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Paper:

Potouroglou, M., Kenyon, E., Gall, A., Cook, K. & Bull, J. (2014). 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. *Marine Pollution Bulletin*, 83(2), 500-507.

<http://dx.doi.org/10.1016/j.marpolbul.2014.03.035>

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Elsevier Editorial System(tm) for Marine Pollution Bulletin
Manuscript Draft

Manuscript Number:

Title: 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

Article Type: Special Issue: Seagrasses

Keywords: density dependence, eelgrass, flowering, long-term, survival, *Zostera marina*

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Abstract: Interaction between density-dependent and environmental drivers of natural populations 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 analysed annual flowering and non-flowering shoot density of *Zostera marina* from 1996-2012 within five discrete meadows around the Isles of Scilly. Data were used to parameterise a population dynamic model, incorporating density-dependent factors and sea surface temperature. Results indicated that flowering is highly structured in time and space, with sea temperature and flowering positively associated at some locations, but not others. However, despite non-random flowering, we found no evidence this contributes to seagrass density. Strong evidence of substantial overwinter survival supports the assumption that long-term dynamics are driven by density-dependent vegetative reproduction. Within the study limits, temperature had little effect on population dynamics, suggesting healthy seagrass meadows may be resilient to moderate climatic warming.

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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 density-dependent and environmental drivers of natural populations 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 analysed annual flowering and non-flowering shoot density of *Zostera marina* from 1996-2012 within five discrete meadows around the Isles of Scilly. Data were used to parameterise a population dynamic model, incorporating density-dependent factors and sea surface temperature. Results indicated that flowering is highly structured in time and space, with sea temperature and flowering positively associated at some locations, but not others. However, despite non-random flowering, we found no evidence this contributes to seagrass density. Strong evidence of substantial overwinter survival supports the assumption that long-term dynamics are driven by density-dependent vegetative reproduction. Within the study limits, temperature had little effect on population dynamics, suggesting healthy seagrass meadows may be resilient to moderate climatic warming.

Keywords: density dependence, eelgrass, flowering, long-term, survival, *Zostera marina*

Highlights:

- **We present long-term eelgrass flowering shoot data from the Isles of Scilly, UK.**
- **Flowering is highly structured in time and space, increasing with sea temperature.**
- **Overwinter survival of vegetation plays a substantial role in population dynamics.**
- **We find no evidence of flowering contributing to long-term population dynamics.**

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Introduction

Identifying the factors that confer resilience or drive change 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 and Brook & Bradshaw, 2006). 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. It has become evident that in order to have a better understanding of ecosystem processes and patterns, the population dynamics of seagrasses over a range of spatial and temporal scale should be explored (Kendrick et al., 2005 and 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 (seeds and flowers) reproduction for the maintenance of existing meadows and colonisation of new areas (den Hartog, 1970 and Orth et al., 1994). Under intense and persistent disturbance, vegetative reproduction may be insufficient to sustain meadows. In this case, the ability to reproduce sexually through flowering and seed development may play a crucial role in the maintenance of meadows. The formation of reproductive shoots and flowers in seagrasses displays patterns that suggest strong environmental controls (Ramage & 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 and Larkum et al., 1984). Laboratory experiments have demonstrated that the effect of temperature on flowering is particularly important, with salinity and day length additional contributing factors (McMillan, 1976).

Zostera marina 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

1 habitats. Annual seagrasses are composed entirely of flowering shoots, and rhizomes
2 rarely persist through winter (Keddy, 1987). Seagrass populations in areas with high
3 environmental stability allocate biomass to the elongation of perennial rhizomes
4 during summer, following a winter die-back (Phillips et al., 1983 and Van Lent &
5 Verschuure, 1994). Thus, it has been assumed that flowers produced by perennial
6 plants probably do not play an important role in the year-to-year survival of the
7 population (Hootsmans et al., 1987). However, importantly, this has remained
8 untested in natural populations over the long term.

15 *Z. marina* meadows in the UK are usually perennial and are believed to persist
16 almost completely as a result of vegetative growth rather than by flower development
17 (Cleator, 1993 and Davison & Hughes, 1998). Its vegetative growth could be
18 associated with disturbed habitats, where it is important for providing a fast local
19 expansion (Phillips et al., 1983), and in this respect the survival of the plant.
20 Moreover, environmental factors can influence the reproductive success on an annual
21 basis. As a result, there can be substantial variation from place-to-place, and from one
22 year to the next at any given location. Therefore, reproductive potential is best
23 determined over a number of years so that the influence of seasonal differences can be
24 partitioned out.

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

48 **Methods**

52 **Study area**

55 Observational data were collected from five discrete eelgrass meadows around
56 the Isles of Scilly, UK, (figure 1) from 1996 to 2012, using consistent and rigorous
57 survey methodology (Cook, 2002). Site details are given in table 1, with depth given
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1 at chart datum (lowest astronomical tide). The average range at springs tides around
2 the Isles of Scilly is 5.0 m. Gradients across meadows are insubstantial, with typically
3 less than 0.5 m depth variation across individual meadows.
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6 Eelgrass was surveyed annually, during the first week of August, by placing
7 25 quadrats (0.0625 m²) at randomized distances (max. 30 m) and bearings from a
8 central datum in each meadow. Within each quadrat, both flowering and non-
9 flowering shoots were counted.
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15 **Table 1. Details of five long-term sampling sites from which *Zostera marina* data**
16 **were collected around the Isles of Scilly, UK.**
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20 Site	21 Latitude, longitude	22 Depth
23 Broad Ledges, Tresco (blt)	24 49° 56.4' N, 06° 19.6' W	0.2 m
25 Higher Town Bay, St. Martin's (htb)	26 49° 57.2' N, 06° 16.6' W	+0.5 m
27 Little Arthur, Eastern Isles (la)	28 49° 56.9' N, 06° 15.9' W	1.0 m
29 Old Grimsby Harbour, Tresco (ogh)	30 49° 57.6' N, 06° 19.8' W	0.6 m
31 West Broad Ledges, St. Martin's (wbl)	32 49° 57.5' N, 06° 18.4' W	0.6 m

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40 The main summer sampling sites are not safely accessible at other times of the
41 year. However, two other nearby locations; one in the Sound of Tean (49° 58.1' N, 6°
42 18.5' W) and a site west of Tean Island (49° 58.1' N, 6° 19.2' W), were surveyed
43 quarterly during 2009 / 2010, again recording number of both flowering and non-
44 flowering shoots in replicated 0.0625 m² quadrats. These data were used to validate
45 our estimates of overwinter survival at the summer sampling locations.
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51 **Sea surface temperature**

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53 HadISST1 satellite measurements of sea surface temperatures, SST, around
54 the UK for each month over the period of this study (1996-2012) were obtained from
55 the British Atmospheric Data Centre (<http://www.badc.nerc.ac.uk>). These data are
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1 resolved into geographical cells (1° latitude × 1° longitude). We used the cell with
2 northwest corner (50° N, 7° W), covering the whole of the Isles of Scilly.
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5 **Model Development**

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8 We explored the long-term population dynamics of *Zostera marina* using a
9 model based on the stage-structured approach of Gillman & Dodd (2000), in which
10 the number of shoots in a given year, $N[t]$, are assumed to result from a proportion, s ,
11 of the previous year's shoot surviving, as well as production of new shoots at a rate,
12 R , subject to density dependence at a rate, b :
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$$17 \quad N[t] = sN[t-1] + RN[t-1] e^{(-bN[t-1])} \quad \text{eqn. 1.}$$

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21 The proportion, s , of overwinter survival can be estimated either directly from
22 time series of summer density, using maximum likelihood, or from the empirical
23 partial autocorrelation coefficients of the time series, or by taking measurements
24 during winter. We compared all three methods in this study.
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30 Once survival, s , has been estimated, the effects of density dependence were
31 tested through the standard rearrangement of equation 1 (Royama, 1992 and Denis &
32 Taper, 1994), giving a linear statistical model that can be fitted to time series:
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$$36 \quad y = \ln(R) - bN[t-1],$$

$$37 \quad \text{where } y = \ln((N[t] - sN[t-1]) / N[t-1]) \quad \text{eqn. 2.}$$

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42 This model was fitted separately to time series of flowering and non-flowering
43 *Zostera marina* shoots using a mixed-effects statistical modelling framework
44 (Pinheiro & Bates, 2000).
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49 All statistical and population dynamic modelling was performed using R
50 2.14.1 (<http://www.r-project.org>).
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54 **Results**

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57 Flowering occurred regularly throughout the study at most of the sites, with
58 the notable exception of Old Grimsby Harbour, ogh. Time series of flowering and
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1 non-flowering shoot densities at each site are shown in figure 2. No overall trend in
2 either flowering or non-flowering shoots was observed through time at any of the
3 sites.
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5 6 **Sea surface temperature**

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10 We regressed both flowering and non-flowering shoot densities on sea surface
11 temperature, SST, using mixed-effects modelling to account for temporal
12 autocorrelation in the data. At all sites, except ogh, we found a positive association
13 between mean numbers of flowering shoots in a given year and SST (table 2).
14 However, we did not find an association between non-flowering shoot density and
15 SST at any of our five sites ($p_{blt} = 0.64$, $p_{htb} = 0.26$, $p_{la} = 0.66$, $p_{ogh} = 0.61$, $p_{wbl} =$
16 0.10).
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24 **Table 2. The relationship between sea surface temperature, SST, and average**
25 **numbers of *Zostera marina* flowering shoots at each of five long-term sampling**
26 **sites around the Isles of Scilly, UK. Slope parameters, with standard errors, from**
27 **linear regressions of average shoot density on SST.**
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32 site	33 slope (SE)	34 <i>t</i> -statistic	35 <i>p</i> -value
36 blt	37 0.027 (0.005)	38 5.72	39 < 0.001
40 htb	41 0.051 (0.005)	42 10.9	43 < 0.001
44 la	45 0.038 (0.005)	46 8.05	47 < 0.001
48 ogh	49 0.002 (0.005)	50 0.51	51 0.61
52 wbl	53 0.018 (0.007)	54 2.55	55 0.01

56 57 **Spatial distribution**

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59 We went on to test the null hypothesis, H0, that shoots (flowering and non-
60 flowering) are randomly distributed spatially at each of the sites. This was compared
61 to a series of alternative statistical models of seagrass biology. The approach was to
62 fit generalized linear models (glm) to time series of flowering shoot quadrats densities
63 at each site and compare alternative likelihood functions using differences between
64 Akaike Information Criteria, ΔAIC , for competing models (Zuur et al., 2009).
65

- 66 • H0: Poisson model: spatially random shoots.

- H1: Negative Binomial model: shoots spatially aggregated.
- H2: Gamma-Poisson mixture model: spatially random shoots, with an increased chance of no shoots at some sampling points compared to chance.
- H3: Gamma-Negative Binomial mixture model: shoots spatially aggregated with an increased chance of no shoots at some sampling points compared to chance.

Flowering shoot data were too sparse to test the more complex mixture models (H2 & H3), but at three out of five sites; htb, la and wbl, there was strong evidence that flowering events were spatially aggregated (H0 vs. H1): $\Delta AIC_{htb} = 71.8$, $\Delta AIC_{la} = 6.05$, $\Delta AIC_{wbl} = 40.9$. The degree of aggregation, θ , was estimated from the negative binomial distributions of the appropriate glm: θ_{htb} (SE) = 0.33 (0.08), θ_{la} (SE) = 0.87 (0.46), θ_{wbl} (SE) = 0.23 (0.08). Decreasing θ indicates stronger aggregation, with the distribution approaching Poisson (random) as $\theta \rightarrow \infty$.

The best descriptor (minimising AIC) of non-flowering shoot distribution was the most complex scenario in each case (table 3), suggesting that *Z. marina* is highly spatially structured within these seagrass meadows, likely with several different environmental drivers of distribution acting concomitantly.

Table 3. Comparison (ΔAIC) of null (spatially random) and alternative models of spatial structure in *Zostera marina* non-flowering shoot distributions at each of five long-term monitoring sites around the Isles of Scilly, UK.

site	H0	H1	H2	H3	θ (95% c.i.)
blt	1511	190.2	221.7	0	4.64 (3.55, 6.06)
htb	2938	2940	344.8	0	5.14 (4.06, 6.51)
la	435.0	134.0	105.2	0	11.4 (8.37, 15.6)
ogh	1147	232.1	77.3	0	8.05 (5.56, 11.6)
wbl	1225	195.3	112.3	0	6.15 (4.43, 8.54)

Temporal dynamics

The roles of flowering and overwinter survival in the long-term dynamics of *Z. marina* around the Isles of Scilly were explored through statistical and population

1 dynamic modelling, as well as being validated using short-term direct sampling at two
2 nearby locations during winter.
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5 1) Statistical model: we calculated empirical lag 1 partial autocorrelation
6 coefficients (the correlation between this year's data and last year's data) at each of
7 the five seagrass meadows. Positive correlation is used as an estimate of the
8 proportion of inter-annual survival (Gillman & Dodd, 2000). All lag 1 coefficients for
9 flowering shoot time series were weakly negative, suggesting that flowering shoots do
10 not generally survive the winter. However, lag 1 coefficients for non-flowering shoots
11 were positive: $PACF[1]_{blt} = 0.33$, $PACF[1]_{htb} = 0.04$, $PACF[1]_{la} = 0.25$, $PACF[1]_{ogh} =$
12 0.12 , $PACF[1]_{wbl} = 0.09$, giving estimates of overwinter survival of non-flowering
13 shoots of between 4 % and 33 %.
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22 2) Population dynamic model: we also estimated the proportion of overwinter
23 survival, s , of shoots (flowering and non-flowering) by fitting a mechanistic model of
24 long-term dynamics to time series (eqn 1). Here too, data for flowering shoots was too
25 sparse to provide evidence for overwinter survival of flowering shoots. However,
26 estimates of overwinter survival of non-flowering shoots of between 47 % and 56 %:
27 $s_{blt} = 0.47$, $s_{htb} = 0.52$, $s_{la} = 0.50$, $s_{ogh} = 0.50$, $s_{wbl} = 0.56$.
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34 3) Direct observation of winter shoots: 40 quadrats were assessed at each of
35 two locations close to the island of Tean, neighbouring our main sampling locations,
36 during September 2009, December 2009, March 2010 and June 2010. At the site in
37 the Sound of Tean, seven flowering shoots were observed in September 2009, none in
38 December 2009, none in March 2010 and five in June 2010. At the other site, west of
39 Tean Island, three flowering shoots were observed in September 2009, one in
40 December 2009, none in March 2010 and none in June 2010.
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48 Average per quadrat non-flowering shoot density (SE), in the Sound of Tean
49 was estimated as 6.60 (1.83) in September 2009, 6.66 (0.49) in December 2009, 6.83
50 (0.95) in March 2010 and 12.3 (1.28) in June 2010; with estimates west of Tean
51 Island: 7.17 (1.14) in September 2009, 8.67 (3.29) in December 2009, 4.83 (0.60) in
52 March 2010 and 7.00 (0.68) in June 2010. This gives winter survival estimates
53 (lowest density / highest density) of 54 % in the Sound of Tean and 56 % west of
54 Tean Island.
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Density dependence

We tested the hypothesis that average eelgrass shoot density is regulated in a density-dependent manner, against the null hypothesis of a random walk (Denis & Taper, 1994), by regressing inter-annual population growth rate on shoot density in the previous year (eqn. 2). At all five long-term sampling sites, we found strong evidence to support the density dependence hypothesis (figure 3a): *Z. marina* density is more likely to return towards equilibrium density after a perturbation, than to follow a random trajectory.

Link between flowering and non-flowering shoots

We regressed current average non-flowering shoot density at each site against the corresponding flowering shoot density from the previous year, using a mixed-effects model to account for temporal autocorrelation at each site. In four of the five long-term sampling time series, we found no evidence of an association between shoot density and previous flowering ($p_{\text{blt}} = 0.41$, $p_{\text{htb}} = 0.21$, $p_{\text{la}} = 0.95$, $p_{\text{ogh}} = 0.28$). Intriguingly, we found a negative relationship between current shoot density and flowering in the previous year at West Broad Ledges, wbl: slope (SE) = -0.717 (0.231), $t = 3.11$, $p = 0.0027$). Overall, this analysis provides no evidence that the effects of flowering, although highly structured in time and space, contribute to eelgrass density or long-term ecological dynamics in this relatively undisturbed setting (figure 3b).

Discussion

Species with a mixed mode of reproduction may exhibit wide variation among locations in the contribution of sexual and asexual reproduction within populations (Eckert & Barrett, 1992). In the present study, *Zostera marina* populations within one geographical region, but growing in different locations, displayed marked variability in flower density. This variability in flowering across the meadows of the Isles of Scilly suggests that sexual reproduction may play a more important role for meadow persistence in some populations than in others. Decreased flowering density was observed particularly at the sites of Old Grimsby Harbour (ogh) and Broad Ledges, Tresco (blt), where high-disturbance conditions occur (e.g. boat traffic and mooring).

1 Here, vegetative reproduction could be important for providing a fast local expansion,
2 and thus maintaining the survival of the plant.
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5 Nevertheless, sexual reproduction is the only way to maintain genetic diversity
6 in seagrass meadows (Ackerman, 2006) and recolonise bare sediments or impacted
7 areas (Marbà & Walker, 1999 and Rasheed, 2004). The reproductive biology of
8 *Zostera* has been well described, indicating that the reproductive processes are highly
9 variable along its geographic distribution (Phillips et al., 1983 and Olesen, 1999).
10 There are considerable variations in spatial and temporal patterns of the species'
11 flowering, which have been related to latitudinal and local gradients (Ackerman,
12 2006), but also with genotypic variation of the populations (Hemminga & Duarte,
13 2000). Temperature appears to be critical for all phases of the reproductive event, but
14 other environmental factors such as irradiance and nutrients may also play a role in
15 the timing and characteristics of the process (Walker et al., 2001).
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26 In our study, there was a direct effect of sea temperature on eelgrass flower
27 density around the Isles of Scilly, at all but one location – Old Grimsby Harbour –
28 which, worryingly, is the most highly impacted by water users. Several studies
29 indicate that phenology of *Zostera spp.* is strongly related also to latitude, with the
30 flowering sequence delayed as latitude increases (Phillips et al., 1983 and Walker et
31 al., 2001). As eelgrass meadows of the Isles of Scilly are situated at intermediate
32 latitude within the geographic range of *Z. marina* and as the summer temperatures in
33 our dataset (16-18 °C) were far from the optimum temperature (20-25 °C) for *Zostera*
34 flowering, we might expect this trend to continue with expected increases in sea
35 temperature in the coming decades. Therefore, it is important to determine the extent
36 to which flowering contributes to reproduction under natural conditions.
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47 Recruitment from sexual reproduction in seagrasses is believed to be
48 extremely low (Hemminga & Duarte, 2000). Their reproductive cycle involves
49 several steps from the flowering to the formation of a new plant, with many of the
50 processes to represent bottlenecks (seed germination and survival) that do not enhance
51 sexual reproduction success (Orth et al., 2006). Apart from sea temperature and light
52 availability, fluctuating salinities has been suggested to affect sexual reproduction,
53 while Van Lent et al. (1995) indicated that the amount of inorganic nitrogen may be
54 of importance for the development and abundance of flowering, as well as site safety
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1 (tidal protection, sediment resuspension etc.). In fact, we found no evidence that
2 flowering in a given year contributes to observed shoot density in the following year.
3 Whilst this largely confirms the predictions of short-term experiments about the
4 minimal contribution of sexual reproduction to eelgrass dynamics, it also raises some
5 interesting questions about why flowering still occurs and is evidently non-random.
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10 In terrestrial ecology, Harada (1999) developed a spatial model to evaluate the
11 evolutionarily stable strategy (ESS) (Maynard Smith, 1982), of a vegetatively and
12 sexually reproducing plant. Plants with an ESS strategy invest more resources into
13 vegetative reproduction than the optimum allocation pattern that would maximise the
14 population size at equilibrium. In fact, the optimal strategy for many clonal plants,
15 such as seagrasses, is to allocate resources to both vegetative and sexual propagation.
16 Sexual reproduction (through seed dispersal) is adaptive as a means of escaping the
17 competitive effect of clonal spread in order to colonise new environments. Generally,
18 when shoot density increases, then competition increases and resource availability
19 decreases. Loehle (1987) expected that sexual propagation should be favored at low
20 density where potential success of sexual reproduction is higher. Likewise, one
21 explanation of decreased flowering and seed production at higher density may be that
22 nutrients get limiting under such conditions.
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35 The ESS scenario would lead to the prediction of greatest flowering, and / or
36 greatest contribution of flowering to subsequent shoot density at the site with lowest
37 observed shoot densities. Worryingly, we do not find this to be the case. In fact, in our
38 study we find lowest levels of flowering at the site with lowest shoot density (ogh).
39 Old Grimsby Harbour is outstanding, in our study, as the site with the greatest direct
40 human disturbance and the hypothesis that this impact is responsible for reduced
41 flowering should be investigated in future research. We also suggest that the relative
42 contributions of seeds, clonal spread and modification of these processes by
43 environmental (natural and anthropogenic) events should be considered in potential
44 seagrass restoration projects.
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54 The lack of evidence for a role of flowering in reproduction strongly suggests
55 that overwinter survival is the primary mode of long-term growth at this location. It is
56 known that sub-surface rhizomes may persist for more than one year (Olesen & Sand-
57 Jensen, 1994). However, the extent to which overwinter survival of shoots provides
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1 resources and continuity for subsequent growth is unknown and, again, likely to be
2 environment dependent. In inter-tidal populations of *Z. marina* it has been shown that
3 grazing by waterfowl can reduce over-winter survival of shoots from c. 40 % to near-
4 undetectable amounts (figure 3 of Tubbs & Tubbs, 1983). In the sub-tidal eelgrass
5 populations of the current study, there are no obvious grazers. We employed three
6 methods of estimating overwinter shoot survival: 1) empirical autocorrelation
7 between summer seagrass densities; 2) mechanistic model fitting to summer densities;
8 and 3) direct winter observations at a neighbouring location. The second and third
9 approaches were in close agreement, with winter shoot densities estimated at around
10 half that of summer density. The empirical time series approach underestimated shoot
11 survival, compared to (2) and (3). This may be because this method lacks statistical
12 power for these relatively short individual meadow time series, or because inter-
13 annual correlation is only a proxy measure of survival. Either way, the important
14 lesson here is not to rely on a single approach when seeking to complex estimate
15 population dynamics from time series data, as well as the need to validate findings
16 with direct measurements where possible.
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30 In conclusion, our long-term study of *Zostera marina* flowering density
31 confirms and also complements existing short-term, manipulative *in situ* or *ex situ*
32 experiments on specific processes occurring at different life stages of the plant and
33 factors controlling its reproduction mode. Our findings indicate that various
34 ecological processes can contribute to the inter-annual changes of a natural
35 ecosystem. The present study illustrates the multi-scale approach needed for
36 developing metrics, but also the knowledge gaps in processes occurring at population
37 level. As seagrass beds are under increasing threat from coastal development,
38 pollution and other forms of human disturbance, this study may offer valuable
39 knowledge which could be used for effective restoration and management plans, as
40 well as conservation policies.
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51 **Acknowledgements**

52 We are grateful to a large number of volunteers who have collected data for the Isles
53 of Scilly seagrass project and the Isles of Scilly Wildlife Trust over many years. In
54 particular, we thank Cyril Nicholas (Natural England) for expert local knowledge and
55 logistical support.
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Figure legends

1
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3 Figure 1. Panel **a** the position of the Isles of Scilly relative to mainland United
4 Kingdom; panel **b** the positions (marked +) of the five seagrass meadows sampled in
5 this study: Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old
6 Grimsby Harbour (ogh), and West Broad Ledges (wbl). The main islands: St. Mary's,
7 St. Martin's and Tresco, as well as Tean Island, where winter monitoring took place,
8 are also shown.
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15 Figure 2. Panel **a** flowering shoot density per 0.0625 m² quadrat; panel **b** non-
16 flowering shoot density per 0.0625 m² quadrat. Grey dots show individual quadrat
17 data; black lines show meadow averages for Broad Ledges Tresco (blt), Higher Town
18 Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges
19 (wbl).
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26 Figure 3. Panel **a** density dependence in population growth rates, $y = \ln((N[t] -$
27 $sN[t-1]) / N[t-1])$, at Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur
28 (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl). Circles show
29 meadow averages for each year. Solid black lines show the predicted relationship
30 between population growth rate and shoot density in the previous year (t-1). Dashed
31 lines show 95 % confidence intervals in model prediction. Panel **b** the relationship
32 between shoot density in a given year and flowering in the previous year.
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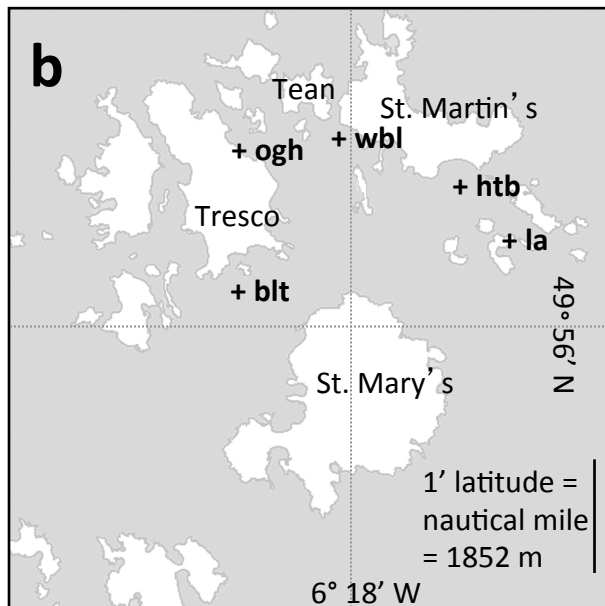
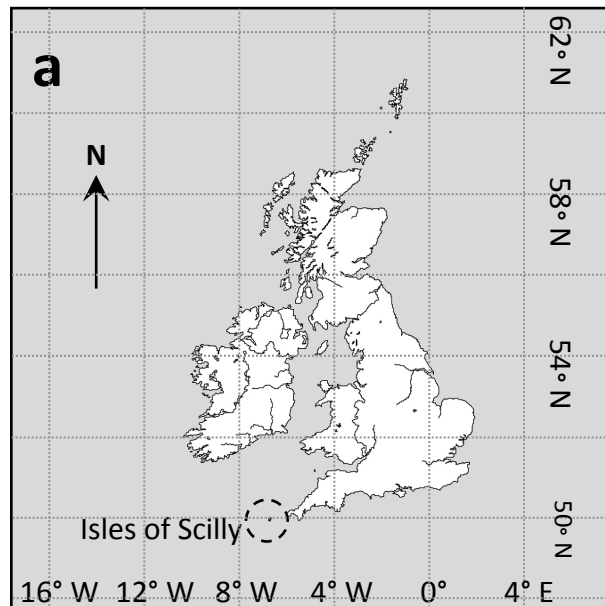


Figure 1

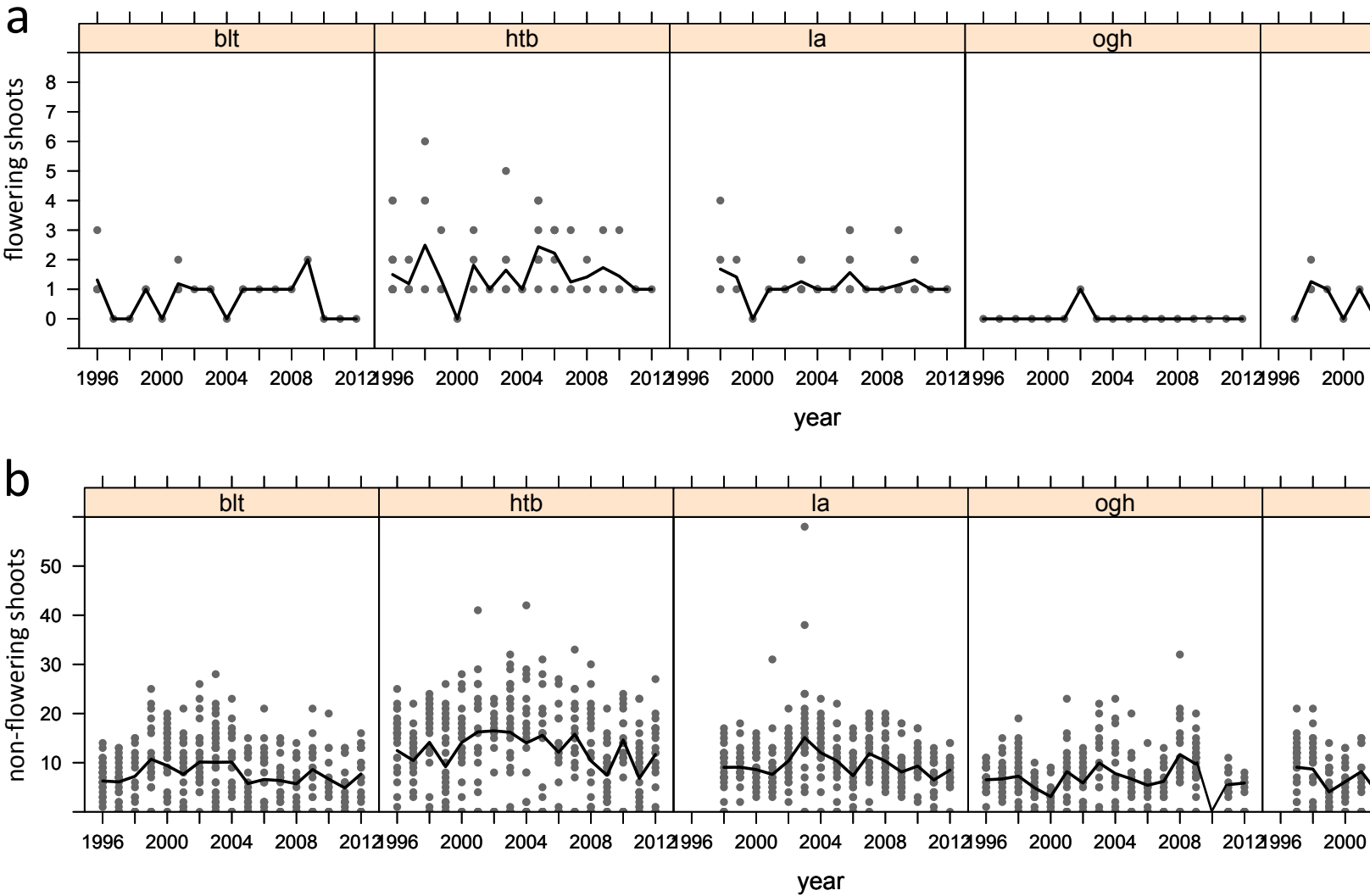


Figure 2

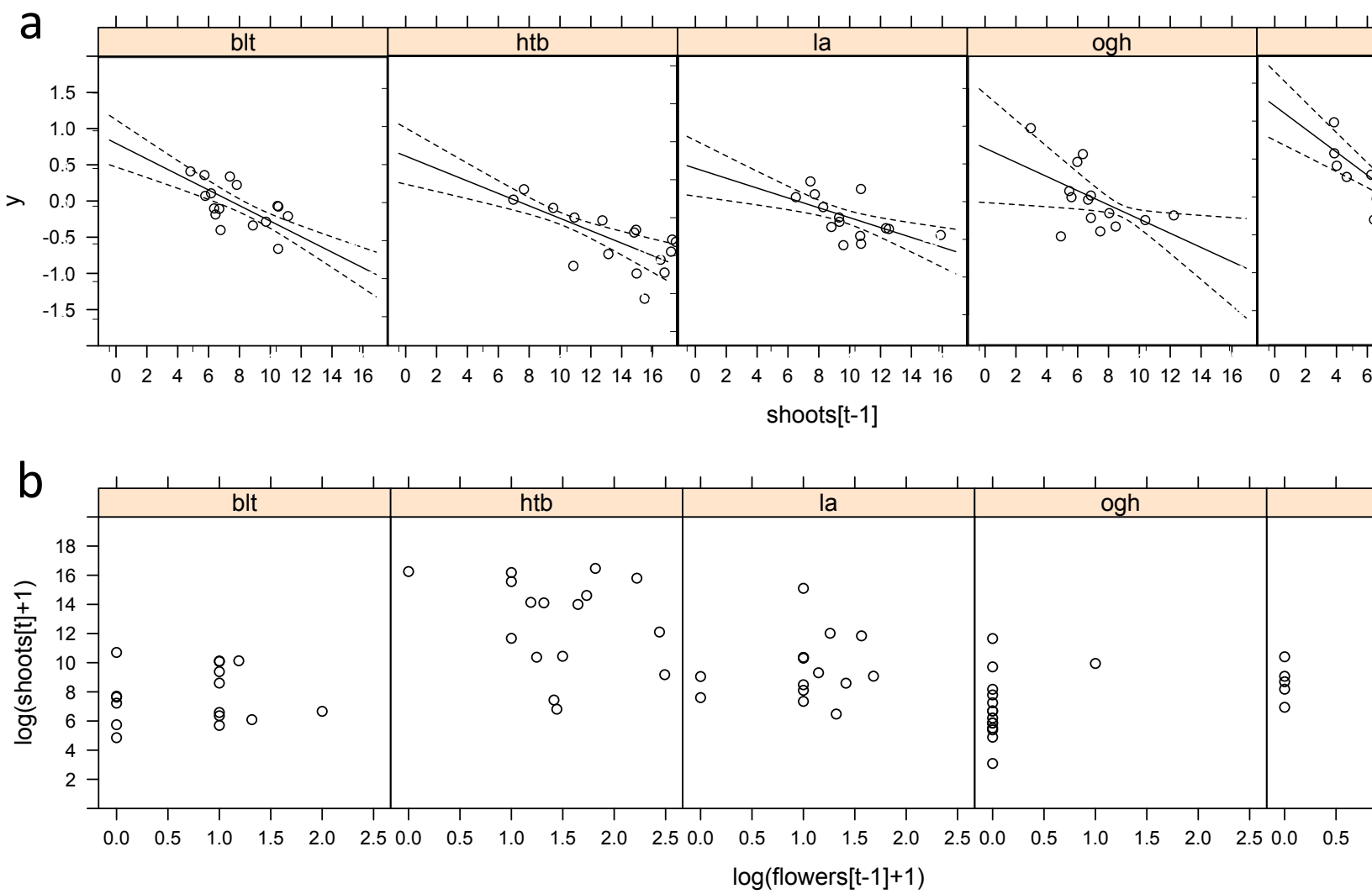


Figure 3