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Patch Distribution and Within-Patch Dynamics of the Seagrass *Zostera noltii* Hornem. in Los Toruños Salt-Marsh, Cádiz Bay, Natural Park, Spain[1]

Fernando G. Brun*, J. Lucas Pérez-Lloréns, Ignacio Hernández and Juan J. Vergara

Area de Ecología, Facultad de Ciencias del Mar y Ambientales, Universidad de Cádiz, 11510 Puerto Real, Cádiz, Spain, e-mail: fernando.brun@uca.es

* Corresponding author

Patch distribution and small-scale (*i.e.*, within-patch) temporal variability in plant morphology, biomass, shoot density, tissue nutrient content and growth were studied in the intertidal seagrass *Zostera noltii* at Los Toruños salt-marsh (Cádiz, Spain). The area covered by *Z. noltii* was 7.3 %, and decreased exponentially with depth. The lack of recruitment from seedlings largely explained the normal patch size distribution observed. Overall, lower biomass, shoot density, above-ground to below-ground biomass ratios and higher leaf elongation rates were recorded at the patch edge, where biomass dynamics were primarily controlled by recruitment and mortality processes. In contrast, temporal variation in above-ground biomass in the patch centre depended largely on changes in shoot leaf number and size. There was no correlation between total biomass and shoot density in the patch centre suggesting that below-ground biomass may be space-limited. Low above-ground biomass and shoot elongation rates were recorded in May, regardless of position within the patch, and were coincident with the abundance of *Ulva* sp. mats. Light reduction by *Ulva* canopies also resulted in a mobilization of carbohydrate reserves. Such resource reallocation may represent an important short-term survival strategy, maintaining leaf and rhizome elongation capacity.

Keywords: biomass; elongation rate; light; phenotypic plasticity; primary production; seagrass dynamics.

Introduction

Seagrass meadows are among the richest and most productive ecosystems (McRoy and Helfferich 1977, Duarte and Chiscano 1999, Mann 2000); they are both ecologically and economically important (Costanza *et al.* 1997). Until the late 1960s, *Zostera noltii* Hornem. meadows were widespread at intertidal and subtidal locations of Cádiz Bay (Seoane 1965). From the early 1970s onwards, there was a sharp reduction in subtidal seagrass cover coincident with coastal development, increased eutrophication and the invasion of the rhizophyte *Caulerpa prolifera* (Forsskäl) J.V. Lamouroux. At present, *Z. noltii* is restricted almost exclusively to scattered intertidal populations. These populations are increasingly affected by mat-forming ephemeral macroalgae (mainly *Enteromorpha* sp. and *Ulva* sp.) (den Hartog 1994, Vergara *et al.* 1998) and anthropogenic disturbances (e.g., hand-raking and shellfishing). Presence and size of the seagrass meadows is a balance between two demographic processes: mortality (natural or man-induced) and recruitment. Mortality often occurs rapidly (days to months), while the temporal scale for recruitment is more variable. Recruitment can be relatively fast (via seedlings, 1–2 growing seasons) or may take several years through vegetative spreading. Seedlings have never been observed in the *Z. noltii* populations in southwestern Europe (Laugier *et al.* 1999, Peralta *et al.* 2000), thus colonization and expansion of these patches may be a relatively slow process.

Much effort has been allocated to record cover (or biomass), production, demography and patch distribution and dynamics of seagrass meadows (Duarte 1999 and references therein). In general, such studies consider seagrass beds as rather homogeneous structures. However, the clonal nature of plants itself confers a high degree of intrinsic heterogeneity to the seagrass patches. In fact, as patches spread out, they become increasingly heterogeneous with a gradient from young colonizing shoots at the border to older shoots at the patch origin (Duarte and Sand-Jensen 1990a). Studies of small-spatial scale variability (*i.e.*, within the patch) in different seagrass properties are rather limited (Brouns 1987, Duarte and Sand-Jensen 1990a,b, Olesen and Sand-Jensen 1994, Nakaoka and Aioi 1999, Nakaoka and Izumi 2000), and as far as we know, they rarely include dynamics (*i.e.*, do not include time as an additional source of variability). The knowledge gained by these studies goes further than the basic information they provide on the functioning

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of the seagrass ecosystem. Such information is very useful for the understanding of seagrass responses to natural and/or human disturbances, which is a requirement for effective management (*i.e.*, conservation and restoration) of these habitats (Short and Wylie-Echevarria 1996).

The objectives of this study were (i) to examine the present condition of the *Zostera noltii* beds in Los Toruños salt-marsh by recording the coverage and distribution of patches, and (ii) to examine within-patch temporal variation of biomass, shoot density, plant morphology, tissue nutrients and growth.

Material and Methods

Sampling site

Zostera noltii grows as scattered patches along the mudflats of Los Toruños salt-marsh (Cádiz Bay Natural Park, 36 °30'N 06 °10'W) at mean depths between 1 and 1.5 m (relative to mean high water level). The tide is semidiurnal with a mean range of 2.5 m, but larger, unpredictable fluctuations in water level are caused by wind. Mean water temperature varied from 12 °C in winter to 25 °C in summer (data from the Meteorological Center of Andalucía Occidental, 10 km from study site). Mean nutrient concentrations in the water column throughout the year were: 0.79 μM nitrate, 16.00 μM ammonium, 0.54 μM phosphate, with sporadic pulses of nitrate and ammonium in winter (*ca.* 8 μM and 42 μM, respectively) (Tovar *et al.* 2000). The attenuation coefficient in the water column at the site fluctuates between 1.5 and 3.5 m^{-1} (Brun 1999).

Patch distribution

Following a preliminary survey, three zones (a, b and c), where the majority of patches occurred, were selected for sampling. Depth, size and number of *Z. noltii* patches were recorded for each zone. The area of each patch (m^2) was estimated from an ellipsoidal equation by measuring the longest and shortest axes. Patch asymmetry index (ratio between longest and shortest axes) was also determined as an estimate of the deviation from the circular shape. Patch size-frequency distributions were constructed for each sampling zone. In addition, the size-frequency distribution of the whole surveyed area (a+b+c = 11,200 m^2) was used to construct a Pareto's cumulative function (Kotz and Johnson 1985) as previously applied in studies on seagrass patch dynamics (Vidondo *et al.* 1997).

A patch radius increase of 0.350 m $year^{-1}$ (derived from rhizome elongation rate for *Z. noltii*, see Results) was used to estimate the age of the patches according to the following relationship

$$\text{patch age (y)} = \frac{\text{patch radius (m)}}{0.350\ (\text{m y}^{-1})} \qquad (1)$$

This estimate will be qualified as either a maximum or minimum estimation of patch age.

Within-patch temporal variation of biomass, shoot density, tissue nutrient content and growth

One of the largest *Z. noltii* patches (143 m^2), with little human disturbance, was selected as a permanent sampling station. Sampling was carried out in August and November 1998 and February and May 1999. On each occasion, four samples were collected haphazardly with a stainless steel frame (20 × 20 cm) from two different positions within the patch, (1) the centre of the *Z. noltii* patch, and (2) the edge of the patch adjoining the unvegetated mudflat. The patch edge was defined as the area within 20 cm from the margin. All *Z. noltii* material in the frame was dug out and rinsed carefully to maintain the physical integrity between modules. Plants were immediately transported to the laboratory for further rinsing with seawater in a 1.5-mm mesh sieve to remove remaining sediment and other debris. Throughout most of the study period, leaves were relatively free of epiphytes; occasionally, organisms were easily removed with fingernails. All shoots (*i.e.*, cluster of leaves supported by a single basal meristem) as well as plants (*i.e.*, single ramets or/and ramets connected by a rhizome axis) were counted. The presence of flowering shoots was also recorded. Vegetative shoots were sorted into three different groups: apical (those showing apical dominance), single small (*i.e.*, short shoots stemming from an older or completely decomposed rhizome system) and lateral (shoots arising from the axils of the rhizomatic leaves; den Hartog 1970). Further architectural or morphometric characteristics were also noted (leaves per shoot, leaf dimensions, number and length of the rhizome internodes and branching pattern). Leaf area index was determined by multiplying mean surface area of shoots (one face only) by shoot density. Subsequently, samples were separated into below-ground (rhizome and roots) and above-ground parts, and oven-dried (60 °C) to a constant weight to determine the dry weight of each fraction. Subsamples of all fractions were powdered and stored for nutrient content analysis. Tissue C and N were determined using a Perkin-Elmer 240 CNH elemental analyzer. Total P was analyzed by acid digestion (Sommer and Nelson 1972). Non-structural carbohydrates (sucrose and starch) were determined following Alcoverro *et al.* (1999).

In addition to biomass sampling, 20–25 shoots from the patch edge and from the centre were marked for growth estimations according to Zieman (1974) as modified by Peralta *et al.* (2000). Rhizome elongation in apical shoots was measured by marking (using a plastic fibre of 45 μm diameter) the sheath of the oldest leaf adjacent to the apex. Marked plants were carefully retrieved after 14 days. After collection, the following seagrass properties were noted: number of leaves per shoot, leaf and rhizome lengths, appearance of new leaves and rhizome internodes, length of the new portion of leaves and rhizomes grown during the marking period, and leaf losses (whole leaves and/or apical parts). To allow production estimates, FW/DW and DW/length relationships were determined for leaves and rhizomes of the marked plants. The leaf plastochrone interval was estimated according to Patriquin (1973).

Above-ground production (g DW m^{-2} d^{-1}) was calculated as the product of the leaf elongation rate (cm $shoot^{-1}$ d^{-1}), DW/length ratio and density (shoots m^{-2}) of the different shoot types. Above-ground losses (g DW m^{-2} d^{-1}) were estimated by multiplying the average above-ground losses (cm $shoot^{-1}$ d^{-1}) by DW/length ratio and density (shoots m^{-2}) of each shoot type. Rhizome production (g DW m^{-2} d^{-1}) was calculated as the product of the average rhizome elongation rate of the main and secondary axis (cm $apex^{-1}$ d^{-1}), the percentage of tagged rhizomes that grew during the marking period, DW/length ratio and density of apical shoots (shoots m^{-2}).

Statistics

Size-frequency distributions of patches were tested for normality using Shapiro-Wilk test. Statistical analyses were conducted using the STATISTICA© computing programme. Since there was pseudoreplication at the patch level, no statistical tests were applied for shoot density and biomass data within a patch. Therefore, only descriptive statistics are given.

Results

Patch distribution

A total area of 11,200 m^2 was surveyed. Zones a and b, with smoother slopes, exhibited the highest cover, mean patch size and number of patches (Table I). Overall, *Zostera noltii* occupied 812 m^2 (7.3 % of the total area surveyed). Cover decreased exponentially with depth ($r^2 = 0.98$), with 50 % of patches occurring between 1.2 and 1.4 m depth (Fig. 1). Shoot density also decreased with increasing depth (Brun personal observations). Patch size was normally distributed at the three sampling zones, but differences in `shape´ parameters (skewness and kurtosis) were observed among zones (Table I, Fig. 2). In zones a and b, 75 % of the patches were smaller than 33 m^2, whereas in zone c the upper quartile was 2.7 m^2. Patch asymmetry index increased with increasing patch size ($r = 0.63$; $p < 0.001$), with the larger axis of the ellipsoidal patches usually oriented parallel to the shoreline (personal observation).

Table I. *Zostera noltii*. Surface occupied by patches, mean patch size and number of patches recorded at three sampling stations (zones a, b and c) at Los Toruños salt-marsh.

	Zone a	Zone b	Zone c	Total
Total area surveyed (m^2)	3200	3500	4500	11200
Area covered by *Zostera noltii* (m^2) (%)	275 (8.6)	505 (14.4)	32 (0.7)	812 (7.3)
Number of patches	30	26	15	71
Mean patch size ± SE (m^2)	10.2±5.2	19.4±11.7	2.2±1.3	12.1±5.1
Skewness	−0.13	0.38	−0.17	−0.07
Kurtosis	−0.60	−0.34	−1.04	−0.32
Mean shore slope (%) [range]; N = 9	1.0 [0.50−1.50]	1.7 [0.75−2.75]	4.8 [2.50−5.40]	–
Mean depth ± SE (m); N = 9	1.26±0.03	1.32±0.02	1.54±0.05	–

Data on mean shore slope and depth, as well as "shape" parameters of the size-frequency distribution of patches (skewness and kurtosis) are also included.

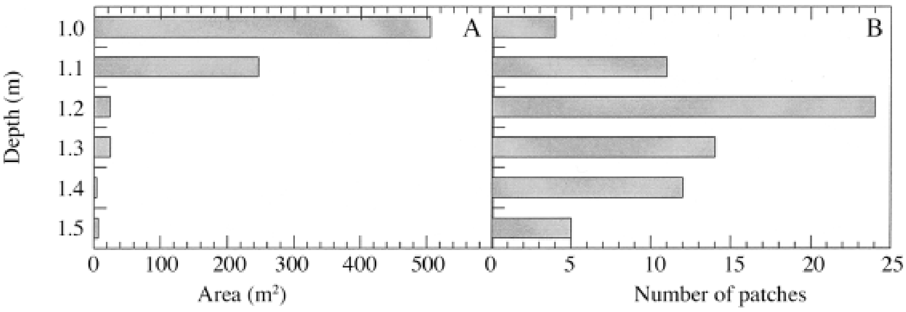

Fig. 1. *Zostera noltii*. Area covered (A) and number of patches (B) occurring at Los Toruños salt-marsh at different depths. Depth is referred to the mean high water level (MHWL). The number of patches sampled was 71 (more information in Table I).

The patch size distribution (for the whole area surveyed), represented as a cumulative function of the Pareto distribution, shows two inflexion points at sizes about 0.20 m^2 and 65 m^2 indicating the existence of three different domains of scale (Fig. 3). Therefore, patches smaller than 0.20 m^2 and those larger than 65 m^2 showed, respectively, lower and higher abundance than expected for entirely self-similar size ranges. We estimated the age of patches (equation 1) by an approach analogous to that used by Duarte and Sand-Jensen (1990a). The patch age-classes (cohorts) conformed well with the measured patch sizes (Fig. 3). The first cohort (0–1 age class) corresponds to those sizes smaller than 0.2 m^2 (the first inflexion point, or the first domain in Figure 3), cohorts 1–2 to 7–8 age class can be also recognized as more or less marked discontinuities (second domain), whereas cohorts > 8 age class are not easily identified (third domain) probably due to a coalescence of neighbouring patches.

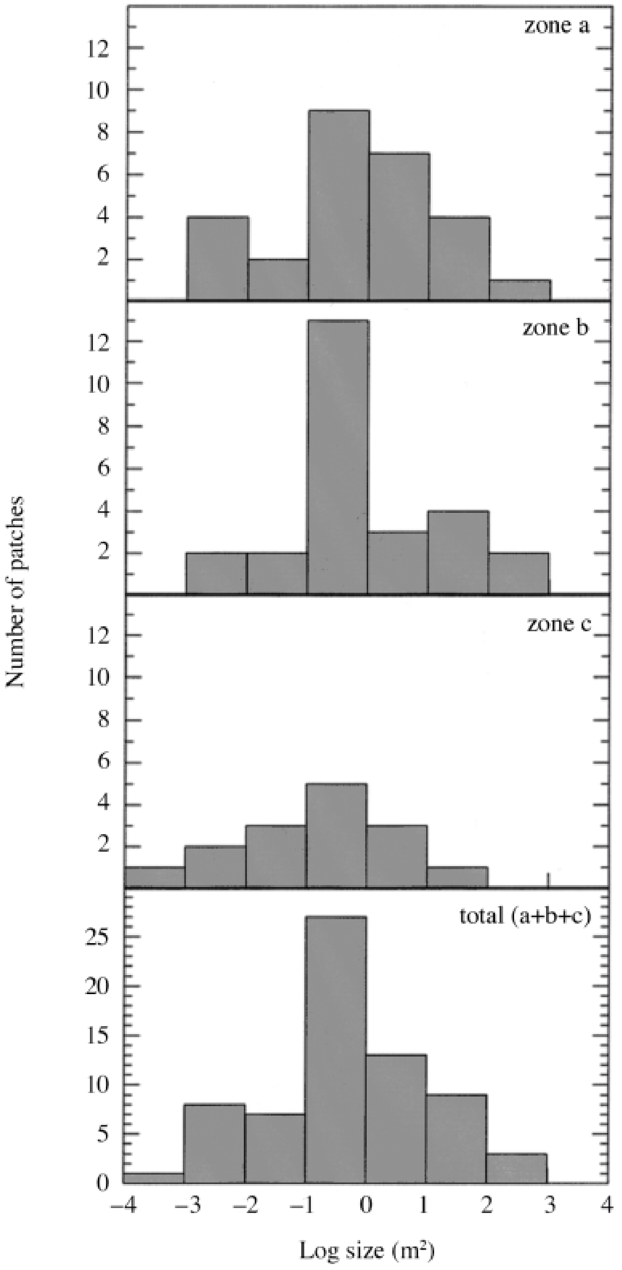

Fig. 2. *Zostera noltii*. Logarithmic size distribution of patches at three sampling zones and at the whole area (zones a, b and c).

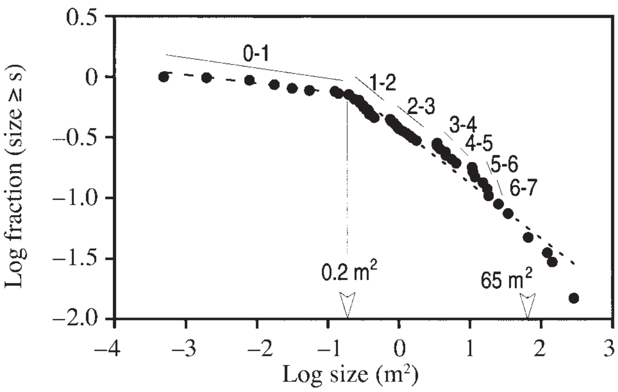

Fig. 3. *Zostera noltii*. Size distribution of patches in the sampled area at Los Toruños salt-marsh (zones a, b and c) represented as cumulative function of the Pareto distribution. Y-axis represents the probability that the size of a patch taken at random (size) will be equal or greater than any given size value (s). Detailed information is given in Kotz and Johnson (1985) and Vidondo *et al.* (1997). Inset numbers show different age classes (y). Arrows show different domains of scale (see Results).

Within-patch temporal variation of biomass and shoot density

At the patch periphery, shoot biomass and leaf area index reached maxima in August 1998 (84.8 g DW m^{-2} and 3.0 m^2 m^{-2}, respectively) and minima in May 1999 (7.03 g DW m^{-2} and 0.2 m^2 m^{-2}, respectively) (Fig. 4A). Similar to the shoot biomass, density peaked in August (9,375 shoots m^{-2}), but no other temporal differences were noted (Fig. 4B). At the patch centre, above-ground biomass, leaf area index and density were much higher than those recorded at the periphery (Fig. 4D). Biomass and leaf area index peaked also in August (215.0 g DW m^{-2} and 7.60 m^2 m^{-2}, respectively), while no temporal differences were detected in density (Fig. 4E).

At the patch edge, single small shoots represented 43 % (August) and 75 % (May) of the total shoot density, but only 4.4 % in February (Fig. 4C). Apical shoots varied between 23 % (May) and 54 % (February). The proportion of lateral shoots was fairly constant (30–40 %), except in May (2 %). By contrast, at the patch centre the relative abundance of the single small shoots was high throughout the year, peaking in February (86.5 %) (Fig. 4F). Apical shoots ranged from 38.6 % (in May) to 7.7 % (in February), whereas lateral shoots varied from 27.4 % (in August) to 5.7 % (in February). Some generative shoots ap-

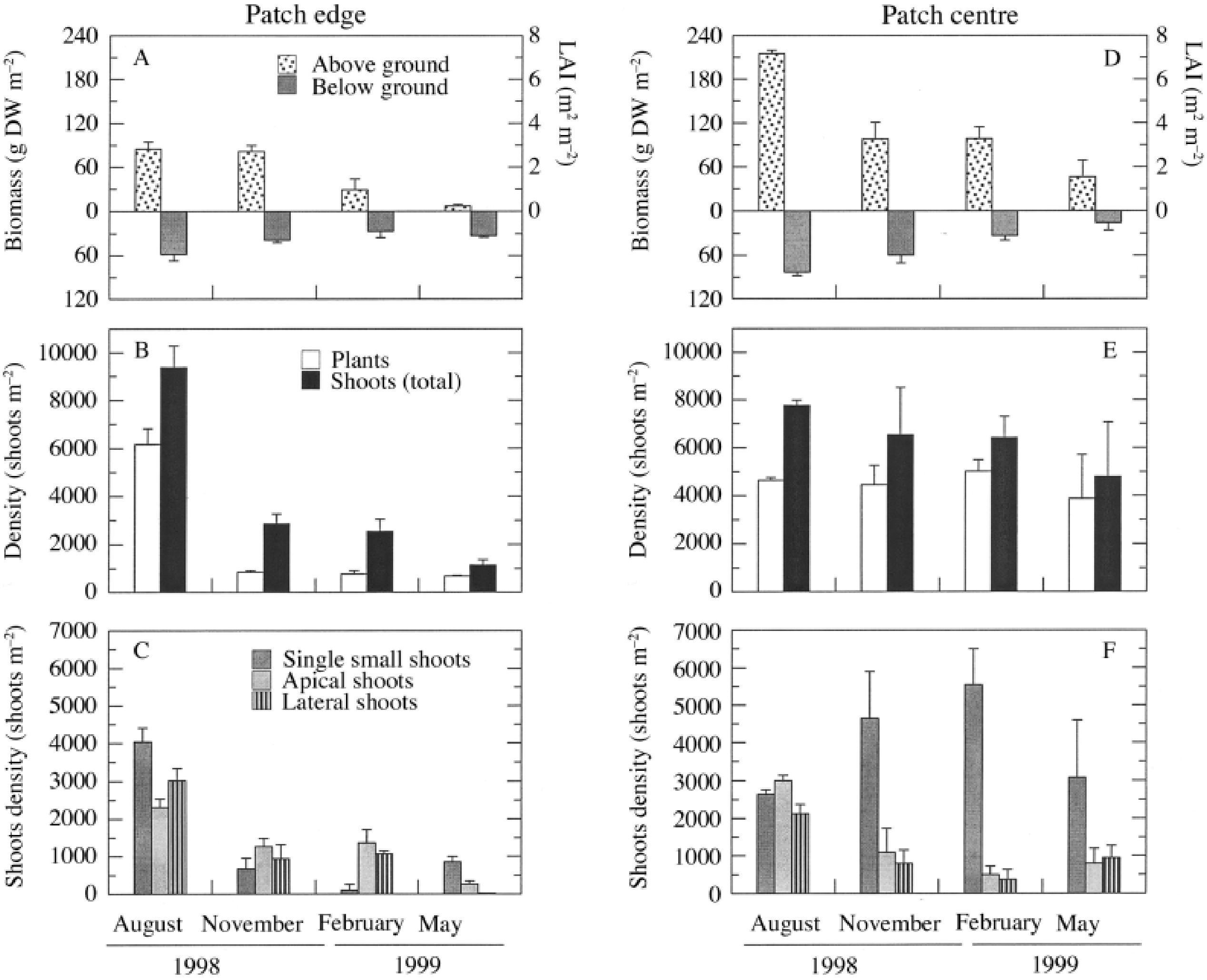

Fig. 4. *Zostera noltii*. Temporal variation in biomass (A, D), density (B, E) and shoot types (C, F) at two different positions (edge and centre) within an intertidal patch. Values are means of two replicates and bars represent SD.

Table II. *Zostera noltii*. Temporal and within-patch variation in morphometric features.

	August 1998	November 1998	February 1999	May 1999
Patch edge				
Leaf length (cm) [range]	7.9 [3.9–10.9]	13.9 [4.2–20.7]	9.3 [0.4–17.5]	7.9 [1.7–13.3]
Leaves per shoot (SE)	4.8 (0.1)	3.8 (0.2)	4.5 (0.5)	4.8 (0.2)
Rhizome internode length (cm) [SE]	1.9 [0.59]	2.3 [0.3]	1.5 [0.4]	1.2 [0.3]
Internodes per rhizome axis (SE)	11.5 (0.6)	4.7 (0.3)	3.1 (0.3)	5.9 (0.5)
Rhizome branching degree (range)	0.65–0.83	0.33–0.55	0–0.10	0.33–0.58
Patch centre				
Leaf length (cm) [range]	8.2 [2.7–10.9]	14.7 [6.6–18.9]	14.1 [3.4–22.1]	9.4 [2.8–13.9]
Leaves per shoot (SE)	3.5 (0.5)	2.8 (0.2)	3.4 (0.3)	3.6 (0.5)
Internodes per rhizome axis (SE)	9.7 (0.6)	4.3 (0.5)	2.6 (0.4)	4.4 (0.4)
Rhizome branching degree (range)	0.56–0.75	0.25–0.30	0	0.10–0.18

The rhizome branching degree was calculated as number of branches/number of nodes.

peared in May, peaked in August (300 shoots m^{-2}), and disappeared in February. The average percentage of generative shoots ranged between 0.4 % and 3.9 % of the total shoot density.

Below-ground biomass peaked in August (58.0 g DW m^{-2}, patch edge; 83.5 g DW m^{-2}, patch centre), with minima in February (26.0 g DW m^{-2}, patch edge) or in May (16.1 g DW m^{-2}, patch centre)

(Fig. 4A). It varied between 82 % (May) and 32 % (August) of the total plant biomass at the patch periphery, but it was nearly constant (25 %) over time at the patch centre. Above- and below- ground dynamics were closely tied to temporal rhizome development and branching pattern (Table II). Highly branched large rhizomes up to 12 internodes, with secondary, tertiary (unusual at the patch centre), even some quaternary axes (only at the patch periphery), all with short internodes (< 2 cm length), were found in August. The rhizome network fragmented at branching points from November onwards, with the main rhizome axis consisting of 3–5 internodes (up to 4 cm length each, at the patch periphery) or mostly single small shoots (at the patch centre). The breakdown process proceeded through February. At the patch periphery, mostly apical shoots with few connected rhizome internodes were found. New growth and branching of the overwintering rhizome segments were observed in May. Below-ground biomass and total plant biomass were positively related to shoot density, suggesting that space did not limit development of below-ground biomass at the patch edge. By contrast, at the patch centre the breakdown process resulted in a high proportion (*ca.* 90 %) of single small shoots (stemming from the senescing rhizome network). In May, the slight elongation of rhizomes (from the single small shoots) resulted in the development of short primary rhizome axes (2–4 internodes) bearing apical and lateral shoots. The elongation and branching of the rhizome network took place in August.

Within-patch temporal variation in tissue nutrient content and non-structural carbohydrates

Usually, shoots had higher nutrient content than below-ground parts (Fig. 5) and were above the critical levels given by Duarte (1990). Tissue N and P contents varied among times and sample sites. This was especially marked in May when plants were covered by overgrowing *Ulva* sp. mats. During this period, plants growing at the periphery showed higher N and P contents in above-ground structures. However, the

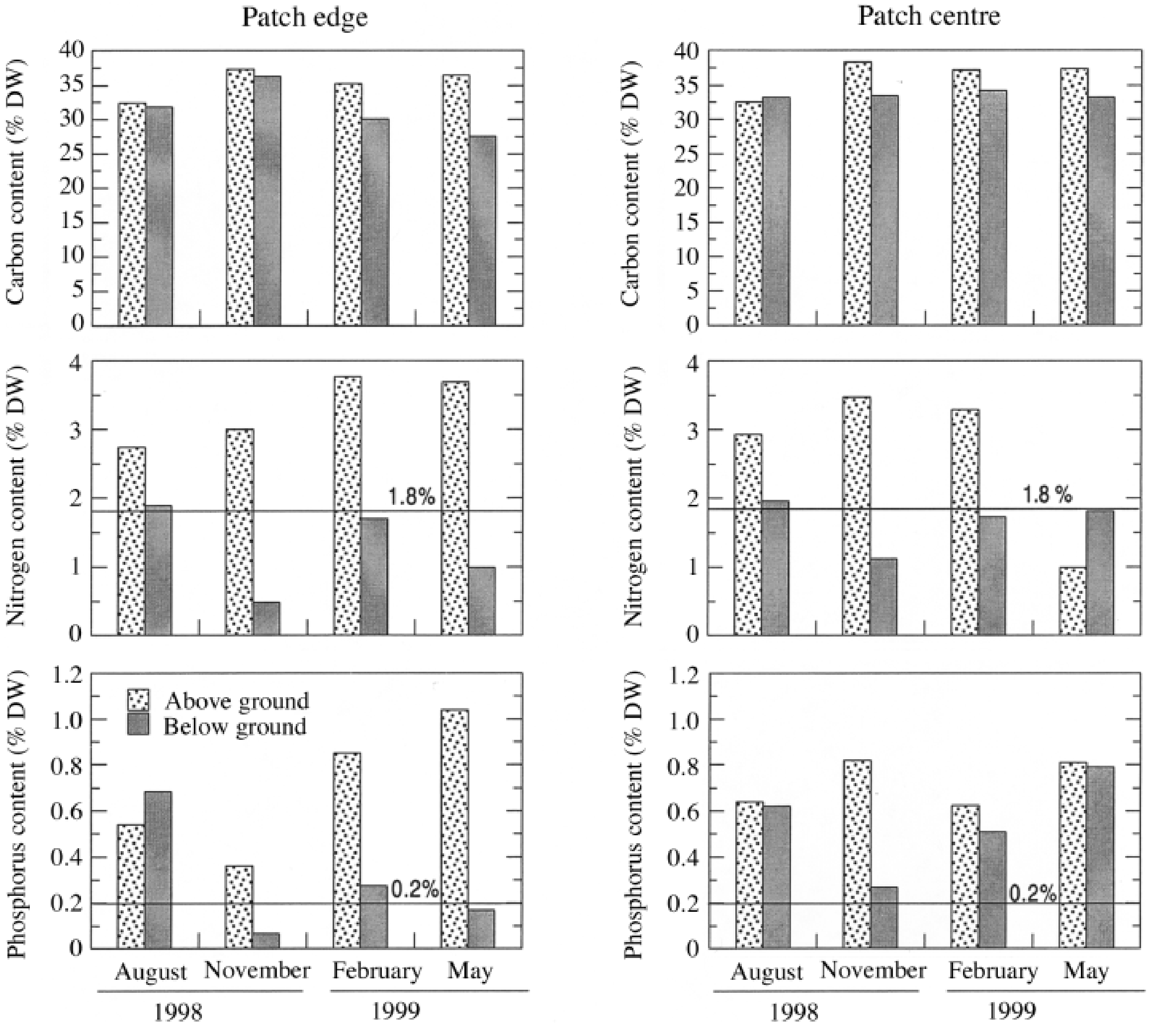

Fig. 5. *Zostera noltii*. Temporal variation in C, N and P contents at two different positions (edge and centre) within an intertidal patch. Horizontal line indicates those levels below which N and P may limit growth (Duarte 1990).

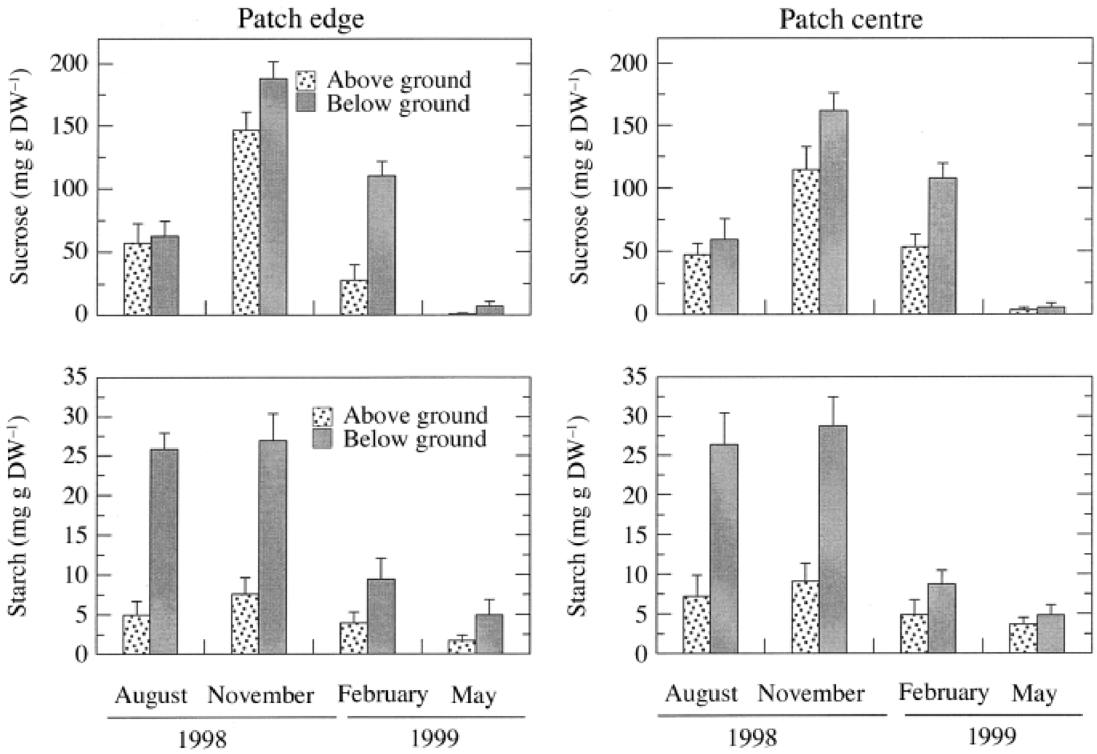

Fig. 6. *Zostera noltii*. Temporal variation in sucrose and starch content in above-ground and below-ground parts of intertidal plants located at different positions within the patch. Values are means of three replicates from pooled samples and bars represent SD.

nutrient quota in below-ground parts was lower than in plants thriving at the patch centre.

Below-ground parts had higher contents of sucrose and starch (temporal means 87.7 mg g DW^{-1} and 17.0 mg g DW^{-1}, respectively) than above-ground parts (56.4 mg g DW^{-1} and 5.4 mg g DW^{-1}) (Fig. 6). Similar temporal patterns were observed with high concentrations in November and low concentrations in May, regardless of compound or the plant location within the patch.

Within-patch temporal variation in leaf and rhizome elongation rates

Once plants were measured in the field and classified in the laboratory, we realized that most of the marked shoots at the patch edge were "apical" shoots while most of the marked shoots at the patch edge were "single small" shoots. Therefore, shoot category is confounded with patch position limiting the statistical analysis to descriptive statistics. In August, shoots from the patch edge showed high elongation and loss rates (2.5 cm d^{-1} and 1.7 cm d^{-1}, respectively) and short plastochrone interval (3 days) (Fig. 7A,C). Similar rates were observed in November, but with longer plastochrone interval (10 days). Throughout the study period (and especially in November and February), leaf gains overcame leaf losses, resulting in positive net growth. Shoots from central parts had lower elongation rates, higher loss rates (in November and February) and higher plastochrone interval than apical shoots, resulting in net losses during these months (Fig. 7B, C).

All main rhizomes exhibited net growth. Elongation rate of the main rhizome axes peaked in May (0.14 cm d^{-1}) with a minimum in November (0.09 cm d^{-1}) (Fig. 7 D). On an annual basis, and assuming no change in elongation rate between sampling periods, the elongation of the main rhizome was 35 ± 2.9 cm. The values recorded for secondary rhizome axes were always lower than those for the main rhizomes ($P <$ 0.05: $F_{1,66}=130.7$; one-way ANOVA). A maximum in August (0.05 cm d^{-1}) and a lack of growth in February were observed. The percentage of tagged rhizomes (secondary) that grew ranged from 0 % (February) to 50 % (August) with an annual value of 10.6 ± 1.68 cm.

Production estimates

Table III shows the seasonal and total annual above-ground and rhizome production, assuming that elongation rates and shoot density measured are somewhat representative for the entire seasons. These estimates account for the temporal variability in the proportion and growth rates of different shoot types and rhizomes. Shoot production ranged from 42 % (spring) to 72 % (winter) of the total plant production. Overall, above-ground parts supported 50 % of the annual production. On average, 73 % of the annual above-ground production was lost, with the high-

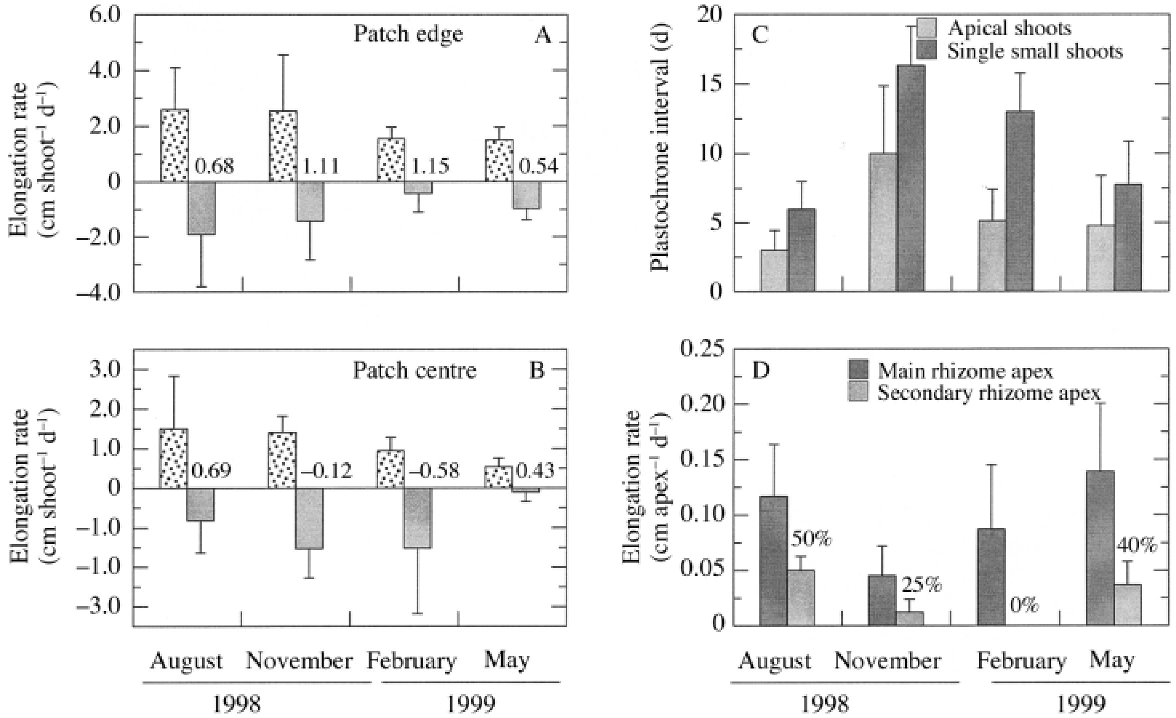

Fig. 7. *Zostera noltii*. Temporal variation in (A) leaf elongation rate of apical shoots, (B) leaf elongation rate of single small shoots, (C) plastochrone interval of apical and single small shoots, (d) rhizome elongation rate. In Figures A and B, negative values are losses and the inset numbers are net changes (*i.e.* elongation minus losses). Numbers at the inset in Figure D are the percentage of all tagged secondary rhizomes showing net growth. Values are means of 18–25 replicates and bars represent SD.

Table III. *Zostera noltii*. Seasonal variation in above-ground production, rhizome production and above-ground losses

	Summer	Autumn	Winter	Spring	Total annual (g DW m^{-2} y^{-1}) (g C m^{-2} y^{-1})	Over-estimation (%)
Above-ground production						
(g DW m^{-2} d^{-1})	8.1 (8.6)	5.4 (6.2)	2.1 (2.1)	2.7 (3.1)	1646 (1804)	9
(g C m^{-2} d^{-1})	2.5 (2.8)	2.0 (2.2)	0.8 (0.8)	1.0 (1.1)	569 (625)	9
Rhizome production						
(g DW m^{-2} d^{-1})	8.4 (12.0)	5.0 (5.2)	0.8 (1.9)	3.7 (5.6)	1611 (2221)	28
(g C m^{-2} d^{-1})	2.7 (3.9)	1.7 (1.8)	0.3 (0.3)	1.1 (1.7)	523 (715)	27
Above-ground losses						
(g DW m^{-2} d^{-1})	4.9	4.9	2.5	0.8	1193	
(g C m^{-2} d^{-1})	1.5	1.8	1.0	0.3	420	
Above-ground losses/production (%)	61	92	118	30	73	
Above-ground production/total production (%)	49	52	72	42	51	

Estimates were made considering the contribution and proportion of the different types of shoots (apical, lateral and single small) and rhizomes (main and secondary axes). These results were compared with those obtained when such premises were not considered (numbers in parentheses), *i.e.*, considering total density and apical shoot values of leaf and rhizome production.

est percentages noted in winter and autumn (118 % and 92 %, respectively).

Since apical shoots are in the bigger size-classes, and are more abundant at the patch edge, the probability of being selected unintentionally for marking is relatively high in field studies. If shoot and rhizome elongation rates (from apical plants) were used to estimate production (elongation rate × density), and the temporal variability in the density of different shoot types were not considered, we calculated that production was overestimated by about 9 % for above-ground parts and by about 28 % for rhizomes.

Discussion

Most of the *Zostera noltii* patches along Los Toruños salt-marsh are intertidal. The exponential decline in cover with increasing depth suggests a control by light (Zimmerman *et al.* 1991, Czerny and Dunton 1995, Lee and Dunton 1997, Peralta *et al.* 2002). Tidal and wind-driven currents often have a large impact on water turbidity and erosion in this shallow coastal system (Muñoz and Sánchez-Lamadrid 1994). Seagrasses may counteract turbidity to some extent by optimizing light absorption and photosynthetic performance over a broad range of light intensities (Hemminga and Duarte 2000). In addition, photosynthesis in *Z. noltii* proceeds under aerial exposure at low tide (Leuschner and Rees 1993, Pérez-Lloréns and Niell 1993b). In summer and/or during windy days, *Z. noltii* occurring at the highest intertidal locations suffers severe desiccation stress during low tide, resulting in die-off. This would partially explain the lack of patches between 0 and *ca.* 1 m depth (Fig. 1).

Since reconstructive techniques to estimate patch age (Duarte and Sand-Jensen 1990a,b, Pergent and Pergent-Martini 1990, Vidondo *et al.* 1997, Kamermans *et al.* 2001) cannot be used in *Z. noltii*, due to the lack of annual marks (e.g., leaf scars), our patch age estimations were based on annual increases in patch radius. Such an approach seems suitable since no significant misclassification errors in patch age were observed considering the variability in rhizome elongation rates.

No recruitment from seedlings was observed in the populations studied, therefore, patch formation and growth must depend on fragmentation of rhizome segments in existing patches (Ramage and Schiel 1999). Reproduction by fragmentation has been recorded in some fast growing coral species, avoiding high rates of larval and juvenile mortality (Highsmith 1982). This reduced recruitment from seedlings and the possible high mortality (natural or human-induced) of the vegetative fragments, would largely explain the normal patch size distribution recorded, which contrasts with the skewed distributions usually reported in other species or populations (Duarte and Sand-Jensen 1990a, Olesen and Sand-Jensen 1994, Vidondo *et al.* 1997, Ramage and Schiel 1999). Skewness is indicative of fast patch formation and high mortality rates (mostly seedlings) observed in seagrass populations depending largely on sexual reproduction (Duarte and Sand-Jensen 1990a). Recruitment in *Cymodocea nodosa* (Ucria) Ascherson populations occurs mainly through seedlings (Duarte and Sand-Jensen 1990a,b, Vidondo *et al.* 1997). Seedlings have never been observed in the *Z. noltii* populations in south-western Europe (Laugier *et al.* 1999, Peralta *et al.* 2000), thus patch recruitment must operate mainly via vegetative propagules from the standing populations. The loss of sexual reproduction is a trait that has been observed in several aquatic clonal plants that fix mutations that disable one or more of the many processes involved in sex (Barret *et al.* 1993, Eckert *et al.* 1999). How or when vegetative propagules become rooted and generate new patches is unknown, but our data suggests that it may be a rather inefficient process: if the total number of patches (22 patches) were to be recruited from propagules and more than 2.3×10^6 shoots were lost during the study period (multiplying total area and lost shoots), the efficiency of the recruitment process would be 1×10^{-5}. Studies or techniques involving molecular markers (*i.e.*, random amplified polymorphic DNA, allozymes, isoenzymes, etc.) as used for other seagrass species (Waycott 1995, Rachel 2002), would be desirable to enlighten this important trait in the biology of *Z. noltii*.

Patch mortality rate diminishes, and heterogeneity (*i.e.*, within patch variability) increases as patch growth proceeds (Duarte and Sand-Jensen 1990a). Structural integrity of small patches (*i.e.*, the first domain in Figure 3: 0–1 age class or < 0.20 m^2) depends mostly on environmental forcing (Duarte and Sand-Jensen 1990a). Several studies (Olesen and Sand-Jensen 1994, Duarte and Sand-Jensen 1990a,b) support the notion of a minimum patch size above which (*i.e.*, the second and third domains in Figure 3: sizes > 0.2 m^2) the probability of patch mortality decreases due to enhanced anchoring, mutual physical protection and physiological integration ("mutually sheltering structure", Thayer *et al.* 1984) among the shoots as patches grow. For *Zostera novazelandica* Setchell, this minimum patch size was 0.4 m^2 (Ramage and Schiel 1999).

Biomass and cover of *Z. noltii* in temperate latitudes usually display unimodal seasonal curves with a maximum in summer and a minimum in winter (Pérez-Lloréns and Niell 1993a, Auby and Labourg 1996, Marbà *et al.* 1996, Vermaat and Verhagen 1996, Sfriso and Ghetti 1998, Laugier *et al.* 1999). Overall, we found a peak in August, but a lower above-ground biomass and shoot elongation rate in May than in February. The sharp reduction in irradiance due to the proliferation of dense *Ulva* sp. mats overgrowing the patch might explain this pattern (Brun *et al.* 2003). Moreover, the associated reduction in light availability could also explain the observed depletion of carbohydrate reserves (Burke *et al.* 1996, Vermaat and Verhagen 1996, Lee and Dunton 1997, Alcoverro *et al.* 1999, Peralta *et al.* 2002, Brun *et al.* 2003) (Fig. 6). Vermaat and Verhagen (1996) estimated that stored carbohydrates in *Z. noltii* could meet 28 % of the respiratory need; photosynthesis must account for the remaining 72 %. The storage capacity and clonal integration (*sensu* Hartnett and Bazzaz 1983) of *Z. noltii* is presumably lower than that in seagrasses with thick and long-lived rhizomes (Tomasko and Dawes 1989, Marbà and Duarte 1998) conferring a very limited tolerance to long-term light deprivation (Peralta *et al.* 2002, Brun *et al.* 2003). Other strategies for surviving long-term light deprivation would include the reduction of respiratory costs by sacrificing part of the oldest tissues (Hemminga and Duarte 2000). Carbohydrate mobilization may represent an important strategy for short-term survival since some leaf growth is maintained and the rhizome elongation capacity increases (*ca.* 0.15 cm apex^{-1} d^{-1}) at the patch periphery. It would allow escape from severe shading by centrifugal occupation of the bare sediment where no *Ulva* mats were present.

Few studies on spatial and/or temporal variability of biomass and production of seagrasses take into account the within-patch heterogeneity (Brouns 1987, Duarte and Sand-Jensen 1990a,b, Olesen and Sand-Jensen 1994, Nakaoka and Aioi 1999, Nakaoka and Izumi 2000). We found small-scale differences in biomass, shoot density, plant morphology, tissue nutrient content and growth rates. Overall, higher biomass, leaf area index, shoot density and above-ground to below-ground biomass ratios were recorded at the patch centre. Biomass dynamics at this site were largely dependent on changes in leaf numbers and size. In contrast, at the patch periphery temporal variation in above-ground biomass was largely dependent on shoot recruitment and mortality. Plant performance was affected by plant position in the patch, resulting in higher elongation rates of the apical shoots (mostly at the patch border) compared to lateral and single small shoots. This suggests some kind of apical meristem dominance or clonal integration between connected shoots, as reported in other seagrass species (Tomlinson 1974, Tomasko and Dawes 1989, Terrados *et al.* 1997a,b). Rhizomes creeping at the patch periphery also displayed higher elongation rates than those at the patch centre, as found in other seagrasses (Patriquin 1973, Duarte and Sand-Jensen 1990a, Gallegos *et al.* 1993, Marbà *et al.* 1996, Nakaoka and Aioi 1999). However, we acknowledge that our sampling design did not allow us to attribute exclusively the variability in the measured variables to shoot category, and other factors as light (quality and quantity), nutrients, sediment and hydrodynamic conditions that change with patch heterogeneity and affect plant development (Fonseca *et al.* 1986, Koch 2001, Peralta *et al.* 2002, Brun *et al.* 2002, Brun *et al.* 2003) should be taken into account. The lower N and P content recorded in peripheral rhizomes may be explained by dilution processes (Stocker 1980), owing to a faster utilization than uptake, so that stored N and P resources are gradually diluted during growth.

The density and proportion of the different shoot types were correlated with light availability. A negative relationship was observed for single small shoots (r^2=0.97), whereas, for apical and lateral shoots the relation was positive (r^2=0.98). This could be a clear symptom of the high phenotypic variability (*sensu* Huber *et al.* 1999) displayed by this seagrass, since shoots with higher above-ground to below-ground ratio (single small shoots) would be favored at low light conditions because photosynthesis could cope with below-ground respiratory demands (Hemminga 1998). The relative biomass allocated to photosynthetic *vs.* non-photosynthetic tissues increases with depth (Stewart 1989) and low light conditions (Sultan 2000). Since the total shoot density remained nearly constant at the patch centre, but the proportion of the different shoot types displayed a temporal variation, an acclimation to reduced irradiance involving biomass partitioning between shoots and root/rhizomes is likely. This could partly explain why patch asymmetry increases with size. If low light favored the appearance (or conversion) of single small shoots, the seaward growth of secondary patch axes will reduce the expansion rate since light availability decreases with depth. This would not be the case for principal axis expansion since it follows approximately the same isobath.

Estimates of total growth (above and below ground) in *Z. noltii* are very few (Marbà *et al.* 1996, Peralta *et al.* 2000, Peralta *et al.* 2002, Brun *et al.* 2002). Unlike the majority of studies on seagrass production, we took into account the temporal variability in the proportion and growth of the different shoot types (Figs 4 C,F, 7 A,B) and rhizome branching and growth (Fig. 7D). Such a time-consuming procedure allowed a rough quantification of the overestimation in above-ground (9%) and, especially, in below-ground production (28%) when such a variability source was excluded. Overall, our production estimates (1646 g DW m^{-2} y^{-1} for above-ground and 1611 g DW m^{-2} y^{-1} for rhizomes) were generally higher than those previously reported for the same species (Auby and Labourg 1996). Higher light availability and temperature, as well as higher shoot density, may largely explain such differences.

In conclusion, *Z. noltii* in Los Toruños salt-marsh is restricted to scattered patches which are normally distributed. The apparent lack of recruitment from seedlings explains, in large part, such a distribution. The present study highlights the importance of within-patch heterogeneity in affecting temporal variation in plant morphology, biomass, density of different shoot types and growth. A high phenotypic plasticity was found in this species, probably as a response to light and space limitation. A proliferation of *Ulva* sp. in May might result in a reduction in light availability and probably modifies the `expected´ temporal variation of biomass, growth and carbohydrate reserves. Although estimations of below-ground production in seagrasses are relatively scarce, future studies should consider small-scale variability (spatial and temporal) to obtain more accurate estimates.

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