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Harkin, Claire and Stewart, Alan J A (2020) Establishment, spread, and impact of an invasive planthopper on its invasive host plant: Prokelisia marginata (Homoptera: Delphacidae) exploiting Spartina anglica (Poales: Poaceae) in Britain. Ecological Entomology, 45 (6). pp. 1327-1336. ISSN 0307-6946

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Establishment, spread, and impact of an invasive planthopper on its invasive host plant: Prokelisia marginata (Homoptera: Delphacidae) exploiting Spartina anglica (Poales: Poaceae) in Britain

CLAIRE HARKIN and ALAN J. A. STEWART School of Life Sciences, John Maynard Smith Building, University of Sussex, Brighton, UK

Abstract. 1. Since its recent arrival in Britain, the planthopper Prokelisia marginata has spread widely around saltmarshes on the east and south coast of England and south Wales, feeding on Common Cordgrass, Spartina anglica, itself an invasive non-native species.

2. Results suggest that P. marginata populations in Britain benefit from a degree of natural enemy release. No evidence of parasitism was found in over 71000 eggs, nymphs, and adults inspected. The only potential natural enemy control was suggested by a positive correlation between the densities of planthoppers and generalist spiders.

3. Experimental exposure under both glasshouse and field conditions to typical field densities of planthoppers resulted in significant negative effects on a number of host plant performance metrics.

4. Spartina anglica is important for stabilising estuarine sediments and has been deliberately planted for this purpose in the past. Its weakening as a result of heavy planthopper herbivory could have serious consequences for the long-term stability of Britain’s vulnerable saltmarsh habitats.

Key words. biological invasion, herbivory, natural enemy release, saltmarsh.

Introduction

Invasive alien species are those that establish in areas outside their native range, subsequently spread beyond the location of their introduction, and have an impact on the recipient community (sensu Colautti & MacIsaac, 2004). Invasive alien species are the subject of considerable political, public, and academic interest (Huenneke, 1988; IUCN, 2000; Mack et al., 2000) and are considered to be among the top five most severe threats to global biodiversity and ecosystem integrity, along with habitat change, climate change, overexploitation, and pollution (Bellard et al., 2016; IPBES, 2019; Millennium Ecosystem Assessment, 2005; Nelson et al., 2006; Vila et al., 2011; Wagner, 2020). Both the rate and extent of biological invasions continue to escalate (McGeoch et al., 2010), with no indication of levelling off (Seebens et al., 2017). Invasions by new species are therefore altering the structure and composition of often long-established communities (Davis, 2003), with consequent effects on ecological interactions and even the physical and chemical structure of the invaded environments (Ehrenfeld, 2010).

Prokelisia marginata Van Duzee is a stenophagous phloem-feeding planthopper that is native to the Gulf and Atlantic coasts of North America, where it is the most abundant herbivore of the Saltmarsh Cordgrass Spartina alterniflora C.E. Hubbard (Denno et al., 1986). Across its entire North American range, the species feeds only on S. alterniflora, S. foliosa and their hybrids, and the introduced S. anglica, avoiding all other sympatrically occurring Spartina and other monocotyledonous species (Grevstad et al., 2003). Studies of P. marginata in its native range show that it exhibits classic r-selected traits, which confer the potential for successful invasion: short generation times and rapid population growth, producing natural densities of up to 1000 adults and 100000 nymphs per m² (Denno et al., 2000; Denno & Grissell, 1979; Gratton & Denno, 2003). Like many planthoppers, P. marginata exhibits phenotypic plasticity in wing morphology, with both brachypterous and macropterous forms present in the same population, enabling the planthopper to maximally exploit the prevailing environmental
conditions (Denno et al., 1986). Macropoters are capable of long-distance migration by flight of up to 30 km (Denno et al., 1996), thereby providing them with the strong dispersal capabilities essential for both insects exploiting transient habitats such as saltmarshes and for the expansion of invading populations (Langellotto & Denno, 2001).

The first record of Prokelisia marginata in Europe was from the Algarve in Portugal in 1994. Later records were reported from Spain in 2008, France in 2009 (Mifsud et al., 2010), the Netherlands (den Bieman & van Klink, 2016), and Norway (Endrestol & Almedal, 2019). Prokelisia marginata was first recorded in Britain on Hythe marshes near Southampton in 2008 (Wilson & Muhlerthaler, 2009). A comprehensive invertebrate survey of the same site in 2000 had found no evidence of the plant hopper (Kirby, 2000), and although it is possible that it was present in extremely low densities earlier, it is likely that it first arrived in Britain sometime between these dates.

Saltmarshes are of high conservation value, providing a unique habitat for a wide diversity of fauna and flora that are unable to survive elsewhere, as well as an important overwintering refuge for wildfowl (Boorman, 2003; Townend et al., 2011). The presence of hard coastal defences can lead to scouring and erosion on the seaward side while simultaneously preventing natural landward migration of the saltmarsh. In combination with rising sea levels and extreme weather events predicted under global climate change scenarios (Lowe & Meiner, 2012), these factors represent a significant threat to this important habitat and its associated species (Barbier et al., 2011; Finch et al., 2007; Irmler et al., 2002). Spartina anglica was first recorded in 1872 in saltmarshes adjacent to Southampton Water and is the fertile allopolyloid of S. x townsendii, itself the sterile F1 hybrid of S. maritima and S. alterniflora (Gray et al., 1991). Although the parental species still occur in isolated remnant populations, S. anglica has become the dominant structuring species in a quarter of Britain’s lower saltmarsh communities (Gray et al., 1997).

In the past, it was planted specifically to stabilise estuarine sediments, although the resultant monospecific stands hold little value for biodiversity (Bouma et al., 2009; Gan et al., 2009).

Although little studied (Gray et al., 1991), the macroinvertebrate communities of S. anglica marshes in Britain appear to be rather sparse; Payne (1973) found only four commonly occurring species in Poole Harbour, three of which appeared to feed on S. anglica, although none exclusively. This contrasts markedly with the situation in North America, where Spartina marshes are heavily attacked by P. marginata and the mirid bug Trigonotylus viligeri, both of which are Spartina specialists (Denno, 1977; Stiling & Bowdish, 2000; Strong & Stiling, 1983) and reach very high densities (Daehler & Strong, 1995; Denno et al., 1986; Denno et al., 2000). Despite high densities, P. marginata apparently has no significant adverse effect on S. alterniflora performance and survival, either where both species have co-evolved (Gustafson, Kilheffer, & Silliman, 2006; Roberts & Pullin, 2008) or in invaded ranges where both have coexisted for a substantial period (Daehler & Strong, 1995). However, S. alterniflora and S. anglica populations that have experienced a lengthy period of separation from P. marginata, or have never been in contact, suffer significant deleterious impacts on growth and survival when exposed to the plant hopper (Daehler & Strong, 1997; Garcia-Rossi et al., 2003; Wu et al., 1999). In glasshouse trials, previously unexposed S. anglica plants suffered 92% mortality after four months of exposure to high densities of P. marginata, with surviving plants averaging only 37% of the biomass of control plants (Wu et al., 1999). Field trials of P. marginata as a biological control agent of invasive S. alterniflora showed an almost 50% reduction in biomass compared to paired controls (Grevstad et al., 2003).

We can assume that British populations of S. anglica had no exposure to P. marginata prior to its arrival in the early 2000s. Here, we test the impact of P. marginata on S. anglica in order to determine the susceptibility of the host to the herbivore after a period of separation and the evolution of the plant as a new species. We hypothesise that: (i) S. anglica performance measures will be negatively affected by exposure to P. marginata feeding and oviposition, and (ii) the strength of this impact will be more severe at greater plant hopper densities. We report on the extent of the invaded range of P. marginata in Britain and the plant hopper’s life history, typical population density, and natural enemy complex.

Materials and methods

Field sites

Regular sampling was conducted at two saltmarsh sites dominated by S. anglica on the south coast of England: Pagham (50°77′N, 0°78′W) and Hythe (50°86′N, 1°39′W). Data on the geographical distribution of P. marginata were collated from records submitted to the UK Auchenorrhyncha Recording Scheme (www.ledra.co.uk) and from invertebrate surveys conducted at Spartina sites around the coast of England and Wales.

Prokelisia marginata demography and invertebrate community sampling

Samples were taken at both sites on 10 approximately monthly occasions from October 2011 to October 2012. On each occasion, a Vortis suction sampler (Stewart, 2002) was used to take four replicate samples from the vegetation, each consisting of ten 10-second ‘sucks’ and covering a total sampled area of 1 m2. Prokelisia marginata and all other Hemiptera were identified to the species level, while all other invertebrates were identified to the family level, and counted. In addition, seven S. anglica tillers were cut at ground level on each occasion from each site and subsequently searched in the laboratory for the presence of P. marginata eggs and egg parasitoids.

Spartina anglica and Prokelisia marginata experimental material

Spartina anglica plants were grown from rhizome material sampled from Pagham that had been washed, cut to approximately 12 cm lengths including at least one node, and planted in 10 cm (then later transferred to 15 cm) diameter pots containing horticultural-grade sand. Pots were watered with fresh
Prokelisia marginata impact on Spartina anglica under glasshouse conditions

Forty-five potted S. anglica plants were placed in individual trays. Individual plants were randomly assigned to one of three treatments: control (no nymphs added), low planthopper density (15 nymphs added), and high planthopper density (30 nymphs added). Five plants of each treatment were randomly assigned to each of three experimental blocks and to a random position within that block in a 3×5 grid configuration. Starting metrics were recorded for each plant: number of leaves, number of tillers, overall plant height, and the length of each leaf (which was then converted to biomass).

Each plant was enclosed by a transparent cylindrical cage constructed from 175μm polyethylene terephthalate polyester film, 13 cm in diameter, 50 cm tall, and with a nylon gauze lid and a 5×7cm gauze-covered ventilation window positioned 18 cm above the base of the cage. Plants were watered and given nutrients as described above. The experiment ran for 8 weeks, at the end of which the same metrics were recorded for each plant, with additional measurements of fresh and dry weight (to an accuracy of 0.01 g) of total above- and below-ground material.

Prokelisia marginata impact on Spartina anglica under field conditions

Field cages, 42 cm tall, 31.5 cm in diameter, and enclosing a ground surface area of 780 cm², were constructed from inverted white opaque polypropylene buckets with the bases removed and covered with nylon gauze and then secured to the ground with steel tent pegs. Pagham was chosen as the experimental site because background densities of P. marginata were very low. Twenty cages were randomly distributed within an area of dense S. anglica subject to a moderate but not excessive level of tidal inundation. Cages were randomly assigned to either Prokelisia addition or control (no Prokelisia added) treatments. Four individual S. anglica stems in each cage were designated as ‘focal’ plants for monitoring. These were loosely tagged with polyvinyl chloride tape, and total leaf length measurements were taken.

Prokelisia marginata were collected the following day from Hythe using the Vortis suction sampler and transported to Pagham. Each Prokelisia addition treatment cage received 200 unsexed adults (equivalent to 256 m⁻²), chosen to reflect the high-density treatment in the glasshouse experiment (224 m⁻²) and mean natural densities at Hythe the previous June (268 m⁻²). The experiment ran for 58 days, after which each focal plant was measured for leaf length, and the above-ground parts were removed and subsequently dry-weighed. The remaining standing crop in each cage was also cut at ground level and later dry-weighed. No attempt was made to retain or count any P. marginata individuals remaining in the cages.

Statistical analysis

Generalised linear models (GLMs) with a quasi-Poisson error structure (due to overdispersion of residuals) were used to test for correlation between the population density of P. marginata and that of other arthropod groups for which at least 200 individuals were collected.

In the glasshouse experiments, differences in plant performance between treatment groups, for continuous response variables, were analysed using linear mixed models (LMMs) with plant change as the response variable, treatment as the explanatory variable, and block as a random factor. Plant change was analysed using relative growth rates (RGRs, i.e. growth during the experimental period divided by the starting measurement) rather than absolute values in order to standardise for unavoidable variation between replicates in the size of plants at the beginning of the experiment. Relative water content was calculated as a percentage of dry biomass. Leaf and tiller count data were analysed using generalised linear mixed-effect models (GLMMs) with a Poisson error structure, log link function, and the Laplace approximation technique (Bolker et al., 2009). As with the LMM structure, plant change was used as the response variable, treatment as the explanatory variable, and block as a random factor.

For the field experiment, all response variables were continuous, normally distributed, and with constant variance. The effect of treatment was analysed using ANOVA, with RGR of focal plants as the response variable and treatment as the explanatory variable. Whole-cage standing crop, the final biomass was used as the response variable.

Analyses were performed with the statistical software R version 3.6.2 (R Core Team, 2019) using the nlme (Pinheiro et al., 2012), lme4 (Bates et al., 2012), and multcomp (Hothorn et al., 2008) packages.

Results

Prokelisia marginata distribution and demography

Prokelisia marginata has been recorded from 41 10-km squares containing Spartina saltmarsh sites from as far north as
the Humber estuary and as far west as the Gower Peninsular in Wales (Fig. 1). All sites containing *S. anglica* and specifically searched for *P. marginata* revealed the plant hopper to be present, although densities varied considerably. Seasonal changes in *P. marginata* density at Hythe revealed a bivoltine life cycle, the second generation being considerably larger than the first, reaching a peak in August with densities of 1252 adults per m² (Fig. 2). The seasonal patterns for eggs and nymphs were similar, with peaks occurring one and two months later, respectively. Densities at Pagham were substantially lower than at Hythe throughout the sampling period. The percentage of macropterous adults at Hythe was 71% in May, reaching a peak of 99% in July and falling no lower than 96% for the rest of the season.

**Invertebrate community composition**

Densities of all other arthropod groups were lower than *P. marginata* by at least one, and more frequently two, order of magnitude (Table S1). The density of *P. marginata* was positively correlated with the density of spiders (both sites: $F = 52.97$, $P < 0.001$; Hythe only: $F = 10.24$, $P = 0.002$; Pagham only: $\chi^2 = 4.47$, $P = 0.03$; Figs 3 and 4). The density of spiders was not correlated with that of any other potential prey group: Hemiptera (excluding *P. marginata*), Collembo, Coleoptera, or Diptera. Over 71 000 *P. marginata* eggs, nymphs, and adults collected over the course of 13 months were examined for the presence of parasitoids, but none were found.

**Effect of Prokelisia marginata on Spartina anglica performance**

Exposure to *P. marginata* under glasshouse conditions had significant negative effects on *S. anglica* relative growth rates in overall height; above-ground and root biomass; and in the number of new tillers gained at high, but not at low, plant hopper density. The number of new leaves gained and the relative water content of shoot material were negatively affected in both the low- and the high-density treatments. There was no effect of either treatment level on the root: shoot ratio of plants (Table 1). Exposure to *P. marginata* under semi-natural field conditions had significant negative impacts on relative leaf length gain of focal *S. anglica* plants and on final whole-cage biomass (Table 2; Fig. 5).

**Discussion**

**The invasion status of Prokelisia marginata in Britain**

Our results show *P. marginata* to be in the successful early stages of invasion in Britain, having reached densities matching those reported from its native range in North America (Denno & Peterson, 2000) and outnumbering other arthropod groups by at least one, frequently two, order of magnitude. The pathway by which *P. marginata* arrived in Britain is unknown, although the most likely is via transport of eggs laid inside plant material. On the assumption that *P. marginata* first arrived in Britain sometime after 2000, however, its colonisation of saltmarshes around the coasts of England and Wales has been exceptionally rapid. Further northward range expansion, at least on the east coast, may be curtailed by the distribution of the host plant (Preston et al., 2002).

*Prokelisia marginata* exhibits functional traits that promote its success as an invasive alien species (Denno et al., 1985). It appears to be bivoltine in Britain, compared to trivoltine in its native range on the Atlantic coast of North America (Denno & Roderick, 1990), as a consequence of the difference in latitude between the study sites (51°N and 39°N, respectively). Despite this difference in voltinism, however, peak adult population densities at one of the British sites were similar to those recorded in the native range (Denno et al., 2000). Growth rates that allow populations to reach such high densities in a single season, together with wing polymorphism enabling rapid dispersal in response to crowding, substantially explain the invasion success of this species. In addition, the relatively unsaturated nature of invertebrate communities in British saltmarshes (Ford et al., 2013), especially the sap-feeding guild, means they are particularly prone to invasion and numerical domination by *P. marginata*.

In Britain, *P. marginata* currently appears to benefit from an absence of specialist natural enemies. In its native range, *P. marginata* can suffer heavily from a parasitoid attack: up to 40% of nymphs and adults by Strepsiptera (Stiling et al., 1991) and 27–100% of eggs by Mymaridae (Stiling et al., 1991) and...
Fig. 2. Mean number (±1 SEM) of adult *Prokelisia marginata* per 0.25 m² between October 2011 and October 2012 at Hythe and Pagham.

Fig. 3. Relationship between number of *Prokelisia marginata* (note log scale) and Araneae per 0.25 m² quadrat sample at Hythe and Pagham. Fitted lines predicted from the generalised linear model with 95% confidence intervals. [Colour figure can be viewed at wileyonlinelibrary.com].

Fig. 4. Mean number (±1 SEM; log scale) of *Prokelisia marginata* (adults and nymphs) and Araneae at Hythe per 0.25 m². Sampling dates as in Fig. 2.
Table 1. Effect of Prokelisia marginata on Spartina anglica performance.

|                          | d.f. | Control mean (SEM) | Treatment mean (SEM) | L ratio | $\chi^2$ | $P$       |
|--------------------------|------|--------------------|----------------------|---------|----------|----------|
| **Biomass relative gain**|      |                    |                      |         |          |          |
| Treatment (whole model)  | 40   | 2.42 (0.63)        | 1.70 (0.29)          | 15.58   | <0.001***|          |
| Low density (post-hoc)   |      | 2.04 (0.47)        | 1.40 (0.40)          | 6.65    | 0.036*   |          |
| High density (post-hoc)  |      | 1.36 (0.32)        | 0.93 (0.25)          | <0.001***|          |          |
| No. new tillers gained   |      |                    |                      |         |          |          |
| Treatment (whole model)  | 40   | 2.07 (0.43)        | 1.17 (0.24)          | 15.09   | <0.001***|          |
| Low density (post-hoc)   |      | 2.04 (0.47)        | 1.40 (0.40)          | 6.65    | 0.036*   |          |
| High density (post-hoc)  |      | 1.36 (0.32)        | 0.93 (0.25)          | <0.001***|          |          |
| No. new leaves gained    |      |                    |                      |         |          |          |
| Treatment (whole model)  | 40   | 15.87 (1.45)       | 11.50 (0.80)         | 15.09   | <0.001***|          |
| Low density (post-hoc)   |      | 12.07 (1.32)       | 10.93 (0.94)         | 6.65    | 0.036*   |          |
| High density (post-hoc)  |      | 10.93 (0.94)       | 10.93 (0.94)         | <0.001***|          |          |
| **Relative water content**|      |                    |                      |         |          |          |
| Treatment (whole model)  | 40   | 2.17 (0.18)        | 1.68 (0.14)          | 17.56   | <0.001***|          |
| Low density (post-hoc)   |      | 1.69 (0.15)        | 1.67 (0.23)          | <0.001***|          |          |
| High density (post-hoc)  |      | 1.67 (0.23)        | 1.67 (0.23)          | <0.001***|          |          |
| **Final root biomass (g)**|      |                    |                      |         |          |          |
| Treatment (whole model)  | 40   | 8.42 (0.65)        | 6.85 (0.72)          | 6.42    | 0.040*   |          |
| Low density (post-hoc)   |      | 8.14 (0.91)        | 5.56 (1.03)          | 0.042*  |          |          |
| High density (post-hoc)  |      | 1.67 (0.23)        | 1.67 (0.23)          | <0.001***|          |          |
| **Relative height gain** |      |                    |                      |         |          |          |
| Treatment (whole model)  | 40   | 0.49 (0.08)        | 0.26 (0.04)          | 13.11   | <0.001***|          |
| Low density (post-hoc)   |      | 0.31 (0.07)        | 0.22 (0.05)          | <0.001***|          |          |
| High density (post-hoc)  |      | 0.22 (0.05)        | 0.22 (0.05)          | <0.001***|          |          |

Individual treatment levels refer to low $P$. marginata density (15 individuals added) and high $P$. marginata density (30 individuals added) treatments. Whole-model analyses refer to comparisons with control (no $P$. marginata added) replicates. Post-hoc test refers to Tukey HSD using 95% CI. Test statistics are log-likelihood ($L$) ratio for LMMs and $\chi^2$ for GLMMs. Relative metrics indicate ratios of post- to pre-experiment measurements. Significance levels indicated by: *≤0.05; **≤0.01; ***≤0.001.

Table 2. Effect of Prokelisia marginata on Spartina anglica performance measures in field conditions.

|                          | d.f. | Control mean (SEM) | Treatment mean (SEM) | $F$ | $P$   |
|--------------------------|------|--------------------|----------------------|-----|-------|
| **Relative leaf length gain**|      |                    |                      |     |       |
| Treatment                | 1    | 1.14 (0.08)        | 0.84 (0.05)          | 4.88| 0.040*|
| Residuals                | 18   |                    |                      |     |       |
| **Final whole-cage biomass (g)**|      |                    |                      |     |       |
| Treatment                | 1    | 83.69 (5.23)       | 60.42 (4.22)         | 5.99| 0.025*|
| Residuals                | 18   |                    |                      |     |       |

Treatments are control (no $P$. marginata) and Prokelisia (200 individuals added). Relative metrics indicate ratios of post- to pre-experiment measurements. Significance levels indicated by: *≤0.05.

The lack of parasitoids of any life history stages in British populations of $P$. marginata fits with the general pattern that parasitoid attack rates tend to be much lower on hosts in their invaded, compared to their native, ranges (Cornell & Hawkins, 1993). For example, parasitism rates in the leaf-mining moth Cameraria ohridella, even of generalist parasitoids, were very low in areas that it had recently invaded but increased as a function of residence time (Grabenweger et al., 2010).

Generalist predators may exert the greatest numerical control on $P$. marginata populations. Spiders have been identified as the primary natural enemies of both adult and nymphal $P$. marginata in their native range (Denno et al., 2002; Gratton & Denno, 2005). Prokelisia marginata appears to be more susceptible to predation than co-occurring prey such as leafhoppers and mirid bugs due to its ineffective predator avoidance behaviour (Dobel & Denno, 1994) and typical adoption of a low position within the Spartina canopy (Vince et al. 1981). The high densities of $P$. marginata at Hythe appear to have elicited a strong numerical response in spiders, although this may still currently be insufficient to regulate planthopper population growth.
Prokelisia marginata are stenophagous on only a small range of Spartina species (Grevstad et al., 2003). As all other Spartina species in Britain are rare and extremely localised (Lacambra et al., 2004), S. anglica provides the main mechanism for the further establishment and spread of P. marginata. Our study is the first to examine the interaction between P. marginata and S. anglica outside North America, where the herbivore showed early promise as a potential biological control agent of the grass (Grevstad et al., 2003). Our findings lend weight to the conclusions of North American studies that long-separated and previously unexposed Spartina populations are vulnerable to attack by P. marginata in a way that co-evolved and coexisting plants are not (Daehler & Strong, 1995; Grevstad et al., 2003; Wu et al., 1999).

British populations of S. anglica have so far benefitted from a degree of natural enemy escape (Gray et al., 1991), in contrast to North American S. alterniflora marshes, which hold a diverse assemblage of host-specific herbivores (Gratton & Denno, 2005). There are no native specialist Spartina herbivores in any part of Europe (Garcia-Rossi et al., 2003). Daehler and Strong (1995) found that the top-down effects of insect herbivores on S. alterniflora in San Francisco Bay were minimal and suggested that this may be because fewer other stressors have a major impact on the plant, which occurs in large, monospecific stands and is subject to little or no interspecific competition (Strong & Ayres, 2013). Dense, monospecific stands are less frequent in Britain, however, where S. anglica is usually present in more mixed communities with other halophytes (Boorman, 2003; Dargie, 2000; Gray et al., 1991; Huckle et al., 2004). S. anglica in Britain may consequently be subject to greater competition-induced stress, already noted as a potential contributing factor to the die-back recorded in recent decades (Lacambra et al., 2004), and may thus be inherently more vulnerable to the deleterious impacts of a novel and abundant insect herbivore.

Prokelisia marginata is still in the relatively early stages of invasion in the United Kingdom. Already, however, it appears to have spread rapidly from its probable site of entry and has reached densities in some populations that, as we have shown under field conditions, will have significant deleterious impacts on the host plant. Invasion lag and other complexities of the invasion process mean that the full effects of an invader may not be seen until a considerable time has elapsed after its arrival (Strayer et al., 2006). Studies have found herbivory by a range of invertebrates to be a significant driver of Spartina sp. die-back (Bertness et al., 2014; Hughes & Paramor, 2004; Jeffries et al., 2006; Silliman & Ziemann, 2001), with a resulting reduction in the sediment retention abilities of the grass (Gleason et al., 1979). In addition, herbivory has been shown to interact with other biological and physical stressors to impact salt-marsh plant productivity and community composition (Alberti et al., 2008; Jimenez et al., 2012; Li & Pennings, 2017; Montemayor et al., 2020). Further investigation is needed to assess whether continued P. marginata population growth and spread may act additively, or even synergistically, with other biotic and abiotic factors to restrain or inhibit growth in British Spartina species or increase the rate of die-back. A reduction in plant vigour, such as has been seen in S. anglica die-back in southern England, may have a deleterious impact on its ability to dissipate wave action and currents across affected saltmarshes (Adnitt et al., 2007), consequently reducing the extent to which it helps to reduce coastal flooding. While the role of S. anglica in stabilising estuarine sediments remains complex, and in some cases contentious, early indications suggest that P. marginata has the potential to contribute to a significant change in the composition of British saltmarsh plant communities over the coming decades. Further research is needed to clarify the nature and extent of these potential impacts on this important and already heavily challenged habitat.
Acknowledgements
The authors thank the Natural Environment Research Coun-
cil [NE/J0500446/1], the University of Sussex School of Life
Sciences, and the Gilchrist Educational Trust for funding this
research. They also thank Dr Ellen Rotheray, University of Sus-
sex, and two anonymous reviewers for helpful comments on
the manuscript and to Natural England for facilitating access to
field sites. The map was produced by the DMAP program, writ-
ten by Alan Morton, Imperial College. Both authors contributed
equally to project design and manuscript preparation. C. Harkin
led on data collection and analysis. The authors declare there
were no conflicts of interest in conducting the research.

Data availability statement
The data that support the findings of this study are available from
the corresponding author upon reasonable request.

Supporting Information
Additional supporting information may be found online in the
Supporting Information section at the end of the article.

Table S1. Number of individuals of classified invertebrate
groups collected at the Hythe and Pagham field sites between
October 2011 and October 2012.

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Accepted 19 June 2020

Associate Editor: Shannon Murphy

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