

# 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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Received 4 April 2005; received in revised form 8 November 2005; accepted 9 December 2005

## 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 to 605 shoots m<sup>-2</sup>, and the annual rate of elongation of the horizontal rhizome, which increased from 23 to 71 cm apex<sup>-1</sup> year<sup>-1</sup>, were different as depth increased from <3 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 DW m<sup>-2</sup> = 480 (±53, S.E.) – 32 (±15, S.E.) 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<sup>-1</sup> year<sup>-1</sup> = 18 (±5.1, S.E.) + 5.0 (±1.33, S.E.) 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.

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**Keywords:** Seagrass; *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, 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

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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 *C. 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 *C. nodosa* growing at depths of 8 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 <3 m) 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 (41°47.227'N, 3°03.206'E), where *C. nodosa* forms a spatially homogeneous meadow (100% cover of the substratum) between depths of 7 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 <7 m. 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; p. 95).  $K_d$  at Sant Pol beach in July 2002 was  $0.095 \text{ m}^{-1}$ , a relatively low value for coastal waters (cf. Kirk, 1983; p. 112).

The abundance of *C. nodosa* was quantified as shoot density (number of shoots  $\text{m}^{-2}$ ) and biomass ( $\text{g DW m}^{-2}$ ). 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 60 °C during 48 h 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  $\text{H}_2\text{SO}_4$ . 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 1 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

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