

Field manipulations of resources mediate the transition from intraspecific competition to facilitation

Karin Svanfeldt*, Keyne Monro and Dustin J. Marshall

Centre of Geometric Biology, School of Biological Sciences, Monash University, Clayton, Vic. 3800, Australia

Summary

1. Population density affects individual performance, though its effects are often mixed. For sessile species, increases in population density typically reduce performance. Still, cases of positive density-dependence do occur in sessile systems and demand explanation. The stress gradient hypothesis (SGH) predicts that under stressful conditions, positive effects of facilitation may outweigh the negative effects of competition.

2. While some elements of the SGH are well studied, its potential to explain intraspecific facilitation has received little attention. Further, there have been questions regarding whether the SGH holds if the stressor is a resource. Most studies of interactions between the environment and intraspecific facilitation have relied on natural environmental gradients; manipulative studies are much rarer.

3. To test the effects of intraspecific density and resources, we manipulated resource availability over natural population densities for the marine bryozoan *Watersipora subtorquata*.

4. We found negative effects of density on colony performance in low resource environments, but mainly positive density-dependence in high resource environments. By adding resources, competition effects were reduced and the positive effects of facilitation were revealed.

5. Our results suggest that resource availability mediates the relative strength of competition and facilitation in our system. We also suggest that intraspecific facilitation is more common than may be appreciated and that environmental variation may mediate the balance between negative and positive density-dependence.

Key-words: coexistence, density-dependence, flow, food, marine invertebrates, population density, SGH

Introduction

A fundamental tenet of ecology is that population density affects individual performance (Watkinson 1980; Damuth 1981; Lawton 1989; Gaston & Blackburn 2008; Silvertown & Charlesworth 2009). For sessile species, density-dependent effects are generally expected to be negative, with conspecific neighbours reducing each other's fitness as they compete for the same resource(s) (Antonovics & Levin 1980; Wilson 1983; Webb & Peart 1999). The negative effects of competition are thought to dominate density-dependent interactions across most taxa in sessile communities, but an increasing number of studies also find positive effects of increasing density (Dickie *et al.* 2005; Leslie 2005; García-Cervigón *et al.* 2013). Positive density-dependence can arise from facilitation, whereby

interactions between individuals benefit one or both of the contributors and are harmful to neither (Stachowicz 2001; Bruno, Stachowicz & Bertness 2003; Callaway 2007).

While the underlying mechanisms may be diverse, increasingly it seems that many systems experience some influence of both positive and negative density-dependence. For example, in birds, the local density of conspecific neighbours can either increase or decrease offspring survival, via increased chick protection from neighbouring parental birds, or chick mortality due to attacks by conspecific neighbours, respectively. If predation pressure is high, the benefits of high conspecific density outweighs the risks, and hence alters the density relationship between density-dependence and fitness (Ashbrook *et al.* 2010). Similarly in tropical tree communities, an increased density of interspecific species can increase the benefits of conspecifics, by decreasing the spread of species-specific herbivores and pests (Peters 2003). In

*Correspondence author. E-mail: karin.svanfeldt@monash.edu

many systems, however, the relative roles of facilitation and competition have traditionally been thought to be mediated by environmental stress.

The idea that environmental stress alters the balance between facilitation and competition has a long history in ecology, and continues to generate debate. An influential idea in this debate is the stress gradient hypothesis (SGH; Bertness & Callaway 1994), first developed for plants. The SGH predicts that the nature of interactions between organisms depends on environmental stress and consumer pressure (for reviews see Callaway 2007; Brooker *et al.* 2008), and most discussion and tests of the SGH have focused on interspecific interactions. In benign environments, the SGH maintains that the dominant force is competition for resources (Connell & Slatyer 1977) but in high stress environments, the benefits of facilitation from habitat amelioration or resource enrichment outweigh the negative effects of competition (Holzapfel & Mahall 1999; Maestre, Bautista & Cortina 2003).

While the SGH was initially formulated for interspecific interactions (Bertness & Callaway 1994; Callaway & Walker 1997), its predictions are equally relevant to intraspecific interactions among plants (Watkinson 1980; Holzapfel & Mahall 1999; Sthultz, Gehring & Whitham 2007; Silvertown & Charlesworth 2009; Soliveres *et al.* 2010; García-Cervigón *et al.* 2013) and sessile invertebrates (Bertness 1989; Leslie 2005). For example, 'nurse' plants can facilitate the establishment of conspecific seedlings during stressful periods (Kitzberger, Steinaker & Veblen 2000; Dickie *et al.* 2005), and barnacle populations can experience either positive- or negative density-dependence across the intertidal zone depending on stress levels (Leslie 2005).

While most SGH studies have focused on non-resource related stressors such as temperature or soil structure (Callaway & Walker 1997; Miriti 2006; Wang *et al.* 2008), Maestre *et al.* (2009) refined the SGH to include variation in interactions when the stressor is a resource such as water, oxygen or food. Their predictions regarding resource-related stressors suggest that for facilitation to occur, neighbours must directly increase the availability of the resource. Okamura (1988) showed that for the encrusting bryozoan *Electra pilosa*, feeding success was increased in high interspecific densities in environments with high flow. If the flow was low, however, interspecific competition decreased the feeding success. The results from Okamura's study stand out from other studies exploring facilitation in the way that they explore resource availability (flow rate) rather than non-resource related stress and density-dependence (Leslie 2005; Goldenheim, Irving & Bertness 2008; Fajardo & McIntire 2011; McIntire & Fajardo 2011).

Important gaps in our understanding of how the environment alters the strength and direction of density-dependence remain. First, few field studies have directly manipulated environmental conditions: rather, natural environmental gradients have been used to explore how

the environment affects intraspecific density-dependence (but see Hart & Marshall 2012). Second, it is unclear whether the SGH applies to intraspecific interactions when the stressor is resource-based (Maestre *et al.* 2009). Here, in a field experiment, we manipulated resource availability and density for the marine encrusting bryozoan, *Watersipora subtorquata* (henceforth referred to as *Watersipora*). Previous studies on this species have shown that neighbouring conspecifics compete for waterborne resources and typically display negative density-dependence (Hart & Marshall 2012). The general assumption for sessile marine species such as *Watersipora*, is that neighbouring individuals compete almost solely for space (Connell 1961; Smally 1984; Bertness 1989). However, recent studies show that even when space is not limiting, sessile individuals compete via non-contact competition for both waterborne food and oxygen (Okamura 1988; Kim & Lasker 1997; Wildish & Kristmanson 2005; Ferguson, White & Marshall 2013; Svensson & Marshall 2015; Thompson, Marshall & Monro 2015). Thus, resource availability for sessile marine species is strongly determined by local flow regimes (Lesser, Witman & Sebnens 1994; Leichter & Witman 1997).

In this study, rather than indirectly testing resource effects on density-dependence along a natural gradient, we orthogonally manipulated two key resources (food and flow) directly. Specifically, we added food to the direct surroundings of colonies growing in various densities using a newly developed experimental technique (Svensson & Marshall 2015), and we obstructed the flow in the direct surroundings of the colonies by baffling the water around our experimental populations, and tested how these manipulations affected density-dependent performance in the field. We used two levels of each resource manipulation (rather than a gradient) because we sought to explore extreme differences in resource availability as a necessary first step to examining functional responses in density-dependence. In contrast to the classic predictions of the SGH, where high stress environments amplifies the role of facilitation, we hypothesised that with resource availability as stressor, reducing stress (by adding resources) would increase the visible effects of facilitation by reducing the effects of competition. We predicted that when resources were scarce, the interactions between neighbouring individuals would be dominated by competition, and density-dependence would be negative. If resources were abundant, however, we expected the effects of competition to diminish. If competition is ameliorated by resource addition, then we expected one of three possibilities: (i) reduced negative density-dependence such that increasing conspecific density reduced performance less strongly in high resource conditions; (ii) the removal of density-dependence effects under high resource conditions; or (iii) a positive relationship between density and performance under higher resource conditions because facilitative effects were unmasked by the addition of resources.

Materials and methods

STUDY SPECIES AND SITE

Our trials were carried out during summer at Royal Brighton Yacht Club, Port Phillip Bay, Australia (37°54'29.9"S 144°58'52.4"E). Water flow within the marina is around 1 cm s^{-1} , and supports a diverse benthic marine sessile community. We chose *Watersipora* as our study organism because it is an easily-accessible species with a relatively well-known and trackable life history. *Watersipora* is a bright red, colonial filter feeder commonly found year-round on hard substrates in the marina. *Watersipora* is a cosmopolitan invader and is considered invasive in most sheltered subtidal areas around temperate regions of the world, including the southern coast of Australia (Hewitt *et al.* 2004). New *Watersipora* colonies are formed by sexual reproduction and the subsequent release of free-swimming larvae into the water column. Once settled, each larva undergoes metamorphosis and forms the first feeding unit of the colony, the ancestrula zooid. Circular bands of feeding zooids (each capable of sexual reproduction upon maturity) then bud outwards from the ancestrula to form the colony. The colony has a shared resource economy, whereby energy from food consumption is distributed through porous cell walls between zooids. New growth occurs at the colony margin. With time, the zooids in the centre of the colony, starting from the ancestrula, lose colour and irreversibly senesce. Zooid senescence is visible as the appearance of a grey inner circle of dead zooids that expands as the colony grows (Hart & Keough 2009; Marshall & Monro 2013). It is debatable if new growth zones can form inwards once senesced zooids are lost due to fragmentation (however this was not observed in our study). In our system, despite being a common member of early successional assemblages, *Watersipora* is a subordinate competitor for space, often overgrown by other encrusting species such as colonial ascidians and sponges. Nevertheless *Watersipora* persists (albeit at much smaller sizes) in quite late-stage communities.

MANIPULATING RESOURCE AVAILABILITY

Watersipora is sessile and filters resources such as food (plankton) and oxygen from the surrounding water. The availability of food and other resources therefore depends on a number of factors: the direct density of resources in the water, the flow rate (more resources per time unit pass feeding structures in higher than lower flow rates), the density of competing neighbours, and the effect of self-shading (the blocking effect of resource capture to zooids at the centre of the colony by zooids growing on the margins) related to colony size. Therefore, we manipulated food availability and flow rate in the field for experimental populations of *Watersipora* colonies at different densities and monitored the growth and senescence of a single, focal colony within each experimental population. We had two levels for each factor: additional food or no additional food, and un-obstructed or obstructed flow. We then crossed the two resource levels over a range of naturally occurring conspecific densities.

To test the effects of food and flow alterations on density in the field, we varied all three factors in an orthogonal design. PVC backing panels, each holding eight $10 \times 10 \text{ cm}$ PVC settling plates with pre-roughened acetate sheets, were horizontally submerged using ropes and wire with the settling plates facing down at 1.5 m

depth along the protected side of a wave-breaking floating attenuator in the field. To manipulate food, we used a technique developed by Svensson & Marshall (2015). Slow-releasing food blocks (30 mL) were created by mixing Reef Phytoplankton (Seachem, Madison, GA, USA) and NutraPlus Reef Feed (Nutra-Kol, Mullaloo, Australia) with Gyprock dental plaster (CSR, North Ryde, BC, Australia) on a ratio of 7 : 7 : 6 respectively. Manipulating food in this manner increases the growth of some sessile marine invertebrates and can reduce the intensity of intraspecific competition (Svensson & Marshall 2015). We made controls by replacing the commercial feed preparations with water (as per Svensson & Marshall 2015). Both food blocks and control blocks were replaced fortnightly. On average, we released $4.6 \times 10^5 \pm 4.9 \times 10^4$ additional food particles (plankton cells) per food block to the direct close environment of our colonies. To manipulate flow, $10 \times 10 \times 5 \text{ cm}$ open-ended PVC boxes surrounded the settlement plates. With the openings facing downwards, the boxes efficiently obstructed the directional flow rate without further affecting access to the surrounding water. Controls for the flow manipulation were open plates, where natural conditions of the site exposed the plates to slow (1 cm s^{-1}) and mainly directional flow from the in- and out-lets of currents through the constructions of the marina. These constructions, in combination with the depth at which we hung the experimental panels, minimised exposure to wave turbulence for plates in both flow treatments. What we created were extremes in environmental conditions that overlap with those experienced naturally by *Watersipora*. In Port Phillip Bay, the natural flow rate at our field site varies from 0.1 to 2.5 cm s^{-1} (Lagos, White & Marshall 2016), and food availability (habitat quality) varies strongly with depth (Lange, Monro & Marshall 2016).

FIELD SET-UP

We created four different treatments: high food – high flow, high food – low flow, low food – high flow, and low food – low flow, with two replicates of each treatment on each panel (8 plates per panel, spread across 20 panels). This resulted in 40 replicates of plates per treatment. Cages attached to the plates held either slow-releasing food blocks (high food) or control plaster blocks (low food). Within each food treatment, half of the plates received the low flow treatment and half received the high flow treatment. In total, we deployed two runs with 10 panels per run (20 panels in total with 8 plates per panel), and with one week's time difference between each run. Before deployment, we used natural variation in the settlement densities of *Watersipora* settlers by leaving empty settlement plates in the field for 1 week. A variety of juvenile invertebrates settled on each plate, so all but *Watersipora* settlers were scraped off. This resulted in a range of densities from one to nine settlers per plate. The plates were thereafter haphazardly allocated to our treatments, and thus our initial densities varied independently of our treatments. By creating our experimental populations before we assigned them to treatments, we effectively controlled for confounding effects of potential differences in initial size or settling density across our treatments – on average all conspecific densities and initial sizes were equal among treatments. Once the experimental populations were established and allocated to their environmental treatments, all new settlers (*Watersipora* or otherwise) were removed weekly. In each experimental population, one *Watersipora* was haphazardly designated as the focal colony and the rest were designated non-focal colonies. We took photographs of the focal colony weekly for 13 weeks, and size was estimated using ImageJ software

(available at <http://imagej.net>). For each focal colony we made weekly estimates of colony size (colony area) and the percentage of the colony that had undergone senescence as per established methods for this species (see Marshall & Monro 2013 for details). Additionally, we aimed to estimate fecundity by monitoring the production of ovicells; however our colonies did not reach sexual maturity during the experimental period. We also monitored the survival of the non-focal colonies to determine whether survival of non-focal colonies differed across treatments over time.

STATISTICAL ANALYSES

To estimate the effects of food availability, flow rate, intraspecific density and time on absolute colony area and senescence, we used repeated linear mixed-effect models (fitted using maximum likelihood) from weeks 1 to 11 for our estimates of colony area, and from weeks 5 to 11 for our estimates of senesced area percentage (excluding weeks 3 and 10 for both colony area and the senescence datasets where measurements were missing). For the parameter 'density', we used estimates of colony numbers per plate at week 0 (before the plates were assigned to the treatments). Given that densities at this stage were randomly assigned to our treatments, we believe this is the most appropriate predictor to use in the analysis. However, to account for mortality amongst colonies on the same plate over time, we performed a mixed model *F*-test to estimate the potential effects of initial density, food, flow, time and their interactions on the survival of non-focal colonies over time (we found no effects, see results). The number of non-focal colonies over time was only estimated at weeks 2, 6, 8 and 11 and therefore, our repeated measure for this test is limited to those time points. A previous study on *Watersipora*, showed that analysing relative growth rates and the absolute size of colonies yield qualitatively similar results. Since we had no initial size differences in our settlers among treatments, and because absolute size is a better measure of fitness, we therefore used absolute size as performance measure for colony area, which we present in our results section. Importantly, we also analysed relative growth and found qualitatively similar results (unpublished analyses). In all of our models, food, flow, density and time were modelled as fixed effects (categorical, categorical, continuous and continuous, respectively)

and panel was modelled as random effect. Since run only had two levels, it was excluded from the analysis (any differences among runs, however, were accounted for by panel effects). To be able to analyse the effects on our response variables over time, we standardised the variation of our predictors (survival, senescence and colony area) for each week to 1 (mean = 0, SD = 1). As the random effects were simply experimental conveniences, we reduced the models according to Quinn & Keough (2002) to test for random slopes, using standard likelihood-ratio tests based on chi-square distributions. We performed model reductions in a hierarchical fashion, where higher order interactions were removed prior to lower order interactions. In this way, all interactions were evaluated before the main effects were tested. The response variables were mean colony size and senescence per plate, as these were the units of replication and the scale at which the treatments were applied. All analyses were run in SAS 9.4 software (SAS Institute Inc., Cary, NC, USA).

Results

We found no effects of initial density, food, flow or density on non-focal survival over time (see Table 1). However, we did see an effect of time (week) on non-focal survival; mortality increased with time. In addition, we found that the effects on both colony size and senescence in all environments varied by panel (spatial arrangement, Fig. 1), but these spatial effects did not interact with our treatments of interest.

We found an interaction between food, flow and density on colony area of *Watersipora* in the field, and this interaction did not vary over time (*Density* × *Food* × *Flow*: $\chi^2 = 3.8$, $P = 0.05$, Fig. 1, for complete final model, see Table 2). Though the three-way interaction of food, flow and density did not vary over time, food and flow interacted with time, as did density and food, and density and flow (*Time* × *Food* × *Flow*: $\chi^2 = 6.0$, $P = 0.01$, *Time* × *Density* × *Food*: $\chi^2 = 7.9$, $P < 0.001$, *Time* × *Density* × *Flow*: $\chi^2 = 5.6$, $P = 0.02$).

Table 1. *F*-test for the parameters time, density, food and flow on the survival percentage of non-focal colonies per plate over time from weeks 1 to 11 for *Watersipora* colonies in the field. All significant effects are presented in bold

Type 3 tests of fixed effects, survival % of non-focal colonies per plate

Effect	Numerator	Denominator	Chi	<i>F</i>	<i>P</i>
Density × Food × Flow × Time	3	559	0.53	0.18	0.91
Density × Food × Time	3	559	0.20	0.07	0.98
Density × Flow × Time	3	559	0.31	0.10	0.96
Food × Flow × Time	3	559	0.85	0.28	0.84
Density × Food × Flow	1	559	0.33	0.33	0.56
Density × Time	3	559	0.32	0.11	0.96
Food × Time	3	559	0.27	0.09	0.97
Flow × Time	3	559	0.16	0.05	0.98
Density × Food	1	559	0.51	0.51	0.48
Density × Flow	1	559	1.26	1.26	0.26
Food × Flow	1	559	0.64	0.64	0.43
Time	3	559	31.18	10.39	< 0.0001
Density	1	559	1.25	1.25	0.26
Food	1	559	2.07	2.07	0.15
Flow	1	559	1.16	1.16	0.28

Fig. 1. Model estimates of the relationship between absolute colony area, food availability, flow rate and initial intraspecific density for *Watersipora* colonies at the latest stage of the experimental trial, at week 11 in the field, with variation due to uncorrelated effects of the experimental panels the *Watersipora* colonies were deployed on. The estimates are presented for each of the four environments of food and flow combinations: high food, low flow (a and b), low food (c and d), high flow (a and c) and low flow (b and d). Lines of best fit for each environment is shown in black and bold, and coloured surrounding lines shows model variations due to the random effect of panel.

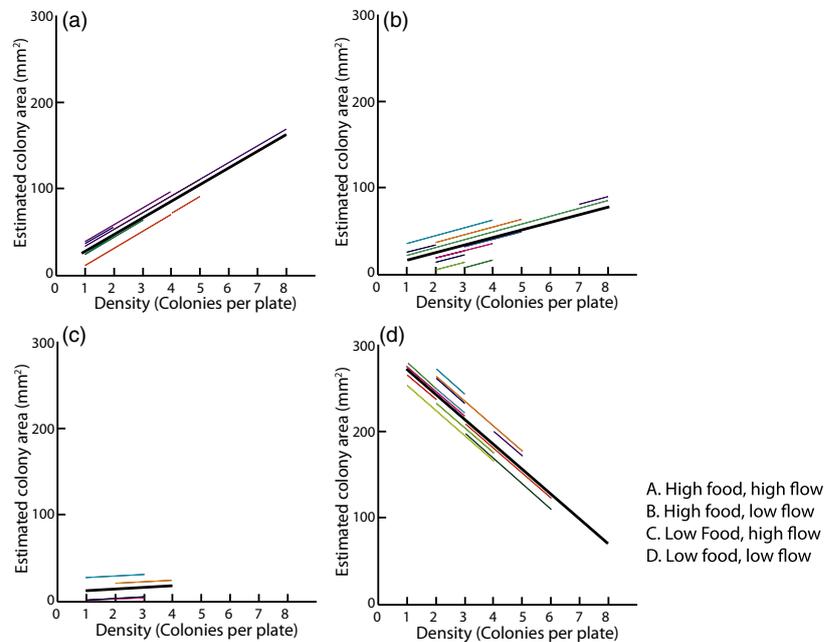


Table 2. Final model and interactions removed from the model for the effects of time, density, food and flow on colony area for *Watersipora* colonies from weeks 1 to 11 in the field. All significant effects are shown in bold

Colony area					
Final model	Chi	<i>P</i>	Interactions removed	Chi	<i>P</i>
Panel	22.6	0.00	Time × Density × Food × Flow	1.6	0.21
Time × Density × Food	7.9	0.00			
Time × Density × Flow	5.6	0.02			
Time × Food × Flow	6	0.01			
Density × Food × Flow	3.8	0.05			
Time × Density	22.1	0.00			
Time × Food	10.4	0.00			
Time × Flow	22.0	0.00			
Density × Food	52.3	0.00			
Density × Flow	3.2	0.07			
Food × Flow	10.5	0.00			
Time	4175.7	0.05			
Density	4.0	0.00			
Food	21.7	0.00			
Flow	39.8	0.00			

For colonies in all environments, colony area increased with time. Exploring the three-way interaction of food, flow and density, we found that increased conspecific density reduced focal colony size in the low food, low flow environment, but the relationship between focal colony size and conspecific density tended to be positive in higher resource environments. In the environment where food availability was low but flow rate was high, colony area was unaffected by the neighbour density, though the range of densities was limited to four colonies per plate, rather than eight as was the maximal number of colonies per plate for all other treatments (due to haphazardly distributed plates with natural settlement to the treatments).

In both environments where food availability was high, focal colony size was positively related to conspecific density, regardless of flow regime.

For percentage of colony senescence from week 5 to 11 in the field, we found an interaction of density and food, and this effect did vary with time (*Time × Density × Food*: $\chi^2 = 4.8$, $P = 0.03$, Fig. 2, for final model, see Table 3). When food availability was low, the percentage of colony senescence did not vary with density. When the food availability was high, however, the senescence percentage of our colonies decreased with intraspecific density. For all colonies, the percentage of colony senescence increased with time.

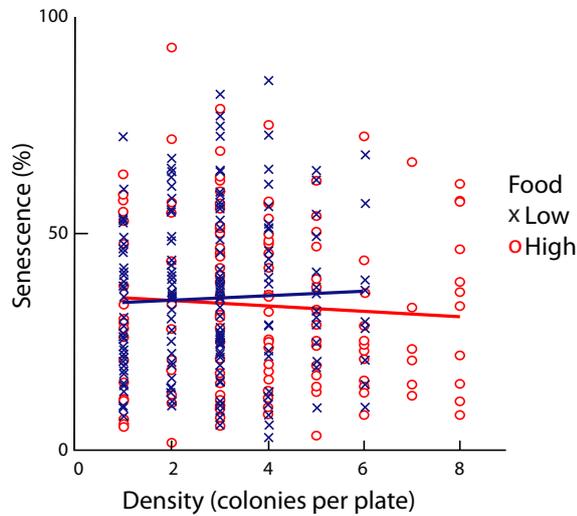


Fig. 2. Relationship between colony senescence percentage, food availability (high or low), and intraspecific density for *Watersipora* colonies from weeks 5 to 11 in the field. Colonies that experienced low food conditions are shown in blue and colonies that experienced high food conditions are shown in red. Note that each point represents an individual colony and lines represent the line of best fit for that treatment combination.

Discussion

Overall, we found evidence that both facilitation and competition operate simultaneously in our system, and that resource availability alters the balance between the two. When resources were abundant, facilitation dominated, but when resources were scarce, competition dominated. In the environment where both food availability and flow rate were low, performance declined with density. In the environment where food was low but flow rate was high, density had no effect on performance. In both environments with added food however, performance

increased with density, indicating that facilitation exceeded the effects of competition. It also appeared that colonies grew more in low flow compared to high flow environments. In addition, in environments with no competitors (density 1), colonies were smaller when food availability was high than when the availability of food was low, which may indicate specialisation towards low resource environments for this species. Whereas colony senescence did not change across densities in the low food environment, the percentage of colony senescence for colonies in the high food environment decreased with density. When no competitors were present, at density 1, the percentage of colony senescence was also marginally higher in the high food environment than in the low food environment. The lower growth and higher senescence rate in low densities under high food environments are puzzling. Our expectations were quite the reverse – namely, that higher food availabilities would increase performance. One possible explanation may be a higher allocation for sexual reproduction, at the expense of colony size, for colonies in the high food environments. However, no colonies in our trials had reached sexual maturity in the space of 13 weeks when the trials concluded. Another explanation may be higher investment in calcification for defence at the expense of size.

The effects of resource availability on colony area and senescence with density varied through time, but there were some consistent signals. With the addition of resources, previously undetected facilitation effects were revealed. When stress is non-resource related, the SGH predicts that high stress environments promote facilitation between neighbours, whereas benign environments promote competition (Bertness & Callaway 1994). Maestre *et al.* (2009) introduced the exception of resource-related stress, where the interactions between neighbours may not follow the predictions of SGH. Our results suggest that altering resources in a population can mediate the

Table 3. Final model and interactions removed from the model for the effects of time, density, food and flow on colony senescence percentage for *Watersipora* colonies from weeks 1 to 11 in the field. All significant effects are shown in bold

Colony senescence %					
Final model	Chi	<i>P</i>	Interactions removed	Chi	<i>P</i>
Panel	22.0	0.00	Time × Density × Food × Flow	3.3	0.07
Time × Density × Food	4.8	0.03	Density × Food × Flow	0.1	0.75
Time × Density × Flow	6.4	0.01			
Time × Food × Flow	5.7	0.02			
Time × Density	2.1	0.15			
Time × Food	4.3	0.04			
Time × Flow	0.4	0.53			
Density × Food	5.0	0.03			
Density × Flow	0.4	0.53			
Food × Flow	0.6	0.44			
Time	1611.5	0.44			
Density	0.6	1.00			
Food	0.0	0.37			
Flow	0.8	0.00			

competition-facilitation balance by suppressing the competition between neighbouring individuals, and thereby reveal facilitative interactions. In such scenarios, competition between neighbours dominates low resource environments (e.g. high resource-related stress) while in high resource environments (e.g. low resource-related stress), neighbours will no longer be affected by competition. If there are no benefits of neighbours, the interaction in a high resource environment would then be neutral. If there are benefits of neighbours, however, these positive interactions would dominate in high resource environments. Our results indicate the latter scenario, demonstrating a beneficial interaction between *Watersipora* individuals that becomes visible in the absence of competition.

However, the interactions in our study only describes those between *Watersipora* colonies in artificial monoculture communities. These conditions, where only *Watersipora* settlers are present in isolation from other species, may apply in the field in early stage communities if *Watersipora* settlers are the primary recruits before other species have had the opportunity to colonise the habitat, and also before contact competition (space limitations) becomes prominent. In other field scenarios, however, the presence of additional species is likely to alter both the direction and magnitude of the interactions we observed. Svensson & Marshall (2015) found that when they added the same food as used in our trials to a mixed species community, most species benefitted and grew significantly larger than in their control treatment. However, in the same study, the growth of *Watersipora* decreased with the addition of food, likely because of the increased interspecific competition pressure.

The mechanism behind facilitation is unclear. Our results indicated that *Watersipora* generally performs better in low-flow environments. It is possible that the slightly disruptive structures of neighbouring conspecific colonies on the smooth settlement substrate decreased local flows and enhanced performance (Sebens 1991), possibly by increasing filtration efficiency (Okamura 1985; Vogel 1996). In line with our results, other studies have shown that bryozoans facilitate filtration by reducing the proportion of water that is refiltered (Pratt 2004), while faster flow rates reduce feeding efficiency for some species (depending on colony size, Okamura 1985). Encrusting species may burn more energy on feeding attempts in higher flow rates, while actual feeding success and thus growth rate and performance may be greater in low flow rates, somewhat explaining the preference for low flow in our species (Okamura 1988). It is also possible that *Watersipora* colonies create a preferable microhabitat that enhances the conditions for conspecific neighbours. These positive density-dependent effects may play a crucial role for the invasion success of *Watersipora* (Taylor & Hastings 2004).

Regardless of the reason behind the facilitation that we have observed, the results of our study show that the abundance of resources alters the balanced relationship

between competition and facilitation at a population level. With this study, we have shown that the balance between competition and facilitation at a population level can be shaped not only by stressors, such as temperature or salinity, but also by resource availability as discussed by Maestre *et al.* (2009). By directly manipulating resource availability, we demonstrate its role in determining the balance of competition and facilitation in our system. Our results add weight to earlier studies that found the role of intraspecific facilitation to vary across environmental gradients (Leslie 2005; Goldenheim, Irving & Bertness 2008; Fajardo & McIntire 2011; McIntire & Fajardo 2011). With our results, we present further evidence for the importance of acknowledging the impacts of both competition and facilitation and how the balance between the two affects interactions within and between populations.

Acknowledgements

We thank Matthew L. Thompson and Henry Wootton for field and technical assistance, Amanda Pettersen and Marie Hennriksen for illustrating assistance, Annie Guillaume for proof reading, Royal Brighton Yacht Club for access to the field site, and the Australian Research Council's Discovery Scheme for funding.

Data accessibility

The data from this study are available online from the Dryad Digital Repository <https://doi.org/10.5061/dryad.sc4s4> (Svanfeldt, Monro & Marshall 2017).

References

- Antonovics, J. & Levin, D.A. (1980) The ecological and genetic consequences of density-dependent regulation in plants. *Annual Review of Ecology and Systematics*, **11**, 411–452.
- Ashbrook, K., Wanless, S., Harris, M.P. & Hamer, K.C. (2010) Impacts of poor food availability on positive density dependence in a highly colonial seabird. *Proceedings of the Royal Society of London B: Biological Sciences*, **277**, 2355–2360.
- Bertness, M.D. (1989) Intraspecific competition and facilitation in a northern acorn barnacle population. *Ecology*, **70**, 257–268.
- Bertness, M.D. & Callaway, R. (1994) Positive interactions in communities. *Trends in Ecology & Evolution*, **9**, 191–193.
- Brooker, R.W., Maestre, F.T., Callaway, R.M. *et al.* (2008) Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology*, **96**, 18–34.
- Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. (2003) Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution*, **18**, 119–125.
- Callaway, R.M. (2007) *Interaction Between Competition and Facilitation*. Springer, Dordrecht, the Netherlands.
- Callaway, R.M. & Walker, L.R. (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*, **78**, 1958–1965.
- Connell, J.H. (1961) Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecological Monographs*, **31**, 61–104.
- Connell, J.H. & Slatyer, R.O. (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist*, **111**, 1119–1144.
- Damuth, J. (1981) Population density and body size in mammals. *Nature*, **290**, 699–700.
- Dickie, I.A., Schnitzer, S.A., Reich, P.B. & Hobbie, S.E. (2005) Spatially disjunct effects of co-occurring competition and facilitation. *Ecology Letters*, **8**, 1191–1200.
- Fajardo, A. & McIntire, E.J. (2011) Under strong niche overlap conspecifics do not compete but help each other to survive: facilitation at the intraspecific level. *Journal of Ecology*, **99**, 642–650.

- Ferguson, N., White, C.R. & Marshall, D.J. (2013) Competition in benthic marine invertebrates: the unrecognized role of exploitative competition for oxygen. *Ecology*, **94**, 126–135.
- García-Cervigón, A.I., Gazol, A., Sanz, V., Camarero, J.J. & Olano, J.M. (2013) Intraspecific competition replaces interspecific facilitation as abiotic stress decreases: the shifting nature of plant–plant interactions. *Perspectives in Plant Ecology, Evolution and Systematics*, **15**, 226–236.
- Gaston, K. & Blackburn, T. (2008) *Pattern and Process in Macroecology*. John Wiley & Sons, Oxford, UK.
- Goldenheim, W.M., Irving, A.D. & Bertness, M.D. (2008) Switching from negative to positive density-dependence among populations of a cobble beach plant. *Oecologia*, **158**, 473–483.
- Hart, S.P. & Keough, M.J. (2009) Does size predict demographic fate? Modular demography and constraints on growth determine response to decreases in size. *Ecology*, **90**, 1670–1678.
- Hart, S.P. & Marshall, D.J. (2012) Advantages and disadvantages of interference-competitive ability and resource-use efficiency when invading established communities. *Oikos*, **121**, 396–402.
- Hewitt, C.L., Campbell, M.L., Thresher, R.E. *et al.* (2004) Introduced and cryptogenic species in Port Phillip Bay, Victoria, Australia. *Marine Biology*, **144**, 183–202.
- Holzappel, C. & Mahall, B.E. (1999) Bidirectional facilitation and interference between shrubs and annuals in the Mojave Desert. *Ecology*, **80**, 1747–1761.
- Kim, K. & Lasker, H.R. (1997) Flow-mediated resource competition in the suspension feeding gorgonian *Plexaura homomalla* (Esper). *Journal of Experimental Marine Biology and Ecology*, **215**, 49–64.
- Kitzberger, T., Steinaker, D.F. & Veblen, T.T. (2000) Effects of climatic variability on facilitation of tree establishment in northern Patagonia. *Ecology*, **81**, 1914–1924.
- Lagos, M.E., White, C.R. & Marshall, D.J. (2016) Biofilm history and oxygen availability interact to affect habitat selection in a marine invertebrate. *Biofouling*, **32**, 645–655.
- Lange, R., Monro, K. & Marshall, D. (2016) Environment-dependent variation in selection on life history across small spatial scales. *Evolution*, **70**, 2404–2410.
- Lawton, J.H. (1989) What is the relationship between population density and body size in animals? *Oikos*, **55**, 429–434.
- Leichter, J.J. & Witman, J.D. (1997) Water flow over subtidal rock walls: relation to distributions and growth rates of sessile suspension feeders in the gulf of Maine water flow and growth rates. *Journal of Experimental Marine Biology and Ecology*, **209**, 293–307.
- Leslie, H.M. (2005) Positive intraspecific effects trump negative effects in high-density barnacle aggregations. *Ecology*, **86**, 2716–2725.
- Lesser, M.P., Witman, J.D. & Sebens, K. (1994) Effects of flow and seton availability on scope for growth of benthic suspension-feeding invertebrates from the Gulf of Maine. *The Biological Bulletin*, **187**, 319–335.
- Maestre, F.T., Bautista, S. & Cortina, J. (2003) Positive, negative, and net effects in grass-shrub interactions in Mediterranean semiarid grasslands. *Ecology*, **84**, 3186–3197.
- Maestre, F.T., Callaway, R.M., Valladares, F. & Lortie, C.J. (2009) Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, **97**, 199–205.
- Marshall, D.J. & Monro, K. (2013) Interspecific competition alters nonlinear selection on offspring size in the field. *Evolution*, **67**, 328–337.
- McIntire, E.J. & Fajardo, A. (2011) Facilitation within species: a possible origin of group-selected superorganisms. *The American Naturalist*, **178**, 88–97.
- Miriti, M.N. (2006) Ontogenetic shift from facilitation to competition in a desert shrub. *Journal of Ecology*, **94**, 973–979.
- Okamura, B. (1985) The effects of ambient flow velocity, colony size, and upstream colonies on the feeding success of Bryozoa. II. *Conopeum reticulum* (Linnaeus), an encrusting species. *Journal of Experimental Marine Biology and Ecology*, **89**, 69–80.
- Okamura, B. (1988) The influence of neighbors on the feeding of an epifaunal bryozoan. *Journal of Experimental Marine Biology and Ecology*, **120**, 105–123.
- Peters, H.A. (2003) Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. *Ecology Letters*, **6**, 757–765.
- Pratt, M.C. (2004) Effect of zooid spacing on bryozoan feeding success: is competition or facilitation more important? *The Biological Bulletin*, **207**, 17–27.
- Quinn, G.P. & Keough, M.J. (2002) *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge, UK.
- Sebens, K.P. (1991) Habitat structure and community dynamics in marine benthic systems. *Habitat Structure: The Physical Arrangement of Objects in Space* (eds S.S. Bell, E.D. McCoy & H.R. Mushinsky), pp. 211–234. Chapman and Hall, New York, NY, USA.
- Silvertown, J. & Charlesworth, D. (2009) *Introduction to Plant Population Biology*. John Wiley & Sons, Carlton, Australia.
- Smally, T. (1984) Possible effects of intraspecific competition on the population structure of a solitary vermetid mollusc. *Marine Ecology Progress Series*, **Oldendorf**, **14**, 139–144.
- Soliveres, S., DeSoto, L., Maestre, F. & Olano, J. (2010) Spatio-temporal heterogeneity in abiotic factors modulate multiple ontogenetic shifts between competition and facilitation. *Perspectives in Plant Ecology, Evolution and Systematics*, **12**, 227–234.
- Stachowicz, J.J. (2001) Mutualism, facilitation, and the structure of ecological communities positive interactions play a critical, but underappreciated, role in ecological communities by reducing physical or biotic stresses in existing habitats and by creating new habitats on which many species depend. *BioScience*, **51**, 235–246.
- Stultz, C.M., Gehring, C.A. & Whitham, T.G. (2007) Shifts from competition to facilitation between a foundation tree and a pioneer shrub across spatial and temporal scales in a semiarid woodland. *New Phytologist*, **173**, 135–145.
- Svanfeldt, K., Monro, K. & Marshall, D.J. (2017) Data from: Field manipulations of resources mediate the transition from intraspecific competition to facilitation. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.sc4s4>
- Svensson, J.R. & Marshall, D.J. (2015) Limiting resources in sessile systems: food enhances diversity and growth of suspension feeders despite available space. *Ecology*, **96**, 819–827.
- Taylor, C.M. & Hastings, A. (2004) Finding optimal control strategies for invasive species: a density-structured model for *Spartina alterniflora*. *Journal of Applied Ecology*, **41**, 1049–1057.
- Thompson, M.L., Marshall, D.J. & Monro, K. (2015) Non-contact competition in a sessile marine invertebrate: causes and consequences. *Marine Ecology Progress Series*, **522**, 115–125.
- Vogel, S. (1996) *Life in Moving Fluids: The Physical Biology of Flow*. Princeton University Press, Princeton, NJ, USA.
- Wang, Y., Chu, C., Maestre, F.T. & Wang, G. (2008) On the relevance of facilitation in alpine meadow communities: an experimental assessment with multiple species differing in their ecological optimum. *Acta Oecologica*, **33**, 108–113.
- Watkinson, A. (1980) Density-dependence in single-species populations of plants. *Journal of Theoretical Biology*, **83**, 345–357.
- Webb, C.O. & Peart, D.R. (1999) Seedling density dependence promotes coexistence of Bornean rain forest trees. *Ecology*, **80**, 2006–2017.
- Wildish, D. & Kristmanson, D. (2005) *Benthic Suspension Feeders and Flow*. Cambridge University Press, Cambridge, UK.
- Wilson, W.H. Jr. (1983) The role of density dependence in a marine infaunal community. *Ecology*, **64**, 295–306.

Received 10 August 2016; accepted 17 January 2017
 Handling Editor: Peter Hambäck