

Magnitude and fate of the production of four co-occurring Western Mediterranean seagrass species

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ABSTRACT: We examined the seasonality and magnitude of the leaf-blade, rhizome and root biomass and production, along with the fate of leaf-blade production, of the 4 Mediterranean seagrass species *Posidonia oceanica*, *Cymodocea nodosa*, *Zostera noltii* and *Zostera marina* in a protected northern Spanish bay (Cala Jonquet, 42° 18.26' N, 3° 18.11' E) to estimate (1) the annual production consumed by herbivores or decomposed by detritivores and (2) the production in excess of consumption and first-year decomposition, which should be an upper limit of long-term burial of refractory detritus. The leaf, rhizome and root biomass of the 4 species displayed a clear seasonal pattern (which is in agreement with past studies), except for that of *Z. noltii*, which suggested a rapid loss of its production either to herbivores or as detritus. *Z. marina* and *P. oceanica* were the most productive species, and transferred to consumers (herbivores and detritivores) about twice the production transferred by *C. nodosa* and *Z. noltii*. Most of the production of the 4 species was decomposed by detritivores, which supports the importance of the detritivore food-web in the use and recycling of seagrass production. Consumption of seagrass leaf production by herbivores appeared to be higher for *C. nodosa* and *Z. noltii*, the species with the greatest leaf turnover rates, than for *Z. marina* and *P. oceanica*. Total heterotrophic use of seagrass production (consumption by herbivores and decomposition by detritivores) accounted for more than 80% of seagrass production in the 4 species. Yet, the excess of production not consumed nor decomposed during the first year ranged over 1 order of magnitude from the most (*Z. marina* and *P. oceanica*) to the least productive species (*C. nodosa* and *Z. noltii*) and represented a larger percentage of the production of the former species (9.2 and 16.8% respectively) compared with the latter species (about 1.5%). That suggests that *Z. marina* and *P. oceanica* may accumulate larger pools of refractory detritus and that their production is recycled more slowly than that of *C. nodosa* and *Z. noltii*. These results show marked differences in the fate of production among the 4 Western Mediterranean seagrass species growing in Cala Jonquet and suggest that differences in the leaf turnover rate could contribute to the explanation of differences in the fate of seagrass production, the species with faster-growing leaves losing a higher percentage of production to herbivores and recycling most of the residual detrital production, therefore storing relatively small pools of refractory detritus.

KEY WORDS: Mediterranean seagrasses · Fate of production · Herbivory · Decomposition · Production excess

INTRODUCTION

Seagrass meadows may be highly productive and therefore may have a strong bearing on the trophic dynamics of many coastal ecosystems (Zieman 1982, Thayer et al. 1984). Seagrasses are key components of such meadows and hence examination of the trophic

routes through which seagrass production is transferred to higher trophic levels is crucial to understanding the role of seagrass meadows in the trophic web of coastal ecosystems. The seagrass production consumed by herbivores and decomposed by detritivores determines all secondary production supported by seagrasses themselves within the meadow or elsewhere when carried out by waves and currents (Thayer et al. 1984, Bach et al. 1986). Conversely, the production

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buried in the sediment as refractory detritus involves a net loss for heterotrophic use and represents the seagrass' capacity to act as a sink for organic carbon (Hemminga et al. 1991, Romero et al. 1994). Hence, seagrasses with similar levels of production may play different trophic roles, depending on what proportion of production follows which of the available routes, and can have, therefore, contrasting trophic implications in the ecosystem.

The fate of seagrass production seems to differ substantially among species. For instance, *Halophila ovalis* and *Halodule uninervis* often support intense consumption by dugongs (cf. Sheppard et al. 1992, De longh et al. 1995) while herbivory only accounts for a minor percentage of the production of other species (e.g. *Posidonia oceanica*; Ott & Maurer 1977, Velimirov 1984, Cebrián et al. 1996a). Moreover, some species develop thick rhizomes and roots with associated low decay rates and consequently store large pools of refractory detritus (for instance: *P. oceanica*, Romero et al. 1994; *Thalassodendron* sp., Lipkin 1979; *Posidonia australis*, Shepherd & Sprigg 1976), in contrast with the much smaller refractory pools for species with faster turnover rates in their belowground parts (for instance: *Cymodocea nodosa*, Mateo 1995; *Zostera marina*, Kenworthy & Thayer 1984, Pellikaan & Nienhuis 1988). Furthermore, although the exportation rates of detrital leaves may vary widely, depending on the physical conditions in the meadows, the published values tend to be higher for species with shorter and narrower leaves (for a review of exportation rates, cf. Hemminga et al. 1991, Pergent et al. 1994), probably because of their greater buoyancy and associated susceptibility to transportation by waves and currents. Whereas estimates of seagrass production are abundant (cf. Duarte 1989, Hillman et al. 1989), estimates of the fate of seagrass production are still few (Duarte & Cebrián 1997).

Four seagrass species grow in the Western Mediterranean Sea. *Posidonia oceanica* (L.) Delile is the dominant species, developing extensive, productive meadows that play an important ecological role (Wittmann 1984). *Cymodocea nodosa* (Ucria) Ascherson dominates in some sheltered bays and coastal lagoons, and it forms dense meadows at considerable depth (e.g. 8 to 20 m on the northern Spanish Mediterranean coast and >30 m at the Balearic Islands and Malta; Ballesteros et al. 1989), whereas *Zostera noltii* Hornem and *Z. marina* L. are much less frequent and are confined to a

few sheltered environments (Ballesteros et al. 1989). Production in the Mediterranean has been evaluated for *P. oceanica*, *C. nodosa* and *Z. noltii*, but not for *Z. marina*. Moreover, the fate of the production of these 4 species is little known, with only some reports of herbivory on *P. oceanica* (cf. Ott & Maurer 1977, Velimirov 1984, Cebrián et al. 1996a) and on *C. nodosa* (Cebrián et al. 1996b) and some reports of burial and export of *P. oceanica* (Romero et al. 1992, Pergent et al. 1994), and of *C. nodosa* (Mateo 1995) production being available. Hence, there is a need to assess and compare the fate of production of these 4 species in order to characterise their trophic role in Mediterranean coastal ecosystems.

The co-occurrence of the 4 Western Mediterranean seagrass species in a sheltered bay (Cala Jonquet) on the northern Spanish Mediterranean coast allows comparison of the magnitude and fate of their production under similar environmental conditions. In this report, we assess the seasonality and magnitude of the leaf-blade, rhizome and root production of these 4 species in Cala Jonquet Bay, and analyse the annual leaf-blade production consumed by herbivores and decomposed by detritivores. Moreover, based on published decay rates of the belowground components of these species, we estimate the belowground production decomposed. We finally combine all these measurements to discuss and compare among the 4 species (1) the total annual production consumed by herbivores or decomposed by detritivores, and (2) the excess of production over consumption and first-year decomposition, which corresponds to an upper limit of the seagrass production buried as refractory detritus.

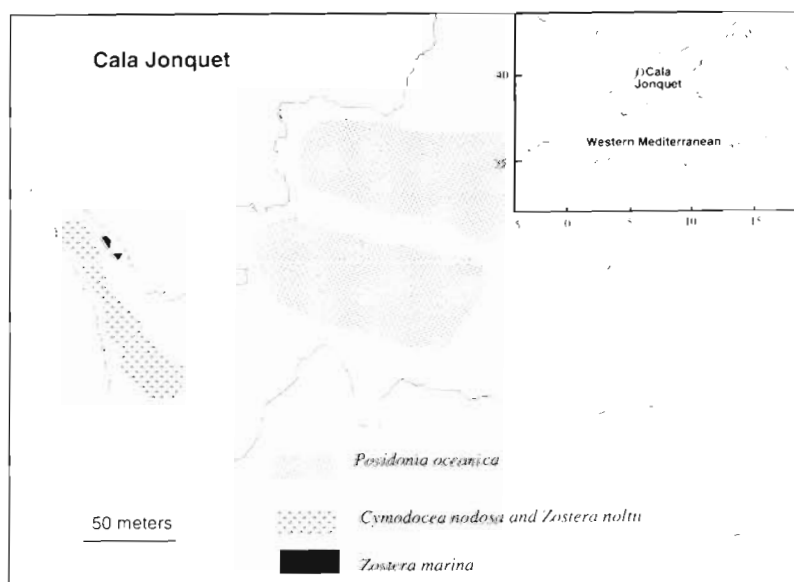


Fig. 1. Locations of the species sampled in Cala Jonquet

METHODS

Cala Jonquet is a sheltered bay located on the northern Spanish Mediterranean coast (42° 18.26' N, 3° 18.11' E) where the 4 Western Mediterranean seagrass species grow (Fig. 1). All the species were sampled at the depth of maximal density, which was 4 m for *Posidonia oceanica* and 1 m for the other 3 species (Marbà et al. 1996a). We visited this bay monthly (bimonthly for some sampling visits) from winter 1991 to summer 1993. On every sampling visit, 3 corers of 20 cm diameter were randomly pushed about 20 cm into the sediment within the seagrass patches to collect *Cymodocea nodosa* and *Zostera noltii*, from which the density of shoots of the 2 species (i.e. leaf clusters for *Z. noltii*) and horizontal apices of *C. nodosa* were registered. Shoot density of *P. oceanica* and *Z. marina* (i.e. leaf clusters for *Z. marina*) and the density of horizontal apices of *P. oceanica* were estimated from 3 replicated 0.25 and 0.1 m² quadrats randomly tossed on the *P. oceanica* meadow and the *Z. marina* patches, respectively, due to the toughness of the *P. oceanica* belowground structure and to preserve the small area covered by *Z. marina* (Fig. 1). In addition, 50 to 100 shoots of each of these 2 species along with their attached belowground material were dug out on each visit.

Leaf (blades and attached sheaths), rhizome and root biomass (g DW m⁻²) of *Cymodocea nodosa* and *Zostera noltii* was calculated from the weight of each respective compartment within the corers after the plant material was dried overnight at 80°C. Leaf biomass of *Posidonia oceanica* and *Z. marina* was estimated as the product of mean shoot density and the mean ratio of leaf dry weight per shoot, which was derived from the collected sample. Similarly, the rhizome and root biomass of *Z. marina* were calculated as the product of the mean shoot density and the mean ratio of dry weight of horizontal rhizomes or roots per shoot, respectively, which were also derived from the collected sample. This procedure, however, did not allow accurate estimation of the belowground biomass of *P. oceanica*, which penetrates several tens of centimetres into the sediment (Romero et al. 1992, Mateo 1995).

On every visit, we marked 10 to 15 apices of horizontal rhizome of each species and 10 to 15 short shoots of *Posidonia oceanica* and *Cymodocea nodosa* as described by Marbà et al. (1996a). That allowed us to derive, for every sampling interval, the horizontal rhizome production rate per apex (g DW apex⁻¹ d⁻¹), the root production rate per apex (g DW apex⁻¹ d⁻¹) and the leaf-blade production rate per shoot (g DW shoot⁻¹ d⁻¹), which is also comprehensively described in Marbà et al. (1996a). For every sampling interval, the horizontal rhizome and root production rates (g DW m⁻² d⁻¹) were calculated as the product of the average density of hor-

izontal apices and the horizontal rhizome or root production rate per apex, respectively. Likewise, the leaf-blade production rate (g DW m⁻² d⁻¹) for every sampling interval was calculated as the product of the corresponding mean shoot density and leaf-blade production rate per shoot. We accounted for the blade-growth of the leaves shed by senescence between consecutive sampling visits by adding, for each sampling interval, the product of the average number of leaves shed per shoot (see below) and the average blade-growth of the oldest standing age rank to the corresponding estimate of leaf-blade production per shoot.

We estimated the annual leaf-blade, horizontal rhizome and root production (g DW m⁻² yr⁻¹) for the 4 species by adding the products of the daily rates and duration of the corresponding sampling intervals over 1 yr. Annual leaf turnover was estimated as the ratio of annual leaf production to maximal leaf biomass. The marking technique used to estimate the production of horizontal rhizomes (Marbà et al. 1996a) may have led to significant underestimation for *Posidonia oceanica* (Pergent 1990, Pergent-Martini et al. 1994), because the internodes appearing during a monthly sampling interval can subsequently exhibit substantial growth. Moreover, this method overlooks the production of vertical rhizome in species with short shoots, i.e. *P. oceanica* and *Cymodocea nodosa*. Hence we compiled estimates of the annual *P. oceanica* horizontal (Marbà et al. 1996b) and *P. oceanica* and *C. nodosa* vertical (Marbà unpubl. data) rhizome production in Cala Jonquet derived from seagrass-growth reconstruction methods (Duarte et al. 1994). The method used for estimation of root production may also result in underestimation (Marbà et al. 1996a) and was not adequate for *P. oceanica* (Marbà et al. 1996a). However, because root production typically represents a minor percentage of total seagrass production (cf. Peduzzi & Vukovic 1990, Sánchez-Lizaso 1993, Van Lent & Verschuure 1994, Vermaat & Verhagen 1996), we believe that this does not affect the differences found in the fate of production among the 4 species. The annual production of leaf sheaths was estimated as the product of the annual leaf formation rate, derived from the leaf marking technique (Marbà et al. 1996a), and the mean sheath biomass of the oldest leaves.

The leaf-blade material produced can be incorporated into standing biomass, be consumed by herbivores, be torn off and subsequently float away as a result of wave action and herbivore bites, or eventually be shed following leaf senescence. In turn, the leaf blades sloughed off either by senescence or by wave or herbivore action decompose gradually within the meadow, or out of it when they are exported by waves and currents. These routes determine the fate of leaf-blade production, which was also estimated in the

study. The mean number of leaf blades per shoot shed by senescence during each sampling interval (S_{st}) was derived from the mean number of standing leaves per shoot at the beginning (N_{t-1}) and end (N_t) of the sampling interval and the mean number of leaves per shoot born during that sampling interval (B_{st}), following the equation (Alcoverro et al. 1995):

$$S_{st} = N_{t-1} + B_{st} - N_t \quad (1)$$

Then, for each sampling period, the rate of leaf-blade shedding by senescence ($g\ DW\ m^{-2}\ d^{-1}$) was derived as the product of S_{st} , the mean blade biomass of the oldest standing age rank and the mean shoot density during the sampling interval, divided by the duration of the sampling interval in days. We also attempted to include leaf-blade shedding due to shoot mortality in the species which displayed a marked seasonal shoot density (i.e. *Zostera marina* and *Cymodocea nodosa*) by adding the product of the difference in shoot density and the average leaf-blade biomass per shoot, divided by the duration of the sampling interval, to the calculation of leaf-blade shedding rates described above for each of the intervals where a significant reduction in shoot density occurred.

Subsequently, the rate of leaf-blade production either consumed by herbivores or torn off by wave action or herbivore bites (i.e. leaf-blade residual loss, RL , in $g\ DW\ m^{-2}\ d^{-1}$) was derived for each sampling interval as:

$$RL = LP - LS - \Delta LB \quad (2)$$

where ΔLB ($g\ DW\ m^{-2}\ d^{-1}$) is the increment in standing leaf-blade biomass during the sampling interval and LP and LS ($g\ DW\ m^{-2}\ d^{-1}$) are the rates of leaf-blade production and shedding by senescence, respectively, measured for the sampling interval. For *Posidonia oceanica*, the loss of leaf production exclusively due to consumption by herbivores may be readily estimated from the bite marks imprinted on the leaf blade (Cebrian et al. 1996a). That cannot be done for the other 3 species because, due to the relative narrowness of their leaf blades, the number of bite marks present is always low regardless of the intensity of herbivory. Hence, for *P. oceanica*, the biomass of any leaf age rank consumed between 2 consecutive sampling dates was derived from the increment in the surface covered by the bite marks on that age rank during the sampling interval, after transforming leaf surface to biomass by means of the leaf specific weight. Subsequently, the consumption per shoot for every sampling interval was calculated by adding the consumption on each age rank during that interval and expressed per unit area ($g\ DW\ m^{-2}\ d^{-1}$) according to shoot density. Estimates of the annual leaf-blade production shed by senescence and either consumed by herbivores or torn off by wave

or herbivore action ($g\ DW\ m^{-2}\ d^{-1}$) were also calculated by adding the products of the daily rates and duration of the corresponding sampling intervals over 1 yr

In order to assess the use of detrital leaf blades by detritivores, litter bag experiments (Josselyn et al. 1986) for each species were carried out from May to October 1994, covering the period when most of the leaf-blade shedding by senescence and subsequent decomposition (cf. Figs. 2 & 4) occurs. These experiments took place in Cala Jonquet for *Posidonia oceanica*, but were carried out, due to logistic constraints, in a similar sheltered bay (i.e. protected bay with similar temperature and depth ranges) closer to our laboratory for the other 3 species. The oldest leaf blade of every sampled shoot was selected to best simulate the decomposition of newly shed leaf blades. A known mass of fresh leaf blades was enclosed in mesh bags (1 mm² pore size), which were just barely buried in the sediment among the standing detrital leaf blades. The dry weight (80°C overnight) of the leaf-blade material remaining in triplicate bags collected at increasing time intervals, spanning a whole experimental period of 4 to 5 mo, was measured to estimate the decomposition of detrital leaf blades. The rate of disappearance of leaf detrital material was described by fitting a simple negative exponential equation (Olson 1963), using least-squares regression analyses:

$$\ln(\text{fraction of initial dry weight remaining}) = -k \times t \quad (3)$$

where k (d^{-1}) and t (d) correspond to the decomposition rate and time elapsed since the beginning of the experiment, respectively. Simple (i.e. linear) exponential models of decomposition assume a constant rate along the entire decay process. Other complex models, such as the double exponential, asymptotic and quadratic equations (Wieder & Lang 1982), in general did not yield a better fit than the equation employed. Disappearance rates of detrital material measured from litter bags include detritus decay, fragmentation by detritivores, and washing off of detrital particles smaller than the mesh size (Harrison 1989). Since most of these exported small detrital particles undergo decomposition, the disappearance rates measured are indicative of the use of seagrass production by detritivores.

We did not attempt to assess exportation of detrital leaf blades from Cala Jonquet Bay. Although Cala Jonquet is a very shallow, protected bay (Fig. 1) which remains calm even during rough sea conditions off the bay, exportation of detrital leaf blades could be significant and differ notably among the 4 species, as demonstrated in other relatively protected bays (Romero et al. 1992, Mateo 1995). Yet, this does not conflict with the aims of this paper, because we intend to compare among the 4 species the extent of seagrass production

consumed by herbivores or detritivores, and the excess of annual production escaping from this consumption, regardless of whether these routes take place inside or outside the meadow.

The error associated with our estimates of biomass, production and fate of leaf-blade production (see Eqs. 1 & 2) was derived by techniques of error propagation (Tsokos 1972). Cross correlation analysis, which derives the Pearson correlation coefficient (r) at a given time lag between 2 time series, was used to describe the similarity between the seasonal patterns of leaf-blade production and its fate for the 4 species.

RESULTS

Leaf biomass was seasonal for all species except for *Zostera noltii* (Fig. 2), with a summer maximum (all values expressed as mean \pm SE) of 555.7 ± 47.1 , 87.7 ± 7.4 and 291.3 ± 40.6 g DW m⁻² for *Z. marina*, *Cymodocea nodosa* and *Posidonia oceanica*, respectively. Minimum leaf biomass occurred in winter and averaged 1.5 ± 0.5 , 10.3 ± 0.9 and 183.5 ± 16.4 g DW m⁻² for these 3 species, respectively. Conversely the leaf biomass of *Z. noltii* varied over an order of magnitude throughout the sampling period (from <1 to 44 g DW m⁻²) with no clear seasonal pattern (Fig. 2). Rhizome and root biomass did not follow, on the whole, a clear seasonal pattern (Fig. 3). Only the rhizome and root biomass of *Z. marina*, and the rhizome biomass of *C. nodosa* exhibited a marked peak in summer, reaching, respectively, 213.1 ± 18.1 and 175.1 ± 6.6 g DW m⁻² for *Z. marina* and 330.5 ± 46.2 g DW m⁻² for *C. nodosa* (Fig. 3).

In contrast, leaf-blade, horizontal rhizome and root production rates were seasonal for all species except for the rhizome of *Posidonia oceanica* (Figs. 2 & 3). Maximal leaf-blade, horizontal rhizome and root production rates occurred in summer, except for the maximal leaf-blade production rate of *P. oceanica*, which occurred in winter and spring, and that of *Zostera noltii*, which occurred in autumn (Fig. 2). Maximal leaf-blade production rates amounted to 8.2 ± 2.4 , 4.5 ± 1.3 , 2.6 ± 0.7 and 3.2 ± 0.7 (for both peaks in winter and spring) g DW m⁻² d⁻¹ for *Z. marina*, *Cymodocea nodosa*, *Z. noltii* and *P. oceanica*, respectively (Fig. 2). The horizontal rhizome and root production rates peaked at 2.1 ± 0.7 and 1.1 ± 0.6 for *Z. marina*, 0.9 ± 0.3 and 1.8 ± 0.6 for *C. nodosa* and 1.2 ± 0.6 and 0.33 ± 0.17 g DW m⁻² d⁻¹ for *Z. noltii* (Fig. 3).

Annual production values for leaf blades and sheaths showed a range of more than 2-fold between the least (*Zostera noltii*) and the most productive (*Z. marina*) species (Table 1). The species with higher annual production of blades and sheaths (*Z. marina* and *P. ocean-*

ica) supported maximal leaf biomasses disproportionately greater than those supported by the species with lower annual production (*C. nodosa* and *Z. noltii*), which resulted in much slower leaf turnover rates for the former species (Table 1). Although root production of *P. oceanica* is not accounted for, and because this production only represents a minor fraction of total *P. oceanica* production (see Table 2), our measurements showed that annual production of rhizomes and roots varied notably among the 4 species, being highest for *Z. marina*. Annual total production was highest for *Z. marina*, which was 1½, 2 and 3 times that of *P. oceanica*, *C. nodosa* and *Z. noltii*, respectively (Table 1).

The seasonal dynamic of leaf-blade shedding by senescence closely matched that of leaf-blade production (except for that of *Posidonia oceanica*) with maximum shedding either coinciding (*Zostera noltii*, time lag = 0 mo, $r = 0.93$, $p < 0.05$) or closely following (*Z. marina* and *Cymodocea nodosa*, time lag = 1 mo, $r = 0.79$ and 0.92 , respectively, $p < 0.05$) maximum production (Fig. 2). Most of the leaf-blade shedding of *P. oceanica* occurred in autumn (Fig. 2). The amount of annual leaf-blade production falling away with senescence varied about 3-fold among the 4 species (Table 1), but it represented a fairly uniform percentage of the annual leaf-blade production (ca 60%) for all 4 species (Table 1).

The seasonal dynamic of the leaf-blade residual loss was associated with that of production for *Zostera marina* and *Cymodocea nodosa* (time lag = 1 and 0 mo, $r = 0.79$ and 0.91 , respectively, $p < 0.05$ for both coefficients), whereas this loss displayed an irregular temporal pattern for *Posidonia oceanica* and *Z. noltii* (Fig. 2). Annual leaf-blade residual loss also varied about 3-fold among the 4 species, representing from 25 to 40% of the annual leaf-blade production (Table 1). Herbivore consumption rates for *P. oceanica* leaves ranged from negligible to 0.3 g DW m⁻² d⁻¹, and only represented about 5% of the annual leaf-blade residual loss.

The decomposition of detrital leaf blades followed a simple negative exponential curve for the 4 species studied (Fig. 4). Leaf blades of *Zostera marina* and *Cymodocea nodosa* decayed faster ($k = 0.0189 \pm 0.0016$ d⁻¹ and 0.0236 ± 0.0045 d⁻¹, respectively) than those of *Posidonia oceanica* ($k = 0.0091 \pm 0.001$ d⁻¹, t -test, H_0 : equality between k , $p < 0.05$). The decay rate for the detrital leaf blades of *Z. noltii* was intermediate ($k = 0.0146 \pm 0.0026$ d⁻¹) and did not differ from the rest of species ($p > 0.05$).

DISCUSSION

The production of leaf blades, horizontal rhizomes and roots of the 4 seagrass species followed a seasonal

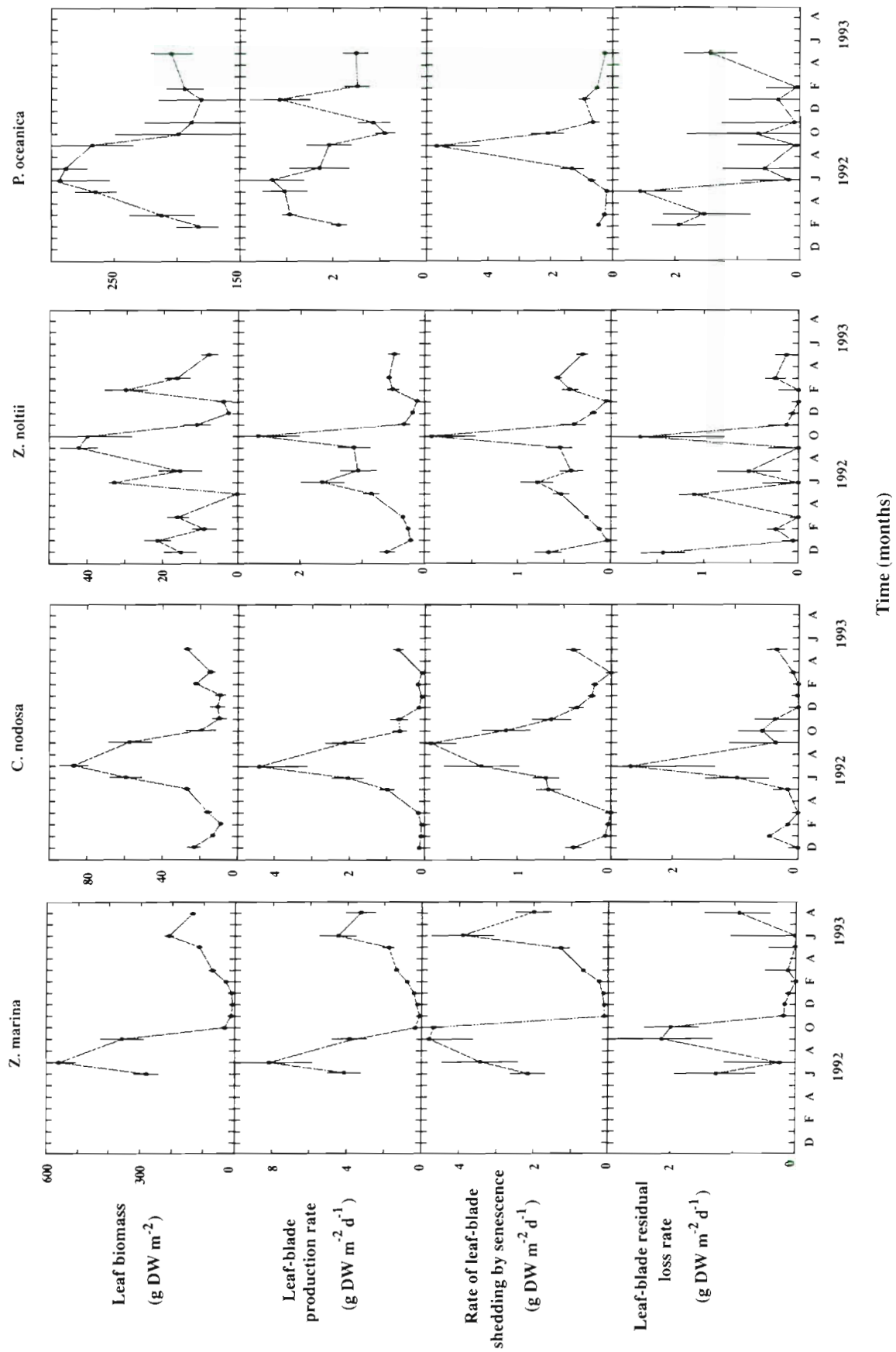


Fig. 2. *Zostera marina*, *Cymodocea nodosa*, *Z. noltii*, and *Posidonia oceanica*. Seasonal dynamics of leaf biomass and rates of leaf-blade production, leaf-blade shedding by senescence and leaf-blade residual loss rate in Cala Jonquet. Vertical bars show \pm SE.

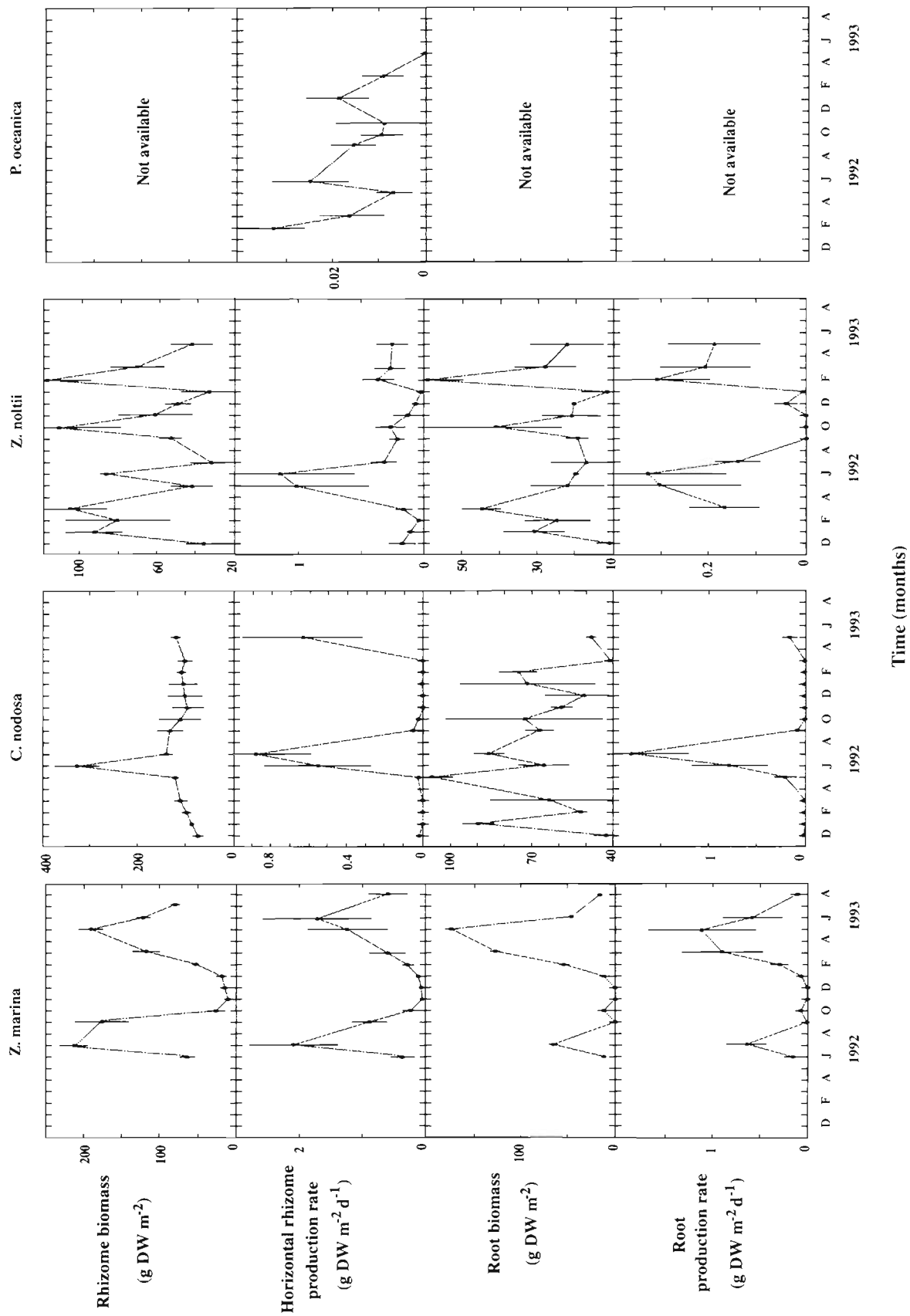


Fig. 3. *Zostera marina*, *Cymodocea nodosa*, *Z. noltii* and *Posidonia oceanica*. Seasonal dynamics of rhizome and root biomass and production rates in Cala Jonquet. Vertical bars show \pm SE

Table 1. *Zostera marina*, *Cymodocea nodosa*, *Z. noltii* and *Posidonia oceanica*. Biomass (g DW m^{-2}) and production ($\text{g DW m}^{-2} \text{ yr}^{-1}$) values and turnover rates (yr^{-1}) for the 4 seagrass species studied. Values in parentheses show the percentage of annual leaf-blade production accounted for. Note that, because of the associated error, the sum of the annual estimates of leaf shedding by senescence and residual loss do not have to coincide with the annual estimate of leaf-blade production. nd: no data

	<i>Z. marina</i>	<i>C. nodosa</i>	<i>Z. noltii</i>	<i>P. oceanica</i>
Maximal leaf biomass	555.7 \pm 47.1	87.7 \pm 7.4	42.9 \pm 4.8	291.2 \pm 40.6
Leaf-blade production	874.5 \pm 202.7	475.6 \pm 120.9	291.8 \pm 69.1	845.3 \pm 144.4
Leaf-sheath production	146.4	64.8	110.5	80.6
Leaf blade + sheath production	1020.9	540.4	402.3	925.9
Leaf turnover rate	1.8	6.2	9.4	3.2
Horizontal rhizome production	259.2 \pm 89.2	65.5 \pm 25.1	117.1 \pm 58.6	6.5 \pm 2.3
Vertical rhizome production		17.9 ^b		42.9 ^a
Root production	145.4 \pm 62.9	120 \pm 24.5	47.4 \pm 25.2	20.5 ^b
Rhizome + root production	404.6 \pm 152.1	203.4	164.5 \pm 83.8	nd
Total production	1425.5	743.8	566.8	63.4 ^c
Leaf-blade shedding by senescence	568.4 \pm 131.1 (65)	258.2 \pm 63.9 (54.3)	188.1 \pm 43.9 (64.4)	500.3 \pm 102.3 (59.2)
Leaf-blade residual loss	228.3 \pm 79.9 (26.1)	211.4 \pm 98.3 (44.4)	120.4 \pm 40.5 (41.3)	300.2 \pm 80.5 (35.5)

^aValue calculated from seagrass-growth reconstructing techniques (Duarte et al. 1995) by Marbà et al. (1996b). This value was used in estimating the total (horizontal + vertical) annual rhizome production value shown here

^bValues calculated from seagrass-growth reconstructing techniques (Duarte et al. 1995) by Marbà (unpubl. data)

^cOnly annual rhizome production

pattern (Figs. 2 & 3) similar to that reported in the past (see references in Table 2). The only exception was the horizontal rhizome production of *Posidonia oceanica*, which fluctuated little at about $0.02 \text{ g DW m}^{-2} \text{ d}^{-1}$ (Fig. 3), in agreement with previous reports of weak seasonality in *P. oceanica* belowground growth (Wittmann 1984). The lack of seasonality of *P. oceanica* horizontal rhizome growth is attributable to its extended life span and large size, which allows storage of enough carbohydrates to support growth independent of environmental conditions over a long time span (Pirc 1985, Marbà et al. 1996a). Our estimates of annual production for the 4 species were within the range of values observed elsewhere (Table 2). It is noteworthy that *Zostera marina* was as productive in this oligotrophic Mediterranean environment (Vidondo & Duarte 1995) as in many relatively nutrient-rich Atlantic locations (Table 2). However, the leaf turnover rates of *Cymodocea nodosa*, *Z. noltii* and *P. oceanica* were high and those of *Z. marina* were low in Cala Jonquet compared with other published values for these species ($1.5\text{--}2.3 \text{ yr}^{-1}$ for *P. oceanica*, cf. Ott 1980, Romero 1989; $2.2\text{--}2.5 \text{ yr}^{-1}$ for *C. nodosa*, cf. Terrados & Ros 1992, Pérez & Romero 1994; 3.4 yr^{-1} for *Z. noltii*, Vermaat et al. 1987; $3.1\text{--}5.3 \text{ yr}^{-1}$ for *Z. marina*, cf. Sand-Jensen 1975, Jacobs 1979, Wium-Andersen & Borum 1984, Van Lent & Verschuure 1994).

The observed seasonality in production was not always conducive to a parallel biomass seasonality (Figs. 2 & 3). Whereas the leaf, rhizome and root bio-

mass of *Zostera marina* and *Cymodocea nodosa* showed, in agreement with previous reports (cf. Sand-Jensen 1975, Orth & Moore 1986, Olesen & Sand-Jensen 1994 for *Z. marina*; Peduzzi & Vukovic 1990, Terrados & Ros 1992, Pérez & Romero 1994 for *C. nodosa*), maximum and minimum values during the summer and winter seasons, respectively, the leaf, rhizome and root biomass of *Z. noltii* did not display a clear seasonal pattern (Figs. 2 & 3). This result is in contrast with previous reports of *Z. noltii* biomass seasonality (Vermaat et al. 1987, Pérez 1989, Pérez-Llorens & Niell 1993). That the seasonal production of *Z. noltii* in Cala Jonquet Bay is not associated with a corresponding seasonal oscillation of biomass (Figs. 2 & 3) indicates that this production must be rapidly lost either to herbivores or as detritus, which is in agreement with reports of the limited capacity of *Z. noltii* rhizomes as storage organs (Dawes & Guiry 1992). In fact, whereas the peak of leaf-blade shedding by senescence of *Z. marina* and *C. nodosa* was observed 1 mo after the peak of leaf-blade production, these peaks coincided for *Z. noltii* (Fig. 2), which further supports the tight temporal coupling between production and losses for this species. This results in a relatively fast leaf turnover rate (9.4 yr^{-1} , Table 1)

Our estimates of leaf-blade residual loss include both the consumption of living leaf biomass by herbivores and the generation of detrital leaf material as fragments torn off by wave or herbivore action. Only for *Posidonia oceanica* has the consumption by herbivores

been directly estimated. Yet, for the 3 other species, an indication of herbivore contribution, both through consumption and sloughing of distal leaf parts, to total residual leaf loss can be obtained by comparing the frequency of leaves showing a bite mark at their tip with those showing only signals of wave breakage. Hence, herbivores must be responsible for most of the leaf-blade residual loss of *Cymodocea nodosa* and *Zostera noltii* because more than 75% of their leaves sampled at any date ended in a bite mark, unlike *P. oceanica*, which had negligible consumption rates, and *Z. marina*, for which the frequency of bitten leaves never amounted to more than 5% at any sampling time. The low herbivore pressure on *P. oceanica* in Cala Jonquet suggested by these results seems to be a general feature of the ecology of *P. oceanica* (Cebrián et al. 1996a), even though herbivory can be intense in certain locations during particular seasons (Kirkman & Young 1981, Nedelec et al. 1981). Similarly, the low herbivory suggested on this Mediterranean population of *Z. marina* is in accordance with previous results for Atlantic populations (about 5% of the leaf production removed by herbivores, Wilkins 1982, Nienhuis & Groenendijk 1986). The higher herbivore pressure on *C. nodosa* and *Z. noltii* suggested by our data is also consistent with previous reports of herbivory on these species elsewhere (25 to 50% of leaf production removed for *Z. noltii* in the Dutch Wadden Sea, Jacobs et al. 1981, Vermaat & Vehagen 1996; 0.5 to 43% for *C. nodosa* along the Spanish Mediterranean coast, Cebrián et al. 1996b).

Although our results strongly suggest contrasting herbivory among the 4 species sampled, they show that most leaf production was channelled as detritus, which is consistent with previous results for other seagrass species and highlights the importance of the detrital trophic route in seagrass meadows (Thayer et al. 1984, Hemminga et al. 1991, Klumpp et al. 1993, Cebrián & Duarte 1995, Duarte & Cebrián 1997). Other trophic routes, such as herbivory on epiphytes (Klumpp et al. 1992, Klumpp et al. 1993, Jernakoff et al. 1996), may contribute substantially to the fueling of food webs in seagrass meadows as well. Overall, the existing literature points to detritivory as the main trophic route within seagrass meadows, because epiphytes normally contribute about 40–50% to total meadow primary production and channel about 40% of their production to herbivores (cf. review by Jernakoff et al. 1996), in contrast with seagrasses, which contribute most of the rest but in general lose only 10% of their production to herbivores (cf. review by Thayer et al. 1984), the greater fraction of total meadow production being then available for detritivores. Yet more research is needed to accurately assess the routes through which primary production is

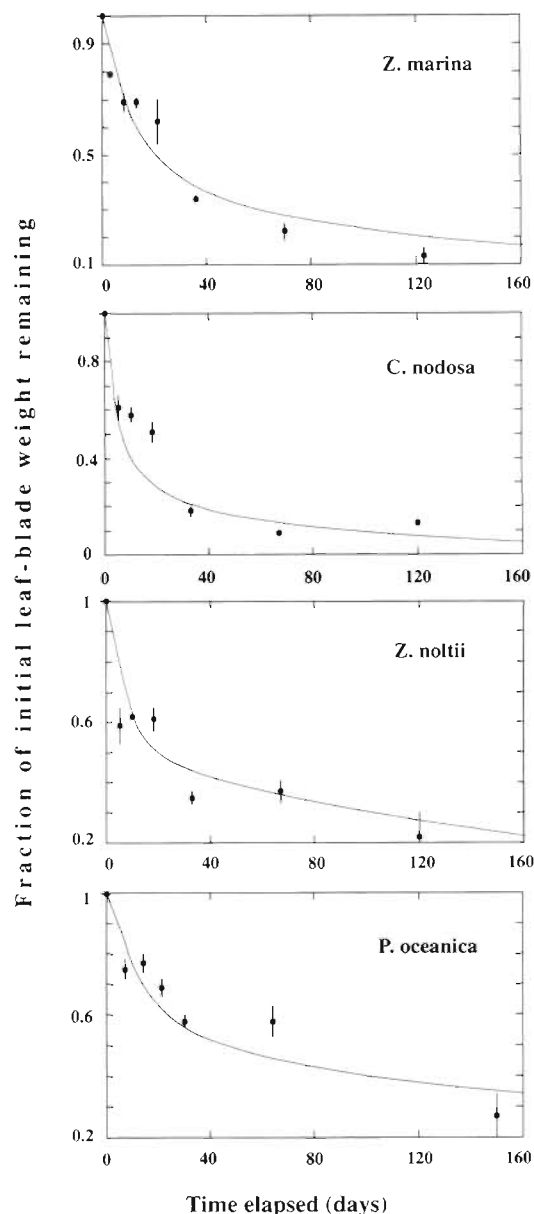


Fig. 4. *Zostera marina*, *Cymodocea nodosa*, *Z. noltii* and *Posidonia oceanica*. Weight loss during decomposition of the leaf-blades in the litter bag experiment. Line depicts the fitted negative exponential equation

transferred to higher trophic levels within seagrass meadows.

We obtained a minimum estimate of the annual trophic flux from seagrass leaf blades to decomposers by multiplying the annual production of detrital leaf-blades and the fraction decomposed annually (Fig. 5), assuming a steady state in the standing biomass of detrital leaf blades (Olson 1963). The annual production of detrital leaf blades by *Posidonia oceanica* and *Zostera marina* is roughly equal to the annual leaf

Table 2. *Zostera marina*, *Cymodocea nodosa*, *Z. noltii* and *Posidonia oceanica*. Published leaf, rhizome and root production values (g DW m⁻² yr⁻¹). Where published values were in grams carbon and in grams AFDW (ash-free dry weight), they have been divided by 0.4 and 0.8, respectively, to be converted into DW (Wium-Andersen & Borum 1984, Hillman et al. 1989, Pedersen & Borum 1993, Van Lent & Verschuure 1994)

	Leaf production	Rhizome production	Root production	Source
<i>Z. marina</i>	856	241		Sand-Jensen (1975)
	1000		455 ^a	Jacobs (1979)
	109	34		Nienhuis & de Bree (1977)
	640	122		Nienhuis & de Bree (1980)
	385–626			Roman & Able (1988)
	1058	789		Wium-Anderson & Borum (1980)
	1000–2000			Sand-Jensen & Borum (1983)
	800–1075		138–255 ^a	Kenworthy & Thayer (1984)
	841–2558	403		Thorne-Miller & Harlin (1984)
	534	385		Robertson & Mann (1984)
	1402	769		Wium-Anderson & Borum (1984)
	1576		812	Pedersen & Borum (1993)
	645–995		177–326 ^a	Olesen & Sand-Jensen (1994)
	200–515		66–165 ^a	Van Lent & Verschuure (1994)
<i>C. nodosa</i>	356–717	34–63	37–171	Peduzzi & Vukovic (1990)
	160–359	46–72		Terrados & Ros (1992)
	420	118	71	Pérez & Romero (1994)
<i>Z. noltii</i>	329			Vermaat et al. (1987)
	379–528			Pérez (1989)
	406		150 ^a	Pérez-Llorens & Niell (1993)
	316–527		202–505 ^a	Vermaat & Verhagen (1996)
<i>P. oceanica</i>	3110	30 ^b	80	Ott (1980)
	604			Wittmann & Ott (1982)
	800–1200			Bedhome et al. (1983)
		42 ^b		Boudouresque et al. (1983)
		27 ^b		Pirc (1983)
	700	2–34 ^b		Bay (1984)
	1742			Frankignoulle & Distèche (1984)
	1100–1200			Thélin & Giorgi (1984)
	613	27 ^c		Wittmann (1984)
	1760–2500			Libes (1986)
		9–66 ^b		Pergent (1987)
	472–557			Esteban (1989)
	730	37–55 ^b	15–73	Romero (1989)
		8–30 ^b		Semroud et al. (1990)
	183–638			Pergent & Pergent-Martini (1991)
	149–438			Buia et al. (1992)
	455–1570	42–173 ^b	9–130	Sánchez-Lizaso (1993)
	126–1231	4–66 ^b		Pergent-Martini et al. (1994)

^aIncludes both rhizome and root production
^bOnly vertical rhizome, i.e. rhizome production of short shoots
^cOnly horizontal rhizome

blade production, since no significant net increment of leaf biomass is observed over the sampling year (Fig. 2) and herbivory is negligible. The annual production of detrital leaf-blades by *Cymodocea nodosa* and *Z. noltii* has been assumed to equal the annual leaf blade production shed after senescence plus half of the annual leaf-blade residual loss. The assumption that 50% of the residual loss corresponds to detrital production represents a best guess and yet has little effect on our estimates of detrital leaf-blade production since leaf-blade shedding by senescence is always much

higher than the residual leaf-blade loss (Table 1). The fraction of detrital leaf-blade production decomposed annually was derived from the decay rates obtained from May to October (see 'Methods'), thereby ignoring the seasonal variability in the decay rates of seagrass leaves (Harrison 1989, Romero et al. 1992). Yet, because most of the total annual leaf-blade shedding by senescence, which accounts for most of the detrital leaf production (see 'Results'), and subsequent decay occur during the period covered by our decay experiment, we believe that our estimates are representative

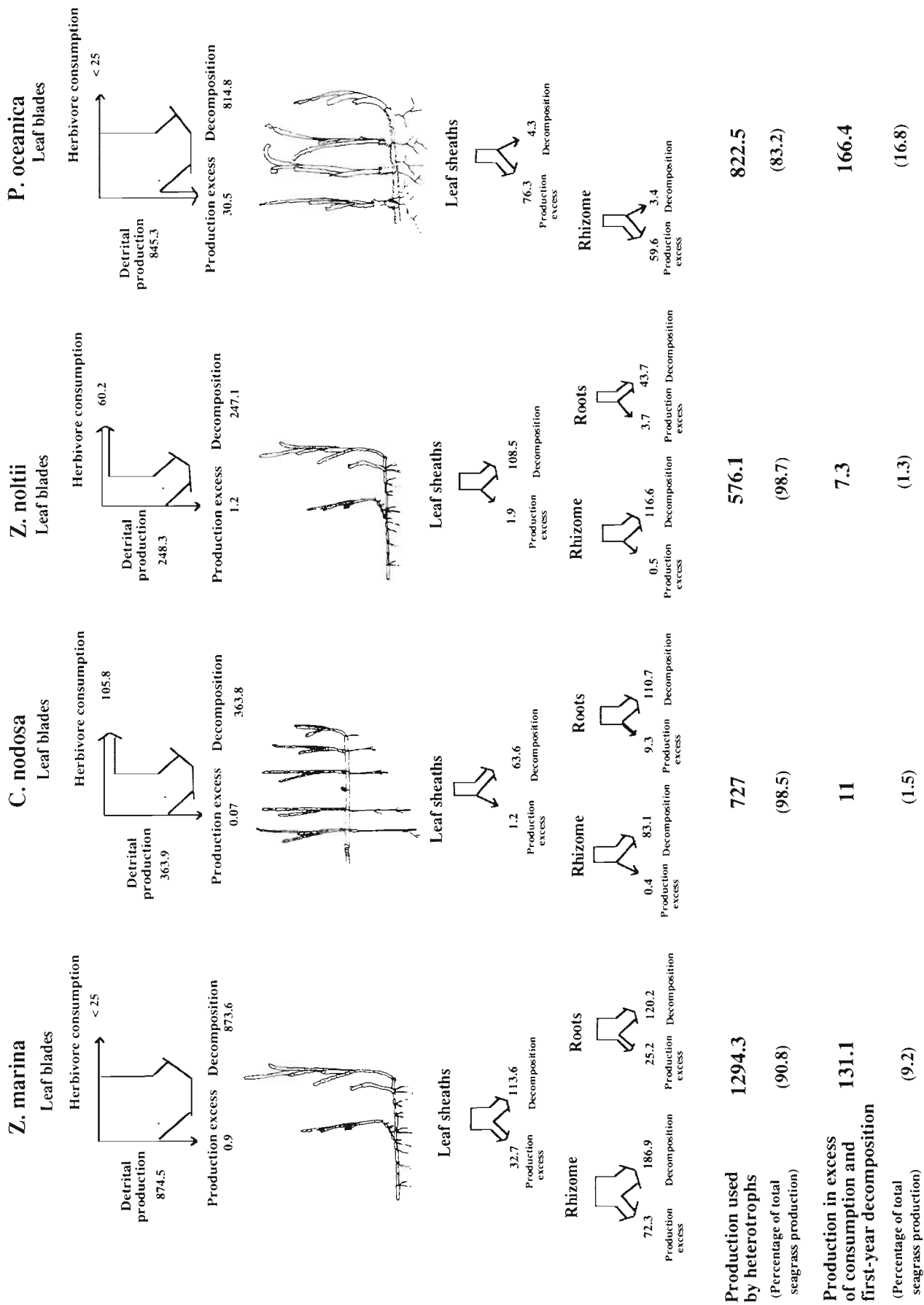


Fig. 5. *Zostera marina*, *Cymodocea nodosa*, *Z. noltii* and *Posidonia oceanica*. Summary of the results reflecting the fate of the production of the species studied. Values are in g DW m⁻² d⁻¹. Herbivore consumption of *C. nodosa* and *Z. noltii* has been assumed to equal 50% of the annual leaf-blade residual loss rate (see 'Discussion')

of the fraction of detrital leaf-blade production decomposed annually. Moreover, because the seasonal variability in decay rates is ignored for the 4 species, our estimates must be indicative of the existing differences in the flux from detrital leaf blades to decomposers among the 4 species.

Likewise, the belowground material (i.e. leaf sheaths, rhizomes and roots) available to decomposers must equal the annual belowground production, since no significant increment in belowground biomass over the sampling year occurred for any of the species (Fig. 3) and herbivory on their belowground parts is thought to be negligible (Ballesteros et al. 1989). The decay rates of belowground material, which allowed a minimum estimate of the fraction of detrital belowground production which is decomposed annually under the assumption of steady state in the standing belowground detrital biomass, were derived from the literature (0.0035 and 0.0048 d^{-1} for rhizomes and roots of *Zostera marina*, respectively, Kenworthy & Thayer 1984; 0.015 and 0.007 d^{-1} for rhizomes and roots of *Cymodocea nodosa*, respectively, Mateo 1995; the decay rates of the leaf sheaths of these 2 species were assumed to be the mean value between the rhizome and root decay rates; 0.00015 d^{-1} for all the belowground components of *Posidonia oceanica*, Mateo 1995). For *Z. noltii*, we assumed the same decay rates as for *C. nodosa*, because they grow in a heterospecific meadow (Fig. 1), and are therefore subject to very similar abiotic conditions which influence decomposition, and because the nutrient content of their belowground parts was relatively similar (Enríquez, Duarte, Marbà & Cebrián unpubl. data). The use of decay rates measured in other environments introduces some variability in our estimates of annual decomposition in Cala Jonquet. Although comparisons of decomposition rates of a given seagrass species among different environments are scarce, this variability seems to lie well below 50% of the average decomposition rate (Harrison 1989, Mateo 1995), provided equality in the methodological conditions (i.e. mesh size of the litterbag and fresh/dry state of the detrital material treated). In spite of considering a variability of 50% around the values of decay rates used, the estimated differences among the 4 species in the amount of production decomposed and the main conclusions reached in this paper (see below) are not altered significantly.

Hence, we believe that our estimates of the trophic flux from seagrass detritus to decomposers, albeit only approximate, are indicative of the existing differences among the 4 species. Moreover, the underestimation of root production entailed by the methods employed (see 'Methods') can little affect our calculation of trophic flux to decomposers because root production only

accounts for a minor fraction of seagrass production (Table 2). The estimated seagrass production used annually by decomposers varies by 2.5 times among species, from $515.9\text{ g DW m}^{-2}\text{ yr}^{-1}$ for the least productive species *Zostera noltii* to $1294.3\text{ g DW m}^{-2}\text{ yr}^{-1}$ for the most productive species *Z. marina*. Hence our results indicate that the most productive species in Cala Jonquet Bay, i.e. *Z. marina* and *Posidonia oceanica*, may support about 2 to 3 times the detritivore production supported by the least productive ones, i.e. *Cymodocea nodosa* and *Z. noltii*, assuming a similar detritivore growth efficiency. In contrast, our results suggest these latter species transfer a greater trophic flux of leaf production to herbivores (Fig. 5), and may, therefore, maintain a higher herbivore production than *Z. marina* and *P. oceanica*, assuming a similar herbivore growth efficiency.

Seagrass production not eaten by herbivores nor decomposed by detritivores during the first year represents an upper limit of the production buried as refractory detritus, which in turn corresponds to production lost for heterotrophic use and thus points to the seagrass' capacity as a sink for organic carbon. Diagenetic losses will act upon the excess of production over consumption and decomposition during the first year and long-term accumulation of seagrass carbon will be only a tiny fraction of this production excess (Middelburg et al. 1993). Still, these estimates should be indicative of the differences in the burial of refractory detritus among the 4 species, provided the differences in long-term decay rates among the species are taken into account. The production excess over consumption and decomposition during the first year is over 1 order of magnitude higher for the most productive species (*Zostera marina* and *Posidonia oceanica*) in relation to the least productive ones (*Cymodocea nodosa* and *Z. noltii*; Fig. 5). On a long-term scale, however, the differences in the production stored as refractory material between *P. oceanica* and the other 3 species will certainly be more pronounced, since long-term decay rates for *P. oceanica* are slower (Pergent et al. 1994, Mateo 1995). Yet, these estimates suggest that *Z. marina* should bury higher amounts of refractory detritus than *C. nodosa* and *Z. noltii*, with *Z. marina* acting, therefore, as a greater sink for carbon in relation to the other 2 species, assuming similar long-term decay rates. Moreover, our estimates of production excess represent a lower percentage of the total production of *C. nodosa* and *Z. noltii* (about 1.5%) in relation to the percentage represented for *Z. marina* (9.2%) and *P. oceanica* (16.8%), further pointing to the limited capacity of *C. nodosa* and *Z. noltii* as sinks for refractory carbon (Fig. 5). Instead, heterotrophs consume virtually all the production of *C. nodosa* and *Z. noltii* (Fig. 5), pointing to fast production recycling.

We show that the trophic flux of seagrass production to secondary consumers, for the 4 species sampled in Cala Jonquet Bay, increases with the magnitude of seagrass production, with decomposition by detritivores being remarkably dominant over consumption by herbivores for the 4 species (Fig. 5). The excess of production over consumption and first-year decomposition is also higher for the most productive species. These results, along with the inferences on the potential secondary production sustained and the capacity to bury refractory detritus by the 4 Western Mediterranean seagrass species, are restricted to Cala Jonquet Bay and cannot be extrapolated to other Mediterranean locations since the levels of production reached by these species may vary widely (Table 1) and *Zostera marina* is almost non-existent elsewhere in the Mediterranean. However, our results are indicative of marked differences in the fate of production among the 4 Mediterranean seagrass species growing in Cala Jonquet Bay which are independent of differences in the level of production reached. Namely, the variability found in herbivore contribution to the total flux of seagrass production to secondary consumers and, then, herbivore pressure on seagrass production (i.e. percentage of seagrass production consumed by herbivores) seems instead associated with differences in the leaf turnover rate, the species with the highest leaf turnover rates (i.e. *Z. noltii* and *Cymodocea nodosa*) losing a greater percentage of their production to herbivores. This is in agreement with the tendency for the percentage of leaf production removed by herbivores to increase with the leaf turnover rate found among seagrass species (Cebrián 1996). This tendency should result from the lower levels of lignin and higher levels of carbohydrates typically found in the leaves of faster-growing species (cf. Cebrián 1996), which would render them more palatable for herbivores and would thus entail herbivore preference for them. The association between the percentage of leaf production consumed and turnover rate has also been found at a general scale comparing different types of primary producers (Cebrián & Duarte 1994) and has also been justified on the basis of a higher trophic quality of faster-growing plants. Moreover, the similarity among the estimates of herbivory on these 4 species registered in very different locations (for instance, herbivory on *Z. marina* and *Z. noltii* in Atlantic populations and in Cala Jonquet Bay, and that on *Posidonia oceanica* in contrasting environments along the Spanish coast) suggests that herbivory variability among seagrass species may be linked to differences in species-specific properties with implications on the seagrass trophic value, such as the leaf turnover rate, apart from being also influenced by environmental variability (Cebrián et al. 1996b).

Our results also suggest that seagrass species with a lower leaf turnover rate could accumulate larger pools of refractory detritus, provided there is variability in long-term decay rates among species, because the percentage of production escaping from consumption by herbivores and first-year decomposition by detritivores is higher for the sampled species with lower leaf turnover rates. This hypothesis is supported by the large pools of refractory detritus observed for seagrass species with relatively slow-growing leaves, for instance *Posidonia oceanica* (Romero et al. 1994, Mateo 1995), *Posidonia australis* (Shepherd & Sprigg 1976) or *Thalassodendron* sp. (Lipkin 1979), in comparison with the much smaller pools supported by other species with faster-growing leaves, such as *Cymodocea nodosa* (Mateo 1995), *Zostera marina* (Kenworthy & Thayer 1984, Pellikaan & Nienhuis 1988) or *Thalassia testudinum* (Kenworthy & Thayer 1984), which could result from the lower decay rates, probably associated with higher lignin content, of the former species (Kenworthy & Thayer 1984, Harrison 1989). This hypothesis is further in agreement with the general dependence of the size and turnover of the plant detrital pool on plant turnover rate for aquatic and terrestrial plant communities (Cebrián & Duarte 1995). Hence we suggest that, whereas the magnitude of production reached by a seagrass species should be indicative of the amount of the total secondary production (herbivores + detritivores) maintained by the seagrass, differences in the leaf turnover rate among species should help explain differences in the percentage of production consumed by herbivores and in the percentage of detrital production recycled or buried as refractory detritus. On this basis, species with faster-growing leaves would transfer greater percentages of production to herbivores and recycle most of the residual detrital production, thereby storing relatively smaller refractory detrital pools, in comparison with species with slower-growing leaves. This hypothesis, if confirmed, should imply that herbivores and detritivores, through consumption of photosynthetic material and recycling of detrital material, respectively, must have a greater impact on the production dynamics of faster-growing seagrass species compared with slower-growing species.

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Erratum

Magnitude and fate of the production of four co-occurring Western Mediterranean seagrass species

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- On page 39, an incorrect unit appeared in the legend to Fig. 5. The correct unit for the values in the figure is $\text{g DW m}^{-2} \text{ yr}^{-1}$