

Why is *Ulva intestinalis* the only macroalga inhabiting isolated rockpools along the Swedish Atlantic coast?

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ABSTRACT: *Ulva intestinalis* (previously called *Enteromorpha intestinalis*) is the principal marine macroalga growing in isolated rockpools along the Swedish west coast. Given that this alga can take up HCO_3^- under the conditions of high pH and low concentrations of inorganic carbon (Ci) that it creates in those pools, we hypothesized that those conditions would be unfavourable for the photosynthetic performance of other algae such that they would not be able to grow in the same pools. This was tested by transferring 2 of the most common macroalgae, *Fucus vesiculosus* and *Chondrus crispus*, from the shallow waters of a bay adjacent to some rockpools, to 2 rockpools containing *U. intestinalis*. Both photosynthetic electron transport rates (ETR) and maximal quantum yields (F_v/F_m) were measured 3 d later. Similar measurements were also performed throughout the day in simulated outdoor rockpools where the 3 species were kept either alone or together for 24 h. It was found that midday ETRs were repressed for all species in the (upper) rockpool as compared to the open bay, but more so for the transferred *F. vesiculosus* and *C. crispus* (33 and 0.6%, respectively, of the bay values) than for *U. intestinalis* (58%). Also, *C. crispus* showed exceptionally repressed midday F_v/F_m values in the rockpools (some 22% of that in the bay), and had largely photobleached after 3 d. Similarly, ETRs declined in the simulated rockpools during the day, especially for *C. crispus* when the other algae were present (to 7% of morning values, compared to 36% when alone). Also, F_v/F_m declined in the simulated rockpools during the day, indeed much more so for *F. vesiculosus* and *C. crispus* when the other algae were present (to ca. 12 and 10% of morning values as compared to 76 and 54%, respectively, when alone). As in the rockpools, the latter alga photobleached when kept together with the other species, but not when alone. Based on these results, and considering their different Ci utilisation mechanisms, it was concluded that the absence in rockpools of algae such as those tested here may be largely due to the adverse conditions of high pH and low Ci concentrations caused by the photosynthetic traits of *U. intestinalis*.

KEY WORDS: *Chondrus crispus* · *Ulva (Enteromorpha) intestinalis* · *Fucus vesiculosus* · Inorganic carbon · Rockpool(s) · pH · Photosynthesis

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INTRODUCTION

Most marine macroalgae utilise bulk HCO_3^- from seawater as their main inorganic carbon (Ci) source for photosynthesis. Such HCO_3^- utilisation may take different forms. Principally, HCO_3^- is either dehydrated extracellularly to form CO_2 , which then diffuses into the cells, or the ion itself is transported across the

plasma membranes (reviewed in Beer 1994). For the common green algae *Ulva* and *Enteromorpha* (today considered to be the same genus, i.e. *Ulva*, Hayden et al. 2003) the mechanisms involved include either the presence of an extracellularly acting carbonic anhydrase (e.g. Björk et al. 1992), the presence of a membrane-bound anion transporter (e.g. Drechsler et al. 1993), or both (Axelsson et al. 1995, Larsson et al.

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1997). While the direct HCO_3^- uptake system of *U. fasciata* was ascribed to facilitated transport via arginine groups of an anion exchange protein (Drechsler et al. 1994), it was recently shown that HCO_3^- transport in *Cladophora glomerata* may involve an ATPase (Choo et al. 2002).

Whereas HCO_3^- utilisation constitutes a logical evolutionary response of marine plants to the ca. 200× higher HCO_3^- than CO_2 concentration in natural seawater, HCO_3^- utilisation via extracellular conversion to CO_2 may in some cases be futile. This is true, for example, if the pH in the close vicinity of the plant surface is high (ca. 9.5 to >10), such as was found for *Ulva fasciata* growing under natural conditions conducive to high photosynthetic rates in Israel (Beer & Israel 1990). Under such conditions, and given that Ci transport within the boundary layer close to the cell membrane is limited by diffusion, the CO_2 concentration in equilibrium with ionic Ci would be in the nM level there, making CO_2 diffusion into the cells ineffectual. It has also been shown that *U. lactuca* can, within 24 h, be induced to switch from carbonic anhydrase-mediated dehydration of HCO_3^- under natural Swedish west coast conditions to direct anion exchange-mediated HCO_3^- uptake (also termed 'DIDS-sensitive HCO_3^- uptake', e.g. Larsson & Axelsson 1999) by increasing the pH experimentally in a flow-through system (Axelsson et al. 1995). Under more natural conditions, it was found that while *U. intestinalis* (then as *Enteromorpha intestinalis*) possesses both systems of HCO_3^- utilisation, only the direct, anion exchange-mediated, HCO_3^- uptake system was functional under the rockpool conditions characterized by high pH and low Ci concentrations (Larsson et al. 1997).

Ulva intestinalis has been reported to be the principal marine macroalga growing in Swedish rockpools (cf. Larsson et al. 1997). During the summer, these rockpools are characterized by daily low Ci concentrations and high pH values (see also Ganning 1971, Truchot & Duhamel-Jouve 1980, Raven 2003), showing that they are out of equilibrium with the atmosphere and that the CO_2 concentrations, thus, are low (cf. Larsson et al. 1997). It was therefore not surprising to find that *U. intestinalis* under such rockpool conditions was induced to utilise HCO_3^- via the anion exchange-mediated direct uptake system (Larsson et al. 1997). It was, however, not clear why *U. lactuca*, which can also adapt its HCO_3^- utilisation system to direct HCO_3^- uptake, did not grow in the rockpools. Secondly, it was not clear to what extent the conditions caused by the photosynthetic traits of *U. intestinalis* in those rockpools could hinder other algae from inhabiting them.

While we have not observed *Ulva lactuca* in the shallow waters adjacent to rockpools on the Swedish west coast, many other algae grow there, with a dominance

of the brown alga *Fucus vesiculosus* and the red alga *Chondrus crispus*. In an attempt to explain why algae other than *U. intestinalis* do not occupy isolated rockpools on the Swedish west coast, we conducted some initial field experiments, in which these 2 macroalgae were transferred from shallow open waters to rockpools inhabited by *U. intestinalis*, and followed the photosynthetic traits of the 3 species. It was found that especially photosynthetic electron transport rates (ETR) decreased excessively in the red alga, and that it photobleached. In separate experiments, simulated outdoor rockpools were generated in which the preliminary results obtained in the natural rockpools were verified.

MATERIALS AND METHODS

All experiments were carried out between July 30 and August 8, 2003. For the initial part of this investigation, 2 rockpools containing dense stands of *Ulva intestinalis* L. were used. Both were located on a small island 2 nautical miles west of Kristineberg Marine Research Station on the Swedish west coast (58° 15' N, 11° 23' E). One rockpool was close (1 m) to a small bay, ca. 0.5 m above the mean seawater level (termed 'lower rockpool', Fig. 1), but occasionally received small amounts of seawater when waves were high. (The diel tidal range here is only 0.1 to 0.3 m, and is of little use for filling the rockpools with seawater.) The other rockpool was situated higher up on the rocks (termed 'upper rockpool'), ca. 2 m above the mean seawater level, and had been isolated from the open sea for at least 2 wk. The weather was bright (ca. 1600 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) and warm (23°C in the open water and up to 27°C in the rockpools) during the days of the experiments. Prior (3 d) to measurements, ca. 50 g FW of *Fucus vesiculosus* and 20 g *Chondrus crispus* were removed from the shallow (0.1 to 0.2 m depth) bottom of the adjacent bay and were placed into the rockpools at similar depths among the *U. intestinalis* thalli, such that they received the same irradiance as in the bay. Measurements were carried out 3 d later between 13:30 and 14:30 h. This experiment was repeated twice (on August 1 and 7).

Rockpool conditions were simulated using 12 white 5 l beakers containing 1 l seawater, placed outside the laboratory. Either 30 g of each species separately, or 10 g each of all 3 species, were placed in the beakers in triplicates. The experiment was repeated 4 times (on July 30 and 31 and August 4 and 6; the latter 2 dates featured the most comparable weather conditions). The irradiance in the beakers reached up to 1800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, and the temperature was 23°C in the morning, reaching a maximum of 28°C during the day.



Fig. 1. The bay (centre right) and the lower rockpool showing *Ulva intestinalis* (lower left)

Irradiance was measured as photosynthetically active radiation (PAR) with a Li-Cor quantum sensor connected to a Li-Cor LI-1000 data logger (Li-Cor), and pH was measured with a pH-meter (Metrohm 632) equipped with a semi-micro combination Ag/AgCl electrode, calibrated according to the NBS pH scale. Concentrations of C_i were determined by injecting 0.1 ml filtered seawater (either collected from the rockpools and transported in the cold to the laboratory or collected from the simulated rockpools) into a gas-stripping acid column and leading the released CO_2 through an infrared gas analyzer (ADC 225 MK3). The CO_2 peak was recorded, and the peak height relative to a 2 mM Na_2CO_3 standard was used to calculate the total C_i concentration.

Effective ($\Delta F/F_m'$) and maximal (F_v/F_m) quantum yields of electron transport through Photosystem II were measured on 3 to 4 specimens in each beaker with a pulse amplitude modulated (PAM) fluorometer (the Diving-PAM, Walz). Photosynthetic electron transfer rates (ETR) were calculated as $\Delta F/F_m'$ multiplied by the incident PAR (measured with the Diving-PAM's quantum sensor under ambient sunlight and calibrated against the Li-Cor quantum sensor connected to a

Li-Cor LI-1000 data logger), 0.5 and an absorption factor (AF, see e.g. Beer et al. 2001). F_v/F_m was measured following 10 min periods of dark adaptation (using so-called dark leaf clips). For general explanations of the use of PAM fluorometry in marine macrophytes, see e.g. Beer et al. (2001), and for limitations of its use at high irradiances, see Beer & Axelsson (2003) and Carr & Björk (2003).

The AF was measured by placing the different thalli on the flat quantum sensor of the Diving-PAM under water and calculating the fraction of absorbed light. These average AF values were found to be 0.50 for *Ulva intestinalis*, 0.82 for *Fucus vesiculosus* and 0.88 for *Chondrus crispus*. For the latter species, the AF value decreased as the thalli bleached (from 0.88 down to a minimum of 0.13).

Insolation and temperature data for the region were supplied by the Swedish Meteorological and Hydrological Institute. The data showed that mean temperature (18.6°C) and insolation (6100 W m⁻²) during the days of the experiments were not extreme compared to the average of the period (means were 16.0°C/5530 W m⁻² for June, 18.4°C/5110 W m⁻² for July and 7.4°C/4660 W m⁻² for August); nor did any particular day of the experiment differ from what could be expected during this period of the Swedish summer.

RESULTS

All 3 species of macroalgae showed significantly lower ETRs in the rockpool than in the open bay (Fig. 2, measured only for the upper rockpool on August 1). This was especially so for *Fucus vesiculosus* and *Chondrus crispus*, for which the afternoon ETRs dropped to 33 and 0.6%, respectively, of the values measured in the bay. Also, all *C. crispus* thalli had visually photobleached during the 3 d they had occupied the rockpools (Fig. 3). This bleaching was also reflected in decreasing AF values (from an average 0.88 to 0.13). In contrast, *Ulva intestinalis* maintained 58% of its ETR in that rockpool. Also, F_v/F_m values were lower in the rockpools than in the open bay (Fig. 4, measured at the same time as the ETRs). This decrease in F_v/F_m was similar for *U. intestinalis* (to 60% in the lower and 44% in the upper rockpools) and *F. vesiculosus* (to 58 and 37% of the bay values in the lower and upper rockpools, respectively). A much larger drop was found for *C. crispus* (down to 23 and 21% of the bay value in the lower and upper rockpools, respectively). During the day, pH in the

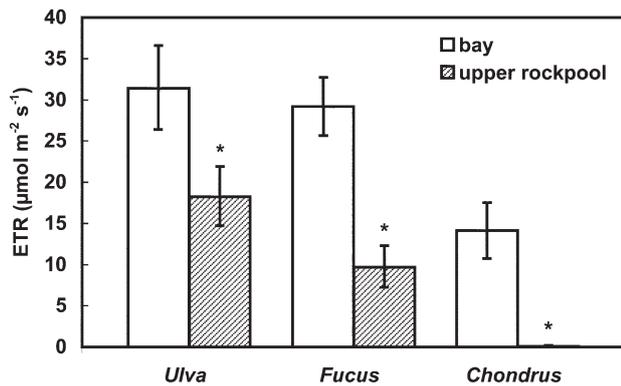


Fig. 2. Photosynthetic electron transport rates (ETR) of *Ulva intestinalis*, *Fucus vesiculosus* and *Chondrus crispus* in the bay and upper rockpool. Data are means of 10 replicate measurements (taken from 13:30 to 14:30 h; 23 to 27°C and 1500 to 1700 µmol photons m⁻² s⁻¹) ± SD; *: significantly different values as compared to those in the bay for each species (*t*-test, *p* < 0.05)

rockpools increased and Ci concentrations decreased (Fig. 5, measured on August 1). At 14:00 h, i.e. close to when ETRs and F_v/F_m values were measured, the pH was 9.8 in the lower and 10.1 in the upper rockpools, while Ci concentrations were around 0.6 mM in both pools. The relatively high pH (8.9) and low Ci concentration (1.5 mM) in the bay deviated from natural open water conditions (pH 8.2, 2.2 mM Ci), showing that the water therein was also affected by the photosynthetic activity of the algae throughout most of the day (but much less so than the rockpools). The same principal results as displayed in Figs. 2, 3 & 4 were also obtained on August 7 (not shown).



Fig. 3. The upper rockpool containing *Ulva intestinalis* and the transferred *Fucus vesiculosus* (upper right) and *Chondrus crispus* (lower left; the thalli were moved to the surface for visibility) 3 d after the latter algae had been transferred there from the bay. Environmental conditions as in Fig. 2

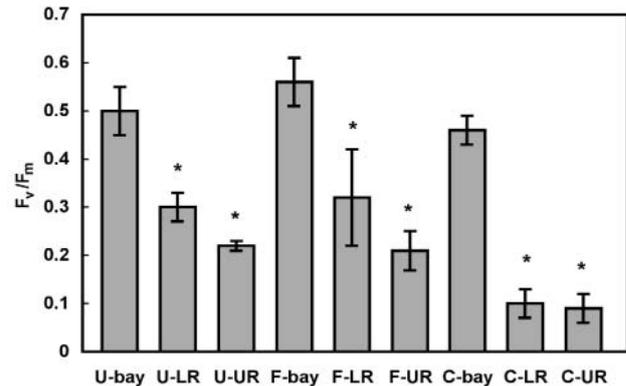


Fig. 4. Maximal quantum yields (F_v/F_m) of *Ulva intestinalis* (U), *Fucus vesiculosus* (F) and *Chondrus crispus* (C) in the bay, lower and upper rockpools (LR and UR, respectively). Data are means of 10 replicate measurements (taken from 13:30 to 14:30 h; environmental conditions as in Fig. 2) ± SD; *: significantly different values as compared to those in the bay for each species (*t*-test, *p* < 0.05)

ETRs also decreased during the day in the simulated rockpools (Fig. 6, presenting data from August 4 and 6, when weather conditions were uniformly sunny). Although the same trend in results was obtained for all days, we chose to present only 2 days with comparable irradiance because irradiance values are included in the ETR calculations. This decline in ETR was especially marked for *Chondrus crispus* when the other species were present (down to 7% of morning values), while 36% was maintained when growing alone (Fig. 6c). This difference was much smaller for *Fucus vesiculosus* (to 29 and 44% of the morning values when in combination with the other species and alone, respectively, Fig. 6b), while ETRs for *Ulva intestinalis* were somewhat higher when the other plants were present (55%) than when alone (43%, Fig. 6a). Also, F_v/F_m declined in the simulated rockpools during the day, especially so for *F. vesiculosus* and *C. crispus* when kept in combination with the other algae (to 12 and 10% of the morning values, respectively), while *U. intestinalis* was not influenced by the other 2 species (Fig. 7, measured on August 6 and 7). There was also a significant decline in afternoon ETR values for *F. vesiculosus* and *C. crispus* in combination with the other algae as compared to when alone, but no such decline was found for *U. intestinalis*. F_v/F_m recovered the following morning, but less so for *C. crispus* when in combination with the other species. It is notable that the initial and recov-

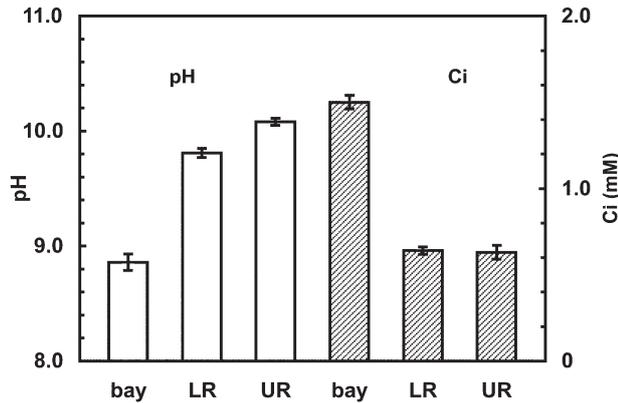


Fig. 5. pH values and concentrations of inorganic carbon (Ci) in the bay, lower and upper rockpools (LR and UR, respectively). Data are means of 5 replicate measurements (taken at 14:00 h) \pm SD

ered F_v/F_m values for *F. vesiculosus* were higher when in combination with the other algae than when alone, but it is not known why. Coinciding with the decreases in ETRs and F_v/F_m values were increases in pH and decreases in Ci (Fig. 8, measured on August 4), and this was especially expressed in the beakers where *U. intestinalis* was present (pH > 10, and 0.6 and 1.0 mM Ci when alone or together with the other species, respectively). Thus, we conclude that the decreased photosynthetic performances noted for especially *F. vesiculosus* and *C. crispus* were due to the drastic changes in pH and Ci caused mainly by *U. intestinalis*, while the former species evidently caused much less change in the seawater media (*F. vesiculosus* could raise the pH in the artificial rockpool water to 9.6 and *C. crispus* to 9.3, Fig. 8). *Chondrus crispus* had photobleached almost completely after 24 h in the beakers (Fig. 9c), and looked much like the photobleached *Chondrus crispus* from the natural rockpools. On the other hand, there was no apparent photobleaching of the other 2 species (Fig. 9a,b). It should be noted that

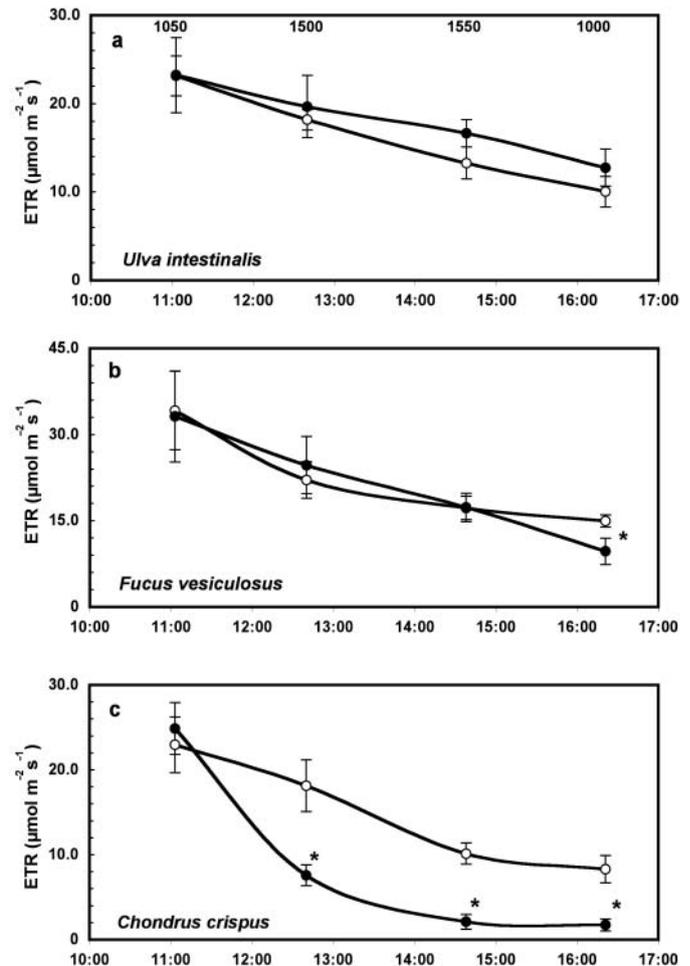
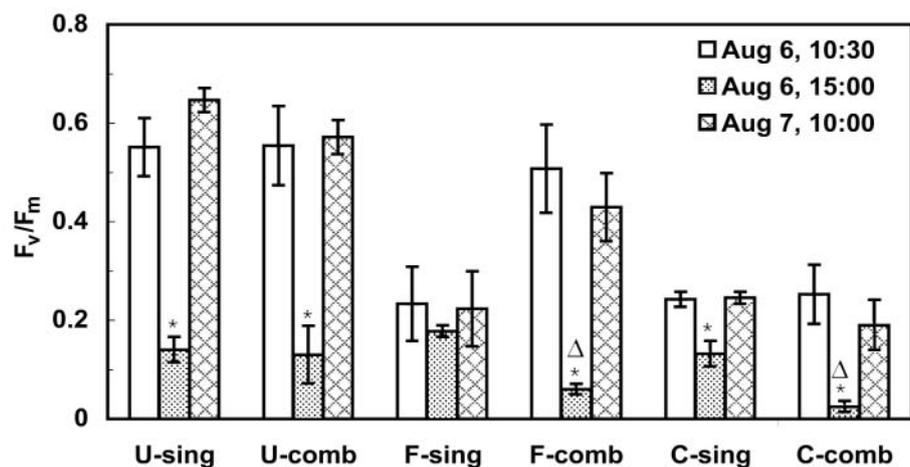


Fig. 6. Daily patterns in photosynthetic electron transport rates (ETR) of (a) *Ulva intestinalis*, (b) *Fucus vesiculosus* and (c) *Chondrus crispus*, placed either alone (○) or in combination with the other species (●) in the simulated rockpools. Data are means of 3 replicate units, 3 to 4 thalli measured in each (20 to 28°C; the irradiance is given at the top of a) \pm SE; *: the rate when in combination with other species was significantly different from the rate when alone at a certain hour (t -test, $p < 0.05$)

Fig. 7. Daily changes in maximal quantum yields (F_v/F_m) of *Ulva intestinalis* (U), *Fucus vesiculosus* (F) and *Chondrus crispus* (C), placed either alone (sing) or in combination with the other species (comb) in the simulated rockpools. Data are means of 3 replicate units, 3 to 4 thalli measured in each (environmental conditions as in Fig. 6) \pm SD; *: that the value was significantly different from that at 10:30 h for each different combination ($p < 0.05$). Δ : that the value for the 'combination' was significantly different from the respective 'single' treatment (t -test, $p < 0.05$)



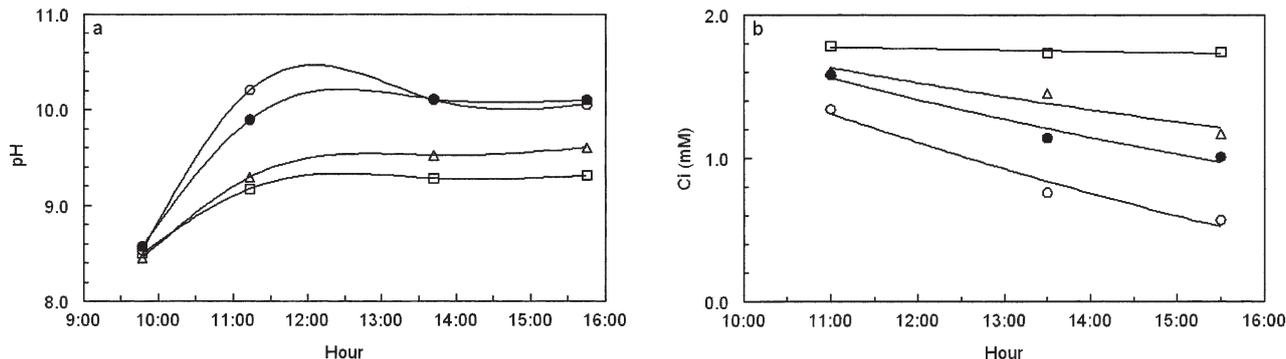


Fig. 8. Daily changes in (a) pH values and (b) concentrations of inorganic carbon (Ci) in the simulated rockpools containing *Ulva intestinalis* (○), *Fucus vesiculosus* (△), *Chondrus crispus* (□) or all species together (●). Data are means of 5 replicate measurements (SD < 5% of the means)

because of the patchy bleaching pattern, the F_v/F_m values for *C. crispus* do not represent the whole thallus area (because only a small proportion of it, i.e. the pigmented patches, was photosynthetically active).

DISCUSSION

The ability of *Ulva intestinalis* to raise the pH of its surrounding seawater to >10 under enclosed conditions while utilising Ci is based on its capacity to transport HCO_3^- across the plasma membrane via an anion exchange protein (Larsson et al. 1997). This HCO_3^- transport system was first detailed for the subtropical *U. fasciata* (Drechsler et al. 1993, 1994), and it was proposed that the high pH created around thalli of this alga (>10, Beer & Israel 1990) was partly caused by OH^- being exchanged outwards in antiport with inward HCO_3^- transport. As a consequence of HCO_3^- transport it was thus visualised that HCO_3^- would dehydrate inside the cells and, while the resulting CO_2 would be fixed by Rubisco, the remaining OH^- would be transported outwards and alkalise the medium. It was also found, however, that the temperate *U. lactuca*, which usually utilises ambient HCO_3^- by carbonic anhydrase catalysed extracellular dehydration to form CO_2 within the diffusion layer, could be induced to transport HCO_3^- via the anion exchange protein by increasing the pH in a flowthrough system for 24 h (Axelsson et al. 1995). Similarly, it was found that while *U. intestinalis* possessed both systems of HCO_3^- utilisation simultaneously, only the latter was effective under the high pH and low Ci conditions found in rockpools inhabited by this alga (Larsson et al. 1997). While *U. lactuca* thus would be a likely candidate for also inhabiting rockpools, the fact that this plant, unlike *U. intestinalis*, was not found in the vicinity of the rockpools indicates that factors other than possible competition with *U. intestinalis* hinder it from inhabiting these rockpools.

Why, then, do other algae growing in the open waters close to the rockpools not inhabit those rockpools? Regarding one of the macroalgal species dominating the shallow open waters adjacent to the rockpools, *Chondrus crispus*, its Ci utilisation system is based on carbonic anhydrase-catalysed extracellular conversion of HCO_3^- to form CO_2 (Axelsson & Beer 2001, Axelsson 2003). This method of HCO_3^- utilisation, which seems to be the one used by most macroalgae (cf. Beer 1994), is effective at relatively low extracellular pH values, but is futile at pH >10 such as found in rockpool waters (cf. Axelsson et al. 1991). This is because (1) the fraction of CO_2 in equilibrium with other Ci forms is extremely low at such high pH values (less than 0.002% of the total Ci at pH 10) and (2) air equilibration is not reached as evidenced by the lower than air equilibrium Ci concentrations found here (0.6 mM as measured here vs 2.2 mM in open seawater). Under such conditions, the CO_2 concentration would be ca. 10 nM and substantial rates of inward diffusion of CO_2 , if any, would be unlikely (cf. Beer & Israel 1990). Indeed, it has been reported that the photosynthetic activity of *C. crispus* ceases at pH 9.5 (Axelsson & Uusitalo 1991). Accordingly, *C. crispus* photosynthesised at extremely low rates both in the natural and simulated rockpools under the high pH and low Ci conditions caused by *Ulva intestinalis*. Regarding the other dominant macroalga in the surroundings of the rockpools, *Fucus vesiculosus*, it was previously shown in pH drift experiments that this species, as well as other Fucaceae, continued to photosynthesise only to pH 9.7 to 9.8 (Axelsson & Uusitalo 1988, Surif & Raven 1989). However, this is based on their ability to excrete protons (Axelsson et al. 1989) such that all Ci can be utilised without raising the pH above this value. Thus, while it is not known if such a system featuring active proton excretion would function at external pH values of >10, it is obvious that *F. vesiculosus* does photosynthesise at a relatively higher



Fig. 9. Examples of thalli of (a) *Ulva intestinalis*, (b) *Fucus vesiculosus* and (c) *Chondrus crispus* either alone (left) or in combination with the other species (right), after 24 h in the simulated rockpools

rate than *C. crispus* (but at a lower rate than *U. intestinalis*) under the high pH and low C_i rockpool conditions as compared with open waters, as well as in the simulated rockpools when *U. intestinalis* was present.

While the inability to photosynthesise at high pH and low C_i concentrations formed by *Ulva intestinalis* may be one direct reason for the absence at least of *Chondrus crispus* from the rockpools, other factors may also be involved. For example, it was reported that *C. crispus* was more susceptible to photoinhibition than *U. lactuca* and the brown alga *Macrocystis pyrifera* (Cabello-Passini et al. 2000), and that its pigments were easily destroyed by UV radiation (Yakoleva & Titlyanov 2001). In our experiments, it is likely that the C_i limitation in the rockpools would exacerbate this susceptibility. This was indicated here by the low F_v/F_m values in the rockpools during the day (an established indication of photoinhibition) and especially by the fact that *C. crispus* photobleached almost completely both in the natural and simulated rockpools when *U. intestinalis* was present. No such photobleaching was observed for *Fucus vesiculosus* and *U. intestinalis*. Another *Fucus* species, *F. distichus*, was reported to be particularly resistant to UV radiation (Hanelt et al. 1997), and photobleaching was not observed for *U. intestinalis* either in a previous study of its photosynthetic traits in rockpools (Larsson et al. 1997).

In addition to C_i limitations, photoinhibition and photobleaching, other factors may also have been involved in restricting the growth of *Chondrus crispus* and *Fucus vesiculosus* in the rockpools investigated here. One potentially contributing factor is the salinity fluctuations in the rockpools (from below to above the normal seawater salinity during rainy events and calm sunny days, respectively), but this was not checked here. Allelopathy, i.e. the excretion of harmful or limiting chemicals by *Ulva intestinalis* that would hinder the growth and development of the other algae, is another possibility. However, the most likely interference here is the direct restriction of photosynthesis by the high pH and low C_i created by the rapidly growing *U. intestinalis* (while the contribution of the other algae was much less, as exemplified in our simulated rockpool experiments). While this is particularly obvious for *C. crispus*, it is possible that further interactions involving competition with *U. intestinalis* for C_i , light and space are important components in the inability of *F. vesiculosus* to establish itself in the developing rockpools.

In summary, we envisage the following macroalgal development in rockpools: out of the spores or algal sections reaching a newly formed rockpool from its nearby waters (e.g. after storm events), it is the thin, opportunistically growing, *Ulva intestinalis* that develops initially. This alga soon causes the C_i to decline

and the pH to rise above 10 because of its high capacity to transport HCO_3^- (possibly in exchange for OH^-). Under such conditions, algae that utilise HCO_3^- via extracellular carbonic anhydrase-catalysed conversion to CO_2 (e.g. *Chondrus crispus*) cannot photosynthesise, because the concentration of CO_2 in the (air-disequibrated) rockpool would be too low to account for any inward diffusion of this carbon form. Also, if any fragment of such an alga would be transported to the developing rockpool, it would photobleach quickly under high irradiances because of the C_i limitation. Other algae that may potentially be able to photosynthesise under the low C_i and high pH conditions caused by *U. intestinalis* are either absent from the habitats close to the rockpools (e.g. *U. lactuca*) or may, because of a slower-growing life strategy, not be able to compete with *U. intestinalis* under the restricting C_i and/or otherwise fluctuating conditions of the rockpools (e.g. *Fucus vesiculosus*).

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LITERATURE CITED

- Axelsson L (2003) The fascinating Rhodophyceae—plasma membrane located CCMs and CO_2 excretion in red macroalgae. Abstract, 3rd Eur Phycol Congr, p 57
- Axelsson L, Beer S (2001) Carbon limitations. In: Rai LC, Gaur JP (eds) Algal adaptation to environmental stresses. Springer-Verlag, Berlin, p 21–43
- Axelsson L, Uusitalo J (1988) Carbon acquisition strategies for marine macroalgae. 1. Utilisation of proton exchanges visualized during photosynthesis in a closed system. *Mar Biol* 97:295–300
- Axelsson L, Uusitalo J (1991) Mechanisms for concentrating and storage of inorganic carbon in marine macroalgae. In: Garcia Reina G, Pedersen M (eds) Seaweed cellular biotechnology, physiology and intensive cultivation. Universidad de Las Palmas de Gran Canaria, Las Palmas, p 185–198
- Axelsson L, Carlberg S, Ryberg H (1989) Adaptations by macroalgae to low carbon availability. II. Ultrastructural specializations, related to the function of a photosynthetic buffer system in the Fucaceae. *Plant Cell Environ* 12: 771–778
- Axelsson L, Uusitalo J, Ryberg H (1991) Mechanisms for concentrating and storage of inorganic carbon in marine macroalgae. In: Garcia Reina G, Pedersen M (eds) Seaweed cellular biotechnology, physiology and intensive cultivation. COST -48, Universidad de Las Palmas de Gran Canaria, Las Palmas, p 185–198
- Axelsson L, Ryberg H, Beer S (1995) Two modes of bicarbonate utilization in the marine green macroalga *Ulva lactuca*. *Plant Cell Environ* 18:439–445
- Beer S (1994) Mechanisms of inorganic carbon acquisition in marine macroalgae (with special reference to the Chlorophyta). *Prog Phycol Res* 10:179–207
- Beer S, Axelsson L (2003) Limitations in the use of PAM fluorometry for measuring photosynthetic rates of macroalgae at high irradiances. *Eur J Phycol* 39:1–7
- Beer S, Israel A (1990) Photosynthesis of *Ulva fasciata* IV: pH, carbonic anhydrase and inorganic carbon conversions in the unstirred layer. *Plant Cell Environ* 13:555–560
- Beer S, Björk M, Gademann R, Ralph P (2001) Measurements of photosynthetic rates in seagrasses. In: Short FT, Coles R (eds) Global seagrass research methods. Elsevier, Amsterdam, p 183–198
- Björk M, Haglund K, Ramazanov Z, Garcia-Reina G, Pedersen M (1992) Inorganic carbon assimilation in the green seaweed *Ulva rigida* C. Ag. (Chlorophyta). *Planta* 187: 152–156
- Cabello-Passini A, Aguirre-von-Wobeser E, Figueroa FL (2000) Photoinhibition of photosynthesis in *Macrocystis pyrifera* (Phaeophyceae), *Chondrus crispus* (Rhodophyceae) and *Ulva lactuca* (Chlorophyceae) in outdoor culture systems. *J Photochem Photobiol* 57:169–178
- Carr H, Björk M (2003) A methodological comparison of photosynthetic oxygen evolution and estimated electron transport rate in tropical *Ulva* species under different light and inorganic carbon conditions. *J Phycol* 39:1125–1131
- Choo KS, Snoeijs P, Pedersen M (2002) Uptake of inorganic carbon by *Cladophora glomerata* (Chlorophyta) from the Baltic Sea. *J Phycol* 38:493–502
- Drechsler Z, Sharkia R, Cabantchik ZI, Beer S (1993) Bicarbonate uptake in the marine macroalga *Ulva* sp. is inhibited by classical probes of anion exchange by red blood cells. *Planta* 191:34–40
- Drechsler Z, Sharkia R, Cabantchik ZI, Beer S (1994) The relationship of arginine groups to photosynthetic HCO_3^- uptake in *Ulva* sp. mediated by a putative anion exchanger. *Planta* 194:250–255
- Ganning B (1971) Studies on chemical, physical and biological conditions in Swedish rockpool conditions. *Ophelia* 9:51–105
- Hanelt D, Wiencke C, Nultsch W (1997) Influence of UV radiation on the photosynthesis of Arctic macroalgae in the field. *J Photochem Photobiol* 38:40–47
- Hayden HS, Blomster J, Maggs CA, Silva PA, Stanhope MJ, Waaland JR (2003) Linnaeus was right all along: *Ulva* and *Enteromorpha* are not distinct genera. *Eur J Phycol* 38: 277–294
- Larsson C, Axelsson L (1999) Bicarbonate uptake and utilization in macroalgae. *Eur J Phycol* 34:79–86
- Larsson C, Axelsson L, Ryberg H, Beer S (1997) Photosynthetic carbon utilization by *Enteromorpha intestinalis* (Chlorophyta) from a Swedish rockpool. *Eur J Phycol* 32: 49–54
- Raven JA (2003) Inorganic carbon concentrating mechanisms in relation to the biology of algae. *Photosynth Res* 77: 155–171
- Surif MB, Raven JA (1989) Exogenous inorganic carbon sources for photosynthesis in seawater by members of the Fucales and the Laminariales (Phaeophyta): ecological and taxonomic implications. *Oecologia* 78:97–105
- Truchot JP, Duhamel-Jouve AI (1980) Oxygen and carbon dioxide in the marine intertidal environment; diurnal and tidal changes in rockpools. *Respir Physiol* 39:241–254
- Yakovleva IM, Titlyanov EA (2001) Effect of high visible and UV irradiance on subtidal *Chondrus crispus*: stress, photoinhibition and protective mechanisms. *Aquat Bot* 71: 47–61