Biomass and primary production of a 8-11 m depth meadow *versus* < 3 m depth meadows of the seagrass *Cymodocea nodosa* (Ucria) Ascherson

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Abstract

Current knowledge about the abundance, growth, and primary production of the seagrass *Cymodocea nodosa* (Ucria) Ascherson is biased towards shallow (depth < 3 m) meadows although this species also forms extensive meadows at larger depths along the coastlines. The biomass and primary production of a *C. nodosa* meadow located at a depth of 8-11 m was estimated at the time of maximum annual vegetative development (summer) using reconstruction techniques, and compared with those available from shallow meadows of this species. A depth-referenced data base of values at the time of maximum annual development was compiled to that end. The vegetative development of *C. nodosa* at 8-11 m depth was not different from that achieved by shallow (depth < 3 m) meadows of this species. Only shoot density, which decreased from 1637 shoots m^{-2} to 605 shoots m^{-2}, and the annual rate of elongation of the horizontal rhizome, which increased from 23 cm $apex^{-1}$ $year^{-1}$ to 71 cm $apex^{-1}$ $year^{-1}$, were different as depth increased from < 3 m to 8-11 m. Depth was a poor predictor of the vegetative development and primary production of *C. nodosa*. The biomass of rhizomes and roots decreased with depth (g D.W. m^{-2} = 480 (± 53, SE) - 32 (± 15, SE) depth (in m), R^2 = 0.12, F= 4.65, d.f. = 35, P = 0.0381) which made total biomass of the meadow to show a trend of decrease with depth but the variance of biomass data explained by depth was low. The annual rate of elongation of the horizontal rhizome showed a significant positive relationship with depth (cm $apex^{-1}$ $year^{-1}$ = 18 (± 5.1, SE) + 5.0 (±1.33, SE) depth (in m); R^2 = 0.50, F= 14.07, d.f. = 14, P = 0.0021). As shoot size and growth did not change significantly with depth, the reduction of shoot density should drive any changes of biomass and productivity of *C. nodosa* as depth increases. The processes by which this reduction of *C. nodosa* abundance with depth occur remain to be elucidated.

Keywords: Seagrasses, *Cymodocea nodosa*, depth gradient, biomass, shoot density, primary production, Mediterranean Sea

1. Introduction

Light availability sets the maximum depth of seagrass colonization (Duarte, 1991). Shoot density of seagrass meadows decreases as depth increases (Romero, 1989; West, 1990; Romero et al., 1998; Krause-Jensen et al., 2000) while seagrass biomass usually reaches a maximum at intermediate depths and decreases towards the depth limit (Duarte, 1991; Krause-Jensen et al., 2000). Strong correlations between light attenuation and the decline of shoot density and seagrass biomass with depth (Duarte, 1991; Krause-Jensen et al., 2000) suggest that light availability is the main factor driving the depth distribution of seagrasses. *In situ* manipulation of light availability and transplant experiments have shown that the leaf growth and biomass of the seagrass *Zostera marina* L. at the deep limit of distribution is dependent on light availability (Dennison and Alberte, 1985; Dennison and Alberte, 1986). The decline of shoot density with depth is considered a plant response to reduce self-shading when light availability is low (Olesen and Sand-Jensen, 1993;Krause-Jensen et al., 2000). Additionally, the size of *Z. marina* shoots increases with depth, and more biomass is allocated to leaves than to rhizomes and roots (Krause-Jensen et al., 2000). *Z. marina* plants grown under an experimental light gradient showed that rhizome growth declined faster than leaf growth as light was reduced (Olesen and Sand-Jensen, 1993). These changes of biomass allocation are interpreted as a plant response to reduce respiration costs and maintain growth under low light availability (Olesen and Sand-Jensen, 1993; Krause-Jensen et al., 2000).

Shoot density, leaf biomass, and productivity of the Mediterranean seagrass *Posidonia oceanica* (L.) Delile decrease from the shallow to the deep limit of distribution of this species (Pirc, 1984;Romero, 1989; Romero et al., 1998; Olesen et al., 2002; Gobert et al., 2003). Shoot size has been shown to remain fairly constant (Pirc, 1984; Olesen et al., 2002) or decrease (Gobert et al., 2003) as depth increases, but the number of leaves per shoot and the growth rate of individual shoots do not change with depth (Pirc, 1984; Romero, 1989; Olesen et al., 2002; Gobert et al., 2003). Hence, the decline of leaf biomass and productivity of *P. oceanica* meadows with depth seems to be driven by the decline of shoot density mainly.

Cymodocea nodosa (Ucria) Ascherson is a common seagrass species in the Mediterranean Sea and the North-Atlantic coast of Africa, including the Canary Islands (den Hartog, 1970), which shows an ample depth distribution from the intertidal (Vermaat et al., 1993) to depths of 33-35 m (Drew, 1978; Reyes et al., 1995a; Canals and Ballesteros, 1997). It can be found on a wide range of substrata too, from coarse sand to muddy sediments (Peduzzi and Vukovič, 1990; Pavón-Salas et al., 2000), and forms extensive meadows in shallow, sheltered places such as lagoons (Terrados and Ros, 1992; Ribera et al., 1997; Agostini et al., 2003), bays (Pérez and Camp, 1986; Pérez and Romero, 1994) or harbor areas (Reyes et al., 1995b). Most part of the knowledge about the magnitude and seasonality of biomass, growth and primary production of *C. nodosa* has been produced in shallow (depth < 3 m) meadows (Caye and Meinesz, 1985; Pérez et al., 1991; van Lent et al., 1991; Terrados and Ros, 1992; Vermaat et al., 1993; Pérez and Romero, 1994; Pérez et al., 1994; Sfriso and Ghetti, 1998; Cancemi et al., 2002; Guidetti et al., 2002; Agostini et al., 2003). Logistical reasons (i.e., shelter from wave action, diving time) might be behind this bias in knowledge for *C. nodosa* also forms extensive meadows at larger depths along the coastlines (Reyes et al., 1995a; Calvín et al., 1999).

The few analysis of the vegetative development of *Cymodocea nodosa* along depth gradients (from 2 to 6 m: Peduzzi and Vukovič, 1990; from 0.4 to 3.8 m: Olesen et al., 2002) show that shoot density and leaf biomass decrease with depth, while the rhizome plus roots to shoot biomass ratio either decreases or does not change, and shoot size remains fairly constant.

In this study we estimated plant size, shoot density, biomass and primary production of *Cymodocea nodosa* growing at depths of 8 m and 11 m, a common location of the meadows formed by this seagrass species in the Mediterranean, and compared the results obtained with those available from shallow (depth < 3m) meadows of this species to evaluate if the vegetative development of deep *C. nodosa* meadows is different from that of shallow meadows. By increasing the depth range from which knowledge about the vegetative development of this species is available we could evaluate if depth-related changes of plant size, shoot density, biomass and primary production of *C. nodosa* were consistent with those observed in other seagrass species.

2. Methods

The study was performed at Sant Pol beach, Sant Feliu de Guixols, NE Spain (41º 47.227'N, 3º 03.206'E), where *Cymodocea nodosa* forms a spatially homogeneous meadow (100 % cover of the substratum) between depths of 7 m and 11 m. The meadow is patchy at a depth of 18.5 m, and isolated plants can be found at a depth of 21 m. *C. nodosa* is not present at depths < 7m. The main sampling station was located at a depth of 11 m with additional samples collected at a depth of 8 m. Sampling was performed in July 2002, when the vegetative development of *C. nodosa* is near its annual maximum (Terrados and Ros, 1992; Pérez and Romero, 1994; Cebrián et al., 1997; Marbà et al., 1996; Rismondo et al., 1997; Sfriso and Ghetti, 1998; Guidetti et al., 2002; Agostini et al., 2003). The vertical attenuation coefficient for downward irradiance (K_d) was estimated by measuring scalar irradiance at noon just below the surface of the sea and at the top of the leaf canopy at the depth of 11 m with a Li-Cor spherical quantum sensor LI-193SB (Kirk, 1983; page 95). K_d at Sant Pol beach in July 2002 was 0.095 m^{-1}, a relatively low value for coastal waters (cf. Kirk, 1983; page 112).

The abundance of *Cymodocea nodosa* was quantified as shoot density (number of shoots m^{-2}) and biomass (g dry weight m^{-2}). Shoot and flower densities were estimated by counting the number of shoots and flowers present in 25 samples collected using a 10.2 cm in-diameter stainless-steel corer that was inserted in the sediment to a depth of 40 cm. The biomass of *C. nodosa* in 10 of the corer samples was sorted into leaves, rhizomes, roots, and flowers, and dried at 60ºC during 48 hours to estimate dry weight. Nitrogen in the leaves was determined using a Carlo-Erba NA-1500 CHN analyzer, and phosphorus was determined spectrophotometrically (Parsons et al., 1984) after wet oxidation with boiling H_2SO_4. Seed abundance was estimated from the number of seeds that were collected in the corer samples.

Growth rates were estimated using reconstruction techniques (Duarte et al., 1994) which are based on the estimation of the age of the shoots using the "plastochrone" concept, the time elapsed between the appearance of two consecutive structural modules (i.e., leaves) in plants (Erikson and Michelini, 1957). The age in years of the shoots was estimated by counting the number of standing leaves and scars left by fallen leaves on the vertical rhizome of each shoot and dividing the resultant number by the average number of leaves produced by *C. nodosa* in one year. Such average was estimated through the analysis of the sequence of lengths of the internodes of large pieces of vertical rhizome (cf. Duarte et al., 1994) which were measured with a stereomicroscope.

The length (cm) of the vertical rhizome of all the shoots collected in the corer samples was measured, and the number of roots, root scars and flower scars present in them was counted. These counts, when divided by the age of the shoots, provide an estimate of the annual elongation of the vertical rhizome and the number of roots and flowers produced by the shoots. Horizontal rhizome pieces of more than 30 cm in-length were collected haphazardly throughout the meadow by hand to estimate their growth rate. The number of standing leaves and leaf scars (i.e. an age estimate) of all the shoots in each rhizome piece collected was counted, as well as the number of internodes and distance (cm) between them. The age difference between shoots in a rhizome piece allowed us to calculate the average elongation and number of internodes produced per leaf plastochrone. The annual rates of elongation and internode production of the horizontal rhizome were estimated by multiplying those per-leaf-plastochrone estimates by the average number of leaves produced during one year. A subsample of 10 fragments of both vertical and horizontal rhizomes was haphazardly chosen and the number of internodes of each fragment was counted and its length measured before drying to estimate average mass and length of vertical and horizontal rhizome internodes. Similarly, three subsamples of 10 small and 10 large unbroken roots were chosen and weighed after drying to estimate the average mass per root. The abundance of apexes of horizontal rhizome was estimated by counting the number of them present in 24 quadrats (1600 cm^2) haphazardly placed within the meadow. Knowledge of the age of each shoot allows to build the age distribution of the population of shoots (cf. Duarte et al., 1994). Mean and median shoot age were estimated, and the resultant age distributions were compared with those available in the literature (Kolmogorov-Smirnov two sample test, Sokal and Rohlf, 1981).

We searched the marine ecology an biology literature for studies describing the vegetative development (plant size, shoot density, biomass, nutrient content of leaves, growth, and productivity) of *Cymodocea nodosa* and compiled a depth-referenced data base of values at the time of maximum annual development (listed in caption of Fig. 1). To evaluate the differences of vegetative development between "shallow" and "deep" meadows we compared the mean of the values obtained at the depths of 8 m and 11m at our study site with the mean of the corresponding values reported by those compiled studies which were performed at depths < 3 m (two-sample t test, two-tailed). Graphing of compiled values against depth suggested that vegetative development was highly variable at shallow meadows and that declines with depth of shoot density, biomass and other variables describing vegetative development occurred at depths > 3 m. We calculated the coefficient of variation of the mean (V*, Sokal and Rohlf, 1981) of selected variables describing the vegetative development of *C. nodosa* in shallow (depth < 3 m) and deep (depth > 3 m) meadows to evaluate the significance of the differences in variability of the vegetative development between them (two-tailed Z test for difference between two coefficients of variation, Zar, 1999). Further, we used linear regression to examine depth-associated changes of the vegetative development of *C. nodosa*.

3. Results

Shoot density of *Cymodocea nodosa* at 8-11 m depth in Sant Pol beach in July 2002 was lower than the annual maximum shoot density reported in most of the meadows of this species studied previously (Fig. 1a). Leaf, rhizome plus roots, and total biomass of *C. nodosa* at the annual maximum at 8-11m depth were also at the low end of the range of reported values (Fig. 1b). The annual maximum shoot density of *C. nodosa* meadows at depth of 8-11 m was lower (two sample t-test, $P < 0.05$) than that of meadows located at depths < 3 m (Table 1). The annual maximum of leaves, rhizome plus roots, and total biomass tended to be also lower at 8-11 m depth than at depths < 3 m but the differences of the means were not significant (Table 1). The relative allocation of biomass to leaves and rhizomes plus roots at 8-11 m depth was not different than that of meadows located at depths < 3 m (Table 1, Fig. 1c).

The average number of leaves of *Cymodocea nodosa* shoots at the time of maximum vegetative development at 8-11 m depth was not different from that of meadows located at depths < 3 m (Table 1, Fig. 1d). The same occurred with the average shoot mass (Table 1, Fig. 1e).

The annual average leaf plastochrone of *Cymodocea nodosa* at 8-11 m depth was not different than that of meadows located at depths < 3 m (Table 1, Fig. 1f). The annual leaf and total production of *C. nodosa* at 8-11 m depth were at low end of the range of values published previously but was not different from the average values estimated in meadows located at depths < 3 m (Table 1, Figs. 1g and 1h). The elongation rate of the horizontal rhizome was, however, higher at 8-11 m depth than the average value estimated in meadows located at depths < 3 m (Table 1). The nitrogen and phosphorus content of *C. nodosa* leaves at 8-11 m depth was not different than the average of values found in meadows located at depths < 3 m (Table 1).

The coefficient of variation of vegetative features and production estimates of *Cymodocea nodosa* was not different (two-tailed Z test for difference between two coefficients of variation, $P > 0.05$) between meadows located at depths lower and higher than 3 m (Table 2). Depth was a poor predictor of the vegetative development of *C. nodosa* for most of the linear regressions of the different variables used to describe the vegetative development against depth were not significant neither considering the whole range of data compiled nor only those data corresponding to depths > 3 m (Table 1). Rhizome plus roots biomass decreased with depth (- 32 ± 14.6 (SE) g D.W. m^{-1}, $P < 0.05$, Table 1) which made total biomass to show a marginally significant trend of decrease with depth too (Fig. 1b, Table 1). The rate of elongation of the horizontal rhizome increased with depth ($P < 0.05$, Fig. 2a).

The average age of *Cymodocea nodosa* shoots varied between 2.5 years and 3.2 years while the median age varied between 2 years and 3 years in meadows located at depths > 3 (Table 3), but were 1.7-1.8 years and 1 year only, respectively, in meadows located at depths < 3 m. The comparison of the age distributions of living *C. nodosa* shoots obtained in this study (Fig. 3a) with those available in the literature showed that most shoot age distributions were different (Table 3). The age distributions of dead shoots at 8 m and 11 m were different (Kolmogorov-Smirnov two sample test, D =0.186

> $D_{0.05}$ = 0.169, Fig. 3b), with average and median ages of 2.0 years and 2 years at the depth of 8 m, and 1.7 years and 1 years, respectively, at the depth of 11 m.

The abundance of *Cymodocea nodosa* flowers at 8-11 m depth was not different than that estimated in meadows located at depths < 3 m (Table 1) but likely mismatches between peak flowering and sampling time make literature comparisons of flower abundance difficult. The average and median age of shoots bearing a flower or flower scars on the vertical rhizome were 3.4 years and 3 years at depth of 8 m, and 3.5 years and 3 years, respectively, at depth of 11 m; the age distributions of these shoots were not different at 8 m and 11 m (Kolmogorov-Smirnov two sample test, D =0.142 < $D_{0.05}$ = 0.290, Fig. 3c). We found flowers in shoots of only 5, 7 and 8 leaf plastochrones in age. Seed abundance tended to be lower at 8-11 m depth than at meadows located at depths < 3 m but the difference of the means was not significant (Table 1).

Discussion

Our results show that the vegetative development of *Cymodocea nodosa* at 8-11 m depth is not different from that achieved by shallow (depth < 3 m) meadows of this species. Only shoot density, which decreased by a factor of 2.7, and the annual rate of elongation of the horizontal rhizome, which increased by a factor of 3, at 8-11 m depth were different. Our results also show that depth is a poor predictor of the vegetative development and primary production of *C. nodosa* for most of the linear regressions of the variables describing the vegetative development of *C. nodosa* against depth were non-significant.

The reduction of seagrass shoot density and biomass with depth has been recognized before and attributed to the parallel decrease of light availability (Duarte, 1991). Further, the reduction of shoot density with depth has been considered the most effective mechanism for seagrasses to acclimate to reductions of light availability as depth increases (Olesen et al., 2002). A threshold light for rhizome branching to occur has been proposed as a mechanism to explain the decrease of shoot density with depth of *Zostera noltii* (Peralta et al., 2002) and *Posidonia oceanica* (Romero, 1989).

Previous studies that have examined the vegetative development of *Cymodocea nodosa* along depth gradients (Peduzzi and Vukovič, 1990; Olesen et al., 2002) show that shoot density and leaf biomass decrease with depth. Given that the range of depths examined by these studies is narrower (from 0.4 m to 6 m) than that examined by us (from 0.3 m to 11 m) we expected to find stronger negative relationships of these variables with depth than we did. The low predicting value that depth had to explain the vegetative development and primary production of *C. nodosa* in our compiled data set might be due to wide spatial variation of water turbidity and light availability among the sites included in it, and apparently higher K_d values at shallow sites (0.57 m^{-1} to 0.35 m^{-1} in the 0.4-1.5 m depth range, cf. Duarte, 1991; Terrados and Ros, 1995; Guidetti et al., 2002) than at deep sites (0.19 m^{-1} to 0.095 m^{-1} in the 4-11 m depth range (Cancemi et al., 2002; this study). Unfortunately, data about irradiance attenuation were not available from most of the sites. Our results are consistent with previous studies on this species (Peduzzi and Vukovič, 1990; Olesen et al., 2002) for neither shoot mass and the number of leaves per shoot nor the average annual leaf plastochrone and productivity of individual shoots changed significantly with depth. Shoot density, leaf biomass and productivity of *Posidonia oceanica* decrease significantly with depth while shoot size and growth remain fairly constant (Pirc, 1984; Romero, 1989; Romero et al., 1998; Olesen et al., 2002; Gobert et al., 2003). In the case of *Zostera marina*, shoot density decreases exponentially with depth while shoot size increases linearly; as a result biomass peaks at intermediate depths (Krause-Jensen et al., 2000).

We found that the rhizome plus roots to shoot biomass ratio of *Cymodocea nodosa* did not change with depth. However, the biomass of rhizomes plus roots decreased significantly with depth driving a marginally significant reduction of total biomass of the meadow which suggests that a slight change of the mass allocation pattern might take place. Previous studies on this species are inconclusive for the rhizome plus roots to shoot biomass ratio either did not change (Olesen et al., 2002) or decreased (Peduzzi and Vukovič, 1990) as depth increased. The rhizome plus roots to shoot biomass ratio of *Posidonia oceanica* does not seem to change with depth (Romero et al., 1998; Olesen et al., 2002) but decreases in *Zostera marina* (Olesen and Sand-Jensen, 1993; Krause-Jensen et al., 2000). Preferential allocation of biomass to leaves as depth increases should not be considered, therefore, a general response of seagrasses to reduce respiration costs and maintain growth under low light availability. Further, our results do not provide support to the hypothesis that the variability of seagrass vegetative development is higher at shallow depths where physical disturbance and light availability are high than at deep meadows where physical disturbance and light availability are low (Krause-Jensen et al., 2000; Middelboe et al., 2003).

Linear regression of the elongation rate of the horizontal rhizome of *Cymodocea nodosa* against depth predicted a rate of increase rate of 5 cm apex^{-1} year^{-1} per m depth, which is consistent with the results of Olesen et al. (2002). However, Peduzzi and Vukovič (1990) did not find any change of the rate of elongation the horizontal rhizome of *C. nodosa* between depths of 2 m and 6 m. The rate of elongation of the horizontal rhizome of *Posidonia oceanica* did not change between depths of 0.7 m and 15.6 m (Olesen et al., 2002). It has been suggested that the elongation of the horizontal rhizome of seagrasses might depend on shoot density (Caye and Meinesz, 1985; Marbà and Duarte, 1998), likely through a self-shading constraint. Shoot density, however, explained little of the variability of the rate of elongation of the horizontal rhizome data included in our depth-referenced data base (Fig. 2b; $R^2 = 0.15$, $F = 2.34$, d. f. = 13, $P = 0.1496$).

The age distributions of *Cymodocea nodosa* shoots show exponential reductions of shoot density since the ≤ 1 year class at shallow meadows (cf. Pérez, 1989; Terrados and Ros, 1992) and since the 2 year class at deep meadows (Reyes et al., 1995b, and this study). These results suggest that shoot turnover decreases with depth. Indeed, the maximum age of shoots at 8-11 m depth was 11-12 years but only 4 to 8 years at shallow meadows (Pérez, 1989; Terrados and Ros, 1992), and median shoot age was lower at shallow than at deep meadows. The age distributions of dead shoots at 8-11 m depth suggest, however, that most part of the shoots die within one year of being produced.

In conclusion, the vegetative development of *Cymodocea nodosa* at 8-11 m depth was not different from that achieved by shallow (depth < 3 m) meadows of this species. Only shoot density, which decreased by a factor of 2.7, and the annual rate of elongation of the horizontal rhizome, which increased by a factor of 3, were different as depth increased from < 3 m to 8-11 m. Depth was a poor predictor of the vegetative development and primary production of *C. nodosa.* As shoot size and growth did not change significantly with depth, the reduction of shoot density should drive any changes of biomass and productivity of *C. nodosa* as depth increases. The processes by which this reduction of *C. nodosa* abundance with depth occur remain to be elucidated.

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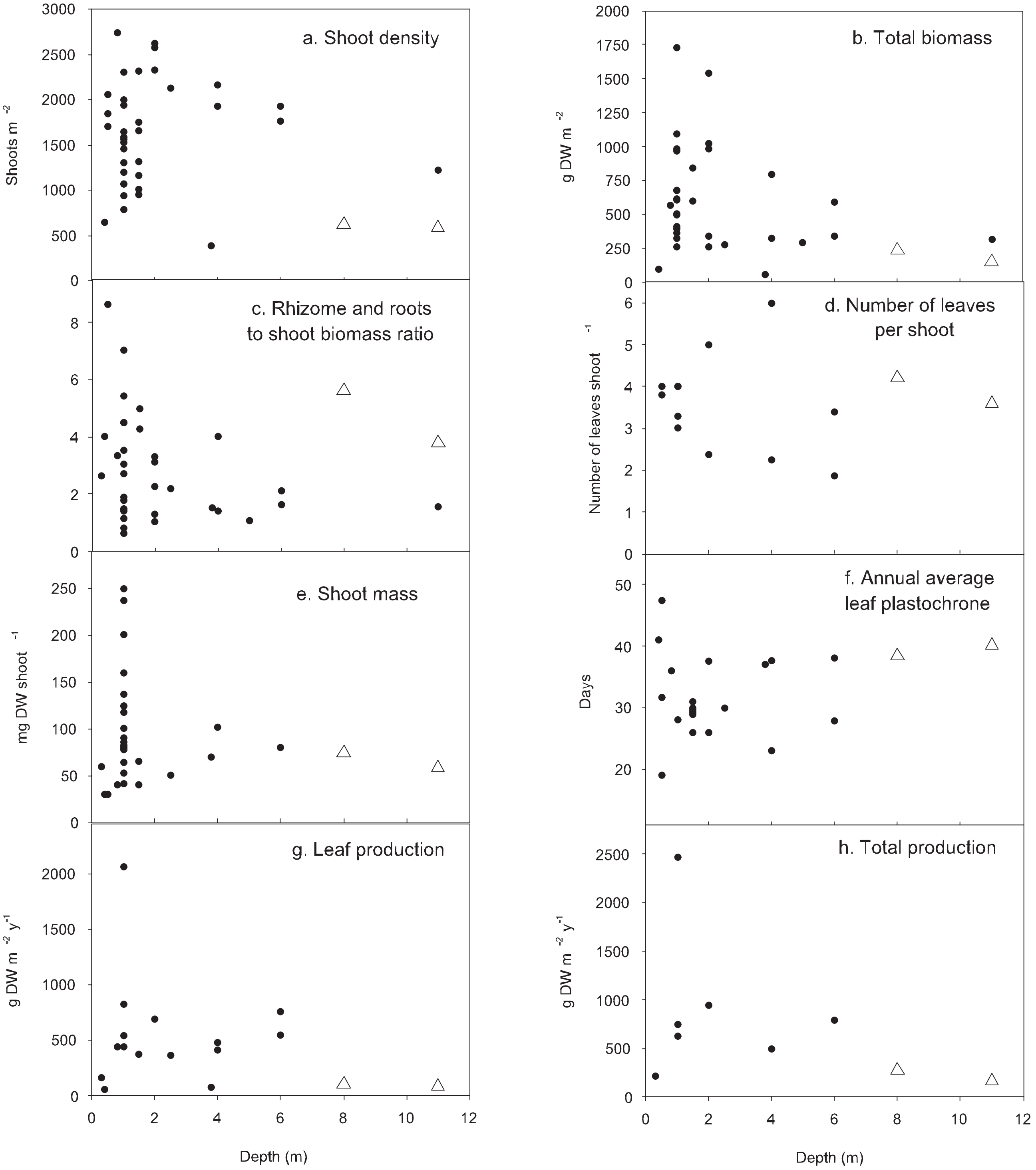
Figure captions

Figure 1. Shoot density (a), total biomass (b), rhizome plus roots to shoot ratio (c), number of standing leaves per shoot (d), and shoot mass (e) at the annual maximum of vegetative development of *Cymodocea nodosa*, and annual average leaf plastochrone interval (f), leaf (g), and total production (h) against depth. Triangles represent the 8-11 m depth meadow studied. Data sources: Pirc et al., 1983; Caye and Meinesz, 1985; Pérez and Camp, 1986; Terrados, 1986; Duarte and Sand Jensen, 1990; Peduzzi and Vukovič, 1990; Buia and Mazzella, 1991; Terrados, 1991; Terrados and Ros, 1992; Terrados, 1993; Terrados and Ros, 1993; Pérez and Romero, 1994; Pérez et al., 1994;Reyes et al., 1995a, 1995b; Vermaat et al., 1997; Pérez et al., 1996; Cebrián et al., 1997; Ribera et al., 1997; Rismondo et al., 1997;Duarte et al., 1998; Zavodnik et al., 1998; Pranovi et al., 2000; Nielsen and Pedersen 2000; Marbà and Duarte, 2001; Cancemi et al., 2002; Guidetti et al., 2002; Olesen et al., 2002; Agostini et al., 2003; Cunha and Duarte, 2005.

Figure 2. Linear regression of the annual rate of horizontal rhizome elongation against depth (a) and shoot density (b) of *Cymodocea nodosa*. Triangles as in Fig. 1

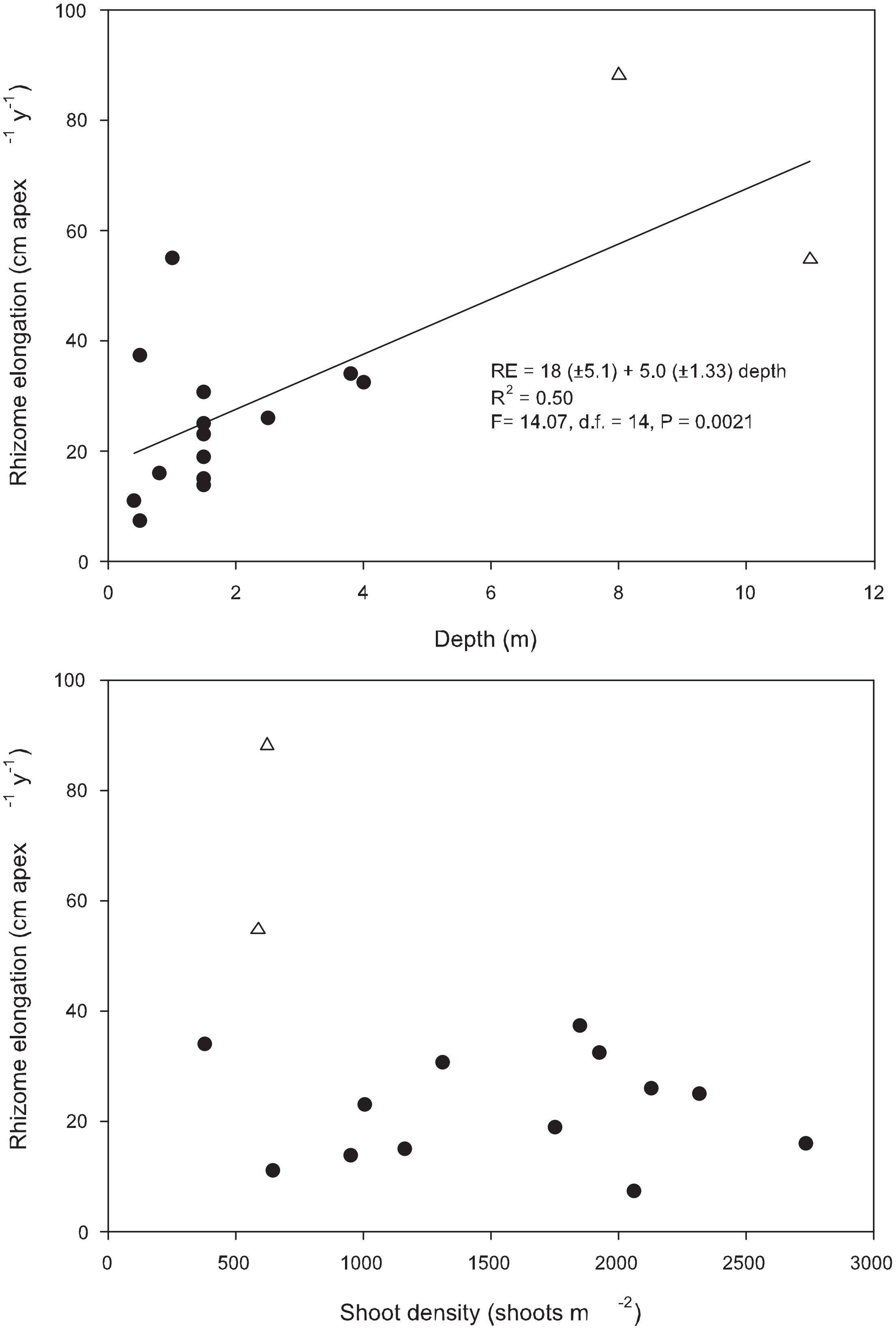
Figure 3. Age distribution of living shoots (a), dead shoots (b), and of shoots that bore a flower and/or a flower scar in the vertical rhizome (c) of *Cymodocea nodosa* at the depths of 8 and 11 m at the study site.

Figure1 rev



a. Shoot density
Shoots m -2
3000
2500
2000
1500
1000
500
0
b. Total biomass
g DW m -2
2000
1750
1500
1250
1000
750
500
250
0
c. Rhizome and roots to shoot biomass ratio
8
6
4
2
0
d. Number of leaves per shoot
Number of leaves shoot -1
6
5
4
3
2
1
0
e. Shoot mass
mg DW shoot -1
250
200
150
100
50
0
f. Annual average leaf plastochrone
Days
50
40
30
20
g. Leaf production
g DW m -2 y -1
2000
1500
1000
500
0
h. Total production
g DW m -2 y -1
2500
2000
1500
1000
500
0
0
2
4
6
8
10
12
Depth (m)
Depth (m)

Figure2 rev



Rhizome elongation (cm apex^{-1} y^{-1})
100
80
60
40
20
0
0
2
4
6
8
10
12
Depth (m)
RE = 18 (±5.1) + 5.0 (±1.33) depth
R^2 = 0.50
F= 14.07, d.f. = 14, P = 0.0021
Rhizome elongation (cm apex^{-1} y^{-1})
100
80
60
40
20
0
0
500
1000
1500
2000
2500
3000
Shoot density (shoots m^{-2})

Figure3 rev


a. Living shoots
8m depth
11m depth
b. Dead shoots
c. Shoot age at flowering
Number of shoots
Age (years)
0
10
20
30
40
50
60
80
5
15
1
2
3
4
5
6
7
8
9
10
11
12

Table 1

Table 1. Vegetative features and production estimates of *Cymodocea nodosa* at depths of 8 m and 11m in Sant Pol beach (NE Spain), corresponding values reported previously of shallow (depth < 3 m) meadows of this species (see caption Fig. 1 for data sources), and results of two-sample t-tests evaluating the significance of the difference between them, and of the linear regressions against depth considering the whole range of depth data compiled and only those depths > 3 m. Bold face indicates significant differences.

Variable	This study Depth: 8 m Mean ± SE	This study Depth: 11 m Mean ± SE	Shallow meadows Depth < 3 m Mean ± SE, n	t-value, d.f., P-value	Linear regression whole depth range R^2, F-value, P-value	Linear regression depths > 3 m R^2, F-value, P-value
Annual maximum shoot density, shoots m^{-2}	623 ± 49	588 ± 38	1637 ± 106.5, 30	**2.50, 30, 0.0179**	0.06, 2.29, 0.1391	0.18, 1.35, 0.2892
Leaf biomass, g DW m^{-2}	46 ± 7.7	33 ± 3.6	188 ± 33.1, 29	1.18, 29, 0.2457	0.03, 1.17, 0.2852	0.07, 0.58, 0.4685
Rhizome and root biomass, g DW m^{-2}	186 ± 36.7	116 ± 16.3	454 ± 48.3, 28	1.68, 28, 0.1043	**0.12, 4.65, 0.0381**	0.07, 0.56, 0.4794
Annual maximum total biomass, g DW m^{-2}	235 ± 44.9	150 ± 20.6	664 ± 81.7, 25	1.64, 25, 0.1141	0.09, 4.13, 0.0504	0.08, 0.67, 0.4382
Rhizome and roots to shoot ratio	5.6 ± 2.11	3.8 ± 0.66	3.1 ± 0.37, 28	1.15, 28, 0.2594	0.01, 0.35, 0.5565	0.09, 0.68, 0.4369
Abundance of flowers, flowers m^{-2}	243 ± 60	153 ± 27	124 ± 33.7, 7	1.15, 7, 0.2876	0.03, 0.37, 0.5537	0.03, 0.10, 0.7767
Abundance of seeds, seeds m^{-2}	7 ± 5	65 ± 29	243 ± 62.8, 7	1.80, 7, 0.1148	0.04, 0.95, 0.3389	0.18, 2.63, 0.1307
Number of leaves per shoot	4.2 ± 0.1	3.6 ± 0.1	3.72 ± 0.265, 9	0.32, 9, 0.7539	0.01, 0.10, 0.7514	0.00, 0.00, 0.9422
Shoot mass, mg DW shoot^{-1}	73.8 ± 10.2	58.3 ± 3.1	97 ± 12.4, 25	0.71, 25, 0.4867	0.02, 0.68, 0.4156	0.48, 2.77, 0.1944
Leaf plastochrone, days	38.5	40.1	31.4 ± 1.82, 15	1.58, 15, 0.1339	0.07, 1.52, 0.2321	0.21, 1.34, 0.2989
Elongation of horizontal rhizome, cm apex^{-1} year^{-1}	88.2 ± 19.1	54.7 ± 8.0	23.3 ± 3.9, 12	**4.40, 12, 0.0009**	**0.50, 14.07, 0.0021**	0.37, 1.17, 0.3928
Leaf production, g DWm^{-2} year^{-1}	104 ± 114.3	87 ± 93.4	594 ± 187.3, 10	1.21, 10, 0.2551	0.07, 1.23, 0.2850	0.14, 0.81, 0.4083
Total production, g DWm^{-2} year^{-1}	275 ± 192.9	169 ± 128.3	998 ± 432.3, 5	1.20, 5, 0.2844	0.18, 1.58, 0.2489	0.50, 2.01, 0.2919
Leaf N, % of dry weight	2.00 ± 0.040	2.06 ± 0.045	1.99 ± 0.089, 22	0.04, 22, 0.9677	0.05, 1.31, 0.2635	0.54, 3.57, 0.1551
Leaf P, % of dry weight	0.206 ± 0.0016	0.149 ± 0.0016	0.138 ± 0.0115, 21	1.04, 21, 0.3085	0.11, 2.82, 0.1074	0.91, 10.80, 0.1880

6

2

Table 2

Table 2. Coefficient of variation of vegetative features and production estimates of *Cymodocea nodosa* in shallow (depth < 3 m) and deep (depth > 3 m) meadows, and Z test to evaluate the significance of the difference between them. See caption Fig. 1 for data sources.

Variable	Depth < 3 m V* ± SE	Depth > 3 m V* ± SE	Z value Critical $Z_{0.05\ (2)} = 1.960$
Annual maximum shoot density, shoots m^{-2}	35 ± 5.1	55 ± 17.4	1.430
Leaf biomass, g DW m^{-2}	94 ± 20.3	61 ± 17.9	0.923
Rhizome and root biomass, g DW m^{-2}	56 ± 9.5	77 ± 26.6	0.891
Annual maximum total biomass, g DW m^{-2}	61 ± 11.3	67 ± 21.3	0.194
Rhizome and roots to shoot ratio	62 ± 11.0	64 ± 19.9	0.013
Abundance of flowers, flowers m^{-2}	69 ± 25.3	122 ± 65.1	0.864
Abundance of seeds, seeds m^{-2}	66 ± 23.5	219 ± 117.7	0.960
Number of leaves per shoot	21 ± 5.1	43 ± 14.5	1.739
Shoot mass, mg DW $shoot^{-1}$	63 ± 12.0	22 ± 7.2	1.507
Leaf plastochrone, days	22 ± 4.2	19 ± 5.3	0.392
Elongation of horizontal rhizome, cm $apex^{-1}$ $year^{-1}$	58 ± 15.1	53 ± 22.7	0.217
Leaf production, g DWm^{-2} $year^{-1}$	97 ± 36.2	79 ± 30.8	0.362
Total production, g DWm^{-2} $year^{-1}$	91 ± 45.5	67 ± 31.9	0.381
Leaf N, % of dry weight	21 ± 3.2	17 ± 5.5	0.562
Leaf P, % of dry weight	38 ± 6.6	55 ± 27.6	0.573

Table 3

Table 3. Number of shoots aged, average and median shoot age (on main diagonal) of *Cymodocea nodosa* at the study location and other meadows of this species. D values and critical $D_{0.05}$ values (below main diagonal) of Kolmogorov Smirnov two sample tests performed to evaluate the significance of the difference between the age distribution of *C. nodosa* shoots at each meadow. Bold face indicates significant differences in shoot age distribution.

	11 m, this study	8 m, this study	6 m, Reyes et al., 1995a	1 m, Pérez, 1989	0.5 m, Terrados and Ros, 1992
11 m, this study	588, 2.5, 2				
8 m, this study	**D = 0.141** >> $D_{0.05}$ = 0.078	623, 3.2, 3			
6 m, Reyes et al., 1995a	**D = 0.156** >> $D_{0.05}$ = 0.069	D = 0.054 < $D_{0.05}$ = 0.068	1112, 3.1, 3		
1 m, Pérez 1989	**D = 0.223** >> $D_{0.05}$ = 0.064	**D = 0.320** >> $D_{0.05}$ = 0.062	**D = 0.347** >> $D_{0.05}$ = 0.051	1920, 1.7, 1	
0.5 m, Terrados and Ros, 1992	**D = 0.224** >> $D_{0.05}$ = 0.065	**D = 0.320** >> $D_{0.05}$ = 0.064	**D = 0.339** >> $D_{0.05}$ = 0.053	**D = 0.056** > $D_{0.05}$ = 0.046	1641, 1.8, 1