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Differences between native and invasive *Caulerpa taxifolia*: a link between asexual fragmentation and abundance in invasive populations

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Abstract The tropical and subtropical marine green alga *Caulerpa taxifolia* has invaded several temperate regions throughout the world, including southeastern Australia. In this study, I examined how invasive *C. taxifolia* from temperate southeastern Australia differed from native *C. taxifolia* from subtropical Moreton Bay, Australia, in the traits proposed as being important to its invasion success: thallus size and density, levels of asexual reproduction (fragmentation) and total biomass. Against the prediction of a large size for invasive *C. taxifolia*, native populations from Moreton Bay had larger stolons and fronds than invasive populations. However, invasive populations consistently had much higher densities of stolons, fronds and fragmented fronds; and a greater biomass compared to native populations. Average densities at invasive sites exceeded 4,700 stolons and 9,000 fronds/m² and were as high as 27,000 stolons and 95,000 fronds/m², which are the highest reported for *C. taxifolia* anywhere. Average densities of fragmented fronds at invasive sites were as high as 6,000/m² and up to 45% of all stolons at invasive sites could be directly linked to asexual recruitment via fragmented fronds. Importantly, at invasive locations there was a strong association between asexual reproduction and abundance demonstrated by positive correlations between the density of fragmented fronds and total biomass. These findings are the first to describe quantitative differences between native and invasive *C. taxifolia* and to demonstrate a link between the high levels of asexual reproduction and high abundance in invasive populations. Although the causes and consequences of high levels of asexual reproduction remain to be explored, this study suggests that changes in

demographic and life-history traits during the invasion by *C. taxifolia* into temperate habitats may contribute to its success there.

Introduction

Invasive species (sensu Kolar and Lodge 2001) are considered among the greatest threats to ecosystems worldwide (Williamson 1996; Mack et al. 2000). Frequently, invasive species occur in higher densities and individuals often obtain a larger size in invasive than in native populations (Crawley 1987; Lohrer et al. 2000; Grosholz and Ruiz 2003) and this is thought to be a major cause of their impact (Torchin et al. 2003). Two main explanations have been proposed to explain the high density and large size often obtained by invasive species. First, phenotypic plasticity occurs because of simply being in a 'better' environment (Crawley 1987) or because of greater allocation of resources to growth and reproduction in response to the absence of natural enemies (Keane and Crawley 2002; Torchin et al. 2003; Mitchell and Powers 2003). Second, evolutionary processes occur resulting in genetic changes (Andrew and Ward 1997; Tsutsui et al. 2000; Krieger and Ross 2002) and rapid adaptation to the new conditions (Maron et al. 2004). Examining how invasive populations differ from the native populations they originated from is an important step in understanding the role of different factors to successful invasion (e.g., Suarez et al. 1999; Lohrer et al. 2000; Tsutsui et al. 2000).

The marine alga *Caulerpa taxifolia* (Vahl) C. Agardh is native to several tropical and sub-tropical regions of the world (Phillips and Price 2002). Invasive populations of *C. taxifolia* now occur in several temperate regions, with invasion almost certainly occurring via accidental release from public or private aquaria (Jousson et al. 1998, 2000; Fama et al. 2002; Komatsu et al. 2003). Invasive populations of *C. taxifolia* were first observed

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in the Mediterranean Sea in 1984 and it now occurs at more than 100 sites where more than 13,000 hectares has been colonized (Meinesz et al. 2001). Invasive populations also occur at nine locations in temperate southeastern Australia (over 800 km south of its native distribution), two locations in southern Australia and two locations in California (Jousson et al. 2000; Creese et al. 2004; Millar 2004), although the Californian populations may have been eradicated (Anderson 2005). All locations invaded in temperate Australia are estuaries or coastal lakes. *C. taxifolia* appears to have a large impact where it has invaded; reaching high abundance (Meinesz et al. 1995; Ceccherelli and Cinelli 1997, 1998; Williams and Grosholz 2002), invading seagrass beds (Ceccherelli and Cinelli 1999), modifying organic and inorganic components of the sediment (Chisholm and Moulin 2003) and potentially threatening biodiversity.

Large thallus size, high population abundance and high levels of asexual reproduction via fragmented thalli have all been proposed as important differences in invasive versus native *C. taxifolia*, and have also been implicated in its success in the invaded sites (Meinesz et al. 1995; Sant et al. 1996; Ceccherelli and Cinelli 1998, 1999; Williams and Grosholz 2002). However, because of the small amount of quantitative data for those variables in invasive and, particularly, native populations (Williams and Grosholz 2002), the extent to which invasive populations differ from native populations remains inconclusive. For example, although they are poorly defined, the broad and narrow morphological forms of *C. taxifolia* have been described at both native and invasive locations (Phillips and Price 2002) and although invasive populations of *C. taxifolia* appear to reach high abundance there are data for only two native populations (Garrigue 1994; Pillen et al. 1998) to which to compare them. Moreover, although sexual reproduction has never been observed in invasive *C. taxifolia* (Žuljevic and Antolic 2000), there are no quantitative data describing densities of asexual fragments in either native or invasive populations. Many *Caulerpa* species, including native *C. taxifolia*, undergo fragmentation naturally (Smith and Walters 1999).

As a first step to understanding *C. taxifolia* invasion in temperate Australia, I measured traits proposed as being important in the success of invasive *C. taxifolia*: thallus size, thallus density, total biomass/m² and levels of asexual reproduction (the density of fragmented fronds and proportion of stolons in populations that originated from fragmented fronds). I compared these among invasive populations of *C. taxifolia* from temperate southeastern Australia and native populations from subtropical Moreton Bay, Queensland. Genetic data indicate that the Moreton Bay area is the likely origin of the invasive *C. taxifolia* in the Mediterranean, southeastern Australia and California (Fama et al. 2002; Meusnier et al. 2002; Murphy and Schaffelke 2003; Meusnier et al. 2004), although in southeastern Australia different populations may have originated from more than one source population (Schaffelke et al. 2002;

Murphy and Schaffelke 2003). Thus, by making these comparisons, any changes in these traits that may have occurred during invasion into southeastern Australia should be revealed. Following these surveys, I then examined correlations between the density of fragmented fronds and biomass within each location to test the prediction that asexual reproduction via fragmented fronds and high abundance are linked in invasive populations.

Material and methods

Study sites

C. taxifolia was sampled from within three geographic locations spanning approximately 1,000 km of the eastern Australian coast: Lake Conjola and Port Hacking (both invasive: Creese et al. 2004; Millar 2004), and Moreton Bay (native: Phillips and Price 2002; Fig. 1, Table 1). All three locations are estuaries and are largely protected from wave action. The dates when *C. taxifolia* invaded Lake Conjola and Port Hacking are unclear. It was first described in both locations in 2000 (Millar 2004), although the high abundance at those locations at that time suggested it had been present for several years. Although *C. taxifolia* is native to Moreton Bay, it appears to be increasing in abundance and spreading in distribution (Thomas 2003). Within each of the three geographic locations three sites were sampled.

Population sampling

C. taxifolia was collected from the same depth at all sites (approximately 1–2 m) where it occurred in 100% cover. At each site, eight cores were haphazardly placed within areas approximately 100 m² in size, pushed through the *Caulerpa* into the sediment to a depth of approximately 5 cm, and all *C. taxifolia* within the core carefully placed into a plastic bag underwater and taken back to the laboratory. The diameter of the core varied slightly because a corer was lost during sampling due to high levels of turbidity. The diameter of the core used at all of the Lake Conjola and Moreton Bay sites, and at Gunnamatta Bay East, was 19.6 cm, while the diameter of the core used at Maianbar and Gunnamatta Bay West was 22.5 cm. Only two cores were sampled at Victoria Point after which the corer was lost, but six additional samples were collected by taking large handfuls of *C. taxifolia* approximately the same area as the corer and placing them into plastic bags. All measures of density and biomass were standardized to unit area to enable comparisons among sites.

For each sample I measured: (1) either the diameter of all stolons or 40–50 randomly chosen stolons, (2) the maximum primary frond length on each stolon, (3) the total number of stolons, primary fronds and fragmented fronds, and (4) total dry weight. Stolon diameter was

Fig. 1 Sites where *Caulerpa taxifolia* was sampled at Moreton Bay, Port Hacking and Lake Conjola on the eastern coast of Australia. Site abbreviations are: Fisherman Islands (FI), North Stradbroke Island (NSI), Victoria Point (VP), Gunnamatta Bay East (GBE), Gunnamatta Bay West (GBW), Maianbar (M), Lake Conjola West (LCW), Adder Bay (AB), Picnic Bay (PB), Roberts Point (RP)

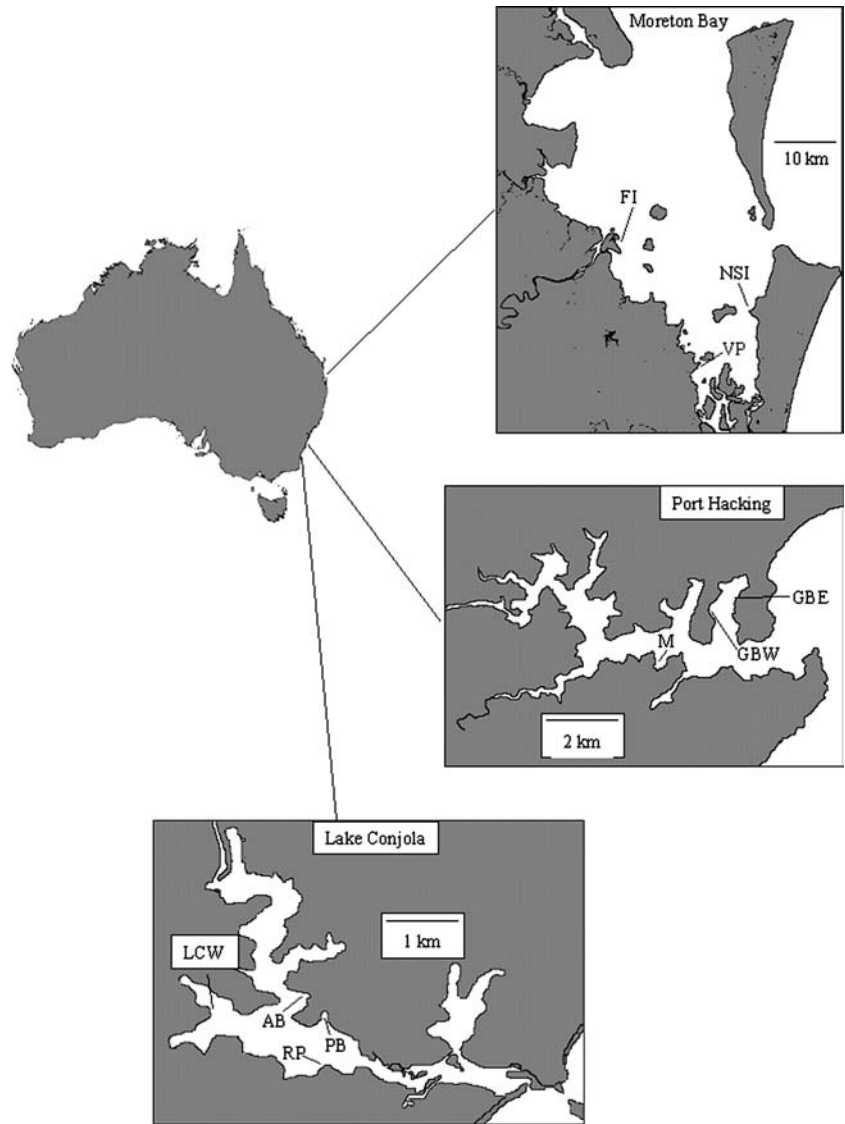


Table 1 Estuary characteristics and sites where *Caulerpa taxifolia* was sampled to determine densities of stolons, fronds, fragmented fronds and biomass. Data for estuary characteristics was sourced from: West and Jones (2001); Phillips and Price (2002); www.dlwc.nsw.gov.au

| Location | Type of estuary | Size (km ²) | Surface seawater temperature (°C) | Sites sampled | Month sampled | Latitude | Longitude |
|--------------|---------------------|-------------------------|-----------------------------------|-------------------------|----------------|-------------|------------|
| Moreton Bay | Semi-enclosed basin | 1,500 | 12.5–32 | North Stradbroke Island | October 2002 | 153°24'E | 27°30'S |
| | | | | Fisherman Islands | October 2002 | 153°11'E | 27°23'S |
| | | | | Victoria Point | October 2002 | 153°19'E | 27°35'S |
| Lake Conjola | Barrier lagoon | 5.9 | 11.2–29 | Lake Conjola West | August 2002 | 150°26'52"E | 35°15'19"S |
| | | | | Picnic Bay | September 2002 | 150°28'11"E | 35°15'23"S |
| | | | | Roberts Point | August 2002 | 150°28'06"E | 35°15'51"S |
| | | | | Maianbar | April 2003 | 151°07'35"E | 34°04'48"S |
| Port Hacking | Drowned valley | 11 | 14–24 | Gunnamatta Bay East | July 2002 | 151°09'00"E | 34°03'28"S |
| | | | | Gunnamatta Bay West | April 2003 | 151°08'36"E | 34°03'26"S |
| | | | | Maianbar | April 2003 | 151°07'35"E | 34°04'48"S |

measured with vernier callipers to the nearest 0.05 mm. A pilot study revealed that for *C. taxifolia* from Lake Conjola, mean stolon diameter (range: 0.41–2.34 mm) of 124 thalli was good predictor of both thallus length

(range: 10–1162 mm, $r^2 = 0.824$, $P < 0.001$) and dry mass (range: 0.019–11.139 g, $r^2 = 0.906$, $P < 0.001$). Mean (± 1 SE) variation in stolon diameter within a thallus was small ($CV = 8.68 \pm 0.54$, $n = 120$ thalli with 3–5

measures of diameter per stolon) but did increase with a decrease in stolon diameter ($n=120$, $r=-0.476$, $P<0.001$). Primary frond length was measured from the frond insertion point on the stolon to its tip (Williams and Grosholz 2002). By using cores to determine stolon densities, there was the potential to resample thalli with ramified stolons if stolons were cut into pieces during the coring, which would inflate stolon densities. However, thalli with ramified stolons generally have very large diameters (>1.8 mm; unpublished data) and, as these make up $<5\%$ of thalli in the populations, it is unlikely that resampling of many thalli would have occurred. Fragmented fronds were defined as fronds that were not attached to a stolon and had new stolons resprouting from their midrib. These fronds were often buried or partially buried in the sediment, and using this definition gives a measure of asexual reproduction because it includes dissemination from the parent thallus. This definition also excludes fronds that were resprouting more fronds (i.e. fronds with proliferative tips; Williams and Grosholz 2002), which occurred mostly on fronds still attached to stolons, and any fronds that may have fragmented during sampling. I focussed on fragmented fronds resprouting stolons as a measure of asexual reproduction as they will go on to form new thalli. The abundance of fragmented stolons that were resprouting new stolons was not quantified, as it was difficult to determine where this had occurred. For fragmented stolons that were resprouting new stolons, the diameter of the original stolon and stolons growing from them were usually similar. Although no sexual reproduction has ever been observed in invasive *C. taxifolia*, and thus it is likely that all reproduction is asexual, my sampling of fragmented fronds gives a measure of the relative abundance of asexual propagules available to recruit into populations. It does not describe the absolute densities of thalli originating from asexual versus sexual reproduction. Total dry weight of each sample was determined by drying samples at 70°C for 48 h.

Nested analyses of variance with the factors location (Lake Conjola, Port Hacking and Moreton Bay) and sites within location were used to test for differences in the size and density of stolons and fronds, the density of fragmented fronds, the proportion of stolons in populations originating from fragmented fronds and total dry weight. For Victoria Point, only data from the two samples collected using cores were included in the density and biomass analyses, but data from all eight samples were included in the analyses for the size of stolons and fronds and the proportion of stolons originating from resprouting fronds. No data on fragmented fronds were collected at Gunnamatta Bay East. Data were log or arcsin transformed to meet ANOVA assumptions. Following ANOVAs, post hoc tests (Tukey's multiple range) for differences among locations were performed. Analyses were carried out using SYSTAT (Version 9, SPSS).

To investigate the link between asexual reproduction and abundance, I first performed correlations between

the density of fragmented fronds and total biomass within each location. I then examined size distributions of stolons originating from fragmented fronds at two sites in Lake Conjola (Lake Conjola West and Adder Bay; $35^{\circ}15'12''\text{S}$, $150^{\circ}27'58''\text{E}$) and one site at Port Hacking (Maianbar; Fig. 1). If the size distribution of stolons originating from resprouting fronds overlaps with the size classes of stolons that are most abundant in the population, it suggests resprouting fronds may be an important determinant of the overall population size distribution. Fragmented fronds (as defined above) were collected in areas of 100% cover of *C. taxifolia* (patches) and where *C. taxifolia* was spreading across uninvaded sand (edges) at the three sites. Both patches and edges were examined as initial observations suggested that the stolons resprouting from fragmented fronds in patches were smaller diameter than those from fragmented fronds in edges. Fragmented fronds were either collected individually underwater or by isolating them from handfuls of collected *C. taxifolia* and their stolon diameter measured as described above. A 2-factor ANOVA was used to test for differences in the diameter of stolons originating from resprouting fronds across sites and habitat (edges versus patches).

Results

There were significant differences in stolon diameter and maximum frond length among locations. Stolons and fronds were larger in Moreton Bay compared to Lake Conjola and Port Hacking, and larger in Lake Conjola compared to Port Hacking (Table 2, Figs. 2, 3). There were also significant differences among sites within locations for both traits (Table 2, Figs. 2, 3). Mean stolon diameters (± 1 SE) for sites at Moreton Bay ranged from 1.33 ± 0.03 mm to 1.37 ± 0.03 mm compared to 1.01 ± 0.02 – 1.26 ± 0.03 mm at Lake Conjola and 0.81 ± 0.02 – 1.17 ± 0.01 mm at Port Hacking. Maximum stolon diameters were largest in Moreton Bay and Lake Conjola, and smallest in Port Hacking (Fig. 2). Maximum primary frond lengths mostly had a larger mean and maximum length in Moreton Bay (mean length ± 1 SE at sites ranged from 7.8 ± 0.2 cm to 11.2 ± 0.3 cm) and Lake Conjola (mean length ± 1 SE at sites ranged from 3.5 ± 0.1 cm to 6.5 ± 0.2 cm) compared to Port Hacking (mean length ± 1 SE at sites ranged from 1.6 ± 0.4 cm to 5.5 ± 0.2 cm; Fig. 3).

There were significantly higher densities of stolons and primary fronds, and biomass/m² at both invasive locations compared to Moreton Bay, and in Port Hacking compared to Lake Conjola (Table 2, Fig. 4). The highest density of stolons and primary fronds occurred at Maianbar, which averaged (± 1 SE) $28\,093 \pm 1,931$ stolons/m² and $98\,719 \pm 5,981$ fronds/m². All invasive sites had greater than 4,777 stolons/m² while all native sites had less than 1,283 stolons/m². The mean biomass in invasive sites was always greater than 170 g dwt/m², with a maximum of 520 ± 16 g dwt/m² at Ma-

Table 2 Nested ANOVAs for the effect of location (Lake Conjola, Port Hacking and Moreton Bay) and site within location on traits of *Caulerpa taxifolia*. Sample sizes for stolon diameter and maximum primary frond length reflect differences in densities within cores. There was no data on fragmented fronds/m² and the proportion of stolons originating from resprouting fragmented fronds for Gunnamatta Bay East. Tukey's test ($P < 0.05$) for the factor Location: MB Moreton Bay; LC Lake Conjola; PH Port Hacking

| Source | df | MS | F | P |
|--|------|-------------|---------|---------|
| Stolon diameter | | | | |
| Location | 2 | 27.585 | 5.627 | 0.042 |
| Site (Location) | 6 | 4.902 | 43.787 | < 0.001 |
| Error | 2477 | 0.112 | | |
| Tukey's: MB > LC > PH | | | | |
| Maximum primary frond length | | | | |
| Location | 2 | 619,318.249 | 7.920 | 0.021 |
| Site (Location) | 6 | 78,201.141 | 113.017 | < 0.001 |
| Error | 1985 | 691.944 | | |
| Tukey's: MB > LC > PH | | | | |
| Stolons/m ² | | | | |
| Location | 2 | 29.104 | 113.592 | 0.021 |
| Site (Location) | 6 | 3.736 | 14.583 | < 0.001 |
| Error | 57 | 0.256 | | |
| Tukey's: PH > LC > MB | | | | |
| Primary fronds/m ² | | | | |
| Location | 2 | 24.089 | 4.991 | 0.050 |
| Site (Location) | 6 | 4.826 | 15.856 | < 0.001 |
| Error | 57 | 0.304 | | |
| Tukey's: PH > LC > MB | | | | |
| Biomass/m ² | | | | |
| Location | 2 | 7.339 | 6.060 | 0.036 |
| Site (Location) | 6 | 1.211 | 7.14 | < 0.001 |
| Error | 57 | 0.170 | | |
| Tukey's: PH > LC > MB | | | | |
| Fragmented fronds/m ² | | | | |
| Location | 2 | 80.094 | 23.182 | < 0.003 |
| Site (Location) | 5 | 3.455 | 3.329 | 0.011 |
| Error | 50 | 1.038 | | |
| Tukey's: LC = PH > MB | | | | |
| Proportion of stolons originating from resprouting fragmented fronds | | | | |
| Location | 2 | 3,810.317 | 60.418 | < 0.001 |
| Site (Location) | 5 | 63.006 | 1.171 | 0.335 |
| Error | 56 | 53.819 | | |
| Tukey's: LC > PH = MB | | | | |

ianbar. The mean biomass in all native sites was less than 115 g dwt/m². Both invasive locations also had a significantly higher density of fragmented fronds than

Moreton Bay (Table 2, Fig. 5). However, Lake Conjola had a significantly higher proportion of stolons in the populations that originated from resprouting

Fig. 2 Stolon diameter distributions for invasive (Lake Conjola and Port Hacking) and native (Moreton Bay) sites. Site abbreviations as in Fig. 1. Numbers in parentheses are sample sizes at each site

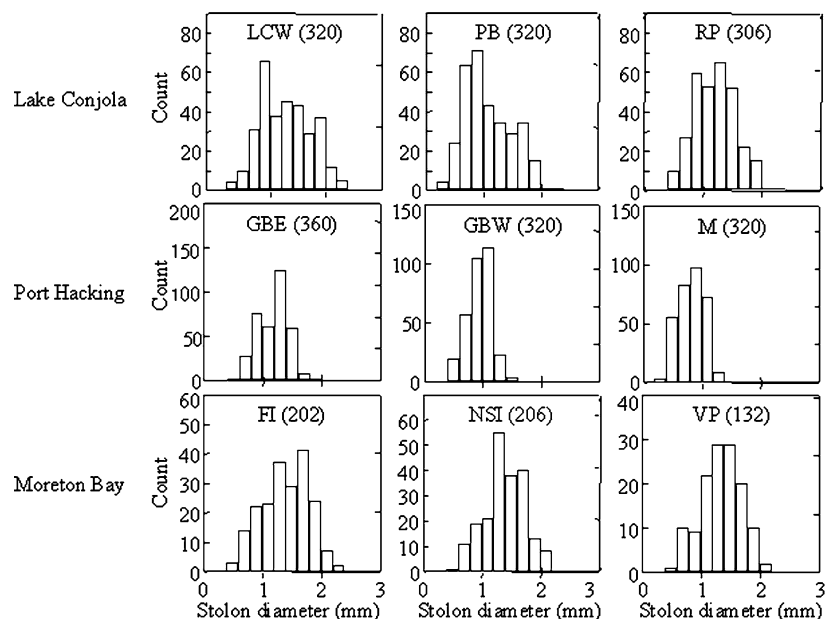
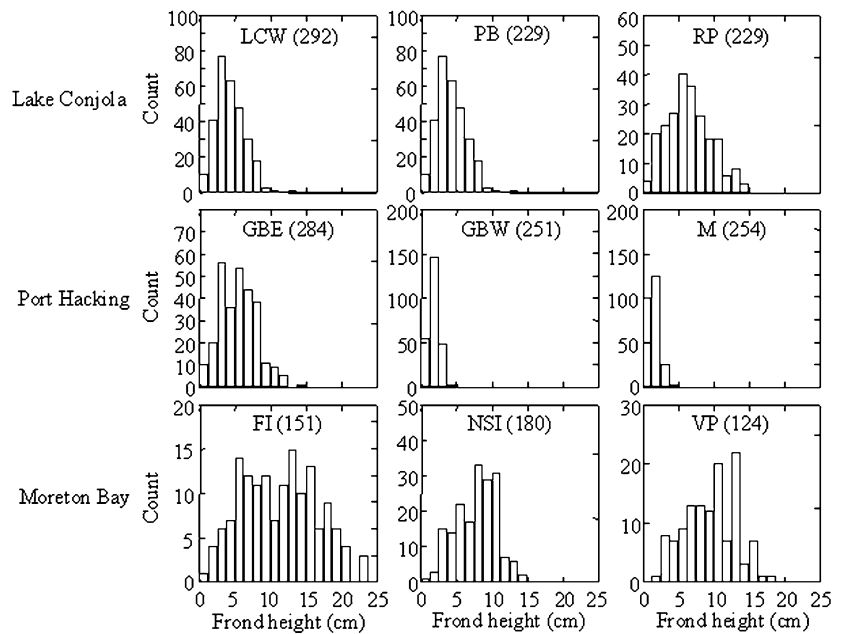


Fig. 3 Maximum primary frond length distributions for invasive (Lake Conjola and Port Hacking) and native (Moreton Bay) sites. Site abbreviations as in Fig. 1. Numbers in parentheses are sample sizes at each site



fragmented fronds than both Port Hacking and Moreton Bay, which were not different from each other (Table 2, Fig. 5). The mean percentage of stolons originating from fragmented fronds at sites at Lake Conjola ranged from 33% to 45% compared to the two sites at Port Hacking which both had less than 12% of their stolons originating from fragmented fronds. Correlations performed between the density of fragmented fronds and biomass within each location showed contrasting results between native and invasive *C. taxifolia*. There were significant positive correlations between fragmented fronds/m² and biomass/m² at the two invasive locations, but not at Moreton Bay (Fig. 6).

The size frequency distributions of stolons originating from resprouting fragmented fronds ranged from 0.4 mm to 1.25 mm at Lake Conjola and 0.35 mm to 1.3 mm at Maianbar (Fig. 7). The 2-factor ANOVA revealed a significant interaction between site and habitat for stolon diameter of resprouting fragmented fronds ($F_{2,261} = 13.421$, $P < 0.001$). Tukey's tests done within each site showed the stolon diameter of resprouting fragmented fronds was larger in the edges versus patches for both sites at Lake Conjola ($P < 0.05$) but was not different between edges and patches at Maianbar ($P > 0.05$).

Discussion

Differences between native and invasive *Caulerpa taxifolia*

Densities of *C. taxifolia* stolons, primary fronds, fragmented fronds and biomass in invasive sites was often an order of magnitude or more higher compared to native sites. The densities of stolons and primary fronds, and

biomass of *C. taxifolia* at Lake Conjola and Port Hacking were also generally higher than reported from the Mediterranean Sea (Meinesz et al. 1995; Ceccherelli and Cinelli 1997, 1998) although the small amount of quantitative data makes comparisons to this study difficult. Similarly, densities of stolons and primary fronds from a study in California are lower than densities recorded in all invasive Australian sites (Williams and Grosholz 2002), and also lower than native Australian sites examined in this study. However, it needs to be noted that the *C. taxifolia* sampled by Williams and Grosholz (2002) had been previously treated with liquid chlorine and covered with tarpaulins in an attempt to eradicate it (Anderson 2005). One further factor that makes comparisons of *C. taxifolia* stolon and primary frond densities among studies difficult is that different methods have been used (Meinesz et al. 1995; Ceccherelli and Cinelli 1997, 1998; Williams and Grosholz 2002). Using cores here may have resulted in a small number of thalli with ramified stolons being resampled, but it enabled the entire size-distribution of thalli in the population to be examined and this indicated a large number of very small thalli that could be overlooked when densities are determined in the field.

The high abundance of fragmented fronds in invasive populations appears a further important difference between invasive and native *C. taxifolia*. It suggests high levels of asexual fragmentation may contribute to the high abundance of invasive populations. Support for a link between asexual fragmentation and high abundance in invasive populations is provided by the strong correlations between the density of fragmented fronds and biomass in Lake Conjola and Port Hacking, which were absent in Moreton Bay. Asexual reproduction is often proposed as the mechanism underlying the rapid spread and high abundance of *C. taxifolia* in the Mediterranean

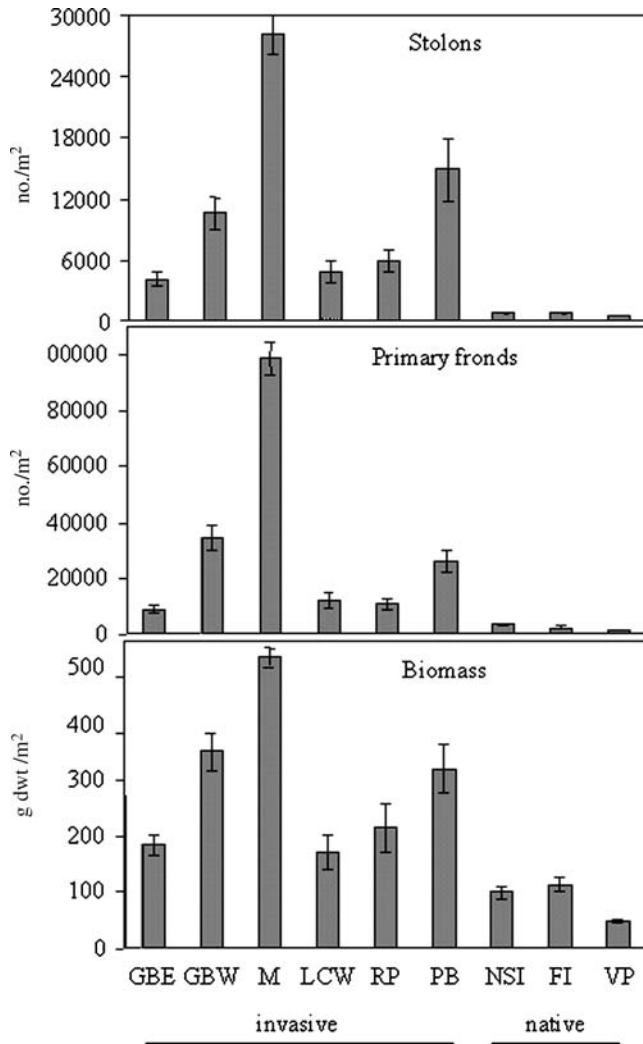


Fig. 4 Density (means \pm SE) of stolons, primary fronds and biomass at invasive and native sites ($n=8$ except *VP* where $n=2$). Site abbreviations as for Fig. 1

Sea (Ceccherelli and Cinelli 1999), but the relationship between asexual fragmentation and abundance has not previously been quantified. It is not known whether *C. taxifolia* from Moreton Bay reproduces sexually as well as asexually. Nonetheless, this study indicates that *C. taxifolia* from Moreton Bay has lower levels of asexual fragmentation than invasive sites, for which sexual reproduction has never been observed. One caveat to the link between asexual reproduction and abundance is that I only examined one type of asexual reproduction. Fragmented resprouting stolons also occur (Creese et al. 2004), but they could not be measured because they were not easily identified in the samples. The overlap in stolon diameter size distributions of resprouting fragmented fronds with the peak in the stolon diameter size distributions for the entire populations in Lake Conjola and Port Hacking suggests the high densities of resprouting fronds may also influence the population size-structure of invasive populations.

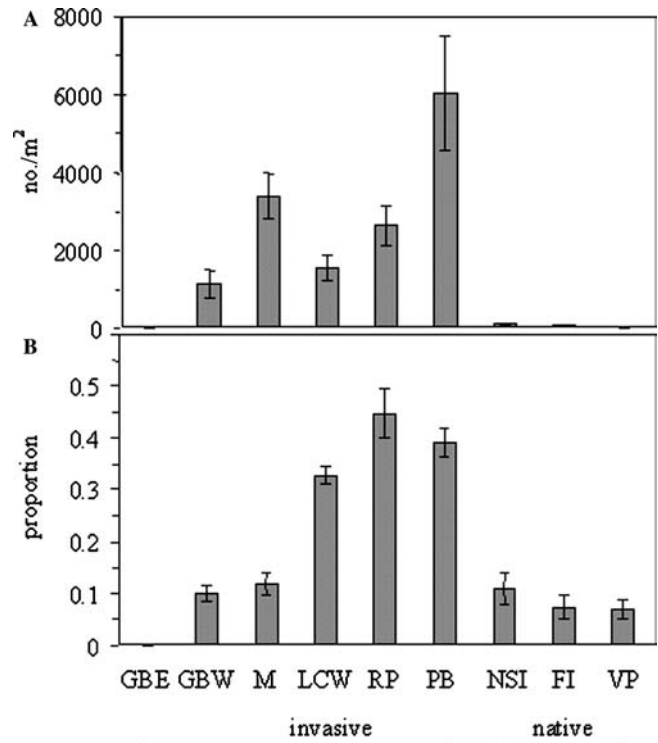


Fig. 5 Mean \pm SE **A** density of fragmented fronds ($n=8$ except *VP* where $n=2$) and **B** the proportion of stolons originating from resprouting fragmented fronds ($n=8$) at invasive and native sites. Site abbreviations as for Fig. 1

The finding that *C. taxifolia* from Moreton Bay was larger than *C. taxifolia* from both Lake Conjola and Port Hacking suggests that invasion of *C. taxifolia* into temperate Australia has not involved an increase in size, although it is possible that not enough time has elapsed for large size to evolve. There appears to be a close genetic relationship between *C. taxifolia* from Moreton Bay and Lake Conjola (Murphy and Schaffelke 2003) and the similar size ranges of *C. taxifolia* stolon diameters in these two locations supports that idea. Tropical Queensland is the likely source of *C. taxifolia* in Port Hacking (Schaffelke et al. 2002) and the smaller size of stolon diameters suggests a different origin than Moreton Bay for *C. taxifolia* in Port Hacking. This apparent absence of an increase in size in *C. taxifolia* during invasion into southeastern Australia contrasts with the apparent increase in size in *C. taxifolia* during invasion into the Mediterranean Sea (e.g., Jousson et al. 2000). However, as discussed previously (Williams and Grosholz 2002), there are few published data on *C. taxifolia* size range, which makes comparisons between native and invasive *C. taxifolia* difficult. Quantitative data for Mediterranean *C. taxifolia* stolon diameter from the field are absent, but the mean diameter of stolons used in a laboratory experiment reached 1.8 mm (Komatsu et al. 1997). Mean frond lengths of *C. taxifolia* reported from the Mediterranean Sea, range from 4 cm to 20 cm (Ceccherelli and Cinelli

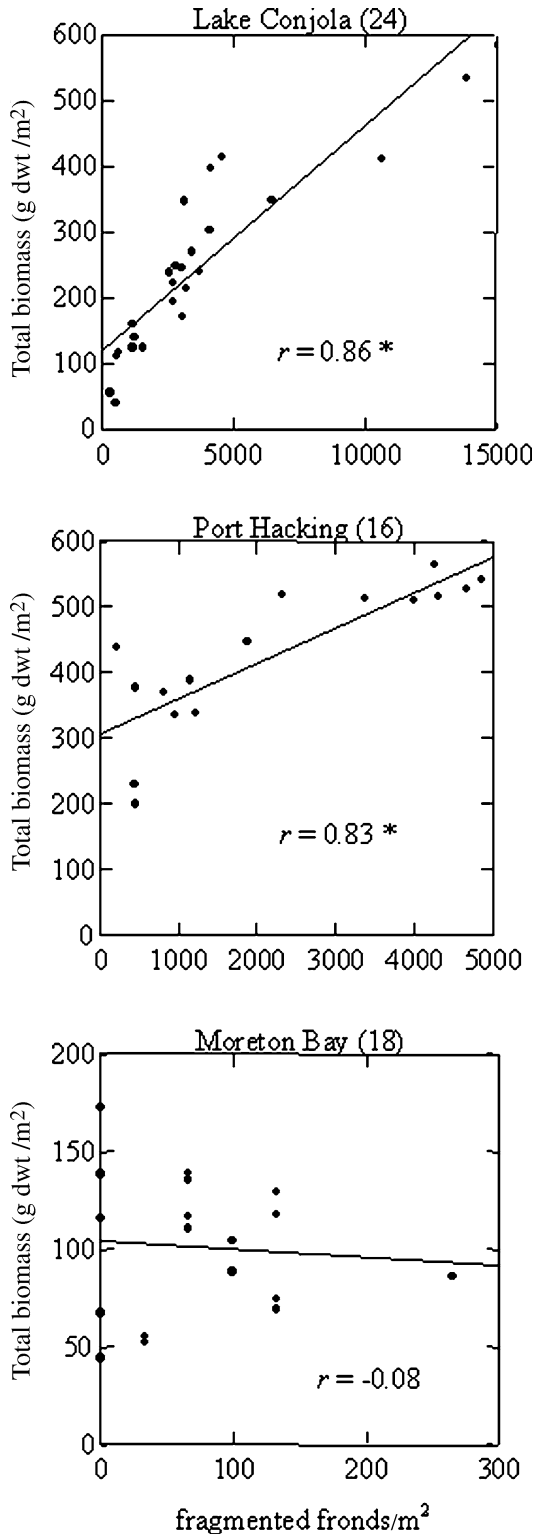


Fig. 6 Correlations between fragmented fronds/m² and biomass/m². Numbers in parentheses are sample sizes. Asterisks indicate significant positive correlations ($P < 0.001$)

1997, 1998) although a maximum size of 60 cm has been described (Meinesz et al. 1995). A mean frond length of 10.4 cm and a maximum of 27 cm were

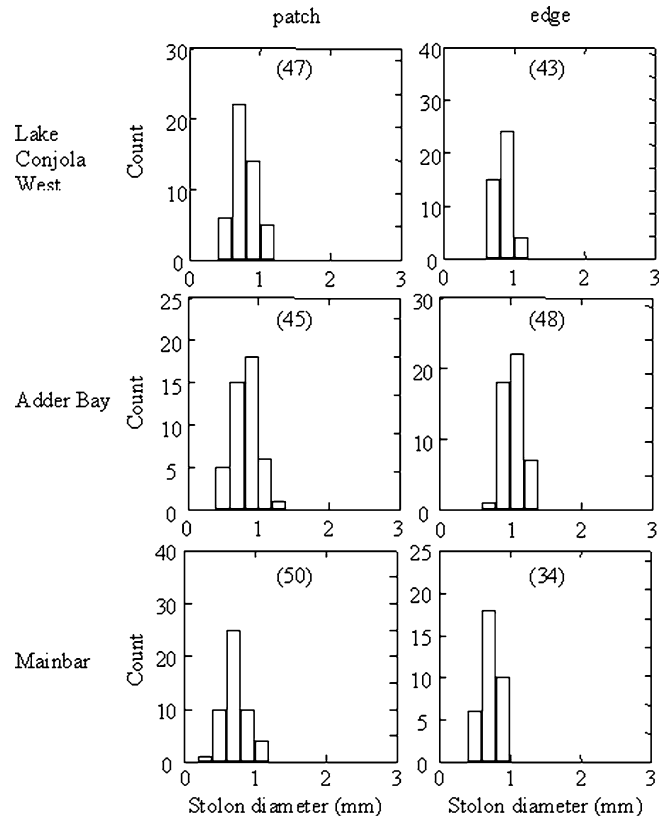


Fig. 7 Size distributions of stolon diameter for resprouting fragmented fronds in patch and edge habitats at two sites in Lake Conjola and one site in Port Hacking. Numbers in parentheses are sample sizes

recorded in California by Williams and Grosholz (2002). Maximum frond length of invasive *C. taxifolia* in southeastern Australia was smaller than in both the Mediterranean Sea and California. Because *C. taxifolia* that invaded the Mediterranean Sea is likely to have come from Moreton Bay (Meusnier et al. 2002) the idea that cold-water tolerance evolved during invasion into the Mediterranean also appears unlikely (see Chisholm et al. 2000). Minimum water temperatures in Moreton Bay (Table 1) are similar to minimum temperatures in the Mediterranean Sea (10–11°C) and considerably lower than the predicted temperature limit for tropical *C. taxifolia* (~20°C; see Komatsu et al. 1997; reviewed in Phillips and Price 2002). Water temperature in Port Hacking and Lake Conjola show a reasonable match to water temperature in Moreton Bay (Table 1), supporting the idea of a similar temperature tolerance being important in the successful invasion of new sites.

These results are the first to quantitatively describe size ranges for two traits (stolon diameter and frond length) that may be useful in defining the different morphological forms of *C. taxifolia*: broad, intermediate and narrow (Phillips and Price 2002). The invasive strain is usually defined as the broad morph although *C. taxifolia* in Port Hacking (an invasive location) has been defined as the narrow form (Phillips and Price 2002).

The results of this study suggest it may be an intermediate form. Given the large size range documented for stolon diameter and frond length within native and invasive locations, the value of qualitative terms to describe the different morphs is probably limited unless they are matched to a quantitative definition, which is consistently applied.

Most traits differed between Lake Conjola and Port Hacking. It has been suggested that *C. taxifolia* in Port Hacking and Lake Conjola are genetically different and may originate from different source populations (Schaffelke et al. 2002). However, any differences between the two locations may reflect seasonal effects, as two sites in Port Hacking were sampled in April and all sites in Lake Conjola were sampled between August and October. In general, any differences in traits within or among locations will be due to both genotypic and environmental effects. Environmental factors such as temperature, light and nutrients influence *C. taxifolia* stolon and frond size and growth, and frond density (Ceccherelli and Cinelli 1997; Komatsu et al. 1997), but their relative effects on traits measured at the sites examined here remains to be explored. For example, the greater extremes in temperature at Moreton Bay and Lake Conjola (Table 1) or differences in nutrient input (see Chisholm et al. 1997) may have influenced these results. Additionally, all locations will be affected by changes in water salinity following heavy rain. There is high mortality of *C. taxifolia* fragments in the laboratory at salinities less than 15 ppt (Creese et al. 2004) and *C. taxifolia* has declined in cover or temporarily disappeared from shallow sites following heavy rain in both Port Hacking and Lake Conjola (personal observations). My aim was to describe patterns of variation in these demographic and life-history traits, not to link them to specific environmental factors. However, the large variation in nearly all traits suggests an important role for environmental factors in the invasion of *C. taxifolia*.

Understanding the causes and consequences of fragmentation to *Caulerpa taxifolia* invasion

High levels of fragmentation in invasive populations and the strong link between fragmentation and abundance in invasive sites are consistent with the idea that asexual reproduction via fragmentation is an important component of *C. taxifolia* invasion. Moreover, it provides a possible mechanistic link between fragmentation and abundance in temperate Australia that emphasizes both the need for a greater understanding of the causes of fragmentation and, allows specific hypotheses about the consequences of fragmentation to abundance of *C. taxifolia* to be examined.

The causes of fragmentation in *C. taxifolia* are likely to be numerous and to be both natural and human-mediated. Human activities such as boating and fishing, and natural causes such as storms and

herbivory, have all been suggested as potential causes of fragmentation of *C. taxifolia in situ* (Sant et al. 1996; Ceccherelli and Cinelli 1999; Meinesz et al. 2001; Žuljevic et al. 2001). There is supporting anecdotal evidence for some of these factors (e.g., finding fragments in boat anchor lockers; Meinesz et al. 2001). However, there is no correlative or experimental evidence that describes the magnitude of the effects of those potential agents of fragmentation or their relative importance to the total fragment load. Moreover, the abundance of fragments in populations will be a function of the probability of a thallus fragmenting or being fragmented, post-fragment survivorship (e.g., Sant et al. 1996) and the recruitment of fragments into populations (e.g., Ceccherelli and Cinelli 1999). A better understanding of all of these factors relating to the supply of fragments into *C. taxifolia* populations is therefore important. Furthermore, the consequences of high levels of fragmentation to the invasion of new sites, population growth and local abundance in sites will in part, depend on its relative importance versus post-recruitment processes (Caley et al. 1996). For example, if density-dependent processes (Arenas et al. 2002) or environmental factors that enhance post-recruitment growth and survivorship are more important than high levels of fragmentation, then fragmentation per se may not contribute greatly to the success of invasive *C. taxifolia*.

Directing research that is based within a sound ecological and evolutionary framework to understand invasive species should contribute to their management (Byers et al. 2001). Despite almost 20 years of invasion by *C. taxifolia* in the Mediterranean, a comprehensive understanding of the factors behind its success, and effective management and control strategies, remain elusive. Control of *C. taxifolia* has only been achieved for relatively small, discrete populations in California using toxic chlorine (Anderson 2005). The findings of differences in demographic and life-history traits between invasive and native *C. taxifolia* and a link between fragmentation and abundance can assist in directing research on invasive *C. taxifolia* in Australia. These directions may include a better understanding of factors causing fragmentation and the importance of the recruitment of fragments to local abundance relative to post-recruitment growth and survivorship and external environmental factors. Given the expansion of *C. taxifolia* in the Mediterranean Sea since establishment (Meinesz et al. 2001), and the very high abundance in invasive sites in southeastern Australia, there is clearly a great need to understand factors determining its success to minimize its impact in Australia.

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