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Desiccation tolerance of the introduced marine green alga *Codium fragile* ssp. *tomentosoides* – clues for likely transport vectors?

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Abstract

The invasive marine green macroalga *Codium fragile* ssp. *tomentosoides* is now considered to be an introduced marine pest along the northwest Atlantic and southern Australian coasts. International or domestic translocation of *C. fragile* ssp. *tomentosoides* is usually attributed to the fouling of ship hulls or shellfish, particularly oysters. A likely domestic vector is shipboard transport, involving the translocation of whole thalli or fragments entangled in fishing nets, ropes, etc. that are then released in a previously unaffected area. Here we investigated the survival of *C. fragile* ssp. *tomentosoides* under emersed conditions, simulating shipboard transport. *C. fragile* ssp. *tomentosoides* was able to survive periods of emersion of up to 90 days in high relative air humidity. Net photosynthesis remained positive at about 50% of the rates of submersed control thalli. After 2 days of emersion and 4 days of rehydration under submersed conditions thalli recover to their initial net photosynthesis rates. Hence, *C. fragile* ssp. *tomentosoides* is likely to survive long shipboard journeys entrapped in fishing nets, anchor wells or other protected, high-humidity areas of a vessel. Furthermore, *C. fragile* ssp. *tomentosoides* may survive emersion on an exposed deck during short trips, especially in cooler conditions such as at night. The incursion sites of *C. fragile* ssp. *tomentosoides* in Australia are generally in modified environments, often associated with shipping-related infrastructure such as wharves, jetties, rip rap, and moorings.

Introduction

Introduced macroalgae are a growing problem worldwide, and species such as *Caulerpa taxifolia*, *Codium fragile* ssp. *tomentosoides*, *Sargassum muticum* and *Undaria pinnatifida* are considered to be high profile invaders (e.g. Ribera and Boudouresque 1995; Cranfield et al. 1998; Trowbridge 1998; Boudouresque and Verlaque 2002; Leppäkoski et al. 2002; Occhipinti-Ambrogi and Savini 2003).

The siphonous green macroalga *Codium fragile* (Suringar) Hariot 1889 has a wide geographic distribution in marine temperate waters, and at least six different subspecies have been recognised (Silva and Womersley 1956; Trowbridge 1998). The subspecies *C. fragile* ssp. *tomentosoides* (Van Goor) Silva is considered to be extremely invasive (Carlton and Scanlon 1985) and is believed to be native to Japan (Trowbridge 1998). High-density populations of introduced *C. fragile* ssp. *tomentosoides* in areas of the Northwest Atlantic

have demonstrated detrimental economic effects on industries such as aquaculture (esp. oysters) and fisheries (Trowbridge 1998). In the Northeast Atlantic region, where *C. fragile* ssp. *tomentosoides* was introduced in the early 1900s, the alga has not attained pest status, which Chapman (1999) attributes to differences in specific biological interactions in the receiving habitats, in particular benthic community composition and grazing pressure.

In the Australasian region, *C. fragile* ssp. *tomentosoides* was first observed in New Zealand in 1973 (Dromgoole 1975) and, presumably as a secondary introduction from New Zealand, in Australia in 1996 (Campbell 1999; Lewis 1999). The alga has since spread rapidly around southeastern Australia and is currently known at several locations in Victoria and eastern Tasmania (Campbell 1999; Trowbridge 1999). The detection of *C. fragile* ssp. *tomentosoides* incursions in the Australasian region is difficult, because there are two native subspecies (*C. fragile* ssp. *tasmanicum*, *C. fragile* ssp. *nova-zealandiae*) and six native congeners that are morphologically similar (Silva and Womersley 1956; Womersley 1984). The rapid spread and high abundance of *C. fragile* ssp. *tomentosoides* at Australian incursion sites has caused concern about potential impacts on shellfish industries and on the remarkable biodiversity of macroalgal communities in temperate Australia (Womersley 1981).

Fouling of ship hulls or shellfish is the most likely vector for international or domestic translocation of *C. fragile* ssp. *tomentosoides* (Dromgoole 1975; Carlton and Scanlon 1985; Trowbridge 1998). Natural dispersal occurs by detached, floating, thalli that are positively buoyant due to internal gas entrapment (Dromgoole 1982). Another likely domestic vector is shipboard transport, involving the translocation of whole thalli or fragments entangled in fishing nets, ropes, etc. that are then released into previously unaffected areas. While fouling stages are most likely juvenile, or dedifferentiated, filamentous phases (see Trowbridge 1998), shipboard translocation will mainly involve mature *C. fragile* ssp. *tomentosoides* thalli or fragments thereof resulting in a higher likelihood of successful establishment.

The objective of this study was to determine survival time of *C. fragile* ssp. *tomentosoides* under emersed conditions such as those conditions likely to be found during shipboard transport: on exposed decks; or, protected from immediate desiccation in fishing nets or anchor wells.

Materials and methods

Collection of algae

Codium species were collected at several locations along Tasmania's east coast and at two locations in New South Wales, and identified to subspecies level. The information was used to produce an updated distribution map of *Codium fragile* ssp. *tomentosoides* in Australia.

For the desiccation experiments, *C. fragile* ssp. *tomentosoides* thalli were collected from two sites in southeastern Tasmania during January 2001: (i) Kettering Marina, from floating moorings, and (ii) Oyster Cove, from shallow subtidal small granite boulders. Thalli at both locations were permanently submerged even at lowest tides, and hence were not acclimated to desiccation. Thalli were placed in individual plastic bags and transported in a cooled, insulated container. In the laboratory, subspecies identification was confirmed by microscopic examination of utricle morphology using descriptions of Silva and Womersley (1956) and Dromgoole (1975). Then thalli were trimmed to size (6–9 g FW) and carefully cleaned of epibiota. All pre-handling of thalli was completed 24 h or more prior to commencement of experiments to avoid results being confounded by handling stress (Drew 1983).

Culture conditions

C. fragile ssp. *tomentosoides* thalli prior to experiments, in control treatments of the desiccation experiment (see below), and in the rehydration phase of the rehydration experiment (see below) were cultivated in a temperature controlled room at 17.5 °C (± 0.5 SE), a photon flux density of around 500 $\mu E\ m^{-2}\ s^{-1}$ (6×36 W 'Cool White' fluorescent tubes), and a light cycle synchronised with the natural daylength at the time of the study of 15 h light: 9 h dark. Up to five labelled thalli were placed in aerated 2 l glass beakers filled with autoclaved seawater, and enriched with half strength PES enrichment (prepared

according to Starr and Zeikus 1987). In the first week 40 µl l^{-1} of a saturated germanium dioxide solution was added to suppress diatom growth (Markham and Hagmeier 1982). The culture solution was exchanged every 3 days.

Desiccation experiment

Three treatments, control (C), humid (H), and dry (D) were used.

- C: thalli were maintained submersed, under culture conditions as above;
- H: thalli were kept emersed in a plastic zip-lock bag in water vapour saturated air (17.5 °C, 90% relative humidity);
- D: thalli were kept emersed, exposed to the air in the culture room (17.5 °C, 59% relative humidity).

The experiments were set up with sufficient thalli in the three treatments that five replicate thalli were measured at 1, 4, 8, 12 days for all treatments, at 16 and 20 days for the C and H treatments only, and at 90 days for the H treatment only. Each *C. fragile* ssp. *tomentosoides* thallus was only used once.

Rehydration experiment

Thalli were exposed to the above-described H and D treatments for either 2 or 8 days. Productivity of five replicate thalli was measured after 1 and 4 days of rehydration ('recovery') in the culture conditions above. Each *C. fragile* ssp. *tomentosoides* thallus was only used once.

Productivity measurements

We used a light and dark bottle method to measure net photosynthesis and dark respiration through changes in oxygen concentration with an oxygen electrode (WTW 340, Germany). Measurements were performed in 0.5 l Schott glass bottles with a specially modified lid to accept the electrode. Bottles were filled to capacity with culture medium (total volume 575 ml) and the algal thallus was attached to the electrode shaft with a loose-fitting rubber band. A magnetic stirrer kept the medium well mixed during measurements. Temperature and light conditions were the same as above, apart from light being provided by vertically mounted fluorescent tubes. Bottles were disinfected and rinsed before each use to prevent microbial contamination.

Each thallus was equilibrated for 20 min in the respective bottle before measurements commenced. Respiration was measured for 20 min in the dark bottle, after transfer to a clear bottle net photosynthesis was measured for 20 min.

Relative water content

Fresh weight of thalli was determined before productivity measurements (FW_1), i.e. prior to reimmersion for emersed thalli. Thalli were re-weighed after productivity measurements (FW_2), before drying in a fan-forced drying oven at 60 °C for 24 h to obtain dry weight (DW). The relative water content (RWC) after desiccation treatment was determined according to:

$$\mathrm{RWC} = [(\mathrm{FW}_1 - \mathrm{DW})/(\mathrm{FW}_2 - \mathrm{DW})] \times 100\%$$

Statistical analysis

Differences in net photosynthesis and respiration of *C. fragile* ssp. *tomentosoides* in the desiccation experiment between the treatments over time were analysed with two-factor ANOVA, with the fixed factors 'treatment' and 'desiccation time'. The ANOVA included only data from days 1 to 12, as after day 12 the D treatment was discontinued. Tukey HSD test was employed as a post hoc test to qualify significant ANOVA results. Differences between treatments in different desiccation and rehydration times in the rehydration experiment were analysed with three-factor ANOVA with the fixed factors 'treatment', 'desiccation time' and 'rehydration time' (each at two levels). Before ANOVA, data were log-transformed and the homogeneity of variances was confirmed with Cochran's test. Analyses were performed using the software package Statistica 5.5 (StatSoft, USA 1999).

Results

Distribution of C. fragile *ssp.* tomentosoides *in Australia*

C. fragile ssp. *tomentosoides* was found at nine of the 20 sampling locations along Tasmania's east

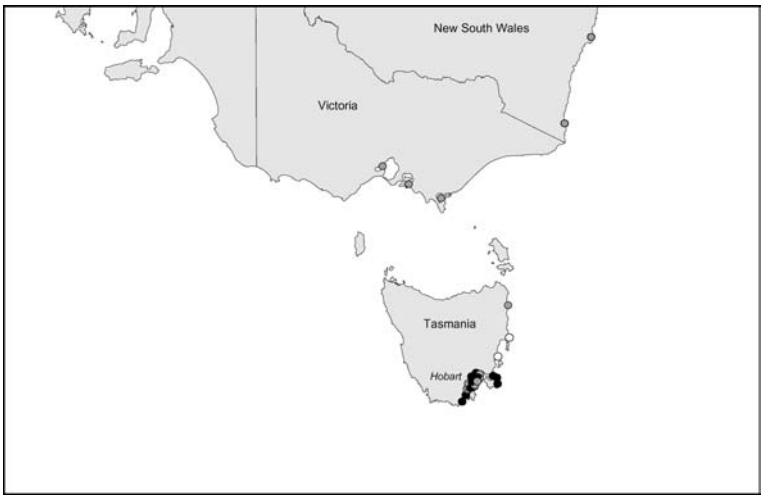

Figure 1. Distribution of *Codium fragile* subspecies at selected locations in Tasmania and New South Wales. Grey circles: *C. fragile* ssp. *tomentosoides*; black circles: *C. fragile* ssp. *tasmanicum* or *C. fragile* ssp. *nova-zealandiae*; white circles: *C. australicum.*

coast (Figure 1). All except one location (Georges Bay, St. Helens, northeast Tasmania) were within 50 km of the city of Hobart. Three of the incursion sites also had native subspecies present in mixed stands with *C. fragile* ssp. *tomentosoides*. The incursion sites in Tasmania and New South Wales were generally modified environments, often associated with shipping-related infrastructure such as marinas, wharfs, jetties, rip rap, and mooring sites. Native subspecies were found in such modified environments as well as on natural rocky shores. Figure 1 also includes two new incursion sites in New South Wales (Jervis Bay, Eden) and three previously known locations in Victoria (Port Phillip Bay, Corner Inlet, Western Port Bay; Campbell 1999; Lewis 1999).

Desiccation experiment

The net photosynthesis rates of *Codium fragile* ssp. *tomentosoides* differed between the three treatments (C, H, D; Figure 2; Table 1). After 1 day of exposure, C and H-treated thalli had similar rates of ~60 μmol O_2 h^{-1} g DW^{-1}, whereas the D-treated thalli had rates of less than 10 μmol O_2 h^{-1} g DW^{-1} (Figure 2). After exposure times of more than 4 days, the H-treated thalli steadily decreased to rates of about 30 μmol O_2 h^{-1} g DW^{-1}, on days 20 and 90. Rates of C thalli first increased then slightly decreased to a level of ~60 μmol O_2 h^{-1} g DW^{-1}. D-treated thalli showed negative rates (i.e. respiration exceeded gross photosynthesis) from day 4 to day 12. This treatment was discontinued because the plants were apparently dead. The two-factor ANOVA showed that the magnitude and direction of the difference between the treatments C and H changes over time (Table 1; treatment × time significant). Inspection of Figure 2 shows that at day 1 net photosynthesis is similar in both treatments, on subsequent days the values in H decrease, whereas values in C first rise slightly and then slowly decrease.

The dark respiration rates of C and H thalli remained on a level of about 15 μmol O_2 h^{-1} g DW^{-1} throughout the experiment with the exception of the very low rate after 90 days of exposure in the H treatment (Figure 2). Statistical comparison of the dark respiration rates in all three treatments over 12 days showed a significant difference between treatments (Table 1). Post hoc comparison of means qualified that the dark respiration rates of the D treatment were significantly higher than in the two other treatments. They increased slightly with increasing exposure time to a maximum value of ~30 μmol O_2 h^{-1} g DW^{-1} at day 12 (Figure 2).

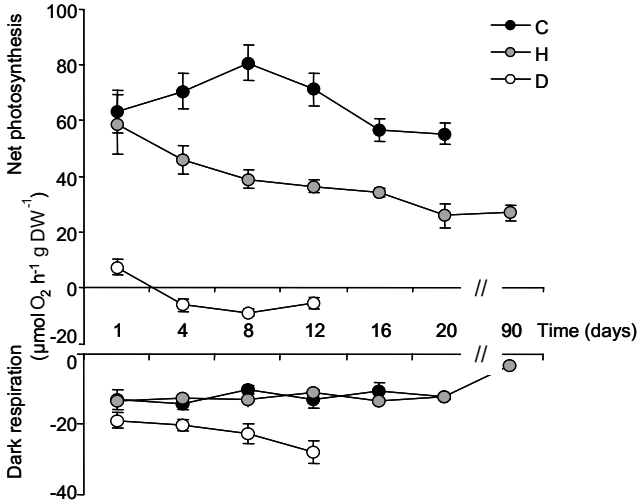

Figure 2. Net photosynthesis and dark respiration rates of *Codium fragile* ssp. *tomentosoides* in three treatments (C = control, H = humid, D = dry) over 90 days. Data points represent average rates ($n = 5$) with error bars indicating standard errors. Note that *x*-axes are not linear.

Rehydration experiment

In this experiment *C. fragile* ssp. *tomentosoides* thalli were allowed to rehydrate under submersed conditions after desiccation. In general, H-treated thalli showed some degree of recovery, whereas D-treated thalli did not (Figure 3). *C. fragile* ssp. *tomentosoides* desiccated in the H treatment for 2 days and allowed to recover for 1 day in submersed conditions exhibited an average net photosynthesis rate of ~40 µmol O_2 h^{-1} g DW^{-1} at day 12 (Figure 3). The same rate was also observed after 8 days desiccation and 1 or 4 days rehydration. Thalli that had recovered for 4 days after 2 days desiccation regained higher net photosynthesis rates of ~60 µmol O_2 h^{-1} g DW^{-1} (Figure 3). Negative net photosynthesis, i.e. respiration exceeded gross photosynthesis, was observed in D-treated thalli in all treatment combinations (Figure 3). The statistical analyses showed a significant interaction between Treatment × desiccation time × rehydration time (Table 2). Inspection of Figure 3 shows that net photosynthesis rate in both treatments changed with rehydration time, however, in opposite directions. Also, net photosynthesis rates changed depending on both desiccation and rehydration time, i.e. after 4 days rehydration the magnitude of the response is different depending on the desiccation time.

The dark respiration rates of the thalli in the H treatment were similar between treatment combinations. The statistical analyses showed a significant interaction treatment × rehydration time (Table 2). Inspection of Figure 3 shows that respiration rates especially in the D treatment varied with rehydration time, and showed increased dark respiration rates after 4 days rehydration.

Table 1. Desiccation experiment*

Source of variation	df	Net photosynthesis			Respiration		
		MS	*F*	*P*	MS	*F*	*P*
Treatment	1	0.152	4.086	0.012	0.061	1.431	0.245
Time	5	5.634	151.940	<0.001	0.483	11.377	0.000
Treat × time	5	0.141	3.793	0.004	0.082	1.924	0.096
Error	48	0.037			0.042		

* Two-factor ANOVA comparing net photosynthesis and respiration of *C. fragile* ssp. *tomentosoides* in two treatments (C, H) and at four measurement occasions (days 1, 4, 8, 12, 16, 20).

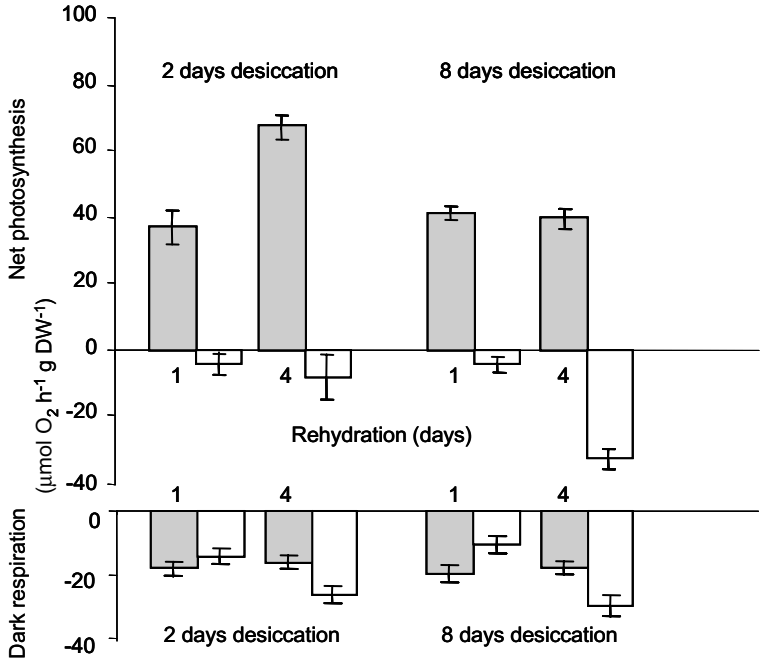

Figure 3. Net photosynthesis and dark respiration rates of *Codium fragile* ssp. *tomentosoides* in eight combinations of treatment (humid = H, dry = D), desiccation time (2 days, 8 days) and rehydration time (1 day, 4 days). Bars represent average rates ($n = 5$) with error bars indicating standard errors. Grey bars represent H treatments and white bars D treatments.

Relative water content

The thalli in the H treatment experienced no water loss after 20 days, and the relative water content (RWC) after the desiccation period was within 3–4% of the initial RWC. The batch that was kept in the H treatment for 90 days had an average RWC of 90% (1% SE). Water loss in the D-treated thalli from both experiments was initially rapid, and after 24 h of desiccation the RWC had been reduced to about 30% (Table 3). After four days the thallus water content remained in equilibrium with atmospheric moisture at around 10% RWC.

The RWC of D-treated *C. fragile* ssp. *tomentosoides* thalli in the rehydration experiment increased slightly after resubmersion. The length of desiccation period appears to control the rehydration rather than the rehydration time (Table 3).

Table 2. Rehydration experiment.[a]

Source of variation	df	Net photosynthesis			Respiration		
		MS	*F*	*P*	MS	*F*	*P*
Treatment	1	4.014	91.249	< 0.001	0.161	4.009	0.054
Desiccation time	1	0.451	10.244	0.003	0.426	10.629	0.003
Rehydration time	1	0.522	11.878	0.002	0.036	0.894	0.352
Treatment × desiccation	1	0.803	18.246	< 0.001	0.594	14.819	0.001
Treatment × rehydration	1	0.312	7.095	0.012	0.005	0.113	0.738
Desiccation × rehydration	1	0.589	13.398	0.001	0.049	1.226	0.276
Treatment × desiccation × rehydration	1	0.270	6.134	0.019	0.058	1.435	0.240
Error	32	0.044			0.040		

[a] Three-factor ANOVA comparing net photosynthesis and respiration of *C. fragile* ssp. *tomentosoides* in two treatments (H, D), two desiccation times (2 days, 8 days) and two rehydration times (1 day, 4 days).

Table 3. Relative water contents (% ± SE) of *Codium fragile* ssp. *tomentosoides* thalli in D treatments of the desiccation and the rehydration experiments.

No. of days desiccated	After desiccation	After 1 day rehydration	After 4 days rehydration
1	35 ± 6		
2	14 ± 3	50 ± 6	44 ± 5
4	11 ± 1		
8	12 ± 1	21 ± 2	21 ± 2
12	11 ± 2		

Discussion

Our experiments indicate that *Codium fragile* ssp. *tomentosoides* is able to survive periods of emersion of at least 90 days in high relative air humidity and, hence, may survive long shipboard journeys entrapped in fishing nets, anchor wells or other protected, high-humidity areas of a vessel. Whole thalli or fragments would resume net photosynthesis after re-immersion at a new location, at rates of at least 50% of submersed control thalli. Furthermore *C. fragile* ssp. *tomentosoides* may survive emersion on an exposed deck during short trips (~1 day), especially in cooler conditions such as at night.

In a similar study Sant et al. (1996) found that the invasive green alga *Caulerpa taxifolia* in the Mediterranean Sea was able to survive up to 10 days under comparable conditions and suggested that local translocation by shipboard transport is an important vector. *C. taxifolia* is known to affect fishing activities, in particular by bottom trawlers and trammel nets, as the sometimes massive presence of the alga interferes with the use of gear (Relini et al. 2000). Fishing nets fouled with *C. taxifolia* would facilitate shipboard translocation. Similarly, introduced bivalves of the genus *Dreissena* in Canada survived emersion for up to 10 days at 10 °C and 95% relative air humidity, and are assumed to survive overland transport in trailered boats between waterbodies (Ricciardi et al. 1995).

Carlton and Scanlon (1985) suggested that fishing vessels dragging up large quantities of *C. fragile* ssp. *tomentosoides* in bottom nets and subsequently releasing it in unaffected locations are important for domestic or local spread of the subspecies, while transoceanic transport vectors are more likely to be hull fouling and epizoic fouling on cultured oysters. The significance of shipboard transport as a vector for invasive macroalgae is enhanced by the capacity of some species to reproduce asexually from fragments (e.g. *C. taxifolia*: Ceccherelli and Cinelli 1999; Smith and Walters 1999). *C. fragile* ssp. *tomentosoides* is able to regenerate from very small fragments of differentiated thalli (Borden and Stein 1969; Fletcher et al. 1989) and can reproduce asexually through parthenogenetic gametes (Ramus 1972). A prerequisite for successful regeneration of *C. fragile* ssp. *tomentosoides* is survival of the journey, which is shown in this study by recovering net photosynthesis after re-immersion. Additionally, translocation of thalli with mature propagules, which are released at a new location without the need of the mature thallus to regenerate, may contribute to enhanced spread of the subspecies (Wassmann and Ramus 1973). This has also been acknowledged for *Sargassum* species (Paula and Eston 1987) and for *Undaria pinnatifida* (Sliwa 1999).

Desiccation tolerance of macroalgae is well studied and different tolerance to desiccation is suggested to be the main factor determining upper shore distribution limits for a species, while biological factors such as competition and predation set lower shore limits (e.g. Lubchenco 1980; Carpenter 1990). Habitats colonised by *C. fragile* ssp. *tomentosoides* range from the low intertidal, with short emersion periods, to the subtidal (to 13 m depth), depending on the geographical region (Trowbridge 1998; Chapman 1999). The Australian incursion sites were generally in modified environments, often associated with shipping-related infrastructure such as wharfs, jetties, rip rap, and mooring sites, and *C. fragile* ssp. *tomentosoides* is usually submersed except for at extreme spring tides. *C. fragile* ssp. *tomentosoides* is not resistant to desiccation and below 30% RWC positive net photosynthesis is not achieved. Thalli that have been desiccated below this RWC do not recover net photosynthesis after re-immersion, except for some thalli that had positive net photosynthesis rates (up to 20% of the control rates) after 4 days recovery and showed rehydration of small portions of the thallus, with disintegrating parts detaching. The present study did not compare desiccation tolerance of introduced versus native subspecies, however,

Dromgoole (1980) found that *C. fragile* ssp. *tomentosoides* is not more resistant to water loss than the native New Zealand subspecies *C. fragile* ssp. *nova-zealandiae*.

This study indicates that successful shipboard translocation of *C. fragile* ssp. *tomentosoides* is physiologically possible. However, to prove the shipboard transport hypothesis it needs to be shown that thalli released after shipboard transport can successfully regenerate or release propagules. Because removal and control of macroalgal invasions is generally resource and time intensive (McEnnulty et al. 2001; Hewitt et al. 2005) we recommend that immediate management options for *C. fragile* ssp. *tomentosoides* focus on the prevention of further invasions. Shipboard translocation is a vector that can be easily managed through public education, emphasising that algae entangled in anchors and their ropes, chains and lockers; fishing equipment such as nets, lines and craypots; and other 'wet' areas of a vessel should be removed and the algal material be stored for disposal on land.

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