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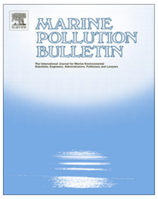

The roles of flowering, overwinter survival and sea surface temperature in the long-term population dynamics of *Zostera marina* around the Isles of Scilly, UK

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ABSTRACT

Interaction between biotic and abiotic drivers of dynamics is an important topic in ecology. Despite numerous short-term studies, there is a paucity of evidence about how environmental structure modifies dynamics in marine systems. We quantified *Zostera marina* flowering and non-flowering shoot density annually from 1996 to 2012 around the Isles of Scilly, UK, parameterizing a population dynamic model. Flowering is structured in time and space, with temperature and flowering positively associated at some locations only. We found no evidence that flower production contributes to seagrass density but 'patchiness' was positively associated with flowering in the previous year. With evidence of substantial overwinter survival, findings support the hypothesis that local populations are maintained largely through vegetative reproduction but sexual reproduction may contribute to colonisation of vacant habitat. This long-term study (1) tests validity of shorter-term investigations, (2) quantifies interaction between biotic and abiotic factors and (3) promotes seagrass as a model ecosystem.

1. Introduction

Identifying the factors that drive changes in population size and distribution is a fundamental goal in ecology, with important implications for the management of over-abundant or endangered species. It is generally accepted that density dependence, acting on fecundity and/or survival, plays an important role in most natural populations (Turchin, 1999; Brook and Bradshaw, 2006) but that both regulatory and environmental processes should be accounted for to understand population dynamics (Coulson et al., 2001; Greenman and Benton, 2001; Bull and Bonsall, 2008). Accordingly, the growth and recruitment dynamics of seagrass habitats are driven by internal regulatory mechanisms that are, in turn, likely to be modified by external forcing events, such as pollution or dredging, and natural environmental factors, including sea temperature and climate (Frederiksen et al., 2004). However, our current understanding of density-dependent processes occurring in seagrass meadows is far from extensive, with analysis of long-term data from natural populations being severely under-represented (although see Rasheed and Unsworth, 2011; Bull et al., 2012; Lobelle et al., 2013). It has become evident that in order to have a better understanding of ecosystem processes and patterns within vegetated, shallow, coastal marine habitats, the population dynamics of seagrasses over a range of spatial and temporal scale should be explored (Kendrick et al., 2005; Lobelle et al., 2013) and we aimed to address this here.

Seagrasses rely on both vegetative (via the clonal lateral spread of rhizomes) and sexual (flowers and seeds) reproduction for the maintenance of existing meadows and colonisation of new areas (den Hartog, 1970; Orth et al., 1994, 2006). Under intense and persistent disturbance, vegetative reproduction may be insufficient to sustain meadows (Plus et al., 2003; Greve et al., 2005; Jarvis and Moore, 2010). In this case, the ability to reproduce sexually through flowering and seed development may play a crucial role in the maintenance and recovery of meadows (Hootsmans et al., 1987). The formation of reproductive shoots and flowers in seagrasses displays patterns that suggest strong environmental controls (Ramage and Schiel, 1999). The onset, duration, and magnitude of flowering can vary widely with temperature, light, depth, sediment characteristics, and perhaps other environmental factors (De Cock, 1981; Phillips et al., 1983; Larkum et al., 1984).

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Z. marina appears to have developed a range of 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). Annual seagrasses are propagated entirely through flowering shoots, and rhizomes rarely persist through winter (Keddy, 1987). Seagrass populations in stable environments allocate biomass to the elongation of perennial rhizomes during summer, following a winter die-back (Phillips et al., 1983; Van Lent and Verschuure, 1994). It has been assumed that flowers produced by perennial plants probably do not play an important role in the year-to-year survival of largely undisturbed populations (Hootsmans et al., 1987). However, importantly, this has remained untested in natural populations over the long term.

Moreover, environmental factors, including temperature, light, salinity, wind and wave exposure can influence the reproductive success of seagrasses. As a result, there can be substantial variation from place-to-place, and from one year to the next at any given location. Whilst light levels are often held to be the most important environmental factor limiting vegetative growth (Orth and Moore, 1986; Dennison, 1987; Short et al., 1995), laboratory experiments have demonstrated the effect of temperature on flowering is particularly important, with salinity and day length additional contributing factors (McMillan, 1976). Here, we focus on temperature as the seagrass population around our study site – the Isles of Scilly, UK – grows in an open ocean environment, with little potential for rainfall and freshwater run-off to change salinity. Furthermore, by conducting our long-term study at the same week each year, variation in day length is effectively controlled for in this study. While exposure is harder to quantify, this is linked to fixed spatial differences such as aspect. As a result, although we do not include wind and wave action as explicit covariates, differences between individual sites are presented with this in mind.

In the present study, we aimed to: (a) identify temporal and spatial patterns in *Z. marina* flowering density in the Isles of Scilly, UK; (b) test the effects of sea temperature on flowering of *Z. marina*; (c) conduct an analysis of density dependence in a natural population based on time series data from annual censuses of flowering and non-flowering shoots of *Z. marina* over a 17 year period; and (d) develop a population dynamic model in order to understand the combined roles of flowering, survival and sea temperature on long-term persistence.

2. Methods

2.1. Study area

Observational data on *Z. marina* above-ground shoot densities were collected from five discrete eelgrass meadows around the Isles of Scilly, UK, (Fig. 1) from 1996 to 2012, using consistent and rigorous survey methodology (Cook, 2002). Site details are given in Table 1. The average range at spring tides around the Isles of Scilly is 5.0 m. Gradients across meadows are insubstantial, with typically less than 0.5 m depth variation across individual meadows.

Eelgrass was surveyed annually, during the first week of August, by placing 25 quadrats (0.0625 m^2) at randomized distances (max. 30 m) and bearings from a central datum in each meadow. Within each quadrat, both flowering and non-flowering shoots were counted.

The main summer sampling sites are not safely accessible at other times of the year. However, two other nearby locations; one in the Sound of Tean (49°58.1′N, 6°18.5′W) and a site west of Tean Island (49°58.1′N, 6°19.2′W), were surveyed quarterly during 2009/2010, again recording number of both flowering and non-flowering shoots in replicated 0.0625 m^2 quadrats. 40 quadrats were assessed at each of two locations (over a comparable area to each of our long term sampling sites), during September 2009, December 2009, March 2010 and June 2010. These data were compared to our estimates of overwinter survival at the summer sampling locations.

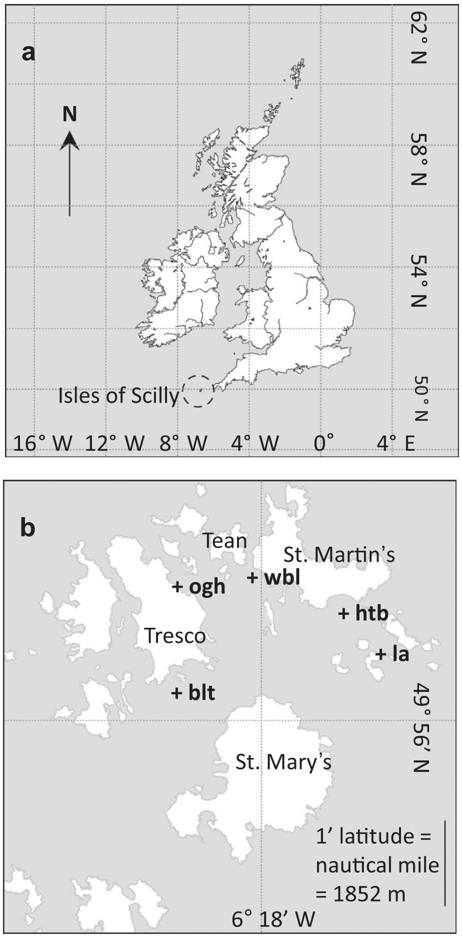

Fig. 1. Panel a the position of the Isles of Scilly relative to mainland United Kingdom. Panel b the positions (marked +) of the five seagrass meadows sampled in this study: Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl). The main islands: St. Mary's, St. Martin's and Tresco, as well as Tean Island, where winter monitoring took place, are also shown.

Table 1

Details of five long-term sampling sites from which *Zostera marina* data were collected around the Isles of Scilly, UK. Depths shown at chart datum (lowest astronomical tide). '+' Indicates drying height.

Site	Latitude, longitude	Depth (m)
Broad Ledges, Tresco (blt)	49°56.4′N, 06°19.6′W	0.2
Higher Town Bay, St. Martin's (htb)	49°57.2′N, 06°16.6′W	+0.5
Little Arthur, Eastern Isles (la)	49°56.9′N, 06°15.9′W	1.0
Old Grimsby Harbour, Tresco (ogh)	49°57.6′N, 06°19.8′W	0.6
West Broad Ledges, St. Martin's (wbl)	49°57.5′N, 06°18.4′W	0.6

2.2. Sea surface temperature

HadISST1 satellite measurements of sea surface temperatures (SST) around the UK for each month over the period of this study (1996–2012) were obtained from the British Atmospheric Data Centre (http://www.badc.nerc.ac.uk). These data are resolved into