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Seasonal dynamics of biomass and nutrient content in the intertidal seagrass *Zostera noltii* Hornem. from Palmones River estuary, Spain

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Abstract

The seasonal dynamics of above- and belowground biomass of *Zostera noltii* Hornem. were studied in a permanent quadrat in the Palmones River estuary, southern Spain (36°11′ N, 5°27′ W) from February 1988 to February 1990. Temporal changes in nitrogen, carbon, different phosphorus fractions (soluble reactive phosphorus, total soluble phosphorus, particulate phosphorus and total phosphorus) and nutrient ratios (C/N, N/P and C/P), were also investigated in the same population from January 1989 to January 1990.

Biomass of above- and belowground structures showed a unimodal seasonal pattern with maxima in summer (180–200 g DW (dry weight)) m^{-2} and 70–75 g DW m^{-2} respectively) and minima in winter (30–50 g DW m^{-2} and 25–30 g DW m^{-2}). Internal concentrations of carbon, nitrogen and phosphorus showed seasonal changes, with minima for nitrogen (3.0% for shoots and 1.2% for underground parts) and total phosphorus (0.45% for underground parts) in summer. Shoots and underground parts of *Z. noltii* contained maximum amounts of nitrogen (5.9 g m^{-2} and 2.1 g m^{-2}, respectively), phosphorus (1.7 g m^{-2} and 0.6 g m^{-2}) and carbon (66.9 g m^{-2} and 27.8 g m^{-2}) in August. The annual flux of nutrients from *Z. noltii* to the detritus compartment has been estimated to be about 14.6 g N, 4.1 g P and 155.3 g C m^{-2} of sediment surface.

Introduction

Seagrass meadows have become recognised as one of the richest and most productive ecosystems, reaching large biomass and being relatively long-lived components of coastal and estuarine ecosystems (Thayer et al., 1977; Zieman and Wetzel, 1980). Their role in the cycling of essential elements (i.e. nitrogen and phosphorus) is important owing to their ability to accumulate these elements, affecting the nutrient turnover in these systems.

Zostera spp. are able to take up nutrients through their roots and shoots

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(McRoy and Barsdate, 1970; Penhale and Thayer, 1980; Iizumi and Hattori, 1982; Thursby and Harlin, 1982; Short and McRoy, 1984; Brix and Lyngby, 1985; Pérez-Lloréns et al., 1993). The internal nutrient content varies depending on species, plant part, environment, season, and age of the plant (Birch, 1975; Augier et al., 1982; Atkinson and Smith, 1983; Pellikaan and Nienhuis, 1988; Piré and Wollenweber, 1988; Pérez-Lloréns and Niell, 1989; Borum et al., 1989; Pérez-Lloréns et al., 1991; Short et al., 1992).

Some of the above studies suggest that regular analysis of internal nutrients can reveal growth strategies in relation to nutrient uptake and storage. Combining nutrient analyses with data on biomass and turnover rates can provide a rough approximation of the amount of these nutrients entering the detritus compartment (Twilley, 1976; Brock et al., 1983), since few organisms feed directly on seagrasses (Nienhuis and Van Ierland, 1978; Den Hartog, 1980; Nienhuis and Groenendijk, 1986). Part of the fixed nutrients in *Zostera* detritus are released by leaching and microbial mineralisation (Harrison and Mann, 1975a; Kikuchi and Pérés, 1977; Godshalk and Wetzel, 1978; Pellikaan and Nienhuis, 1988), increasing the nutrient levels, and consequently, the energy flow in these environments.

The purpose of the present investigation was to measure seasonal changes in biomass and nutrient content (carbon, nitrogen and phosphorus) in the intertidal seagrass *Zostera noltii* Hornem., because of the important role that this species plays in the nutrient cycling processes in the Palmones River estuary.

Materials and methods

The study area

The Palmones River estuary is located in Algeciras Bay, southern Spain (36°11′ N, 5°27′ W) (Fig. 1). The estuary is 2500 m long and 1500 m wide at the mouth. The water depth is shallow, 1.0 m in the sampling area and 3 m in the central channel. Salinity ranges between 29 and 35‰ and the water is muddy, corresponding to type 9 of the Jerlov classification (1976). Soluble reactive phosphorus (SRP) concentrations in water and sediment are highly variable (0.5–15 μM and less than 50 μM, respectively) depending upon tide and wastewater discharge (Clavero et al., 1991). The intertidal mudflats are covered by *Z. noltii* beds, which become exposed at low tide. The tide is semidiurnal with small amplitude (1 m), greater fluctuations being caused by the wind.

Biomass

Monthly plant samples were collected from January 1988 to February 1990. A permanent sampling area of 14 m×5 m was situated in a homogeneous

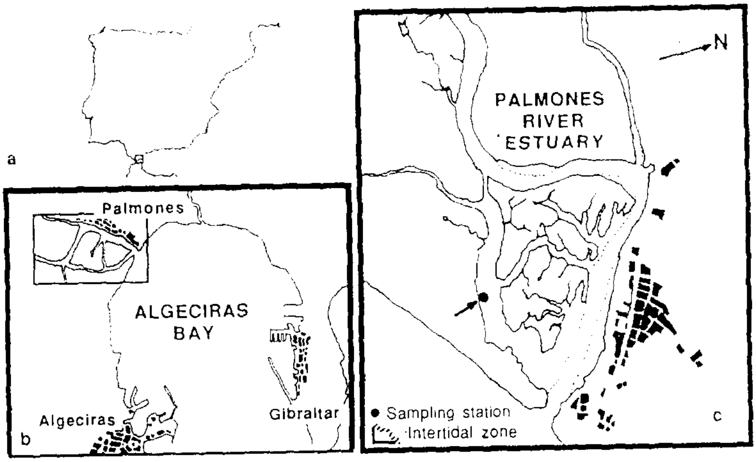

Fig. 1. Location of (a) Algeciras Bay in southern Spain, (b) Palmones River estuary and (c) sampling site in the intertidal mudflats (arrow).

Zostera noltii bed. Three randomly distributed seagrass samples were collected within a 16 cm×16 cm iron frame (minimum representative area, Pérez-Lloréns, 1987). All sampled quadrats were marked with a stick to ensure that the same quadrats were not re-sampled over the 2 year period. All plant material (above- and belowground parts) collected monthly in the three quadrats was dug out, sieved (2 mm mesh) and transported to the laboratory in polyethylene bags, washed further with tap water to remove sea salt, cleaned of epiphytes by careful scraping, and sorted into above- and belowground parts (no inflorescences were observed). Plant material from each sampling quadrat was oven dried at 60°C to constant weight, pulverised and stored separately.

Tissue nutrients

Samples of the seagrass homogenate (1–1.5 mg dry wt.) were taken for determination of carbon and nitrogen with a Perkin-Elmer® C–N–H 240-C analyser (Perkin-Elmer, Norwalk, USA). Samples for the analysis of the different phosphorus fractions (6 mg dry wt. (DW)) were crushed in a mortar with deionised water. Solid particles and filtrate were obtained after filtration (Whatman GF/C): 1 ml of filtrate was used to obtain SRP values using a Technicon® AAII Autoanalyser (Technicon Swords, Co. Dublin, Ireland) (malachite green method, Fernández et al., 1985). Solid particles and 1 ml of filtrate were acid-digested (Sommer and Nelson, 1972) and analysed to obtain particulate phosphorus (PP) and total soluble phosphorus (TSP), respectively. Total phosphorus (TP) was considered to be the sum of the TSP and PP fractions (Pérez-Lloréns and Niell, 1989). The analyses were performed in triplicate.

Results

Biomass

The biomass changes of aboveground parts of *Z. noltii* showed a regularly fluctuating pattern over the years 1988–1989 (Fig. 2a) with significant maxima in August (180 g and 202 g DW m^{-2} in 1988 and 1989 respectively) (*t*-test, $P<0.01$). This was followed by a biomass decrease during autumn,

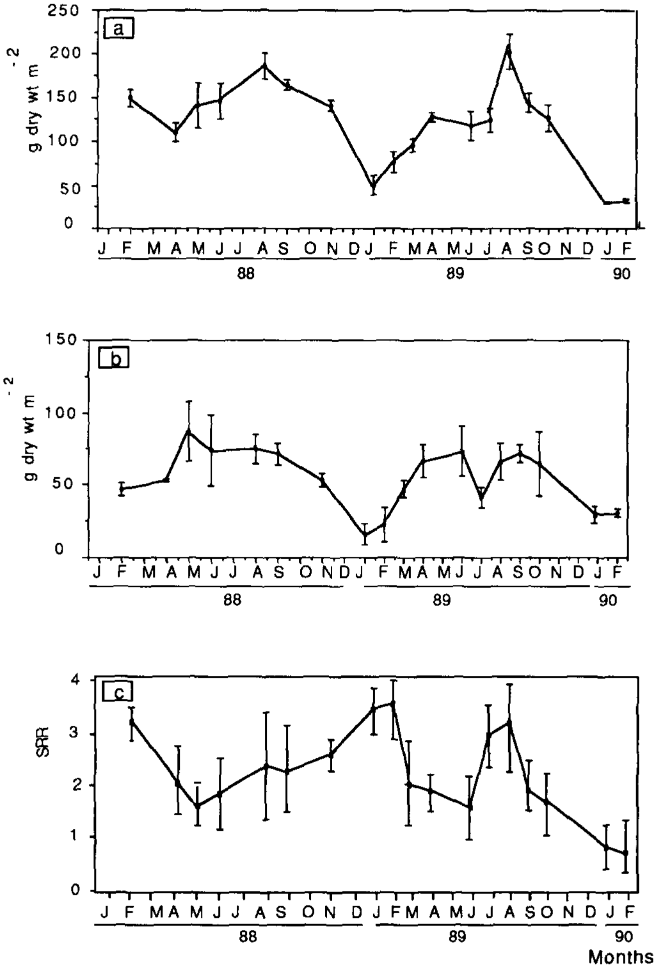

Fig. 2. Seasonal changes in shoot standing stock (a), living belowground biomass (b), and shoot/living belowground biomass ratio (c) of the intertidal seagrass *Z. noltii* in the Palmones estuary. Mean ± SD of three samples on each date is given.

reaching minimum values (30–50 g DW m^{-2}) in January. The biomass curve of the living belowground parts (Fig. 2b) showed a long peak in the period May–September (75 g DW m^{-2}) and minimum values during January (25–30 g DW m^{-2}). The total biomass increased from 164.5 g DW m^{-2} in April 1988 to 254.3 g DW m^{-2} in August 1988, and from 65 g DW m^{-2} in January 1989 to 268 g DW m^{-2} in August 1989.

The shoot:root (including rhizome) ratio was higher than 1 (during 1988 and 1989) showing a bimodal seasonal pattern, with minima in mid to late spring (Fig. 2c) and peaks in winter and summer. The seasonal variations in this ratio were more affected by biomass variations in above- than belowground parts because the latter have a lower turnover, owing to their protection against mechanical wear and from most grazers. However, the ratio was lower than 1 during 1990 (only January and February data are shown) because large amounts of shoots became detached during the floods in November–December 1989.

Tissue nutrients

Internal concentrations of carbon, nitrogen and phosphorus in the seagrass *Z. noltii* are presented for 1989.

Carbon

The annual pattern of carbon in shoots and belowground parts was much more variable than that for nitrogen and phosphorus. Values fluctuated between 25.1 and 40.2% of dry weight, with greater fluctuations in below- than in aboveground parts (Fig. 3a). The amount of carbon accumulated by *Z. noltii* per square metre of sediment surface (nutrient standing stocks) was calculated for each sampling day by multiplying the carbon concentrations (g C g^{-1} DW) by the biomass of the shoots and/or belowground parts per square metre. Shoots accumulated the highest amounts of carbon (Fig. 4a) reaching a maximum level in August (66.9 g C m^{-2}). Shoots contained 69%, on average, of the total plant carbon during the whole year.

Nitrogen

Nitrogen concentrations in the shoots and belowground parts showed a clear annual trend with minima in summer (3.0% and 1.2% of dry weight respectively) and maxima in winter (4.0% and 3.0%) (Fig. 3b).

The accumulation of nitrogen was highest in the shoots, reaching a maximum in August (5.9 g m^{-2}) and a minimum in winter (Fig. 4b). Shoots on average contained 75% of the total plant nitrogen during the whole year.

Phosphorus

The amount of phosphorus in the tissues showed a clear seasonal trend (Fig.

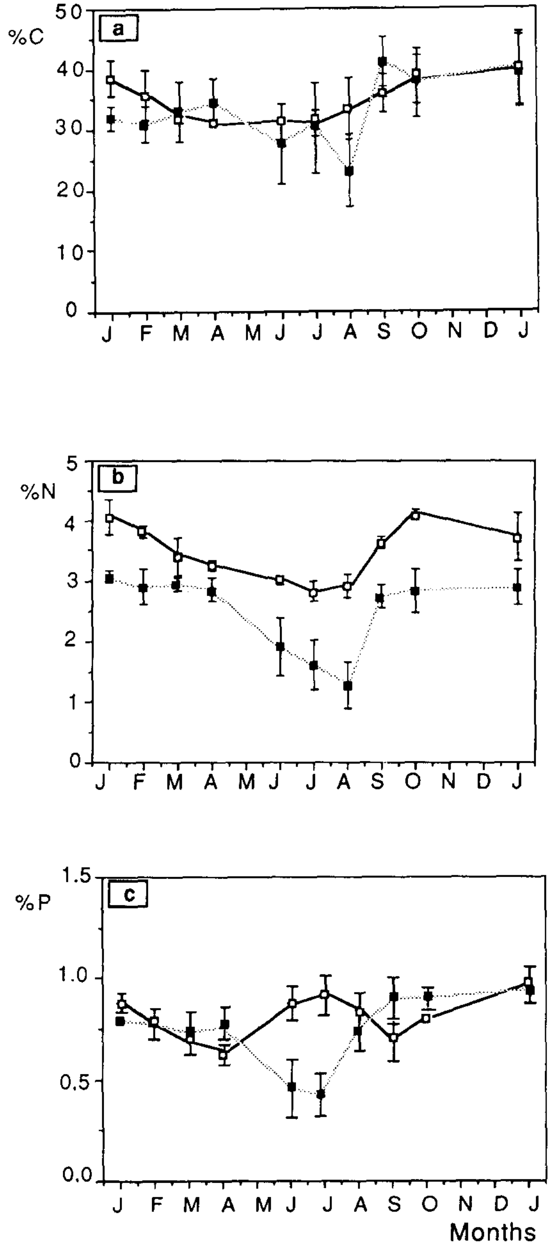

Fig. 3. Seasonal changes in carbon (a), nitrogen (b) and total phosphorus (c) contents (as percentage of dry weight) of shoots (open symbols, solid lines) and living underground biomass (closed symbols, broken lines). Mean ± SD of three samples on each date is given.

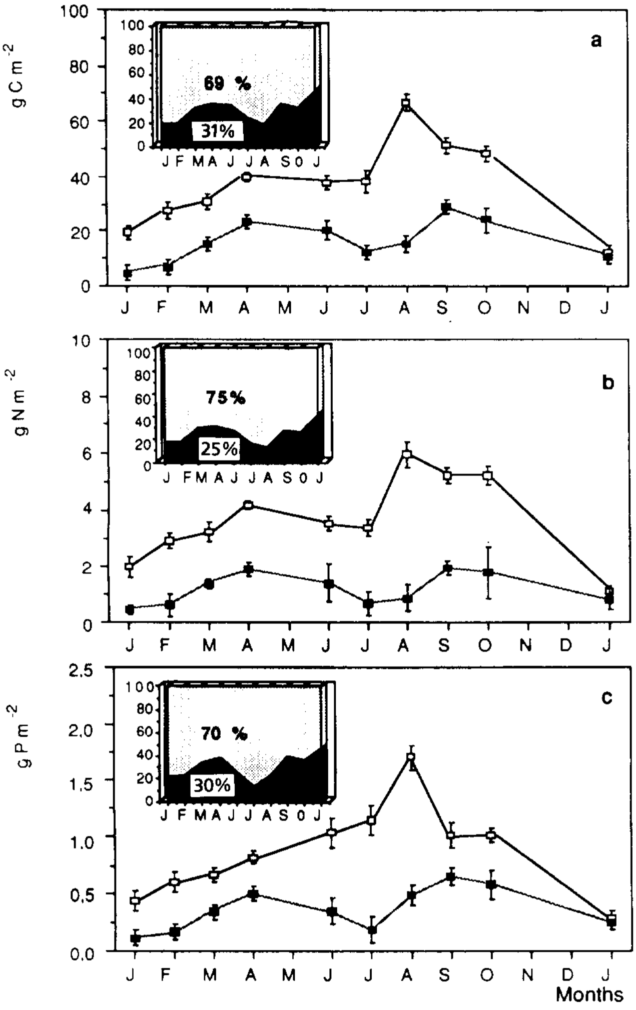

Fig. 4. Seasonal changes in carbon (a), nitrogen (b) and total phosphorus (c) accumulated in shoots (open symbols, solid lines) and in living belowground parts (closed symbols, broken lines) of *Z. noltii* per square metre of sediment surface. Inset: the relative distribution (%) of these nutrients in shoots (lighter area) and belowground parts (darker area). Mean±SD of three samples on each date is given.

3c). SRP and TSP concentrations were always highest in the shoots (Figs. 5a and 5b), which possess an increased metabolism and enhanced turnover rates. SRP in shoots showed a minimum in summer (58.1 μmol P g^{-1}) and a maximum in winter (86.8 μmol P g^{-1}). TSP in shoots reached maxima in summer and early winter (approximately 275.0 μmol P g^{-1}) and minima in spring and autumn (150.3 μmol P g^{-1}). Belowground parts contained higher PP

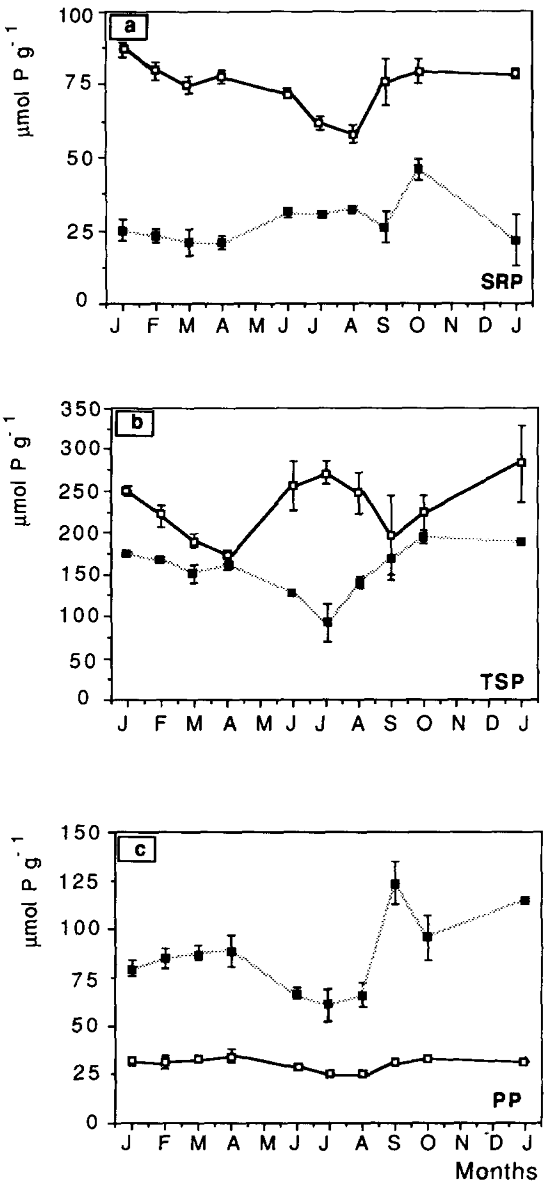

Fig. 5. Seasonal changes in different phosphorus fractions of shoots and belowground parts: (a) soluble reactive phosphorus (SRP); (b) total soluble phosphorus (TSP); (c) particulate phosphorus (PP). Mean ± SD of three samples on each date is given.

concentrations than aboveground parts, reaching a sharp peak in September, and in the shoots a small minimum in summer (Fig. 5c). TP concentrations in above- and belowground parts showed a complementary pattern, mainly

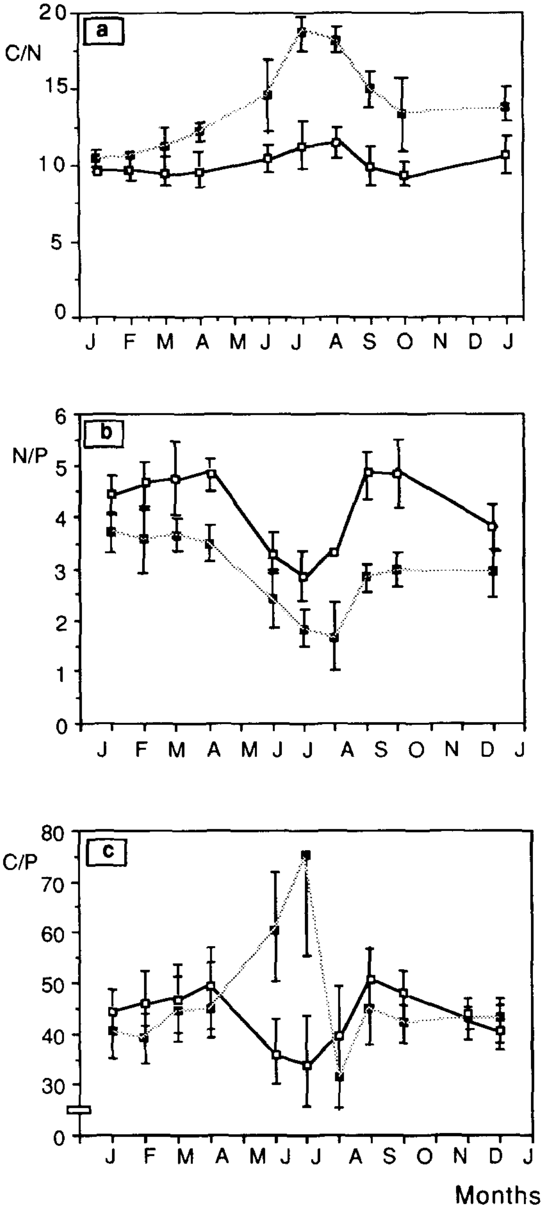

Fig. 6. Seasonal changes of C/N (a), N/P (b) and C/P (c) weight ratios in shoots (open symbols, solid lines) and living belowground parts (closed symbols, broken lines) of *Z. noltii*. Mean ± SD of three samples on each date is given.

between April and October (Fig. 3c): a foliar increase in TP coincided with a belowground decrease of this nutrient during April–July, and the opposite trend occurred between July and October.

The amount of phosphorus accumulated by *Z. noltii* (m^{-2}) is shown in Fig. 4c. Shoots contained the highest amount, reaching a maximum in August (1.70 g m^{-2}) and a minimum in winter (0.25 g m^{-2}). The phosphorus accumulated in the belowground parts showed a bimodal curve, reaching maxima in April and October and minima in winter and July. Over the course of a year, 70% of the total phosphorus was found in the shoots.

C/N, N/P and C/P ratios

C/N weight ratios of shoots and belowground parts showed a clear seasonal trend, with maxima in summer (10 and 18, respectively) and minima in winter (10.5 and 9.9) (Fig. 6a). Ratios in the belowground parts were always higher than those of the shoots. As an index of seasonal changes in the nutritional value, this ratio is less informative than either the carbon or nitrogen data alone (Harrison and Mann, 1975b). Because of the large variations in nitrogen and the relative stability of carbon, the C/N curves simply reflect changes in nitrogen.

N/P weight ratios of above- and belowground parts showed a similar seasonal pattern, with minima in summer (2.7 and 1.7, respectively) and maxima in winter (4.6 and 3.6). N/P ratios were always highest in shoots (Fig. 6b).

Above- and belowground parts of *Z. noltii* differed in the seasonal pattern of the C/P weight ratios (Fig. 6c). The lowest values were recorded in the shoots during mid-summer (35.1). Higher values were obtained in belowground parts with a remarkable peak in July (75.2), followed by a sharp decrease in August.

Discussion

Biomass

The temporal variation of biomass of above- and belowground parts of *Z. noltii* showed the same unimodal curve as reported for *Zostera marina* L. by several authors (Sand-Jensen, 1975; Jacobs, 1979; Nienhuis and DeBree, 1980; Wium-Andersen and Borum, 1980; Sand-Jensen and Borum, 1983; Orth and Moore, 1986) and for *Z. noltii* (Vermaat et al., 1987; Pérez, 1989).

Production of *Z. marina* and *Z. noltii* usually peaks in summer, simultaneously with the irradiance and temperature values, forming the main basis of the maximum increase in the shoot biomass. It is generally agreed that light is more likely to be the true controlling factor in *Z. marina* production (Sand-Jensen, 1975; Backman and Barilotti, 1976; Nienhuis and DeBree, 1977; Jacobs, 1979; Short, 1980; Sand-Jensen and Borum, 1983; Short et al., 1992). Calculations of the minimum light requirements of *Z. noltii* populations growing in the Palmones River estuary were carried out by Pérez-Lloréns (1991). These estimations, based on photosynthetic performances and measurements of light attenuation (self-shading and water turbidity), showed that light, instead of nutrients, is the major factor controlling seasonal variation of these populations. This finding agrees with recent studies (Dennison et al., 1987; Hemminga et al., 1991) suggesting that a lack of nutrient limitation in what are most probably eutrophic estuaries (e.g. the Palmones River estuary) produces conditions of light limitation partly induced by reduction in water clarity.

Although we lack reliable estimations of primary production in *Z. noltii* populations in the Palmones River estuary, a rough approximation can be made by multiplying the annual mean standing stock (119 g DW m^{-2}) by the mean annual leaf turnover (3.4 $year^{-1}$) reported by Vermaat et al. (1987) for this species. The production value obtained (406 g DW m^{-2} $year^{-1}$) is close to those reported for this species (Vermaat et al., 1987; Pérez, 1989) and for *Z. marina* (Sand-Jensen, 1975; Nienhuis and DeBree, 1980; Verhagen and Nienhuis, 1983; Roman and Able, 1988) (Table 1).

There are two explanations for the marked decrease in aboveground biomass during January–February 1990: firstly, lowered winter production as a consequence of decreased insolation and the enhanced grazing pressure from the wintering populations of herbivorous birds (Jacobs et al., 1981), mainly *Anas acuta* (L.), *Anas penelope* (L.) and *Anas crecca* (L.) in the Palmones River estuary (Pérez-Lloréns, 1991); secondly as a consequence of the floods of November and December 1989. During these floods large quantities of silt

Table 1

Comparison of annual aboveground production of *Z. noltii* and *Z. marina*

Species	Annual aboveground production (g DW m^{-2})	Location	References
Z. marina	856	Denmark	Sand-Jensen, 1975
	640	The Netherlands	Nienhuis and DeBree, 1980
	385–626	Massachusetts, USA	Roman and Able, 1988
Z. noltii	329	The Netherlands	Vermaat et al., 1987
	379–528	NE Spain	Pérez, 1989
	406	S Spain	This study

were deposited on the *Z. noltii* beds; consequently the shoots were badly abraded, and the proportion of above- to belowground biomass diminished significantly (Fig. 2c; $P<0.01$) from 3.5 in January 1988 and 1989 to less than 1 during January and February 1990. Similar effects have been reported by Hanekom and Baird (1988) from a population of *Zostera capensis* Setchell in South Africa. Other consequences of the floods were the sharp decrease in underwater irradiance and in salinity due to the high amount of resuspended silt and the high input of freshwater, respectively. A decrease in seagrass populations in response to lowered irradiance and salinity has been recorded by several authors (Biebl and McRoy, 1971; Backman and Barilotti, 1976; Jacobs, 1979; Short, 1980; Bulthuis, 1983; Hanekom and Baird, 1988).

Nutrients

Total nitrogen and phosphorus concentrations (% DW) in shoots and belowground parts of *Z. noltii* showed a clear seasonal pattern, while no clear annual picture was observed for carbon, because of its high variability and fluctuating pattern, especially in the belowground parts.

For nitrogen, our results are in accordance with the data of Harrison and Mann (1975b) and Pellikaan and Nienhuis (1988) for *Z. marina*, those of Pirć and Wollenweber (1988) and Pérez (1989) for *Cymodocea nodosa* (Ucria) Aschers. and those of Short et al. (1992) for *Syringodium filiforme* Kütz. High concentrations of nitrogen before the main growing season may be, as Brock et al. (1983) pointed out, the result of active nutrient uptake, followed by a period of rapid protein synthesis before the start of fast growth. The period of rapid biomass increase (mainly in summer) coincides with a generalised decrease of nitrogen and phosphorus (the latter in belowground parts) concentrations within the plants. This response has also been observed in other species of aquatic angiosperms (Harrison and Mann, 1975b; Brock et al., 1983; Pellikaan and Nienhuis, 1988; Pérez, 1989; Short et al., 1992). The low nitrogen concentrations during summer have been explained by dilution processes (Stocker, 1980) owing to a faster utilisation than uptake in this period, so that stored nitrogen and phosphorus resources are gradually 'diluted' during growth.

The C/N ratio may be used as an index of nutritive food quality (Wahbeh, 1988). According to Russell-Hunter (1970) a ratio of 17/1 is adequate for animal food. Thus, above- and belowground parts of *Z. noltii* would constitute a good quality food since the ratio is lower than this value, mainly in the shoots, the parts most exposed to the grazers.

The different fractions of phosphorus showed a seasonal trend. The increase of TSP fraction observed in shoots from April to August, was accompanied by a decrease in SRP and PP, suggesting that these latter fractions may act as precursors for the former (Pérez-Lloréns and Niell, 1989). A decrease in TP was observed in the belowground parts (during spring–summer), coinciding with a shoot biomass increase, suggesting that this nutrient is translocated from below- to aboveground parts during this active growing season. However, the increase of TP in the belowground parts from late summer, coinciding with leaf senescence, could be explained by the translocation of phosphorus from shoots to the belowground parts or simply by a reduction in upward translocation, resulting in an accumulation of phosphorus in the belowground parts. This role of belowground parts as storage/sink organs for organic compounds and nutrients has already been suggested for several aquatic angiosperms (Harrison and Mann, 1975b; Hocking et al., 1981; Pérez-Lloréns and Niell, 1989; Borum et al., 1989).

Nutrient concentrations within the plants were always higher than the critical, limiting values of 0.75% for nitrogen and 0.07% for phosphorus (Gerloff, 1975) reported for aquatic macrophytes. If these critical values are correct for *Z. noltii*, it implies that nitrogen and phosphorus are not the limiting factors for growth of this species in the Palmones River estuary.

The mean phosphorus concentrations of shoots (0.78%) and belowground parts (0.65%) of *Z. noltii* in the Palmones River estuary, are at the upper limit of those recorded in various seagrasses (Short, 1987; Pellikaan and Nienhuis, 1988; Pérez-Lloréns et al., 1991), resulting in lowered mean atomic N/P and C/P ratios of shoots (9/1 and 113/1 respectively) and belowground parts (7/1 and 119/1). The atomic N/P ratios are in the lower limit of those mentioned by Fenchel and Jørgensen (1971) (10/1 to 70/1), but the C/P atomic ratios are lower than those mentioned by the same authors (200/1) for benthic plants. The mean atomic C/N/P ratios for shoots (113/9/1) and belowground parts (119/7/1) deviate highly from the Redfield ratio (106/16/1), being even lower than the average ratio of 507/21/1 reported by Atkinson and Smith (1983) for benthic marine macroalgae and seagrasses. This indicates that the plants had an ample phosphorus supply, as is expected by the relatively high phosphorus concentration in the Palmones River estuary with a highly organic muddy sediment (Clavero et al., 1991). In this way, Short (1987) using experimental mesocosm tanks to grow eelgrass in different substrates, reported that shoots and belowground parts accumulated higher levels of phosphorus in the plants grown in the mud tank than those in the sand tank, as expected from the availability of organic matter in the mud substratum (Fenchel and Blackburn, 1979).

The shoot: root (including rhizome) ratio in *Z. noltii* populations growing on the high organic muddy sediments of the Palmones River estuary for 1988–1989 was always higher than 1. This finding is in accordance with those of Burkholder et al. (1959) and Margalef (1962) in *Thalassia testudinum* Banks ex König and Burkholder and Doheny (1968) in *Z. marina* which demonstrated a decrease in shoot/root (including rhizome) ratios from muddy substrate to sandy substrate. This would seem to show the need for a better developed nutrient absorptive system in the coarser sediments (Short, 1983) which generally tend to be lower in nutrients and organic matter (Zieman and Wetzel, 1980).

Twilley (1976), Brock et al. (1983) and Short et al. (1992) calculated the annual phosphorus and nitrogen cycling by *Nuphar* sp., *Nymphoides peltata* (Gmel.) O. Kuntze and *Syringodium filiforme*, respectively, multiplying the turnover rate of the biomass by the annual mean nutrient stocks of the plants. This method is applied in this work to obtain a rough estimation of the annual flux of these nutrients entering the detritus compartment, since it is assumed that few organisms feed directly on seagrasses (Nienhuis and Van Ierland, 1978; Den Hartog, 1980; Nienhuis and Groenendijk, 1986). Among these organisms are the wintering populations of herbivorous birds (*A. acuta, A. penelope* and *A. crecca*) on the Palmones River estuary. Our own observations agree with findings of Jacobs et al. (1981) who pointed out that grazing pressure by seagrass-consuming birds becomes important in intertidal populations. Thus, we are aware that the accuracy of these calculations will depend on the degree of grazing. As we lack reliable estimations of the turnover of above- and belowground parts, the calculations are based on data from Vermaat et al. (1987) and Jacobs (1979). Shoots contributed to a higher degree to the annual flux of nitrogen (11.9 g m^{-2}), phosphorus (3.4 g m^{-2}) and carbon (126.1 g m^{-2}) than the belowground parts (2.7 g m^{-2}, 0.7 g m^{-2} and 29.2 g m^{-2}, respectively) (Table 2), because of their higher biomass turnover rates and nutrient standing stocks. Our calculations could result in an overestimation, depending on the degree at which the nutrients are translocated from old senescent leaves to the newly formed leaves (Brock et al., 1983; Borum et al., 1989). This remobilisation has already been pointed out for nitrogen in *Z. marina* (Borum et al., 1989). Further studies on nitrogen, phosphorus and carbon release during the decomposition processes of *Z. nol-*

Table 2

The annual nutrient stocks of shoots and belowground parts of *Z. noltii* and the estimated annual flux of nitrogen, phosphorus and carbon from these structures to the detritus compartment (g m^{-2} sediment surface)

Plant part	Mean nutrient standing stock (g m^{-2})			Turnover rate ($year^{-1}$)	Cycled annually (g m^{-2})		
	N	P	C		N	P	C
Aboveground	3.5	1.0	37.1	3.4[1]	11.9	3.4	126.1
Belowground	1.5	0.4	16.2	1.8[2]	2.7	0.7	29.2
Total plant					14.6	4.1	155.3

[1] Data from Vermaat et al. (1987).

[2] Data from Jacobs (1979).

tii as well as on the quantification of seagrass consumption by birds and other animals, will be carried out to complete our knowledge of their role in nutrient cycling. These data together with those of seasonal changes of nutrients in the various compartments of the Palmones River estuary, will be helpful in identifying the role of *Z. noltii* in the nutrient balance of the whole system.

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