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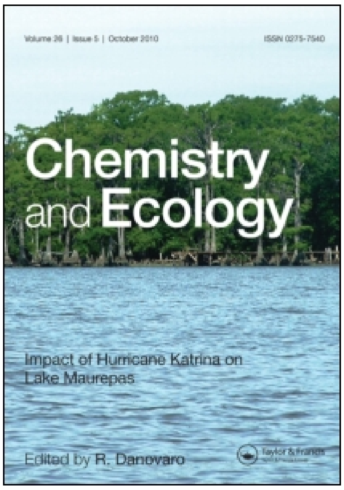

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Multiscale lepidochronological analysis of *Posidonia oceanica* (L.) Delile rhizome production in a northwestern Mediterranean coastal area

M. Montefalcone[a]; E. Amigoni[a]; C. N. Bianchi[a]; C. Morri[a]; A. Peirano[b]; G. Albertelli[a]
[a] DipTeRis, University of Genoa, CoNISMa Local Research Unit, Genoa, Italy [b] ENEA, Marine Environment Research Centre, Santa Teresa, La Spezia, Italy

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Multiscale lepidochronological analysis of *Posidonia oceanica* (L.) Delile rhizome production in a northwestern Mediterranean coastal area

M. Montefalcone[a]*, E. Amigoni[a], C. N. Bianchi[a], C. Morri[a], A. Peirano[b] and G. Albertelli[a]

[a]*DipTeRis, University of Genoa, CoNISMa Local Research Unit, Genoa, Italy;*
[b]*ENEA, Marine Environment Research Centre, Santa Teresa, La Spezia, Italy*

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The influence of geographical location and depth on the rhizome primary production of *Posidonia oceanica* was investigated over different spatial scales: large (the whole Ligurian coast), medium (the individual meadows) and small (the sites of each individual meadow). Six *Posidonia oceanica* meadows, separated by 30 to 60 km from each other, were sampled in summer 2002 along the 300 km of the Ligurian coast (NW Mediterranean). In each meadow, two sites, 100 to 200 m apart, were chosen and in each site 10 orthotrophic shoots were sampled at three depth zones: shallow (1.5–10 m), intermediate (10–15 m), and deep (15–26 m). The annual primary production of the rhizomes was reconstructed through lepidochronology for three previous years (1999, 2000 and 2001). Three-way analysis of variance showed no significant differences in rhizome production at small scale whereas differences at medium scale were significant. These differences were strictly confined at the shallow depths suggesting that local impacts from the coastline are likely to be responsible for the variability in the rhizome primary production among meadows.

Keywords: *Posidonia oceanica*; lepidochronology; primary production; multiscale analysis; Mediterranean Sea; Ligurian coast

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1. Introduction

The endemic *Posidonia oceanica* (L.) Delile is the most important and abundant seagrass in the Mediterranean Sea, where it covers about 40,000 km^2 of the seafloor [1] and forms one of the most productive seagrass beds worldwide [2]. *P. oceanica* meadows have been listed as priority natural habitats (SCIs, Sites of Community Interest) on Annex I of the EC Habitat Directive 92/43/EEC [3] for which special plans of management and conservation must be designated. The need to implement such conservation measures has become even more urgent since *P. oceanica* is experiencing a widespread decline throughout the whole Mediterranean basin due to human activities [4,5]. The regression of the *P. oceanica* meadows was particularly severe in the Ligurian Sea (NW Mediterranean), where the heavy urban and industrial coastal development that have impacted the Ligurian coasts since the 1960s led to a massive decline of most of the meadows [6,7].

*Corresponding author. Email: montefalcone@dipteris.unige.it

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Its susceptibility to changing environmental conditions, due to either climate fluctuations or human disturbances, makes *P. oceanica* an indicator of water quality and health [8], in accordance with the Annex V of the Water Framework Directive (WFD, 2000/60/EC) where seagrasses are listed as biological quality elements to be used in defining the ecological state of a coastal water body [9].

Reconstructive techniques, such as lepidochronology, have been recommended as tools of analysis of seagrass dynamics, including annual growth and production [10,11]. These techniques, based on the possibility to estimate the age of leaf sheaths (leaf bases persisting along the rhizome after the fall of the leaf blade), have been frequently employed for estimating the primary production of both above-ground and below-ground tissues, i.e. leaves and rhizomes, for several years preceding the sampling dates [12]. Lepidochronology has also been shown effective in providing information on past environmental disturbances [8,13].

Apart from the Mediterranean-wide evaluation recently made by González-Correa et al. [14], few studies compared *Posidonia oceanica* meadows over an entire region [15–17]. In the present paper, lepidochronology was used to test the influence of geographical location and depth on the *Posidonia oceanica* rhizome primary production across different spatial scales along the Ligurian coast (NW Mediterranean). The Ligurian *P. oceanica* meadows have been affected since the 1960s by various kinds of impact that synergically act over different spatial scales. Increased water turbidity and climate change mostly work at the basin-wide scale [18]. Individual meadows are also affected by a number of anthropogenic local impacts from the coastline caused by coastal development and by urbanization [6,19]. Notwithstanding the comparatively small size of the *P. oceanica* meadows in the Ligurian Sea [15], sectors of an individual meadow might, in addition, be differently exposed to more point-source impacts from the coastline, i.e. beach replenishments, seawall constructions, coastal revetments, terrigenous discharges, etc., which are often hardly quantified [20,21]. In order to identify the scale at which the six Ligurian meadows showed the greatest differences in their productivity, a hierarchical sampling design was therefore employed [22].

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2. Materials and methods

2.1. *Study area and field activities*

Six *Posidonia oceanica* meadows were randomly chosen over a large spatial scale of the 300 km of the Ligurian coast, an administrative Region of Italy. The six meadows are separated by 30 to 60 km from each other (see Figure 1): Mortola (MO), Gallinara (GA), Cogoleto-Arenzano (CA), Pagana (PA), Manara (MA), Monterosso (MM). A description of the Ligurian seagrass meadows can be found in [15].

Field work was carried out by scuba diving at the beginning of summer 2002, when the cycle concerning the lepidochronological year 2001 could be considered as concluded. According to the hierarchical sampling design adopted, in each meadow two sites (1 and 2, separated by 100 to 200 m from each other) were randomly selected to estimate small scale differences, to be contrasted with medium scale (i.e. among meadows) ones. In each site three stations were also identified within three depth zones: shallow (S), in correspondence of the upper limit of the meadow (1.5–10 m depth); intermediate (I), in the middle of the meadow (10–15 m depth); deep (D), in correspondence of the lower limit of the meadow (15–26 m depth). In each station, 10 randomly selected orthotrophic shoots were collected; also, percent cover of *P. oceanica* canopy was estimated visually by two divers independently on a seabed surface of about 25 m^2, and 5 randomly replicated counts of shoot density (using a 40 cm $\times$ 40 cm PVC frame) were taken [23].

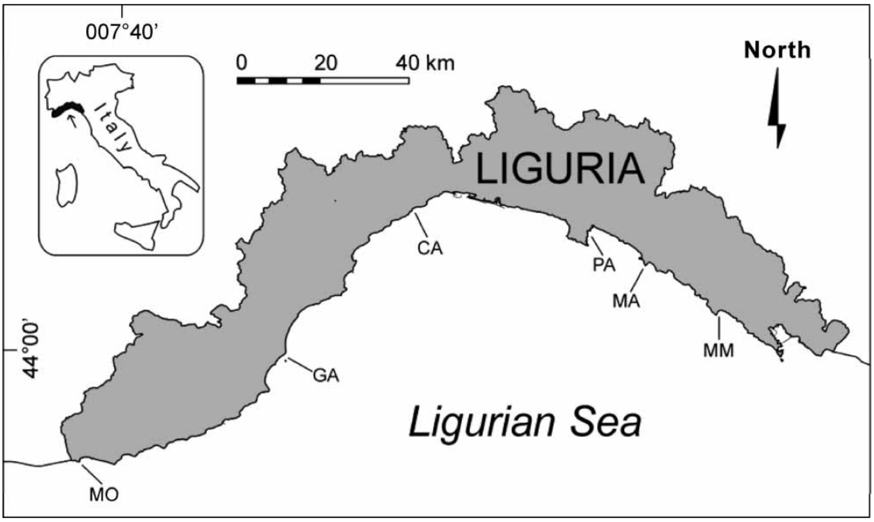

Figure 1. Location of the six *Posidonia oceanica* meadows investigated along the Ligurian coast: Mortola (MO), Gallinara (GA), Cogoleto-Arenzano (CA), Pagana (PA), Manara (MA), Monterosso (MM).

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2.2. *Laboratory analyses*

Annual primary production of the rhizome (gDW year^{-1}) was assessed by lepidochronology, according to the standardized procedure proposed by Pergent-Martini et al. [11]: the portions of the rhizome produced between each pair of two minima (corresponding to the tissue produced during one year) were cut and then dried for 48 h at 70°C, until constant dry weight was achieved. The primary production was reconstructed only for the previous three years (2001, 2000, 1999) in all the rhizomes.

2.3. *Data treatment*

Three-way analysis of variance (ANOVA) was used to test for differences in the rhizome primary production among and within the six meadows. Because many authors hypothesised that *P. oceanica* rhizomes go on growing for 3 years before lignifying definitively [24,25], it would be unwise to compare the mean values of the rhizome production among the three years reconstructed in this study, thus, three distinct ANOVAs were performed for the three years separately in order to ensure the homogeneity in the age of the analysed rhizomes (only for 1999 the growth was likely to be completed). The model of the analysis consisted of three factors: meadow (six levels, random); site (two levels, random and nested within meadows); depth (three levels, fixed and orthogonal), with $n = 10$ replicates (shoots) per combination of factor levels. Prior to analysis, homogeneity of variances were tested by Cochran's C-test and, when necessary, data were transformed using ln(x) to assure homogeneity [22]. When a treatment factor was significant, differences were explored using the Student–Newman–Keuls test (SNK test).

The Pearson's correlation coefficient (r) was used for investigating the relationships between mean annual primary production of the rhizome and different variables: mean shoot density, mean *P. oceanica* percent cover, and mean relative shoot density computed as shoot density $\times$ percent cover [23].

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3. Results

In the shallow zones, the mean annual production of the rhizome showed a great variability among meadows (see Figure 2) in all the three reconstructed years, i.e. 1999, 2000, 2001, ranging from 0.0326 (±0.0051) gDW year^{-1} at MO in 2001 to 0.2184 (±0.0829) gDW year^{-1} at GA in 2001. In the intermediate zones, the mean rhizome annual production varied from 0.0334 (±0.0062) gDW year^{-1} at PA in 1999 to 0.1385 (±0.0363) gDW year^{-1} at MO in 1999. In the deep zones, the mean rhizome annual production was comparatively homogeneous among meadows in all the three reconstructed years, ranging from 0.0305 (±0.0075) gDW year^{-1} at MO in 2001 to 0.0932 (±0.01664) gDW year^{-1} at MA in 2000.

In all the three reconstructed years, ANOVAs revealed significant differences in the annual rhizome primary production among the six meadows (see Table 1). No differences were observed

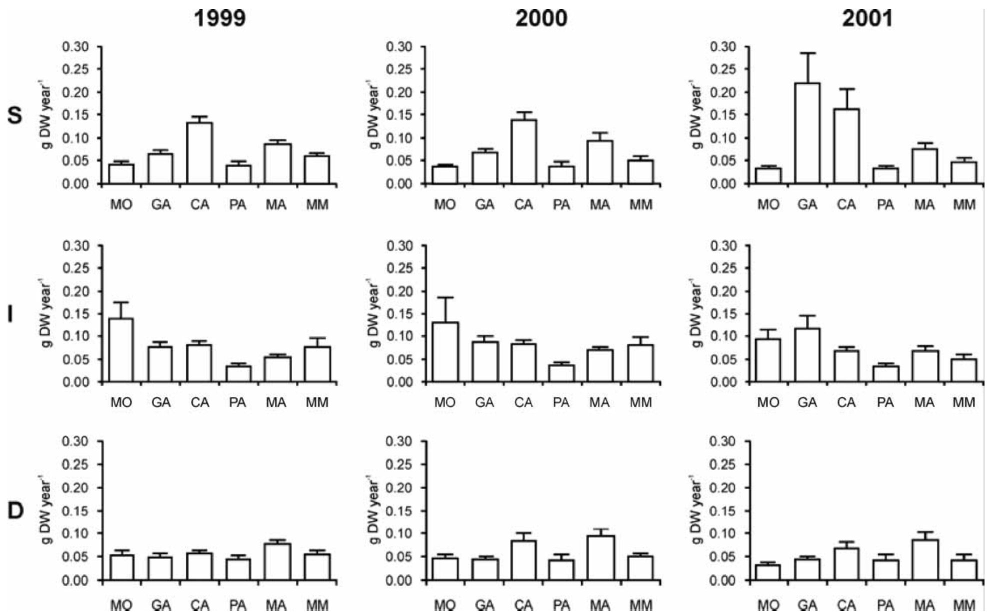

Figure 2. Mean annual primary production of the rhizome (+SE) in the three depth zones (S, shallow; I, intermediate; D, deep) during the three reconstructed years (1999, 2000, 2001) in the six *Posidonia oceanica* meadows investigated. Individual meadows are indicated by their code as in Figure 1.

Table 1. Results of the 3-way ANOVAs on annual primary production of the rhizome during the three reconstructed years 1999, 2000, 2001. Bold numbers indicate significant differences ($p < 0.05$).

		1999			2000			2001		
	df	MS	*F*	*p*	MS	*F*	*p*	MS	*F*	*p*
Meadow	5	5.3003	15.45	**0.0023**	7.3605	16.56	**0.0019**	9.9197	12.50	**0.0040**
Site(M)	6	0.3430	1.32	0.2454	0.4445	1.58	0.1515	0.7936	1.83	0.0934
Depth	2	1.6335	0.71	0.5154	2.5248	1.42	0.2873	6.7872	2.94	0.0989
M×D	10	2.3049	1.57	0.2256	1.7821	1.41	0.2834	2.3070	0.71	0.7043
D×S(M)	12	1.4638	5.65	**0.0000**	1.2654	4.51	**0.0000**	3.2629	7.51	**0.0000**
RES	324	0.2589			0.2809			0.4346		
TOT	359									
		Cochran's C-test=0.0843 Transformation: ln(x)			Cochran's C-test=0.0746 Transformation: ln(x)			Cochran's C-test=0.0402 Transformation: ln(x)		

in the annual rhizome production between the two sites (1 and 2) and among the three depth zones (shallow, intermediate and deep) in all the meadows. A significant Depth × Site (M) interaction was detected and the SNK test revealed that values of the annual rhizome primary production recorded in the shallow stations of many meadows were different from those recorded in either the intermediate or deep stations.

No direct relations were detected between production of the rhizome and shoot density, between production of the rhizome and cover of *P. oceanica*, and between production of the rhizome and relative shoot density.

4. Discussion

The hierarchical sampling design adopted in this study provided evidences of the great variability in the annual primary production of the rhizome among the six individual meadows, i.e. over the medium spatial scale, which was mostly ascribable to their shallow zones. As depth was likely to not directly influence the primary production of the rhizome, variability among meadows might reflect differences in type of habitat and in hydrodynamic regime [12,26], as well as in human induced disturbances [19]. The Ligurian meadows had been notoriously affected by different stressors from the coastline that exerted their effects at both medium and small scales [15]; moreover, the shallow and the deep portions of a meadow were usually more impacted than the intermediate portions [6,21].

The absence of significant differences between the two sites within each meadow allow us to exclude the variability of the rhizome primary production over the small spatial scale; in contrast, the local impacts that influenced the Ligurian coast from the 1960s [6] still have visible effects on the health state of the meadows in shallow waters. The regressive condition of the lower limits already described in most meadows [27], was consistent with the basin-wide increased water turbidity that affected especially the lower portions of the Ligurian *P. oceanica* meadows [15,28]. Nevertheless, in correspondence of the lower limits, all positioned at different depths, the primary production of the rhizome was comparable among meadows and showed nearly the same values of those recorded in the intermediate zones, where the health state of the meadows was comparatively higher [7]. The observed homogeneity in the rhizome primary production within the meadows may be due to endogenous mechanisms of compensation, possibly linked to genetic differences with depth [29] or among sites in a same meadow [30]. Also the absence of apparent relationships between the primary production of the rhizome and shoot density or cover pointed out that production is modulated neither by depth nor by the structural features of the meadow. This partially contrasts with the results reported by Peirano et al. [31] that identified a strong negative relationship between the rhizome growth rate and the shoot density in seven shallow Ligurian meadows.

Notwithstanding the generalised regressive state of the Ligurian meadows [31], values of annual primary production of the rhizome obtained in the six Ligurian meadows investigated were similar to those reported from other meadows in the Mediterranean Sea located in comparatively less anthropised areas [11]. Environmental protection measures have been shown effective in checking the decline of *Posidonia oceanica* meadows across the whole Mediterranean Sea, favouring positive population dynamics of this species [14]. Only in very recent years, the Liguria region has undertaken coastal management actions aimed at preventing and reducing the amount and the effects of anthropogenic impacts on *P. oceanica* meadows through ad hoc legislation (e.g. the Ligurian regional laws on beach replenishments of 1999). However, it is unlikely that the enforcement of this legislation is already producing effects on the status of Ligurian meadows that still show alarming signs of degradation [7]. The lack of evidence of point-source impacts

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shown by the similarity between sites within meadows cannot be therefore interpreted as clues of rapid recovery: impacts of beach replenishments, for instance, need a period of about five years to be adsorbed, as shown by lepidochronology [20]. A combination of reconstructive techniques and long term monitoring, as already on going along the French side of the Ligurian Sea [17], is essential for weighting the effectiveness of coastal management actions and for verifying the potentiality of recovery in those meadows affected by older local impacts.

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