum*, in May 1998) and phosphorus contents between 0.35 % dw (*Gracilaria bursa-pastoris*, in December 1998) and 0.06 % dw (*Dasya sessilis*, December 1998) (Table 1). Neither nitrogen nor phosphorus contents exhibited significant differences amongst the groups. Furthermore, contrary to carbon and phosphorus content, nitrogen content in tissues was negatively correlated with water temperature ($r^2=0.15$, $p=0.004$), with annual maximums always found during winter.

Dark respiration rates

Measured *Rd* ranged between 6.7 µmol O$_2$ g^{-1} dw h^{-1} (*Rytiphlaea tinctoria* in February 1999) and 793.5 µmol O$_2$ g^{-1} dw h^{-1} (*Dasya sessilis* in July 1998) (Table 2). As expected, water temperature had a clear impact on the overall respiration rates (ANOVA, $p<0.001$), whereas no effect of salinity was found (ANOVA, $p=0.30$). Typically, low respiration rates were recorded during autumn and winter while high respiration rates were recorded during spring and summer. The best fit was obtained with an exponential regression ($R_d=8.96 \times e^{(0.12 \times Temp)}$, $p<0.001$), which corresponds to a Q$_{10}$ of 3.3. No significant difference was found when comparing *Rd* among groups.

Photosynthetic parameters

Gross maximal photosynthetic rates (P_{max}^b, Table 3) ranged between 1316.8 µmol O$_2$ g^{-1} dw h^{-1} (*Monostroma obscurum*, recorded in May 1998) and 31.1 µmol O$_2$ g^{-1} dw h^{-1} (*Rytiphlaea tinctoria*, in February 1999), and was positively correlated with water temperature (r^2=0.22, $p<0.001$). When comparing the gross maximal photosynthetic rates between groups, only Chlorophyceae and Rhodophyceae exhibit significant differences (Tukey multiple comparison, $p<0.05$), with higher P_{max}^b for the Chlorophyceae.

The maximum I_k (Table 4) was measured on *Zostera marina* leaves in July 1998 (501 µmol photons m^{-2} s^{-1}), and the minimum I_k, 55 µmol photons m^{-2} s^{-1}, was recorded on *Cutleria multifida* during winter (February 1999). As expected, overall I_k variations (all species together) exhibited a positive relationship with water temperature (r^2=0.33, $p<0.001$). It appears furthermore that Phaeophyceae have significantly lower I_k than Phanerogams, whilst no significant difference has been found between the other groups.

Effect of water temperature on R_d, P_{max}^b and I_k intra-specific variations

When looking at the six species studied at every season, only two species, *Ulva* spp. and *Nanozostera noltii* (leaves), did not show significant differences in respiration rates amongst the temperatures tested (Table 5). For *Z. marina*, *C. linum* and *G. bursa-pastoris*, best fits were obtained with an exponential relationship, with regression coefficients above 0.8. On the contrary, *S. muticum* exhibited a linear relationship with temperature with a mediocre regression coefficient.

No overall correlation between the photosynthetic parameters (P_{max}^b, I_k, α) and the chlorophyll *a* contents was found. Nonetheless in order to discard intra-specific variations due to chlorophyll contents, the effect of temperature was tested on parameters normalized to the pigment concentrations. In contrast to *N. noltii*, *Ulva* spp. and *S. muticum*, for which a high temperature tends to increase the maximum production, no effect of water temperature on P_{max}^b has been recorded for *Z. marina*, *C. linum* and *G. bursa-pastoris* (Table 5).

An effect of water temperature on I_k was detected only for two species, *Z. marina* and *G. bursa-pastoris*. For both species a linear positive correlation was obtained.

The effect of temperature on photosynthetic efficiency was very contrasted from one species to another (data not shown). A clear impact (ANOVA, $p<0.01$) has been found for three species (*Z. marina*, *Ulva* spp. and *G. bursa-pastoris*) while for the others a slight effect (ANOVA, $p=0.03$, *S. muticum*) or no effect at all (ANOVA, $p>0.05$, *N. noltii*, *C. linum*), was recorded. Moreover, when there is an effect, it varies according to the species: for *Z. marina* and G. *bursa-pastoris* a negative effect was observed (the highest was the temperature, the lowest was α) whilst for *Ulva* spp. the contrary occurred.

Calculated P/I curves

Seasonal P/I curves for *Z. marina*, *N. noltii*, *C. linum*, *M. obscurum*, *Ulva* spp., *G. bursa-pastoris* and *S. muticum* are presented in Fig. 2. In a general way, highest productions were found during spring and summer, excepted for two species, *G. bursa-pastoris* and *S. muticum* that exhibited different seasonal trends with maximums in December and February respectively. Highest net production rate was recorded for *M. obscurum* in May 1998 (temperature 17°C). This species also showed at this season a very high dark respiration rate (335 µmol O_2 g^{-1} dw h^{-1}) as well as a relatively low I_k, which led to a very high photosynthetic efficiency (9.1 µmol O_2 g^{-1} dw h^{-1} / µmol photons m^{-2} s^{-1}). Only *Cutleria multifida* (Phaeophyceae) exhibited a higher photosynthetic efficiency with 9.9 µmol O_2 g^{-1} dw h^{-1} / µmol photons m^{-2} s^{-1} recorded in December 1998, although having a lower maximum net production rate (478.9 O_2 µmol g^{-1} dw h^{-1}). Two other species exhibited remarkable photosynthetic capacities: *Dictyota dichotoma* (Phaeophyceae, foliaceus thallus) and *Dasya sessilis* (Rhodophyceae, filamentous thallus). Both exhibited high maximum net production rates and photosynthetic efficiencies: 5.1 and 8.1 µmol O_2 g^{-1} dw h^{-1} / µmol photons m^{-2} s^{-1} for *D. sessilis* (at 25°C) and *D. dichotoma* (at 17°C), respectively. Nevertheless, these species have not been studied at every season and thus further experiments performed under differing conditions should be of interest.

In the Thau lagoon, macrophytes are present on the whole lagoon bordure, between the shore and 7 m deep. Nonetheless, within this limit, attempts to rely photosynthetic parameters to species bathymetric distributions resulted unsuccessful. No correlations were found between the P/I curves parameters and either the mean depth of the zone where the species show high biomasses, or their distribution maximum depth.

4. DISCUSSION

A total of 23 species of macrophytes was collected in the Thau lagoon at different seasons and the main photosynthesis and respiration parameters were measured using the polarographic method. No photoinhibition was detected, probably due to the short incubation times and the experimental conditions maintained close to field conditions (water temperature and salinity, nutrients, oxygen). Nonetheless, this methodology does not allow direct extrapolations to *in situ* diel production because of natural light-acclimatation mechanisms and photoinhibition that could lead to a misestimate of field primary production (Henley et al., 1991 a, Macedo et al., 2002).

Chlorophyll concentrations in tissues were found within the range of usually published values. High seasonal variations were recorded, illustrating the fact that pigment contents depend directly on the light regime to which the populations were acclimated (Rosenberg and Ramus, 1982; Fillit, 1995; Pérez-Lloréns et al., 1996).

Mean C:N and N:P ratios were respectively 14.1 and 11.3 for the macroalgae and 16.6 and 10.4 for the seagrasses. Nitrogen contents exhibited seasonal variations, with higher tissue concentrations found in autumn and winter, following the usually reported maximum ammonium and nitrate concentrations in the Thau lagoon (Picot et al., 1990, Mazouni et al., 1998).

Like other biochemical reactions, dark respiration (all species together) was positively influenced by temperature, since the range of temperature tested (from 7 to 25°C) remained within the physiological limits. However no effect of temperature on *N. noltii* and *Ulva* spp. respiration rates was detected. For both species, the high variability of respiration recorded in February 1999, maybe due to an experimental stress (tissues cut) as mentioned by Littler & Arnold (1980), and this could explain the absence of effect. Moreover, one can notice that the respiration rates recorded for *D. sessilis* in July 1998 was

very high. Although no evidence of tissue senescence was noticed during the experiment, this possibility cannot be discarded since no specific measurements (protein contents, bacterial activity…) was done.

In the same way as the respiration, the dark reactions of the photosynthesis are directly dependent on the temperature (Bulthuis, 1987). Thus, as expected, maximum photosynthetic rates were found to be temperature dependent. However, the effect of temperature on P_{max}^b appears to be less marked than on R_d since the photosynthetic capacities of the plants are also dependent on other factors like prior thermal or light history (Bulthuis, 1987).

The study results support the commonly accepted idea that most productive macroalgae have a high surface/volume ratio (King & Schramm, 1976; Arnold & Murray, 1980; Littler & Arnold, 1982). Indeed, Fig. 3 shows that all the sheet-like and tubular thalli (*sensus* Littler and Arnold, 1982) exhibited the highest oxygen productions. Our results illustrate moreover that, even if not considered by the former authors, seagrasses should be considered at least as productive as the most productive, sheet-like and short-life algae. Light saturated net photosynthesis estimates for *N. noltii* and *Z. marina* ranged from 127.2 to 583 and from 70.9 to 476.5 O_2 μmol g^{-1} dw h^{-1}, respectively, and compared well with Jiménez et al. (1987), Latala (1995) and Vermaat & Verhagen (1996) results.

Contrary to the respiration rates that, each time a relationship was found, exhibited a positive correlation with temperature, the photosynthetic parameters exhibited among species showed contrasting variations with temperature. For example the net photosynthesis of the two seagrasses showed different trends with increasing temperature. For *N. noltii* the maximum net production rate was reached at 25°C and the minimum corresponded to the lowest temperature while for intermediate temperatures (13 and 17°C)

the responses were similar. On the contrary *Z. marina* exhibited highest production rates at 17°C. Indeed, the P/I curve at 25°C is characterised by high leaf respiration rates and a very low photosynthetic efficiency (0.6 µmol O_2 g^{-1} dw h^{-1} / µmol photons m^{-2} s^{-1}) leading to very low potentialities at low PFD. Furthermore, an eventual nutrient limitation in July 1998 seems unlikely since the N and P content in *Z. marina* leaves were higher or equal to Duarte (1990)'s thresholds, i. e. 0.2 and 1.8 % dry weight for phosphorus and nitrogen respectively. Thus, *Z. marina* seems to be photosynthetically better adapted to lower temperatures than *N. noltii*. The observation of below-ground organs respiration rates, very high for *Z. marina* in summer, reinforce this hypothesis. These results are in accordance with the P_{max}^b optimum found for *Z. marina* between 19 and 23°C by Evans et al. (1986).

In the same way, *C. linum*, *G. bursa-pastoris* and *S. muticum* showed clear preferences for temperatures below 25°C. In particular, *S. muticum* exhibited the highest photosynthetic efficiency and maximum production rates at the lowest tested temperature (7°C). Nonetheless, if a summer nutrient limitation seems to be unlikely for *C. linum* (the nitrogen concentrations in tissues were higher than in spring and in autumn, and higher than the critical tissue nutrient concentrations found by Lavery & McComb (1991), it cannot be discarded for either *G. bursa-pastoris* or for *S. muticum*, since the summer period corresponded to low nitrogen contents. In any case, our results for *G. bursa-pastoris* are in accordance with growth measurements performed in the Thau lagoon by De Casabianca et al. (1997), who found a predominant effect of temperature with an optimum growth at around 15°C.

The *Ulva* spp. photosynthesis parameters have been widely studied and the maximum production rates measured in the present study fall within the ranges reported by Latala (1995), Viaroli et al. (1999) or Menéndez et al. (2001). The highest production rates

for *Ulva* spp. were reached in spring and summer. P/I curves at 17 and 25°C were roughly similar although a lower I_k was recorded in July 1998. Furthermore, this species exhibited surprisingly low production rates in December 1998, with higher P^b_{max} recorded at 7°C during February 1999. A nitrogen limitation can reasonably explain these patterns since internal nitrogen concentration in May, July and December (respectively 1.3, 1.01 and 1.2% dw) were far below the critical levels considered by Fujita et al. (1989, 2.4% dw), Lavery & McComb (1991, 2% dw), and Pedersen & Borum (1994, 2.2% dw).

The results presented here confirm the very high photosynthetic acclimatation capabilities exhibited by macrophytes when exposed to varying light conditions (Henley et al., 1991a, Henley, 1993). Indeed, due to a very high intra-specific seasonal variability, no correlation was found between the photosynthetic capacities of species and their distribution along the depth gradient. However, using photosynthetic capacities as a basis, it has been possible to distinguish between species with a preference for colder or warmer conditions, as well as to detect periods of likely nutrient limitation for some species. When looking at the general light regime in the Thau lagoon, a high annual insolation coupled with a somewhat low extinction coefficient, it is likely that the spatial distribution of macrophytes is rather controlled by nutrient availability and/or interspecific competition than by light availability. In the context of anthropogenic pressure (local activities or global change) that lead to changes in the environmental characteristics, this study may help to predict which species are likely to survive under certain conditions.

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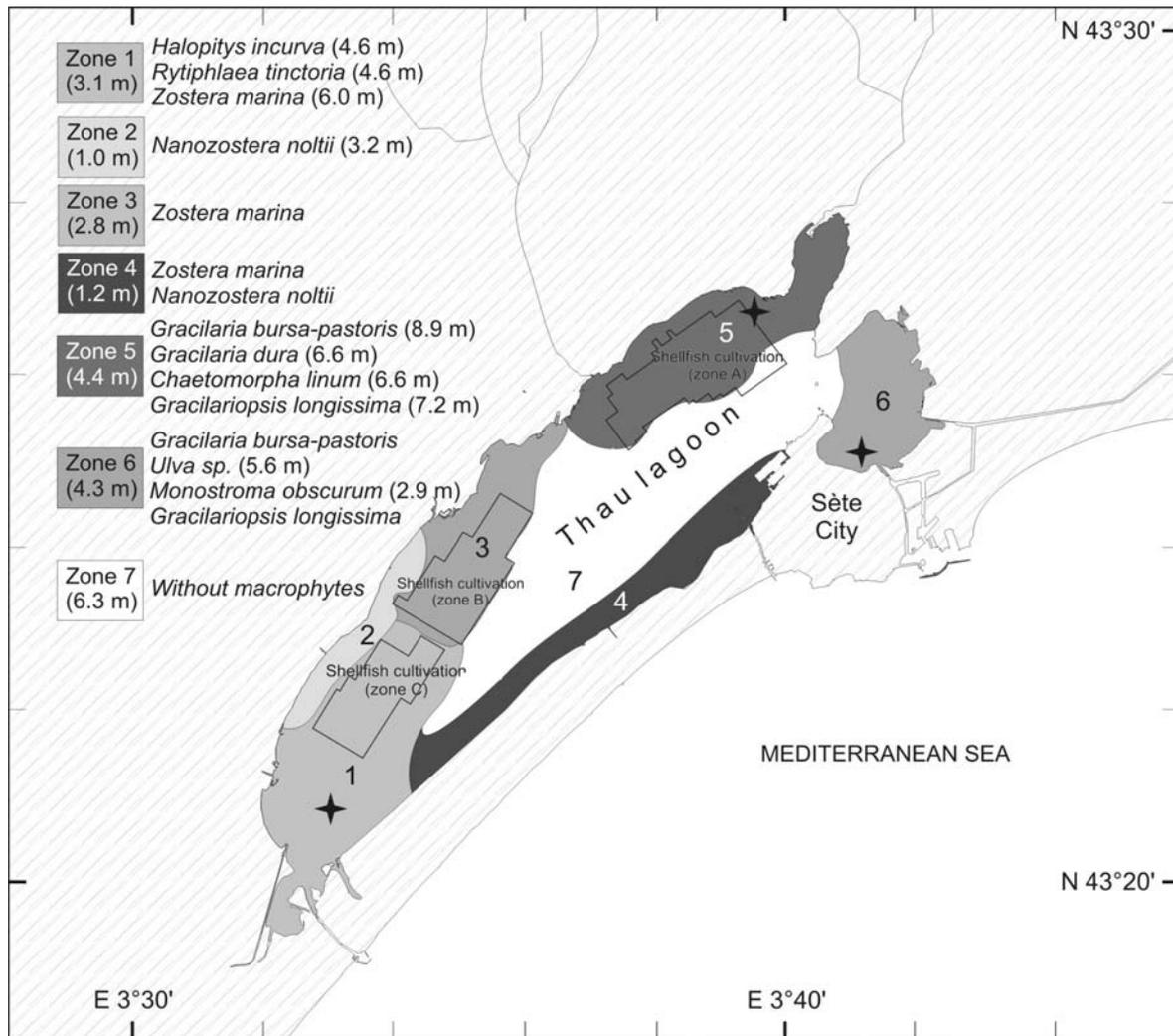
Figure 1. Macrophyte distribution map (after Plus et al., 2003). Mean depth for each zone is reported, as well as the maximum depth at which characteristic species was found. Black stars show where the species were collected.
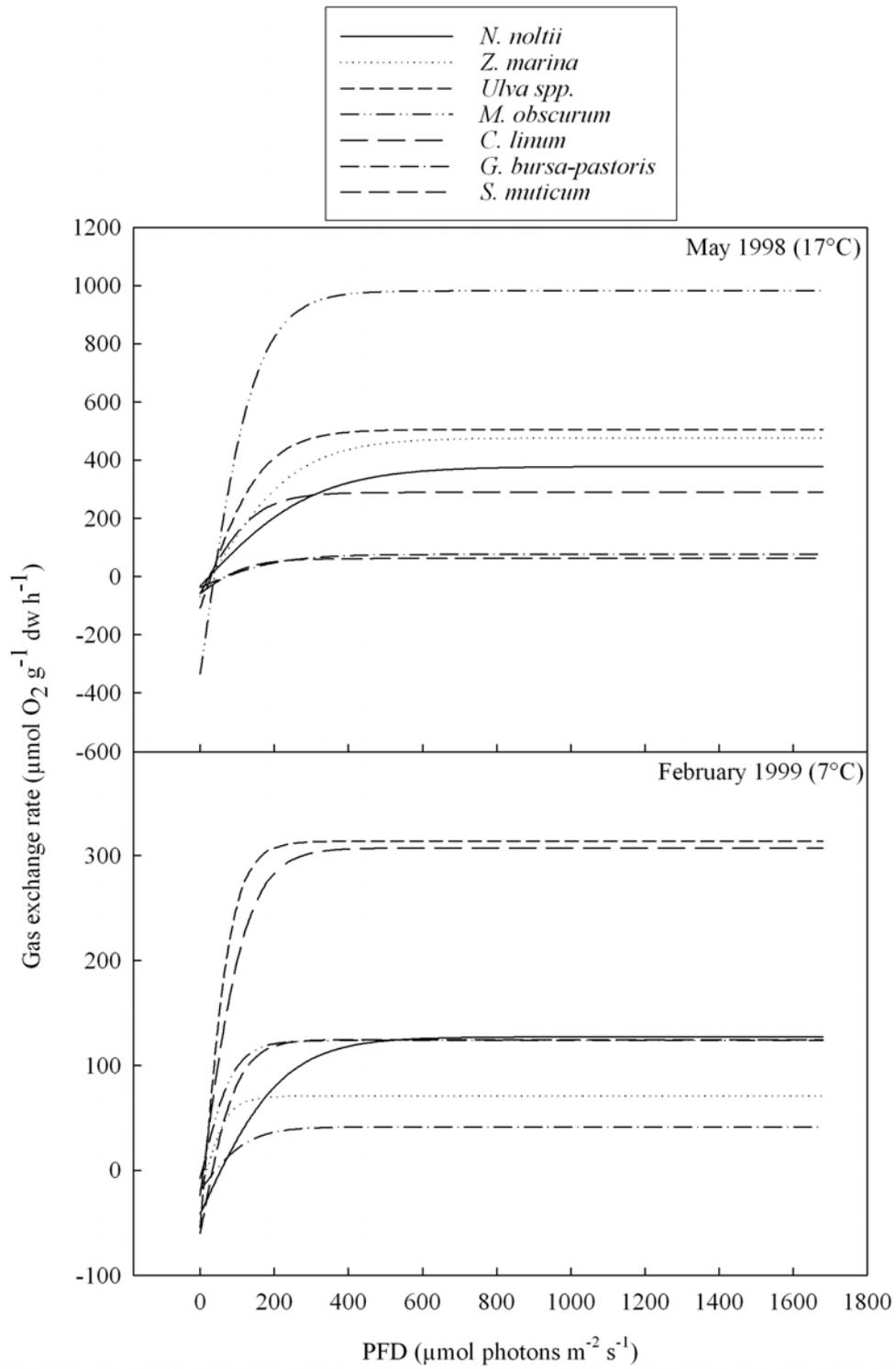
Figure 2. Calculated P-I curves found for May 1998 and February 1999.
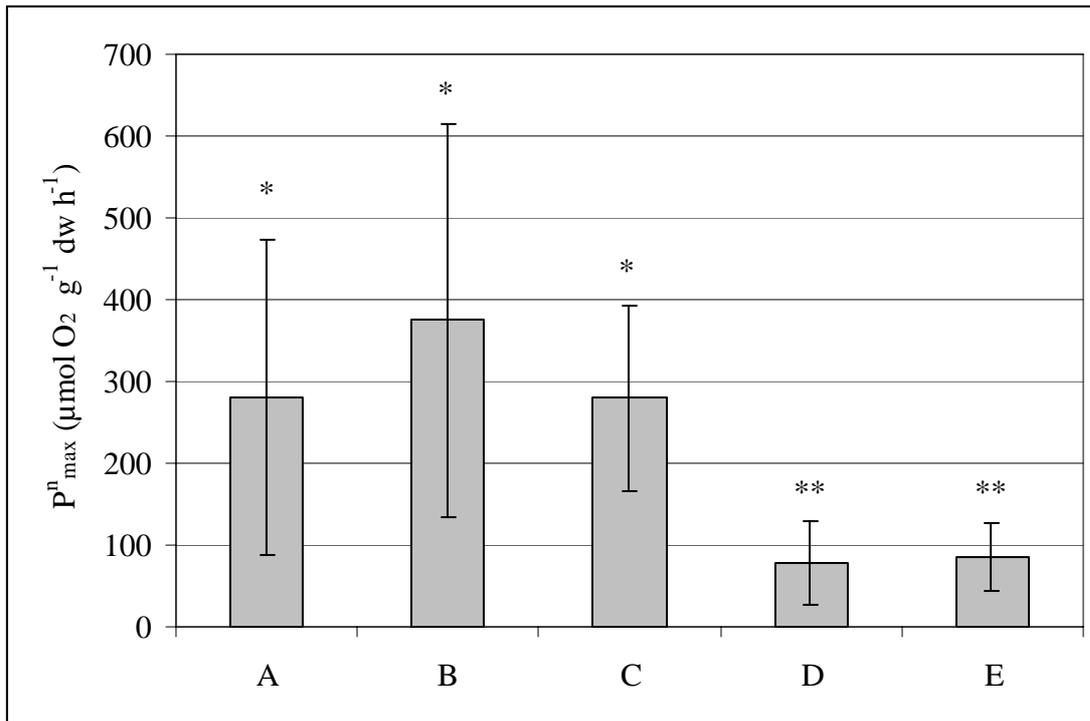
Figure 3. Mean light saturated net production rates (P^n_{max}) for the different thallus/leave shape categories (all seasons were pooled). Species were grouped into five categories : the functional-form groups B, C, D and E were precisely defined by Littler and Littler (1980) and Littler and Arnold (1982) : B (*M. obscurum*, *Ulva* spp., *C. multifida*, *E. intestinalis*, *D. dichotoma*) = thin (one to several cells thick) tubular and sheet like (laminate) forms, C (*C. vagabunda*, *C. linum*, *D. sessilis*) = delicately-branched (lightly corticated) filamentous forms, D (*G. bursa-pastoris*, *G. longissima*, *G. dura*, *G. asiatica*, *H. incurva*, *G. gracilis*, *A. corallinum*, *Grateloupia spp.*, *R. tinctoria*) = fleshy to wiry forms (coarsely branched), E (*U. pinnatifida*, *S. muticum*, *C. barbata*, *C. filum*) = thick blades and branched leathery forms. Seagrass leaves were added as a new group (A : *N. noltii* and *Z. marina*). Groups sharing the same sign (* or **) are not statistically different (p > 0.05, Kruskall-Wallis rank test).

Table 1. Carbon, nitrogen and phosphorus contents measured on the different species at the four seasons. Results are means of triplicates and their standard deviations (in brackets) except for phosphorus (single data). All values are expressed in % of dry weight.

	C	N	P	C	N	P	C	N	P	C	N	P
		(% dry wt)			(% dry wt)			(% dry wt)			(% dry wt)	
		May 1998			July 1998			December 1998			February 1999	
Zostera marina (leaves)	34.9 (0.04)	1.9 (0.04)	0.3	35.7 (0.00)	1.8 (0.17)	0.2	36.1 (0.03)	1.7 (0.01)	0.2	35.2 (0.12)	3.2 (0.04)	0.3
(rhizomes-roots)	31.8 (0.03)	1.2 (0.04)	0.1	36.6 (0.01)	0.7 (0.02)	0.1	34.2 (0.04)	1.0 (0.01)	0.1	31.3 (0.02)	1.2 (0.01)	0.1
Nanozostera noltii (leaves)	37.0 (0.05)	1.9 (0.02)	0.2	35.1 (0.03)	2.1 (0.00)	0.2	36.9 (0.08)	2.2 (0.03)	0.1	38.9 (0.08)	2.6 (0.03)	0.2
(rhizomes-roots)	31.1 (0.06)	0.9 (0.05)	0.2	31.8 (0.03)	0.8 (0.01)	0.1	36.0 (0.08)	0.9 (0.02)	0.2	35.7 (0.05)	1.4 (0.02)	0.2
Chaetomorpha linum	20.9 (0.05)	1.1 (0.05)	0.1	37.1 (0.05)	1.7 (0.01)	0.2	27.8 (0.01)	1.6 (0.05)	0.1	25.7 (0.10)	2.3 (0.02)	0.1
Cladophora vagabunda	m. d.[*]	m. d.	m. d.	24.0 (0.02)	1.9 (0.03)	0.1	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.
Enteromorpha intestinalis	m. d.	m. d.	m. d.	26.8 (0.18)	1.4 (0.01)	0.1	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.
Monostroma obscurum	23.6 (0.08)	2.9 (0.02)	0.1	m. d.	m. d.	m. d.	31.5 (0.08)	2.4 (0.04)	0.1	27.0 (0.08)	1.4 (0.02)	0.1
Ulva spp.	25.7 (0.04)	1.3 (0.02)	0.1	29.5 (0.09)	1.0 (0.00)	0.1	31.5 (0.02)	1.2 (0.03)	0.1	32.6 (0.04)	2.8 (0.01)	0.2
Alsidium corallinum	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.	27.8 (0.08)	3.2 (0.04)	0.2	27.5 (0.29)	3.8 (0.07)	0.2
Dasya sessilis	m. d.	m. d.	m. d.	35.1 (0.10)	4.3 (0.04)	0.1	25.7 (0.03)	2.6 (0.02)	0.1	33.7 (0.05)	3.9 (0.01)	0.2

Gracilaria bursa-pastoris	24.3 (0.03)	0.7 (0.02)	0.1	18.3 (0.07)	0.9 (0.02)	0.2	24.9 (0.04)	2.5 (0.08)	0.4	25.8 (0.12)	2.8 (0.05)	0.2
Gracilaria dura				31.0 (0.08)	3.2 (0.04)	0.3	31.9 (0.11)	2.0 (0.03)	0.2	30.3 (0.29)	2.7 (0.23)	0.3
Gracilaria gracilis	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.	33.0 (0.50)	3.6 (0.11)	0.20
Gracilariopsis longissima	33.2 (2.56)	1.0 (0.07)	0.1	m. d.	m. d.	m. d.	32.4 (0.18)	1.9 (0.02)	0.1	m. d.	m. d.	m. d.
Grateloupia asiatica	27.7 (0.59)	2.2 (0.08)	0.2	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.
Grateloupia spp.	29.2 (2.07)	1.9 (0.67)	0.2	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.
Halopitys incurva	m. d.	m. d.	m. d.	26.8 (0.07)	2.3 (0.03)	0.3	30.7 (0.03)	1.8 (0.01)	0.1	29.6 (0.01)	2.4 (0.01)	0.1
Rytiphlaea tinctoria	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.	30.2 (0.15)	1.2 (0.02)	0.2	28.6 (0.30)	2.0 (0.11)	0.3
Chorda filum	24.4 (0.10)	0.4 (0.03)	0.1	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.
Cutleria multifida	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.	20.1 (0.04)	2.7 (0.04)	0.4	24.2 (0.01)	1.4 (0.01)	0.3
Cystoseira barbata	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.	29.7 (0.01)	1.2 (0.02)	0.2	m. d.	m. d.	m. d.
Dyctiota dichotoma	24.9 (12.3)	2.1 (1.04)	0.2	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.
Sargassum muticum	36.7 (0.03)	1.5 (0.02)	0.1	28.8 (0.04)	1.5 (0.02)	0.3	31.7 (0.03)	2.0 (0.02)	0.2	31.3 (0.06)	2.2 (0.09)	0.2
Undaria pinnatifida	29.7 (0.03)	1.5 (0.01)	0.3	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.	m. d.

[*] m. d. = missing data

Table 2. Mean dark respiration rates (R_d, expressed in µmol O_2 g^{-1} dry wt h^{-1}) measured on the different species. Results are means and standard deviations (in brackets) of three replicates.

	Dark Respiration Rate (µmol O_2 g^{-1} dry wt h^{-1})			
	May 1998	July 1998	December 1998	February 1999
Z. marina (leaves)	69.4 (17.2)	141 (26.8)	54.5 (20.8)	22.2 (2.0)
(rhizomes-roots)	46.5 (6.0)	49.7 (17.4)	8.2 (4.6)	3.5 (1.5)
N. noltii (leaves)	33.2 (17.9)	66.1 (10.7)	32.9 (11.4)	41.3 (39.5)
(rhizomes-roots)	14.1 (2.2)	17.8 (3.2)	8.1 (2.9)	11.4 (4.2)
C. linum	59.1 (23.6)	187 (26.1)	70.3 (14.5)	23.8 (3.7)
C. vagabunda	m. d.*	412 (140)	m. d.	m. d.
E. intestinalis	m. d.	606 (157)	m. d.	m. d.
M. obscurum	335 (58.5)	m. d.	49.5 (7.2)	7.3 (0.8)
Ulva spp.	109 (21.5)	69.5 (21.2)	22.7 (3.7)	54.6 (22.2)
A. corallinum	m. d.	m. d.	38.6 (12.8)	21.8 (3.5)
D. sessilis	m. d.	794 (31.0)	73.9 (7.8)	14.2 (10.6)
G. bursa-pastoris	37.3 (8.4)	228 (37.8)	28.2 (10.2)	18.9 (13.5)
G. dura	m. d.	49.6 (30.6)	19.4 (11.4)	17.1 (4.8)
G. gracilis	m. d.	m. d.	m. d.	20.3 (3.4)
G. longissima	27.7 (2.8)	m. d.	26.0 (4.1)	m. d.
G. asiatica	57.7 (12.9)	m. d.	m. d.	m. d.
Grateloupia spp.	52.6 (17.9)	m. d.	m. d.	m. d.
H. incurva	m. d.	139 (26.3)	32.0 (11.9)	10.0 (3.2)
R. tinctoria	m. d.	m. d.	17.8 (1.9)	6.7 (3.4)
C. filum	27.3 (14.0)	m. d.	m. d.	m. d.
C. multifida	m. d.	m. d.	36.5 (13.3)	m. d.

C. barbata	m. d.	m. d.	183 (51.2)	62.6 (13.1)
D. dichotoma	306 (74.3)	m. d.	m. d.	m. d.
S. muticum	57.8 (5.3)	180 (9.6)	49.5 (10.9)	59.9 (25.4)
U. pinnatifida	63.2 (38.8)	m. d.	m. d.	m. d.

[*] m. d. = missing data

Table 3. Gross maximal photosynthetic rate (P^b_{max}, in µmol O_2 g^{-1} dry wt h^{-1}) for the different species. Results are means and standard errors (in brackets) of triplicates, t values for the nonlinear least squares regression are also given.

	P^b_{max}	t value	P^b_{max}	t value	P^b_{max}	t value	P^b_{max}	t value
	May 1998		July 1998		December 1998		February 1999	
Z. marina	546 (27.3)	20.0	290 (18.7)	15.5	163 (24.4)	6.7	93.1 (4.6)	20.2
N. noltii	411 (24.6)	16.7	649 (32.8)	19.8	383 (10.2)	37.4	169 (15.8)	10.7
C. linum	349 (48.2)	7.2	257 (10.0)	25.7	327 (11.0)	29.8	331 (4.6)	72.0
C. vagabunda	m. d.*		901 (83.1)	10.8	m. d.		m. d.	
E. intestinalis	m. d.		1017 (35.5)	28.7	m. d.		m. d.	
M. obscurum	1319 (9.6)	136.6	m. d.		280 (8.5)	32.9	131 (6.1)	21.4
Ulva spp.	614 (30.6)	20.0	526 (17.5)	30.0	228 (9.9)	23.0	368 (9.5)	38.7
A. corallinum	m. d.		m. d.		114 (4.2)	27.1	68.4 (2.6)	25.9
D. sessilis	m. d.		1075 (34.7)	31.0	332 (9.9)	33.4	301 (11.1)	27.0
G. bursa-pastoris	114 (13.1)	8.7	284 (21.4)	13.3	266 (12.1)	22.0	60.4 (1.6)	36.8
G. dura	m. d.		168 (14.9)	11.3	109 (6.8)	16.0	45.7 (1.7)	26.5
G. gracilis	m. d.		m. d.		m. d.		111 (4.0)	27.7

G. longissima	93.2 (10.1)	9.2	m. d.		179 (5.8)	31.0	m. d.	
G. asiatica	160 (4.3)	37.4	m. d.		m. d.		m. d.	
Grateloupia spp.	115 (10.6)	10.8	m. d.		m. d.		m. d.	
H. incurva	m. d.		235 (22.5)	10.5	90.6 (3.3)	27.3	45.0 (2.3)	19.4
R. tinctoria	m. d.		m. d.		56.5 (2.6)	21.8	31.1 (1.0)	30.7
C. filum	52.5 (5.6)	8.8	m. d.		m. d.		m. d.	
C. multifida	m. d.		m. d.		122 (4.5)	27.1	m. d.	
C. barbata	m. d.		m. d.		661 (32.8)	20.1	277 (12.3)	22.5
D. dichotoma	505 (30.9)	16.4	m. d.		m. d.		m. d.	
S. muticum	120 (3.0)	40.0	245 (9.1)	27.0	134 (3.7)	36.2	185 (7.9)	23.5
U. pinnatifida	212 (8.1)	26.3	m. d.		m. d.		m. d.	

[*] m. d. = missing data

Table 4. Saturation irradiance (I_k, µmol photons m^{-2} s^{-1}) for the different species (standard error, in brackets, and t value for the nonlinear least squares regression are given).

	I_k	t value	I_k	t value	I_k	t value	I_k	t value
	May 1998		July 1998		December 1998		February 1999	
Z. marina	245 (44.2)	5.6	501 (76.2)	6.6	99.2 (53.9)	1.8	69.5 (11.0)	6.3
N. noltii	305 (50.3)	6.1	254 (34.6)	7.3	174 (12.3)	14.2	222 (52.3)	4.24
C. linum	143 (66.5)	2.1	128 (17.1)	7.4	139 (13.2)	10.5	122 (4.7)	25.8
C. vagabunda	m. d.		226 (64.1)	3.5	m. d.		m. d.	
E. intestinalis	m. d.		255 (24.0)	10.6	m. d.		m. d.	
M. obscurum	146 (3.5)	42.0	m. d.		118 (10.5)	11.2	89.1 (12.9)	6.9
Ulva spp.	163 (25.9)	6.3	96.0 (11.9)	8.1	58.0 (10.0)	5.8	82.8 (6.8)	12.2
A. corallinum	m. d.		m. d.		96.1 (11.1)	8.7	91.5 (10.8)	8.5
D. sessilis	m. d.		211 (19.0)	11.1	67.7 (7.6)	9.0	95.9 (10.6)	9.0
G. bursa-pastoris	208 (79.0)	2.6	343 (65.5)	5.2	209 (24.2)	8.7	128 (10.5)	12.2
G. dura	m. d.		300 (73.8)	4.1	107 (20.8)	5.1	63.8 (8.6)	7.4
G. gracilis	m. d.		m. d.		m. d.		93.7 (10.2)	9.2

G. longissima	230 (80.3) 2.9	m. d.	348 (25.1) 13.9	m. d.
G. asiatica	89.3 (12.0) 7.5	m. d.	m. d.	m. d.
Grateloupia spp.	94.8 (39.2) 2.4	m. d.	m. d.	m. d.
H. incurva	m. d.	293 (81.3) 3.6	73.9 (10.5) 7.1	100 (15.3) 6.6
R. tinctoria	m. d.	m. d.	104 (15.6) 6.7	84.5 (9.1) 9.3
C. filum	95.4 (42.1) 2.3	m. d.	m. d.	m. d.
C. multifida	m. d.	m. d.	87.2 (9.7) 9.0	m. d.
C. barbata	m. d.	m. d.	66.8 (11.6) 5.8	55.6 (9.0) 6.2
D. dichotoma	62.5 (31.3) 3.0	m. d.	m. d.	m. d.
S. muticum	133 (11.6) 11.5	146 (18.7) 7.8	103 (8.4) 12.3	97.6 (12.4) 7.9
U. pinnatifida	127 (16.5) 7.7	m. d.	m. d.	m. d.

[*] m. d. = missing data

Table 5. Regressions between water temperature (Temp) and R_d, P_{max}^b or I_k. P_{max}^b has been normalized to the Chl a contents (P_{max}^b expressed in µmol O_2 mg^{-1} Chl a h^{-1}). ns = non significant ($p \geq 0.05$), * = significant ($0.01 \leq p < 0.05$), ** = very significant ($0.001 \leq p < 0.01$), *** highly significant ($p < 0.001$).

Species	Var.	p	R^2	n	Type[*]	a	b
Z. marina	R_d(leaves)	***	0.90	12	exponential	12.3	0.1
	R_d(rhizomes)	***	0.75	12	exponential	1.25	0.16
	P_{max}^b	ns					
	I_k	**	0.52	12	linear	22.2	-116.2
N. noltii	R_d(leaves)	ns					
	R_d(rhizomes)	*	0.42	12	linear	0.40	7.19
	P_{max}^b	***	0.69	12	exponential	38.8	0.06
	I_k	ns					
Ulva spp.	R_d	ns					
	P_{max}^b	*	0.46	12	exponential	86.1	0.06
	I_k	ns					
C. linum	R_d	***	0.84	12	exponential	12.4	0.11
	P_{max}^b	ns					
	I_k	ns					
G. bursa-pastoris	R_d	***	0.82	12	exponential	4.38	0.15
	P_{max}^b	ns					
	I_k	*	0.46	12	linear	0.11	2.52
S. muticum	R_d	**	0.61	10	linear	6.30	-10.4

P_{max}^b	*	0.50	10	linear	3.50	23.0
I_k	ns					

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* Linear ($R_d = a \times \mathrm{Temp} + b$) and exponential ($R_d = a \times \mathrm{e}^{(b \times \mathrm{Temp})}$) regressions were tested. The a and b values for the best regression coefficient (R^2) are shown.