Mar Biol (2007) 151:99–107
DOI 10.1007/s00227-006-0459-1

RESEARCH ARTICLE

Photosynthesis in *Codium fragile* (Chlorophyta) from a Nova Scotia estuary: responses to desiccation and hyposalinity

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Received: 1 November 2005 / Accepted: 10 August 2006 / Published online: 7 September 2006

Abstract *Codium fragile* ssp. *tomentosoides* from Caribou Harbour, an estuarine site in the southern Gulf of St. Lawrence, was extremely tolerant to stresses from desiccation and reduced salinity. Photosynthetic responses of both rhizomatous and erect growth forms were measured using pulse amplitude modulation (PAM) fluorometry of chlorophyll *a* fluorescence to determine effective quantum yield (Φ_{PSII}) and relative electron transport rate (rETR). After 5 h of desiccation, thalli lost 20% of their mass, but still showed high levels of Φ_{PSII}. Thalli survived for at least 6 h in freshwater, and showed virtually complete recovery of photosynthetic capacity within a few hours of return to full seawater. Immersion in 8 psu showed virtually complete recovery until the 24 h treatment period. Combining desiccation and salinity stresses produced a synergistic effect, but plants still showed strong recovery even after 86% dehydration and reimmersion in 16 psu. These results suggest that the photosynthetic physiology of *Codium fragile* is highly adapted to growth in estuarine conditions.

Communicated by M. Kühl, Helsingør.

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Introduction

Codium fragile (Suhr) Hariot ssp. *tomentosoides* (van Goor) Silva is an invasive seaweed, and it has spread to many temperate parts of the world (Trowbridge 1995, 1998, 2002; Campbell 1999). The species has become well established on both sides of the Atlantic Ocean from Scandinavia to Spain, and from the Gulf of St. Lawrence to the Carolinas (Chapman 1999). In most areas, *C. fragile* occurs on rocky substrata, where it grows primarily in the subtidal zone, low intertidal zone or in intertidal rock pools at full salinity. In eastern North America, *C. fragile* has been able to grow in estuarine conditions (Malinowski and Ramus 1973; Hanisak 1979; Garbary et al. 1997; Hubbard and Garbary 2002; Garbary et al. 2004). Malinowski and Ramus (1973) suggested that *C. fragile* would not become a nuisance in soft bottom habitats because of substratum limitations. These large populations in estuarine habitats were not predicted based on the fully marine origin of the species. Traits that have been suggested as the basis of the success of *C. fragile* include the ability for rapid growth, low light requirements, tolerance to high light levels, and high temperature and salinity tolerances (Ramus et al. 1976; Hanisak 1979; Trowbridge 1998; Mathieson et al. 2003).

Since at least 1996 when *Codium* was first discovered in northern Nova Scotia in Caribou Harbour, it has become well established in the southern Gulf of St. Lawrence (Garbary et al. 1997, 2004; Hubbard and Garbary 2002; Locke et al. 2003). Two morphological forms of *C. fragile* were described from Caribou Harbour: the normal erect form with a basal disk from which arise erect exes, and a prostrate form in which rhizomatous axes grow along the sediment and produce erect branches (Garbary et al. 2004). The rhizomatous growth form would appear to be better adapted for this habitat in that it allows for multiple attachment sites to the various substrata (e.g., small stones, shells and shoots and rhizomes of *Zostera marina* L. Here we examine the physiological differences in these forms to determine if physiological adaptation (greater resistance to light and desiccation stress) is coincident with morphological adaptation.

In this paper we examine the photosynthetic responses of *C. fragile* from an estuarine habitat in Nova Scotia to determine the extent of physiological adaptation to both hyposalinity and desiccation stress. The ability to withstand reduced salinities should reflect the extent to which populations of *C. fragile* can prosper in the reduced and fluctuating salinities of estuaries. In addition, thalli and propagules may be exposed on the shore as a consequence of wind and tides. Many thalli in estuarine conditions are free-floating for shorter or longer periods, and desiccation tolerance will be a significant adaptive trait. Desiccation causes cellular dehydration, which increases the concentration of electrolytes within the cell, causing changes to membrane-bound structures including the thylakoid (Wiltens et al. 1978). Since chlorophyll protein complexes are contained within the thylakoid membrane, chlorophyll *a* fluorescence is therefore a sensitive indicator of structural damage to this membrane (Schreiber and Bilger 1987). Consequently, long-term survival and dispersal in estuaries will be enhanced if plants have significant physiological adaptations to both low salinity and desiccation.

Materials and methods

Thalli of erect and rhizomatous forms of *Codium fragile* ssp. *tomentosoides* (hereafter *C. fragile* or *Codium*) were collected in August 2003 in Caribou Harbour, Pictou County, Nova Scotia (45.74°N, 62.66°W). Thalli were collected in the low intertidal zone to shallow subtidal zone (ca. +10 to –30 cm). Caribou Harbour (ca. 15 km^2) is a soft-bottom estuary (25–28 psu) with large areas dominated by meadows of *Zostera marina* L. The shorelines are primarily sandy beaches, salt marshes or cobble beaches, the latter dominated by *Fucus vesiculosus* L.

For the current experiments, *Codium* thalli were acclimated for 30 days in a 500 l fiberglass tank, filled to a depth of 0.5 m and maintained at 18–20°C using standard fluorescent lights at 25–30 μmol photons m^{-2} s^{-1} of photosynthetically active radiation (PAR) in unsupplemented seawater at 30 psu. The low light and long acclimation period resulted in plants being acclimated to low irradiance. Daylength was the same as in situ (ca. 12 h light per day), with room lights being regulated using an exterior sensor. Seawater was replenished every 2 weeks and constantly circulated. During acclimation, no evidence of thallus bleaching or senescence was apparent.

The photosynthetic performance of *Codium* under different experimental conditions was measured via chlorophyll *a* fluorescence using a Diving-PAM fluorometer (Walz GmbH, Effeltrich, Germany). Fluorescence parameters F (chlorophyll fluorescence of a light-acclimated thallus), F'_m (maximal chlorophyll fluorescence of a light-acclimated thallus), and $\Phi_{PSII} = (F'_m - F)/F'_m$ (effective quantum PSII yield of a light-acclimated thallus) were measured for fragments from the mid portion of non-terminal branches. Here there was less variation in chlorophyll *a* fluorescence relative to older thallus portions with darker color, or terminal branches with variable chlorophyll content. Leaf clips (Diving-LC, Walz) were positioned onto the sample, with their shutters open, and a reading was made for fluorescence parameters. All experiments were conducted at room temperature (ca. 20°C) with illumination provided by cool-white fluorescent lights.

Experiment 1. Adaptation to low irradiance

We examined the effect of levels of irradiance (20, 38 and 60 μmol photons m^{-2} s^{-1} on plants with the rhizomatous and erect morphologies ($n = 6$–10). *Codium* fragments 15–20 cm long were placed in experimental chambers with flow-through seawater. The effective quantum yield of photosynthesis (Φ_{PSII}) was measured initially, and then at eight or nine intervals over 70–80 h. Rapid light curves (RLCs) of photosynthesis were produced for the two growth forms following low light adaptation at 25–30 μmol photons m^{-2} s^{-1} in the tank before the start of salinity and desiccation experiments. The RLCs were obtained from nine measurements after 10 s sample illumination with increasing levels of actinic light from 0 to 1,400 μmol photons m^{-2} s^{-1} ($n = 6$–10). The relative electron transport rate (rETR) between PSII and PSI is calculated as:

$$\mathrm{rETR} = \Phi_{PSII} \times \mathrm{PPFD} \times 0.5 \times 0.84$$

where PPFD is photosynthetic photon flux density of photosynthetically active radiation (PAR 400–700 nm).

This equation assumes that PSII absorbs half (0.5) the quanta of available light (Schreiber et al. 1994) and an average photosynthetic unit absorbs about 84% of incident PAR (Björkman and Demmig 1987).

Experiment 2. Desiccation effects on two forms

To determine the effects of increasing desiccation on two forms of *C. fragile* (rhizomatous and erect), thallus fragments 15–20 cm long and one per thallus were removed from the seawater tank and transferred to a constant environment room (relative humidity (72–75%) and room temperature (20°C). The effective quantum yield was measured in 6–10 thalli from each form. To determine dehydration, we measured the initial fresh weight after gentle blotting to remove surface moisture (W_f), and then at intervals during air drying (W_t). At the completion of the experiment, thalli were oven dried (at 65°C) to a constant mass to determine a final dry weight (W_d). Percentage dehydration (%D) was calculated as follows:

$$\%D = (W_f - W_t)/(W_f - W_d) \times 100$$

Prior to measuring photosynthesis, the sampled tissue was immersed in seawater for at least 2 h prior to ensure fully imbibed tissue.

Experiment 3. Effect of hyposalinity on photosynthesis

The objective of this experiment was to determine the photosynthetic performance of the erect form of *C. fragile* following exposure time to a range of reduced salinities. Ten *Codium* fragments were pre-exposed to a given osmotic solution (0, 8, 16 psu) and duration (1, 3, 6, 14, 24, 48 h), then immediately returned to the original seawater (30 psu) aquaria (n = 6–10 per treatment). Effective quantum yield was then measured.

Experiment 4. Combined effects of desiccation and hyposalinity

This experiment was carried out to assess the effects of hyposaline conditions on the speed and capacity of desiccated tissue to recover its photosynthetic activity. Thallus portions were desiccated for 2, 7, 15, and 24 h (20–24, 51–65, 88–90, >90% dehydration, respectively). Thalli were then immersed in seawater at different salinities (8, 16, 32 psu) and the effective quantum yield was measured following rehydration.

Data analysis

All results are presented as means ± SD. Effective quantum yield (Φ_{PSII}) and rETR data were tested using ANOVAs for significant differences among treatments. These data were not analyzed as a time series due to statistical dependence between samples through time within a trial. When a significant difference was detected ($P < 0.05$), the means were analyzed using Turkey's test to determine where the differences occurred. Variance heterogeneity was checked using Cochran's test, and data were transformed when required. When normality and equal variance were not achieved, the non-parametric Kruskal–Wallis test was performed to assess variation among treatments. These analyses were performed using the software SPSS Release 11.0.1 (SPSS Inc., Chicago, IL, USA)

Results

Rhizomatous and erect growth forms

The effective quantum yield (Φ_{PSII}) of photosynthesis varied considerably based on irradiance and duration of exposure. Despite clear morphological differences between thalli with a prostrate habit and those with a standard morphology, there was no evidence for physiological differentiation between primary prostrate axes and primary erect axes in non-stressed conditions. Thus at 20, 38 and 60 μmol photons m^{-2} s^{-1}, there was no significant difference between the two growth forms ($F_{1,330} = 0.684$; $P = 0.409$) (Fig. 1). There was a major response to irradiance; however, in that at the two lowest irradiances there was little reduction in Φ_{PSII} even after 65 h. At the highest irradiance, there was significant reduction of Φ_{PSII} after only 5 h from 0.68 to 0.53. The decline continued until 40 h exposure after which quantum yield stabilized at about 0.4.

The sensitivity to high irradiance is also shown in thalli maintained in the laboratory for 1 month in a tank with illumination provided by overhead fluorescent lamps. Both rhizomatous prostrate and normal erect morphs of *C. fragile* gave similar responses ($F_{1,142} = 0.070$; $P = 0.791$). Relative electron transport rate (rETR) peaked at about 20, at an irradiance of 180 μmol photons m^{-2} s^{-1} over the course of the rapid light curves (RLCs). There was a continual decline in rETR at higher irradiances (data not shown).

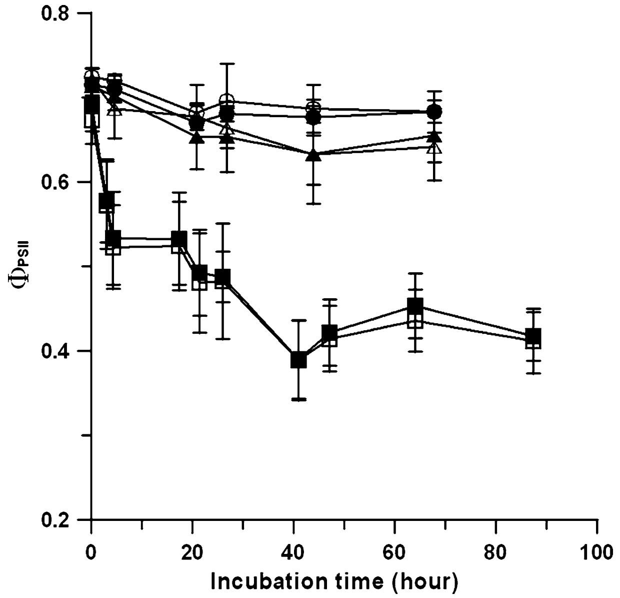

Fig. 1 Effective quantum yield (Φ_{PSII}) of erect (*open triangle, open circle, open square*) and rhizomatous (*filled triangle, filled circle, filled square*) growth forms of *Codium fragile* at three irradiances (*open triangle, filled triangle* 20*; open circle, filled circle* 38*; open square, filled square* 60 μmol photons m^{-2} s^{-1})

Desiccation and quantum yield

Thalli exposed completely have slow desiccation, losing about 80% of their wet mass after exposure of 16 h (Fig. 2). It then took an additional 8 h to lose another 13% of the original wet mass. Hence, desiccation was almost linear between 1 and 7 h and then slowed. Thalli showed about a 10% reduction in Φ_{PSII} after 1 h of desiccation, and there was a further 10–15% decline with up to 5 h of desiccation. Ten hours of desiccation resulted in a 60% desiccation and a 50% loss in Φ_{PSII}. After 17 h of desiccation and about 80% dehydration, effective quantum yield was reduced by two-thirds. These thalli showed only partial recovery of photosynthetic yield over the next 7 h, and the full recovery of these plants is doubtful. The two growth forms did not differ during early stages of the experiment; however, after 6 h, the rhizomatous form showed lower dehydration ($F_{1,40}$ = 2.831; P = 0.100) and significantly higher quantum yield ($F_{1,98}$ = 10.010; P = 0.002).

Hyposalinity stress

Hyposalinity clearly had a significant effect ($F_{2,213}$ = 41.835; $P < 0.001$) on photosynthetic performance. Up to 6 h of immersion in freshwater and then return to full salinity had little effect on Φ_{PSII} following 60 h of recovery (Fig. 3). Although the thalli placed in freshwater for 6 h had an initial reduction of Φ_{PSII} of around 25%, and Φ_{PSII} remained below 1 at 3 h immersion times, there was little difference in any of these thalli after 60 h of recovery. After 14 h in freshwater, quantum yield dropped dramatically by almost 60%. Despite some recovery in the first 10 h, there was a gradual decline over the next 45 h suggesting that full recovery is not possible following this exposure.

Plants recovered better after immersion in 8 psu seawater (Fig. 4) although there were significant

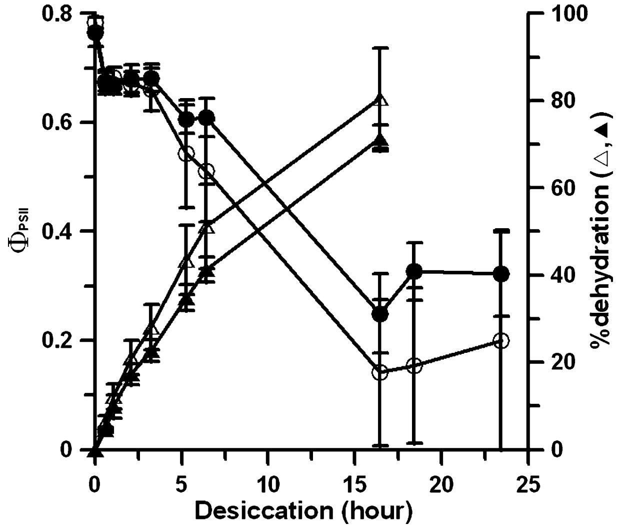

Fig. 2 Effective quantum yield (Φ_{PSII}) of erect (*open triangle, open circle*) and rhizomatous (*filled triangle, filled circle*) growth forms of *Codium fragile* at different levels of % dehydration

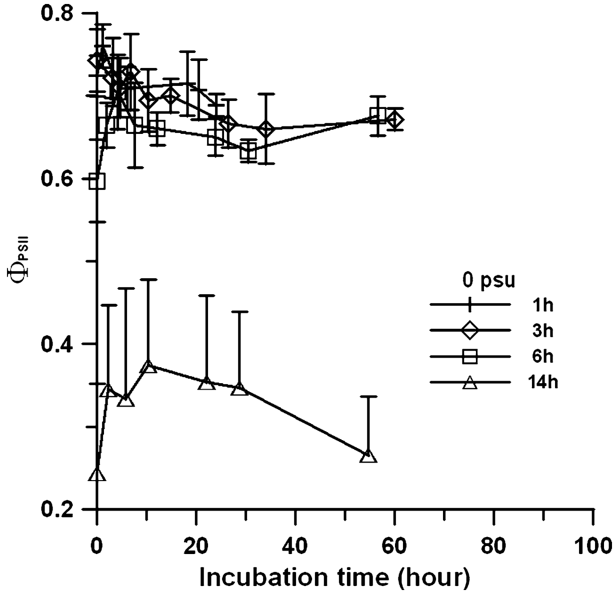

Fig. 3 Effective quantum yield (Φ_{PSII}) of recovering *Codium fragile* after different times of exposure to 0 psu

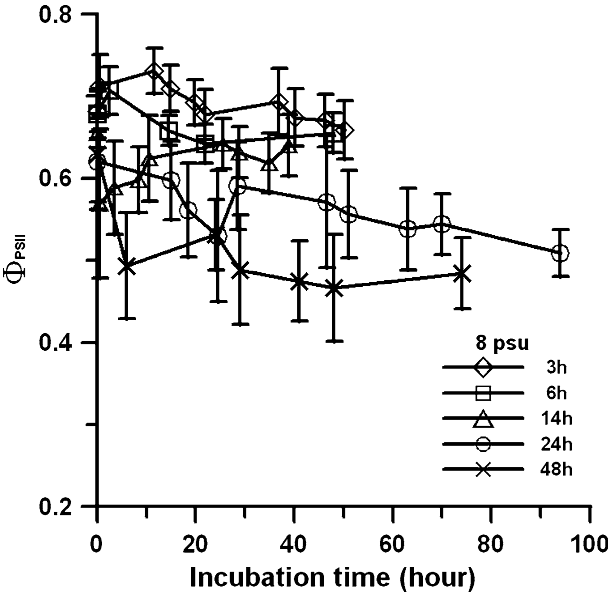

Fig. 4 Effective quantum yield (Φ_{PSII}) of recovering *Codium fragile* after different times of exposure to 8 psu

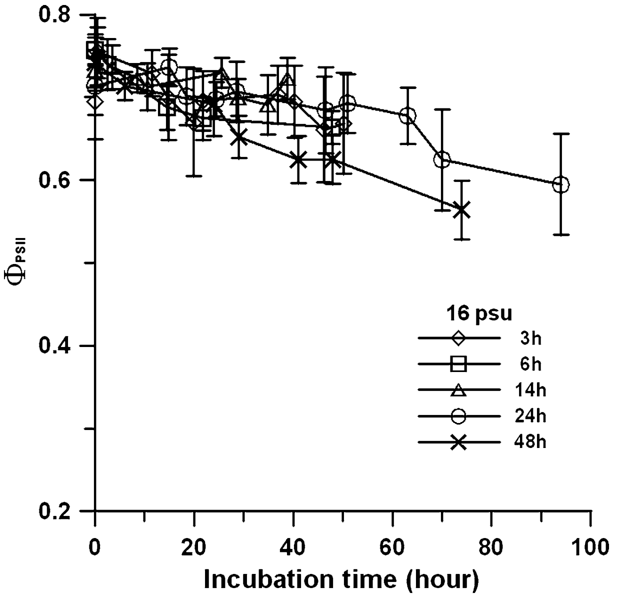

Fig. 5 Effective quantum yield (Φ_{PSII}) of recovering *Codium fragile* after different times of exposure to 16 psu

responses to the different immersion times ($F_{4,346}$ = 130.817; $P < 0.001$). Only differences between 3 and 6 h were not significant (post hoc test; $P = 0.187$). Three and 6 h immersion at 8 psu showed no decline in Φ_{PSII}, and values remained stable even after 50 h of recovery, suggesting no long-term damage to photosynthetic machinery by this exposure. With 14 h of exposure to 8 psu there was an initial 20% drop in Φ_{PSII}, but over the next 40 h in standard seawater, Φ_{PSII} recovered such that it was only slightly lower (*post hoc* test; $P < 0.001$) than values for 6 h.

A 24 h exposure to 8 psu caused an initial 10% drop in Φ_{PSII}; however, these algae did not recover, and entered a slow photosynthetic decline such that after 90 h of recovery, thalli still only had Φ_{PSII} of 0.55. A 48 h exposure to 8 psu resulted in an immediate drop in Φ_{PSII} to 0.5, with no recovery after 70 h in full seawater. At 16 psu, ANOVA indicated a significant response to immersion times ($F_{4,346}$ = 15.233; $P < 0.001$). This was despite the fact that thalli showed little in the way of reduction in Φ_{PSII} with up to 48 h of exposure (Fig. 5). After 50 h of recovery it was only the algae that had been immersed for 48 h in half strength seawater that showed significant reduction in Φ_{PSII} (post hoc test; $P < 0.001$).

Combined desiccation and salinity stress

Combined salinity and desiccation treatments showed synergistic reductions in Φ_{PSII} than either factor alone (Table 1, Fig. 6). In all experimental conditions, Φ_{PSII} increased for 3–10 h following reimmersion. For a given level of desiccation, recovery of Φ_{PSII} was related to salinity. At 20–24% dehydration, only 8 psu showed incomplete recovery after 45 h. Even at 8 psu these thalli had a strong Φ_{PSII} (>0.5). With increasing dehydration (56%) there was a greater loss of Φ_{PSII}, and thalli at 8 psu showed a declining Φ_{PSII} such that at 45 h the mean was at 0.4. The high variances among these thalli suggest that survival would be variable. At 90% dehydration all thalli showed reductions in Φ_{PSII}, and the extent of recovery was related to salinity. Upon rehydration, Φ_{PSII} was initially uniform in all thalli (ca. 0.2) and then increased rapidly to 0.4–0.5. By 10 h after rehydration, thalli at different salinities showed different quantum yield that were directly related to salinity. Following 93% dehydration, Φ_{PSII} was dramatically reduced, and only thalli incubated in full seawater showed photosynthetic activity. This was extremely limited (Φ_{PSII} = 0.1), and within 24 h the response dropped to zero.

Table 1 Two-way ANOVA table showing statistical results for combined desiccation and salinity experiment. Note: results for 24 h (93% dehydration) were not included in this analysis

Source	Sum of squares	*df*	Mean square	*F*-ratio	*P*
Desiccation	7.232	2	3.616	208.744	<0.001
HypoSalinity	1.404	2	0.702	40.539	<0.001
Interaction	0.601	4	0.150	8.671	<0.001
Error	11.536	666	0.017		

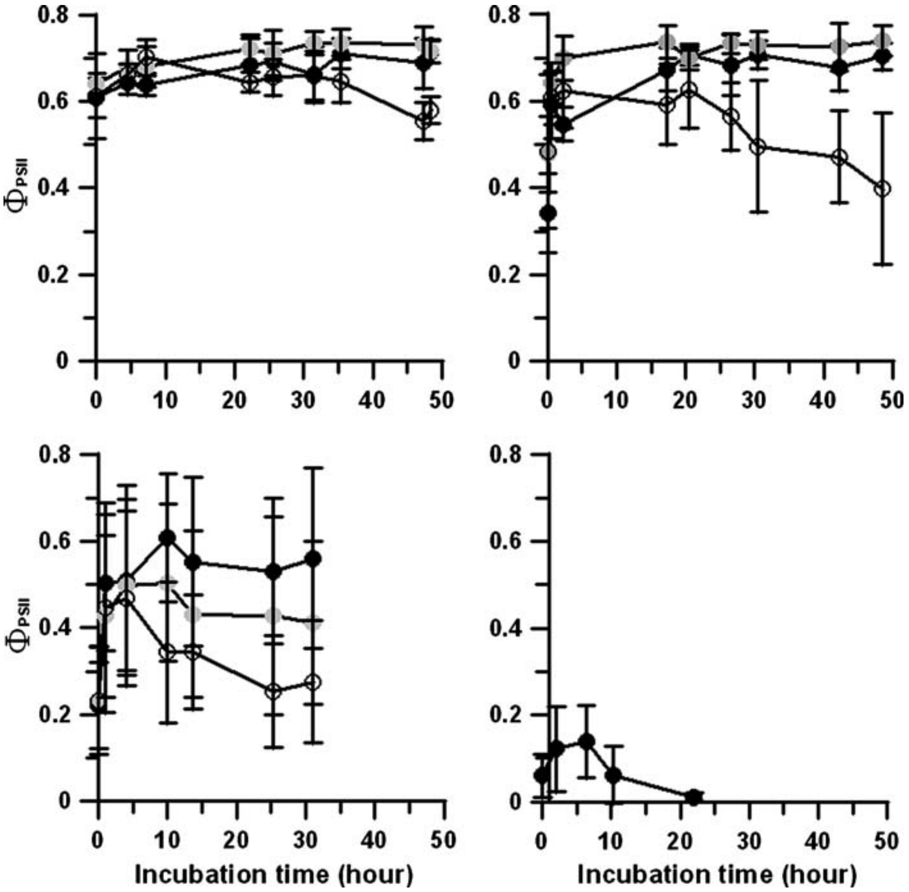

Fig. 6 Effective quantum yield (Φ_{PSII}) of recovering *Codium fragile* in a range of salinities (*filled circle* 32, *filled gray circle* 16, *open circle* 8 psu) following: **a** 20–24% dehydration, **b** 51–56% dehydration, **c** 86–90% dehydration, and **d** 93% dehydration

Discussion

Hyposalinity is a major environmental factor affecting the distribution and growth of marine algae (e.g., Bird and McLachlan 1986; Kirst 1989; Lüning 1990; Lobban and Harrison 1994; Kim and Lee 1996). On the one hand, the distribution and survival of many seaweeds are constrained by reduced salinity (e.g., Munda 1978; Lee 1998) and fluctuating salinities (e.g., Kamer and Fong 2000). On the other hand, many seaweeds have considerable adaptive abilities to lowered salinity (e.g., *Gelidium coulteri* Harvey, Macler 1988), and several marine algae have made the transition from marine into freshwater (Sheath 1987). *Blidingia minima* (Nägeli ex Kützing) Kylin, *Bostrychia radicans* Montagne and *Enteromorpha intestinalis* (L.) Link are clearly estuarine species, and their photosynthesis and growth are still substantial at 10 psu (Karsten and Kirst 1989a, b; Kim and Lee 1996; Kamer and Fong 2000). The long exposures to which these species were subject during experiments (up to 4 weeks) suggest full adaptation to hyposaline conditions. Hanisak (1979) showed that *Codium* in New England could survive and grow at 24 psu, although growth was strongly reduced at 18 psu and ceased at 12 psu. The tolerance to hyposalinity reported here for *Codium* is not as complete as in *Enteromorpha*, *Blidingia* or *Bostrychia*; however, tolerance is at least equivalent to that reported for estuarine and non estuarine populations of *Cladophora rupestris* (L.) Kützing (Wienke and Davenport 1987; Thomas et al. 1988). The fact that *Codium fragile* still has high rates of effective quantum yield after 24 h at 8 psu, or 48 h at 16 psu, and can maintain high levels after 90 h of recovery, shows remarkable tolerance for a fundamentally marine species.

The photosynthetic characteristics of *C. fragile* show adaptation for life in temperate estuaries. Relative ETR peaks at irradiances of less than 200 μmol photons m^{-2} s^{-1}, suggesting that *C. fragile* is a shade adapted thallus, and can survive in beds of *Zostera marina* L. *Codium* can survive in freshwater for 6 h and show full recovery. Lagoons and estuaries are naturally turbid environments and hence it should be advantageous to be optically dense to allow for efficient light absorption. *C. fragile* is considered to have very efficient light utilization at low light levels (Ramus et al. 1976; Ramus 1978). Specifically, Ramus (1990) suggested that *C. fragile* could outgrow *Ulva curvata* at low light levels based on photosynthetic *P–E* curves. Thus, except for the areas immediately adjacent to sites of freshwater inflow, photosynthetic responses suggest that thalli would have no problem surviving in the estuaries in the southern Gulf of St. Lawrence. Recovery of photosynthetic capacity even after 80% dehydration suggests that unattached plants that may be cast onto the shore can recover, if conditions of wind and tide allow for reimmersion.

Codium fragile has high water content relative to other intertidal and subtidal algae (Dromgoole 1980). Along with the cylindrical axes and low surface to volume ratio, the high water content partly explains the slow dehydration in our experiments. *Codium* may function similar to the intertidal saccate algae *Halosaccion americanum* (Gmelin) Ruprecht and *Colpomenia peregrina* (Sauvageau) Hamel, that retain seawater in their thalli. These species have slow desiccation rates and relatively stable photosynthetic rates regardless of whether they are submerged or emersed (Oates 1985, 1986).

There is a wide range of responses among taxa and growth forms to desiccation. In intertidal algae from New Zealand, Brown (1987) concluded that recovery following desiccation was correlated with vertical distribution on the shore. Ji and Tanaka (2002) concluded, however, that decline in photosynthetic rate following desiccation was not correlated with height on the shore, but with lower rates of water loss during desiccation. The slow desiccation rate, and the high levels of effective quantum yield (i.e., above 0.5) associated with 30% desiccation in *C. fragile*, are more consistent with conclusions of Ji and Tanaka (2002). However, the improvements in photosynthetic performance reported for many intertidal algae following slight desiccation (Brinkhuis et al. 1976; Quadir et al. 1979; Ji and Tanaka 2002) did not occur in *C. fragile*.

Johnson et al. (1974) showed that for six intertidal algae that a 10–60% water loss was required for a reduction of 50% of the maximal photosynthetic rate. The intertidal *Porphyra haitanensis* Chang and Zheng can tolerate a 30% loss of water before major reduction in photosynthetic capacity occurs (Zou and Gao 2002). In the high intertidal *Mazzaella parksii* (Setchell and Gardner) Hughey, Silva and Hommersand, major reduction in photosynthetic rate occurred after 20% desiccation [Scrosati and DeWreede 1998, as *Mazzaella cornucopiae* (Postels and Ruprecht) Hommersand]. *C. fragile* is at the upper limit of these species, with ca. 60% dehydration required to reduce Φ_{PSII} by 50%. Abe et al. (2001) described the relationship between drying, water potential and photosynthetic rate for a range of intertidal and subtidal algae. Again, *Codium fragile* fits into the mid range of the tolerant intertidal species in terms of photosynthetic capacity following desiccation. Given the high water content and relatively slow rate of water loss compared to other species (Dromgoole 1980), *C. fragile* appears to have the physiology consistent with being a highly tolerant intertidal species.

Codium fragile reproduces extensively through vegetative propagation. This occurs through fragmentation of mature plants to produce propagules (Garbary et al. 2004). Seasonality is such that fragmentation of overwintering algae occurs in late spring. This is well after snow melt and the potential impact of low salinity on survival. Isolated filaments can also serve as propagules, and these are also resistant to brackish conditions (Yang et al. 1997). Thus, even if propagules are more sensitive to low salinity than mature plants, dispersal and colonization by vegetative means should not be constrained through most of the estuaries in the southern Gulf of St. Lawrence. The lack of dependency on spores or sexual reproduction as the primary method of propagation makes the physiology reported here a central aspect of population maintenance.

The synergy in negative reactions to desiccation and salinity stress were expected; however, the ability of *C. fragile* to recover what would be considered strongly adverse conditions, points to the highly adaptive nature of the species. Most estuaries in the southern Gulf of St. Lawrence are shallow, with low freshwater inflows and high flushing rates based on exchange with coastal seawater (e.g., Pomquet Harbour, Kim et al. 2004b). Thus, salinity is typically above 20 psu for most of the estuarine area (e.g., Antigonish Harbour, Garbary and Barkhouse 1987).

Codium fragile has maximum rETR at an irradiance of about 200 μmol photons $\mathrm{m}^{-2}\ \mathrm{s}^{-1}$; above this irradiance photoinhibition occurs. The *P-E* curve based on rETR suggests that *Codium* is a shade species (Ramus 1978, 1990; Herbert and Waaland 1988) with about half the light required for saturation as in *Ulva pertusa* Kjellman (Kim et al. 2004a). Many intertidal and shallow subtidal seaweeds show photoinhibition at midday, and even short exposures cause major reduction in photosynthetic parameters (e.g., Sagert et al. 1997; Häder et al. 1998, 1999, 2001; Jiménez et al. 1998; Yakovleva and Titlyanov 2001). Except for populations in rock pools (Begin and Scheibling 2003), where shading from overhanging plants and the water column occurs, photoinhibition may explain the absence of significant intertidal populations of *C. fragile* on rocky intertidal shores and soft sediment shores in eastern Canada.

Another environmental constraint on the distribution of *C. fragile* is ultraviolet (UV) radiation. After 23 days exposure to PAR and UVA, Φ_{PSII} dropped by 30% and ETR_{max} by 50% (Michler et al. 2002). *C. fragile* was the most sensitive species tested. In *C. adhaerens* (Cabrera) C. Agardh, there was virtually no recovery during 6 h after 60 min exposure to solar radiation. In *C. taylori* Silva, a 30 min exposure to unfiltered solar radiation markedly decreased photosynthetic quantum yield relative to conditions where UVA and UVB were filtered (Häder et al. 2000). These UV treated plants did not show full recovery even after 6 h in the absence of UV. In intertidal seaweeds from Chile (not including *Codium*), species were particularly tolerant of solar radiation. Natural UV caused <25% photoinhibition, with rapid recovery (Gómez et al. 2004). These experiments are consistent with observations by Ramus (1978) who showed that *C. fragile* had extremely high absorbance down to 380 nm, the lowest wavelength that was used. High UV absorbance would likely continue much further into UVA wavelengths. Thus, despite considerable tolerance to desiccation and low salinities, the ecological range of *C. fragile* may be more constrained by impacts of UV radiation on photosynthesis than the factors we considered.

Acknowledgments We thank Sarah Fraser for technical support and AG Miller and Ricardo Scrosati for helpful discussion and comments on the manuscript. This work was supported by grants from MarineBio21, Ministry of Maritime Affairs and Fisheries, Korea to KYK and the Natural Sciences and Engineering Research Council of Canada to DJG.

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