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Disturbance influences the invasion of a seagrass into an existing meadow

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ABSTRACT

Future impacts from climate change and human activities may increase the likelihood of invasions of native marine species into existing habitats as a result of range shifts. To provide an understanding of the invasion of a native seagrass species (*Syringodium isoetifolium*) into a tropical multi-species meadow, detailed field assessments were conducted over a six year period. After establishing in a discrete patch, the extent and standing crop of *S. isoetifolium* increased 800 and 7000 fold, respectively, between 1988 and 2003 ($\sim$300–260,000 m^2 and <1 kg DW to 7596 ± 555 kg DW). The expansion of *S. isoetifolium* was confined to subtidal areas and appears primarily from clonal growth. The observed expansion of this species into a new locality was found to be clearly influenced by cumulative impacts and chronic small-scale physical disturbances. This study has immediate relevance to managing impacts which influence the spread of invasive species.

1. Introduction

Predicating species responses to environmental change requires knowledge not just of their physiology and their interactions with other existing species, but also of new interactions with species that are invading due to range shifts (He et al., 2013; Rahel and Olden, 2008). Given the increasing likelihood of species geographic range shifts due to environmental change (McCarty, 2001) the capacity to understand the consequences of these shifts in terms of the resultant species interactions is of wide reaching importance.

An invasive species can affect ecosystem structure, functioning and resultant provision of ecosystem services through changes such as habitat availability, associated biota, and biogeochemical cycling (Pejchar and Mooney, 2009; Vicente et al., 2013). As a result of such changes, biological invasions in many ecosystems have resulted in major biodiversity loss (Bax et al., 2003; Butchart et al., 2010) and are generally considered a threat to the integrity of natural communities and to the preservation of endangered species (Walker and Kendrick, 1998; Lodge, 1993; Carlton and Geller, 1993; Ribera and Boudouresque, 1995; Vitousek et al., 1997). Not all species invasions result in biodiversity loss as new species interactions induced by an invasion can have positive effects upon that system. In natural communities, species have been found to affect each other through both negative and positive interactions (He et al., 2013).

Invasive plants are recognised as species or strains that rapidly increase their spatial distribution by expanding into existing plant communities (Kercher and Zedler, 2004). Although some invasions simply result from natural or human induced dispersal mechanisms, providing an invader species the opportunity to rapidly out-compete existing species, a range of biological and physical factors can drive such processes (Bax et al., 2003; He et al., 2013; Williams, 2007). For example, physical disturbance can provide an opportunity for an invasive species to have a competitive advantage (Williams, 2007) which may depend upon the life history traits of the invasive species and the interactions of that species with native species (He et al., 2013).

Tropical seagrass meadows are characterised by high disturbance regimes which can occur at a range of scales and are thought to be of importance in driving species composition and interactions (Carruthers et al., 2002; Rasheed, 2000). Such disturbance can be ecophysiological (e.g. light limitation, elevated nutrients) or physical (e.g. grazing, bioturbation, waves) (Larkum et al., 2006). Physical disturbance is common and has multiple forcing factors including both natural and human related (Williams, 1988; Preen et al., 1995; Creed and Amado Filho, 1999; Kenworthy et al., 2002). Physical disturbances may cause seagrass loss (Orth et al., 2006a; Waycott et al., 2009) or through subsequent recovery

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processes, can lead to changes in seagrass species and structural composition (Birch and Birch, 1984; Preen, 1993; Campbell and McKenzie, 2004). These drivers of change may occur over a range of spatial and temporal scales such that impacts from some disturbances may not be immediately apparent.

Although relatively rare, changes to seagrass meadows have been associated with the spread of invading introduced seagrass species (Posey, 1988; Larned, 2003; Bando, 2006; Williams, 2007). Specific examples of this are the invasion of *Zostera japonica* into the Pacific NE (Harrison, 1982). Given the proposed scenarios of future environmental change, such phenomena are likely to increase in prevalence as geographic ranges change. Given the continued global declines of seagrass, understanding factors that may drive further change is of importance to their conservation and management. Detailed examples of how a marine species such as seagrass naturally expands its range into new localities and the resultant inter-species dynamics are rarely documented and hence poorly understood and have the capacity to provide inferences about future invasions.

Syringodium isoetifolium has a wide Indo-Pacific distribution and inhabits sandy substrates in shallow waters often associated with reef platforms (Green and Short, 2003). It often occurs in multi-species meadows and is usually considered a competitor species for its ability to rapidly recolonise disturbed areas (Birch and Birch, 1984; Rollon et al., 1998). Here we document the expansion in extent and standing crop (above ground biomass) of a native seagrass *S. isoetifolium* since its first record at a new tropical locality. We discuss the competitive ability of this species, and the role that disturbance, both natural and anthropogenic, may have contributed to its apparent introduction and expansion.

2. Methods

Green Island is a vegetated coral cay located situated approximately 27 km north-east of Cairns (16°46′S, 145°58′E), within the Great Barrier Reef (GBR) Marine Park and World Heritage Area (Fig. 1). It is an inner shelf planar reef (about 710 ha) orientated north-west–south-east extending approximately 4 km along its longest axis and 2 km along its shortest axis. A shallow and indistinct lagoon on the north and north-west lee of the cay gently deepens to the back-reef slope (Beach Protection Authority, 1989).

Green Island tides are diurnal with a mean sea level of 1.54 m and a mean lower low water at 0.6 m above Australian Height Datum (Department of Transport, 2006). Winds from the south-east predominate throughout the year, strongest during winter but weaker and with a north easterly element in summer months (Maxwell, 1968).

Seagrasses at Green Island were first described in October 1967 (den Hartog, 1970) and increases in their distribution have been a topic of debate for many years (den Hartog, 1970; Kuchler, 1978; Udy et al., 1999; Hopley, 1982, 1989; Gourlay, 1983; Van Woesik, 1989; Wolanski, 1994; Brodie, 1995). The first detailed examination of the seagrass meadows on Green Island was from May 1987 to April 1988 (Mellors and Marsh, 1993; Mellors et al., 1993). The most abundant seagrass meadows (dominated by *Halodule uninervis* with *Cymodocea serrulata, Cymodocea rotundata* and *Halophila ovalis*), were located in the lagoon on the sheltered north-western side of the cay. Less abundant meadows (dominated by *Thalassia hemprichii* and *C. rotundata*) were reported on the reef flat located on the north-eastern and southern sides of the cay. Although *S. isoetifolium* is reported throughout the GBR region, on Green Island it was rare and only a few plants were found in early 1988 (Baxter, 1990).

Detailed mapping of seagrass distribution was conducted in 1992, 1993, 1994, 1997 and 2003 from August and September of each year, to factor out seasonal variation (see McKenzie, 1994). Points were systematically mapped every 20 m along permanent north–south orientated transects (100–1000 m in length), located 100–500 m apart, each year (Fig. 2). A theodolite and/or differential

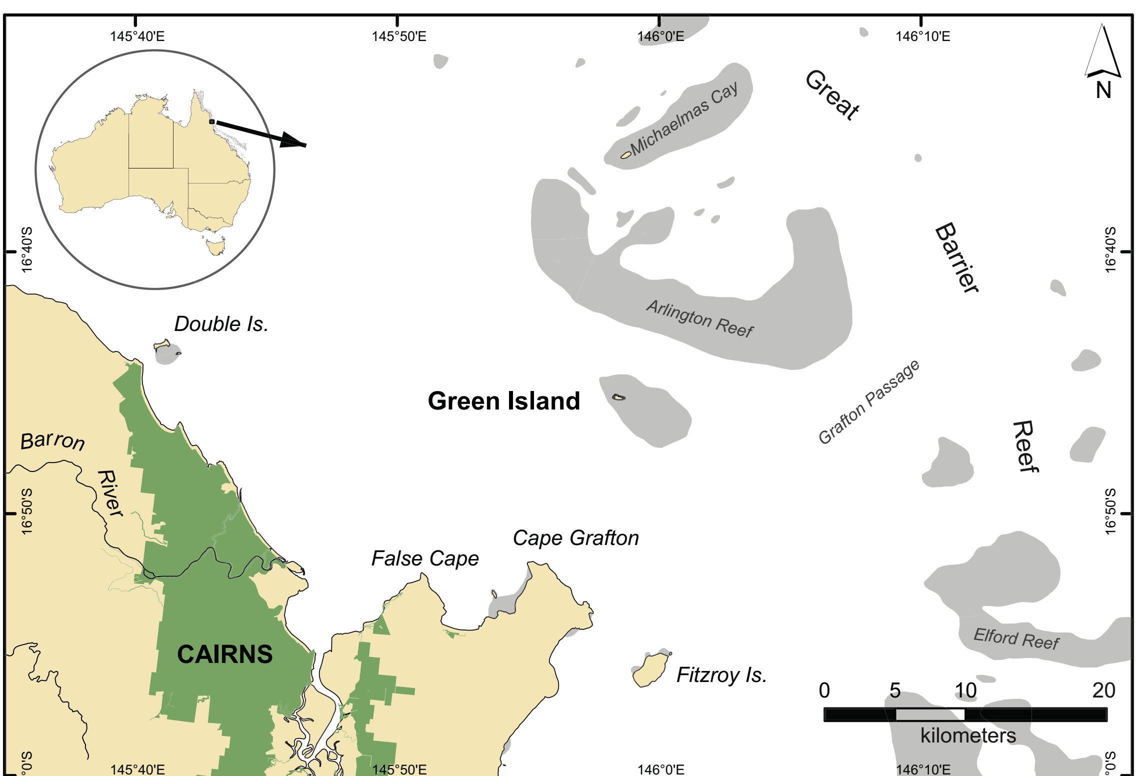

Fig. 1. Green Island is located 27 km NE of the Australian mainland in the middle of the Great Barrier Reef lagoon.

global positioning system (dGPS) was used to accurately record geographic positions of survey points (±1.5 m). Digitally scanned and rectified vertical aerial photography (1:12,000 and 1:6000) was used to assist with mapping.

Seagrass above ground biomass (standing crop, grams dry weight (g DW)) and community structure were determined using a non-destructive visual estimates of biomass technique (Haydock and Shaw, 1975), previously used for this locality (Mellors and Marsh, 1993) and for assessing seagrass biomass change (Mumby et al., 1997; Rasheed et al., 2008; Coles et al., 2009; Rasheed and Unsworth, 2011). Observers ranked seagrass above ground biomass by referring to a series of agreed reference quadrats (5 for each of the dominant lagoon and reef flat seagrass communities) which represented the range of biomass to be encountered. The five reference quadrats were ranked from 1 (least biomass) to 5 (maximum biomass expected) on a linear scale (Haydock and Shaw, 1975). Reference quadrats were left in place until sampling was completed to provide observers with the opportunity to reacquaint themselves with the scale. For subsequent surveys, photographs of the calibration quadrats (see below) were used to supplement the reference quadrats to improve the resolution of field estimations and ensure consistency between years (Kutser et al., 2007). In the field, observers ranked seagrass biomass within 3 haphazardly placed 0.25 m^2 quadrats, at each survey spot, by assigning a rank value (to 0.1 accuracy) by referring to the reference quadrats and photographs. In addition to biomass estimates, the relative proportion of each seagrass species within each quadrat and the presence of seagrass flowers and fruits were also recorded. Seagrass species were identified according to Kuo and McComb (1989) and Jacobs et al.(2006).

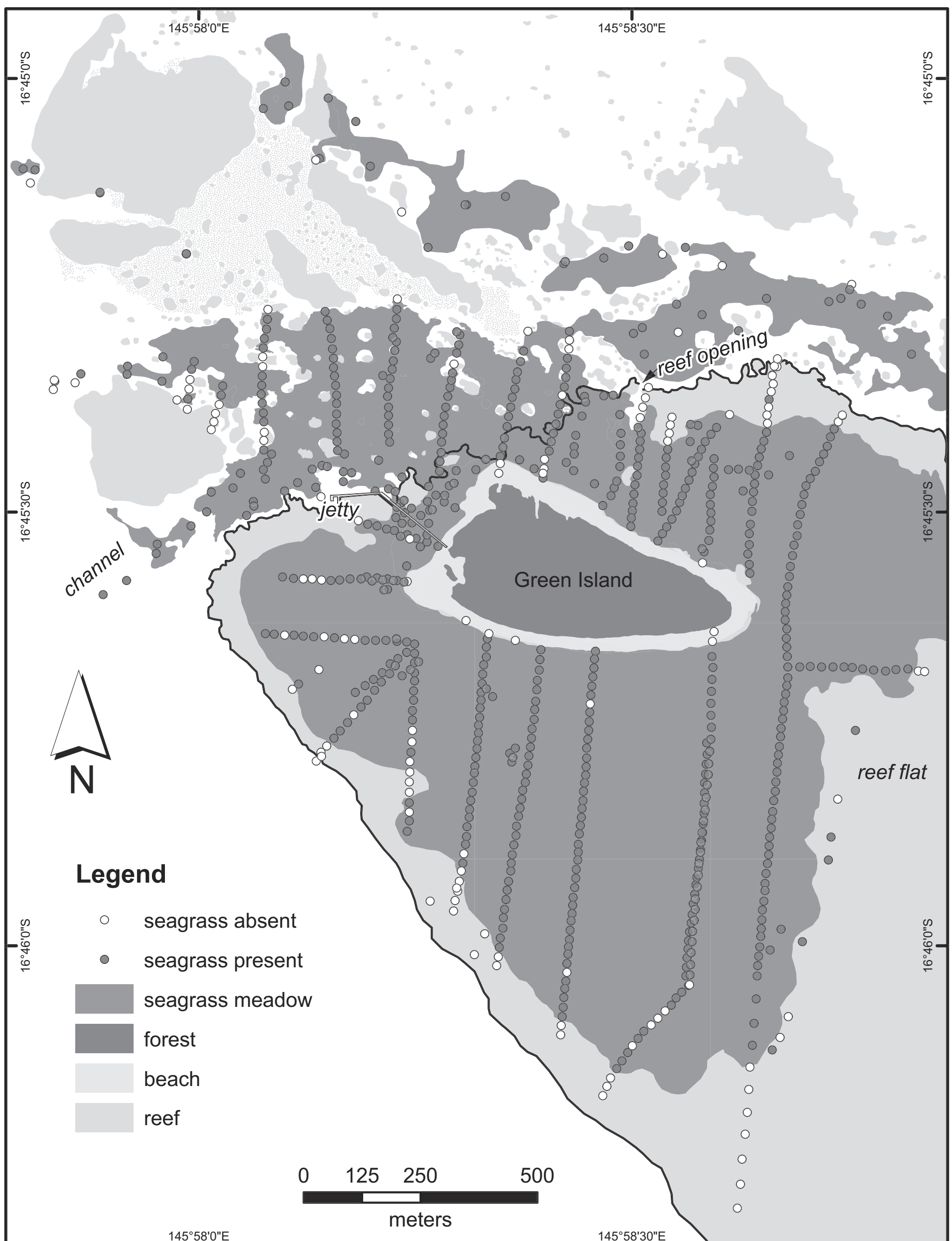

Fig. 2. Location of mapping points in the lagoon and on the reef flat surrounding Green Island. Seagrass distribution is maximum extent of all years merged (1992–2003) and edge of reef flat delineated from lagoon.

At the completion of each survey, each observer's ranks were calibrated against a set of quadrats ($n = 10$, covering the range of survey ranks), which were photographed, harvested, dried and converted into above-ground biomass in grams dry weight (DW) per square metre. The calibration exercise was performed in the field by each observer assigning a rank to a series of 10 calibration quadrats, in the same manner as for the survey (calibration quadrats only covered the range of survey ranks). A linear regression was determined for each individual observer, which was then applied to survey ranks to convert data to above-ground biomass. As per Rasheed and Unsworth (2011) data from each individual observer was only used if the linear regression had an $r^2 > 0.90$.

All survey data were entered into a Geographic Information System (GIS). Boundaries of seagrass meadows were determined in the field by observers and where available from aerial photograph interpretation. Bathymetry (elevation above Australian height datum) along transects was mapped in 1993 using a theodolite. Elevations were measured every 50 m along transects. The error in determining the seagrass distribution in this study was set at 5 m either side of the meadow boundary. Other errors associated with mapping, such as the position of a diver under the vessel, were embedded within this range. Taking these factors into account, an 'estimate of reliability' (R) of the areal extent (ha) of each monitoring meadow was calculated (McKenzie et al., 2001) using the buffering function in ArcGIS® (Environmental Systems Research Institute).

The above-ground *Syringodium* biomass data were used to generate spatial interpolation distribution/abundance maps (surface plots) using the spatial analyst extension in ArcGIS®9.3 (Environmental Systems Research Institute). A linear variogram model was used and gridded with an ordinary Kriging algorithm (no drift) to quantitatively assess the spatial continuity of data. Kriging was chosen as the geostatistical gridding method because the data was irregularly spaced and the generated surface plots express the trends suggested in the data by connecting high points along a ridge rather than isolating in bulls-eye type contours. Kriging also incorporates anisotropy and underlying trends in an efficient and natural manner. The standing crop was estimated from the abundance categories generated by the surface plots (using lower, median and upper category values).

3. Results

Eleven species of seagrass were found in the Green Island survey area over the monitoring period. These were: *C. serrulata*, *C. rotundata*, *H. uninervis* (wide and narrow leaf varieties), *Halophila capricorni*, *Halophila decipiens, Halophila minor, H. ovalis*, *Halophila spinulosa*, *S. isoetifolium*, *T. hemprichii* and *Zostera muelleri* ssp. *capricorni.*

H. capricorni, *H. decipiens* and *H. spinulosa* were only reported from the deeper waters (20–34 m) adjacent to the access channel entrance and to the far north of the survey area (Fig. 3). *Z. muelleri* ssp. *capricorni* was reported on one occasion (1992) in a small isolated patch in the lagoon adjacent to the jetty. *H. minor* was present on the high intertidal sand flat off the west of the cay prior to 1997, after which it was displaced by other species.

In 1992, seagrass meadows in the lagoon were multispecies dominated by *H. uninervis* with *C. serrulata* and *C. rotundata* (Fig. 4a). Small patches of *S. isoetifolium* were also present in the multispecies meadow, to the north and closer to the reef flat. Monospecific meadows of *H. ovalis* were located in the northern extremes of the lagoon. On the reef flat, multispecies meadows were dominated by either *T. hemprichii, C. rotundata* or *H. uninervis* (Fig. 4b). On the reef flat south of the cay, the meadows were dominated by *T. hemprichii* and *C. rotundata* with some *H. uninervis* closer to the beach. East of the cay the meadows were predominately *T. hemprichii* and *H. ovalis* with a few patches (~30 m radius) of *C. rotundata*. On the reef flat to the north of the cay, meadows were *H. uninervis* and *T. hemprichii* with patches of *C. rotundata* and *C. serrulata*.

The total area of seagrass meadows surrounding Green Island was 113.7 ± 6.4 ha in 1992, and progressively increased to 151.6 ± 10.7 ha in 2003 (Table 1, Fig. 3). The greater portion of meadows surrounding Green Island were located on the reef flat (Table 1) and although the extent increased over the study period, it was not as great as the increase which occurred in the lagoon (Fig. 3). Between 1992 and 1997, the area of seagrass in the lagoon more than doubled. By 2003, the lagoon meadows had nearly tripled the 1992 mapped area (Table 1).

Throughout the period the meadow has been assessed in area (since 1988) it has not only changed in extent, but also in species composition (Fig. 4) and standing crop (above ground biomass) (Table 1). In the mid 1990's, *H. uninervis* spread further south across the reef flat and *C. serrulata* increased within the lagoon and on the reef flat immediately north of cay (Table 1). The main expansion in seagrass meadows occurred on the western section of the reef flat adjacent to the cay (south of the channel) and in the northern regions of the patch reefs, where *H. ovalis* meadows spread into the sandy deeper waters (Fig. 3). Over the study period, all species expanded beyond their 1992 extent and, with the exception of *C. serrulata*, distribution of all species was greatest in 2003 (Table 1, Fig. 5). The distribution of *C. serrulata* peaked in 1993 and gradually declined until 2003 (Table 1, Fig. 5). The greatest change in the late 1990s and new millennium was the spread of *S. isoetifolium* throughout the lagoon and north western regions of the reef flat. *S. isoetifolium* covered an area of approximately 300 m^2 in 1988, and in 2003 was estimated to have covered 260,300 m^2; a significant linear increase of over 800 times (Figs. 6 and 7). Patches of *S. isoetifolium* occasionally occurred in meadows on the intertidal regions of the reef flat throughout the study period (1992, 1993 and 1994), but never persisted (Fig. 7). The shallowest *S. isoetifolium* persisted was 1.24 m below MSL.

S. isoetifolium never colonised outside existing meadows of other species (Fig. 7). The increased composition of *S. isoetifolium* in the meadows was significantly correlated with a decrease in *H. uninervis* biomass in the lagoon ($F_{1,3} = 22.81$, $p < 0.05$), and *H. ovalis* biomass on the reef flat ($F_{1,3} = 12.33$, $p < 0.05$), with the relationships explaining 88% and 80% of the variance, respectively.

Seagrass standing crop (all species pooled) more than tripled over the study period from 9261 ± 2665 kg DW in 1992 to 36,662 ± 4441 kg DW in 2003 (Table 1). Most of this increase occurred in the lagoon and on the subtidal reef flat immediately north of the cay. This was primarily a consequence of the spread of *S. isoetifolium*, which increased exponentially from an estimated <1 kg DW total standing crop in 1988 to 7596 ± 555 kg DW in 2003 (Figs. 6 and 7). The locations where *S. isoetifolium* standing crop was the greatest were surrounding the turning basin in the boat access channel near the elbow in the jetty and near the break in the reef flat to the north of the cay (Fig. 7).

Female inflorescence of *S. isoetifolium* were reported throughout it's distribution in 1997 and 2003. No male inflorescence were found during the study period.

4. Discussion

The present study provides evidence of the competitive nature of a seagrass species invading an existing high speciose seagrass meadow through vegetative propagation. The extent of the invasion of which was found to be influenced by processes of disturbance. The arrival of this plant was probably the result of human translocation of a fragment or seed. Knowledge of such

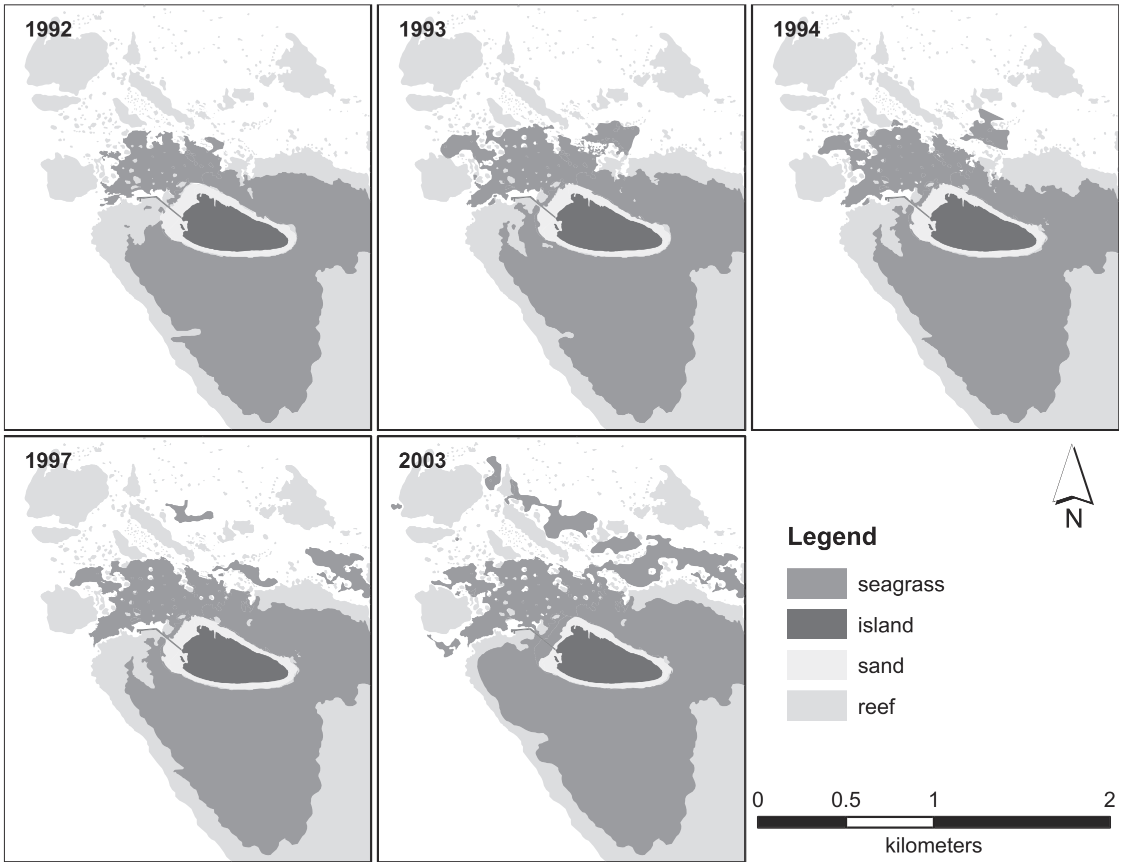

Fig. 3. Distribution of seagrass meadows (all species pooled) surrounding Green Island, from 1992 to 2003.

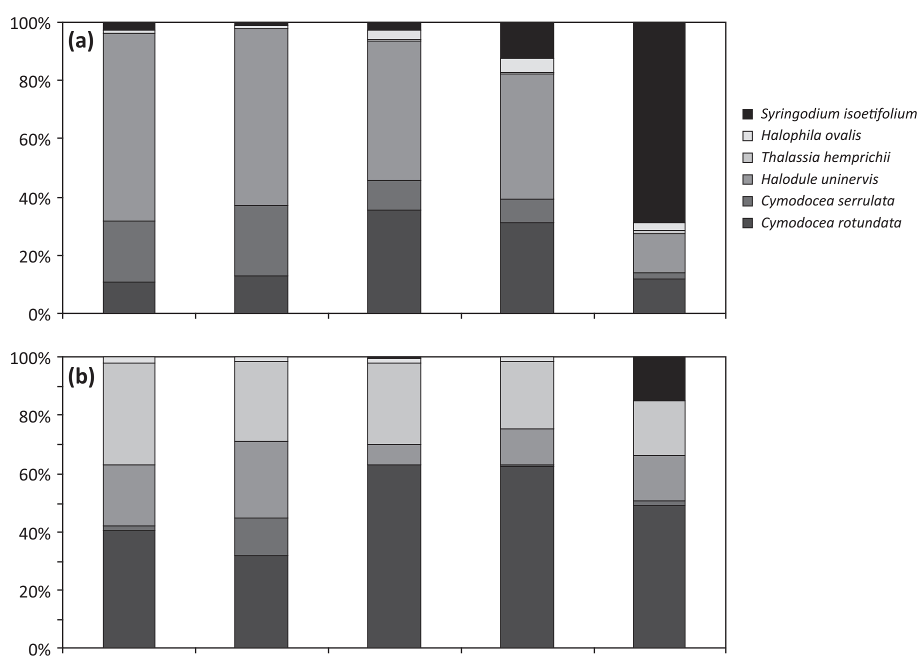

Fig. 4. Change in above ground seagrass biomass species composition in the meadows located in the lagoon (a) and on the reef flat (b) surrounding Green Island from 1992 to 2003.

incidences of the colonisation of a new seagrass species into a multi-species meadow are rare and this research provides a novel insight into that process. Understanding of how marine species can expand into new habitat is of importance given the potential for species range shifts with future climatic change and anthropogenic threats.

The seagrass species *S. isoetifolium* was a recent arrival at Green Island (not reported until 1988). Since establishing as a discrete

Table 1
Area (hectares ± R) and standing crop (kg DW) of seagrass species and meadows mapped in the lagoon and reef flat regions surrounding Green Island each year.

Species	Region	1959	1972	1992	1993	1994	1997	2003
Cymodocea rotundata	Reef flat	NA	NA	29.17 ± 2.25	30.77 ± 2.61	36.74 ± 3.12	50.87 ± 4.61	54.05 ± 3.63
	Lagoon	NA	NA	4.35 ± 0.98	6.81 ± 1.45	12.96 ± 2.21	16.96 ± 2.11	22.67±2.60
Cymodocea serrulata	Reef flat	NA	NA	0.67 ± 0.41	4.68 ± 0.79	4.14 ± 1.29	2.35 ± 0.84	2.91 ± 0.43
	Lagoon	NA	NA	9.40 ± 1.96	13.63 ± 2.74	11.12 ± 3.09	11.00 ± 2.55	11.12 ± 3.12
Halophila ovalis	Reef flat	NA	NA	27.21 ± 3.20	23.93 ± 5.12	29.34 ± 7.13	18.58 ± 4.63	18.21 ± 4.79
	Lagoon	NA	NA	7.18 ± 2.19	11.10 ± 3.71	7.68 ± 2.91	19.4 ± 4.67	28.08 ± 6.60
Halodule uninervis	Reef flat	NA	NA	15.37 ± 3.23	28.76 ± 3.83	24.19 ± 3.65	24.01 ± 3.47	19.05 ± 3.17
	Lagoon	NA	NA	14.44 ± 2.10	14.50 ± 2.18	16.6 ± 2.58	23.94 ± 3.78	33.77 ± 5.98
Syringodium isoetifolium	Reef flat	NA	NA	0.18 ± 0.09	0.87 ± 0.26	1.62 ± 0.46	1.47 ± 0.48	6.64 ± 0.99
	Lagoon	NA	NA	4.15 ± 0.74	4.40 ± 0.95	10.68 ± 1.49	14.25 ± 2.03	19.36 ± 3.19
Thalassia hemprichii	Reef flat	NA	NA	92.13 ± 3.69	90.92 ± 3.84	90.54 ± 4.54	94.78 ± 3.95	105.17 ± 4.15
	Lagoon	NA	NA	0	0.38 ± 0.24	0.42 ± 0.27	1.02 ± 0.36	0.77 ± 0.53
Merged (species pooled)	Reef flat	NA	NA	98.83 ± 3.97	99.91 ± 4.29	97.06 ± 4.24	108.2 ± 3.8	112.1 ± 3.8
	Lagoon	1.1 ± 0.3[a]	6.5 ± 1.3[a]	14.89 ± 2.44	22.48 ± 4.07	21.98 ± 3.73	31.38 ± 9.72	39.52 ± 6.9
Standing crop		NA	NA	9261 ± 2665	7153 ± 1309	21,154 ± 3277	27,064 ± 3825	36,662 ± 4441

NA = not available/measured.
[a] From Udy et al. (1999).

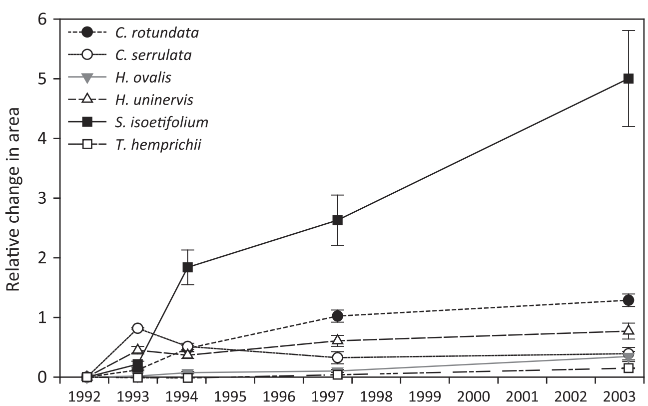

Fig. 5. Change in seagrass meadow extent each year relative to 1992, for each seagrass species (lagoon and reef flat pooled).

patch, its distribution increased considerably together with that of the whole meadow, a finding in contrast to the reported global seagrass decline (see Waycott et al., 2009). *Syringodium* established only in the sheltered subtidal area of the lagoon and reef flat to the north-west of the cay. Isolated plants occasionally occurred on the reef flat but never persisted, possibly a consequence of the species sensitivity to desiccation (Björk et al., 1999; Bridges and McMillan, 1986), high light (Fokeera-Wahedally and Bhikajee, 2005) and elevated temperatures (Campbell et al., 2006).

Isolated plants of *S. isoetifolium* were first reported at Green Island in the area north of the cay, which is sheltered from the SE trade winds and adjacent to the main anchorage/mooring area for resident and transient vessels. Natural introductions of *S. isoetifolium* to Green Island are unlikely as the closest source locations are over 120 km (McKenzie et al., 1997; Lee Long et al., 1993; den Hartog, 1970; Coles et al., 1989) and the buoyancy potential of seeds, fruits and vegetative fragments is poor/low (Orth et al., 2006b; Kendrick et al., 2012). Our data and observations cannot confirm that this species was introduced through human intervention, but if *S. isoetifolium* was never present at Green Island before this period, the most plausible explanation is that reproductive structures or vegetative fragments travelled to Green Island via the anchors of visiting vessels. *S. isoetifolium* is a dioecious plant and is capable of producing seeds that remain viable for extended periods (McMillan, 1991) and all *S. isoetifolium* locations within 500 km of Green Island are popular coastal or continental island boat anchorages.

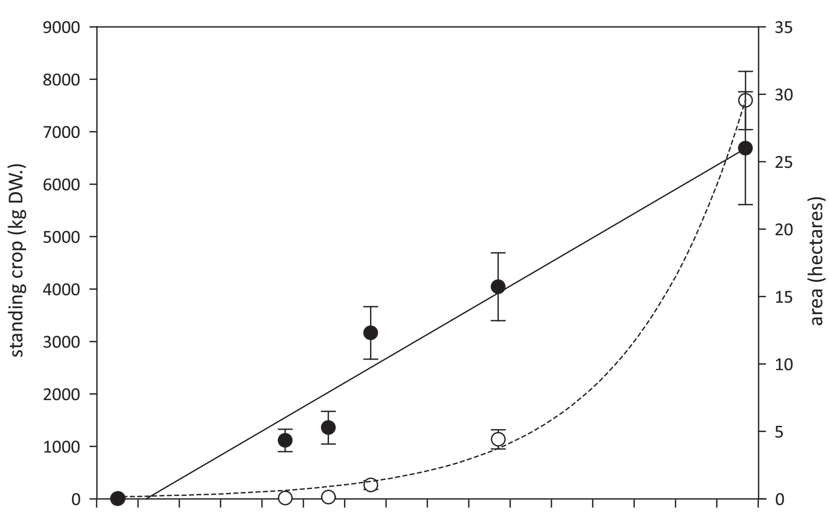

Fig. 6. Change in standing crop (○, kg dry weight ± SE) and extent (●, hectares ± R) of *Syringodium isoetifolium* meadows surrounding Green Island from 1988 to 2003. Extent increased linearly over time ($r^2 = 0.959$, $p < 0.001$), however, standing crop was exponential growth ($r^2 = 0.998$, $p < 0.001$).

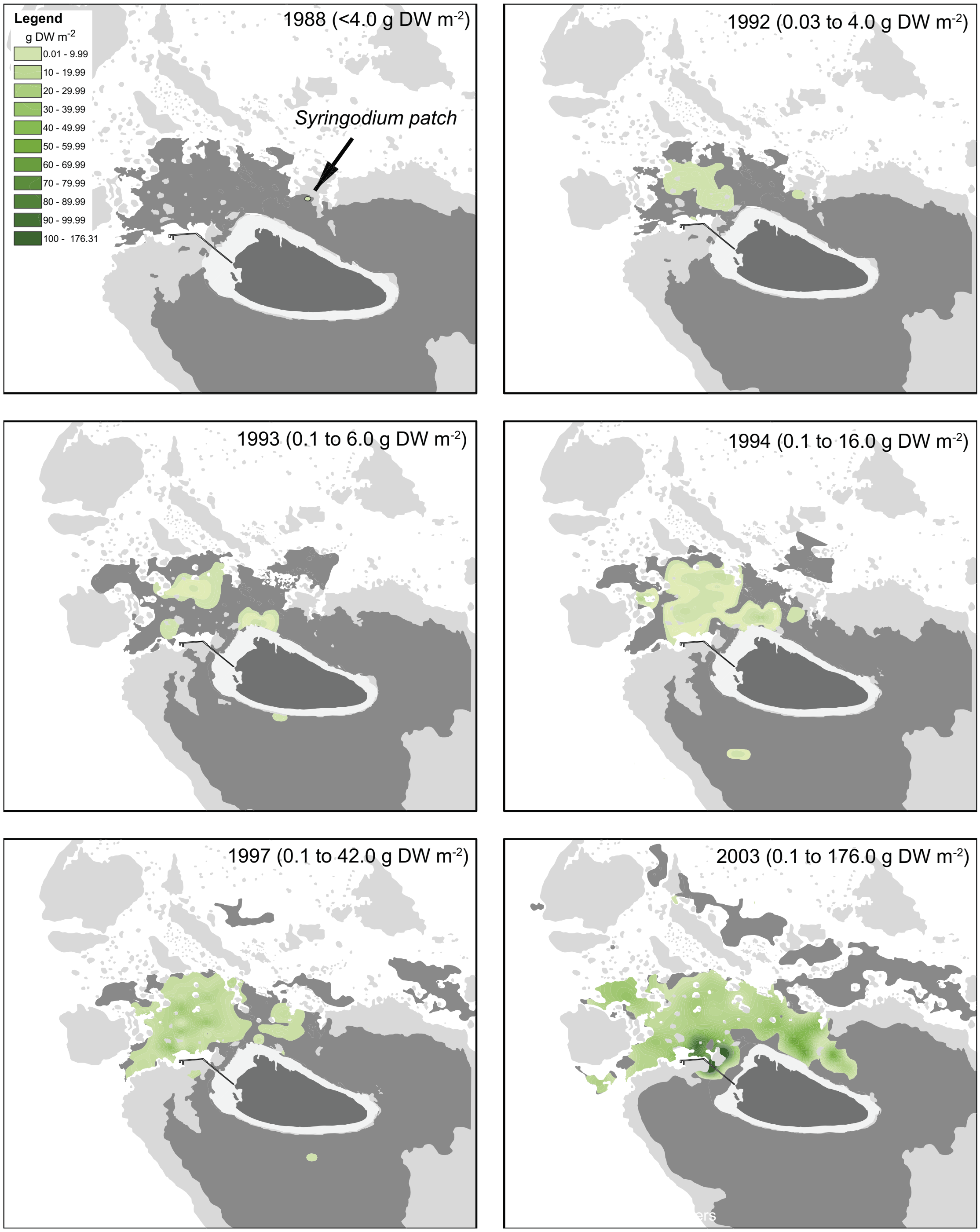

Fig. 7. Kriging interpolations of the *Syringodium isoetifolium* mean standing crop (grams dry weight per square meter) in context of the total seagrass distribution (all species pooled) surrounding Green Island from 1988 to 2003.

Inflorescence was commonly observed throughout the study period, however, only female flowers were found. Rasheed (2004) similarly observed flowering of *S. isoetifolium*, but found no seeds. In the absence of seeds, patch initiation and colonisation could only occur by vegetative fragments. Limited patch initiation by *S. isoetifolium* was observed in the present study and by Rasheed (2004), although vegetative fragments were often observed drifting across meadows (Personal Observation). This suggests the entire population of *S. isoetifolium* at Green Island may have developed clonally from a single female plant following a lone introduction, genetic studies are required to confirm this.

Expansion of *S. isoetifolium* patches have been reported to generally occur as a front, with the density decreasing some distance behind the front (Brouns, 1987), however, this did not appear to be the situation in the present study. Once established, plants remained and formed a dense rhizome mat; spreading via rhizome expansion. Rhizome elongation of *S. isoetifolium* at Green Island (4.6–6.9 mm day^{-1}) (Rasheed, 2004) was greater than recorded for this and similar species elsewhere (Brouns, 1987; Vermaat et al., 1995; Williams, 1990).

S. isoetifolium is often classed as a competitor species (Birch and Birch, 1984) and its ability to recolonise disturbed areas rapidly

(Rollon et al., 1998) and to withstand competition from other species offers a possible explanation for its recent spread around Green Island. Prior to its probable introduction in the 1980s, recovery of harvested plots (0.25 m^2) of seagrass between May 1987 and April 1988 were only by *H. uninervis*, *C. rotundata* and *H. ovalis* (M. Pearce, Personal Observation, DAFF Unpublished data); a finding in agreement with Heijs and Brouns (1986). However, when Rasheed (2004) conducted recovery experiments at the same location in 1995–1996, *S. isoetifolium* rapidly colonised disturbed plots and remained at a higher density than in undisturbed plots, at the expense of *H. uninervis*. This suggests the increased abundance of *S. isoetifolium* may have provided a completive advantage and/or that the factors controlling seagrass growth had changed.

With sufficient nutrients available (Udy et al., 1999), the overriding forcing factors for seagrass growth in the subtidal meadows are likely to have been light, herbivory and physical disturbance (Larkum et al., 2006). Floodwaters and agricultural runoff from the mainland have been reported to impact the reefs of Green Island (Petus et al., 2014), reducing light availability. As *S. isoetifolium* has a lower light requirement than *H. uninervis* or *C. rotundata* (Rasheed, 2000; Fokeera-Wahedally and Bhikajee, 2005), the reduced light availability would have provided *S. isoetifolium* a completive advantage.

The primary seagrass herbivores on Green Island are likely to be parrotfish, urchins, Green turtles and the occasional dugong (Baxter, 1990). Fishing has been limited around Green Island since 1974, and prohibited since November 1983 (Baxter, 1990). The elimination of fishing has probably led to increased predation on herbivores, limiting their abundance and consumption of seagrass, leading to an increase in seagrass abundance (Heck and Valentine, 2007; Lewis and Anderson, 2012). This may partly explain the overall increase in seagrass extent, but unlikely to explain the change in species composition as *S. isoetifolium*, *C. rotundata* and *H. uninervis* are reported to be equally preferred by herbivorous topical fish (Mariani and Alcoverro, 1999).

Dugong (*Dugong dugon*) are seagrass community specialists (Marsh et al., 2011), however, individuals or evidence of their grazing are rarely observed in Green Island seagrass meadows. Green Island is an important feeding ground for immature green turtles (*Chelonia mydas*) (Limpus et al., 1994) which spend 90% of their time feeding on seagrass and algae in waters shallower than 4 m (Hays et al., 2002; Read, 1991; Forbes, 1996; Brand-Gardner et al., 1999). The seagrass feeding preference for green turtles is reported to be *H. ovalis* > *Syringodium* > *H. uninervis* > *Zostera* (Brand-Gardner et al., 1999; Ross, 1985; Jupp et al., 1996). At Green Island, green turtles were often observed selectively feeding on *Cymodocea* spp. in the lagoon (Personal Observation) and only *C. rotundata* was identified from stomach analysis of individuals on the reef flat in October 2003 (Personal Observation). It is also unlikely that the seagrass compositional change or increase in extent is due to changing green turtle populations, as turtle densities at Green Island have stayed relatively stable and similar to other locations of the same genetic southern GBR stock (Ian Bell, Personal Observation EHP Unpublished data).

Large-scale natural disturbances, such as impact by severe tropical storms, have been reported as a causal mechanism for assisting the spread of deepwater *Syringodium filiforme* via seed and seagrass fragment dispersal (Kendall et al., 2004). There is, however, no evidence that such large scale natural disturbances were a primary or major contributing factor to the spread of *S. isoetifolium* at Green Island.

Natural small-scale disturbances are common at Green Island from currents and waves. Waves and current velocities greater than 100 cm/s can disrupt the integrity of the seagrass mat and bottom velocities of 50–100 cm/s would be sufficient to maintain erosion (Patriquin, 1975). A small reef opening in the outer coral crest on the north of the cay at Green Island (Fig. 2), funnelled waves through a narrow opening onto the shallow (<4 m) reef flat, creating strong currents, particularly during low tide periods and northerly winds. *S. isoetifolium* was first observed at this location (in 1988) where over the study period it formed a dense monospecific meadow (Fig. 7). Although current speeds were not measured at this section of the reef, they were significantly higher (Personal Observation) than the 27 cm/s recorded at an adjacent area of reef flat (Yamano et al., 2000). The persistence of *S. isoetifolium* could be attributed directly to erosion associated with waves and strong currents, because of its greater tolerance of unstable substrates and higher rhizome growth rates preceding other colonising species (Patriquin, 1975; den Hartog, 1977).

The greatest physical disturbances at the island result from intensive human use, probably longer than anywhere else on the GBR. Green Island has been a popular tourist destination since the 189Os, and the first regular tourist ferry service began in 1924. The island became a national park in 1937, a marine national park in 1974 and amalgamated into the GBR World Heritage Area in 1981 (Baxter, 1990). Between 1990 and 1998, an average of 281,000 people visited Green Island annually, with daily peaks as high as 1900 people (Udy et al., 1999; Mau, 2003). In 2004, visitor numbers had increased to 385,211 per year (Quicksilver Connections, 2010). Despite its small size, the resources of Green Island are important to the region (Cullen-Unsworth et al., 2013) and environmental management is complex due to the various legislative obligations, in particular with respect to the levels and types of activities conducted. The majority of activities occur within the lagoon and in 1990 the Green Island Recreation Area Management Plan was implemented to control activities (Fig. 8). Nevertheless, the ecology of Green Island and the reef have been degraded in a variety of ways over the past century by human activities, including: construction of buildings, jetties and groynes; disposal of wastes, especially sewage; low-level pollution of air, water and soil; extraction of ground water; dredging of sediments; and the removal of fish or shells.

The major physical disturbance to seagrasses surrounding Green Island, however, appears the result of boating activities. Intensive boat activity may result in direct physical damage to a seagrass meadow by propellers (scarring) or anchors and the resuspension of sediment from water movement (Creed and Amado Filho, 1999). *S. isoetifolium* can rapidly recolonise disturbed areas and the variable light reduction (from suspended sediments) increases blade chlorophyll and growth rates (Fokeera-Wahedally and Bhikajee, 2005).

The greatest physical disturbance observed at Green Island was the result of large (up to 38 m) tourist vessels manoeuvring within the boat access channel (Fig. 8), which would generate wash and turbulence, and create blowholes (excavation of the seagrass and underlying substrate) and suspend sediments. The areas of highest *S. isoetifolium* standing crop were immediately adjacent to the vessel turning area (Fig. 7). Similarly, from mid 1992, barges transporting cargo created blowholes in the meadows to the north of the cay as they traversed the reef flat during high spring tides to land/unload on the beach (Fig. 8). Such disturbance coincided with the rapid establishment of *S. isoetifolium* in the immediate vicinity of the landing site. Chronic disturbance from smaller vessels was also common in the meadows to the NW of the cay during the study period, in the beach hire and overnight mooring precincts (Fig. 8). Propeller scars from dive vessels driven into the shallows to alite passengers from the beach and anchor/mooring scars from visiting and permanent craft were rapidly recolonised by *S. isoetifolium*.

The present study clearly illustrates the role of disturbance in influencing the spread of an invasive species in the marine environment. In terms of management this has immediate relevance

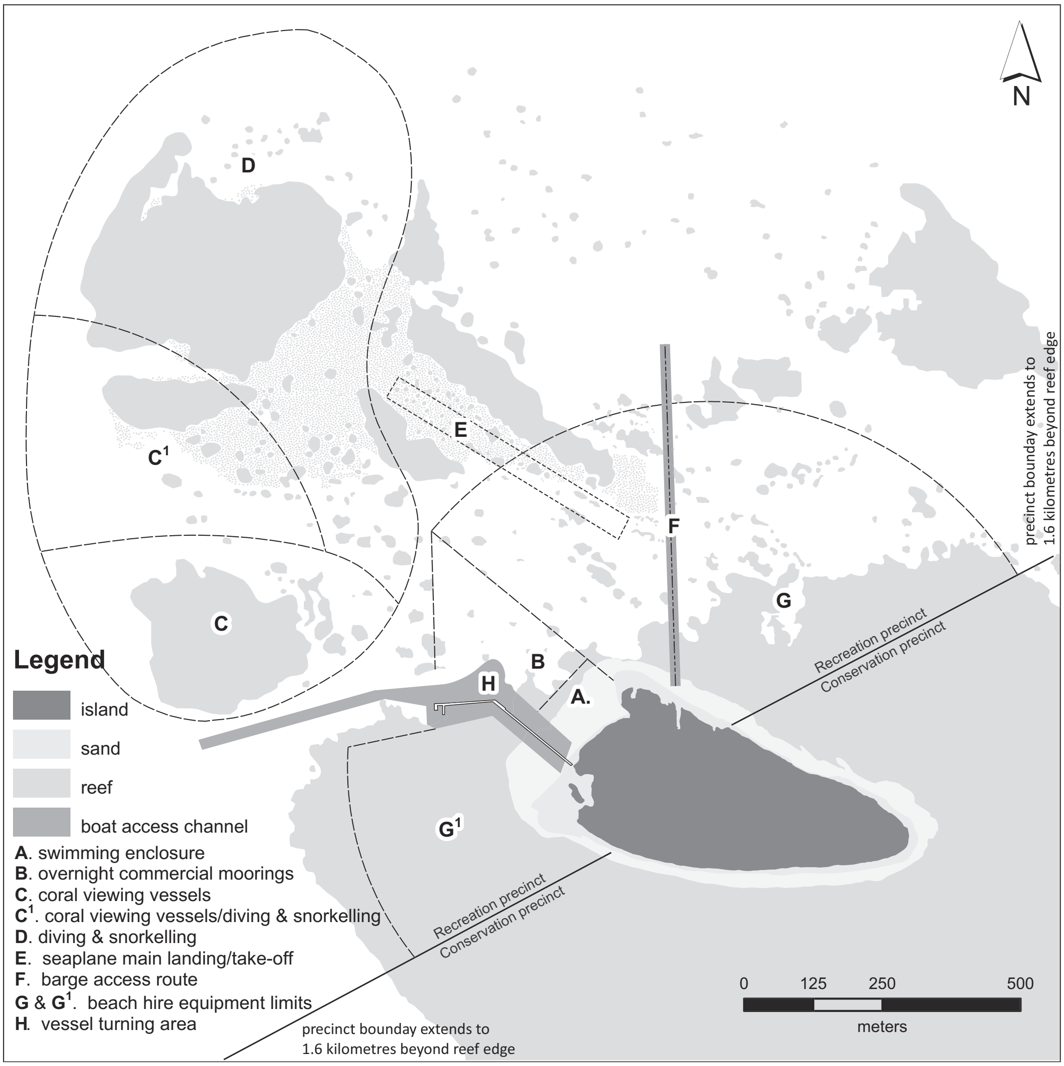

Fig. 8. Location of recreational activity precincts surrounding Green Island, implemented as part of the Green Island Recreation Area Management Plan. Modified from Environmental Protection Agency (2003).

to managing how the spread of invasive species are dealt with. Whether the invasion in discussion requires management relates to its functional consequences. The functional differences between the seagrass communities before and after the *S. isoetifolium* invasion, are not clear and require consideration. This study also illustrates the significance of chronic small-scale and cumulative impacts, and the importance of long-term monitoring to identify emerging trends in a globally changing environment.

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