Population-level effects of clam harvesting on the seagrass *Zostera noltii*

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ABSTRACT: Seagrass declines have been reported worldwide, mostly as a consequence of anthropogenic disturbance. In Ria Formosa lagoon, southern Portugal, the intertidal meadows of *Zostera noltii* are highly disturbed by clam harvesters. The most common technique used to collect the clams consists of digging and tilling the sediment with a modified knife with a large blade. Here we present both descriptive and experimental evidence of the negative effects of clam harvest on the *Z. noltii* populations of Ria Formosa. A comparison between disturbed and undisturbed meadows suggests that clam harvesting activities change the species population structure by significantly reducing shoot density and total biomass, particularly during August, when the harvest effort is higher. Experimental harvest revealed a short-term impact on shoot density, which rapidly recovered to control levels during the following month. An experimental manipulation of rhizome fragmentation revealed that plant survival is reduced only when fragmented rhizomes are left with 1 intact internode. Shoot production and rhizome elongation and production of fragmented rhizomes having 2 to 5 internodes were not significantly affected, even though growth and production were lower when only 2 internodes were left. Experimental shoot damage at different positions along the rhizome had a significant effect on plant survival, rhizome elongation, and production only when the apical shoot was removed. Our results show that clam harvest can adversely affect *Z. noltii* meadows of Ria Formosa while revealing a low modular integration that allows the species to rapidly recover from physical damage.

KEY WORDS: Clam harvest · Physical damage · *Zostera noltii* · Seagrass · Disturbance · Population recovery

INTRODUCTION

Seagrass decline is a worldwide phenomenon. Although natural disturbances are recognized, most declines are attributed to anthropogenic disturbances (Short & Wyllie-Echeverria 1996). Direct mechanical damage reported to disturb seagrasses include dredging (Zieman 1982, Phillips 1984, Thayer et al. 1984, Coles et al. 1989), propeller scarring (Zieman 1976, Walker et al. 1989, Dawes et al. 1997), boat mooring and anchoring (Williams 1988, Walker et al. 1989, Creed & Amado Filho 1999), and docks (Burdick & Short 1999). Fishing gear practices (Ardizzone et al. 2002, Orth et al. 2002, Uhrin et al. 2005) and fishing techniques associated with clam harvest and clam cul-

ture (Peterson et al. 1983, 1987, Fonseca et al. 1984, Everett et al. 1995, Boese 2002, Neckles et al. 2005) have also been shown to negatively impact seagrasses, including declines in seagrass cover and failure of seagrass restoration in the Dutch Wadden Sea (De Jonge & De Jong 1992).

Sporadic and continuous mechanical damage results in partial or complete removal of plants from the substratum (Short & Wyllie-Echeverria 1996). As a result of plant removal, secondary effects like decreased seagrass cover, productivity, and biodiversity and increased habitat fragmentation, sediment resuspension, erosion, and alteration of physical processes (e.g. water currents) may result in long-term effects such as community restructuring (Hemminga & Duarte 2000).

The Ria Formosa lagoon, southern Portugal, is a highly productive ecosystem dominated by the intertidal seagrass *Zostera noltii*. *Z. noltii* is a small species that develops extensive meadows sustaining high gross primary production (Santos et al. 2004). These meadows play an important role in the bivalve recruitment (A. H. Cunha & R. Santos unpubl. data) and biodiversity of Ria Formosa lagoon, including economically important species such as cephalopods, crustaceans, and fish. Clam harvest and clam culture are the main commercial activities of the lagoon, representing more than 90% of national clam production (Direcção Regional das Pescas e Aquicultura do Sul pers. comm.). These activities take place along the intertidal areas, where *Z. noltii* meadows develop. The most common technique used by local clam harvesters consists of manually digging and tilling the sediment using a modified knife with a large blade. This technique severs shoots and rhizomes and causes plant burial.

The main objectives of this study were to (1) analyze the effects of clam harvesting, as it is performed by local fishermen, on *Zostera noltii* population density and biomass through the comparison of disturbed and undisturbed meadows; (2) test the effects of clam harvesting on *Z. noltii* density and its recovery through *in situ* experimental manipulation; and (3) determine the effects of physical damage caused by clam harvesting technique in plant survival, growth, and production, through the experimental manipulation of both rhizome and shoot fragmentation at different modular levels, i.e. altering the intact number of modular units.

MATERIALS AND METHODS

This study was conducted from June to November 2001 in the Ria Formosa lagoon, southern Portugal (Fig. 1). The lagoon is a mesotidal system with a high spring tide surface area of 84 km^2 and an exposed intertidal area of about 80% (Andrade 1990). The lagoon is separated from the Atlantic Ocean by a system of 5 sand barrier islands and 6 inlets. The tidal amplitude ranges from 3.50 m on spring tides to 1.30 m on neap tides. Sampling was performed in a *Zostera noltii* meadow under clam harvesting disturbance and in an adjacent undisturbed meadow. The disturbed meadow is a free access area frequently used for commercial clam harvest. The undisturbed meadow is part of a private clam culture concession where trespassing is not allowed. Clam harvest did not occur in this area for several years. Five randomly distributed samples were collected biweekly from each meadow, with a 12 cm diameter core. In each sample, the number of shoots was counted to estimate shoot density. The total biomass (above plus belowground material) of *Z. noltii* was determined by drying the sample at 60°C for 48 h. The effects of clam harvest on *Z. noltii* population density and its recovery were assessed by *in situ* experimental manipulation. Fourteen permanent plots of 10 × 10 cm were randomly placed in a homogeneous, undisturbed *Z. noltii* meadow. Half of the plots were disturbed using the same technique employed by the local clam harvesters, while the other half remained as control (undisturbed). After the plots were disturbed, the area was allowed to settle for a day, so that the tidal currents would flatten the sediment and remove the loose plants. Plots were monitored the following day and every 2 wk thereafter for 5 mo, by counting all the shoots within each plot.

The physical impact of the clam digging on plant survival, growth, and production was assessed by experimental manipulation to varying degrees of rhizome and shoot fragmentation. In the first experiment, rhizomes were severed at increasing distances from the apical meristem, creating 5 levels of modular units (ramets) composed of 1, 2, 3, 4, or 5 rhizome internodes and including the respective aerial shoots (Fig. 2A).
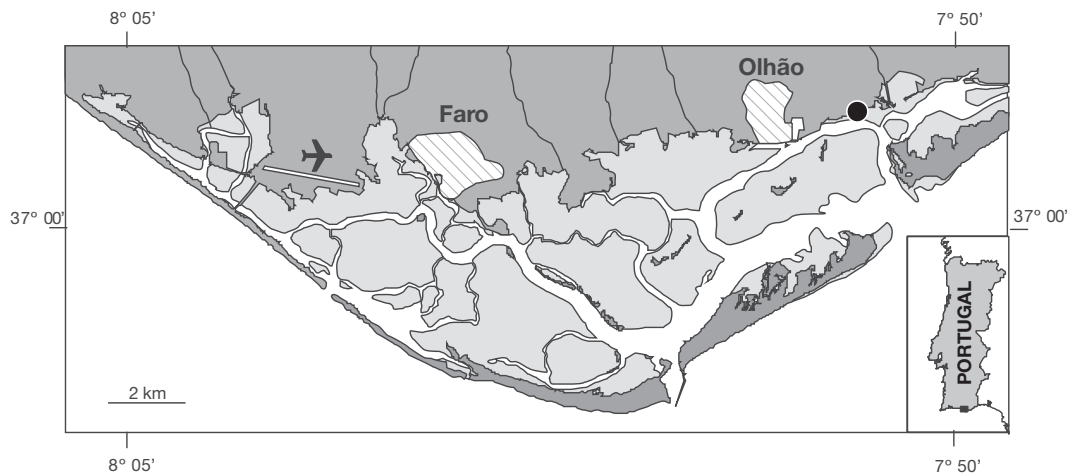

Fig. 1. Map of Ria Formosa, southern Portugal, with the location of *Zostera noltii* study meadows (●)

Each treatment was independently applied to 10 replicate plants. Plants were carefully collected, severed, and immediately placed in perforated plastic containers filled with local sediment. Apex shoots were tagged to distinguish new modular sets produced during the experimental period. The containers were randomly placed in the same meadow maintaining the local sediment level. The experiment was initiated in August 2003 and concluded after 30 d. Plant survival was determined and plants were examined for the number of new shoots and internodes produced to estimate the shoot and internode production rates (no. d^{-1}) and for the length of newly developed rhizome to calculate rhizome elongation rate (mm d^{-1}). The new internodes were dried at 60°C for 48 h, to estimate rhizome production rate (g DW d^{-1}).

In a second experiment, shoots were cut at their base, removing the basal meristem, to simulate damage caused by clam digging. Four levels of shoot damage, relative to shoot position on the rhizome, were generated: no damage (control), 1 shoot cut off (the closest to the apex shoot), 2 shoots cut off (leaving the apex shoot only), and only the apex shoot cut off (Fig. 2B). Each treatment was independently applied to
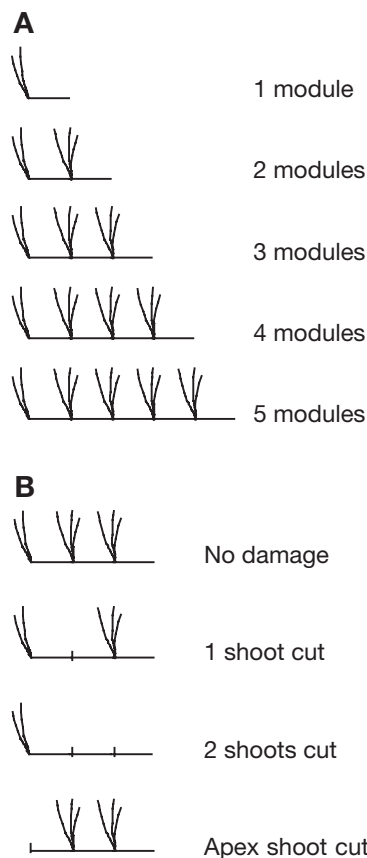

Fig. 2. *Zostera noltii*. Schematic representation of the experimental manipulation of (A) rhizome fragmentation and (B) shoot damage of *Z. noltii* plants

10 replicate plants consisting of 3 rhizome nodes and associated shoots, including the apical shoot. Plants with 3 modules were selected, as there were no significant differences in growth and production of plants with 3, 4, or 5 modules and it is very difficult to find intact plants with 5 modules. Plants were harvested, severed, and immediately placed in perforated plastic containers as described above. The experiment was initiated in September 2003 and concluded after 30 d. The plant parameters were analyzed as described above.

Prior to statistical analyses, data were tested for homogeneity of variance and normality of distribution. When necessary, data were log-transformed to fit assumptions. Differences in shoot density and biomass between disturbed and undisturbed meadows were investigated using 2-way ANOVA with disturbance and date as main effects. The recovery of shoot density after experimental disturbance was compared with controls using a Student's *t*-test for each sampling moment after data log-transformation. One-way ANOVA was used to test the effects of experimental damage of rhizomes and shoots on shoot and internode production, and in rhizome growth and production. When ANOVA indicated a significant difference, Tukey's multiple comparison test was applied to determine where significant differences occurred. Significant differences were considered at a probability value of p < 0.05 (Sokal & Rohlf 1995).

RESULTS

The shoot density of the *Zostera noltii* meadow under clam harvest disturbance was significantly lower than the undisturbed meadow (Fig. 3A), except on 1 June, 1 July, 15 July, and 1 October. The biomass of the disturbed meadow was 2 to 8 times lower during the whole sampling period (Fig. 3B). Shoot density and biomass showed no significant differences among sampling dates.

Experimental clam harvest significantly reduced the density of *Zostera noltii* shoots until 15 d after the digging event (Fig. 4). Immediately following disturbance, 43 % of shoots were lost and 19 % of the remaining shoots had damaged leaves. Thirty days post-disturbance, densities had recovered to non-disturbed levels. From then on, no significant differences were found between treatment and control plots (Fig. 4).

Survival of experimentally damaged plants having 1 modular unit was much lower (10 %) than plants with 2 to 5 modules (80 to 100 %, Fig. 5A). This treatment level was not considered in further statistical analysis as only 1 plant had survived. Rhizome elongation and rhizome production rates were lower in plants with
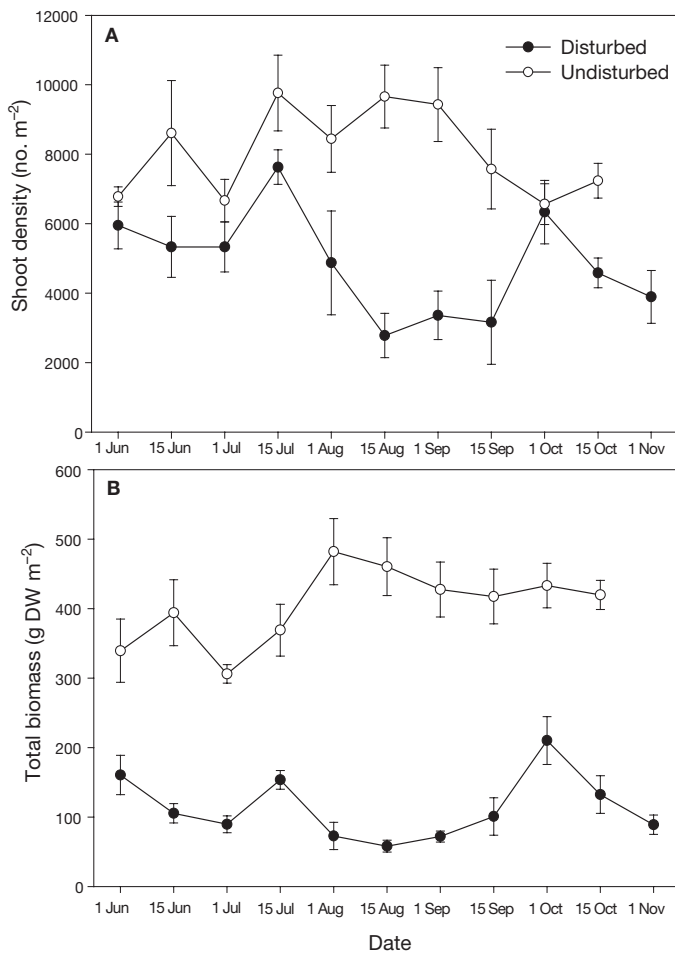
Fig. 3. *Zostera noltii*. (A) Shoot density and (B) total biomass of *Z. noltii* meadows under varying levels of clam harvest disturbance (mean ± SE)
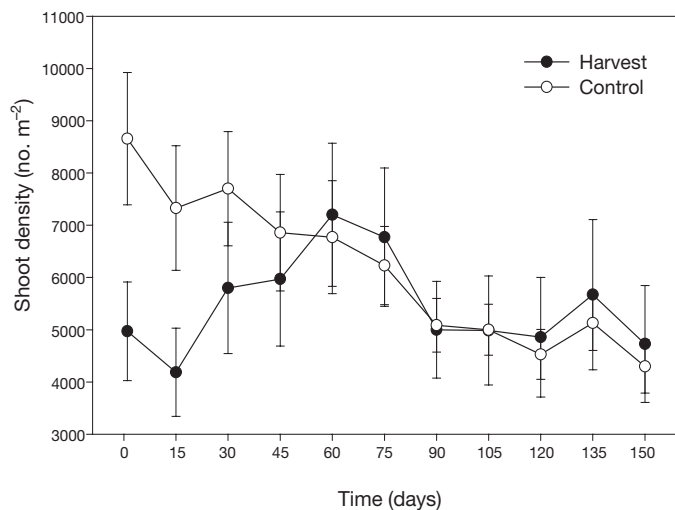

Fig. 4. *Zostera noltii*. Effects of clam harvest on shoot density (mean ± SE)

1 and 2 internodes, compared to plants with 3 to 5 internodes, but no significant effects of rhizome fragmentation (2 to 5 modules) were found in shoot production, internode production, rhizome elongation, or rhizome production rates (Fig. 5). The shoot damage experiment showed a negative effect of manipulation on plant survival, as 20% of all plants did not survive the initial cutting (Fig. 6A). No differences were found in the survival of plants with 1 or 2 shoots severed. Plant survival was lowest when the apex shoot was cut off (20%). The effects of cutting the apex shoot on shoot production, internode production, rhizome elongation, and rhizome production rates were extreme as practically no growth and production were observed with this treatment (Fig. 6). On the other hand, no significant effects were found when shoots other than the apical were severed (Fig. 6). No rhizome branching occurred during the experiment.

DISCUSSION

The *Zostera noltii* meadows of Ria Formosa, southern Portugal, are heavily utilized by clam harvesters and have a visually fragmented aspect and a lower sea-grass cover. The results of this study provide both descriptive and experimental evidence of the negative effects of clam harvest activity on *Z. noltii* populations. Both shoot density and total plant biomass were lower in meadows described as disturbed, and experimental harvest significantly reduced shoot density up to 15 d post-harvest. Our results indicate that recovery of isolated disturbances in *Z. noltii* meadows will occur for approx. 1 mo, as suggested by experimental harvest (Fig. 4). The high growth rates and production of *Z. noltii* (Vermaat & Verhagen 1996, Marbà & Duarte 1998, Laugier et al. 1999) seem to buffer the long-term effects of isolated disturbances. Besides the initial reduction in shoot density (43%), shoot damage was also found the day after the experimental disturbance. However, no significant evidence of shoot damage was found 15 d after disturbance and beyond, which illustrates the fast leaf growth of the species (Vermaat et al. 1987, 1993). Boese (2002) found slower recovery for *Z. marina* subjected to experimental clam digging. Significant declines in above- and belowground biomass were observed for 1 mo post-digging, and persisted for 10 mo, although not significant. Recovery of disturbed *Z. noltii* meadows may occur through vegetative development, as long as modular units with at least 2 rhizome internodes with the respective connected shoots remain on the sediment (Figs. 5 & 6). This result can be directly applied to the management of *Z. noltii* meadows in Ria Formosa, allowing them to sustain the impacts of local clam harvesting. A secondary effect of
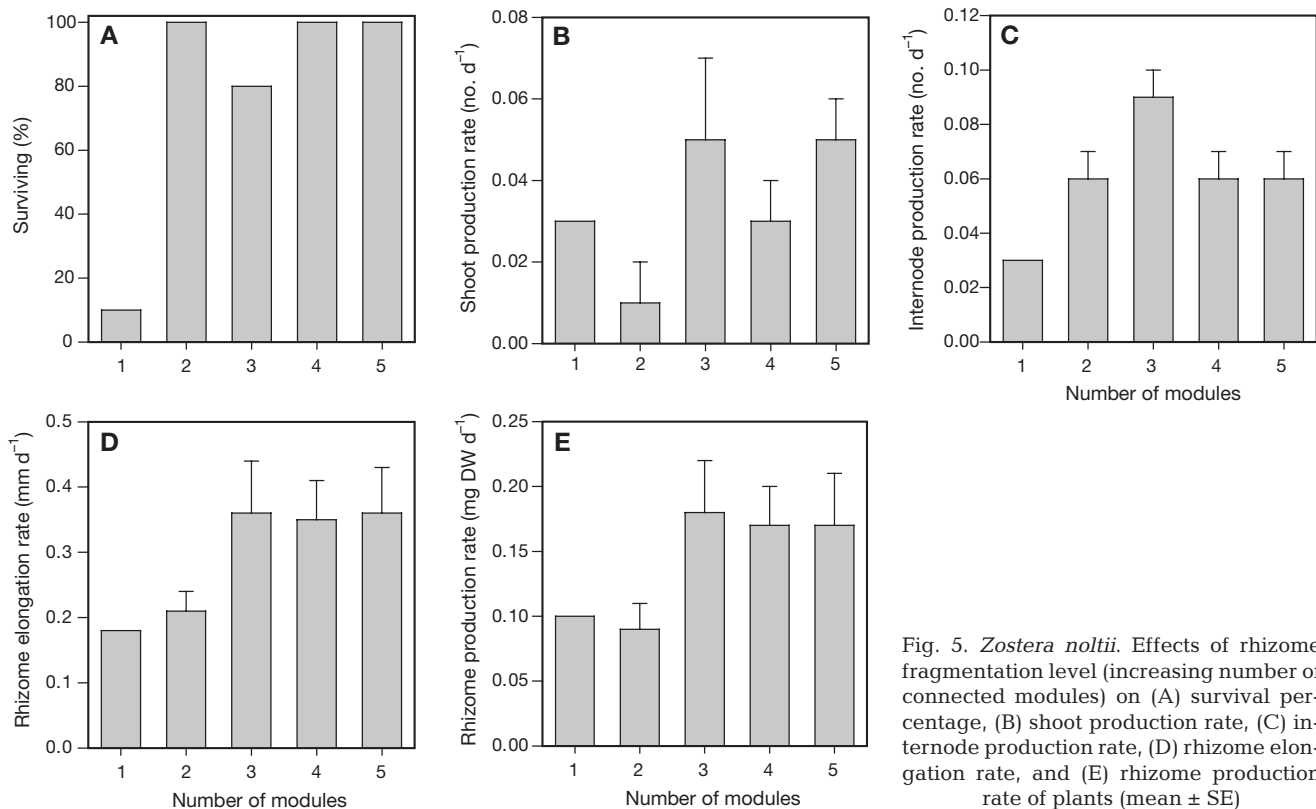
Fig. 5. *Zostera noltii*. Effects of rhizome fragmentation level (increasing number of connected modules) on (A) survival percentage, (B) shoot production rate, (C) internode production rate, (D) rhizome elongation rate, and (E) rhizome production rate of plants (mean ± SE)

exploiting clams or other resources such as molluscs within the *Z. noltii* meadows of Ria Formosa is the disturbance caused by trampling. Negative impacts on seagrass shoots and rhizomes as a result of repeated trampling have been demonstrated elsewhere (Eckrich & Holmquist 2000).

The recovery of commonly disturbed seagrass meadows depends not only on the level of disturbance but also on its frequency (Short & Wyllie-Echeverria 1996). The experimental manipulation of clam harvest in this study consisted of isolated disturbances. Extrapolation to the intertidal areas of Ria Formosa under frequent and intense clam harvest activity must be done with caution. A slower recovery of *Zostera noltii* shoot density than that found here would be expected.

Sexual reproduction of *Zostera noltii* may also contribute to the recovery of disturbed meadows as indicated by the higher reproductive effort of this species under clam harvesting disturbance (Alexandre et al. 2005, this volume). The relevance of sexual reproduction to the species recruitment was demonstrated by Diekmann et al. (2005), who found high genetic variability of *Z. noltii* meadows in Ria Formosa.

Rhizome fragmentation drastically reduced plant survival when only 1 module remained connected to the apical meristem (Fig. 5A). The damaged plants were not observed to decay but instead disappeared from the meadow, probably as a result of the buoyancy

of the leaves, which caused the limited root system of the modules to disengage. Shoot production, internode production, rhizome elongation, and rhizome production rates were not significantly affected by rhizome fragmentation (Fig. 5), even though growth and production were lower when only 2 modules were left. This indicates a low modular integration for *Zostera noltii* compared with other seagrasses. Terrados et al. (1997b) found negative effects on both rhizome and leaf growth of the seagrass *Cymodocea nodosa* when the horizontal rhizome was severed up to 11 internodes away from the apical meristem. Marbà et al. (2002) observed that the maximum translocation of carbon and nitrogen along *Z. noltii* rhizomes was lowest among seagrasses, about 9 cm, which is equivalent to a maximum of 3 internodes. The low modular integration observed in *Z. noltii* suggests that the high rhizome elongation and clonal growth rate for this species do not depend much on accumulated reserves in the rhizome. Rather, a direct and immediate investment of photosynthates (soluble carbohydrates) in growth and a low accumulation of insoluble carbohydrate reserves (starch) are expected. In fact, this was observed in a current investigation of the circadian and seasonal variation of *Z. noltii* carbohydrates (J. Silva & R. Santos unpubl. data). This strategy may constitute a valuable feature of *Z. noltii* when withstanding physical disturbances such as those caused by clam harvest.
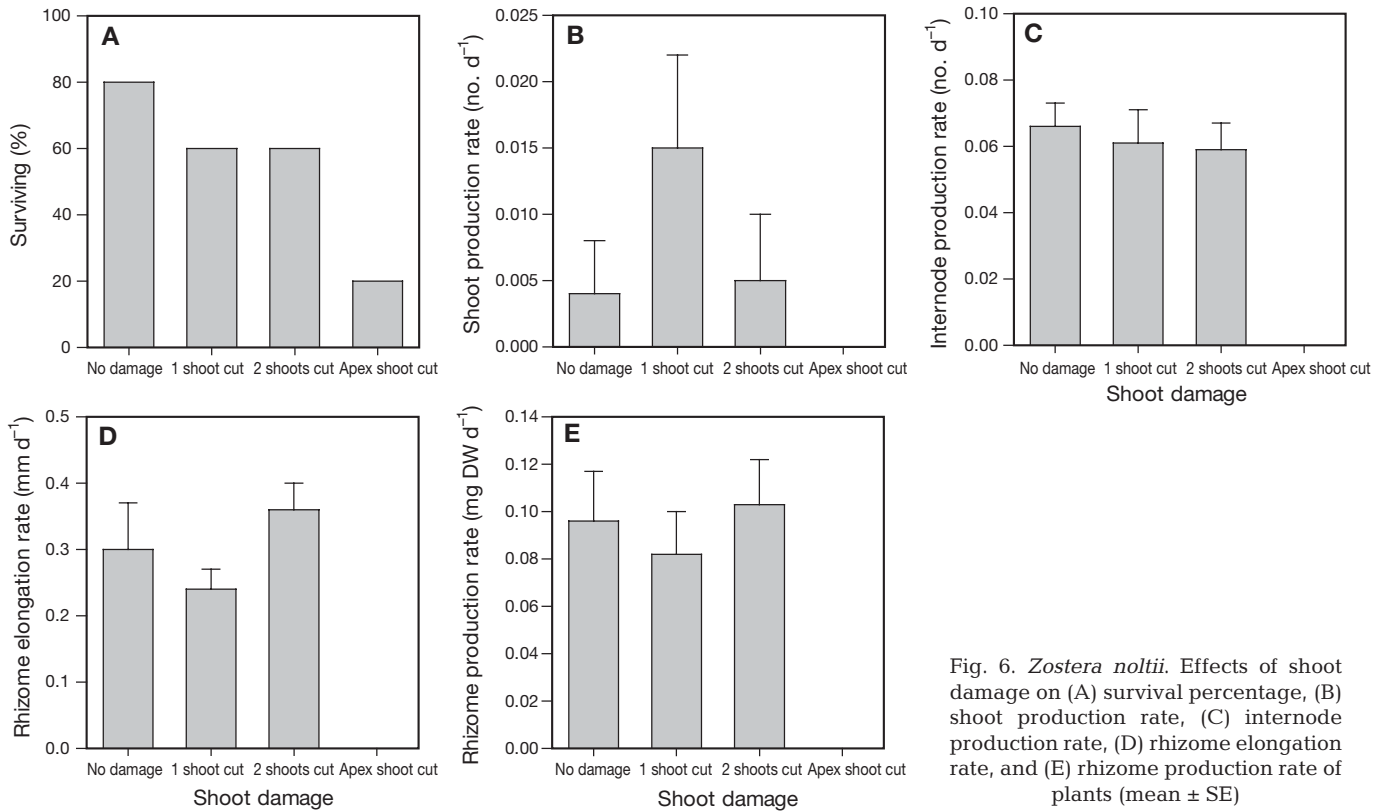
Fig. 6. *Zostera noltii*. Effects of shoot damage on (A) survival percentage, (B) shoot production rate, (C) internode production rate, (D) rhizome elongation rate, and (E) rhizome production rate of plants (mean ± SE)

When shoots were severed at different positions along the rhizome, a strong effect was found on shoot production, internode production, rhizome elongation, and rhizome production rates only when the apical shoot was removed (Fig. 6). This supports the hypothesis that apical growth in *Zostera noltii* is mostly dependent on apical shoot photoassimilates, contrary to what was observed in other seagrasses that rely on internal translocation of resources along the rhizome (Marbà et al. 2002). Physiological integration between shoots has been interpreted as an adaptive advantage for seagrasses, such that different modules can share resources produced by neighboring modules and contribute to vegetative spread by apical meristem growth (Marbà et al. 2002). The *Z. noltii* strategy must differ from most seagrasses as it depends less on module integration yet is more able to react to heavy physical disturbance that fragment its clonal structure. In addition, no rhizome branching occurred in *Z. noltii* within the time of the experiment, indicating that apical dominance does not occur in *Z. noltii*, at least within a 30 d response time. Removal of the apical meristem in *Cymodocea nodosa* not only promoted branching but also elongation of the rhizome branches (Terrados et al. 1997b). A change in the growth form of the closest vertical rhizome into horizontal growth was also observed in *C. nodosa* as a result of apical dominance (Terrados et al. 1997a).

In conclusion, clam harvesting activity adversely affects *Zostera noltii* populations, despite the great recovery capacity of the species. Meadow recovery may occur even if plants with only 1 or 2 modules, including the apical shoot, remain on the sediment. Clam harvesting in Ria Formosa may not allow the full recovery of *Z. noltii* meadows due to high frequency and intensity of disturbance, particularly during summer. Our results suggest that *Z. noltii* meadows may sustain clam harvest disturbance provided that the meadows are allowed to recover from isolated disturbance for about 1 mo.

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