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Demography of shallow eelgrass (*Zostera marina*) populations – shoot dynamics and biomass development

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Summary

1 Although *Zostera marina* (eelgrass) is a widespread and well examined seagrass we provide here a first study of shoot demography and growth, conducted by following cohorts of eelgrass shoots during an annual cycle in six perennial populations in Limfjorden, Denmark.

2 The formation of leaf shoots on side-branches occurred throughout the year but peaked in May-June and declined at reduced light availability. Maximum mortality of over-wintering leaf shoots coincided with the flowering season, whereas new leaf shoots had the highest mortality in late summer and most were lost at an early age (mean half-life of 50 days) presumably due to shading within the dense stands. The cumulative production of new leaf shoots was between 525 and 1296 $\text{m}^{-2}\ \text{year}^{-1}$ and total shoot mortality ranged from 541 to 1483 $\text{m}^{-2}\ \text{year}^{-1}$, so that net shoot density changed only little (16–491 shoots $\text{m}^{-2}\ \text{year}^{-1}$). Because no seedlings were established within the vegetation, population maintenance was achieved by rhizome branching.

3 Average leaf production per shoot was high (17 leaves $\text{shoot}^{-1}\ \text{year}^{-1}$) compared to formation of new shoots (0.97 shoots $\text{shoot}^{-1}\ \text{year}^{-1}$). Biomass losses due to the continuous leaf turnover constituted 74% of total biomass losses, and growth of the over-wintering shoot population was the major contributor to seasonal biomass increases. Thus, during an annual cycle with low frequency of disturbance, biomass in these stable eelgrass populations was predominantly allocated to increased shoot size, despite the high shoot recruitment.

4 Eelgrass is not easily assigned to a particular growth strategy but resembles clonal terrestrial plants with phalanx growth by forming dense meadows of restricted horizontal spread and maintaining control of shoot recruitment. Cost effective reconstruction techniques, not applicable to eelgrass with short lived rhizomes, hold great promise for future comparative studies of demography and growth strategy of long-lived seagrasses and terrestrial rhizomatous plants.

Keywords: biomass allocation, population structure, shoot demography, *Zostera marina*

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Introduction

Seagrasses are clonal plants that form dense monospecific meadows by vegetative propagation in shallow waters in temperate and tropical regions (Tomlinson 1974; den Hartog 1970). Seagrass meadows are very important to the ecology of coastal waters (Mann 1982) but are vulnerable to physical perturbations caused by severe climatic conditions or human activities (e.g. eutrophication) and therefore vary in areal cover due to shoot mortality (den Hartog & Polderman 1975; Orth & Moore 1983; Orth & Moore 1986; Shepherd *et al.* 1989). The recovery of seagrass populations from a decline in abundance predominantly relies on the recruitment of shoots through branching and expansion of the rhizomes (Duarte & Sand-Jensen 1990; Williams 1990). Thus, seagrass populations are subject to a continuous turnover of shoots and the overall balance between shoot mortality and recruitment determines whether populations expand or decline. The time interval required to recover after severe die-back and the ability to form meadows in frequently perturbed areas are greatly influenced by the capacity for rhizome elongation and the subsequent production of new shoots on side-branches to occupy available space (Duarte 1991).

The shoot demography of terrestrial plants has been studied intensively and has led to recognition of general patterns of shoot density regulation via either shoot natality or shoot mortality (Lovett Doust 1981; Schmid & Harper 1985) and formulation of general theories of biomass-density regulation in even-aged monocultures (e.g. -3/2 law; Westoby 1984). Similar studies have not been conducted for seagrasses, although monospecific seagrass stands should provide optimal opportunities for comparisons among seagrass species of different growth form and tissue turnover and for interesting parallels to terrestrial plants. This neglect is particularly surprising for eelgrass, which is widely distributed in temperate waters throughout the northern hemisphere (den Hartog 1970) and whose ecology is otherwise well known. Eelgrass rhizomes are, however, relatively short-lived (1–2 years) and shoot densities are high ($\sim 1000\ m^{-2}$) making it laborious and technically difficult to reconstruct shoot life tables or to follow tagged shoots over long time intervals. In contrast, reconstruction techniques and age determinations are easily applicable in most large, long-lived subtropical and tropical seagrass species and should provide a valuable tool to evaluate their regulation of shoot recruitment and longevity (Duarte *et al.* 1993).

Here, we attempt to quantify the capacity for clonal growth and its regulation in six adjacent perennial eelgrass (*Zostera marina*) populations subject to low frequency of disturbances, by considering the dynamics of leaf shoot cohorts during the annual cycle. Population age structure was used to determine the production of new leaf shoots and the fate of shoots recruited in successive time intervals. More specifically we ask whether eelgrass shoots are indeed subject to extensive turnover as suggested by the closely related *Zostera japonica* in intertidal habitats (Bigley & Harrison 1986) and we examine the importance of shoot density regulation via shoot natality or mortality with reference to the strategies for terrestrial clonal plants.

The biomass of perennial eelgrass populations usually follows a distinct seasonal pattern showing minimum values in winter and peak values in mid-summer following a period of extensive growth (Sand-Jensen 1975; Jacobs 1979; Wium-Andersen & Borum 1984). Measurements of eelgrass production have revealed fast and continuous turnover of leaves and rhizomes (Sand-Jensen 1975), but usually ignore the flux of shoots within the population. Here, we were able to quantify the cumulative losses of biomass via mature and newly recruited leaf shoots in comparison to biomass losses through leaf shedding and, thereby, determine the relative importance of seasonal biomass allocation to increased shoot weight and density.

THE STUDY SPECIES *Zostera marina*

Zostera marina L. (eelgrass) is a perennial seagrass with a simple shoot system consisting of a horizontal, below-ground rhizome with associated roots and one terminal and several lateral leaf shoots (Fig. 1). A leaf shoot consists of a bundle of leaves supported by a single basal meristem. Each eelgrass leaf is formed in synchrony with a rhizome segment (internode). All leaf axils contain a potential branch-producing meristem and side-branches are initiated within the third or fourth leaf of the parent leaf shoot (Tomlinson 1974). Eelgrass does not seem to develop dormant meristems. Terminal shoots may develop inflorescences from the end of their first year and they senesce after flowering.

Methods

Eelgrass shoot demography was studied in six shallow-water (~ 0.7 m) eelgrass populations, located within 500 m of each other in a well-protected region of the western part of Limfjorden (Nees Sund; salinity 26‰), Denmark. Daily measurements of surface irradiance were obtained from a nearby (70 km) meteorological centre. The light availability below the canopy was calculated, based on a biomass specific attenuation coefficient of $0.0143\ m^2\ g^{-1}$ dry wt as previously determined (Wium-Andersen & Borum 1984). Light absorption within the canopy was estimated as the difference between light availability at the surface and below the canopy, assuming that light reflection within the vegetation was 10% of incoming light.

Above- and below-ground biomass was harvested monthly from March to October 1990 and in March

Fig. 1 Schematic illustration of *Zostera marina* showing a terminal and several lateral leaf shoots from a common rhizome.

1991 within three randomly located 0.25-m × 0.25-m quadrates in each population. The age of all side-branches was recorded from their position on the rhizome chain and rhizome internodal length sequences were measured on 10–15 of the oldest shoots present. Seedlings were identified by the presence of the seed coat if still attached to the roots or by a scorpioid base, indicative of a seedling (Setchell 1929). Finally, leaves and rhizomes were separated, dried and weighed.

The shoot age of side-branches was recorded in terms of the number of leaves (number of standing leaves plus the number of rhizome internodes) produced by the parent after the branch was initiated and subsequently converted into absolute shoot age based on the measured time interval between formation of successive leaves. These plastochrone intervals (*PI*) were determined from the sequence of rhizome internodal lengths, which follows a seasonal cycle with short segments being produced during winter and long ones during summer. Therefore, the number of leaves (= number of rhizome segments) formed since winter growth can be estimated as the change in number of standing leaves plus the number of rhizome internodes following the shortest segment. The leaf formation rate was also measured directly by the leaf marking technique of Sand-Jensen (1975) as modified by Perez *et al.* (1991).

Leaf shoot recruitment and mortality were estimated from constructed life tables, where the monthly transition of leaf shoots between age-classes was followed. Because the rhizome linkage between individual leaf shoots decays relatively fast, only shoots younger than 17 *PI*s (~1 year) could be separated into distinct age-classes. The majority of the overwintering leaf shoots were older than 4 *PI*s and capable of branching. These shoots comprised one group of mixed age ('old shoots') in the constructed life-table. Leaf shoots recruited during our study period ('young shoots') were included in the life-table in accordance with their appearance between successive sampling dates. Leaf shoot recruitment rate (r_b) was calculated as

$$r_b = \ln\left(\frac{N_t}{N_t - N_{new}}\right)t^{-1}, \qquad (1)$$

where N_t is total leaf shoot density at the sampling date and N_{new} is the number of leaf shoots recruited during the period (t) preceding sampling. Leaf shoot mortality rate (r_m) was calculated as

$$r_m = \ln\left(\frac{N_t - N_{new}}{N_0}\right)t^{-1}, \qquad (2)$$

where N_0 is the shoot density at the preceding sampling date.

Above-ground production was calculated by adding the biomass which was lost due to shedding of shoots and old leaves to the monthly changes in above-ground biomass. Biomass losses through leaf shoot mortality were calculated from changes in the number of leaf shoots from each age class and their corresponding weights. Leaves lost per shoot were estimated from monthly changes in leaf number per shoot minus the number of new leaves produced (estimated from the measured *PI*). The biomass of shed leaves was calculated from the weight proportion (F_b) of the oldest leaf of all leaves per shoot. Assuming no leaf turnover in lost shoots between successive sampling dates, total biomass loss due to leaf shedding ($Loss_{leaves}$) was then

$$Loss_{leaves} = [0.5(B_0 + B_t) - Loss_{shoots})\ F_b n, \qquad (3)$$

where B_0 is the initial and B_t the final above-ground biomass for the period (t), $Loss_{shoots}$ is biomass losses due to leaf shoot mortality and n is the number of leaves lost during the period preceding sampling. Above-ground production (P) during each sampling period was

$$P = B_t - B_0 + Loss_{leaves} + Loss_{shoots}. \qquad (4)$$

The annual production was calculated as the sum of the production estimates of each sampling period from March 1990 to March 1991.

Below-ground (rhizomes + roots) production was estimated from the mean weight of rhizome segments produced between sampling dates and the number of leaf shoots per unit area. To avoid overestimation of rhizome production, the number of newly produced leaf shoots (younger than 4 *PI*) were subtracted from the areal leaf shoot density because they had very small internodes on their rhizomes.

Results

SEASONAL BIOMASS DEVELOPMENT AND LEAF PRODUCTION

Daily surface irradiance (Fig. 2) is presented as mean values over periods corresponding to one P.I. for eel-

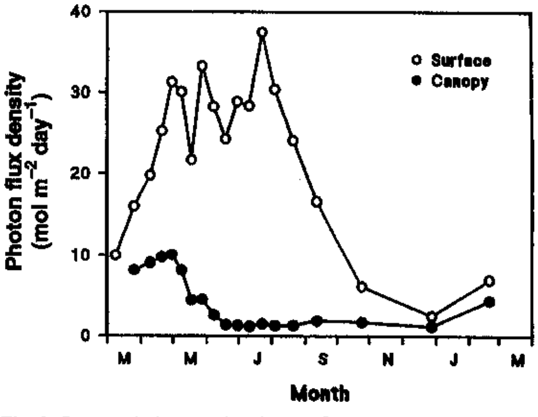

Fig. 2 Seasonal changes in photon flux density at the water surface (○) and below the eelgrass canopy (●). Symbols represent mean values during time intervals equivalent to plastochrone intervals of eelgrass leaf shoots.

grass at that time of year (see later). Mean surface irradiance varied from 2.5 mol photons m^{-2} day^{-1} during winter to 37.5 mol m^{-2} day^{-1} in late July. Maximum light below the canopy was reached in early May prior to extensive biomass development (Fig. 3), and it declined gradually to 3 mol m^{-2} day^{-1} in mid-June and 1 mol m^{-2} day^{-1} in late summer (Fig. 2), close to the light compensation point for eelgrass photosynthesis (Dennison 1987). Water temperature, measured less frequently, ranged from 25 °C in July to below zero during thin ice cover in January and February. All the eelgrass populations examined were exposed to the same surface irradiance and water temperature because of their close proximity and, unless otherwise is stated, data were similar from all six populations and are presented as mean values.

The six eelgrass populations displayed seasonal biomass patterns, with increasing values from March to August followed by a decline in autumn (Fig. 3). Mean above-ground biomass ranged from 38 to 219 g dry wt m^{-2} and below-ground biomass (rhizomes and roots) from 63 to 119 g dry wt m^{-2}. Leaf shoot density, on the other hand, remained relatively constant at about 840 shoots m^{-2} from March to August and declined to 600 shoots m^{-2} in autumn (Fig. 3). Flowering shoots were found between March and August with maximum densities in May, ranging from 29 to 150 shoots m^{-2} among populations.

Leaf formation rate, measured by the leaf marking technique, was in close agreement with rates estimated from rhizome internodal length sequences (Fig. 4). Leaf formation rate showed maximum values during May (0.10 leaves shoot^{-1} day^{-1}, *PI* = 9.6 days), when light availability in the canopy was greatest (Fig. 2), and low values during winter, yielding an annual production of 17 leaves shoot^{-1}.

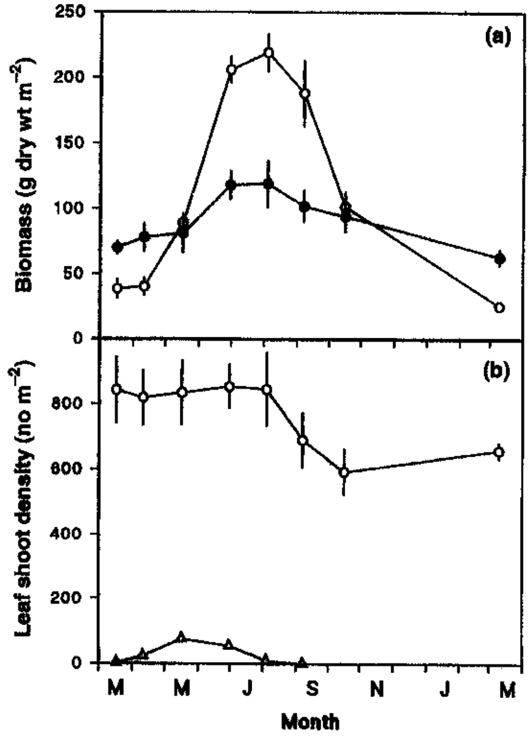

Fig. 3 Seasonal changes in (a) biomass of eelgrass leaf shoots (○) and rhizome + roots (●) and (b) leaf shoot density of all eelgrass leaf shoots (○) and flowering eelgrass shoots (△). Symbols are mean values (± SE) for six adjacent eelgrass populations.

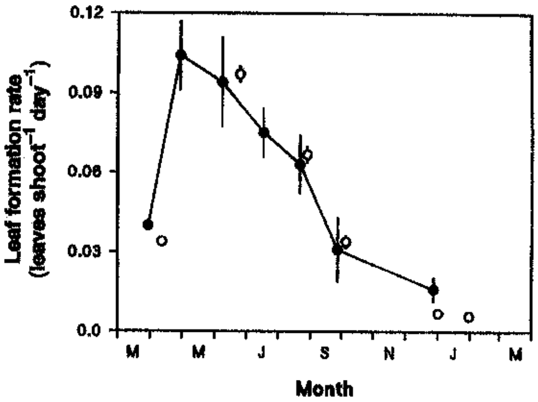

Fig. 4 Seasonal changes in the appearance rate of new eelgrass leaves (mean ± SE) measured by rhizome internodal length sequences (●) and leaf marking (○).

LEAF SHOOT RECRUITMENT AND MORTALITY

The seasonal changes in age structure of leaf shoots are presented as average values for the six adjacent populations (Fig. 5). During winter and early spring, leaf and leaf shoot formation was very low and the majority of leaf shoots present in March–April were recruited before the winter. During May, coinciding with extensive leaf and biomass development (Figs 3 and 4), many new leaf shoots appeared and the total number of young leaf shoots reached a maximum level in August. The high frequency of young leaf shoots (1–3 *PI*s of age) in March 1991 (Fig. 5), resulted from a much higher frequency of branching from October 1990 onwards than over the previous winter.

The seasonal cycle of leaf shoot recruitment rate, presented as the number of side-branches formed per m^2 per day within each *PI*, is shown in Fig. 6 for all six populations. The initiation of new branches was significantly correlated ($r^2 = 0.45$, $P < 0.005$) to the amount of light absorbed within the eelgrass canopy. Overall, the six populations showed similar seasonal patterns of leaf shoot recruitment with highest rates during early summer when seasonal light availability was high and self-shading within the vegetation was low. However, the initiation of high branching activity differed somewhat. Two populations showed an early start and reached maximum leaf shoot recruitment of 11.4 and 14.4 shoots m^{-2} day^{-1} in May (Fig. 6d and f). The other populations reached maximum rates in June (range 7.4–11.7 shoots m^{-2} day^{-1}).

The cohorts of eelgrass leaf shoots that appeared between successive sampling dates, faced a steady

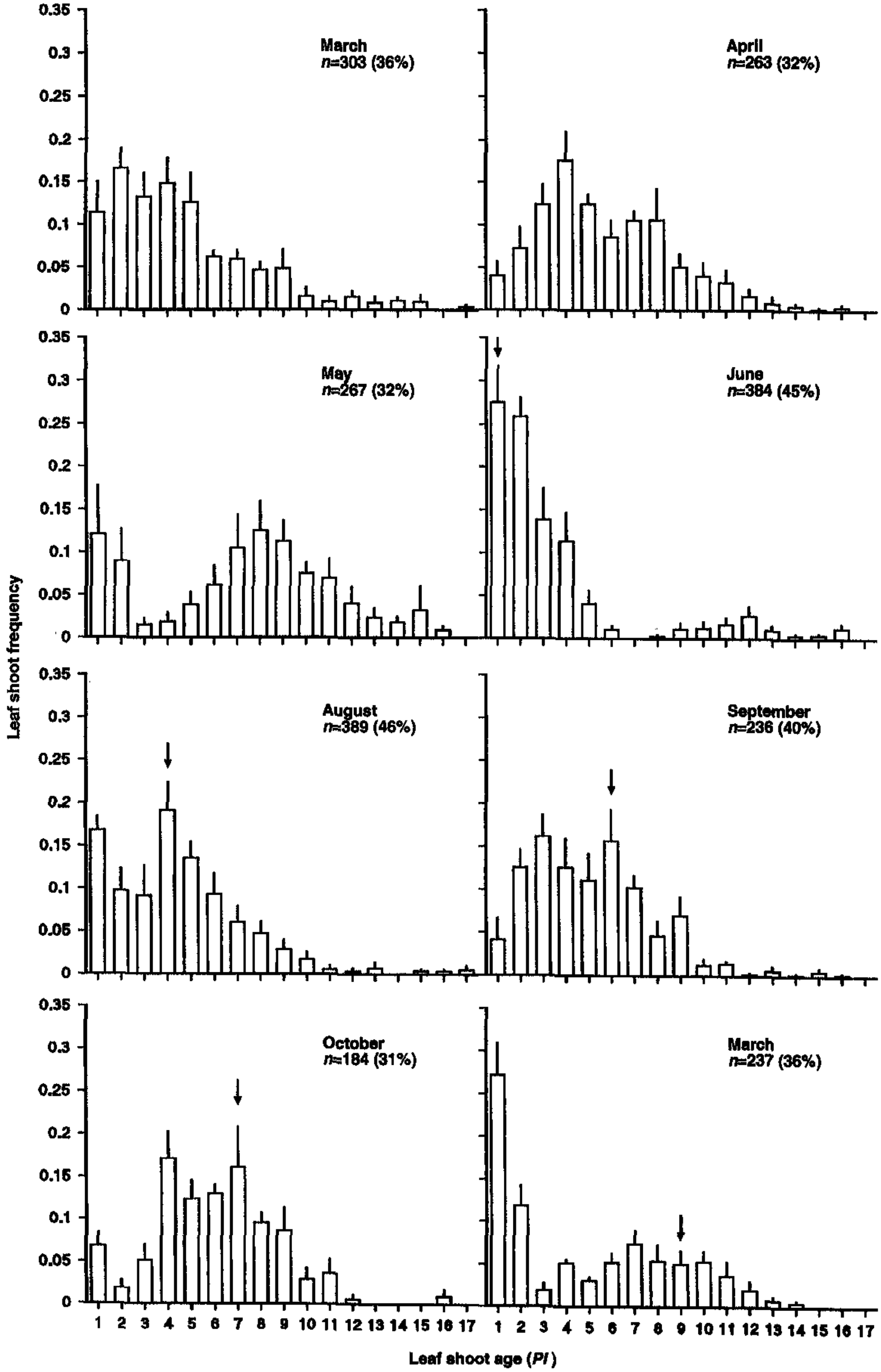

Fig. 5 Seasonal changes in age-structure combined for six adjacent eelgrass populations (mean ± SE). Only age-classes younger than 17 *PIs* (~ 1 year) are included. Because new leaf shoots are not formed synchronously, the youngest age-class is not complete and therefore omitted from the constructed tables. *n* is the number of leaf shoots per m^2 younger than 17 *PIs* with their proportion of all leaf shoots (%) in brackets. Arrows mark the appearance of the largest age-class recorded (in June) and its subsequent transition to older age-classes.

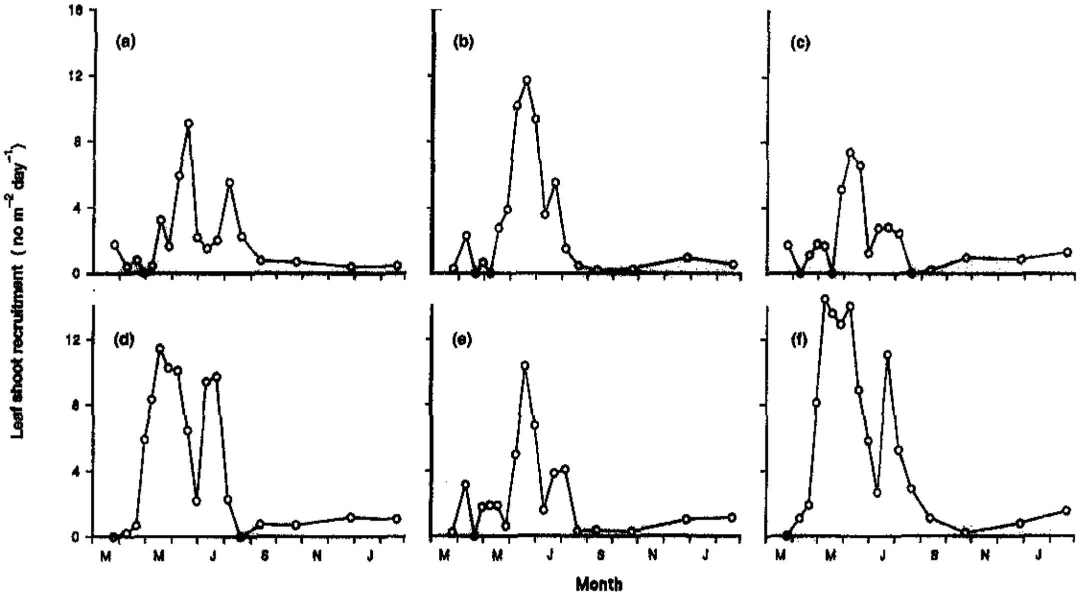

Fig. 6 Seasonal production of new shoots on side branches in the six shallow eelgrass populations (a–f).

decline with time albeit slowing down during winter (Fig. 7A). All cohorts showed a significant ($P < 0.05$) linear relationship between log-transformed shoot number per cohort and time during the growth season and, thus, exhibited a constant mortality risk independent of age and month of recruitment. The mixed age class of shoots surviving from the previous year showed a much smaller decline from 840 to 500 m^{-2} during early summer and, thereafter, remained constant (Fig. 7B). The mortality rate of old leaf shoots peaked in June (7.7 10^{-3} ln-units day^{-1}) when recruitment rate was also at a maximum (Fig. 8). The

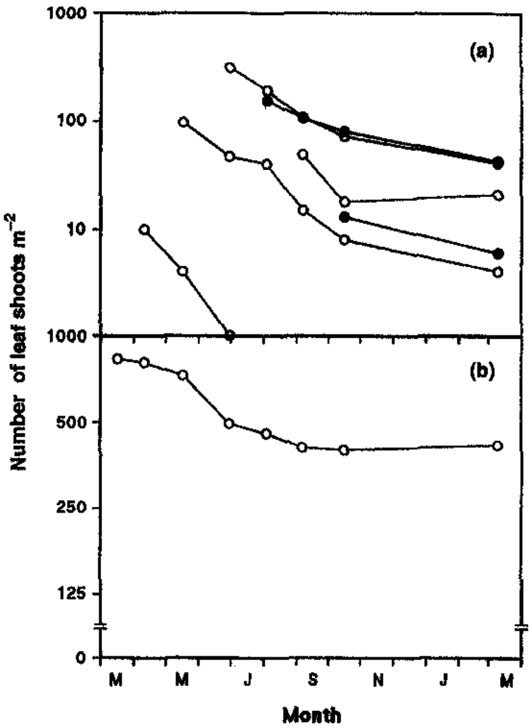

Fig. 7 Depletion curves (mean ± SE) of leaf shoot cohorts recruited between successive sampling dates (a) and of the over-wintering leaf shoot population present at the initiation of this study in March 1990 (b). The start of the curves in (b) represents the time of cohort recruitment. Filled and unfilled symbols are used for clarity only.

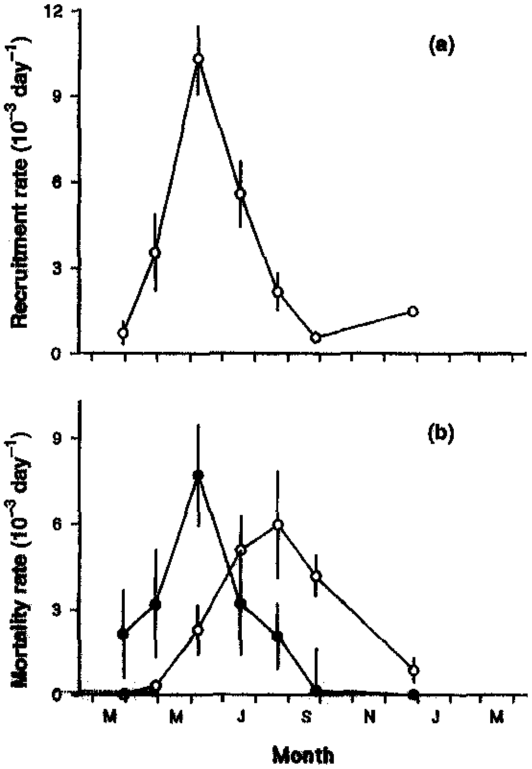

Fig. 8 Seasonal changes in eelgrass leaf shoot recruitment rates (a) and mortality rates (b) of old leaf shoots present at the initiation of the study (●) and of leaf shoots recruited during the study (○). Recruitment and mortality are relative rates normalized to the number of shoots present according to equations 1 and 2, respectively, and constitute mean values (± SE) of six adjacent eelgrass populations.

maximum mortality rate (6.0 10^{-3} ln-units day^{-1}) of new leaf shoots occurred in September, 8–10 weeks after the maximum recruitment rate.

Cumulative shoot recruitment achieved through rhizome branching and shoot mortality in each of the six eelgrass populations are summarized in Table 1. Only few seedlings (mean 7 m^{-2}, range 0–11 m^{-2} in May) became established within the populations and none of these were still alive by June. Variability in annual leaf shoot recruitment among the six populations was not significantly correlated to the standing leaf shoot density in March 1990 ($r^2 = 0.091$, $P > 0.1$) and ranged from 0.6 to 1.5 branches per leaf shoot. The net reduction in leaf shoot density experienced by the six populations between March 1990 and March 1991 averaged 187 shoots m^{-2} $year^{-1}$ (range 16–491 shoots m^{-2}) and occurred despite an annual mean recruitment of 796 shoots m^{-2} (range 525–1296 shoots m^{-2}). Thus, despite a dynamic flux of leaf shoots the changes in shoot density were relatively small. The initial survival of newly recruited leaf shoots was low since half of the shoots died within one to two months of their appearance (Fig. 7, Table 1). During the period of maximum mortality of young leaf shoots (June–September), variability in the number of leaf shoots lost among the six adjacent populations was not significantly related ($r^2 = 0.24$, $P > 0.1$) to the average number of shoots present, suggesting that leaf shoot mortality was density independent. The relative death risk decreased with age for leaf shoots surviving their first year and the population of old shoots lived considerably longer (average half-lives of 389 days, Table 1).

ABOVE-GROUND PRODUCTION AND BIOMASS LOSSES

To ensure sufficient leaf shoot numbers to describe age-size relationships of eelgrass shoots, data from all populations were combined. Eelgrass median leaf shoot weight increased with age and approached a constant level beyond about 12 *PI*s (~9 months) (Fig. 9). The weight development of old leaf shoots present in March 1990 and of leaf shoots recruited during successive months is shown in Fig. 10. The median weight of old leaf shoots showed a 11.7-fold increase from March to August, parallel to the seasonal development of above-ground biomass (Fig. 3a). The period of emergence affected leaf shoot weight, as the size of newly recruited leaf shoots changed during the season according to the seasonal growth pattern of the old leaf shoots. Thus, leaf shoots recruited in April and May were small, but the longer growing season allowed extensive growth compared to leaf shoots recruited later during the growing season (Fig. 10). Leaf shoots recruited after the peak biomass in August continued to grow in size, such that October leaf shoots became heavier during winter. The remaining age-classes lost weight during winter and leaf shoot sizes were less age dependent the following spring.

The monthly contributions of new leaf shoots to total above-ground biomass and leaf shoot density are shown in Table 2. Because leaf shoots added to the populations within this year never reached the same size as the old leaf shoots (Fig. 10), the biomass proportion of young leaf shoots remained low (< 14%) compared to the larger number of young leaf shoots present (< 45%).

Biomass losses through the continuous leaf turnover of eelgrass leaf shoots was high (612 g dry wt m^{-2} $year^{-1}$) compared to losses through leaf shoot mortality (214 g dry wt m^{-2} $year^{-1}$) and constituted 74% of total annual losses of above-ground biomass (Table 3). Although the mortality of mature shoots (vegetative and generative) was lower (176–660 shoots m^{-2} $year^{-1}$) than that of young leaf shoots recruited during the study period (245 to 1011 shoots m^{-2} $year^{-1}$), the biomass loss was 2.4-fold higher because of larger leaf shoot size (Table 1 and 3). Annual above-ground production ranged from 654 to 995 g dry wt m^{-2} $year^{-1}$ (Table 3) and the below-ground

Table 1 Cumulative leaf shoot recruitment and mortality during an annual cycle (March 1990 – March 1991) in six adjacent eelgrass populations (A–F). Old leaf shoots are the overwintering shoot population of mixed age structure present in March 1990 and survival and half-lives of newly recruited leaf shoots are given for the cohort produced in June

	A	B	C	D	E	F
Leaf shoot density (m^{-2}) in						
March 1990	651	720	677	923	1200	891
March 1991	635	555	635	704	709	704
Fractional change of leaf shoot density	0.98	0.77	0.94	0.76	0.59	0.79
Recruitment (leaf shoots m^{-2} $year^{-1}$)	525	710	569	1015	661	1296
Mortality (leaf shoots m^{-2} $year^{-1}$)	541	875	611	1234	1152	1483
Fractional survival of						
old leaf shoots	0.73	0.48	0.46	0.45	0.45	0.47
newly recruited leaf shoots	0.16	0.13	0.18	0.12	0.22	0.15
Half-life (days) of						
old shoots	662	344	333	326	326	337
newly recruited shoots	31	36	64	38	56	74

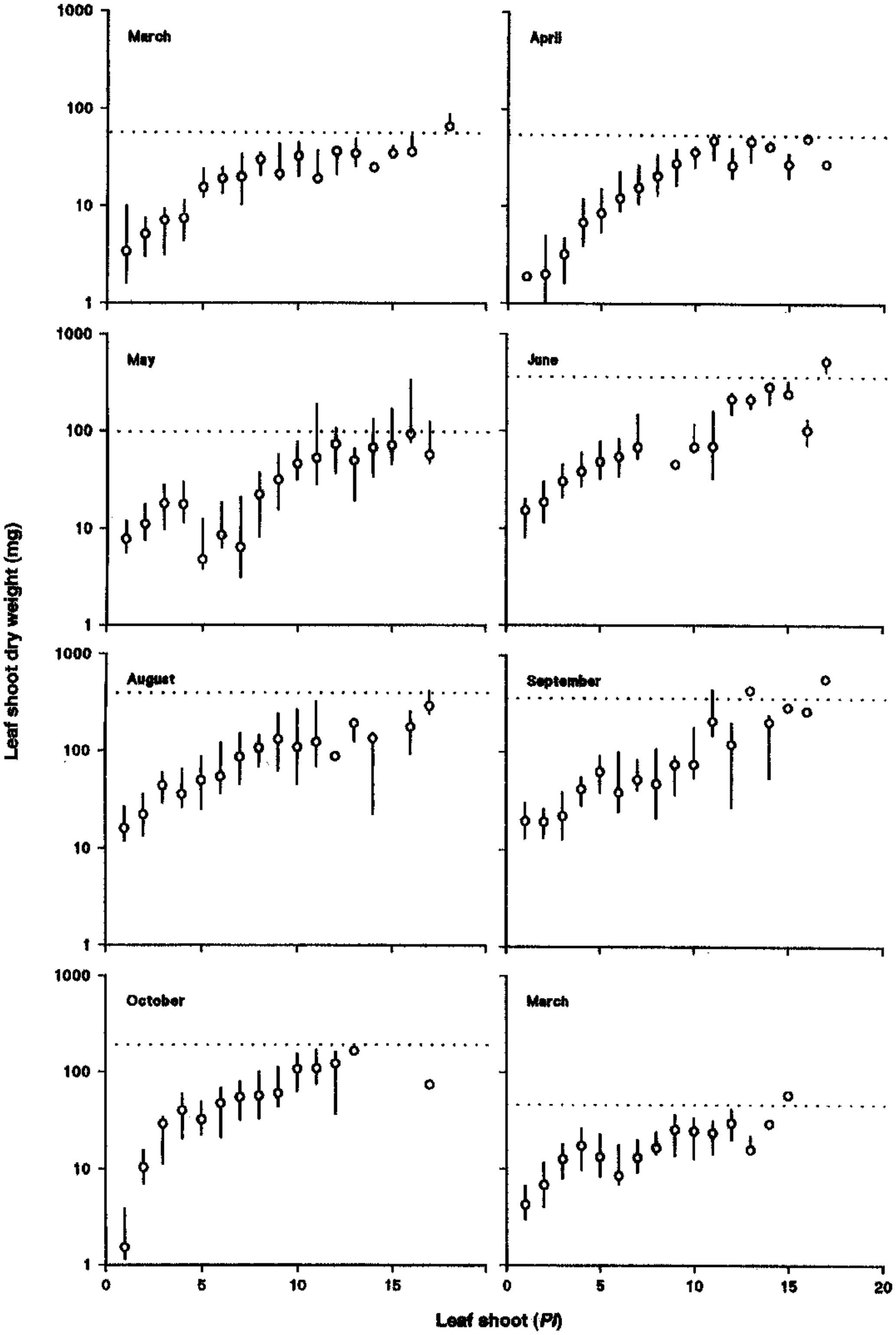

Fig. 9 The relationship between the median leaf shoot weight and age (as *PI*s) of eelgrass leaf shoots during an annual cycle. Vertical bars show upper and lower quartiles and the dotted line the median weight of leaf shoots older than 17 *PI*s. In absolute time 17 *PI*s is approximately 1 year.

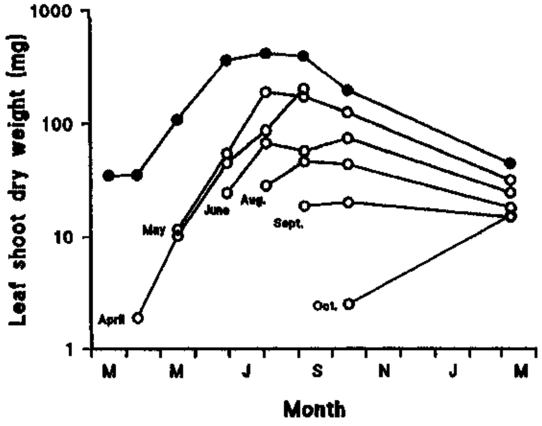

Fig. 10 Seasonal weight development of over-wintering eelgrass leaf shoots, present in March 1990 (●) and of leaf shoot cohorts recruited at successive time intervals from April to October 1990 (○). Leaf shoot weights are shown as median values.

Table 2 Density and biomass of young eelgrass leaf shoots produced during the study as a proportion of total leaf shoot density and total leaf biomass. Mean and range of six adjacent populations

	Proportion of leaf shoot density		Proportion of leaf biomass	
Month	Mean	Range	Mean	Range
April	0.013	0.00–0.04	0.0004	0.000–0.003
May	0.113	0.04–0.28	0.017	0.003–0.054
June	0.413	0.28–0.55	0.066	0.037–0.107
August	0.445	0.33–0.58	0.127	0.059–0.192
September	0.400	0.20–0.48	0.101	0.048–0.142
October	0.307	0.12–0.47	0.119	0.049–0.198
March	0.365	0.23–0.51	0.142	0.080–0.262

Table 3 Annual leaf production of six adjacent eelgrass populations (A–F) and the cumulated biomass losses due to shedding of leaves and leaf shoot mortality. Old leaf shoots had overwintered and were present at the initiation of the study (March 1990) and new leaf shoots were formed on side-branches during the study

		Biomass losses (g dry wt m^{-2} $year^{-1}$)		
	Leaf biomass production (g dry wt m^{-2} $year^{-1}$)	Leaves	Old leaf shoots	New leaf shoots
A	654	520	84	36
B	738	550	149	58
C	767	536	161	65
D	778	604	133	70
E	974	732	200	52
F	995	729	165	115

(rhizome and roots) production ranged from 177 to 326 g dry wt m^{-2} $year^{-1}$ resulting in a combined eelgrass production between 831–1284 g dry wt m^{-2} $year^{-1}$ in the six populations.

Discussion

SHOOT RECRUITMENT AND MORTALITY

Eelgrass leaf shoot density was relatively constant during the year due to a nearly synchronous seasonal cycle of shoot natality and mortality. Similar population stability between successive years has been found in several perennial clonal herbs of contrasting growth patterns (Callaghan 1976; Hutchings 1979; Noble *et al.* 1979; Lovett Doust 1981). Competitive (phalanx type) species, at one extreme, show population regulation through a close control on shoot recruitment (Schmid & Harper 1985), thereby preventing emergence into already crowded habitats. At the other extreme, plants with a more opportunistic growth strategy (guerrilla type) tend to control the number of shoots by their death rates rather than their birth rates (Lovett Doust 1981; Schmid & Harper 1985). Eelgrass may be viewed primarily as a competitive species due to the development of dense stands composed of large shoots with relatively slow lateral growth (Schmid & Harper 1985; Duarte 1991). Moreover, the gradual decline of eelgrass leaf shoot recruitment coinciding with high self-shading within the stands during late summer (Figs 2 and 6) suggested that leaf shoot density may, in part, be regulated through branching frequency. Likewise, in a broader global comparison we found the net increase in leaf shoot density from spring to summer to be significantly negatively related to the initial biomass of leaf shoots (Olesen & Sand-Jensen 1994). Such light induced growth pattern has been found for other clonal plants, where shading caused inhibition of lateral shoot development, leading to small investment in side-branches and lateral spread under low light conditions and, thereby, reducing the effects of density-mediated competition (Kays & Harper 1974; Slade & Hutchings 1987; de Kroon & Knops 1990). However, other environmental factors and internal growth rhythms may also influence the branching pattern of eelgrass and, hence, experimental manipulation of leaf shoot density would be needed to evaluate further the control of shoot recruitment rate within individual populations.

The seasonal cycle of eelgrass leaf shoot mortality was separated into a period of prevailing mortality of the over-wintering shoot population and one where mortality of newly recruited shoots dominated (Fig. 8b). Part of the mortality of over-wintering leaf shoots (8.9–38.8%) was directly associated with the death of shoots that are shed after flowering. It is possible that the cost of producing flowering shoots also affected the survival of the remaining shoots as indicated in other studies of clonal plants (Carlson & Callaghan 1990). Flowering shoots of *Zostera americana* may act as sinks for photoassimilates (Harrison 1978), which may influence the viability of adjacent shoots on the same rhizome by withdrawing carbon sources from connected shoots (Marshall 1990). The shoot dynamics of monocarpic flowering species may therefore be greatly affected by the extent of flowering as has been demonstrated during a five-years study of *Carex bigelowii* populations (Carlson & Callaghan 1990) where annual flowering frequency ranged from 1 to 37% causing large fluctuations in shoot density among years. For eelgrass, however, actual leaf shoot density was kept at a relatively constant level as the mortality rate of old leaf shoots was significantly correlated to ($r^2 = 0.87$, $P < 0.01$) and balanced by an equal production of new leaf shoots.

The high mortality of predominantly young and small leaf shoots during late summer was presumably caused by a combination of reduced surface light at this point in the season and high self-shading in the canopy as the estimated light availability below the canopy approximated the light compensation point for eelgrass photosynthesis (1–3 mol photons m^{-2} day^{-1}, Dennison 1987). Such negatively size-dependent mortality of shoots has been reported for many clonal species (Hutchings & Barkum 1976; Pitelka *et al.* 1985; Carlson & Callaghan 1990; de Kroon *et al.* 1992) and is often confined to late summer and fall where biomass approaches a maximum level.

Because of gradual rhizome degradation, it was not possible to estimate the maximum longevity of eelgrass leaf shoots. The oldest shoots we recorded were less than two years old (30 *PI*s), which is low compared to maximum ages of 7 and 9 years reported for the seagrasses *Cymodocea nodosa* (Duarte & Sand-Jensen 1990) and *Thalassia testudinum* (Gallegos *et al.* 1993). Mean shoot longevity of *C. nodosa* and *T. testudinum* populations, however, has been estimated at 2.4 and 1.5 years, respectively (Duarte 1991; Gallegos *et al.* 1993). This is similar to our estimate for mature eelgrass shoots, since approximately half of the over-wintering shoot population present in March 1990 survived until March 1991, yielding an average lifetime of one year plus the age they had already achieved in March 1990 (Table 1). Newly recruited eelgrass shoots, on the other hand, had life expectancies of about 0.14 year (the time to which half the shoots survived), which is similar to the mean longevity of small fast growing seagrass species (e.g. *Ruppia maritima*, *Halophila ovalis*; Duarte 1991). Accordingly, early stages of eelgrass shoots were subject to high mortality risk and only a minor fraction survived the growing season (Table 1) whereas the population of over-wintering shoots consisted of large, long-lived shoots, displaying high survival until flowering.

The annual production of leaf shoots on side-branches (800 m^{-2}) exceeded the losses of old shoots (430 m^{-2}), yielding a substantial surplus of young leaf shoots. Thus, maintenance of the six eelgrass populations was achieved by vegetative propagation, where leaf shoots lost from the populations were replaced by branching of survivors. Recruitment of new genets in stable populations of clonal plants is generally very infrequent (Noble *et al.* 1979; Lovett Doust 1981; Pitelka *et al.* 1985) and the probability of establishment and survival of seedlings is low compared to vegetatively produced shoots (Cook 1985). Likewise, seedlings were only of minor importance to eelgrass shoot recruitment as none survived past the period of peak biomass. Seedlings will, however, contribute to patch maintenance following catastrophic decline of seagrass abundance, leaving open space available for seedling establishment and growth (Duarte & Sand-Jensen 1990).

PRODUCTION ESTIMATES AND BIOMASS LOSSES

Estimates of eelgrass production are usually based on measurements of leaf elongation rates, ignoring the flux of leaf shoots within the population. In this study the inclusion of leaf shoot turnover in productivity estimates yielded an annual above-ground production between 654 and 995 g dry wt m^{-2} year^{-1} among the six populations, equivalent to a biomass turnover rate (P/B_{max}) of 3.6 (range 3.3–3.8). The higher turnover of eelgrass leaves (17 leaves shoot^{-1} year^{-1}) relative to that of leaf shoots (0.97 year^{-1}), demonstrates that individual leaf shoot growth was the major contributor to biomass production. Biomass losses through the continuous shedding of leaves contributed on the average 74% (range 70–81%) of the total annual biomass losses (Table 3). Thus, biomass production in previously examined eelgrass populations, measured by the leaf marking technique alone, is of the same magnitude, with biomass turnover rates ranging from 3.8 to 5.3 (Sand-Jensen 1975; Jacobs 1979; Wium-Andersen & Borum 1984).

Eelgrass leaf shoot weight was highly variable (e.g. 1–1570 mg dry wt in August) because shoot age (up to ~ 12 *PI*s) and seasonally changing growth conditions influenced the weight. Shoots recruited during this study year never reached the weights exhibited by over-wintering shoots and therefore the density of old shoots was a critical determinant of total above-ground biomass (Table 2). Also, biomass losses due to mortality of newly recruited shoots in eelgrass was low compared to that of fewer but much heavier mature shoots, despite significant losses in terms of numbers.

In conclusion, the observed shoot dynamics of the studied eelgrass populations showed an overall balance between recruitment and mortality rates during the annual cycle, emphasising the importance of clonal growth for population maintenance. It is suggested that population regulation took place mainly through shoot recruitment as low formation rates of new leaf shoots on side-branches coincided with reduced light availability as a result of low surface irradiance or self-shading within the dense stands. Clonal plants with phalanx growth strategy display similar efficient regulation of shoot density through tight control on shoot recruitment, thereby reducing shoot mortality due to crowding (Lovett Doust 1981; Schmid & Harper 1985). However, mortality of young leaf shoots was high probably because of the density stress generated by growth of old eelgrass shoots, combined with the seasonal declining light availability, although mortality of these small shoots caused only minor biomass losses. Thus, newly recruited shoots may be considered as short-living expendable shoots which may recolonize the space liberated by previous mortality or will otherwise die. In contrast, the population of over-wintering shoots displayed longer life span and was the major contributor to biomass development and sexual reproduction.

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