Probing the role of propagule pressure, stochasticity, and Allee effects on invasion success using experimental introductions of a biological control agent

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Abstract. 1. Although most populations of non-native species arriving in new environments fail to establish, mechanisms behind failed biological invasions are still poorly understood.

2. Propagule pressure has been found to be a dominant driver of establishment success, underpinned by processes such as stochasticity and Allee effects. While studies have revealed the presence of a component Allee effect in field populations, empirical support for demographic Allee effects has been limited.

3. We used the leaf-feeding beetle *Neolema ogloblini*, a biological control agent against the plant *Tradescantia fluminensis*, as a proxy invasive species to experimentally study the process of establishment. We investigated how the initial size of the population released affects the probability of establishment and population growth in the first season after introduction at isolated sites in New Zealand.

4. The probability of establishment was found to increase with numbers of individuals released. A significant quadratic relationship was found between population size released and per capita population growth rate; that is per capita population growth rate initially increased as population size released increased but decreased at higher population levels.

5. These results support the presence of a demographic Allee effect. However, as the influence of stochasticity (environmental and demographic) could not be completely separated from that of a demographic Allee effect, we conclude that extinction probability in the experimental populations of *N. ogloblini* was influenced by both a demographic Allee effect and stochasticity.

6. Our study demonstrates and supports the concept that experimental biocontrol agent releases can be used for testing hypotheses regarding invasion biology.

Key words. Demographic Allee effect, establishment, *Neolema ogloblini*, invasive species, *Tradescantia*.

Introduction

New populations of non-native insect species arrive in areas outside their natural range on a continuous basis (Brockerhoff

et al., 2014; Edney-Browne *et al.*, 2018; Liebhold *et al.*, 2018; Seebens *et al.*, 2018). This trend is widely attributed to unprecedented growth in global trade and travel (Brockerhoff *et al.*, 2010; Ward, 2014; Liebhold *et al.*, 2018). To become successful invaders, these newly arrived non-native species populations must pass through the three sequential stages of the invasion process (e.g. arrival, establishment, and spread)

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and the barriers that separate them (Liebhold & Tobin, 2008; Blackburn *et al.*, 2011). In this paper, we focus on population processes (e.g. propagule pressure, Allee effects, etc.) that may act as barriers or filters during the establishment stage. While the arrival of most populations of non-native insect species do not lead to establishment, some do, and it is this variability in establishment success that has motivated a sustained effort to understand the factors that influence establishment (Blackburn *et al.*, 2015; Cassey *et al.*, 2018b).

Successful establishment occurs when newly arrived non-native populations are able to form self-sustaining populations, which grow to sufficient levels such that extinction is highly unlikely (Liebhold & Tobin, 2008; Lockwood *et al.*, 2013). Establishment success of a non-native species depends on several factors. Among these are characteristics of the recipient area called 'invasibility', which includes climatic suitability, presence and quality of host resources, and interspecific interactions such as herbivory, competition, predation, and mutualism (Brockerhoff & Liebhold, 2017). Other factors are those of the arriving non-native species, termed 'invasiveness', such as life history traits, evolutionary history, and genetic diversity (Szűcs *et al.*, 2014; Hui *et al.*, 2016). In addition, characteristics that vary independently of species and location, such as propagule pressure, also play a role in affecting establishment (Blackburn *et al.*, 2015; Cassey *et al.*, 2018b).

Propagule pressure is a dominant driver of establishment success in small populations of introduced non-native species (Lockwood *et al.*, 2005; Cassey *et al.*, 2018a; Duncan *et al.*, 2019). Propagule pressure refers to the number of individuals in the arriving population, the frequency of arrival, the physical distance between individuals, as well as their quality and genetic diversity (Hufbauer *et al.*, 2013; Lange & Marshall, 2016). The arrival of a large founding population is more likely to lead to establishment than arrival of small founding populations (Lockwood *et al.*, 2005; Drake & Lodge, 2006). Several processes may underpin the widespread influence of propagule pressure on establishment success; these include demographic and environmental stochasticity, Allee effects, emigration/dispersal, inbreeding and genetic drift, natural enemies, and habitat quality and connectivity (Lande, 1993; With, 2004; Jonsen *et al.*, 2007; Courchamp *et al.*, 2008; Paynter *et al.*, 2012; Hufbauer *et al.*, 2013; Morel-Journel *et al.*, 2016). The low establishment rates of small populations can be the result of any one or combinations of the above processes, making it difficult to determine, which is acting in any given case.

The Allee effect is broadly defined as a decline in individual fitness with decreasing population size or density (Stephens *et al.*, 1999). Allee effects are typically strongest at low densities and can create critical population thresholds, below which populations can decline to extinction (Stephens *et al.*, 1999; Courchamp *et al.*, 2008). In addition, the Allee effect may increase the duration of the first two stages of the invasion process (e.g. arrival and establishment) (Potapov & Rajakaruna, 2013). Stephens *et al.* (1999) distinguish between component and demographic Allee effects. When a population experiences a component Allee effect, some component of individual fitness has a positive relationship with density (e.g. individual survival or reproduction is reduced at low density) (Stephens

et al., 1999). In some cases, a component Allee effect leads to a demographic Allee effect where for a small population at low density the per capita growth rate of the population is reduced, potentially leading to negative growth and local extinction (Stephens *et al.*, 1999). A component Allee effect does not necessarily always give rise to a demographic Allee effect as one component of fitness may be offset by an increase in other components of fitness (Angulo *et al.*, 2007; Gregory & Courchamp, 2010). For example females at low density may have access to fewer potential mates, but simultaneously, more resources (because of lower competition) may enhance their fecundity.

Mechanisms giving rise to component Allee effects often involve social or cooperative processes among conspecifics, such that individuals do better collectively than alone (Courchamp *et al.*, 2008). Well-known causes include mate-finding failure, loss of cooperative defence, loss of environmental conditioning, foraging inefficiency, and predator saturation failure (Hunter, 2000; Kramer *et al.*, 2009; Kanarek & Webb, 2010; Fauvergue *et al.*, 2012).

While many studies have revealed a component Allee effect, empirical support for a demographic Allee effect has been limited (Kramer *et al.*, 2009; Gregory *et al.*, 2010; Fauvergue, 2013; Drake *et al.*, 2019). This is thought to be mainly due to the difficulty and high measurement error in censusing low-density populations (Courchamp *et al.*, 2008). In addition, extinction rates at low densities may be simultaneously elevated by other factors like demographic stochasticity and thus may mask the influence of Allee dynamics (Roush & Hopper, 1993; Dennis, 2002; Liebhold & Bascompte, 2003).

Nonetheless, evidence for demographic Allee effects has been found for a limited number of species across diverse taxa, including the saltmarsh Cordgrass *spartina alterniflora* loisel. (Davis *et al.*, 2004), the aquatic crustaceans *Hesperodiaptomus shoshone* (SA Forbes) (Kramer *et al.*, 2008) and *Daphnia magna* Straus (Kramer & Drake, 2010), the Glanville fritillary butterfly (*Melitaea cinxia* L.) (Kuussaari *et al.*, 1998), the Eurasian Gypsy moth (*Lymantria dispar* (L.))(Johnson *et al.*, 2006), a parasitoid wasp *Aphelinus asychis* Walker (Fauvergue & Hopper, 2009), and the Californian Channel Island fox (*Urocyon littoralis*) (Angulo *et al.*, 2007). Just how common place and widespread demographic Allee effects are in natural populations is an ongoing subject of research and debate (Kramer *et al.*, 2009; Gregory *et al.*, 2010; Fauvergue, 2013; Drake *et al.*, 2019). Even so, it is an important ecological phenomenon relevant to the fields of biological invasion, biological control, conservation, and sustainable harvesting (Drake *et al.*, 2019). In addition, global environmental change may affect Allee dynamics in populations (e.g. they may become weaker or stronger, appear or disappear) (Berec, 2019) as a result of changes in organismal physiology, population abundances and distribution, and species interactions due to global environmental change (Tylianakis *et al.*, 2008). Using population models to study the effect of increasing temperature, Berec (2019) found that whereas the Allee effect driven by predation generally weakens as temperature increases, the Allee effect due to the need for finding mates is predicted to become stronger when warming occurs. Knowledge on the presence and strength of Allee effects is,

therefore, crucial in order to understand changes in Allee effect dynamics due to global environmental change (Berec, 2019).

Similar to the Allee effect, stochasticity (demographic and environmental) plays an important role in the extinction of small populations (Lande, 1993). Both the Allee effect and demographic stochasticity give rise to a similar, positive relationship between initial population size and probability of establishment, and it can be difficult to distinguish between the two processes (Fauvergue *et al.*, 2012). Demographic stochasticity occurs because the birth or death of an individual in a populations is a random event, such that individuals identical in their expected reproduction or longevity still differ by chance in the number of offspring they produce or how long they will live (Lande, 1993). Environmental stochasticity arises from fluctuations in environmental factors such as temperature, wind, and rainfall that may drive population-level fluctuations in birth and death rates (Lande, 1993). Unlike the Allee effect and demographic stochasticity that are dominant in small populations, the impact of environmental stochasticity is independent of population size, and influences both small and large populations (Lande, 1993). However, environmental stochasticity can interact with demographic stochasticity to increase the extinction rate in small populations, where a random reduction in population growth rate can drive population size down to where the effects of demographic stochasticity come into play (Grevstad, 1999a).

Understanding the factors that explain the success or failure of species establishment is not only important for preventing biological invasions, but also for the preservation and reintroduction of threatened species and for successful establishment of biological control agents (Shea & Possingham, 2000; Fowler *et al.*, 2006; Yeates *et al.*, 2012; Hufbauer *et al.*, 2013). Usually little information exists about the early stages of establishment of accidentally introduced species, as most invasion events are detected only years after their arrival and there is seldom any knowledge of the original arrival, the pathway involved, and how many individuals were introduced (Marsico *et al.*, 2010; Brockerhoff *et al.*, 2014).

Invasion biology and biological control are essentially sides of the same coin, and their linkage has long been recognised (Ehler, 1998; Fagan *et al.*, 2002; Marsico *et al.*, 2010). Introductions of species used as classical biological control agents offer unique opportunities to experimentally study the process of establishment by non-native species (Grevstad, 1999b; Fowler *et al.*, 2006; Marsico *et al.*, 2010; Fauvergue *et al.*, 2012; Roderick *et al.*, 2012). In particular, introduction of biological control agents targeting invasive plants can serve as a model system for studying invasions of non-native insect species attacking plants. Releases of biological control agents are principally planned biological invasions, and in general are subjected to the same biogeographic, demographic, and genetic processes operating during unwanted biological invasions (Fagan *et al.*, 2002; Fauvergue *et al.*, 2012). Such planned introductions allow (i) observation of mechanisms at work at very small population sizes during the establishment stage, (ii) experimental manipulation of initial conditions, and (iii) experimental testing that a population has indeed established or failed to establish after being introduced.

A number of studies have used manipulative field experiments with introductions of biocontrol agents to test hypotheses regarding invasion biology (Grevstad, 1999b; Memmott *et al.*, 2005; Fauvergue *et al.*, 2007; Fauvergue & Hopper, 2009). Among these, only two studies found evidence for a demographic Allee effect after introductions (Grevstad, 1999b; Fauvergue & Hopper, 2009), but two other studies found no Allee effect (Memmott *et al.*, 2005; Fauvergue *et al.*, 2007). Therefore, there is a need for more empirical evidence for the occurrence of demographic Allee effects in biological invasions, to broaden our understanding of this phenomenon, how common it is, and to improve our ability to draw general conclusions about the mechanisms involved.

To study the role of population size and how it relates to the Allee effect in the early stage of establishment, the leaf beetle *Neolema ogloblini* (Monrós) (Chrysomelidae) a biocontrol agent released against *Tradescantia fluminensis* Vell. (Commelinaceae) in New Zealand, was used as a model species. By manipulating initial population size over replicated releases, we examined how population size influences: (i) the probability of establishment and (ii) the per capita population growth of established populations. We predicted there would be a greater probability of establishment at higher population sizes and that lower per capita growth rates in smaller populations would be indicative of a demographic Allee effect.

Materials and methods

Study system

Neolema ogloblini is a specialist leaf-feeding chrysomelid beetle found on *T. fluminensis* and *Tradescantia mundula* Kunth (Fowler *et al.*, 2013). The adults are glossy, metallic-black, and notch leaves from edges as they feed, while the larvae are pale greyish-brown and graze externally on the epidermal tissue on the underside of leaves. Pupation occurs inside a pupal case made from threads of a white oral extrusion resembling foam, which solidifies (Hayes, 2016). Most pupal cases are found on the underside of leaves, or on the soil surface attached to plant detritus. Development time from egg to adult is approximately 31 days at 24°C (H. Williams, unpublished data), with two to three generations expected in the field in New Zealand (Hayes, 2016). A colony of *N. ogloblini* was obtained from beetles reared by Landcare Research (Lincoln, New Zealand) for the biocontrol programme against *T. fluminensis* in New Zealand, originally imported from Brazil (Lages and Curitiba). For the purposes of this study, a population was maintained year-round in a glasshouse environment on caged, potted plants of *T. fluminensis* (hereafter referred to as the 'general population'). Temperatures in the glasshouse varied between 15°C and 25°C in winter and 15°C and 30°C in summer.

Tradescantia fluminensis is native to south-east Brazil and northern Argentina, but has escaped cultivation and is now considered one of New Zealand's worst invasive temperate forest weeds (Syrett, 2002). *Tradescantia mundula* (previously *T. albiflora* Kunth) is native to Argentina, Brazil, and Uruguay and is naturalised in New Zealand (Fowler *et al.*, 2013; Pellegrini, 2018). Both species are frost intolerant with their

distribution within New Zealand restricted to frost-free areas (Fowler *et al.*, 2013). *Tradescantia fluminensis* plants used for rearing and *T. mundula* plants used for field trials were grown from cuttings in plant trays under greenhouse summer conditions, using a well-draining, compost-rich potting medium. Cuttings of both plant species were obtained from stock plants maintained at Landcare Research.

Experimental design

The initial sizes of *N. ogloblini* populations were manipulated over replicated releases at 30 isolated sites in the Selwyn district of Canterbury, New Zealand. All sites were located in an area classified as the Canterbury-Otago tussock grasslands ecoregion (Department of Conservation, 1987).As Both N.*ogloblini* and its host plant prefer shady conditions, all sites were situated under trees (most sites were set up in conifer shelter belts of rural properties, surrounded by pasture land), with no access to livestock and a minimum distance of 500 m between sites to prevent cross-over dispersal. Adults of *N. ogloblini* rarely disperse over substantial distances without host patches as stepping-stones(in a mark-release-recapture study, only 1% (N = 1200) of adults were able to locate an unoccupied host patch 60 m away (H. Williams, unpublished data)), and sea distance of 500 m was deemed as sufficient isolation between sites. The Selwyn district experiences between 10 and 50 frost days in winter (Macara *et al.*, 2020), and as *T. mundula* is frost sensitive, it is currently not widespread in the district. Care was taken though to ensure sites were not close to naturalised patches of *T. mundula* or *T. fluminensis* that could act as refuge host patches. This was done through visual survey of the area within 200 m around each site and questioning the landowners on the presence of the plant species on their properties.

At each site, potted plants were arranged to form arectangular patch size with a leaf-cover of ca. 1 m^2. As a ground-cover species, the *T. mundula* foliage filled the entire area of the plant trays they were grown in, and therefore, patch size was determined by the area of adjoining trays. The potted plants were placed on weed-mat to prevent rooting and minimise the likelihood of becoming established. Plants were watered on a regular basis to ensure plants stayed in a healthy growing condition. The use of patches of potted host plants grown in a shade house enabled control of confounding factors such as host quality patch size, stem density, nitrogen content, plant physiological stage, and soil type and drainage, thereby reducing the influence of environmental stochasticity on *N. ogloblini* populations.

Six population sizes were used for releases and consisted of either2, 4, 8, 16, 32, and 64 unmated adults released onto patches. These population size treatments were assigned randomly to the 30 sites, resulting in five replicates for each of the six population sizes. To obtain unmated adults of similar ages for the field releases, eggs were collected from the general population and reared on *T. fluminensis* leaves in ventilated, plastic containers (30 × 15 × 15 cm) under laboratory conditions (25:18 °C temperature regime, 14L:8D photoperiod). The use of laboratory-reared adults not only aided obtaining unmated

adults, but also reduced the influence of demographic variance on probability of establishment and growth rate of *N. ogloblini* populations. Under controlled rearing conditions, the high quantity and quality of resources and absence of stressors (e.g. predation, intra-, and interspecific competition) tend to minimise inter-individual variance in reproductive success (Vercken *et al.*, 2013).

On the day before the release, newly emerged adults were collected from the rearing containers. Adults of *N. ogloblini* display a pre-oviposition period of 5 days when no mating takes place, therefore, only adults that emerged in the previous 48 h were used to ensure that they were unmated. For population sizes of 32 and 64 adults, individuals were chosen at random, while equal numbers of each sex were used for populations of ≤16 adults. Morphologically it is not possible to distinguish between male and female beetles, but females tend to be larger than males (Hayes, 2016). Therefore, selection of males and females was based on size. In a test to corroborate this method, adults (N = 530) were confined individually to small vials with cut leaves of *T. mundula* and monitored for oviposition. Containers with eggs were assumed to be female (*N. ogloblini*females lay eggs irrespective of being mated, though at a lower rate), while those without eggs assumed to be male. Results indicated that the sex of only four beetles (0.75%) were assigned incorrectly. Upon selection, adults were confined overnight on cut leaves in small mesh bags to settle and feed. The leaves with adults were then gently released in a single location in the host plant patches the next morning when temperatures were cooler, in order to reduce immediate dispersal. Releases were made between 16 and 29 November 2017, and populations were left in the field through mid-April 2018.

Visits to sites depended on weather and the watering needs of the potted plants, which ranged from once a week during hot, dry weather (November to February), to every 2nd week during cooler, rainy weather (March to April). During selected visits, each plant patch was inspected for 10 minutes by carefully lifting stems and turning leaves, and the presence of adults (or signs indicating the presence of adults – fresh feeding marks, newly-laid eggs, and newly-emerged larvae) was noted. Such observations were done to determine whether failed establishments could be traced back to the immediate dispersal or disappearance from the site by the adults.

To estimate the number of adults produced in the field during one season, we used the number of pupae found, rather than the number of adults present. Adult numbers may vary because of death (e.g. old age or predation) or dispersal (e.g. prompted by patch decline/competition), or other unknown factors. The characteristic white 'foamy' pupal cases of *N. ogloblini* are very distinctive and usually attached to the underside of leaves or to leaf litter around the host plant, and therefore, relatively easy to find. The original intent was to use the number of pupal cases with exit holes as estimate of adult numbers produced. During the experiment though, it was not always possible to find a distinct exit hole (and thus indicating successful adult eclosion), and the number of pupae was used instead. Although using pupal number as an estimate meant that the population would not be tracked for an entire generation, this provided a consistent estimate of population growth under

the unconfined, open-field situation of the experiment. Under laboratory conditions, survival rate between the pupal stage and the adult stage did not vary substantially; with survival from egg to the pupal stage 87.7% (N = 285 eggs) and to the adult stage 84.2% (N = 285 eggs). It is acknowledged that factors such as predation or environmental conditions could additionally reduce survival from the pupal phase to the adult phase. In the context of this study, population establishment was thus defined as successful development to the pupal stage of any offspring produced within the first growing season after introduction.

After 10 weeks following release (mid-summer census), plants at all sites were carefully searched for pupal cases. As development from egg to adult takes approximately 6 weeks (under lab conditions), all populations had been in the field long enough such that at least some offspring should have reached the pupal stage (even under the cooler conditions expected in the field). The number of pupae was determined by counting and recording the number of pupal cases. Those pupal cases with exit holes were then removed (as per original methodology), while those still containing pupae were left in the patch. As empty pupal cases would not normally be intentionally removed in a natural setting, the impact of this methodology on the behaviour and population dynamics of *N. ogloblini* is unknown.

At the completion of the field trials (19 weeks following release), all plants were transferred to sealed plastic bags and brought to the laboratory, where all plants were carefully searched for all life stages of *N. ogloblini* and the number of each stage was recorded. The presence of pupal cases with exit holes indicated that populations were able to produce at least one generation during the growing season. To prevent double counting of pupae recorded at week 10, the number of pupal cases left in patches at that time was subtracted from the final pupal count.

Statistical analysis

All statistical analyses were executed in the open source statistical environment R version 3.4.3 (R Core Team, 2017). Values for AICc were determined using the R package "AICcmodavg" (Mazerolle, 2017).

We analysed the effect of initial population size released on the probability of establishment at the field sites (N = 30). A binomial logistic regression model (maximum likelihood estimation) was used to determine if release size influenced whether populations established (1 = established (supporting development of offspring to pupal stage), 0 = extinction (no development to pupal stage)). The model was fitted using the *glm* function in R.

To identify the presence of a demographic Allee effect, a linear regression model was used to examine the relationship between population size released and per capita population growth rate. The model was fitted using the function *lm* in R. Per capita growth rate (r) was calculated as $r = \ln(N_1/N_0)$, with (N_1) the number of pupae produced during the season and (N_0) the population size released. A small non-zero number (0.001) was added to each growth rate data point prior to calculation to enable inclusion of extinct populations. Apart from measures such as using similarly-aged, laboratory reared adults, and potted host plants of similar quality, the influence of demographic

stochasticity was further reduced by, including only sites where adults were present for an extended time in the statistical analysis on the relationship between population size released and per capita population growth rate. This was done with the rationale that, the closer the actual longevities of individuals in a population are to the average, the lower the influence of demographic stochasticity, at least in terms of longevity and survival. *Neolemaogloblini* adults have been reported to live up to 5 months in captivity (Hayes, 2016), but under the optimum conditions experienced in the laboratory, this period is most likely at the upper limits of adult longevity. Information in the literature suggests average adult longevity of Criocerinae beetles to be between 2 and 3 months (e.g. *Plectonycha correntina* Lacordaire = 76 ± 40 days (Cagnotti *et al.*, 2007), *Crioceris* sp. = 103 ± 13 days (Witt & Edwards, 2002), *Lemapraeusta* (Fab.) = 78 ± 1 days (Das *et al.*, 2019), and *Lilioceris cheni* Gressit and Kimoto = 84 ± 19 days (Manrique *et al.*, 2017)) and our observations indicated this same range for the average longevity of *N. ogloblini* adults. Thus, only sites where adults were present for a minimum of 4 weeks after initiation of the experiment (about a third of the expected average longevity) were included in the statistical analysis (N = 26). This resulted in the omission of four sites (one site where two adults were originally released, and three sites where four adults were originally released). Initial inspection of the data suggested nonlinearity (a hump-shaped relation); therefore, both linear and quadratic functions of population size released were fitted to explain population growth rate. Adjusted R^2 and Akaike's Information Criterion corrected for small samples (AICc) were used to determine the most parsimonious model.

Results

Establishment probability

The number of weeks that adult activity was noted at sites following initial release increased with increasing population size (Fig. 1). At only four sites (one site with initial population size of two individuals, and three sites with initial population size of four individuals) no signs of any adult activity were noted
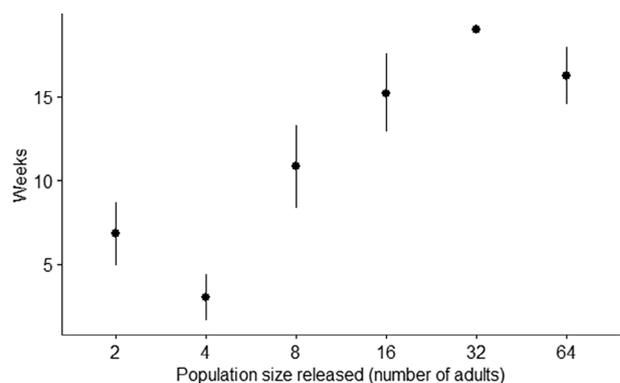
Fig. 1. Mean number of weeks (from a maximum of 19) that *Neolema ogloblini* adult activity was observed at field sites (n = 30) for different population sizes released. Error bars indicate standard errors.
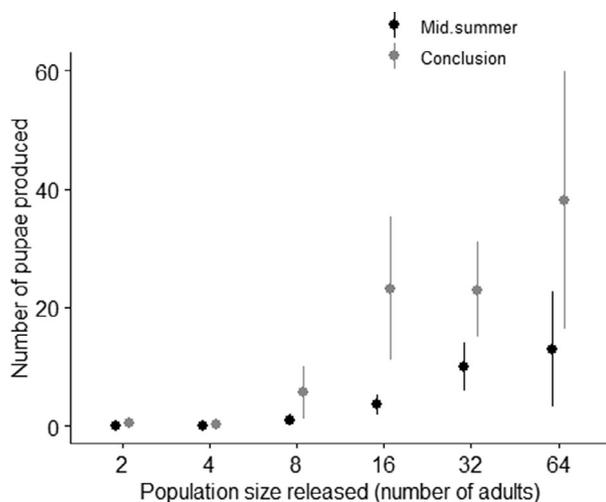
Fig. 2. Mean numbers of pupae produced by *Neolema ogloblini* populations at field sites (n = 30) during growing season 2016–17. Experiment replicates were staggered and started 16–19 Nov 2016, a mid-summer census was taken 10 weeks after start of experiment (25 January to 8 February 2017), and the experiment was concluded at 19 weeks after start of experiment (29 March to 11 April 2017). Error bars indicate standard errors.

1 week after release and for the duration of the experiment. At these sites, it was presumed that adults dispersed, died, or were preyed upon within the first week after release at these sites. No eggs were ever noted at these sites.

Pupal case counts during the mid-summer census (10 weeks following initial release) indicated that limited numbers of pupae were produced at sites with smaller initial population sizes (two to eight adults released). No pupae were produced at sites where initially two and four adults were released, and only one out of five sites where initially eight adults were released produced pupae (Fig. 2). At these sites with smaller initial population sizes, no pupae were produced, even though adult feeding and egg-laying were observed for several weeks (with the exception of the four sites where adults disappeared within the first week after release) (Fig. 1).

At the conclusion of the experiment (19 weeks following initial release), no pupae were found at 11 out of the 30 sites and these populations were deemed extinct. Although all initial population sizes produced pupae from at least one site (Fig. 2); all populations that went extinct were from releases of 16 adults or less. Initial population size was positively related to the probability of establishment and the statistical significance was confirmed by a logistic regression model ($X^2 = 17.122$; $P \leq 0.001$) (Fig. 3).

Per capita population growth rate

Per capita population growth rate ($\ln(N_1/N_0)$) was highly variable among sites, even among those with the same starting population size (Fig. 4). The statistical analysis indicated a significant quadratic relationship between population size and per capita population growth rate ($F_{2,23} = 3.60$; $P = 0.04$; Adj.$R^2 = 0.17$, AICc = 133.4) (Fig. 4). Thus, per capita population growth rate
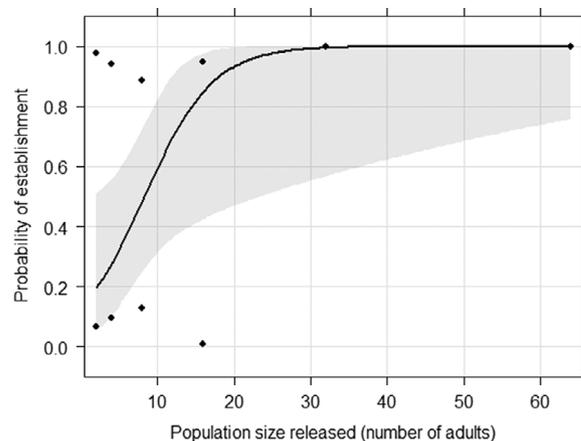
Fig. 3. The relationship between population size released and the probability of establishment of *Neolema ogloblini* at field sites (n = 30). The solid line represents values predicted from a logistic regression model. The shaded area is a pointwise confidence band for fitted values, based on standard errors computed from the covariance matrix of the fitted regression coefficients. Diamonds are partial residuals points.
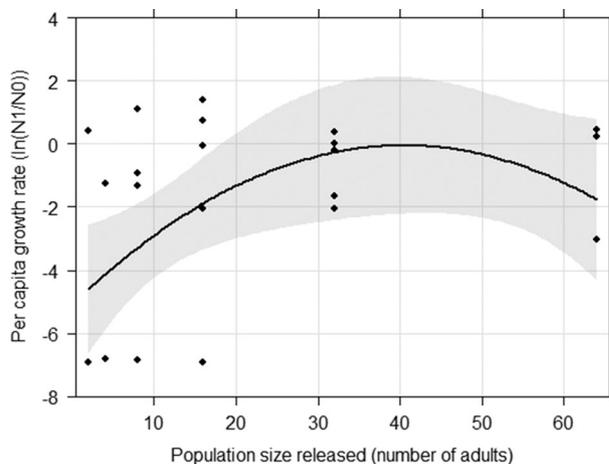
Fig. 4. The relationship between population size released and per capita growth rate ($\ln(N_1/N_0)$) of *Neolema ogloblini* at field sites. To take into consideration the influence of demographic stochasticity, only sites where adults (or their activities) were noted for more than 4 weeks after the initiation of the experiment were included in the analysis (n = 26). The shaded area is a pointwise confidence band for fitted values, based on standard errors computed from the covariance matrix of the fitted regression coefficients. Diamonds are partial residuals points.

initially increased as population size increased but decreased or levelled off at higher population levels (Fig. 4). A linear relationship between population size released and per capita growth rate provided a poorer model fit to the data ($F_{1,24} = 2.50$; $P = 0.13$; Adj.$R^2 = 0.06$, AICc = 135.1).

Discussion

In this study, we focussed on only one component of propagule pressure, that is population size during one introduction event,

and how it influences the probability of establishment and per capita population growth rate of introduced populations. Our results indicated that initial population size was positively associated with the probability of establishment of the model organism, *N. ogloblini*. This is consistent with other studies on propagule pressure as a predicator of establishment success (Cassey *et al.*, 2018a). In our study, although establishment occurred at all tested population sizes, smaller populations failed to establish more often. Our observations suggest that failed establishment was in some cases due to immediate dispersal or predation of adults (e.g. at the four sites where no signs of any adult activity (feeding and/or oviposition) were noted one week after release and for the duration of the experiment), while in other cases, failed establishment was due to a gradual decline in adult numbers and poor survival of offspring. The positive relationship between initial population size and probability of establishment suggests that demographic factors (stochasticity and Allee effects) influenced by population size or density, played a role in determining establishment (Lande, 1993; Grevstad, 1999a; Shaffer, 2006; Fauvergue *et al.*, 2012). In addition, the relationship between initial population size and probability of establishment was strong enough not to be entirely swamped by variability in density-independent environmental factors such as micro climate or other unknown influences.

Several other studies have used releases of biocontrol agents to investigate the relationship between population size released and establishment probability (Grevstad, 1999b; Memmott *et al.*, 2005; Paynter *et al.*, 2016). Paynter *et al.* (2016) analysed the influence of biological control agent release size on weed biocontrol programmes in New Zealand. Their results indicated that agents can be established from relatively small numbers (<500), but very small releases (<50) are likely to fail. Through experimental introductions of populations (2, 4, 10, 30, 90, and 270 adults) of a psyllid weed biocontrol agent *Arytainillaspartiophila* Förster, in New Zealand, Memmott *et al.* (2005) found the probability of establishment was significantly and positively related to initial release size. Similarly, Grevstad (1999b) introduced two species of chrysomelid beetles, *Galerucella calmariensis*(L.) and *G. pusilla* (Duftschmidt), into stands of purple loosestrife (*Lythrumsalicaria*L.) at four different population sizes (20, 60, 180, and 540) and monitored changes in population size over 3 years. For both *Galerucella* species, the probability of establishment increased with increasing number of individuals initially released (Grevstad, 1999b).

A further objective of our study was to investigate the existence of a demographic Allee effect by examining the relationship between population size released and per capita population growth rate. A demographic Allee effect is typically characterised by a hump-shaped relationship between population density and per capita population growth rate, wherein growth at low population density shows positive density dependence before transitioning to negative density dependence at a higher population density (Berec *et al.*, 2007; Courchamp *et al.*, 2008). Technically, ourexperiment did not allow for the exact estimation of the demographic Allee effect since populations could not be tracked for a full generation, however, the measurement of population numbers from adults to pupae nearly consists of a full generation and was deemed the more reliable estimate of the number of next generation adults. Our results indicated a hump-shaped relationship between per capita population growth rate and population size released, with a reduced per capita population growth rate at low population size, increasing as population size increased and reduced or levelling off at higher population size (Fig. 4), suggesting the presence of a demographic Allee effect in the experimental *N. ogloblini* populations. Likewise, Grevstad (1999b) investigated the relationship between release size and per capita growth rate of experimental populations of *G. calmariensis* and *G. pusilla*, and found per capita population growth rate increased with increasing release size, indicating the presence of a demographic Allee effect. In contrast, experimental introductions of psyllids provided no evidence of Allee effects (Memmott *et al.*, 2005). In established populations in our experiment, the per capita population growth rate varied considerably among sites for a given population size released, potentially due to both demographic and environmental stochasticity. Similarly, both Grevstad (1999b) and Memmott *et al.* (2005) reported strong variation in growth rate among sites, even for populations initiated with the same population sizes. In these two studies, environmental stochasticity seemed to play a major role in establishment success, either because the rate of catastrophic events was high (about 30% of release sites went extinct due to site destruction within the 5 years of study (Memmott *et al.*, 2005)), or because variance in population growth rate was not explained by population size (Grevstad, 1999b). Since initial population sizes were very low in our study, stochasticity may also mask Allee dynamics. Omitting 'extinct sites', where adults disappeared within the first 4 weeks from the statistical analysis, somewhat reduced the influence of stochasticity, but asignificant hump-shaped relationship was retained between per capita population growth rate and population size released. This cautiously supports the presence of a demographic Allee effect. As we could not completely separate the influence of stochasticity (environmental and demographic) from that of a demographic Allee effect in the data analysis, we conclude that extinction probability in the experimental populations of *N. ogloblini* was influenced by both a demographic Allee effect and stochasticity.

In our experiment, per capita population growth rate was either negative or generally low across the range of release sizes used. Studies have shown that habitat loss, habitat degradation, and habitat isolation may decrease population-carrying capacity, population growth rate, and survival (Fischer & Lindenmayer, 2007; Griffen & Drake, 2008; Heinrichs *et al.*, 2016).Griffen and Drake (2008) studied the effects of habitat size and quality on extinction time in experimental populations of *D. magna* and found that extinction risk is reduced by improving habitat quality or increasing habitat size. In our study, the quadratic relationship found between per capita population growth rate and population size (Fig. 4) suggests the presence of negative density dependence at higher population sizes, possibly as a result of competition. Therefore, limited patch size could have resulted in depleted resources, which prompted earlier emigration than what would have occurred at larger patch sizes, causing lower population sizes and overall lower per capita growth rates. It is, therefore, possible that the minimum patch size required to maintain populations throughout the duration of the experiment was considerably larger than what was provided

in the experiment. In the small patches used, the population size range between the Allee threshold and carrying capacity of the patch was very narrow and populations were easily tipped from a positive density dependent situation to a negative density situation. In its native range, patches of *T. fluminensis* are often small ($\leq 0.25\,m^2$) and ephemeral, and the plant has been found to virtually disappear from sites where it had been abundant in previous years (Fowler *et al.*, 2013). *Neolema ogloblini* may, therefore, be adapted to an ephemeral and patchy distribution of its host, but in our experiment no other host patches were available in the vicinity, therefore, any adult that dispersed away was effectively lost to the population, and, simultaneously, there was no opportunity for the 'rescue effect' through immigrating adults (Brown & Kodric-Brown, 1977).

The mechanism(s) driving the demographic Allee effect in small populations of *N. ogloblini* is unknown, but two candidate component Allee effects, generalist predation and mate-finding failure, may explain the positive effect of population size released on establishment probability and per capita growth rate.

While not quantified, the presence of spiders and predatory mites was frequently noted and predation on eggs and smaller instars (1st and 2nd) was often observed. Smaller populations, although continuously producing offspring, may not have been able to produce enough offspring to saturate generalist predators and allow at least some of the larvae to develop to the adult stage. In addition, the adult beetles themselves may be more vulnerable to predation while living in smaller populations, as the chance of an individual being captured by a predator decreases as group size increases (Turchin & Kareiva, 1989; Gascoigne & Lipcius, 2004). In our analysis to examine the relationship between population size released and per capita population growth rate, we did not include data on sites where adults disappeared within the first 4 weeks from the model. While this somewhat reduced the influence of demographic stochasticity, it may also have resulted in an underestimation of the impact of predation.

Another frequent cause of the Allee effect in small populations is the failure of mates to locate each other at low population densities (Gascoigne *et al.*, 2009; Kramer *et al.*, 2009; Yamanaka & Liebhold, 2009; Berec *et al.*, 2017). As a sexually reproducing organism, mate-finding failure could potentially be an additional component Allee effect that scales up to produce a demographic Allee effect in populations of *N. ogloblini*. But, as we did not specifically measure mating success in the current study, we could not attribute mate limitation to the measured differences in population growth rates. Further studies are needed to investigate possible interactive effects of generalist predation and mate-finding failure on the overall demographic Allee effect in populations of *N. ogloblini*.

Despite the potential for a strong Allee effect, success has been achieved with *N. ogloblini* as a biological control agent in New Zealand (Paynter, 2018). Establishment and subsequent spread have been confirmed at several sites, particularly at warmer North Island sites (Paynter, 2018). Perhaps this species has been successful because release sizes used (approximately 200 adults, L. Hayes, personal communication, June 2019) have been above the critical level where Allee effects adversely impact establishment. Although our study suggests that release sizes as low as 40 adults could potentially result in establishment, winter would likely reduce persistence to the next growing season. In addition, per capita growth rates of our field populations varied considerably among sites for a given population size released. Release sizes of at least 100 adults are therefore, recommended for biological control purposes. Establishment success will also depend on factors such as generalist predation levels and climatic suitability. Paynter (2018) reported at sites further south in New Zealand, cooler climatic conditions potentially reduced establishment probability. Cooler climatic conditions could potentially affect the number of generations produced per season, while generalist predation could reduce population growth rates. With slower population build-up, higher initial release sizes (or multiple releases) may be needed to ensure beetle establishment at cooler sites or sites with high predator levels.

Our study has demonstrated how propagule pressure, underpinned by processes such as Allee effects and stochasticity, influences establishment success. This supports the concept that experimental biological control releases have the potential to serve as a testing ground for studying the population ecology of invading species (e.g. Allee effects, propagule pressure, genetic diversity, dispersal, adaptation, etc.), as well as practical applications (e.g. detectability of incipient populations, management actions, etc.), and can ultimately aid in the management of biological invasions and improving biological control programmes (Ehler, 1998; Fagan *et al.*, 2002; Fauvergue *et al.*, 2012).

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Contributions of authors

Research was conceived and designed by all authors; HEW performed research and analysed data; and HEW wrote the manuscript with input from all authors.

Data availability statement

The data that support the findings of this study are openly available in Figshare (www.figshare.com) with the identifier DOI: 10.17608/k6.auckland.12609581

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