

D. L. Ramage · D. R. Schiel

## Reproduction in the seagrass *Zostera novazelandica* on intertidal platforms in southern New Zealand

Received: 25 June 1997 / Accepted: 24 September 1997

**Abstract** This study investigates the reproductive periodicity and reproductive output of the seagrass *Zostera novazelandica* on two intertidal reefs. Peak numbers of flowering shoots occurred during March (late summer) of two years at both sites and no flowering shoots occurred during the winter months of July to September. There were greater numbers of flowering shoots in seagrass patches in the low intertidal zone (up to an average of 55 per 0.1 m<sup>2</sup>) compared to the middle (up to 20 per 0.1 m<sup>2</sup>) and upper (up to 9 per 0.1 m<sup>2</sup>) zones, and about three times greater reproductive output in patches associated with tidepools compared to those not bordering tidepools. The average number of inflorescences per shoot was 3.1 ( $\pm 0.25$ ) at one site vs 1.2 ( $\pm 0.08$ ) at the other, and showed a progressive decrease from the lower shore to the upper shore. Patches associated with tidepools had twice the number of inflorescences per shoot ( $2.8 \pm 0.24$ ) than patches not bordering tidepools ( $1.5 \pm 0.16$ ). The number of flowering shoots was highly correlated with leaf width, leaf length, and ramet density, while the leaf-area index decreased from the lower shore to the upper shore. The reproductive effort of plants, as measured by the percent biomass invested in flowering shoots during peak reproduction, was significantly different between sites, tidepool associations, and shore level. For all the variables measured, there was considerable spatial variation, with significant interaction terms between most factors investigated. In laboratory experiments, more inflorescences were produced at light intensities of 30 and 300  $\mu\text{E m}^{-2} \text{s}^{-1}$  than at 100  $\mu\text{E m}^{-2} \text{s}^{-1}$ . At a salinity of 17‰, 1.5  $\times$  the number of flowers was produced than at 33‰, while none was formed at 70‰. Plants cultured at 5 °C had about three times the number of inflorescences than those at 15 °C, while none was formed at 25 °C.

### Introduction

The perennial endemic seagrass *Zostera novazelandica* forms prominent patches throughout the lower to mid intertidal zone on rocky platforms in southern New Zealand, but despite its abundance there are no published field-based studies on reproduction in this species. Seagrasses, generally, rely on both vegetative and sexual reproduction for the maintenance of existing beds and colonization of new areas (Tomlinson 1974; Orth et al. 1994). Reproductive output tends to increase in habitats that exert great physiological stress, particularly when plants are distributed throughout a heterogeneous environment, both for seagrasses and for taxonomically unrelated terrestrial plants (Kingsbury et al. 1976; Grime 1979; Phillips et al. 1983; van Lent and Verschuure 1994a).

Seagrasses that are exposed to high summer water-temperatures and large fluctuations in salinity favour an annual life history with plants growing during spring and dying off during autumn (Harrison 1979; Keddy 1987). In these cases, recruitment is entirely by germination of seeds the following spring (Harrison 1982). Annual seagrasses are composed entirely of flowering shoots, and rhizomes rarely persist through winter (Harrison 1979; Keddy 1987). Seagrass populations in areas with high environmental stability allocate biomass to the elongation of perennial rhizomes during summer, following a winter die-back (Tomlinson 1974; Phillips et al. 1983; Robertson and Mann 1984; van Lent and Verschuure 1994b). In this case, seeds produced by perennial plants probably do not play an important role in the year-to-year survival of the population (Hootsmans et al. 1987).

One widely distributed intertidal species, *Zostera marina* L., appears to have developed two life history strategies in response to different environmental regimes. In areas where both annual and perennial forms of the eelgrass occur, the two types are clearly partitioned into different habitats (Phillips et al. 1983; Keddy 1987).

---

Communicated by G.F. Humphrey, Sydney

D.L. Ramage · D.R. Schiel (✉)  
Marine Ecology Research Group, Zoology Department,  
University of Canterbury, Private Bag 4800,  
Christchurch 1, New Zealand

Annual plants dominate upper intertidal areas that are drained at low tide and exposed to the air for several hours during a tidal cycle, while perennial plants are more abundant low in the intertidal zone and in creeks and pools which are exposed only briefly at low tide, if at all (Harrison 1979; Phillips et al. 1983; Keddy 1987).

Anthesis (the stage at which flowers open) and seed production are two critical stages in the life cycle of seagrasses, but although several *Zostera* species have been intensively studied in recent years, there is little quantitative information about the timing of sexual reproduction and the processes associated with flowering (Jacobs and Pierson 1981; Silberhorn et al. 1983; Orth et al. 1994). North American studies have documented the onset of flowering as being late winter to early summer, depending on the latitude of the study site (Marmelstein et al. 1968; Harrison 1979; Silberhorn et al. 1983; Larkum et al. 1984; Hootsmans et al. 1987; Ferguson et al. 1993; Conacher et al. 1994). Tropical and subtropical seagrass populations tend to flower early, and have an extended flowering season of up to 8 mo (Conacher et al. 1994), while seagrasses in higher latitudes begin flowering in summer and continue briefly into autumn (Hootsmans et al. 1987; Harrison 1979).

McMillan (1976) studied the effects of salinity, temperature and photoperiod on the production of flowering shoots in five seagrass genera under controlled laboratory conditions. This and similar studies indicated that the primary influence on reproduction is temperature, but that salinity, day length and light intensity may also contribute to the timing and intensity of reproduction at a particular location (Setchell 1922; McMillan 1976; De Cock 1981a, b; Larkum et al. 1984; Conacher et al. 1994).

Flowering has been recorded as only a rare occurrence for many seagrass species (McMillan 1980). The discovery of reproductive shoots in patches at our study sites provided an opportunity to examine reproductive events in *Zostera novazelandica*. This is a widespread species in New Zealand (Moore and Edgar 1970; Wilson 1994), is apparently confined to the intertidal zone (Webb et al. 1990), and is monoecious. One habitat inhabited by this species is rocky reefs along the east coast of the South Island. The hard substratum is unsuitable for root and rhizome growth but, once established in cracks and tidepools, plants accumulate sand around their roots and extend along tidal cracks to form discrete patches, most of which are  $<1 \text{ m}^2$  in surface area.

Here we describe the timing of events in the flowering process of *Zostera novazelandica* patches on intertidal platforms, test for relationships between reproduction and seagrass plant characteristics, and test whether reproduction is related to various physical factors.

## Materials and methods

The study was carried out at two sites on the Kaikoura Peninsula, on the central east coast of the South Island of New Zealand ( $42^{\circ}25'S$ ;  $173^{\circ}42'E$ ; Fig. 1), from March 1994 through March 1995

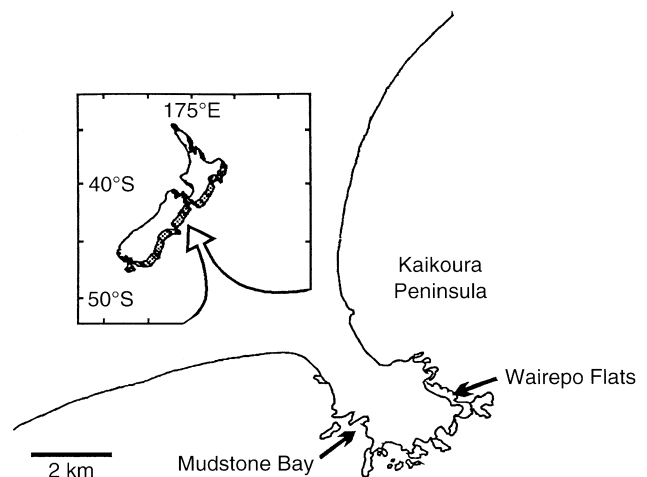


Fig. 1 Map of New Zealand, showing location of two study sites on Kaikoura Peninsula

(further information about study sites and general characteristics of the region can be found in Hickford and Schiel 1995 and Woods and Schiel 1997). Wairepo Flats is a gently sloping mudstone reef exposed to northeasterly swells, but protected from severe southerly storms. Mudstone Bay,  $\approx 3 \text{ km}$  away on the opposite side of the peninsula, is a mudstone reef exposed to a southwesterly swell but protected by the peninsula from the full force of southerly storms. The tidal range is 2.4 m. Patches of *Zostera novazelandica* cover  $\sim 15\%$  of the reef surface in the mid to low intertidal zone in these sites and extend from  $\sim 0.3$  to 1.3 m above chart datum (Schiel unpublished data); the other major habitats are patches dominated by the fucalean alga *Hormosira banksii* and bare elevations dominated by limpets.

Flowering shoots appear seasonally amongst the vegetative blades of *Zostera novazelandica*, and are easily recognised on close examination of patches. A flowering shoot is comprised of one or more branches which can have several inflorescences; each inflorescence is enveloped in a leaf sheath (spathe).

The reproductive status of seagrass patches and how it was affected by position on the shore was determined through stratified sampling. Thirteen monthly samples were taken, beginning in March 1994. The positional strata were sites ( $n = 2$ ), shore height ( $n = 3$ ), and association with tide pools (i.e. patches either with or without a bordering tide pool). Shore height was determined by distance from the low-water mark and the abundance of *Hormosira banksii*, which extends from the low to the upper middle tidal zone. The high-shore zone had no significant algal cover, the mid-shore zone was distinguished as having up to 50% algal cover, and the low-shore had virtually 100% cover of *H. banksii* and other fucalean algae interspersed with *Zostera novazelandica* patches. The number of flowering shoots, the number of inflorescences per flowering shoot, and leaf-blade characteristics (width, length and density) of surrounding vegetative shoots were counted within  $0.1 \text{ m}^2$  quadrats ( $n = 15$ ) randomly placed within patches in each sampling stratum each month.

To determine the relative proportions of plant biomass invested in vegetative and reproductive material, cores of 80 mm diam and 15 cm deep ( $n = 3$ ) were removed from randomly selected patches within each sampling stratum at the peak flowering period. All plant material was removed from the sediment using a sieve (1 mm mesh) and divided into rhizomes, roots, leaves, and flowering shoots. Each portion was then dried separately in an oven at  $105^{\circ}\text{C}$  for 24 h, and weighed (Young and Kirkman 1975; Dawson 1976; Larkum et al. 1984; Vermaat et al. 1993). From this, "reproductive effort" could be determined, calculated as the percentage of total plant biomass made up of reproductive shoots.

Laboratory-based experiments were done to test the effects of light intensity, salinity and temperature on inflorescence formation.

Core samples of 80 mm diam and 10 to 12 cm in depth were removed from a vegetative 9 m<sup>2</sup> seagrass patch in the mid-shore height of Wairepo Flats and placed in 500 ml polyethylene pots (12 cm diam, 12 cm deep). Blade density, rhizome biomass, and the appearance of plants were similar in all cores. Fine sand from an adjacent beach area was used to pack the cores firmly into the pots before transportation to the laboratory. Only nine aquaria (40 cm × 30 cm × 20 cm deep) were available for experiments. Replicate cores ( $n = 6$ ) were randomly assigned to each aquarium and 8 litres of natural seawater (33‰ S) were added to achieve a depth of 5 to 7 cm above the surface of the plants. Each aquarium was randomly assigned to one of nine treatments encompassing three experimental factors: light intensity (30, 100 and 300  $\mu\text{E m}^{-2} \text{s}^{-1}$ ); salinity (17, 33 and 70‰) and temperature (5, 15 and 20 °C). Experiments were performed in temperature-controlled rooms with cool-white fluorescent tubes as the light source. Light intensity was varied using layers of shade cloth (0, 1 or 3 layers) over the aquaria, 8 cm from the surface of the cores. Light intensity was measured with a photometer at several points within each aquarium, and a variation of <10% was found within each aquarium and within treatments. Salinity was elevated in one salinity treatment using natural sea salt and lowered in another treatment by dilution with distilled water. Salinity was monitored every 3 to 4 d using a refractometer and distilled water was added as required to maintain original treatment salinities. Because of the limited number of temperature-controlled rooms available, it was not possible to test simultaneously for effects of photoperiod on inflorescence formation or for interactive effects.

All aquaria were exposed to a summer (14 h light:10 h dark) photoperiod (McMillan 1976); the light intensity in the salinity and temperature treatments was held at 100  $\mu\text{E m}^{-2} \text{s}^{-1}$ , the temperature in the light intensity and salinity treatments was held at 15 °C, and the salinity in the light intensity and temperature treatments was 33‰. Aquaria were maintained in these conditions for 28 d,

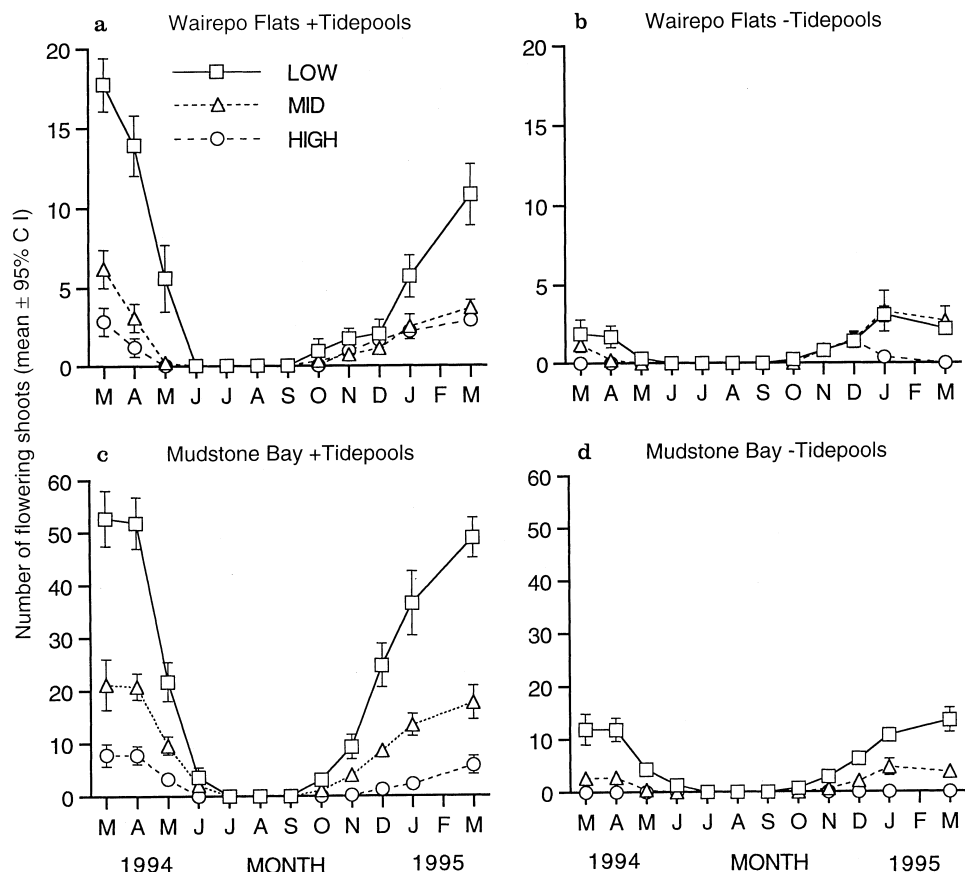
and at the end of this period the number of flowering shoots and number of inflorescences per shoot were counted.

To replicate the treatment aquaria, the entire experiment was done twice, from 15 December 1994 to 11 January 1995, and from 5 February to 4 March 1995, with time as a blocked factor. Results from the two time periods were tested and found to be non-significant ( $p > 0.25$ ). Data were pooled to increase the number of degrees of freedom for analysis of variance (Sokal and Rohlf 1995; p. 284).

## Results

Immature inflorescences were first observed during late October in *Zostera novazelandica* patches in all parts of the low intertidal zone and in patches in the mid intertidal zone associated with tidepools. Six weeks later in early December, flowering shoots began appearing in patches higher on the shore. The quantitative sampling at both sites showed that peak densities in patches adjacent to tide pools occurred in March in both 1994 and 1995, while in patches not associated with pools peak flowering was recorded from January through March (Fig. 2). Mature embryos and seeds were seen from late December to March, and seeds appeared to overwinter and germinate the following spring (September). The length of the flowering period varied between tidal heights from 8 mo in the low intertidal zone in patches adjacent to tidepools to only 3 mo in patches not asso-

**Fig. 2** *Zostera novazelandica*. Number of flowering shoots per 0.1 m<sup>2</sup> at three tidal heights (low, mid, high shore) for patches at Wairepo Flats and Mudstone Bay associated with tidepools and patches not associated with tidepools (CI confidence interval)



ciated with pools high on the shore at Wairepo Flats (Fig. 2a, b). At Mudstone Bay, no reproductive shoots were ever found in patches in the high intertidal zone that were not associated with tidepools, while further down on the reef patches were devoid of flowering shoots for only the winter months of July to September (Fig. 2c, d).

All the main spatial factors (sites, tidal heights, pools) were significant, as were the interactions among these factors (Table 1). For example, Mudstone Bay had about triple the number of flowering shoots per 0.1 m<sup>2</sup> as Wairepo Flats in both tidepool treatments (Fig. 2). However, the effects of tidal height varied among sites and treatments. For example, the number of flowering shoots per 0.1 m<sup>2</sup> were similar on the low shore and mid shore at Wairepo Flats (– Tidepools: Fig. 2b), but the mid- and high-shore levels were similar where patches

were adjacent to tidepools (Fig. 2a). The number of flowering shoots in the peak period did not vary significantly between years, but the year × pool interaction was significant because of a slight decrease in 1995 in tidepools at Wairepo Flats, while there was a slight increase where tidepools were absent. Overall, tidal height and tidepools were the most important factors affecting the number of flowering shoots. Tidal height alone accounted for 23% of the total variation in numbers, while tidepools alone accounted for 18% (Table 1). Most of the variation in flowering shoots, therefore, was accounted for by the spatial factors, rather than by years.

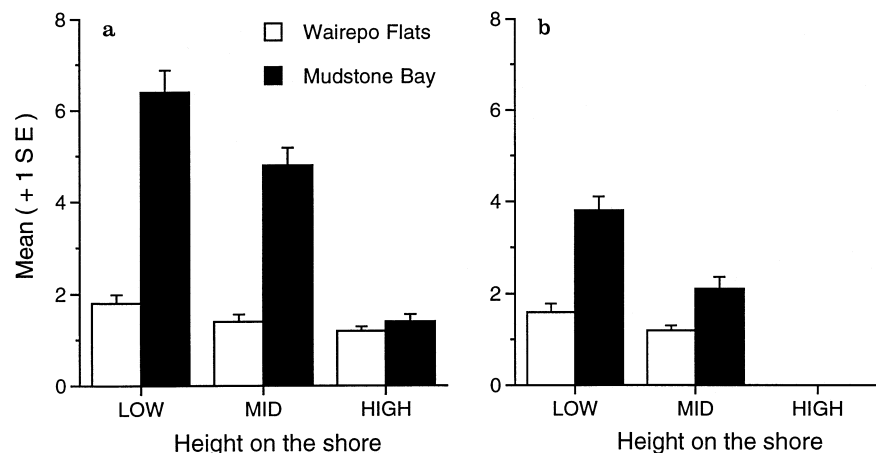
Not only was the density of flowering shoots significantly greater at Mudstone Bay than at Wairepo Flats at all tidal heights, but the number of inflorescences per shoot was also significantly greater at Mudstone Bay ( $F_{1,168} = 204.1, p < 0.001$ ; Fig. 3). For example, where tidepools were associated with seagrass patches there were six inflorescences per shoot at Mudstone Bay on the low shore, while Wairepo Flats had only two per shoot (Fig. 3a). There was a greater number of inflorescences in patches associated with tidepools ( $F_{1,168} = 108.6, p < 0.001$ ), but this effect varied between the two sites (Fig. 2a, b;  $F_{2,168} = 40.8, p < 0.001$ ). Wairepo Flats had similar numbers of inflorescences per flowering shoot among tidal heights, except on the high shore in patches not associated with tidepools (Fig. 3b); patches at neither site reproduced on the high shore where tidepools were absent. There was generally a progressive decrease in the number of inflorescences per shoot from the low shore to the high intertidal zone, but this was most pronounced at Mudstone Bay. As for the number of flowering shoots, there was a significant interaction among the three main factors (site, tidal height, tidepools;  $F_{2,168} = 7.9, p = 0.0005$ ).

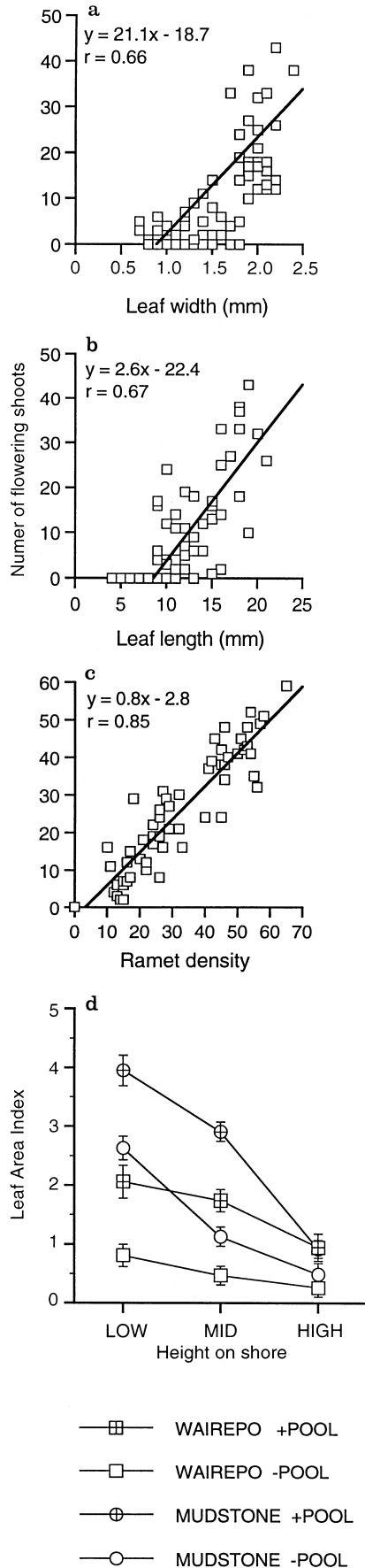
Overall, the density of flowering shoots was positively associated with the leaf-blade characteristics of width, length and density per patch (Fig. 4). Plants in patches that produced large numbers of flowering shoots had wider (Fig. 4a) and longer (Fig. 4b) leaf blades than those with fewer flowers. Sixty-six percent of the varia-

**Table 1** *Zostera novazelandica*. ANOVA for mean number of flowering shoots per 0.1 m<sup>2</sup> at peaks of two flowering seasons (March 1994 and March 1995) at two sites (Wairepo Flats and Mudstone Bay), three shore heights (low, mid and high), and for patches either associated or not associated with tidepools. % variance = treatment SS ÷ total SS (Welden and Slauson 1986; Raimondi 1990; Schiel 1990) (SS sum of squares)

Source	(df)	SS	F	p > F	%
Year (Y)	(1)	149.511	2.52	0.1132	0.17
Site (S)	(1)	11334.444	191.18	0.0001	12.91
Height (H)	(2)	19892.600	167.77	0.0001	22.67
Pool (P)	(1)	15471.111	260.96	0.0001	17.63
Year × site	(1)	0.044	0.00	0.9782	0.00
Year × height	(2)	68.022	0.57	0.5640	0.08
Year × pool	(1)	313.600	5.29	0.0221	0.36
Site × height	(2)	7678.956	64.76	0.0001	8.75
Site × pool	(1)	4494.400	75.81	0.0001	5.12
Height × pool	(2)	6554.756	55.28	0.0001	7.47
Y × S × P	(1)	0.044	0.00	0.9782	0.04
Y × S × H	(2)	33.356	0.28	0.7550	0.00
Y × H × P	(2)	92.867	0.78	0.4578	0.10
S × H × P	(2)	1728.600	14.58	0.0001	1.97
Y × S × H × P	(2)	23.022	0.19	0.8236	0.03
Residual	(336)	19920.267	22.70		

**Fig. 3** *Zostera novazelandica*. Number of inflorescences per flowering shoot in March 1995 at three tidal heights and two sites (Wairepo Flats and Mudstone Bay) for patches associated with tidepools (a), and patches not associated with tidepools (b)





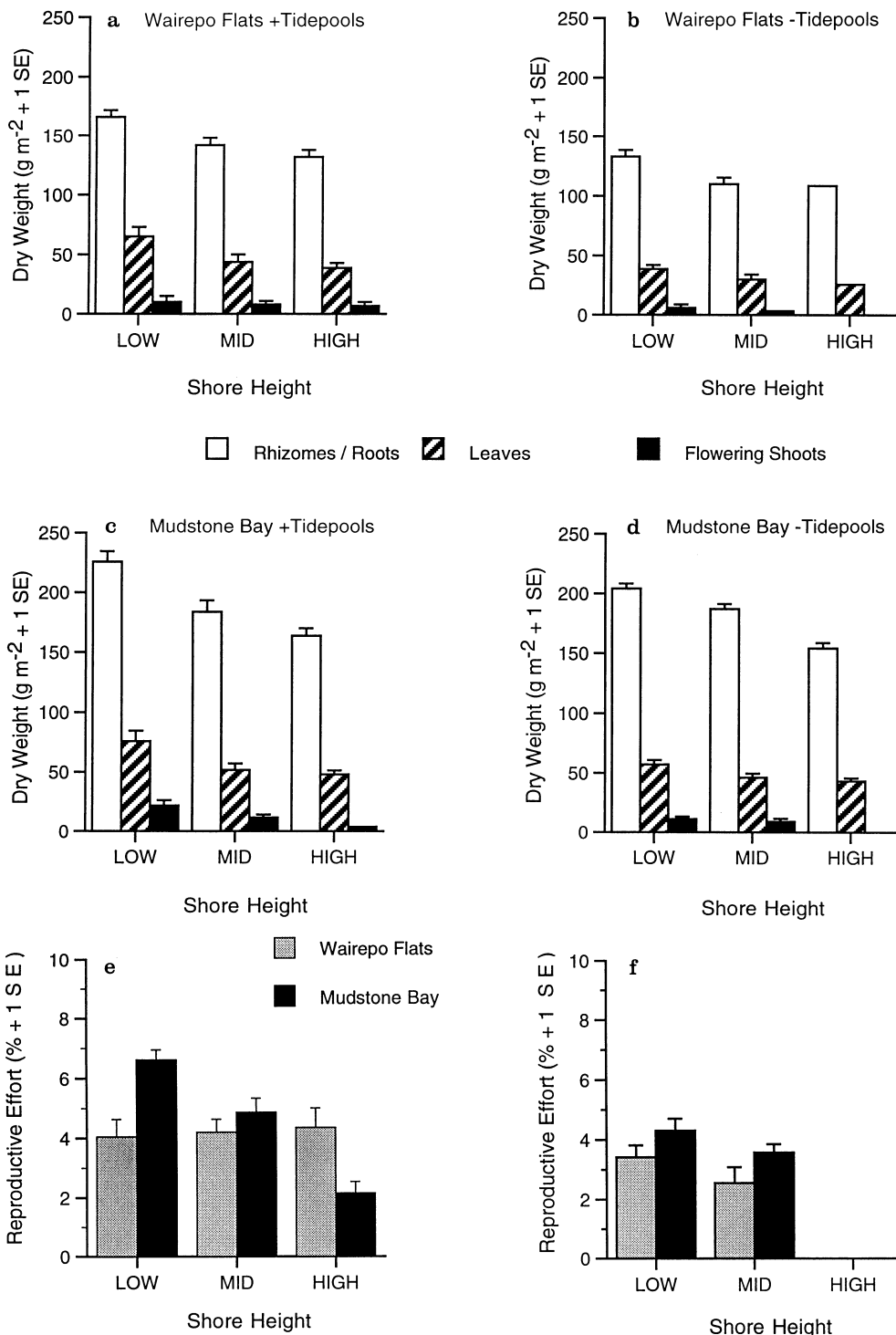
**Fig 4** *Zostera novazelandica*. **a-c** Relationships between number of flowering shoots per 0.1 m<sup>2</sup> and average leaf width, average leaf length, and average ramet (blade) density, and regression equations describing relationships; **d** relationship between leaf area index and tidal height for patches at the two sites, with and without tidepool associations

tion in flowering shoot density is explained by either leaf width or leaf length. Reproduction was strongly density-dependent, with 72% of the variation in the numbers of flowering shoots being accounted for by the average ramet (blade) density of patches (Fig. 4c). This effect was independent of site, shore height, or tidepool association of plants. These plant characteristics were used to calculate the leaf-area index, a dimensionless parameter representing the area of leaf surface over unit area of ground. This was significantly lower in the upper shore zone ( $F_{[2,48]} = 889.0, p < 0.001$ ); Fig. 4d), although there was a significant interaction among all factors ( $F_{2,48} = 11.3, p < 0.001$ ).

The allocation of plant biomass among rhizomes and roots, leaves, and reproductive shoots varied among sites, shore heights, and tidepool association (Fig. 5a-d). At Wairepo Flats, rhizomes and roots of patches associated with tidepools averaged 165 g dry wt m<sup>-2</sup> in the low tidal zone (Fig. 5a) compared to 135 g dry wt m<sup>-2</sup> in patches not associated with pools (Fig. 5b). At Mudstone Bay, rhizomes and roots of patches associated with tidepools averaged 230 g dry wt m<sup>-2</sup> (Fig. 5c) compared to 200 g dry wt m<sup>-2</sup> in patches not associated with pools (Fig. 5d). Leaves accounted for around a third of total patch biomass. The biomass for all plant parts declined with increasing tidal height. Reproductive effort was calculated as the percentage of the total plant biomass per core made up of flowering shoots. This generally decreased with increasing tidal height (Fig. 5e,f). This effect was more pronounced at Mudstone Bay than at Wairepo Flats ( $F_{1,24} = 14.7, p < 0.001$ ). Plants in patches associated with tidepools allocated a significantly greater proportion of their total biomass to reproduction than did plants not associated with pools ( $F_{1,24} = 1857.6, p < 0.001$ ). However, all effects varied spatially (site × height × pool interaction:  $F_{2,24} = 65.7, p < 0.001$ ).

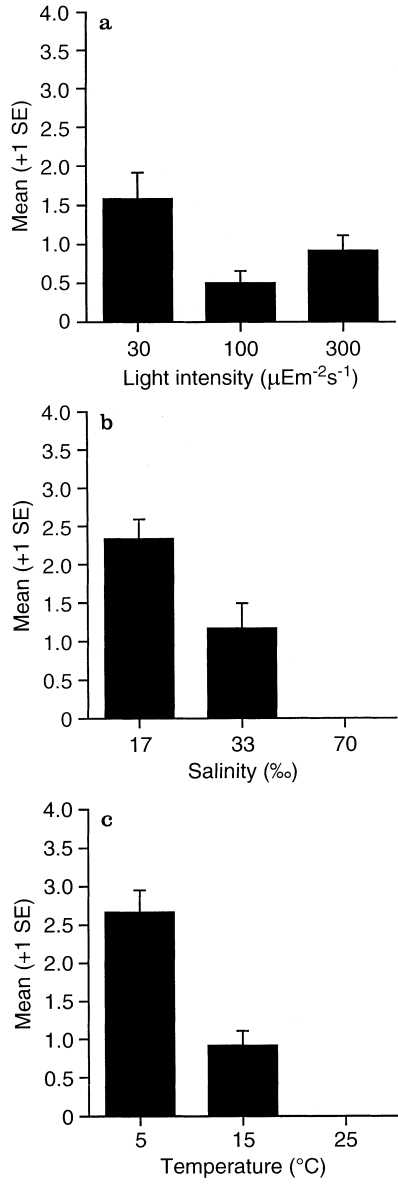
*Zostera novazelandica* plants produced flowers 2 to 3 wk after transplantation into laboratory aquaria. Flowers were borne on short, erect peduncles, 6 to 8 cm long, that produced a single inflorescence each (i.e. one inflorescence per shoot). Light intensity had a significant effect on the formation of reproductive shoots ( $F_{2,33} = 4.78, p = 0.02$ ; Fig. 6a). The fewest inflorescences were produced at 100 μE m<sup>-2</sup> s<sup>-1</sup>. An a posteriori test of means showed there was no significant difference between cores exposed to 30 and 300 μE m<sup>-2</sup> s<sup>-1</sup> or between cores at 100 and 300 μE m<sup>-2</sup> s<sup>-1</sup> ( $p < 0.05$ , Duncan's multiple-range test). The only clear difference, therefore, lay between the 30 and 100 μE m<sup>-2</sup> s<sup>-1</sup> treatments.

**Fig. 5** *Zostera novazelandica*. **a-d** Dry weight of seagrass rhizomes and roots, leaves, and flowering shoots at three tidal levels (low, mid, high shore) in patches at Wairepo Flats and Mudstone Bay associated with tidepools and not associated with tidepools; **e, f** reproductive effort (% of total plant biomass in reproductive shoots) + 1 SE at three shore heights in the two sites for patches associated with tidepools (e) and patches not associated with tidepools (f)



The number of inflorescences produced per core was significantly different between each of the three salinity regimes (Fig. 6b). Half-strength seawater (17‰ S) appeared to promote the formation of flowers, while the plants maintained in 70‰ S failed to produce any reproductive shoots and died after 14 to 18 d. Plants growing in standard seawater (33‰ S) produced an intermediate number of inflorescences per core.

Temperature also had a significant effect on the production of inflorescences at each of the three levels tested (Fig. 6c). Plants cultured at 5 °C produced almost three times the number of inflorescences per core as those at 15 °C, while those maintained at 25 °C appeared to suffer heat rigor and did not produce any reproductive or new vegetative shoots during either experiment.



**Fig. 6** *Zostera novazelandica*. Number of flowering shoots per core (50 cm<sup>2</sup> surface area) for plants grown in laboratory at three levels of light intensity, three salinities, and three temperatures

**Discussion**

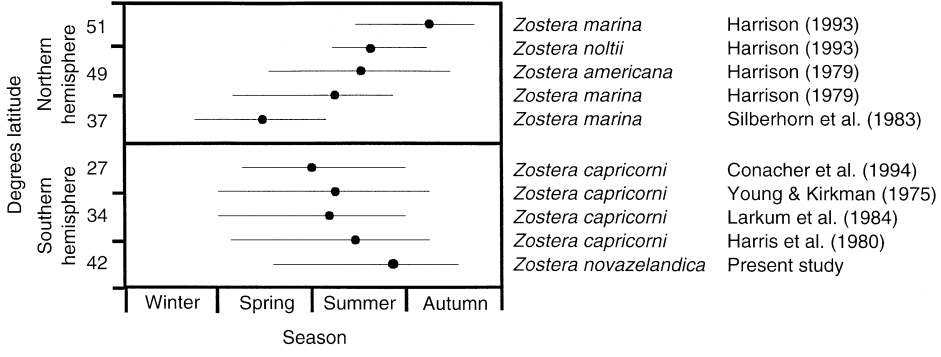
The flowering season of *Zostera novazelandica* lasts for up to eight full months of the year, from October to June, with peak flower production from January to March. This pattern of reproducing from spring to late autumn, with peak flower production in summer, is typical of *Zostera* species at higher latitudes. Within the genus there is an overall trend of peak reproduction occurring later in the summer with increasing latitude in both hemispheres (Fig. 7). This is particularly pronounced in the northern hemisphere for *Z. marina*, which spans a wide latitudinal range.

On the Kaikoura Peninsula, flowering of *Zostera novazelandica* lasts longest in the low intertidal zone, while high on the shore plants that are not associated with tidepools are reproductive for only 3 mo at most. The density of flowering shoots and the number of inflorescences per shoot also vary along the intertidal gradient. Many seagrass patches high on the shore do not contain any sexually reproducing plants or else have single inflorescences at very low densities. Large, branching, reproductive shoots comprised of multiple inflorescences were located only on the lower shore.

Plants associated with tidepools and tidal cracks exhibit much higher reproductive output than those in patches not associated with pools. Moore and Edgar (1970) also observed that intertidal *Zostera capricorni* plants in the North Island of New Zealand flowered exclusively in pools left in hollows on the shore when the tide was low. Anecdotal evidence also suggested that this species usually flowers only when permanently submerged (Webb et al. 1990). The affiliation of sexually reproductive plants with water may be due to the requirement for a liquid medium for pollen dispersal and effective pollination. The filiform pollen strands of *Zostera* species form a network over the surface of the water (if exposed to air) which enables surface pollination to occur under suitable tidal conditions (McConchie and Knox 1989).

The inverse correlation of leaf width and length, ramet density, leaf area index and biomass with tidal height and the positive correlation with tidepools may also correspond with the production of flowering shoots. Patches low on the shore contain larger plants in terms

**Fig. 7** *Zostera* spp. Timing of flowering in different species from temperate regions, showing peak period of reproduction (●) and range



of both above-ground and below-ground biomass than those in the high intertidal zone. This may be attributable not only to increased submersion time but also to the surrounding *Hormosira banksii* further down on the reef which probably enhances water retention around the patches and provides some relief from desiccation. Plant growth is also stimulated when ramets remain submerged in pools throughout the tidal cycle (Keller and Harris 1966; Jacobs 1979).

Measures of reproductive success such as the numbers of flowers and fruit are typically correlated with overall plant size (Sohn and Policansky 1977; Waller 1988). There may be a threshold size to produce flowers or viable fruit and seeds, but this depends on the morphology and physiology of plants (Waller 1988). The correlation between plant size and the density of flowering shoots of *Zostera novazelandica* indicates that the best predictor of reproduction mode (i.e. sexual or vegetative) may be plant biomass, possibly because nutrients can be transferred from the rhizomes during flower development (Phillips 1972; Sohn and Policansky 1977; Harrison 1979). Rhizome biomass probably reflects a critical metabolic state in which limited resources must be allocated between flower and rhizome production (McNamara and Quinn 1977; Sohn and Policansky 1977; Silvertown 1987). The distribution of biomass among organs involved in vegetative growth and sexual reproduction in a species is not fixed, however, particularly in populations growing under different conditions (Abrahamson 1975; Harrison 1982). For example, in contrast to *Z. novazelandica*, populations of *Phyllospadix torreyi* in California showed a decrease in the density of flowering shoots, the number of inflorescences per shoot, and reproductive biomass with decreasing tidal height (Williams 1995). The reproductive characteristics of plants were greatest at a subtidal depth of 1.5 m, and declined with increasing water depth; Williams ascribed this to light-limitation.

Many biotic and abiotic factors, including climate, density, and disease, affect the amount of stored nutrients available for flower and fruit production and rhizome growth. *Zostera novazelandica* in patches low on the shore or in tidepools may therefore have greater reproductive activity because they have a biomass and rhizome nutrient store more capable of supporting the production of flowers and fruit. Correlations of reproductive effort and reproductive shoot biomass with vegetative biomass, shoot density and leaf size (width and length) (Larkum et al. 1984; Conacher et al. 1994) provide a foundation for this hypothesis. Among marine angiosperms there is a general trend, in habitats ordered along a disturbance continuum, for greater sexual reproductive effort among plants in highly disturbed or stressful habitats (Phillips et al. 1983; Keddy 1987; Harrison 1993; Conacher et al. 1994). *Z. novazelandica* plants that are high on the shore or not adjacent to permanent pools are presumably in a more stressful environment, and therefore an increase in reproductive effort relative to plants low on the shore might be ex-

pected. The lower biomass (and nutrient supply) of plants in this upper zone may, however, inhibit their ability to respond to stress by sexual reproduction (Gallegos et al. 1992). Under these conditions, where vegetative growth is favoured, the formation of flowers and fruit requires a large energetic input (Gadgil and Solbrig 1972; Sohn and Policansky 1977). Vegetative growth is frequently associated with early succession or with frequently disturbed habitats where it is important for maintaining the survival of the plant as well as providing a relatively fast, low-risk local expansion (Salisbury 1942; Koller and Roth 1964; Schaffer 1974; Abrahamson 1975; Lovett Doust 1981; Waller 1988).

In refining the R-C-S (ruderal, competitive, stress-tolerant) life-history strategies proposed by Grime (1974), Kautsky (1988) classified plants according to habitat predictability (frequency of disturbance, particularly wave action and desiccation) and habitat favourableness (degree of stress such as salinity and light-limitation). Stress-tolerant plants were placed into two groups: "stunted strategists", which exploit high-stress and high-disturbance conditions, and "biomass storers" such as *Zostera marina*, which occur under low-disturbance and high-stress conditions. An important difference between *Z. marina* and *Z. novazelandica* is the tidal heights at which each occurs. *Z. marina* plants growing 3 to 10 m below mean water level are not subjected to periodic disturbance by wave action, but the strictly intertidal *Z. novazelandica* plants are. The higher stress and higher disturbance conditions in the intertidal zone would therefore put *Z. novazelandica* in an intermediate position between being a biomass storer and a stunted strategist. *Z. novazelandica* conforms to the specifications of Kautsky in having an extensive root system, low turnover rate, and little reliance on sexual reproduction. Instead, there is mostly vegetative growth of rhizomes with a large proportion of the biomass overwintering.

The formation of reproductive shoots and flowers in seagrasses displays patterns that suggest strong environmental controls. Laboratory experiments show that the primary influence is temperature, and that salinity and day length are contributing factors (McMillan 1976). Setchell (1929) proposed that temperature alone determined periodicity in the reproductive cycle of *Zostera marina*, and several other studies have supported the hypothesis that temperatures  $>15^{\circ}\text{C}$  are required for anthesis (Tutin 1938; Churchill and Riner 1978). There is, however, contradictory evidence from Puget Sound, where flowering occurs when water temperatures are only 8 to 9  $^{\circ}\text{C}$  (Phillips 1974); Chesapeake Bay, where inflorescences were obtained at the end of winter when water temperatures were just 3  $^{\circ}\text{C}$  (Silberhorn et al. 1983); and the present study, where *Z. novazelandica* cores maintained at 5  $^{\circ}\text{C}$  produced more inflorescences than at 15 and 25  $^{\circ}\text{C}$ . It may be that the development of reproductive shoots is not inhibited by temperatures  $<15^{\circ}\text{C}$  as suggested by Setchell, but that maturation of inflorescences and the timing of anthesis may be expressed in lower temperatures (De Cock 1981c).

For seagrass populations in the intertidal zone, the effect of fluctuating temperatures on flowering is particularly important (De Cock 1981b). Temperature is influenced by time of day and tidal height, so the temperature regime depends on the timing of flood and ebb events. Laboratory experiments have demonstrated that the alternation of temperatures induces the formation of more inflorescences than do periods with a stable low temperature (De Cock 1981b).

A rise in water temperature may be the cue for reproduction in many *Zostera* populations (Setchell 1929; Jacobs and Pierson 1981; Phillips et al. 1983; Conacher et al. 1994), but it is necessary to examine the other environmental influences on flowering and the interactions between different factors (McRoy 1970; Phillips 1974). It is unlikely that a single factor is responsible for floral induction. A laboratory study on *Thalassia testudinum* by Marmelstein et al. (1968) demonstrated that the role of photoperiod is to initiate floral development. There is a minimum day length required for flowering to occur, and perhaps also a minimum night length, as flowering was suppressed under constant illumination (Marmelstein et al. 1968). This suggests that shorter day lengths during the winter months could inhibit flowering even under inductive salinity and temperature conditions (McMillan 1976). In *Z. novazelandica*, cores exposed to 5 °C and a 14 h light:10 h dark photoperiod produced the greatest number of inflorescences, indicating that although winter temperatures around the Kaikoura Peninsula are unlikely to suppress the formation of reproductive shoots, the shorter day lengths may be inhibitory at this time.

It is difficult to separate the effects of light intensity and temperature, because in intertidal and shallow-water environments increased irradiance is usually accompanied by a rise in temperature (De Cock 1981c). In situ shading experiments have shown that flowering is affected by changes in irradiance, and the induction of flowering is primarily correlated with increases in insolation (Backman and Barilotti 1976; Jacobs 1979; Jacobs and Pierson 1981; Dennison and Alberte 1985). The lack of a clear trend in our light-intensity experiments could be explained by the need for an interaction between light intensity and temperature to generate a flowering response. The only treatment to yield viable fruit was at 300  $\mu\text{E m}^{-2} \text{s}^{-1}$  (at 15 °C), suggesting that the combination of a higher temperature and the highest light intensity was responsible for the formation of reproductive shoots and anthesis.

The role of salinity in the flowering of several seagrass species was investigated in the laboratory by Setchell (1924), Bourn (1935), and Phillips (1960) who found that flowering of *Ruppia maritima* was confined to lower salinities, and viable seeds were produced only at a salinity of  $\leq 28\text{‰}$ . *R. maritima* plants maintained in salinities  $> 30\text{‰}$  do not flower, but those at lower salinities, including tap water, produce reproductive shoots (McMillan unpublished data, cited in McRoy and McMillan 1977). Similarly, *Halophila engelmanni* and

*Thalassia testudinum* flowered in experimental cultures of 28 to 32‰ S, and most seagrasses have a flowering tolerance within this range (Marmelstein et al. 1968; McMillan 1974; McRoy and McMillan 1977). Low salinities enhance the flowering of *Zostera novazelandica* in laboratory cultures, which could explain the abundance of this species in brackish waters of estuaries. Vegetative growth is also stimulated under conditions of low salinity. On the intertidal platforms of the Kaikoura Peninsula the diluting action of intense rainfall and freshwater runoff occurs mostly in winter, when plants are not reproductive. Decreased salinity due to rainfall in summer is only occasional, and its influence on flowering is, therefore, probably minor.

The pattern of reproductive output of *Zostera novazelandica* plants on the intertidal platforms of the Kaikoura Peninsula does not conform to the traditional model of stress-induced flowering (Phillips et al. 1983; Keddy 1987; Harrison 1993). Plants high on the shore do not adopt an annual life history, but rather exist as perennial forms dependent on vegetative growth for the survival and maintenance of patches. Plants in the low intertidal zone and those associated with permanent tidepools and creeks, respond to stimuli that induce the formation of reproductive shoots and initiate flowering. Differences in flowering intensity between shore heights and tidepool treatments reflect limitations imposed by plant size and morphological form (Gallegos et al. 1992; Conacher et al. 1994). Overall, reproduction in *Z. novazelandica* is a product of patch location along the gently sloping intertidal platforms of the eastern South Island.

**Acknowledgements** We thank C. Ramage, M. Hickford, H. Cochran, J. van Berkel for logistic help and support and Dr. L Field for help with computer software. We gratefully acknowledge the financial support of the Foundation of Research, Science and Technology, Grants UOC318, UOC412, and UOC511.

## References

- Abrahamson WG (1975) Reproductive strategies in dewberries. *Ecology* 56: 721–726
- Backman TW, Barilotti DC (1976) Irradiance reduction: effects on standing crops of the eelgrass *Zostera marina* in a coastal lagoon. *Mar Biol* 34: 33–40
- Bourn WS (1935) Sea-water tolerance of *Ruppia maritima* L. *Contr Boyce Thompson Inst Pl Res* 7: 249–255
- Churchill AC, Riner MI (1978) Anthesis and seed production in *Z. marina* L. from Great South Bay, New York, USA. *Aquat Bot* 4: 83–93
- Conacher CA, Poiner IR, O'Donohue M (1994) Morphology, flowering and seed production of *Zostera capricorni* Aschers. in subtropical Australia. *Aquat Bot* 49: 33–46
- Dawson FH (1976) The annual production of the aquatic macrophyte *Ranunculus penicillatus* var. *calcareous* (R.W. Butcher) C.D.K. Cook. *Aquat Bot* 2: 51–73
- De Cock AWAM (1981a) Influence of light and dark on flowering in *Zostera marina* under laboratory conditions. *Aquat Bot* 10: 115–123
- De Cock AWAM (1981b) Influence of temperature and variations in temperature on flowering in *Zostera marina* under laboratory conditions. *Aquat Bot* 10: 125–131

- De Cock AWAM (1981c) Development of the flowering shoot of *Zostera marina* L. under controlled conditions in comparison to the development in two natural habitats in the Netherlands. *Aquat Bot* 10: 99–113
- Dennison WC, Alberte RS (1985) Role of daily light period in the depth distribution of *Zostera marina* (eelgrass). *Mar Ecol Prog Ser* 25: 51–61
- Ferguson RL, Pawlak BT, Wood LL (1993) Flowering of the seagrass *Halodule wrightii* in North Carolina, USA. *Aquat Bot* 46: 91–98
- Gadgil M, Solbrig OT (1972) The concept of r- and K-selection: evidence from wild flowers and some theoretical considerations. *Am Nat* 106: 14–31
- Gallegos ME, Merino M, Marba N, Duarte CM (1992) Flowering of *Thalassia testudinum* Banks ex König in the Mexican Caribbean: age dependence and interannual variability. *Aquat Bot* 43: 249–255
- Grime JP (1974) Vegetation classification by reference to strategies. *Nature, Lond* 250: 26–31
- Grime JP (1979) Plant strategies and vegetation processes. John Wiley & Sons, Ltd. Bath, England
- Harris M McD, King RJ, Ellis J (1980) The eelgrass *Zostera capricorni* in Illawara Lake, New South Wales. *Proc Linn Soc NSW* 104: 23–33
- Harrison PG (1979) Reproductive strategies in intertidal populations of two co-occurring seagrasses (*Zostera* spp.). *Can J Bot* 57: 263–268
- Harrison PG (1982) Spatial and temporal patterns in abundance of two intertidal seagrasses: *Zostera americana* and *Zostera marina*. *Aquat Bot* 12: 305–320
- Harrison PG (1993) Variations in demography of *Zostera marina* L. and *Zostera noltii* on an intertidal gradient. *Aquat Bot* 45: 63–77
- Hickford MJH, Schiel DR (1995) Catch vs count: effects of gill-netting on reef fish populations in southern New Zealand. *J exp mar Biol Ecol* 188: 215–232
- Hootsmans MJM, Vermaat JE, van Vierssen W (1987) Seed-bank development, germination and early seedling survival of two seagrass species from the Netherlands: *Zostera marina* L. and *Zostera noltii* Hornem. *Aquat Bot* 28: 275–285
- Jacobs RPWM (1979) Distribution and aspects of the production and biomass of eelgrass, *Zostera marina* L., at Roscoff (France). *Aquat Bot* 10: 45–60
- Jacobs RPWM, Pierson ES (1981) Phenology of reproductive shoots of eelgrass, *Z. marina*, at Roscoff (France). *Aquat Bot* 10: 45–60
- Kautsky L (1988) Life strategies of aquatic soft bottom macrophytes. *Oikos* 53: 126–135
- Keddy CJ (1987) Reproduction of annual eelgrass: variation among habitats and comparison with perennial eelgrass (*Zostera marina* L.). *Aquat Bot* 27: 243–256
- Keller M, Harris SW (1966) The growth of seagrass in relation to tidal depth. *J Wildl Mgmt* 30: 280–285
- Kingsbury RW, Radlow A, Mudie PJ, Rutherford J, Radlow R (1976) Salt stress responses in *Lasthenia glabrata*, a winter annual composite endemic to saline soils. *Can J Bot* 54: 1377–1385
- Koller D, Roth N (1964) Studies on the ecological and physiological significance of amphicarp in *Gymnarrhena micrantha* (Compositae). *Am J Bot* 51: 26–35
- Larkum AWD, Collett LC, Williams RJ (1984) The standing stock, growth and shoot production of *Zostera capricorni* Aschers. in Botany Bay, New South Wales, Australia. *Aquat Bot* 19: 307–327
- Lent van F, Verschuure JM (1994a) Intraspecific variability of *Zostera marina* L. (eelgrass) in the estuaries and lagoons of the southwestern Netherlands. I. Population dynamics. *Aquat Bot* 48: 31–58
- Lent van F, Verschuure JM (1994b) Intraspecific variability of *Zostera marina* L. (eelgrass) in the estuaries and lagoons of the southwestern Netherlands. II. Relation with environmental factors. *Aquat Bot* 48: 59–75
- Lovett Doust L (1981) Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*) I. The dynamics of ramets in contrasting habitats. *J Ecol* 69: 743–755
- Marmelstein AD, Morgan PW, Pêquegnat WE (1968) Photoperiodism and related ecology in *Thalassia testudinum*. *Bot Gaz* 129: 63–67
- McConchie CA, Knox RB (1989) Pollination and reproductive biology of seagrasses. In: Larkum AWD, McComb AJ, Shepherd SA (eds) *Biology of seagrasses*. Elsevier Science Publishers, New York, pp 74–111
- McMillan C (1974) Salt tolerances of mangroves and submerged aquatic plants. In: Reimold RJ, Queen WH (eds) *Ecology of halophytes*. Academic Press, New York, pp 379–390
- McMillan C (1976) Experimental studies on flowering and reproduction in seagrasses. *Aquat Bot* 2: 87–92
- McMillan C (1980) Flowering under controlled conditions by *Cymodocea serrulata*, *Halophila stipulacea*, *Syringodium isoetifolium*, *Zostera capensis* and *Thalassia hemprichii* from Kenya. *Aquat Bot* 8: 323–336
- McNamara J, Quinn JA (1977) Resource allocation and reproduction in populations of *Amphicarpum purshii* (Gramineae). *Am J Bot* 64: 17–23
- McRoy CP (1970) Standing stocks and other features of eelgrass (*Zostera marina*) populations on the Coast of Alaska. *J Fish Res Bd Can* 27: 1811–1821
- McRoy CP, McMillan C (1977) Production ecology and physiology of seagrasses. In: McRoy CP, Helfferich C (eds) *Seagrass biology: an ecosystem perspective*. Marcel Dekker, New York, pp 297–344
- Moore LB, Edgar E (1970) *Flora of New Zealand*. Vol. II. A.R. Shearer, Government Printer, Wellington, New Zealand
- Orth RJ, Luckenbach M, Moore KA (1994) Seed dispersal in a marine macrophyte: implications for colonization and restoration. *Ecology* 75: 1927–1939
- Phillips RC (1960) Observations on the ecology and distribution of the Florida seagrasses. *Prof Pap Ser mar Lab Fla* 2: 1–72
- Phillips RC (1972) Ecological life histories of *Zostera marina* L. (eelgrass) in Puget Sound, Washington. Ph.D. thesis. University of Washington, Seattle
- Phillips RC (1974) Temperate seagrass flats. In: Odum HT, Copeland BJ, McMahan EA (eds) *Coastal ecological systems of the United States*. Conservation Foundation, Washington, DC, pp 244–299
- Phillips RC, Grant WS, McRoy CP (1983) Reproductive strategies of eelgrass (*Zostera marina* L.). *Aquat Bot* 16: 1–20
- Raimondi PT (1990) Patterns, mechanisms, consequences of variability in settlement and recruitment of an intertidal barnacle. *Ecol Monogr* 60: 283–309
- Robertson AI, Mann KH (1984) Disturbance by ice and life-history adaptations of the seagrass *Zostera marina*. *Mar Biol* 80: 131–141
- Salisbury EJ (1942) *The reproductive capacity of plants*. Bell & Sons, London
- Schaffer WM (1974) Optimal reproductive effort in fluctuating environments. *Am Nat* 108: 783–790
- Schiel DR (1990) Macroalgal assemblages in New Zealand: structure, interactions and demography. *Hydrobiologia* 192: 59–76
- Setchell WA (1922) *Zostera marina* in its relation to temperature. *Science, NY* 56: 575–577
- Setchell WA (1924) *Ruppia* and its environmental factors. *Proc natn Acad Sci USA* 10: 286–288
- Setchell WA (1929) Morphological and phenological notes on *Zostera marina* L. *Univ Calif Publ Bot* 14: 389–452
- Silberhorn GM, Orth RJ, Moore KA (1983) Anthesis and seed production in *Zostera marina* L. (eelgrass) from the Chesapeake Bay. *Aquat Bot* 15: 133–144
- Silvertown JW (1987) *Introduction to plant population ecology*. Longman Scientific & Technical, New York
- Sohn JJ, Policansky D (1977) The costs of reproduction in the mayapple *Podophyllum peltatum* (Berberidaceae). *Ecology* 58: 1366–1374

- Sokal RR, Rohlf FJ (1995) *Biometry – The principles and practice of statistics in biological research*. 3rd edn. W.H. Freeman & Co., New York
- Tomlinson PB (1974) Vegetative morphology and meristem dependence – the foundation of productivity in seagrasses. *Aquaculture*, Amsterdam 4: 107–130
- Tutin TG (1938) The autecology of *Zostera marina* L. in relation to its wasting disease. *New Phytol* 37: 50–71
- Vermaat JE, Beijer JAJ, Gijlstra, R, Hootsman MJM, Phillippart CJM, van den Brink NW, van Vierssen W (1993) Leaf dynamics and standing stocks of intertidal *Zostera noltii* (Hornem) and *Cymodocea nodosa* (Ucria) Ascherson on the Banc d'Arguin, Mauritania. *Hydrobiologia* 248: 59–72
- Waller DM (1988) Plant morphology and reproduction. In: Lovett Doust J, Lovett Doust L (eds) *Plant reproductive ecology: patterns and strategies*. Oxford University Press, Oxford, pp 203–227
- Webb C, Johnson P, Sykes B (1990) Flowering plants of New Zealand. The Caxton Press, Christchurch
- Welden CW, Slauson WL (1986) The intensity of competition versus its importance: an overlooked distinction and some implications. *Q Rev Biol* 61: 23–44
- Williams SL (1995) Surfgrass (*Phyllospadix torreyi*) reproduction: reproductive phenology, resource allocation, and male rarity. *Ecology* 76: 1953–1970
- Wilson HD (1994) *Stewart Island plants*. Manuka Press, Christchurch, New Zealand
- Woods CMC, Schiel DR (1997) Use of seagrass *Zostera novaezelandica* (Setchell, 1933) as habitat and food by the crab *Macrophthalmus hirtipes* (Heller, 1862) (Brachyura: Ocypodidae) on rocky intertidal platforms in southern New Zealand. *J exp mar Biol Ecol* 214: 49–65
- Young PC, Kirkman H (1975) The seagrass communities of Morton Bay, Queensland. *Aquat Bot* 1: 191–202