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Seasonal uncoupling of demographic processes in a marine clonal plant

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A B S T R A C T

In temperate regions, climatic factors impose a general seasonal pattern on seagrass growth that can be observed in leaf growth rates and, in small species, also in shoot density. Large variations in shoot density suggest a strong temporal uncoupling between shoot recruitment and shoot mortality, and the dependence of each of these processes on different drivers. Here we examine seasonal patterns of recruitment and mortality in the seagrass *Cymodocea nodosa*, one of the species most sensitive to seasonal forcing in the Mediterranean. We sampled two local populations submitted to different nutrient availability in Alfacs Bay (NW Mediterranean) and determined recruitment and mortality rates, as well as other plant traits, on a monthly basis. Our results confirm the hypothesized uncoupling, with maximum mortality 2 months after maximum recruitment. Whereas timing of recruitment was associated with light availability, and was supported by carbohydrate remobilisation, mortality was related to high water temperatures and probably also to light limitation in late summer due to self-shading. In the high-nutrient population, algal overgrowth caused further light deprivation, with mortality rates higher than in the low-nutrient population. It is emphasised that the demographic balance of the studied populations was negative for most of the year, with the exception of August and September. Therefore, caution is necessary when overall population trends are inferred from single annual sampling events.

1. Introduction

Seasonal changes in climatic factors such as light and temperature shape the growth dynamics of temperate seagrasses (e.g. Sand-Jensen, 1975; Pérez and Romero, 1992; Alcoverro et al., 1995; Enríquez et al., 2004). The observed growth patterns arise not only from the interplay between such large-scale external factors (light and temperature) and local conditions (e.g. nutrient availability, sediment redox potential; Alcoverro et al., 1995; Wolfer and Strailer, 2004; Lee et al., 2007), but they are also strongly modulated by intrinsic factors, i.e. species-specific constraints. Of these, plant architecture and size, plasticity, extent of clonal integration and storage capacity (Pérez et al., 1994; Marbà et al., 1996; Agawin et al., 2001; Enríquez et al., 2004) are of key importance in determining the timing and magnitude of seagrass responses to climate forcing (Duarte, 1991; Laugier et al., 1999).

Thus, the seasonal response to climate forcing of the largest temperate seagrass species (e.g. *Posidonia oceanica*) is restricted to variations in shoot growth, which results from the combination of a large storage capacity (favoured by long-lived shoots and thick rhizomes) that buffers environmental variability, and long plastochron intervals (Marbà et al., 1996). In contrast, smaller seagrass species (e.g. *Cymodocea nodosa)* show strong variations not only in shoot growth but also in shoot density, the latter indicating possible seasonal uncoupling between recruitment and mortality (Tomlinson, 1974; Duarte, 1991). This may be the result of greater dependence on environmental conditions, probably caused by limited storage capacity (short-living shoots and thin rhizomes) in combination with high rates of module addition (short plastochron intervals; Marbà et al., 1996).

While the seasonality of some of the processes related to shoot growth, such as carbon balance, biomass changes, and leaf elongation and turnover, has received considerable attention (Alcoverro et al., 1995; 2001; Duarte, 1989; Duarte and Chiscano, 1999), annual patterns of shoot recruitment and mortality have been rarely examined (Olesen and Sand-Jensen, 1994a; Laugier et al., 1999). In seagrasses, shoot recruitment is mainly based on vegetative growth since the recruitment of new shoots via sexual reproduction, through seed establishment and germination, seems to be relatively infrequent (Olesen and Sand-Jensen, 1994a; Duarte et al.,

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2006). Vegetative shoot recruitment depends on rhizome growth and ramet addition (e.g. rhizome elongation capacity, branching frequency and angle; Kendrick et al., 2005), both modulated by resource (light, nutrients and space) availability. Shoot mortality is either due to internal (ageing) or external causes (competition, light deprivation, defoliation and mechanical disturbances; Duarte et al., 2006). The balance between shoot recruitment and mortality will largely determine the seagrass population trend: increasing, declining or stable (Olesen and Sand-Jensen, 1994a; Hemminga and Duarte, 2000).

The seagrass *Cymodocea nodosa* has been reported to experience one of the largest seasonal fluctuations known in seagrass shoot density (Terrados and Ros, 1992; Pérez and Romero, 1994; Marbà et al., 1996), with a marked pattern of biomass and productivity strongly coupled to seasonal changes in light and temperature (Pérez and Romero, 1992; Marbà et al., 1996). Previous studies on the demography of *Cymodocea nodosa* populations from both the Atlantic and the Mediterranean have focused on the annual net balance between shoot recruitment and mortality. This approach has mostly been based on reconstructive methods from single annual sampling events, inferring recruitment and mortality rates from seagrass shoot age distributions (Pérez et al., 1994; Cancemi et al., 2002; Cunha and Duarte, 2005). Although the reported estimates of annual recruitment and mortality provide useful information on population dynamics, they are subject to interpretative limitations (Ebert et al., 2002; Fourqurean et al., 2003) and suffer from the lack of information at shorter time-scales (i.e. within-year variability). Yet this information with higher time resolution can be especially important to understand the drivers of the individual processes (recruitment and mortality), as well as to infer more robustly the population trend.

Thus the present work aimed to elucidate the seasonal pattern of shoot recruitment and shoot mortality underlying the seasonal variation in shoot density in *Cymodocea nodosa*. We hypothesize the existence of temporal uncoupling between shoot recruitment and shoot mortality as the immediate cause of this variation, and we discuss the possible driving factors of these two basic demographic processes. We conducted monthly sampling, over one year, of two local populations of *Cymodocea nodosa* in Alfacs Bay, Western Mediterranean, and, by means of reconstructive techniques, we calculated monthly shoot recruitment and mortality rates, and examined their statistical association with several environmental (temperature and irradiance) and plant (biomass and carbon reserves in rhizomes) variables. Finally, we compared our results (annually-integrated) to demographic balances obtained using single annual sampling events.

2. Methods

2.1. Study site

Alfacs Bay is an estuarine bay situated on the southern side of the Ebro river delta (NW Mediterranean, Fig. 1). The shallow (0–2 m depth) areas are colonised by macrophytes, mostly *Cymodocea nodosa*, forming either monospecific stands or mixed with the green alga *Caulerpa prolifera* (Pérez and Camp, 1986; Mascaró et al., 2009). We chose two sampling sites, one on the northern shore and one on the southern shore. The two sites differ in nutrient availability, as the northern shore is subjected, from May to October, to the influence of freshwater carrying high nutrient and organic matter concentrations as runoff from rice paddy fields. In contrast, conditions on the southern shore are more similar to the general oligotrophic regime of nearby Mediterranean waters (Pérez et al., 2001). Consequently, the average concentrations of inorganic nitrogen and inorganic reactive phosphate in the water column are approx. 30-fold higher on the northern than on the southern shore, and even greater differences are found concerning pore waters (more than 200-fold higher nutrient concentration in the northern than in the southern zone; Vidal et al., 1992; Pérez et al., 1994). This difference in nutrient availability is reflected in the abundance of overgrowing green macroalgae during the summer on the northern shore and in a notably higher nutrient content in *Cymodocea nodosa* tissues, especially leaves (Pérez et al., 2001). Both sites also differ in salinity, with annual averages of 34.7 psu and 36.6 psu (northern and southern sites, respectively). These differences are not relevant for plant performance (growth and mortality), as its optimum is between 30 and 40 psu (Fernández-Torquemada and Sánchez-Lizaso, 2011).

In order to quantify the influence of the main climatic factors, monthly averaged values (mean ± SD) of irradiance (Global Solar

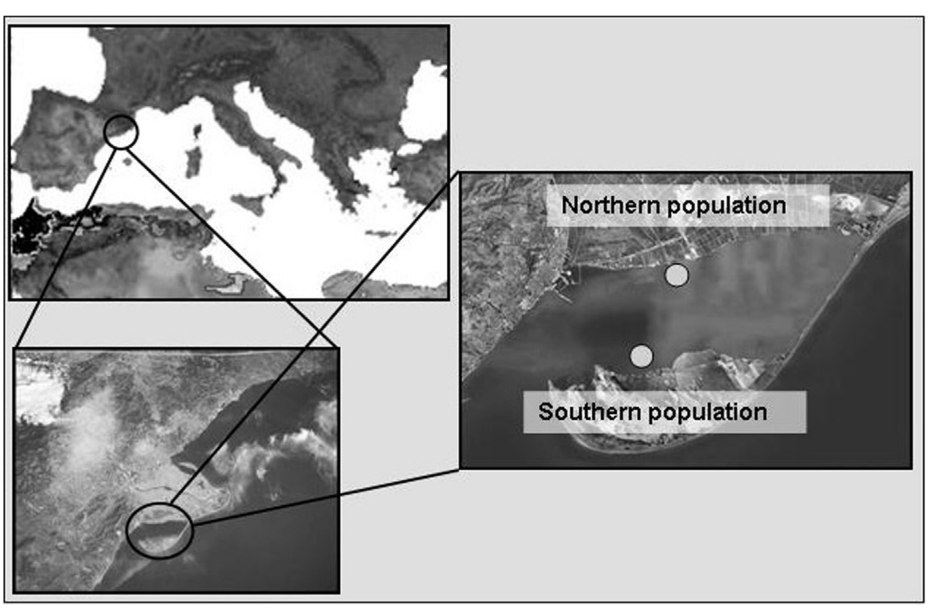

Fig. 1. Location of the study area and the two *Cymodocea nodosa* populations.