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Edaphic resource foraging by *Zostera marina* (Linnaeus) patches

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ABSTRACT

Clonal foraging in response to heterogeneously distributed water, light or mineral resources has been demonstrated for a number of terrestrial plant species. The existence of similar behavior in seagrasses and the cross-scale effects of clonal foraging on patch development, however, have not fully been explored. Our objective was to test whether spatial exploration by independent ramet clusters could generate emergent patch behavior consistent with clonal foraging theory. We also examined the effect of nutrient amendment on reproductive effort and seedling recruitment. Working in Shinnecock Bay, New York, USA, with the clonal marine angiosperm, *Zostera marina*, we attempted to stimulate directional growth along ten patch edges over a two-year period using subterranean fertilizer. Changes in ramet demography, patch expansion, seedling emergence and reproductive effort were quantified through repeated shoot censusing. We found that nutrient addition accelerated patch expansion. Enriched edges exhibited significantly higher shoot densities, indicating that a ramet proliferation, selective ramet placement or a combination of the two responses had occurred. The seasonality of this effect was different between treatments and consistent among years, representing a fundamental shift in the pattern and phenology of seagrass growth. Within patches, no detectable differences in per capita branching rates or reproductive effort were observed. This study provides the first evidence of foraging behavior by patches of *Z. marina*, and offers new insight into its seasonal growth patterns during the as yet poorly understood colonization period.

1. Introduction

The modular growth of clonal plants provides an observable framework from which to explore the genet-environment interaction in both space and time. As an iterative record of plant responses, the spatial structure of genet growth (termed` 'ramet architecture') is a complex product of anatomical constraints, ontogeny and phenotypic plasticity (Huber et al., 1999). For many species, natural variation in key parameters, such as branching angle, branching frequency and spacer length, can lead to large differences in ramet placement and distribution (de Kroon and Hutchings, 1995). Simulation models of clonal growth for a number of terrestrial (Cain, 1990; Cain and Damman, 1997; Cook, 1985; Wong et al., 2011) and marine (Brun et al., 2007; Marba and Duarte, 1998, 2003; Sintes et al., 2006) species have shown that this plasticity can explain emergent patch behavior, including: (1) non-linear edge growth, (2) effective sweeping of un-vegetated space, (3) self-thinning and (4) central die-back or ring-like growth patterns.

Flexibility in ramet architecture has important implication for resource acquisition, because clonal plants generally inhabit environments that are heterogeneous at spatial scales approaching that of the genet. For example, it is well established that mineral resources in terrestrial (de Kroon and Mommer, 2006; Jackson and Caldwell, 1993; Rajaniemi and Reynolds, 2004) and marine (Jensen and Bell, 2001) ecosystems exhibit marked spatiotemporal variability, with patchiness mostly driven by plant-soil (Jackson and Caldwell, 1993; Stuefer, 1996) and animal-sediment (Peterson and Heck, 1999; Peterson and Heck, 2001) interactions, respectively. Clonal plants have shown the capacity to exploit such heterogeneity by asexually reproducing at rates differential to resource availability (i.e., ramet proliferation) and/or adjusting their architecture to maximize ramet placement within high quality zones (i.e., clonal foraging) (Birch and Hutchings, 1994; Humphrey and Pyke, 1997; Ikegami et al., 2007; Oborny and Englert, 2012). Together with similar processes acting on individual ramets (i.e., root proliferation and root foraging; de Kroon and Mommer, 2006), elements of clonal growth have been implicated in controlling resource acquisition (Oborny and Hubai, 2014; Sutherland and Stillman, 1988), invasiveness (Keser et al., 2014; Song et al., 2013) and competitive dominance (Grime, 2007; but see Kembel et al., 2008).

In reality, however, the relationship between resource distribution and clonal trait expression is often complicated by (1) physiological integration, (2) physiological plasticity and (3) reproductive investment. For many clonal plants, neighboring ramets remain vascularly connected, existing as integrated physiological units ('IPU'; Watson, 1986) or ramet hierarchies (Briske and Derner, 1998). For each IPU, translocation of photosynthate, water and nutrients (Price and Marshall, 1999) can

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subsidize the growth of impoverished ramets (Oborny and Hubai, 2014), resulting in uptake specialization among IPU members (i.e., 'division of labor'; Stuefer, 1996). Modeling (Oborny and Hubai, 2014) and empirical (Humphrey and Pyke, 1997; Roiloa and Hutchings, 2013) studies have demonstrated that this sort of integration greatly influences foraging behavior, enhancing foraging efficiency and increasing competitive advantage, particularly when coupled with resource storage and a root or ramet proliferation response. However, because IPUs respond to resource availability collectively, integrated clones can exhibit phenotypic responses counter to those predicted for isolated individuals (Roiloa and Hutchings, 2013); for example, root biomass of unitary plants lessens in nutrient replete soils, while IPUs tend to increase the root biomass of ramets within resource rich zones.

The temporal stability of resource patches also has significance. Whereas permanent changes in root biomass and ramet architecture may be effective for long-lived or seasonally predictable resources, time lags and construction costs ill-adapt them to transient nutrient pulses. More ephemeral resources can be exploited by elevating nutrient uptake rates at the point of contact (Kembel et al., 2008; Keser et al., 2014; Roiloa and Hutchings, 2013). For terrestrial species, such kinetic adjustments have been shown to satisfy whole-plant demand from extremely small fractions of the root system (Caldwell, 1994). Indeed, malleability in uptake performance underpins the 'sit and wait' strategy (i.e., 'high scale' root foraging) of many unitary, as well as clonal, plants (Grime, 2007; Stuefer, 1996).

Finally, the induction and development of reproductive structures represents a considerable energetic investment on the part of the IPU (Verhagen and Nienhuis, 1983). The degree to which this influences long-term spatial patterns in vegetative growth has not been adequately explored; however, 'Division of Labor Theory' suggests that resource-rich portions of the IPU or genet may act as reproductive hotspots within the larger landscape (Price and Marshall, 1999; Stuefer, 1996). If so, the resultant genet architectures might be affected, particularly for species with monocarpic shoots. Given the rich interplay between clonal trait expression, physiological integration and plasticity, and reproductive allocation, visually assessing the relative contribution of clonal traits and generating a priori predictions regarding ramet dynamics can be quite challenging even for single genet systems (Brun et al., 2006; Humphrey and Pyke, 1997), let alone for patches composed of multiple genets or species.

For seagrasses, architectural responses to variations in mineral resources have not received much attention; however, the effects of nutrient addition on plant and meadow performance have been well studied. In a recent review of 28 studies involving 14 seagrass species, Cabaco et al. (2013) found that short-term fertilization resulted in nonlinear biomass-density relationships depending on initial shoot densities – with increasing shoot biomass and densities occurring below species-specific thresholds and declines, indicating a self-thinning response, above. Others have found reduced belowground biomass investment with increased nutrient loading, consistent with optimal partitioning theory (Lee and Dunton, 2000; Statton et al., 2014 and references within; Wicks et al., 2009). Translocation of resources among physiologically connected individuals has been confirmed for many species, including *Cymodocea serrulata*, *Cymodocea nodosa*, *Halophila stipulacea*, *Halodule uninervis*, *Posidonia oceanica*, *Thalassodendron ciliatum*, *Thalassia hemprichii* and *Zostera noltii* (Duarte and Sand-Jensen, 1996; Marba et al., 2002; Vermaat, 2009), but has not yet been demonstrated for *Zostera marina* or *Zostera novazelandica* (Duarte et al., 2006). As with terrestrial species, subsidies to patch edges are more common for species with relatively high growth rates than among k-selected taxa (Vermaat, 2009). To date, only a single study (Jensen and Bell, 2001) has looked at the effect of sediment nutrient heterogeneity on the shape of seagrass patch development, despite the clear importance of vegetative growth to patch expansion and coalescence (Duarte et al., 1994; Duarte and Sand-Jensen, 1990). Jensen and Bell (2001) used subterranean fertilizers to examine ramet architectural responses by *Halodule wrightii* along a tidally influenced patch edge over a 5-week period. They reported significant reductions in rhizome internode distance and increased shoot biomass for phosphorus (P), but not for nitrogen (N) or N and P treatments (branching frequency was unchanged). Neither were they able to match natural variation in these parameters to in situ soil conditions.

As a first step toward understanding the potential role of clonal foraging and ramet proliferation in the pace and shape of *Z. marina* colonization, we attempted to stimulate directional growth at the patch level using asymmetric nutrient additions within ten radially-expanding, sub-tidal patches of perennial *Z. marina*. In the absence of clear a priori expectations regarding the form of this response, we simply asked: (1) can heterogeneously distributed mineral resources elicit an edge growth response, (2) does this response manifest as phalanx- or guerrilla-like growth along the expanding patch margin, (3) what effect does clonal foraging and/or small-scale nutrient amendment have on reproductive effort, and (4) what role might seedling recruitment play in patch-scale foraging? In this study, we monitored the spatial exploration of *Z. marina* patches and evaluated aspects of their growth for emergent behavior consistent with clonal foraging theory.

2. Materials and methods

2.1. Study site

All fieldwork was conducted in Shinnecock Bay, a backbarrier lagoon in southeastern Long Island, New York, USA. Tides are semi-diurnal with a range of 0.8 m (USACE, 2004). In the southeast portion of the bay, roughly 400 m from shore and 2.5 km east of the Inlet (40.857237° N, 72.450289° W), we selected ten mono-specific *Z. marina* patches (five in October 2011, increased to ten in July 2012). All were <4 m^2 and at least 0.5 m from adjacent seagrass at the time of choosing. Depths ranged from 0.33–0.39 m MLLW (mean $\pm$ 1 s.d.: 0.36 $\pm$ 0.02 m). Surficial sediments consisted of siliceous sands and were uniformly low in organic content ($<1\%$ by loss on ignition at 500 °C for 5 h, B. T. Furman unpubl.).

2.2. Experimental design

At each patch, permanent markers were installed to allow for consistent placement of a 4-m^2 quadrat with 100 equally sized cells. Counts of vegetative and generative shoots were conducted once in 2011 and 4$\times$ per annum, 2012 thru 2014. Periodicity corresponded to seasonal shoot growth and flowering cycles, with sampling at the onset of growth, during the time of maximal flowering, at peak aboveground biomass, and at or near the end of the growing season (i.e., March/April, May, July and October, respectively). During the spring, mid-summer and fall periods, one 100-g 15:3:3 (N:P:K) Jobe's Tree and Shrub® fertilizer spike was added to the center of every cell in each of two non-consecutive quadrants; i.e., 25 per quadrant in an upper-left/lower-right or lower-left/upper-right arrangement, randomly selected at the start of the experiment. A pilot study, conducted in sub-tidal mesocosms using similar beach sand, confirmed the presence of a stable nutrient signal out to 20 cm. This pattern was persistent in quiescent, tidal conditions over the course of several days to weeks. Therefore, we anticipated a spatially limited, triannual pulse of N and P availability.

Physical confirmation of nutrient uptake (by *Z. marina*) and treatment contrast was prevented by *Mytilus edulis* recruitment during the spring of 2014. Settlement of mussel spat occurs annually in this portion of the bay, with individuals remaining confined to the leaves of *Z. marina*, and perishing as juveniles (approx. 5–10 mm, total length) to heat stress and predation by mid to late summer (B. J. Peterson, person. obs.). In October of 2013, however, recently settled juveniles were beginning to migrate to the sediment-water interface. In 2014, many had recruited to form adult aggregations. This had the dual effect of (1) inhibiting effective vegetative shoot censusing, as byssal threads

tended to mangle and bind leaf material, and (2) contributing to sediment nutrient pools within ambient quadrants (Vinther et al., 2012). Unexpectedly, generative shoots were unaffected by mussel presence, arising from among even the densest mussels. Because floral induction occurs in mid to late fall (Churchill and Riner, 1978), concurrent with initial mussel migration – but prior to mussel maturation – and because no impact on floral condition was observed, we chose to terminate vegetative growth analysis in October 2013 and reproductive analysis in May 2014. By early summer of 2014, mussel presence had severely affected the experimental patches, barring any assessment of *Z. marina* nutrient concentration or description of rhizome architecture.

As a proxy, vegetative leaf tissue was sampled from twenty, unaffected, similarly sized patches located within the same meadow but unaffected by mussels. These patches were amended (10 ambient and 10 enriched) at the same periodicity (beginning in 2012), using the same fertilizer, but at a quarter of the application density. Eight weeks following nutrient addition, three replicate groups of 5 haphazardly selected shoots were collected from each patch. The two youngest leaves from each shoot were retained, gently cleaned of epiphytic growth, and dried at 60 °C for >72 h. Samples (N = 60) were then ground to a fine homogeneous powder with a mortar and pestle, and total carbon and nitrogen contents were determined by oxidation in a Thermo EA1112 elemental analyzer following Fourqurean et al. (1992). The single effect of treatment status on the C:N ratio of aboveground vegetative biomass was compared using a Student's *t*-test.

2.3. Cell-level dynamics

Consistent quadrat placement allowed for fine-scale accounting of vegetative growth dynamics over a 2-year period. At the cell level, we evaluated patterns in ramet-specific recruitment rate (RSR; d^{-1}), adapted from Marba et al. (2005), with the calculation taking the form:

$$RSR = \frac{(N_{t_1} - N_t)}{[(t_1 - t) \times N_t]} \quad (1)$$

where N_t and N_{t1} are the number of ramets at time t and t + 1, respectively. RSR was estimated for all cells that contained seagrass at the onset of the experiment and converted to seasonal anomalies by subtracting season means; balanced nutrient treatment representation was achieved by re-sampling with replacement. The mean seasonal anomaly was then calculated for each cell over the available observation period, eliminating the effect of repeated measurement. The main effect of nutrient addition was assessed using a one-way ANOVA on ranked data. To explore possible density-dependent effects of season and nutrient condition on cellular RSR, we simulated vegetative shoot recruitment over a 1-yr period for both nutrient enriched and ambient treatments. RSR estimates were calculated for all seagrass-containing cells. Seasonal durations were constructed using mean seasonal sampling intervals, yielding a model year of 362.73 d. At the start of a randomly selected season, a single ramet was placed within an isolated cell (one cell per treatment) and allowed to propagate for one year at rates re-sampled from appropriate season, treatment and cell density pools. To delineate initial cell density groups, empirical RSR distributions were binned into 5-ramet units (0–70 ramets per cell) based on the cell densities observed at the start of each season. Any time-step that produced a season-density-nutrient combination for which an estimate of RSR was unavailable was allowed to carry forward with no change in ramet abundance. All modeled cells falling to or below zero remained at that value for the balance of the model year. Final ramet densities (10,000 per nutrient treatment, N = 20,000) were compared using a one-way ANOVA.

2.4. Patch-level dynamics

Patch edge expansion rate (EER; cells per edge cell d^{-1}; Fig. 1) was calculated for each quadrant at each sampling period, as

$$EER = \frac{\sum D_{t_2}}{E_{t_1}} / t_2 - t_1 \quad (2)$$

where D is the distance score in number of cells at t_2 and E is the number of edge cells at t_1. A distance field, expressed as the number of quadrat cells from seagrass present in the previous time-step, was determined for each patch at each sampling period using an 8-neighbor rule; distance scores (D) represent the distance value achieved by each newly acquired cell during the following time-step. The number of edge cells (E) was determined using a 4-neighbor rule (as this encompasses the entire patch perimeter) and included an extra row on either side of the quadrant boundary to account for cross-border growth. EER values are sensitive to un-mapped seagrass entering at the edges of the sampling quadrat. Such encroachment occurred in only 2 patches, and affected only 1 and 3 quadrants, respectively (10 cells total). These cells were disqualified upon first appearance, but allowed to factor into EER calculation thereafter. A one-way ANOVA was used to test for the main effect of nutrient enrichment on EER; data were converted to seasonal anomalies and ranked prior to analysis.

We also simulated annualized edge growth using EER estimates for both nutrient enriched and ambient edges. EER values were randomly selected by season and treatment (re-sampled with replacement, 10,000 iterations per treatment), and edge growth was simulated using mean seasonal durations to produce annual distance values, measured in distance score per edge cell. Modeled distributions for ambient and enriched treatments were compared using one-way ANOVA.

To quantify patterns in ramet density along the active growth margin (hereafter, 'edge density'), we calculated the sum of all ramets at time t_1 within the eight cells neighboring any central cell that had acquired seagrass during the following time-step (t_2; Fig. 2). Edge densities were then pooled by nutrient treatment. As with the EER analysis, encroaching seagrass was removed upon first appearance. A one-way ANOVA on ranked data was used to evaluate the effect of nutrient enrichment on edge density.

2.5. Seedling recruitment

Assuming that (1) local seed production varied positively with floral abundance, and (2) local seed retention exceeded trapping of exogenous seeds, then seedling recruitment should manifest as a spike in patch-level RSR during the season of maximum seedling emergence. This spike should also be proportional to the magnitude of the previous flowering event. To investigate this possibility, patch-level RSR values

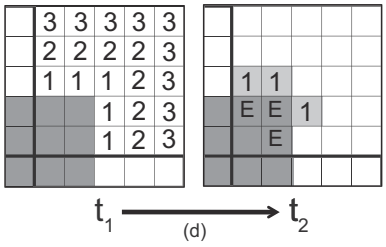

Fig. 1. Illustration depicting the edge expansion rate (EER; cells per edge cell d^{-1}) calculation for vegetative growth recorded within the upper right quadrant of a *Z. marina* patch between two successive time-periods (t_1 and t_2). Dark gray cells denote seagrass presence at t_1, light gray new growth at t_2. The distance field generated using the 8-neighbor rule is shown as numeric values radiating from existing seagrass at t_1; the distances obtained by vegetative growth are shown at t_2. Edge cells representing new growth at t_2 (marked 'E') are identified using the 4-neighbor rule with an additional row bounding the target quadrant. Time between sampling is recorded in days.

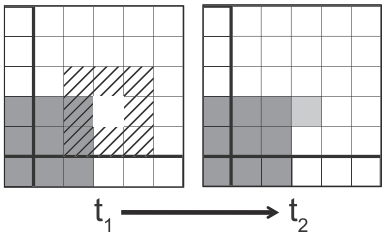

Fig. 2. Illustration of an edge density calculation for vegetative growth within the upper right quadrant of a *Z. marina* patch between two successive time-periods (t_1 and t_2). Dark gray cells denote seagrass presence at t_1, light gray new growth at t_2. The hatched region shows the area within which the sum of all ramets at t_1 is calculated.

were calculated, converted to seasonal anomalies, and compared to whole-patch floral abundances using Pearson and Spearman correlations.

2.6. Reproductive effort

Differential impact of nutrient treatment on reproductive investment was evaluated using (1) per capita flowering effort, (2) flowering probability by quadrat cell and (3) proportional flowering by quadrant as metrics of comparison. Because flowering is induced in the late fall, all flowers recorded in May were descendent from IPUs present during the previous October (Churchill and Riner, 1978). To compare ramet-specific flowering intensity at the cell level, we standardized flowering abundance for all flowering cells in May to the vegetative shoot density observed within an 8-cell neighborhood (9 cells, total) during the previous October. These data were expressed as reproductive to vegetative shoot ratios (R:V) and analyzed using a two-way, interactive, Type III ANOVA on ranked data, with nutrient treatment and sampling period as fixed factors. The probability that seagrass-containing cells would undergo flowering was evaluated using logistic regression and ANOVA, with nutrient condition as a fixed factor. Cell-specific states (i.e., flowered or not flowered) from all three floral censuses were pooled by nutrient treatment and transformed via a binomial logit function prior to analysis. We used a one-way generalized linear model with a quasi-binomial error distribution to investigate the impact of fertilization on the proportion of flowering cells per quadrant, i.e., standardized to the number of seagrass-containing cells. The resultant model was evaluated for data dispersion, goodness-of-fit and cooks distance prior to interpretation.

2.7. Statistical analysis

Parametric and non-parametric univariate analysis and data simulations were performed using the statistical software, R version 2.14.1 (R Development Core Team, 2012). In all cases, response data were appropriately transformed to meet the assumptions of ANOVA. Effect patterns obtained using ranked data and/or unbalanced ANOVA designs were corroborated via permutation tests of main- and interaction-effect F-statistics; confirmatory results are not presented. Statistical significance was assessed at an alpha of 0.05.

3. Results

3.1. Treatment diagnostics

During the 720-day ($n = 5$; 444 d, $n = 10$) manipulative experiment, cell-level estimates of shoot density fell between 25 and 1650 shoots m^{-2} (404 ± 305 shoots m^{-2}), exhibiting no clear long-term temporal trend. Mean density by sampling period ranged from 255 ± 161 to 566 ± 331 shoots m^{-2} with substantial seasonal and intra-patch variability. Percent coverage by patch (i.e., percent of sampling quadrat within which seagrass was present) began reasonably low at between 5 and 57% (33.1 ± 18.2%), reaching 58 to 92% (72.6 ± 12.7%) by October 2013. The ambient and enriched sections of each patch underwent similar changes: starting at 32.6 ± 19.8% and 33.6 ± 19.3% and ending at 69.0 ± 14.0% and 76.2 ± 16.4%, respectively. Only a single quadrant was filled during the observation period (an enriched quadrant within patch no. 6, July and October 2013), although quadrat-level treatment space was never exhausted. Maximum values were 90% and 94% for ambient and enriched halves, respectively. Patch growth did, however, commonly reach or exceed quadrat boundaries, continuing beyond our monitoring design to distances of no more than 40 cm.

Leaf tissue C:N analysis confirmed that nitrogen released by subterranean fertilizer spikes was (1) available to *Z. marina* roots and rhizomes, (2) still being incorporated into new growth 8 weeks post-addition, and (3) in excess of surrounding ambient conditions (square transformed, $t_{33} = 3.57$, $p = 0.001$). Mean enriched foliar C:N was 11% lower than ambient (20.67 ± 2.61, enriched; 23.22 ± 1.73 ambient). This supports the nutrient-limited status of *Z. marina* growth in Shinnecock Bay, particularly for populations inhabiting well-sorted, sandy sediments (Carroll et al., 2008; Wicks et al., 2009). Although direct measurement of treatment contrast and integrity could not be made, we maintain that pore-water transfer among adjacent quadrants was likely limited and could only have served to diminish the observed treatment effects.

3.2. Cell-level dynamics

Ramet-specific recruitment rates (RSR), calculated for seagrass-containing cells, ranged from −0.016 to 0.122 d^{-1} (enriched: $n = 168$, 0.007 ± 0.014 d^{-1}; ambient: $n = 163$ 0.008 ± 0.018 d^{-1}). Seasonally-adjusted mean RSR values were unresponsive to nutrient addition ($F_{1,329} = 0.407$, $p = 0.524$). Visual inspection of ramet recruitment as a function of initial cell density (Fig. 3) revealed patterns consistent with cell crowding, as per capita recruitment fell to zero at between 5 and 35 shoots per cell (125–875 m^{-2}) depending on the season. Nutrient-enriched cells generally outperformed ambient at the lower end of the density spectrum, particularly in the spring; however, this pattern was reversed in the fall, when enriched RSR mirrored winter profiles, while ambient cells maintained higher recruitment rates. Simulated on an annual basis, these differences resulted in a statistically significant, 31% increase in recruitment within enriched cells ($F_{1,19,998} = 943.5$, $p < 0.001$). Final ramet densities ranged from 0 to 44.59 $cell^{-1}$; ambient and enriched means were 8.12 ± 6.00 and 10.64 ± 5.58 $cell^{-1}$, respectively.

3.3. Patch-level dynamics

Monthly edge growth rate ranged from 0.00 to 1.36 cells per edge cell. The upper limit was on par with patch expansion as visually assessed in quadrat time-series; however, because seagrass expansion occurs at scales smaller than the quadrat cell, often incompletely filling newly acquired cell-space, there is no direct method to convert EER to sensible distance units. Mean monthly EER was 0.153 ± 0.171 and 0.206 ± 0.224 cells per edge cell for ambient and enriched quadrants, respectively. Results of the one-way ranked ANOVA on seasonally adjusted EER confirmed a significant nutrient response ($F_{1,\ 257} = 9.492$, $p = 0.002$) with 35% faster growth for fertilized seagrass edges (Fig. 4). Simulations based on empirical EER distributions found 38% further annual spreading relative to ambient patches ($F_{1,19,998} = 3.428$, $p < 0.001$). On a seasonal basis, the effect of nutrient addition was not uniform (nutrient × season: $F_{3,251} = 4.0903$, $p = 0.007$). A visual assessment of seasonal EER patterns revealed distinctly different annual cycles in edge growth, with fertilized quadrants out-performing ambient ones during all seasons except autumn, during which ambient growth continued at near-summer pace, while enriched edges decelerated to winter levels (Fig. 5). This pattern was consistent among years.

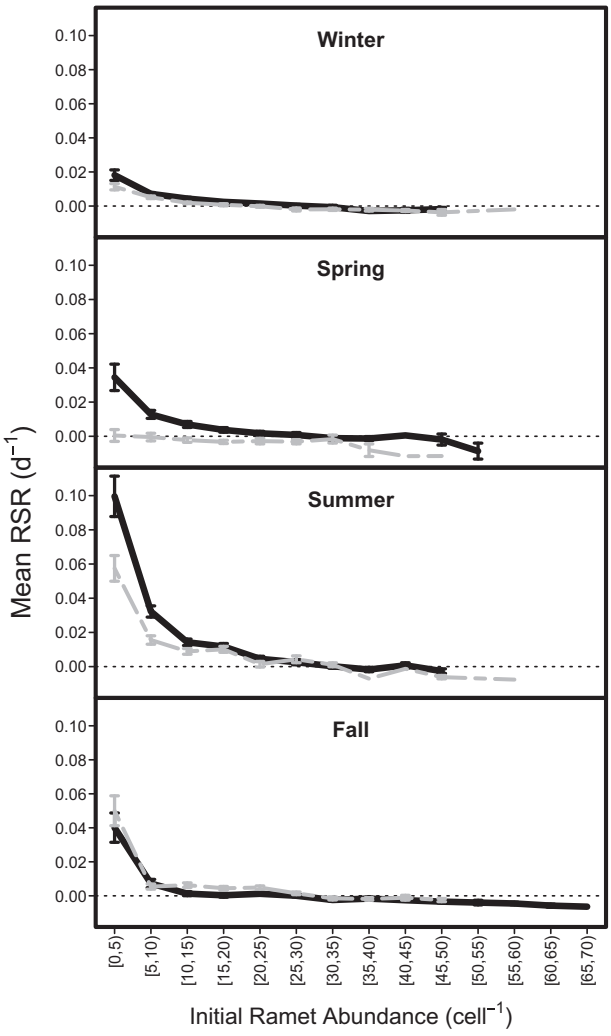

Fig. 3. Seasonal patterns of mean (±SE) ramet-specific recruitment rate (RSR; ramets d^{-1}) for enriched (solid black line) and ambient (gray dashed line) cells displayed as a function of initial cell densities (ramets quadrat cell^{-1}; binned at 5-ramet intervals prior to median calculation).

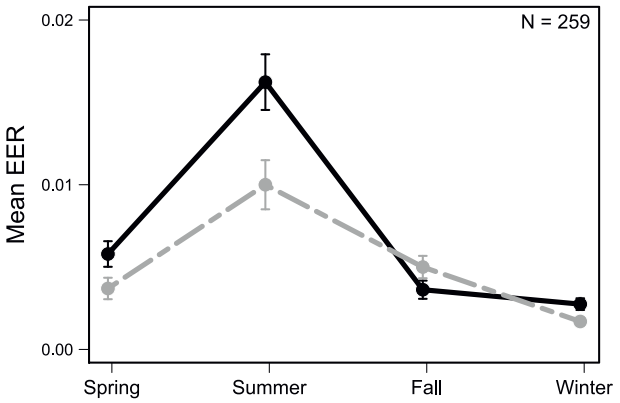

Fig. 5. Seasonal patterns in mean edge growth rate (EER; cells per edge cell d^{-1}) for enriched (solid black line) and ambient (gray dashed line) quadrants over the 2-year observation period. Error bars represent standard error (SE).

Edge growth habit analysis identified a total of 586 examples of edge expansion. In 2.7% of these cases, gains greater than one cell from the edge were recorded. This happened 3 times more often in enriched (n = 12) than ambient (n = 4) quadrants; however, because neighboring cell densities were not quantified prior to edge advancement, these data were removed from our edge density analysis. Among the 264 ambient and 306 enriched instances of single-cell expansion, neighboring ramet abundance varied from 1 to 152 vegetative shoots (equating to 3 and 475 shoots m^{-2}). Fertilization resulted in a significant 12% increase in neighboring ramet density preceding lateral growth ($F_{1, 568} = 7.548$, p = 0.006), representing a shift in ramification toward a more phalanx-like pattern of advance.

3.4. Seedling recruitment

Experimental patches varied in vegetative shoot abundance from 44 to 2444 (748.1 ± 556.1) shoots per patch over the course of the experiment with nearly all patches exhibiting seasonal oscillation amid net-positive inter-annual growth. Generative shoot abundance was equally variable, 0 to 473 (167.6 ± 146.9) per patch, with increasing floral abundance and R:V across the observation period. Successive Pearson and Spearman correlations between patch-level floral abundance and RSR seasonal anomalies provided a crude estimate of seedling

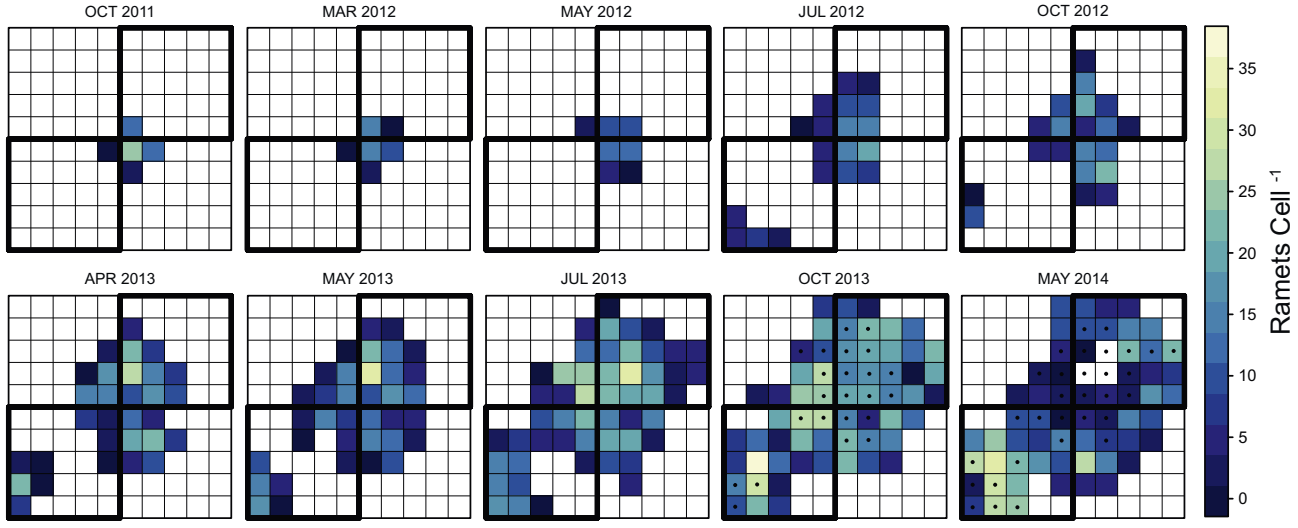

Fig. 4. Heat map of radial growth for a selected patch during the 2-year experiment. Color intensity corresponds to cellular ramet densities. Nutrient enriched quadrants are highlighted with thick black borders. Black circles denote cells where *M. edulis* individuals were noted at the sediment-water interface, as juveniles in October of 2013 and later as adults in May of 2014.

recruitment (Fig. 6). Of the 8 time periods we examined, spanning > 1.5 years post-flowering, we found significant evidence of seedling contribution during the second summer only, that is, between May and July of the year following seed dispersal. The relationship between flowering magnitude and RSR at the patch level was relatively strong, with a Pearson correlation coefficient of 0.90 ($p = 0.039$). This supports previous genetic work that showed germinants readily compete with established genets at this site (Furman et al., 2015).

Intriguingly, both Pearson and Spearman correlation tests identified a significant, albeit small, reduction in per capita ramification during the first winter following flowering (Pearson: $r = -0.59$, $p = 0.022$; Spearman: $r = -0.65$, $p = 0.008$). Given that genets begin flowering in their second spring (Granger et al., 2003), RSR reductions in the winter reflect a two-year lifespan for a portion of vegetative growth associated with a flowering IPU. Two-year longevity of *Z. marina* shoots was first proposed by Pedersen in 1913, and later reviewed by Duarte et al. (1994). Alternatively, this signal might represent the shunting of resources away from younger IPU members (Olesen, 1999), resulting in their loss, or an overall reduction in branching rates for sexually active IPUs.

3.5. Reproductive effort

A total of 985 flower-containing cells were censused during the course of the experiment (ambient: 448, enriched: 537). Conventional R:V ratios incorporate vegetative information collected only at the time of flowering. For comparison, our cell-level data, calculated in this way, varied from 0 to 0.72 with an overall mean of 0.23 ± 0.20. Annual means were 0.13 ± 0.18, 0.14 ± 0.11 and 0.37 ± 0.20 for 2012, 2013 and 2014, respectively. However, because our assessments were made at comparatively small spatial scales, encroachment of flowering ramets from adjacent cells could not be ignored; indeed, 7 to 16% of flower-bearing cells were unoccupied during the previous October, indicating that cross-cell transfer of flowers was a measurable component of cellular R:V. Furthermore, the magnitude of correlation between reproductive and vegetative shoot abundance was consistently higher for October than for any other time period, regardless of whether the target cell or an 8-cell neighborhood was used. Despite diagnostic evidence that our revised R:V metric more accurately depicted cell-level dynamics, no significant response to fertilization was found in either the interactive model ($F_{1,971} = 0.1101$, $p = 0.740$) or a one-way model with nutrient condition as a fixed factor ($F_{1,975} = 0.0232$, $p = 0.879$). Similarly, no effect on the probability that grass-containing cells would flower [$df = 1/1352$, deviance $= 1.1729$, $p(\chi^2) = 0.279$] or on the proportion of flowering cells per quadrant [$F_{1,96} = 0.2597$, $p(>F) = 0.612$] was observed.

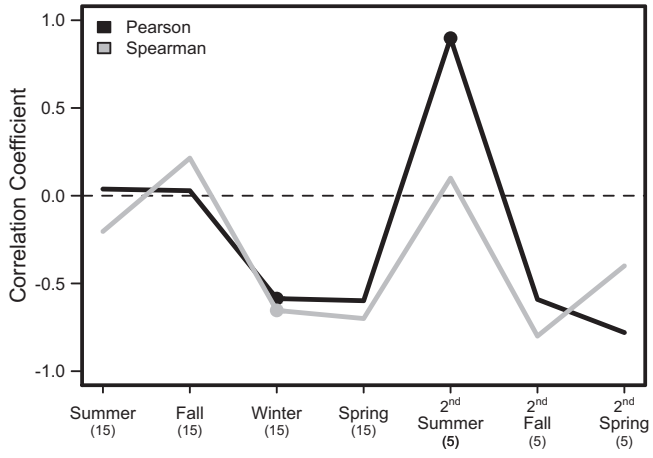

Fig. 6. Temporal patterns in Pearson (solid black line) and Spearman (solid gray line) correlation coefficients obtained between the magnitude of floral abundance (flowers per patch) and patch-level, seasonal RSR anomalies for successive seasons following flowering. Filled circles denote a statistically significant relationship. Parenthetical values on the abscissa represent the number of observation per test.

4. Discussion

Within the scope of phenotypic plasticity lies the potential for resource foraging by clonal plant modules ranging from the roots and rhizomes of single ramets to the emergent architecture of competing genets. In this study, we provide experimental evidence for the existence of edaphic resource foraging by *Z. marina* patches. Differential ramet proliferation along patch margins led to accelerated growth within resource-rich zones, with patch edges advancing in a phalanx-like manner. Meanwhile, within patches, no detectable differences in per capita branching rates or reproductive effort were observed. Elicitation of patch-scale foraging by experimental nutrient addition occurred while under otherwise natural growth and competitive conditions, making the 2-year experiment a realistic demonstration of foraging potential, and a logical first step toward understanding its role in space acquisition by *Z. marina*.

Marine and terrestrial studies on clonal plant demography have reported that ramet emergence rates are often matched by density-dependent mortality along resource gradients or following nutrient enrichment (Cook, 1985). Investigators have cited competitive stress brought on by above- and belowground crowding, as well as strategic ramet senescence as potential causes for resource-mediated mortality (Duarte et al., 2006; Duarte and Sand-Jensen, 1990; Herbert and Fourqurean, 2009). Our data support this view, as no cell-level changes in RSR were found. Instead, ramet demography appears to have become de-coupled only at patch margins, where crowding effects were minimized. Because individual ramets were not marked during this study, no direct measurement of ramet turnover could be made; however, we posit that ramet birth rates may have been uniform within patch quadrants. If true, nutrient amendment would have altered shoot age distributions (Herbert and Fourqurean, 2009), driving median age downward and increasing the amount of dead belowground biomass, ultimately affecting patch-level attributes such as reproductive potential, carbon sequestration and sediment stabilization.

The study of clonal foraging has built upon four decades of terrestrial work on root proliferation (de Kroon and Mommer, 2006) and recognizes similar distinctions between (1) biomass allocation responses, where structural components of individual ramets are modified (Birch and Hutchings, 1994), (2) selective ramet placement, where elements of clonal architecture control ramet location (Ikegami et al., 2007), and (3) ramet proliferation, where branching probability becomes differential to resource availability (Sutherland and Stillman, 1988). Of these, only the second element meets the strictest definition of clonal foraging. However, a lack of sufficient plasticity, interaction among the three elements, and the countervailing effects of clonal integration and physiological plasticity bring into question its prevalence in natural systems (Birch and Hutchings, 1994; de Kroon and Hutchings, 1995; Humphrey and Pyke, 1997; Sutherland and Stillman, 1988). For example, ramet spacer lengths have been found to be relatively insensitive to nutrient condition (Birch and Hutchings, 1994) and manipulative studies of terrestrial species report greater responses of branching frequency relative to internode length or branching angle (Sutherland and Stillman, 1988). Nevertheless, modeling studies notionally support the idea of selective ramet placement, particularly for resource patches greater than 5 times mean internode length (Sutherland and Stillman, 1988) and those persistent enough for successive ramet generations to curtail directional inertia imposed by monopodial growth (Oborny and Englert, 2012).

For *Z. marina*, ramets tend to be separated by rhizome lengths of 5 cm (Sintes et al., 2006), equating to an optimal resource grain of no less than 25 cm. In the present study, nutrient patches were 100 cm (diagonally, 141 cm), providing ample space for architectural modification to operate, while the 2-year observation period should have allowed for

between 6 and 24 branching events per baseline genet (Greve et al., 2005; Harrison, 1993). Resolving the influence of selective ramet placement and opportunistic ramet proliferation, however, requires physical examination of the rhizome architecture, which was prohibited by mussel recruitment in the last months of the experiment. Even with this information the two processes are often confounded, as adjustments to spacer length or angle also result in a concentration of rhizome buds, thereby increasing branching potential (Oborny and Englert, 2012). We can, however, assert that selective ramet placement, if it did occur by means of architectural adjustment, did not impede patch expansion, as it was higher for enriched margins.

Annually, the effect of nutrient addition resulted in different seasonal patterns of patch elongation, with fertilized edges exhibiting a biphasic response, growing vigorously spring through summer, while ambient edges followed a more broader unimodal pattern. Seasonal effects on shoot length, biomass and density are all well understood for temperate seagrasses, with *Z. marina* increasing in all three measures upon onset of vernal growth (Duarte et al., 1994; Guidetti et al., 2002; Olesen, 1999). Asexual recruitment of an annual cohort continues through late summer (Duarte and Sand-Jensen, 1990; Poumian-Tapia and Ibarra-Obando, 1999), during which time ramet populations experience their highest mortality rates (Olesen, 1999), due to heat stress and the resultant carbon imbalance (Jarvis et al., 2014; Zharova et al., 2001). These effects are mitigated by rhizome storage of nonstructural carbohydrates, typically taking the form of sucrose (Burke et al., 1996; Vermaat, 2009). Reserves have been shown to provide roughly 3–4 weeks of foliar support under adverse growing conditions and appear to be accumulated primarily during the spring (Burke et al., 1996). The shift in patch growth phenology, then, could alter the magnitude and mobilization of carbohydrate reserves with important downstream impacts on heat and shade tolerance. For example, if ramet proliferation draws resources away from typical storage patterns then the reduced fall growth rates we observed could have been the result of insufficient buffering capacity. If so, this might expose ramet populations to greater seasonal losses during anomalously harsh years. Concomitant monitoring of rhizome carbohydrate patterns along active growth margins, therefore, represents a valuable research objective, with implications for patch stability during the critical colonization phase.

At the landscape level, the foraging response we observed could allow developing *Z. marina* patches to exploit sediment nutrient signals generated by seagrass-associated fauna, including tube-building amphipods (e.g., *Ampelisca* spp. and *Corophium* spp.) or polychaetes (e.g., *Clymenella* spp.), as well as larger bivalves such as *Mercenaria mercenaria*. Because these species commonly occur among seagrass patches, but are not obligate seagrass residents (Bostrom et al., 2006), their nutrient footprints might generate resource-rich conduits for seagrass expansion. This could potentially speed patch coalescence, providing faster access to the disturbance protection conferred by greater patch size (Olesen and Sand-Jensen, 1994), jointly adding to meadow coverage and stability during periods of colonization. Over time, differential rates of lateral spreading might also reveal landscape patterns in edaphic condition, such as nutrient heterogeneity left by perished seagrasses, exposed glacial peat deposits or subtidal groundwater outflows.

Surprisingly, fertilization did not enhance flowering rates, regardless of the scale of observation. We know from previous work conducted at this site (Jackson et al., in review) that nutrient addition can have significant effects on the pace of floral development, the size of generative shoots, and the number of seeds per inflorescence. Vegetative proliferation within nutrient hot spots could therefore still have broad indirect effects on reproductive performance. Increasing overall ramet abundance, decreasing ramet age and reducing inter-patch distances would all enhance reproductive potential and success within developing meadows, providing vital dispersal capability and seed bank density at precisely the time of greatest space availability (i.e., during the establishment phase; Greve et al., 2005; Lee et al., 2007).

In conclusion, we found that pulsed delivery of mineral resources to the active growing margin of *Z. marina* patches resulted in vegetative growth and accelerated patch expansion. Incremental edge advances were characterized by significantly greater ramet numbers, indicating that a ramet proliferation, selective ramet placement or a combination of the two responses had occurred. The seasonality of this effect was consistent among experiment years and suggestive of a fundamental shift in the growth pattern and phenology of seagrass edges exposed to nutrient enhancement. Direct effects on reproductive intensity were not recorded; however, patch-level foraging may function indirectly in sexual performance at the meadow scale. This study establishes, for the first time, the role of foraging behavior in the space acquisition strategies of *Z. marina*, providing vital information regarding vegetative growth patterns during the poorly understood colonization period.

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