Short communication

Meadow fragmentation and reproductive output of the SE Asian seagrass *Enhalus acoroides*

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Abstract

Flower and fruit production of the abundant, tall, long-lived, dioecious, surface-pollinating seagrass species *Enhalus acoroides* (L.) Royle were estimated at seven sites in the reef flats off Bolinao (NW Luzon, The Philippines) featuring different fragmentation of the seagrass meadows. Fragmentation of the seagrass meadow was quantified as cover of *E. acoroides* and all seagrass species present in 20×20 m plots. *E. acoroides* and overall seagrass cover were correlated positively. The proportion of female flowers of *E. acoroides* that developed a fruit increased sharply as overall seagrass cover was around 50%. Apparent sex ratio bore no relationship with overall seagrass cover. This threshold-type of relationship suggests that fragmentation of seagrass meadows can have a major effect on the reproductive output of this species. A possible mechanism underlying these results would be a non-linear increase of the efficiency of trapping the surface-dispersed pollen with increasing seagrass canopy density. This provides the first evidence based on real data that fragmentation can affect the population dynamics of seagrass species.
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Keywords: Pollen dispersal; Hydrochorous pollination efficiency; Landscape heterogeneity; Nonlinear thresholds; Tropical seagrass meadows

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1. Introduction

Seagrasses are rooted angiosperms inhabiting unconsolidated sediments of shallow coastal waters where physical disturbance by waves and currents is a natural phenomenon (Marbà and Duarte, 1995; Ver-

maat et al., 1997). Such disturbance has been related to the spatial structure and fragmentation of seagrass meadows (Patriquin, 1975; Fonseca and Kenworthy, 1987; Fonseca and Bell, 1998). Human activities in coastal waters have also resulted in increased fragmentation of seagrass meadows (Walker et al., 1989; Pasqualini et al., 1999; Bell et al., 2002). Large-scale declines of seagrass meadows (Short and Wyllie-Echeverria, 1996) call for in-depth understanding of the ecological processes involved in seagrass recovery. Although some seagrasses can show a high recolonisation capacity through vegetative growth (Kendrick et al., 1999; Hemminga and Duarte, 2000), seeds are considered crucial for the recovery and recolonisation of declining or disappeared seagrass beds (Orth et al., 1994, 2000).

Several environmental factors may indirectly affect the reproductive success of seagrasses through their effect on plant growth, for example light and nutrient availability (Agawin et al., 1996; Rollon, 1998). Pre- and post-dispersal seed predation can reduce the reproductive success of seagrasses (Fishman and Orth, 1996; Nakaoka, 2002; Orth et al., 2002; Balestri and Cinelli, 2003). Seagrass canopies modify hydrodynamics (Fonseca, 1996; Koch and Gust, 1999; Verduin and Backhaus, 2000) with consequences for habitat conditions and processes (Ward et al., 1984; Koch, 1999a; Gacia and Duarte, 2001; Gacia et al., 2002) which can affect plant growth (Koch, 1994, 1999b) and possibly sexual reproduction output. Additionally, pollen dispersal, pollination efficiency and fruit production might be directly influenced by the effect of seagrass canopies on water motion (cf. Lovett Doust and Laporte, 1991; Verduin et al., 1996). Hence, increased fragmentation of seagrass meadows may affect their reproductive output and, consequently, their capacity for long-term maintenance.

The large, long-lived, dioecious seagrass *Enhalus acoroides* (L.) Royle is abundant in SE Asian seagrass meadows (Johnstone, 1979; Nienhuis et al., 1989; Chansang and Poovachiranon, 1994; Terrados et al., 1998). Contrary to most seagrass species, *E. acoroides* invests substantial resources in reproduction (Duarte et al., 1997: 20% of annual aboveground productivity), and pollination occurs at the water surface (Troll, 1931; Den Hartog, 1970; Pettitt, 1984; Cox, 1988). The length of the female peduncle limits successful pollination to low tide depths shallower than ca. 0.5

m (Den Hartog, 1970). Vegetatively, the species occurs substantially deeper (Rollon, 1998). Rhizome branching frequency and longevity of shoots and rhizomes give rise to a patchy distribution of clonal fragments (Marbà and Duarte, 1998), with the gaps filled by other seagrasses, macroalgae or bare sediment. The natural patchiness of *E. acoroides* meadows and its abundant production of fruits (Duarte et al., 1997) make this species an appropriate model for our purpose: to elucidate if reproductive output of *E. acoroides* was affected by fragmentation of the seagrass meadows.

2. Materials and methods

Enhalus acoroides is common in the mixed seagrass beds covering the reef flats surrounding Santiago Island off Bolinao, NW Philippines. (Fig. 1; Vermaat et al., 1995; Rollon, 1998). In March 2000, we searched the reef flat for sites that differed in fragmentation of the seagrass meadow and selected 7 sites (Table 1) in larger areas of approximately homogeneous patchiness over distances of at least
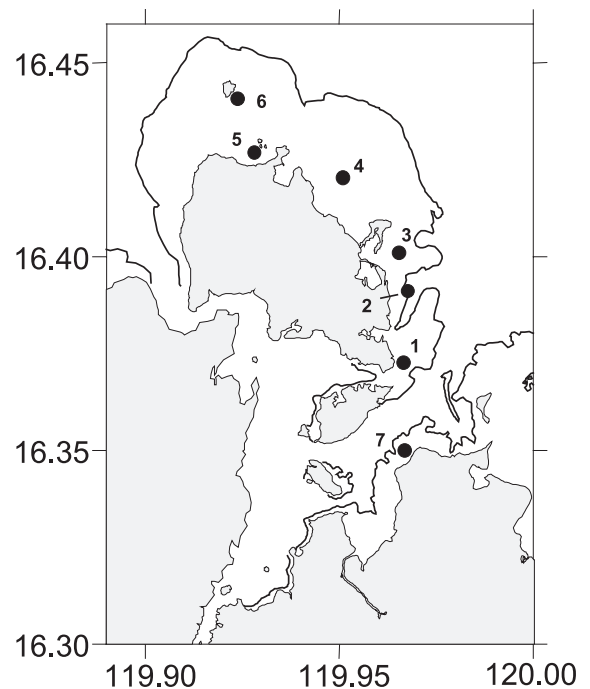

Fig. 1. Map of Santiago Island and surrounding reef flat. Sites are indicated with ●. Station numbers are as in Table 1.

Table 1
Site description of the sampled plots on the Bolinao reef flats in March 2000

Site	Coordinates	Mud in sediment (% of dry weight)	Calcium in sediment (% of dry weight)	Light attenuation water (K_d, m^{-1})
1. Pilar	16°37.18 N, 119°97.00 E	NA	NA	0.39±0.02
2. Victory	16°37.45 N, 119°97.10 E	NA	NA	NA
3. Dewey	16°38.35 N, 119°97.00 E	0.9	34.9	NA
4. Makandong	16°42.43 N, 119°93.41 E	8.1	39.3	0.40±0.02
5. Binabalian Labas	16°42.40 N, 119°92.50 E	8.1	34.4	NA
6. Silaqui	16°43.77 N, 119°92.21 E	5.5	37.6	0.30±0.01
7. Carot	16°34.88 N, 119°96.48 E	2.6	34.1	0.65±0.10

Mud (% of sediment particulates <63 μm) and calcium contents of sediments are taken from Kamp-Nielsen et al. (2002), light attenuation data are from Rivera (1997). NA=data not available; light attenuation at station 2 is probably similar to that of station 7, at station 3 to that of 4 and at station 5 to that of station 6. Note that coordinate minutes and seconds are decimal as in (Fig. 1).

500 m. Water depth varied little between sites (0.3–0.7 m at mean low tide) and would not preclude water surface pollination of female flowers during low tide. All sites had comparable sediment conditions and water turbidity (Table 1). A 20×20 m plot was delimited in each site (but 4 of such plots were established in Silaqui and Carot sites) and we quantified cover of both *E. acoroides* and all seagrasses, as well as the abundance of reproductive structures of *E. acoroides*. Seagrass cover, which quantifies the presence of seagrass at specific points or within quadrats of a certain size, is a well established variable to describe the spatial structure and fragmentation of the comparatively simple seagrass landscapes formed by mosaic of plant canopies and bare sediment gaps (Fonseca and Bell, 1998; Hovel and Lipcius, 2001, 2002; Fonseca et al., 2002; Hovel et al., 2002; Hovel, 2003).

The large 20×20 m plots were partitioned into 64 quadrats of 2.5×2.5 m. Quadrat and plot sizes were chosen to encompass the smaller scales of patchiness present, since small single-clone patches of *E. acoroides* have areas in the order of 0.05 m^2 and patch size increases continuously when these merge into closed meadows. Total seagrass and *E. acoroides* cover were estimated in each quadrat using the following scale: 0 (no cover), 1 (cover<25% of quadrat surface), 2 (25–50%), 3 (50–75%), 4 (75–90%) and 5 (≥90%). We then allotted each quadrat to one of the following cover class strata: no cover (0), intermediate (<25%) and dense (≥25%). From each of the last two cover class strata ('intermediate' and 'dense') we selected 10 random quadrats in each plot and harvested all flowering plants encountered.

Upon return to the laboratory, we counted in each quadrat sample the number of male inflorescences (including the number of pollen-bearing flowerlets per inflorescence), the number of female flowers (including the number of ovaries per flower), the number of fruits (including enclosed seeds), as well as lengths and widths of all male inflorescences and female flowers. An apparent sex ratio was calculated from the observed number of male and female flowers. Fruiting shoots were excluded here, since their long ripening period of 2–3 months (Rollon, 1998) would bias the ratio to the female side.

We consider that our snapshot sampling during successive days in March provides unbiased results on the reproductive output of *E. acoroides* in meadows with different fragmentation because (a) flowering is synchronised throughout the Bolinao area with two reproductive seasons, one in March–July and one in November–December (Rollon, 1998), (b) we took a random sample from each of the two flushes in reproductive shoots, one already with fruits and the other still developing; and (c) the life span of clones, shoots and reproductive structures is long compared to our sampling (Vermaat et al., 1995; Rollon, 1998). Although density of individual species may show substantial seasonality, within-year variability in cover is limited in these mixed seagrass beds (Rollon, 1998). We used correlation and regression analysis to describe the relationship between fragmentation and reproductive output. The elucidation of the effects of fragmentation requires landscape-scale studies but practical and logistical constraints impose limits to the size of the areas that can be manipulated in field experiments (McGarigal and Cushman, 2002). Large study areas are

bound to include large levels of inherent, natural variability which makes it difficult to obtain true replicates of any experimental treatment (McGarigal and Cushman, 2002), and this study was not designed to test for differences in reproductive output at fixed fragmentation levels. Our approach cannot support strong inferences but we feel that it is useful as a comparative and correlative approach suggesting explanatory patterns, i.e. hypotheses to guide future research.

3. Results

Overall seagrass cover as well as *Enhalus acoroides* cover varied substantially among plots and were
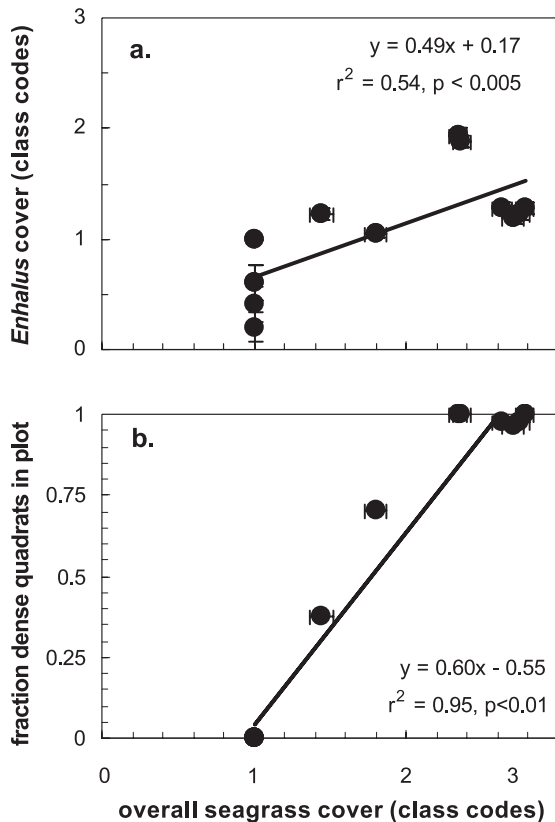

Fig. 2. Scatterplots of the cover of (a) *Enhalus acoroides* and (b) the fraction of dense quadrats in a plot against overall seagrass cover averaged over a plot. For significant linear regressions, the equation, explained variation as r², and the level of significance is presented. Data are presented as means±1 standard error. Cover is a class code (see Materials and methods).

correlated positively (Fig. 2a). At the scale of quadrats, cover class 0 (no seagrass) did not occur in our plots. The seagrass meadows inside the plots differed substantially in fragmentation as is evident from both overall cover and the fraction of dense (seagrass cover≥25% of quadrat surface) quadrats in a plot. Since these two variables were significantly correlated (Fig. 2b), we chose to use overall seagrass cover as a proxy for the fragmentation of the seagrass meadow within the plots.

The abundance of male flowers was positively correlated to overall seagrass cover, but this was not the case for female flowers (Fig. 3a, b), although the scatterplot suggests an increasing upper bound with increasing cover. When fruit abundance is expressed as a ratio to female flower abundance, a highly significant non-linear pattern emerges (Fig. 3c): we found a sharp increase in the ratio of female flowers with developing fruits above an overall cover of 2.5, which corresponds to a mean seagrass cover around 50% of quadrat surface (i.e., dense quadrats). No relationship with cover was observed for apparent sex ratio, the number of seeds per fruit, or the number of flowerlets per male inflorescence (Fig. 3d, e, f). None of the variables used to quantify the reproductive output of *Enhalus acoroides* were correlated with the cover of this species alone (data not shown).

4. Discussion

We found that the proportion of female flowers of *Enhalus acoroides* that developed a fruit increased sharply as overall seagrass cover was around 50%. This threshold-type of relationship suggests that fragmentation of seagrass meadows can have a major effect on the reproductive output of this species. The abundance of male and possibly also female inflorescences of *E. acoroides* increased with overall seagrass cover, which is an expected consequence of the higher plant abundance featured by the less fragmented seagrass meadows. The increase of *E. acoroides* fruit set relative to flowering above an overall seagrass cover of 50% did not seem to be driven by changes in the sex ratio, which bore no relationship with fragmentation. Our correlative approach cannot pinpoint the actual mecha-
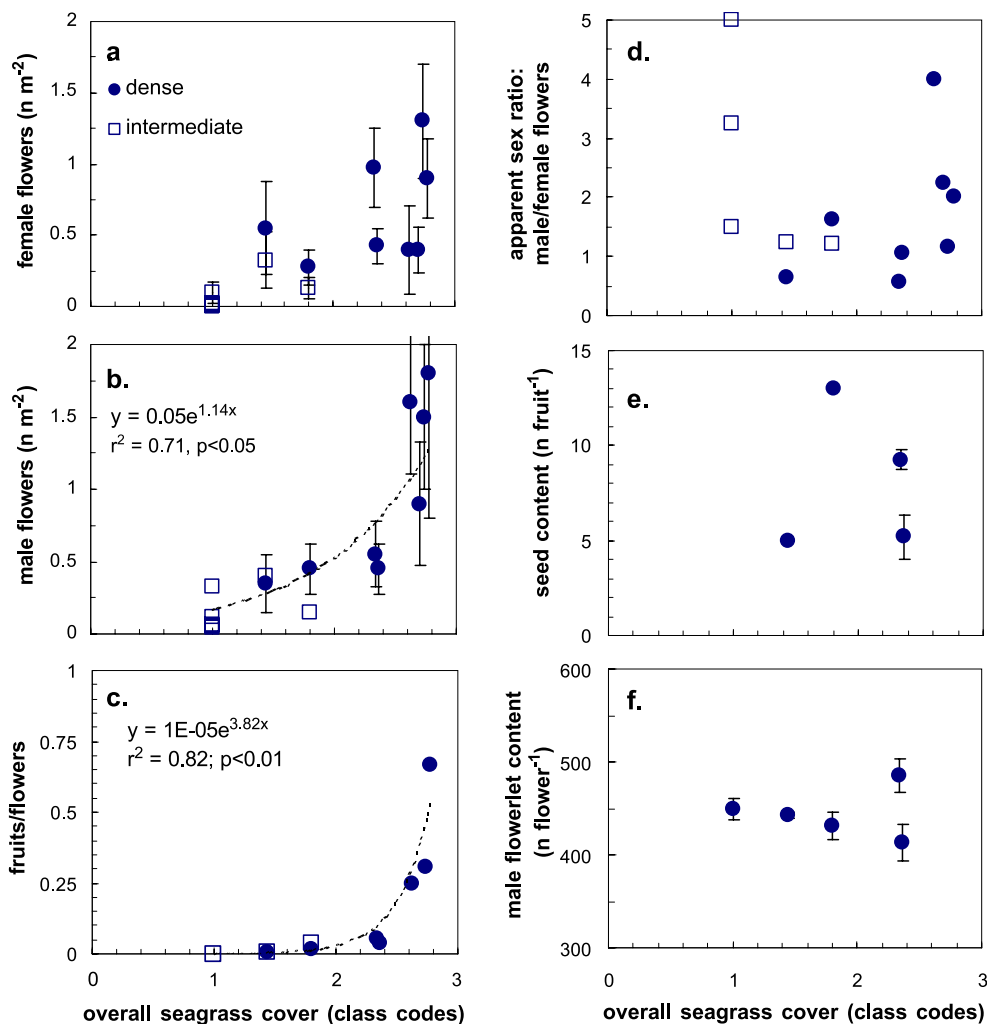
Fig. 3. Scatterplots of (a) density of stage 1 female flowers, (b) density of male inflorescences, (c) the ratio of fruits over stage 1 female flowers, (d) apparent sex ratio, (e) the number of seeds within a fruit, and (f) the number of male flowerlets within a male inflorescence, all against overall seagrass cover in a plot. Apparent sex ratio is the ratio of male flowers over female stage 1 flowers. Female stage 1 flowers have not yet risen to the water surface but are clearly visible between the leaf sheaths. Data derived from intermediately dense quadrats are depicted with open symbols, those from dense quadrats with filled symbols. Further as (Fig. 2). The non-linear fit in (b) did not provide a significantly better fit than a linear fit, although the r^2 of the latter was 0.59; in (c) the non-linear fit was significantly better than a linear one (with $r^2 = 0.23$), F=4.3, 12 and 12 df, $p < 0.01$.

nism by which fragmentation affects the probability for a female flower to produce a fruit. Still, our study provides a first indication that fragmentation of seagrass meadows can affect the population dynamics of seagrass species by reducing seed output.

Several mechanisms may explain the trend we observed. For example, *E. acoroides* can be severely nutrient limited in the area (Agawin et al., 1996; Terrados et al., 1999), and small-scale spatial variation in sediment nutrient availability might determine the capacity of a female plant to develop fruits successfully as well as that of male plants to complete a flowering event. Further, seagrasses can modify sediment conditions through the release of oxygen by the roots (Pedersen et al., 1998; Enríquez et al., 2001) and this capacity increases with plant abundance (Marbà and Duarte, 2001; Halun et al., 2002). If fruit set of *E.*

acoroides is affected by reducing conditions or sulphide levels in the sediment it can be surmised that non-linear interactions may be established between the fragmentation of seagrass meadows and the reproductive output of *E. acoroides* through seagrass abundance.

Another possible mechanism could be based on the influence of seagrass canopies on water motion and its consequences for pollination. As seagrass meadows become less fragmented their capacity to reduce water movement should increase. We postulate that seagrass canopies need to be sufficiently dense (i.e. cover>50%) to affect hydrodynamic conditions so that drifting pollen or male flowerlets are efficiently trapped within the meadow and pollination of *E. acoroides* is promoted. During mass-release of male flowerlets, these get entangled in the leaves at the water surface along the edges of seagrass patches and subsequently disperse into the stand (Rollon, 1998). Because relative fruit set of *E. acoroides* was not related to the cover of this species alone but to overall seagrass cover we speculate that it is the whole ensemble of different seagrass species forming the meadow that effectively modify hydrodynamic conditions to promote pollination. Pollination-enhancement might be a mutualistic effect of dense canopies (cf. Vermaat et al., 1987; Worm and Reusch, 2000). Our results provide support to the postulated limited efficiency of surface pollination for *Vallisneria americana* (Lovett Doust and Laporte, 1991). Further, they also support the pattern of enhanced pollen limitation observed in fragmented populations of wind-pollinating oaks (Knapp et al., 2001).

Short pollen life (cf. *Zostera marina*, Cox et al., 1992) could be a third alternative mechanism to explain why fragmentation of seagrass meadows might affect pollination, for a large fraction of pollen grains could be dead when contacting the stigmas in highly fragmented meadows. Dispersal of *E. acoroides* pollen occurs not only through pollen grains on the water surface but also through floating male flowerlets which carry the grains (Cox, 1988). The life span of *E. acoroides* pollen grains is unfortunately unknown, but should be comparatively short (not more than 2 days).

A level of seagrass cover around 50% has been proposed as a transition point delimiting seagrass sites with main differences in habitat conditions along a gradient of hydrodynamic activity, and below which seagrass landscapes tend to exist as discrete patches (Fonseca and Bell, 1998). Coincidentally, damage caused to seagrass meadows by boat propeller scarring did not seem to affect fish and shrimp populations inhabiting seagrass meadows when scarring was up to 50% of the surface of the meadow (Bell et al., 2002). Our results suggest a comparable threshold for the effect of seagrass fragmentation on reproductive output. A similar non-linear threshold was proposed to exist around 50–60% for landscapes that provided fragmented habitat to birds and mammals (Andrén, 1994).

In summary, we found that increased fragmentation of a multispecific seagrass meadow correlated with a reduced probability of *E. acoroides* female flowers to develop fruits. Despite the apparent limitations of our results, they highlight the relevance of spatial fragmentation for the maintenance and recovery of seagrass meadows.

Acknowledgements

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