

# Meiofaunal production and energy transfer efficiency in a seagrass *Posidonia oceanica* bed in the western Mediterranean

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**ABSTRACT:** Measurements of secondary production of meiofaunal assemblages are limited, and for most seagrass systems no information is available yet. In the present study meiofaunal production was estimated in a *Posidonia oceanica* bed in the NW Mediterranean Sea using the summation of biomass increments and different equations based on the production:biomass ratio (i.e. biomass turnover). Total meiofaunal production ranged from 7.5 to 13.2 gC m<sup>-2</sup> yr<sup>-1</sup>, according to the approach utilised (mean value 10.0 ± 1.9 gC m<sup>-2</sup> yr<sup>-1</sup>, median value 9.6 gC m<sup>-2</sup> yr<sup>-1</sup>). These values are among the highest reported worldwide, indicating that seagrass systems are hot spots of meiofaunal production. Despite the numerical dominance of nematodes, harpacticoid copepods were responsible for about 50% of total meiofaunal production, followed by polychaetes and nematodes (34 and 12%, respectively). Daily meiofaunal production rates were highest in February–March (21.3 mgC m<sup>-2</sup> d<sup>-1</sup>), late May–June (31.4 mgC m<sup>-2</sup> d<sup>-1</sup>) and October–December (44.6 to 52.0 mgC m<sup>-2</sup> d<sup>-1</sup>). Analysis of daily secondary production of the dominant taxa suggested that different meiofaunal components dominated in different periods. During February–March, May–June and September–October harpacticoid copepods displayed highest production rates, but in November and December daily meiofaunal production was largely accounted for by polychaetes and nematodes. Temporal analysis of total meiofaunal production also revealed that, conversely to what is expected for temperate environments, only ca. 15% of the meiofaunal carbon was produced in summer, whereas 23% was observed in spring and 45% in autumn. Temporal changes in total meiofaunal daily production were apparently not dependent upon temperature, but rather reflected changes in the content and bio-availability of sediment organic matter in the seagrass bed. The seagrass *P. oceanica* was responsible, together with microphytobenthos, for high primary production values (169 to 300 gC m<sup>-2</sup> yr<sup>-1</sup>). The fraction of total benthic primary production potentially consumed by meiofauna (as a measure of seagrass trophic efficiency) ranged from 10 to >50%. These estimates provide evidence of the relevance of meiofauna in benthic energy flows. At the same time, the production efficiency in the *Posidonia* bed (calculated by the ratio of total meiofaunal production to total primary production) was only 3.0 to 5.3%. These values, comparable to those observed in estuarine/organic-rich systems, are 2 to 10 times lower than those estimated in *Cymodocea nodosa* or *Zostera noltii* seagrass meadows, indicating that the *Posidonia* system is less efficient than other seagrass systems in channelling primary production to higher trophic levels.

**KEY WORDS:** Meiofauna · Secondary production · Energy transfer efficiency · *Posidonia oceanica* · Mediterranean Sea

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## INTRODUCTION

Seagrasses are among the most productive ecosystems worldwide and contribute significantly to the pro-

ductivity of coastal areas in both temperate and tropical waters (Phillips & McRoy 1980). In the oligotrophic Mediterranean Sea, *Posidonia oceanica* meadows are extensively distributed at depths ranging from <0.5 to >35 m, and reach primary production (PP) values up to 3000 gC m<sup>-2</sup> yr<sup>-1</sup>, playing a key ecological role (Ott

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1980). Seagrasses indeed represent an important food source for benthic consumers, offer refuge from predation to several benthic species, are nursery areas for fish juveniles, and have an important structuring role, enhancing habitat complexity, supporting epiphytes and modifying sediment texture and hydrodynamic regime (Kikuchi & Pérès 1977, Heck & Orth 1980, Orth & Van Montfrans 1984, Gambi et al. 1990, Renones et al. 1995, Gacia et al. 1999, De Falco et al. 2000).

Trophic interactions in *Posidonia* meadows are highly complex. Though grazing activity on epiphytes can be important to vagile fauna inhabiting the leaf stratum (Gambi et al. 1992), seagrass ecosystems are assumed to be characterised by detritus-based food webs (Mateo & Romero 1997), in which the direct consumption of living seagrass is restricted to few consumers (Mazzella et al. 1992). Due to the dominance of structural carbohydrates and to the very low protein content, phytodetritus produced by these phanerogams is highly refractory (Lawrence et al. 1989). The low degradability of seagrass carbon results in a low bio-availability of sediment organic matter (Danovaro et al. 1994). Phytodetritus produced by seagrasses needs bacterial 'aging' to become available to secondary producers (Velimirov 1986) and once degraded or converted into bacterial biomass, enters the benthic food web mostly through benthic consumers (i.e. meiofauna [Novak 1982, Danovaro 1996] and macrofauna [Lepoint et al. 2000]).

Trophic-efficient ecosystems are those able to channel PP to secondary production with minor losses. Whether seagrass systems act as detritus traps or as promoters of high secondary production is an important issue from an ecological point of view. The complexity of seagrass habitats makes it difficult to take into account all components contributing to secondary production (epiphytes, lower and upper leaf fauna, vagile fauna, benthic epifauna, infauna; Gambi et al. 1992, Zupo & Nelson 1999). One alternative way for estimating trophic efficiency of seagrass systems is relating total primary production to the secondary production of a single benthic component. In *Posidonia oceanica* systems, macroinfaunal assemblages, despite their high diversity, generally show low biomass and production values (Albertelli et al. 1996), and similar values have been reported for *Halophila/Heterozostera* habitats from Australia (Edgar 1990). This would support the hypothesis that seagrass systems have a low trophic efficiency, but quantitative estimates are still lacking. Moreover, estimates of trophic efficiency based on macrofaunal production can be biased by the supply and/or export of larvae from/to other systems.

Meiofaunal assemblages are highly suitable for trophic efficiency assessments as: (1) they are charac-

terised by life cycles spent entirely in the sediment (i.e. lack of pelagic dispersion); (2) their production is not masked by allochthonous inputs; (3) they respond promptly to all different organic matter sources and are closely coupled to primary production inputs; (4) they display high densities ( $>10^6$  ind.  $m^{-2}$ ), high turnover rates and high secondary production values (often higher than macrofaunal production), thus playing a key role in benthic energy flows (Heip et al. 1982, Feller & Warwick 1988, Higgins & Thiel 1988, Ceccherelli & Mistri 1991, Danovaro & Fabiano 1996, Albertelli et al. 1999). Moreover, meiofauna represent a direct link between producers and higher trophic levels because they are efficient in exploiting organic detritus and, at the same time, are predated upon by both macrofauna and juvenile fish (Watzin 1983, De Morais & Bodiou 1984, Lindquist et al. 1994).

Estimates of meiofaunal production and food requirements are particularly important in seagrass systems, where the fate of the organic material released by leaf decay is unclear and estimates of the fraction of PP actually entering benthic food webs are lacking. Despite the increasing evidence of meiofaunal relevance in *Posidonia oceanica* meadows (Novak 1992, Danovaro 1996), information on meiofaunal secondary production and their contribution to organic carbon pathways in seagrass food webs is completely lacking.

In this study we estimated meiofaunal secondary production and provided quantitative estimates of the efficiency of a Mediterranean seagrass system (*Posidonia oceanica*) in channelling primary production to higher trophic levels. To do this we analysed the ratio of meiofaunal secondary production (the component assumed to be able to channel organic carbon to higher trophic levels) to total benthic primary production. Temporal patterns in meiofaunal production were also investigated to better understand factors controlling production efficiency. Finally, these estimates were compared to those calculated in different environments to provide new insights on the production efficiency of vegetated and non-vegetated coastal ecosystems.

## MATERIALS AND METHODS

**Study area.** This study was carried out from January 1991 to January 1992 in a *Posidonia oceanica* bed in Prelo Bay, Golfo Marconi, Ligurian Sea (NW Mediterranean Sea; 44° 20' 08" N, 9° 12' 09" E). Sediment samples were collected by SCUBA divers on a monthly basis. Sampling frequency was increased to 2 wk intervals from March to June. The study area was sheltered and characterised by the presence of a large *P. oceanica* meadow that formed an almost continuous

and dense belt from 0.4 to 9.0 m depth. The sampling station was located at 4 m depth where ca. 375 shoots  $\text{m}^{-2}$  were found. From 4 to 6 m depth, seagrass primary production was homogeneous, but displayed interannual changes from a minimum value of 104.5 to a maximum of 235.2  $\text{gC m}^{-2} \text{yr}^{-1}$  (Boyer 1991 and Guidetti 2000, respectively). In this study area, primary production values within this range have been consistently reported in different years (Danovaro 1993, Danovaro et al. 1994). Microphytobenthic production, estimated in the same sampling station where seagrass primary production was measured, reached values of 64.8  $\text{gC m}^{-2} \text{yr}^{-1}$  (Danovaro 1993).

**Meiofaunal biomass and production.** Meiofauna samples were collected in replicate cores ( $n = 2$  to 4, internal diameter 3.7 cm, surface area 10.7  $\text{cm}^2$ ) down to a depth of 12 cm. Sediment samples were first placed in a hot (60°C) 0.4  $\mu\text{m}$  prefiltered seawater solution to relax the animals, thus allowing a better morphometric analysis, and then fixed with a 4% formaldehyde buffered solution. Sediments were sieved through 1000 and 37  $\mu\text{m}$  mesh. The fraction remaining on the 37  $\mu\text{m}$  sieve was centrifuged 3 times in Ludox HS (density 1.18  $\text{g cm}^{-3}$ ) in order to separate the lighter organisms from the heavier sediment grains (Heip et al. 1985). All meiobenthic animals were counted and classified under a stereo microscope after staining with Rose Bengal (0.5  $\text{g l}^{-1}$ ).

Body volume of meiofaunal organisms was derived from measurements of body shape. For nematodes, body volume was calculated using Andrassy's formula:

$$V = L(W/2)^2\pi \times 10^{-6} \quad (1)$$

where  $V$  = the volume (nl);  $L$  = the length ( $\mu\text{m}$ );  $W$  = the width at the middle of the oesophagus ( $\mu\text{m}$ ).

For all other meiofaunal organisms, individual biovolume was estimated from body length and width using the formula:

$$V = L \times W^2 \times C \quad (2)$$

where  $L$  = body length (mm);  $W$  = body width (mm);  $C$  = the approximate conversion factors for each meiofaunal taxon (Feller & Warwick 1988). The body volume was then multiplied by an average density (1.13  $\text{g cm}^{-3}$ ; Feller & Warwick 1988) to obtain the biomass and the dry:wet wt ratio was taken to be 0.25 (Warwick & Gee 1984).

The overall meiofaunal production on an annual basis was calculated in various ways to facilitate comparability of our data to those available in the literature (Heip et al. 1982):

(1) Production estimates were based on the method of summation of biomass increments at each sampling period during a year's sampling (also defined as 'minimal production', Arntz 1971):

$$P_{\text{tot}} = \Delta B_{t_1-t_0} + \Delta B_{t_2-t_1} + \dots + \Delta B_{t_n-t_{n-1}} \quad (3)$$

where  $P_{\text{tot}}$  = total annual meiofaunal production;  $\Delta B_{t_1-t_0}$  = the total biomass increment between 2 subsequent samplings;  $t_n-t_0 = 1$  yr.

(2) Production estimates were calculated by multiplying the annual mean biomass of the entire meiofaunal assemblage by their ratio of production to biomass (i.e. biomass turnover, PB) on an annual basis ( $P/B = 9$ , according to Gerlach 1971, or  $P/B = 10$ , according to McIntyre 1964):

$$P_{\text{tot}} = P/B \times B_{\text{annual}} \quad (4)$$

where  $B_{\text{annual}}$  = mean annual meiofaunal biomass.

(3) Production estimates were based on production:biomass ratios specific for each taxon (i.e.  $P/B = 8.4$  for nematodes, 18 for harpacticoids, and 5 for annelids and turbellarians, according to Warwick et al. 1979; or  $P/B = 9.75$  for nematodes, 21 for copepods, 11.3 for turbellarians, 9.7 for annelids, and 9.12 for other taxa according to Lasserre et al. 1976):

$$P_{\text{tot}} = P_{\text{nem}} + P_{\text{cop}} + P_{\text{anel}} + P_{\text{turb}} + P_{\text{oth}} \quad (5)$$

and

$$P_{\text{taxon}} = P/B_{\text{taxon}} \times B_{\text{taxon}} \quad (6)$$

where  $P_{\text{nem}}$  = total nematode production;  $P_{\text{cop}}$  = total harpacticoid copepod production;  $P_{\text{anel}}$  = total annelid production;  $P_{\text{turb}}$  = total turbellarian production;  $P_{\text{oth}}$  = total production of all others meiofaunal taxa;  $P_{\text{taxon}}$  = annual production of each taxon;  $P/B_{\text{taxon}}$  = annual biomass turnover of each taxon;  $B_{\text{taxon}}$  = annual mean biomass of each taxon.

Direct methods for estimating total meiofaunal production (e.g. species-specific growth increments, identifiable cohorts) are operationally not feasible at a community level, because of the taxonomic difficulty in identifying meiofauna to species level, and because of the small size of meiofaunal organisms (Higgins & Thiel 1988). Moreover, *in situ* estimates based on oxygen consumption are not possible because meiofauna respiration can not be efficiently distinguished from bacteria and protozoa oxygen consumption. At the same time, the approaches we used are limited since the methods of biomass-increment summations underestimate the value of total meiofaunal production. Methods based on annual  $P:B$  ratios are subjected to problems of accuracy (Warwick 1980).  $P:B$  ratios are variable within each taxon (a range of 4 to 63 was observed for nematodes, Vranken et al. 1986). Moreover, it is not easy to establish a single  $P:B$  ratio for the entire community (Vranken & Heip 1986). Therefore, we recognise that methods used here need further validation with other specific estimates, but still remain the only way to provide comparable values of total meiofaunal secondary production (McIntyre 1964, Ankar & Elmgren 1976, Warwick et al. 1979, Escar-

average et al. 1989, Chardy & Dauvin 1992, Chardy et al. 1993, Danovaro & Fabiano 1996).

The temporal analysis of meiofaunal secondary production (MP) was investigated by identifying which periods displayed highest biomass increments, and which biotic/environmental factors were responsible for such changes. In this case we applied the Warwick's fractionated *P:B* ratios to each sampling period, as follows:

$$\text{MP} = \sum_{i=1}^n \frac{\text{MBM}_i \times P/B_i}{T_1} + \sum_{i=1}^n \frac{\text{MBM}_i \times P/B_i}{T_2} + \dots + \sum_{i=1}^n \frac{\text{MBM}_i \times P/B_i}{T_n} \quad (7)$$

and

$$\text{MP}_{T_1} + \text{MP}_{T_2} + \text{MP}_{T_n} \dots = 1 \text{ yr} \quad (8)$$

where MP = meiofaunal secondary production ( $\text{g C m}^{-2} \text{ yr}^{-1}$ );  $n$  = number of taxa;  $\text{MBM}_i$  = the average meiofaunal biomass of each taxon at each sampling interval;  $P/B_i$  = the production to biomass ratio utilised for each taxon on a daily basis and calculated by dividing the annual *P:B* ratio by the number of days of each sampling period;  $T$  = the number of days between 2 subsequent samplings;  $T_1, T_2, T_n$  = is the sequential number of sampling intervals;  $\text{MP}_{T_1}$  = is meiofaunal production determined for each sampling interval.

**Meiofaunal energetic demand and estimates of trophic and production efficiency.** Information available on conversion factors applicable for estimates in meiofaunal energetic demand is extremely limited. Carbon conversion factors are needed to estimate the amount of carbon required (i.e. food demand) for yielding a unit of secondary production. Estimates of food demand are generally made using conservative factors, which have the main limit of not taking into account temporal variability in benthic metabolism and/or organic carbon bioavailability (Danovaro et al. 2001). The C-conversion efficiency factors utilised in literature are: (1) 32.5%, based on direct metabolic measurements (Warwick et al. 1979). This value has been corroborated by direct estimates based on respiration rates (30 to 40%, Herman et al. 1984); (2) 10%, based on the Lindeman concept of flux energy through trophic levels within an ecosystem (Bouvy 1988). In order to take into account errors due to the use of different conversion factors, meiofauna food demand was estimated using both factors as follows:

$$\text{MFD} = \text{MP}/\text{CCE} \quad (9)$$

where MFD = meiofaunal food demand (as  $\text{g C m}^{-2} \text{ yr}^{-1}$ ); CCE = carbon conversion efficiency (i.e. 32.5 or 10%).

The ratio of meiofauna food demand to total primary production (microphytobenthic production plus *Posidonia oceanica* production) represents the fraction of

primary production utilised for meiofaunal growth (i.e. trophic efficiency expressed as percentage).

$$\text{TE} = \text{MP}/\text{BPP} \times 100 \quad (10)$$

where TE = trophic efficiency; BPP = total benthic primary production (as  $\text{g C m}^{-2} \text{ yr}^{-1}$ ). The production efficiency (PE) was estimated as the ratio of MP to total primary production (as seagrass plus microphytobenthic primary production, from the same sampling station and based on synoptic samplings):

$$\text{PE} = P_t/P_{t-1} \quad (11)$$

where PE = production efficiency (expressed as percentage);  $P_{t-1}$  = the production of the exploited trophic level (in this case BPP);  $P_t$  = the production of the higher trophic level (in this case MP).

## RESULTS AND DISCUSSION

### Meiofaunal biomass and production in seagrass *Posidonia oceanica* beds

The range of individual body weights of the main meiofaunal taxa encountered in the *Posidonia oceanica* bed (Table 1a) overlapped with those previously reported from other coastal environments (see Higgins & Thiel 1988: review). The only exception was represented by nematodes, which displayed an individual biomass higher than values reported in the Atlantic and North Sea coasts ( $0.2$  to  $0.5 \mu\text{g C ind.}^{-1}$ ; Witte & Zijlstra 1984, Escaravage et al. 1989). However, this feature can be typical of seagrass systems as similar values have been repeatedly reported by Novak (1989) and Danovaro et al. (1999) from different Mediterranean *Posidonia* systems. Despite their body size and their dominance in terms of density (on annual average nematodes accounted for 44% of total meiofaunal density), nematodes biomass (range:  $0.2 \pm 0.1$  to  $4.8 \pm 2.5 \text{ g C m}^{-2}$  in April and November, respectively; Table 1b) accounted only for 12% of total meiofaunal biomass, which was mostly accounted by polychaetes (58%) and harpacticoid copepods (23%). The average individual biomass of all taxa was characterised by a high degree of variability (Table 1). Such large variability requires great caution when *P:B* ratio-based estimates of secondary production are calculated.

Total meiofaunal biomass in the investigated *Posidonia oceanica* bed (on average  $1.0 \text{ g C m}^{-2}$ ) was comparable to values reported from other Mediterranean seagrass systems (Novak 1989) and in a nearby sandy areas characterised by the presence of *Cymodocea nodosa* (average meiofaunal biomass:  $0.8 \text{ g C m}^{-2}$ ; Danovaro & Fabiano 1996). High meiofaunal biomass values (range:  $1.2$  to  $2.4 \text{ g C m}^{-2}$

equivalent to 2.98 to 6.01 g dry wt m<sup>-2</sup>) have been also reported in *Zostera noltii* beds along the Atlantic coast (Escaravage et al. 1989). Such comparisons are not biased by variability in biomass estimates since, on annual average, the coefficient of variation for total meiofaunal biomass was 42.9%. Therefore, it is possible to conclude that meiofaunal biomass in the *Posidonia oceanica* bed was high, thus reflecting the large organic carbon inputs provided by benthic primary production.

Often comparisons of secondary production from different areas are difficult because different methods are used for their estimation. In the present study, all different calculation methods of total meiofaunal production provided similar results (Table 2), displaying a coefficient of variation of 19%. As expected, the lowest estimate of total meiofaunal production (7.5 gC m<sup>-2</sup> yr<sup>-1</sup>) was obtained using Arntz's method (also defined

minimal production because it does not take into account predatory losses), whereas the highest value (13.2 gC m<sup>-2</sup> yr<sup>-1</sup>) was obtained using the fractionated *P:B* ratios proposed by Lasserre et al. (1976). Meiofaunal production estimates in the *Posidonia oceanica* bed (mean value 10.0 ± 1.9 gC m<sup>-2</sup> yr<sup>-1</sup>, median value 9.6 gC m<sup>-2</sup> yr<sup>-1</sup>) were 4 to 5 times higher than those reported in the North and in the Baltic Sea (McIntyre 1964, Ankar & Elmgren 1976) or in the Atlantic (Chardy & Dauvin 1992, Chardy et al. 1993). Similarly high values in subtidal sediments have been reported only from other seagrass systems and estuarine environments (Warwick et al. 1979, Escaravage et al. 1989). Such differences are so important that they cannot be masked by the variability associated with the method used for estimating secondary production nor by the variability associated with the meiofaunal biomass estimates.

Table 1. Individual (a) and total biomass (b) of nematodes, copepods, polychaetes, turbellarians and others organism (0 to 4 cm) during 1991–1992 study period. na: not available

<b>(a)</b>												
Date	Nematodes		Copepods		Polychaetes		Turbellarians		Other taxa			
	µgC ind. <sup>-1</sup>	±SD										
17 Jan 91	0.8	1.3	1.8	1.5	28.7	32.5	8.0	7.9	1.3		0.5	
20 Feb 91	0.8	0.9	1.6	6.3	33.1	31.3	3.8	4.1	7.0		2.8	
21 Mar 91	0.7	0.9	1.8	6.1	5.3	15.6	4.9	6.2	1.3		0.5	
08 Apr 91	0.8	0.4	1.6	1.8	66.2	18.2	5.6	4.4	4.0		1.6	
22 Apr 91	1.0	0.7	1.4	0.3	43.0	6.1	3.7	0.4	2.1		0.8	
08 May 91	1.0	1.2	0.5	0.4	18.9	21.6	1.8	1.2	4.6		1.8	
30 May 91	1.0	2.1	0.9	2.9	19.3	19.2	1.8	0.8	1.8		0.7	
28 Jun 91	0.6	0.5	1.3	1.7	36.9	47.8	3.0	3.3	9.4		3.8	
18 Jul 91	0.6	1.0	0.7	0.8	14.9	19.8	0.6	0.2	0.0		0.0	
01 Aug 91	0.5	0.3	0.3	0.4	7.2	5.7	2.2	1.7	48.1		19.3	
05 Sep 91	0.8	1.4	1.4	1.8	8.9	7.8	2.2	3.0	3.2		1.3	
31 Oct 91	0.4	0.5	0.3	0.2	7.8	6.4	na	na	2.3		0.9	
30 Nov 91	1.5	2.0	1.7	4.2	43.9	28.2	3.6	4.0	5.6		2.2	
23 Dec 91	0.3	0.2	0.4	0.4	18.8	23.7	1.3	1.1	2.3		0.9	
07 Jan 92	0.1	0.1	0.2	0.2	7.5	9.5	0.5	0.4	2.7		1.1	
<b>(b)</b>												
Date	Nematodes		Copepods		Polychaetes		Turbellarians		Others		Meiofauna	
	gC m <sup>-2</sup>	±SD	gC m <sup>-2</sup>	±SD								
17 Jan 91	0.17	0.24	0.09	0.09	0.35	0.00	0.18	0.20	0.01	0.01	0.79	0.55
20 Feb 91	0.06	0.01	0.29	0.20	0.63	0.02	0.12	0.07	0.03	0.01	1.13	0.32
21 Mar 91	0.04	0.05	0.25	0.08	0.08	0.02	0.09	0.01	0.01	0.00	0.48	0.17
08 Apr 91	0.05	0.02	0.01	0.09	0.12	0.00	0.02	0.00	0.02	0.01	0.22	0.12
22 Apr 91	0.03	0.02	0.18	0.06	1.23	0.19	0.10	0.01	0.01	0.01	1.54	0.28
08 May 91	0.11	0.15	0.06	0.04	0.19	0.23	0.02	0.02	0.01	0.01	0.39	0.44
30 May 91	0.14	0.14	0.42	0.08	0.44	0.10	0.03	0.01	0.02	0.01	1.05	0.34
28 Jun 91	0.04	0.06	0.48	0.12	0.43	0.13	0.04	0.09	0.04	0.02	1.03	0.41
18 Jul 91	0.08	0.06	0.16	0.06	0.26	0.05	0.02	0.02	0.02	0.02	0.53	0.21
01 Aug 91	0.15	0.06	0.08	0.04	0.18	0.05	0.07	0.05	0.02	0.02	0.50	0.21
05 Sep 91	0.23	0.09	0.32	0.08	0.15	0.04	0.01	0.00	0.02	0.01	0.73	0.22
31 Oct 91	0.10	0.01	0.32	0.03	0.41	0.13	0.00	0.00	0.02	0.00	0.85	0.18
30 Nov 91	0.34	0.27	0.32	0.13	4.00	2.05	0.07	0.05	0.01	0.00	4.75	2.50
23 Dec 91	0.07	0.05	0.06	0.06	0.28	0.08	0.02	0.01	0.03	0.01	0.46	0.21
07 Jan 92	0.20	0.11	0.03	0.02	0.23	0.11	0.03	0.01	0.01	0.01	0.50	0.26

Table 2. Meiofaunal production in Prelo Bay and other areas

Location	Depth (m)	Method	Production (gC m <sup>-2</sup> yr <sup>-1</sup> )	Source
North Sea	Subtidal	<i>P/B</i> = 10	2.5–3.8	McIntyre (1964)
Baltic Sea		<i>P/B</i> = 10	2.7	Ankar & Elmgren (1976)
Lynher UK		<i>P/B</i> <sup>a</sup>	13.5	Warwick et al. (1979)
South Africa	Mud-sand	<i>P/B</i>	0.6–8.0	Dye (1979)
South Africa	Mangrove	<i>P/B</i>	4.3	Dye (1983)
North Sea	Subtidal		9.0	Heip et al. (1983)
North Sea	117	<i>P/B</i> = 2	2.4	Faubel et al. (1983)
Wadden Sea	Intertidal		3.6	Witte & Zijlstra (1984)
Brittany	0–10		16.1	Bodin et al. (1984)
USA	10	<i>P/B</i> <sup>a</sup>	10.1	Rudnick et al. (1985)
New Zealand	Muddy-shelf	<i>P/B</i>	3.6	Probert (1986)
North Sea		<i>P/B</i> = 9	1.1	De-Wilde et al. (1986)
		<i>P/B</i> = 10	1.2	
Canada	Intertidal		15.7	Schwinghamer et al. (1986)
Kerguelen	Intertidal	Arntz, 1971	15.2	Bouvy 1988
		<i>P/B</i> = 9	14.6	
Atlantic	Intertidal	<i>P/B</i> <sup>b</sup>	6.5–29.4	Escaravage et al. (1989)
Atlantic	20	<i>P/B</i> = 14.5	4.1	Chardy & Dauvin (1992) <sup>c</sup>
Atlantic	10	<i>P/B</i> = 14.6	4.4	Chardy et al. (1993)
Marconi Gulf,	10	Arntz, 1971	3.2	Danovaro (1993)
Ligurian Sea		<i>P/B</i> = 10	10.6	
		<i>P/B</i> = 9	9.5	
		<i>P/B</i> <sup>a</sup>	8.5	
		<i>P/B</i> <sup>b</sup>	10.9	
Seagrass bed,	4	Arntz, 1971	7.5	Present study
Ligurian Sea		<i>P/B</i> = 10	10.7	
NW Mediterranean		<i>P/B</i> = 9	9.6	
		<i>P/B</i> <sup>a</sup>	9.0	
		<i>P/B</i> <sup>b</sup>	13.2	

<sup>a</sup>Warwick et al. (1979)  
<sup>b</sup>Lasserre et al. (1976)  
<sup>c</sup>Production value not reported by the authors; data are based on average biomass (0.28 gC m<sup>-2</sup>)

Using equations provided by Warwick et al. (1979) for the calculation of the meiofaunal production of each taxon, it was possible to estimate that copepods provided the highest contribution (ca. 50%, i.e. 4.45 gC m<sup>-2</sup> yr<sup>-1</sup>) to the total meiofaunal production, followed by polychaetes and nematodes (34 and 12%, respectively; Table 3). The high secondary production of harpacticoid copepod in this seagrass bed confirmed the relevance of this taxon in systems characterised by strong vegetation cover (Coull et al. 1983, Hicks 1985). Our values of secondary production, though based on a whole taxon, are comparable to those reported for dominant copepod species from different coastal environments, such as *Canuella perplexa* (2.4 to 2.7 gC m<sup>-2</sup> yr<sup>-1</sup> from a brackish-water Mediterranean lagoon, Ceccherelli & Mistri 1991); *Huntemannia jadensis* (0.7 to 1.7 gC m<sup>-2</sup> yr<sup>-1</sup>, Feller 1982), *Microarthridion littorale* (0.6 gC m<sup>-2</sup> yr<sup>-1</sup>, Fleeger & Palmer 1982), and

*Tachidius discipes* (0.98 to 1.01 gC m<sup>-2</sup> yr<sup>-1</sup>, Herman et al. 1984).

The annual turnover rate (as life cycle turnover × number of generations) has been estimated to approximate 9 to 10 for the meiofauna (Coull 1988). Turnover rates are a very difficult parameter to quantify as they depend upon the reproductive potential of the different meiofaunal species, but also on a number of environmental factors (temperature, food supply and availability), which can influence total meiofaunal production and benthic trophic efficiency in exploiting food sources. Biomass turnover rates can be expressed as the ratio of production to biomass. Danovaro (1993) reported a *P:B* ratio for the entire meiofaunal assemblage of ca. 3 from sandy sediments. Similar *P/B* values have been calculated from respiration experiments based on different life stages of crustacean meiofaunal populations (*P/B* = 3, Herman et al. 1984; *P/B* = 3.6, Feller 1982). In the present study, total meiofaunal production estimated using Arntz's method allowed estimating the overall annual biomass turnover rate of 7.5 (*P/B*, calculated as the

ratio of total annual meiofaunal production to annual average biomass). This value was close to those generally reported for meiofaunal assemblages (McIntyre 1964, Gerlach 1971) and about double of those reported for more oligotrophic sandy habitats (Danovaro 1993), suggesting the presence of higher rates in these organic-rich environments. However, *P:B* ratio-based estimates of secondary production must be viewed with caution since the assumption of

Table 3. Relative contribution of different taxa to total meiofaunal production (0 to 4 cm) calculated using the method of Warwick et al. (1979)

	<i>P/B</i>	Biomass (gC m <sup>-2</sup> )	Production (gC m <sup>-2</sup> yr <sup>-1</sup> )	Contribution (%)
Nematodes	8.40	0.13	1.05	11.6
Harpacticoid copepods	18.00	0.25	4.45	49.7
Polychaetes	5.00	0.62	3.11	34.4
Turbellarians	5.00	0.05	0.26	2.8
Others	9.12	0.02	0.18	2.0
Total		1.07	9.05	

average turnover ratios accrues errors due to sampling variance and the variability of biomass estimates.

Temporal changes in meiofaunal production are reported in Table 4. Total daily meiofaunal production displayed evident temporal changes, with highest values in February–March ( $21.3 \text{ mg C m}^{-2} \text{ d}^{-1}$ ), late May–June ( $31.4 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) and October–December ( $44.6$  to  $52.0 \text{ mg C m}^{-2} \text{ d}^{-1}$ ). However, conversely to what is generally expected for temperate environments (in which higher meiobenthic density and production are expected in summer, Soyer [1985]), our estimates of daily meiofaunal production indicated that about 45% of the  $P_{\text{tot}}$  occurred in autumn, ca. 23% in spring, 17% in winter and 15% in summer. Since most daily production values during the ‘warm season’ (e.g. those from July to September, when water temperature is  $>20^\circ\text{C}$ ) lie  $<20 \text{ mg C m}^{-2} \text{ d}^{-1}$ , it is possible to conclude that temporal trends of total meiofaunal production are not temperature-dependent. Therefore, temporal fluctuations in daily production rates must be driven by other factors. In the seagrass system, all periods of high secondary production corresponded to microphytobenthic blooms in February–March and late May–June, and to the release of seagrass leaves and their epiphytes in November–December (Danovaro 1996). Therefore, it is likely that temporal changes in total meiofaunal daily production reflected changes in the content and bio-availability of sediment organic matter in the seagrass bed.

The analysis of daily secondary production of the dominant taxa also suggested that different meiofaunal components dominated in different periods. During February–March, May–June and September–October harpacticoid copepods displayed high daily production rates. However, total daily meiofaunal production in

November and December was largely accounted for by polychaete and nematode production.

### Trophic and production efficiency in *Posidonia oceanica* seagrass systems

In this paper we provided the first estimates of trophic efficiency and production efficiency in a seagrass system. The trophic efficiency was defined as the fraction of total PP that was directly or indirectly channelled (or converted) into meiofaunal production. The fraction of total PP potentially utilised by meiofauna can be estimated from meiofaunal food demand. Using the 2 conversion factors available in the literature (32.5 and 10%, Warwick et al. 1979 and Bouvy 1988, respectively), it is possible to estimate a meiofauna food demand of 27.9 to  $90.5 \text{ g C m}^{-2} \text{ yr}^{-1}$  (Table 5). Though phytoplankton PP in the same area can reach  $61.5 \text{ g C m}^{-2} \text{ yr}^{-1}$  (Fabiano 1984), this contribution was not considered in our budget of total PP since the production of phytoplankton reaching seagrass sediments at 4 m depth was included into estimates of microphytobenthic PP. Therefore, assuming a range of total benthic primary production (BPP as seagrass plus microphytobenthic PP) of 169 to  $300 \text{ g C m}^{-2} \text{ yr}^{-1}$  (this range is the widest possible and includes all errors associated with the spatial and temporal variability) meiofaunal food demand would be equivalent to 17 to 54% and 10 to 30% (assuming the lowest and the highest BPP values, respectively) of the total benthic primary production (Table 5). Overall, these estimates provide quantitative evidence of the relevance of meiofauna in benthic energy flows, indicating that 10 to 50% of the PP in a seagrass system

Table 4. Nematode, copepod, polychaete, turbellarian and other group production during the sampling period, daily production of each taxon and their relative contribution to the total annual meiofaunal production (MP)

Sampling periods	Interval (d)	Production (gC m <sup>-2</sup> interval <sup>-1</sup> )					Total production	Daily production (mgC m <sup>-2</sup> d <sup>-1</sup> )	Control to total MP (%)
		Nematodes	Copepods	Polychaetes	Turbellarians	Others			
Jan–Feb	34	0.09	0.31	0.23	0.07	0.02	0.72	21.1	8.2
Feb–Mar	29	0.03	0.39	0.14	0.04	0.01	0.62	21.3	7.0
Mar–Apr 1	18	0.02	0.12	0.03	0.01	0.01	0.18	10.0	2.0
Apr 1–Apr 2	14	0.01	0.07	0.13	0.01	0.00	0.22	16.0	2.5
Apr 2–May 1	16	0.03	0.10	0.16	0.01	0.00	0.29	18.3	3.3
May 1–May 2	22	0.06	0.26	0.09	0.01	0.01	0.43	19.7	4.9
May 2–Jun	29	0.04	0.64	0.17	0.02	0.02	0.91	31.4	10.3
Jun–Jul	20	0.04	0.47	0.14	0.01	0.02	0.69	34.5	7.8
Jul–Aug	14	0.01	0.02	0.01	0.00	0.00	0.05	3.6	0.6
Aug–Sep	35	0.15	0.35	0.08	0.02	0.02	0.62	17.6	7.0
Sep–Oct	56	0.21	0.88	0.22	0.01	0.03	1.34	24.0	15.3
Oct–Nov	30	0.15	0.47	0.91	0.01	0.01	1.56	52.0	17.7
Nov–Dec	23	0.11	0.22	0.67	0.01	0.01	1.02	44.3	11.6
Dec–Jan	16	0.05	0.03	0.05	0.01	0.01	0.15	9.1	1.7

Table 5. Energetic demand of meiobenthos compared to microphytobenthic and *Posidonia oceanica* production as potential food sources

	Meiofauna		Microphyto- benthos production	<i>P. oceanica</i> production
	Production	Food demand <sup>a</sup>		
	(gC m <sup>-2</sup> yr <sup>-1</sup> )			
Total	9.05	27.85	90.50	64.8
Nematodes	1.05	3.23	10.50	
Copepods	4.45	13.69	44.50	
Polychaetes	3.11	9.57	31.10	
Turbellarians	0.26	0.80	2.60	
Others	0.18	0.55	1.80	

<sup>a</sup>Estimated assuming a conversion factor of 32.5 %  
<sup>b</sup>Estimated assuming a conversion factor of 10 %

can be channelled through meiofauna (including all possible errors in our estimates).

The production efficiency (PE) is generally employed as a measure of the efficiency of energy transfer from one trophic level to the next, and is calculated as the energy produced by one trophic level compared to the production of the exploited trophic level. Besides the difficulties in obtaining reliable production estimates, the ecological efficiency calculated in this way can be biased by the fact that meiofaunal organisms do not represent all consumers of PP present in a seagrass meadow (Velimirov 1991, Gambi et al. 1992). Nonetheless, PEs based on meiofaunal assemblages represent wide-spectrum indicators of the energy transfer from producers to consumers (Higgins & Thiel 1988). In the *Posidonia oceanica* system, the PE was 3.0 to 5.3% (calculated as the ratio of  $P_{tot}$  to total PP; Table 6). The detailed analysis of the PE from different locations (based on homogeneous calculation methods and conversion factors) revealed that our values were very low

and comparable to those observed for high-energy or estuarine organic-rich systems. One might conclude that this is the obvious consequence of the highly refractory composition of seagrass leaves and their phytodetritus, which is known to be largely unavailable to benthic consumers (Pirc & Woltenveber 1988, Danovaro et al. 1999). However, estimates of PE from a *P. oceanica* system were 2 to 10 times lower than those calculated in *Cymodocea nodosa* and *Zostera noltii* seagrass systems from Mediterranean and Atlantic coastal areas (Table 6). It is possible that such low PEs are bal-

anced by a fraction of PP entering benthic food webs through macrofauna or other benthic boundary components. Nonetheless, our results suggest that *P. oceanica* meadows are less efficient than other seagrass systems in the transfer of energy to higher trophic levels.

Further investigations are needed to clarify the reason of such different ecological efficiencies and the extent of errors associated to estimates of MP, but the development of this approach for estimating benthic trophic efficiency, and its extension to other benthic components, can be a promising approach for comparing carbon transfer and energy budgets in different benthic coastal systems.

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Table 6. Comparison of production efficiency from different locations

Location	Environmental features	Depth	Meiofauna production (gC m <sup>-2</sup> yr <sup>-1</sup> )	Benthic primary production (gC m <sup>-2</sup> yr <sup>-1</sup> )	Production efficiency (%)	Source
Atlantic	Estuarine mud flat	Intertidal	19.5	57.3–87.9	22.1–33.9	Escaravage et al. (1989)
Atlantic	<i>Zostera</i> bed	Intertidal	13.0	40.6–85.7	15.2–32.1	Escaravage et al. (1989)
Atlantic	<i>Zostera</i> bed	Intertidal	29.4	95.1–141.2	20.8–30.9	Escaravage et al. (1989)
Atlantic	Sand unvegetated	Intertidal	6.5	26.1–44.2	14.7–24.9	Escaravage et al. (1989)
Atlantic	Sand unvegetated	Intertidal	5.1	25.7–34.0	15.1–19.9	Escaravage et al. (1989)
Mediterranean	<i>Cymodocea</i>	10 m	8.5	72.5–95.1	8.9–11.7	Danovaro & Fabiano (1996)
Atlantic	Oyster Park	Intertidal	11.8	121.3–162.1	7.3–9.7	Escaravage et al. (1989)
Atlantic	Fine coastal sands	7 m	8.1	87.2–109.4	7.4–9.3	Escaravage et al. (1989)
Atlantic	Estuarine silt-clay	Intertidal	11.0	250–300 <sup>a</sup>	3.7–4.4	Rudnick et al. (1985)
South Africa	Dune slacks	Intertidal	3.6	95.0	3.8	McLachlan et al. (1996)
Wadden Sea	Silt	Intertidal	3.6	200.0	1.8	Witte & Zijlstra (1984)
Atlantic	Fine sand	20 m	4.1	219.0	1.8	Chardy & Dauvin (1992)
Mediterranean	<i>Posidonia</i> bed	Intertidal	9.0	169.3–300.0	3.0–5.3	Present study

<sup>a</sup>Net plankton PP

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