Resources mediate selection on module longevity in the field

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Abstract

The life histories of modular organisms are complicated, where selection and optimization can occur at both organismal and modular levels. At a modular level, growth, reproduction and death can occur in one module, independently of others. Across modular groups, there are no formal investigations of selection on module longevity. We used two field experiments to test whether selection acts on module longevity in a sessile marine invertebrate and whether selection varies across successional gradients and resource regimes. We found that selection does act on module longevity and that the strength of selection varies with environmental conditions. In environments where interspecific competition is high, selection favours colonies with longer zooid (module) longevity for colonies that initially received high levels of maternal investment. In environments where food availability is high and flow rate is low, selection also favours colonies with longer zooid longevity. These patterns of selection provide partial support for module longevity theory developed for plants. Nevertheless, that selection on module longevity is so context-dependent suggests that variation in module longevity is likely to be maintained in this system.

Introduction

Unlike solitary organisms, modular organisms have an indeterminate structure comprised of multiple subunits, which can undergo independent development (Hamilton *et al.*, 1987). This allows each module to experience its own life history, in some ways separated from, but at the same time within, the life history of the whole organism (Watkinson & White, 1986). In principle, growth, reproduction and death can all occur autonomously in separate modules (Thomas, 1994). Throughout the whole organism, resources are often shared between modules and can be redistributed from one module to the next. This sharing and redistribution of resources throughout the colony allows modules to be allocated separate functions, such as feeding, growth or reproduction (Palumbi & Jackson, 1983; Watson, 1984; Haggar & Ewel, 1995). Counter-intuitively, this also allows deteriorating processes, like module mortality, to sometimes be beneficial for the organism – for example, when allocation of

resources from older modules to newer, more vital ones maximizes whole-colony fitness.

In both theory and empiricism, module mortality has best been studied in plants. In plants, the modular units are the totipotent shoots (Tuomi & Vuorisalo, 1989), from which both flowers (reproductive units) and leaves (feeding units) can develop. Although it is known that the longevity of shoots depends on environmental cues (Eleuterius & Caldwell, 1981; Silva *et al.*, 1982), it is not certain how or when shoots senesce. The longevity of both flowers and leaves, on the other hand, has been thoroughly modelled and may shed some insight in module longevity for plants, as it has been shown that shoot and leaf longevity are positively correlated (Eleuterius & Caldwell, 1981). For leaves, the optimal leaf longevity is predicted to reflect whole-plant energy budgeting (Kikuzawa & Ackerly, 1999; Wright *et al.*, 2004). With time, the energy acquisition rate of a leaf will decline, either by shading from newer leaves ('self-shading'), physical damage or from the accumulation of metabolic waste products (Gan & Amasino, 1997; Ackerly, 1999; Guiboileau *et al.*, 2010). Eventually, the energetic costs of maintaining the leaf will exceed what the leaf can produce. As a result, energy and nutrients (mainly nitrogen) are reabsorbed

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by the plant, and the old leaves will senesce and die (Thomas & Stoddart, 1980; Smart, 1994). This resource-recycling strategy, based on nitrogen economics, is what allows plants to optimize resource allocation and maximize whole-plant lifetime fitness (Kikuzawa, 1991, 1995; Ackerly, 1999; Kikuzawa & Ackerly, 1999).

As for shoots, the timing of leaf senesce can be mediated by resource competition and environmental conditions (Monk, 1966; Ashman & Schoen, 1994). However, the strength and direction on selection for leaf longevity in varying conditions is still debated. For example, leaf longevity is affected by the availability of local environmental resources (Kikuzawa, 1991). If sunlight is the limiting resource, then by shading some but not all leaves of a plant, the available nitrogen will be redistributed from the shaded to the unshaded leaves. As leaf nitrogen content is positively correlated with leaf lifespan, the shaded leaves will therefore experience a shorter lifespan (Evans, 1989; Hikosaka *et al.*, 1994; Ackerly & Bazzaz, 1995). Surprisingly, if the whole plant is shaded, leaf longevity will increase, and growth of the plant will decrease, due to energy retention within the plant (Hidema *et al.*, 1991; Kikuzawa & Ackerly, 1999; Terashima *et al.*, 2005). For the same reasons, selection on plant traits, including leaf lifespan, is also affected by competition from neighbours. In line with studies on partial shading, neighbouring plants that compete for sunlight (and hence partially blocking the available sunlight for each other's canopies) have shorter leaf lifespans, as fast growth and fast leaf turnover is favoured (Grime & Hodgson, 1987). If plants are competing for soil nutrients, however, the impact of competition is unclear, although evidence suggests that selection favours nutrient retention and thus prolonged leaf lifespan (for a full review, see Aerts, 1999). These studies suggest that the interplay of competition, resources and selection on module longevity is complex.

For modular animals, selection on module longevity is even less clear than for plants and has been largely overlooked in the literature. The life histories of sessile marine organisms are similar to those of modular plants, where the modules are termed 'zooids' rather than 'shoots' (Hughes, 2005). The zooids of sessile marine organisms contribute to a variety of functions, and many species experience zooid senescence separate to organism mortality. Zooids are totipotent: for some species, the same zooid goes through different life stages with a variety of functions; but in others, clusters of zooids have specialized functions, like feeding or reproduction, throughout their life cycles. There have been a number of intriguing studies on how zooid turnover may maintain whole-colony lifespans in marine invertebrates (Jackson & Winston, 1981; Petralia *et al.*, 2014; Rinkevich, 2017), but to our knowledge, no study has formally examined selection on zooid longevity. Some studies suggest senescence in some marine colonial species is a fixed intrinsic trait (Rinkevich *et al.*, 1992), and

others suggest it is plastic (Harvell & Grosberg, 1988); either way, rates of module senescence are likely to be subject to selection. For example, laboratory trials show that zooids of the marine bryozoan *Electra pilosa* experience shorter lifespans in high food environments (Bayer *et al.*, 1994), and that zooids of the marine bryozoan *Watersipora subtorquata* show different turnover rates at varying depths (Lange *et al.*, 2016); however, manipulative studies examining selection on module longevity for any sessile marine invertebrate are exceedingly rare.

Selection on module longevity thus remains relatively unexplored across modular groups, and the consequences of variation in resources for selection on module longevity remain particularly unclear. To examine how environments with varying resource conditions affect selection on module longevity, we examined the strength and direction of selection on module longevity across a range of manipulated environments under field conditions. We used unanalysed data (on zooid longevity) from a field experiment conducted by Marshall & Monro (2013), and unanalysed data (also on the trait zooid longevity) from a field experiment conducted by Svanfeldt *et al.* (2017). In the first experiment, interspecific competition (and thus variation in resource availability) was manipulated in three levels (Marshall & Monro, 2013). In the second experiment, food availability and flow rate were manipulated by altering the local abundances over a natural gradient of intraspecific density.

Materials and methods

Study site and species

The first experiment was conducted at Redcliffe Marina, Brisbane, Australia, in 2008, and the second at Royal Brighton Yacht Club (RBYC), Port Phillip Bay, Australia, in 2013. These sites are both protected by man-made structures and would be considered low exposure environments, with mainly directional flow from one effective inlet and one outlet. In RBYC, the local flow rate ranges from 0.1 m s^{-1} to 2.5 cm s^{-1} (Lagos *et al.*, 2016) and flow rates are similar to Redcliffe Marina. In our trials, we used the colonial marine bryozoan *Watersipora subtorquata* (hereafter referred to as *Watersipora*), which is an invasive species, commonly found in coastal Australian waters (Hewitt *et al.*, 2004). *Watersipora* colonies typically grow in sheltered areas and are easily recognized by their characteristic bright red colour. New *Watersipora* colonies are formed by sexual reproduction and the subsequent release of free-swimming larvae into the water column. The larvae are lecithotrophic and therefore completely reliant on maternal investment in larval energy reserves until settlement (Svanfeldt *et al.*, 2016). After settlement, each larva goes through metamorphosis and forms the first

feeding unit of the colony – the ancestral zooid. The size of the ancestrula is highly correlated with larval size prior to settlement, making it a good indicator of maternal provisioning (Marshall & Keough, 2004). Once metamorphosed, the ancestrula starts budding, where circular bands of feeding and sexually reproducing zooids start forming the circular colony. Growth occurs in zooids on the colony margin. With time, the zooids in the centre of the colony lose their colour and irreversibly senesce. Although other bryozoan species can initiate senescence from other regions of the colony than the centre (for some species to create excurrent chimneys), *Watersipora* typically only senesces from the centre out. Zooid senescence is visible as the appearance of a grey inner circle of older, dead zooids that expands as the colony grows (Hart & Keough, 2009; Marshall & Monro, 2013). Within the colony, energy acquired from food capture is shared among zooids via porous cell walls (Banta, 1969; Bone & Keough, 2010).

Interspecific competition

At Redcliff Marina, the interspecific competition was manipulated over a range of settler (ancestrula) sizes. *Watersipora* colonies were collected at the field site and spawned in the laboratory. The released larvae were allowed to settle in water drops on acetate sheets, and the sheets then glued onto 10 × 10 cm PVC plates. To reflect the range of natural competition conditions in the field in a way that affect performance for *Watersipora*, the environment was manipulated in accordance with a previous study by Marshall & Keough (2009): newly settled ancestrulae were numbered and assigned randomly to one of three field treatments: low, intermediate and high competition. In the low competition treatment, settlers were attached to blank settlement plates that were cleaned weekly throughout the experiment to remove natural recruitment from external organisms. In the intermediate competition treatment, settlers were attached to blank settlement plates that were allowed to accumulate natural recruitment of external organisms (including sponges, bryozoans, worms and ascidians) throughout the experimental period. In the high competition treatment, settlers were attached to settlement plates that had been exposed to natural recruitment of external organisms for 3 weeks in the field prior to attachment and therefore already held young developing fouling communities. Treatments were applied independently and at the scale of settlement plate. In total for this experiment, 60 replicates of each treatment were deployed. Plates with one of the three treatments were then haphazardly attached to PVC backing panels, such that all three treatments were represented on each panel, and the panels submerged at 1 m depth in the field. Equal numbers of each treatment were attached to each backing panel, and the position of the plates on the panels was

rearranged weekly throughout the experiment, to prevent artefactual covariance between spatial arrangement and the life history traits of interest. In total, 30 backing panels were deployed, holding a total of 180 plates (60 per treatment). After deployment, the plates were photographed weekly for 6 weeks in the field, and the photographs analysed in ImageJ software (available at http://imagej.net; Marshall & Monro, 2013). Colony traits were then analysed from the photos. In the previous study by Marshall & Monro (2013), senescence was measured as the proportion of live vs. senesced zooids. Here, we used landmarked photographs of colonies to follow individual zooids over time to determine zooid lifespan from the initial budding stage until zooid death, where the mean lifespan of four zooids per colony was used. Furthermore, we analysed ancestrula size, and the reproductive output of the colonies (ovicell count per week) was used as a measure of colony fitness.

Intraspecific density and resource availability

At RBYC, resource availability was manipulated over a natural gradient of intraspecific density of *Watersipora* colonies. *Watersipora* colonies are sessile filter-feeders that compete exploitatively for food particles and depend on the rate at which the particles pass their feeding structures (Pratt, 2008). We manipulated food availability by adding or not adding food blocks (see below for details), and flow rate by obstructing or not obstructing the natural flow. The two resource manipulations were then crossed over the range of *Watersipora* density in an orthogonal design, with the aim to create extremes in environmental conditions, overlapping with natural conditions experienced by *Watersipora*.

Resource availabilities and intraspecific density were manipulated according to the following procedures. The range of intraspecific density was obtained by submerging 80 10 × 10 cm acetate plates attached to backing panels at 1.5 m depth at the field site. After a week in the field, the settlement plates were examined, and all non-*Watersipora* settlers were scraped off, resulting in 1–8 *Watersipora* settlers per plate. The plates were then haphazardly assigned to the resource manipulation treatments. To manipulate the availability of food, artificial slow releasing food blocks were made by mixing commercial filter feeder mixture and dental plaster (see Svensson & Marshall, 2015 for details). Control blocks were made with dental plaster and water. The food and control blocks were then attached with mesh cages at the centre of each settlement plate respective to treatment. Flow rate was manipulated by surrounding settlement plates with 10 × 10 × 5 cm flow obstructing boxes. The boxes effectively obstructed the directional flow rates on the plates, without reducing access to open water. Controls for the flow obstruction treatment were open settlement plates. By crossing the food and

flow treatments orthogonally, we created four environments with the combinations of high and low food and flow availabilities. In the field, 20 backing panels, each holding two replicates of each treatment (in total eight plates per backing panel), were submerged over two runs (10 panels per run), with 1 week between the initiation of each run. In total, there was a replication of 40 plates per treatment. After deployment, the plates were monitored by weekly photographs from week 1 to week 13 in the field. The images were then analysed in ImageJ software (Svanfeldt *et al.*, 2017). As in Marshall & Monro (2013), Svanfeldt *et al.* (2017) had used the rate of live vs. dead zooids to estimate senescence. Again, for this study, we measured actual zooid longevity from bud formation until the death of the individual zooids and used the average lifespan of four zooids per colony. As fitness proxy, we used asexual reproduction (colony size per week). For colonial organisms, growth, just like sexual reproduction, increases reproductive output and is therefore integral to fitness (Pedersen & Tuomi, 1995). Preferably, both sexual and asexual reproduction should be measured for total organismal fitness (Winkler & Fischer, 1999), but our colonies did not reach sexual maturity before a mortality event wiped out all of our colonies. For *Watersipora* and other colonial species, though, reproductive output is highly correlated with size (Hughes, 1984; Hart & Keough, 2009) which further strengthens the appropriateness of our use of asexual rather than sexual reproduction as fitness measure.

Statistical analyses

To estimate the strength and direction of selection on the zooid traits in the two experiments (zooid longevity plus ancestrula size in the interspecific experiment, and zooid longevity in the intraspecific experiment), and to obtain standardized estimates of linear (β) and nonlinear (γ) gradients of selection, we used the classic multiple-regression approach of Lande & Arnold (1983). Prior to analysis, zooid traits were transformed to units of standard deviation within each environment, and relative fitness (asexual reproduction and reproductive output, respectively) was calculated by dividing each absolute value by the mean value within each environment, in accordance with standard methods for selection analyses (Kingsolver & Pfennig, 2007). The strength of selection was tested by comparing our models using likelihood ratio tests.

To estimate selection on the zooid traits, we first analysed the effect of environment (competition for the interspecific experiment, and density, food and flow for the intraspecific experiment) on relative fitness. In our analyses, zooid traits were modelled as fixed effects and spatial arrangement (backing panel) was modelled as random. These mixed models for each environment thereafter served as our base models. Second, we tested

for significant directional selection on the zooid traits (zooid longevity for the interspecific experiment, and zooid longevity and ancestrula size for the intraspecific experiment) on fitness, by adding only linear regression coefficients to our base model terms. Third, we tested for quadratic selection by adding quadratic terms to the linear model and again tested whether quadratic selection varied across environments. As we had multiple traits for the interspecific experiment, we also added interactions between the zooid traits to our models to estimate correlational selection within environments and also if there was variation in correlational selection on the traits across environments. All analyses were performed in SAS, version 9.4 using ML estimation in PROC MIXED.

Results

For the interspecific competition experiment, we found a strong effect of environment (competition level) on colony performance (ovicells per week; Table 1), where colonies performed best in the environment where competition was low, and worst in the environment where competition was high. Further, we explored if there was selection on the zooid traits (zooid longevity and ancestrula size) and if this selection differed across environments. We found significant directional selection for the zooid traits that differed with environment ($\chi^2 = 7.3$, d.f. = 1, $P = 0.03$). However, when exploring selection for each trait, we found that no significant directional selection with environment for either trait (Table 1). We also found evidence for differences in correlational selection among environments (Table 1); under high competition, individuals had highest fitness when ancestrula size was larger and zooid longevity was longer, while individuals with lower values in both traits had lower fitness (Table 2; Fig. 1). In low and intermediate competition environments, however, there was no evidence for correlational selection. In addition, we found significant quadratic selection on ancestrula size that differed with environment (Table 1). In the environments with low and high

Table 1 Effects of environment (variations of competition), zooid longevity and ancestrula size on colony performance (ovicells per week) for *Watersipora subtorquata* colonies in the field.

	χ^2	d.f.	P
Environment	106.4	1	**< 0.001**
Environment*Zooid longevity	3.7	1	0.054
Environment*Ancestrula size	3.7	1	0.054
Environment*Zooid longevity*Ancestrula size	7.5	1	**< 0.001**
Environment*Zooid longevity*Zooid longevity	0.0	1	1.000
Environment*Ancestrula size*Ancestrula size	5.1	**1**	**0.020**
Zooid longevity*Zooid longevity	0.0	1	1.000

Significant effects are shown in bold.

Table 2 Standardized gradients of linear selection (β) and nonlinear selection (γ) on zooid longevity and ancestrula size with competition environments in *Watersipora subtorquata*.

		$\gamma \pm$ SE	
	$\beta \pm$ SE	Zooid longevity	Ancestrula size
Low competition			
Zooid longevity	−0.07 (0.09)	0.00 (0.00)	
Ancestrula size	0.06 (0.31)	0.01 (0.07)	0.03 (0.05)
Intermediate competition			
Zooid longevity	−0.19 (0.11)	0.00 (0.00)	
Ancestrula size	0.33 (0.41)	−0.06 (0.09)	**−0.17 (0.07)**
High competition			
Zooid longevity	0.18 (0.31)	0.00 (0.00)	
Ancestrula size	−1.05 (0.56)	**0.39 (0.13)**	−0.01 (0.10)

Errors are shown in parentheses next to each estimate, and all significant effects ($P < 0.05$) are shown in bold.
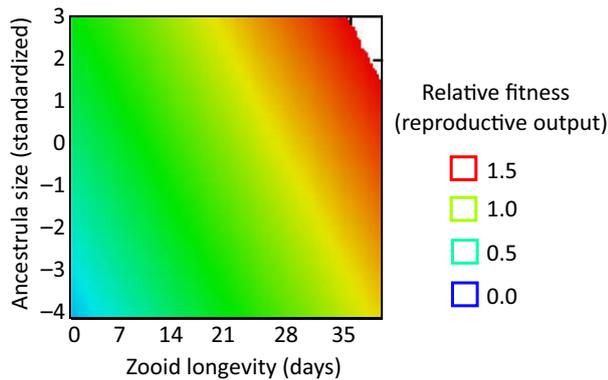

Fig. 1 The predicted effect of zooid longevity and ancestrula size on fitness in high interspecific competitive environment for *Watersipora* colonies in the field. The x- and y-axes show the standardized traits, and the heat plot shows relative fitness from low (blue) to high (red). In this environment (high competition), selection favours colonies originating from larger ancestrula with longer zooid longevity.

competition, quadratic selection on ancestrula size was nonexistent, whereas in the intermediate competition environment, there was strong stabilizing selection on ancestrula size (Table 2). Quadratic selection on zooid longevity did not differ among environments (Table 1), and there was no evidence for quadratic selection on zooid longevity overall (Table 1).

For the intraspecific density experiment, we found a strong main effect of overall environment (density, food and flow combinations) on colony performance (colony size per week; Table 3), where there was a significant interaction of density, food availability and flow rate (Table 3) on colony performance. Colonies in environments where food availability was high (regardless of

flow) showed positive density dependence on fitness, as did colonies in the environment where food availability was low but flow rate was high. In the environment where both food availability and flow rate were low, however, colonies experienced negative density dependence (Svanfeldt *et al.*, 2017). Further, we explored if selection acted on zooid longevity and if this selection varied with environments. Directional selection did not vary with any of the interactions between zooid longevity, colony density and food or zooid longevity, colony density and flow (Table 3). However, the strength (and direction) of selection on zooid longevity varied with the interaction of zooid longevity, food and flow (Table 3). In the environment where food availability was low and flow rate was high, selection favoured longer zooid longevity (Tables 4 and 5; Fig. 2). In all

Table 3 Effects of environment (variations in density, food and flow), and zooid longevity on colony performance (colony size) for *Watersipora subtorquata* colonies in the field.

	χ^2	d.f.	P
Environment	37.5	**6**	**< 0.001**
Density*Food*Flow	3.8	**1**	**0.05**
Density*Food*Zooid longevity	0.0	1	1.00
Density*Flow*Zooid longevity	0.0	1	1.00
Food*Flow*Zooid longevity	102.2	**1**	**0.01**
Environment*Zooid longevity*Zooid longevity	4.2	1	0.65
Zooid longevity*Zooid longevity	0.3	1	0.58

Significant effects are shown in bold.

Table 4 Effects of variations of food availability, flow rate and zooid longevity on colony performance (colony size) for *Watersipora subtorquata* colonies in the field.

	χ^2	d.f.	P
Low food, high flow*Zooid longevity	5.1	**1**	**0.02**
High food, high flow*Zooid longevity	2.6	1	0.11
High food, low flow*Zooid longevity	0.8	1	0.38
Low food, low flow*Zooid longevity	0.9	1	0.34

Significant effects are shown in bold.

Table 5 Standardized gradients of linear selection (β) on zooid longevity with variation in resource (food and flow) environments in *Watersipora subtorquata*.

		$\beta \pm$ SE
High food, high flow	Zooid longevity	−0.19 (0.12)
High food, low flow	Zooid longevity	0.16 (0.18)
Low food, high flow	Zooid longevity	**0.47** (0.20)
Low food, low flow	Zooid longevity	−0.22 (0.22)

Standard errors are shown in parentheses next to each estimate, and all significant effects ($P < 0.05$) are shown in bold.
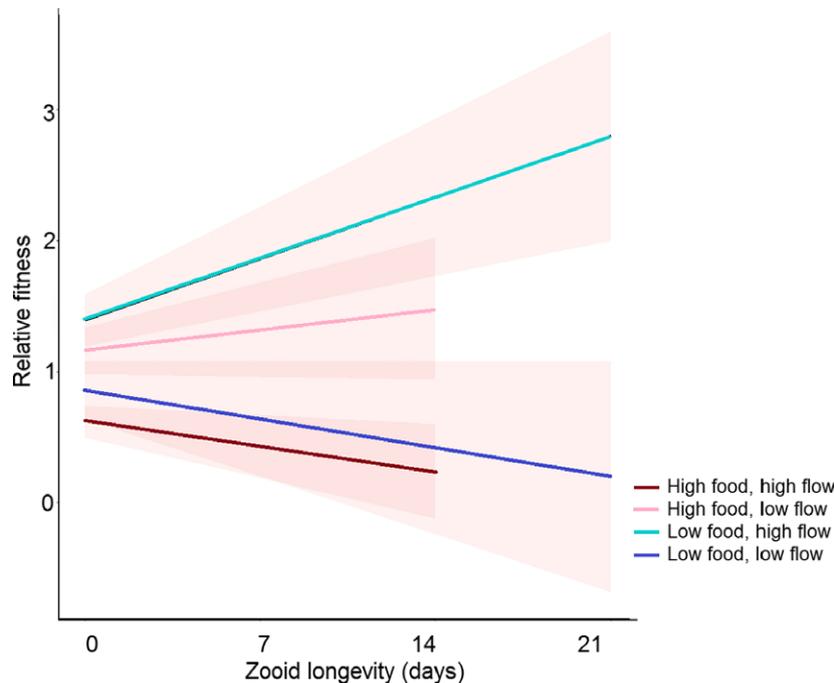
Fig. 2 The predicted effects of zooid longevity on fitness in four environments with varying food and flow conditions on *Watersipora* colonies in the field. The *x*-axis shows zooid longevity, and the *y*-axis shows relative fitness. The linear effects of zooid longevity on relative fitness are shown in maroon for the environment with high food and high flow, pink for the environment with high food and low flow, teal for the environment with low food and high flow, and indigo for the environment with low food and low flow (±SE as shades). When food availability is high and flow rate is low, selection favour colonies with longer zooid longevity. In all other combinations of food and flow environments, selection did not act on zooid longevity.

other environments, selection was weak or nonexistent (Tables 4 and 5; Fig. 2). Quadratic selection on zooid longevity did not differ among environments (Table 3), and there was no evidence for quadratic selection on zooid longevity overall (Table 3).

Discussion

We found that selection acts on module lifespan in a modular animal species and that this selection is mediated by environmental conditions. In environments with low or intermediate interspecific competition, selection on zooid longevity was nonexistent. In environments with high interspecific competition, selection favoured colonies with longer zooid longevity if the ancestrula size of those colonies were larger. In this high competition environment, colonies with shorter zooid longevity were least favoured by selection, but only if the colonies were small as ancestrulae. Colonies in this environment that had higher values in one trait but lower in the other trait (smaller ancestrula and longer zooid longevity or larger ancestrula and shorter zooid longevity) had intermediate fitness. We also found quadratic selection for ancestrula size, as further discussed in Marshall & Monro (2013), where in

environments with intermediate competition, there was strong stabilizing selection on ancestrula size. In our second experiment, where we manipulated the availability of resources, selection favoured colonies with longer zooid longevity in environments with low food availability and high flow rate. In all other environments, colonies experienced no selection on zooid longevity. As indicated by multiple studies on modular plants (Eleuterius & Caldwell, 1981; Silva *et al.*, 1982; Kikuzawa, 1991, 1995; Ackerly, 1999; Kikuzawa & Ackerly, 1999), we have shown that module longevity is under selection, and that selection varies with environmental conditions.

Previously, it has been shown that sessile marine invertebrate colonies growing in conditions with high food availability have shorter zooid longevity (Bayer *et al.*, 1994). This finding aligns well with observations and theories of modularity in plants. The similarities between modular organisms are numerous, and there responses to environmental cues also show possible parallels between modular groups. In plants, high nutrient availability promotes shorter leaf lifespans, encouraging plant growth overall. It has been shown that shoot and leaf longevity can be positively correlated, where short-lived shoots in populations with

high turnover rates where leaf longevity is short have high net productivity and thus high fitness (Eleuterius & Caldwell, 1981). In high nutrient environments, the limiting factor for plant growth is sunlight. As new leaves grow, they will effectively shade the older leaves, inducing 'self-shading'. By adapting faster leaf turnover (and thereby shorter leaf longevity), the negative properties of the 'self-shading' effect are minimized (Grime & Hodgson, 1987). Similarly, high nutrient environments will promote rapid growth of neighbours, which could further induce shading, and therefore enhance the benefits of shorter leaf lifespans (Grime & Hodgson, 1987). In low nutrient availability, plants are shown to prolong leaf lifespans in order to efficiently retain nutrients (Grime & Hodgson, 1987; Escudero et al., 1992). While it might be intuitively appealing to assume that low flow conditions for marine invertebrates are analogous to low nutrient conditions in plants, the aspects of flow on food availability are somewhat complicated. For colonial marine invertebrates, higher flow rates indicate that more food particles per unit time are passing the feeding apparatus (Cahalan et al., 1989). However, multiple studies by Okamura (1984, 1985, 1990) and also by Pratt (2008) have shown that feeding rates of sessile marine invertebrates, specifically bryozoans, are either unaffected by flow rate, or decrease with increased flow. The reason that increased flow rate does not increase feeding is explained in an additional study by Okamura (1988), where it was shown that for bryozoans, feeding attempts are higher under high flow rates, whereas the actual food particle capturing success is higher under lower flow rates. That colonies in the environment with low food availability in combination with higher flow rate experienced selection for longer zooid longevity could therefore be the result of nutrient retention, similar to the responses of plants in low nutrient environments (Escudero et al., 1992).

That selection favours the covariation of longer zooid longevity and larger offspring size (ancestrula) in environments with high interspecific competition, may also be a result of similar strategies to those acting on plant modules in competitive environments. In plants, it has been shown for several species that seed mass (offspring size) is positively correlated with leaf longevity (Seiwa & Kikuzawa, 1991, 1996). Classic offspring size theory predicts that there is a relationship between offspring size and fitness, where larger offspring have higher fitness than smaller offspring. It also predicts that this relationship is stronger in harsher rather than benign environments (Parker & Begon, 1986). Therefore, our finding of a correlational selection between offspring size and zooid longevity for our marine invertebrate in the environment with high competition was not surprising, but rather confirms the patterns of classic theory of correlated evolution of these two traits.

Our results suggest that there are stabilizing forces acting on module longevity, where the phenotypic diversity of this trait may persist due to variation in selection pressure across environments (Kassen, 2002). We found that selection acts on zooid longevity in a modular species and that this selection is mediated by environmental conditions. With this study, we have provided a starting point for understanding selection pressures in modular organisms, and the role of modules in the life history. By addressing the aspects of modular life history, we hope to understand how selection of module lifespan shapes the evolution of modular species.

References

Ackerly, D. 1999. Self-shading, carbon gain and leaf dynamics: a test of alternative optimality models. *Oecologia* **119**: 300–310.

Ackerly, D. & Bazzaz, F. 1995. Leaf dynamics, self-shading and carbon gain in seedlings of a tropical pioneer tree. *Oecologia* **101**: 289–298.

Aerts, R. 1999. Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedbacks. *J. Exp. Bot.* **50**: 29–37.

Ashman, T.-L. & Schoen, D.J. 1994. How long should flowers live? *Nature* **371**: 788–791.

Banta, W.C. 1969. The body wall of cheilostome Bryozoa. II. Interzoidal communication organs. *J. Morphol.* **129**: 149–169.

Bayer, M., Cormack, R. & Todd, C. 1994. Influence of food concentration on polypide regression in the marine bryozoan Electra pilosa (L.)(Bryozoa: Cheilostomata). *J. Exp. Mar. Biol. Ecol.* **178**: 35–50.

Bone, E.K. & Keough, M.J. 2010. Does polymorphism predict physiological connectedness? A test using two encrusting bryozoans. *Biol. Bull.* **219**: 220–230.

Cahalan, J.A., Siddall, S.E. & Luckenbach, M.W. 1989. Effects of flow velocity, food concentration and particle flux on growth rates of juvenile bay scallops Argopecten irradians. *J. Exp. Mar. Biol. Ecol.* **129**: 45–60.

Eleuterius, L.N. & Caldwell, J.D. 1981. Growth kinetics and longevity of the salt marsh rush Juncus roemerianus. *Gulf. Caribb. Res.* **7**: 27–34.

Escudero, A., Del Arco, J., Sanz, I. & Ayala, J. 1992. Effects of leaf longevity and retranslocation efficiency on the retention time of nutrients in the leaf biomass of different woody species. *Oecologia* **90**: 80–87.

Evans, J. 1989. Partitioning of nitrogen between and within leaves grown under different irradiances. *Funct. Plant Biol.* **16**: 533–548.

Gan, S. & Amasino, R.M. 1997. Making sense of senescence (molecular genetic regulation and manipulation of leaf senescence). *Plant Physiol.* **113**: 313.

Grime, J. & Hodgson, J. 1987. Botanical contributions to contemporary ecological theory. *New Phytol.* **106**: 283–295.

Guiboileau, A., Sormani, R., Meyer, C. & Masclaux-Daubresse, C. 2010. Senescence and death of plant organs: nutrient recycling and developmental regulation. *C.R. Biol.* **333**: 382–391.

Haggar, J.P. & Ewel, J.J. 1995. Establishment, resource acquisition, and early productivity as determined by biomass allocation patterns of three tropical tree species. *For. Sci.* **41**: 689–708.

Hamilton, N.S., Schmid, B. & Harper, J. 1987. Life-history concepts and the population biology of clonal organisms. *Proc. R. Soc. Lond. B Biol. Sci.* **232**: 35–57.

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.

Harvell, C.D. & Grosberg, R.K. 1988. The timing of sexual maturity in clonal animals. *Ecology* **69**: 1855–1864.

Hewitt, C.L., Campbell, M.L., Thresher, R.E., Martin, R.B., Boyd, S., Cohen, B.F. *et al.* 2004. Introduced and cryptogenic species in Port Phillip Bay, Victoria, Australia. *Mar. Biol.* **144**: 183–202.

Hidema, J., Makino, A., Mae, T. & Ojima, K. 1991. Photosynthetic characteristics of rice leaves aged under different irradiances from full expansion through senescence. *Plant Physiol.* **97**: 1287–1293.

Hikosaka, K., Terashima, I. & Katoh, S. 1994. Effects of leaf age, nitrogen nutrition and photon flux density on the distribution of nitrogen among leaves of a vine (Ipomoea tricolor Cav.) grown horizontally to avoid mutual shading of leaves. *Oecologia* **97**: 451–457.

Hughes, T.P. 1984. Population dynamics based on individual size rather than age: a general model with a reef coral example. *Am. Nat.* **123**: 778–795.

Hughes, R.N. 2005. Lessons in modularity: the evolutionary ecology of colonial invertebrates. *Sci. Mar.* **69**: 169–179.

Jackson, J.B. & Winston, J.E. 1981. Modular growth and longevity in bryozoans. Recent and fossil Bryozoa: 121-126.

Kassen, R. 2002. The experimental evolution of specialists, generalists, and the maintenance of diversity. *J. Evol. Biol.* **15**: 173–190.

Kikuzawa, K. 1991. A cost-benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern. *Am. Nat.* **138**: 1250–1263.

Kikuzawa, K. 1995. The basis for variation in leaf longevity of plants. In: *Global Change and Terrestrial Ecosystems in Monsoon Asia* (T. Hirose & B.H. Walker, eds), pp. 89–100. Springer, Berlin.

Kikuzawa, K. & Ackerly, D. 1999. Significance of leaf longevity in plants. *Plant Species Biol.* **14**: 39–45.

Kingsolver, J.G. & Pfennig, D.W. 2007. Patterns and power of phenotypic selection in nature. *Bioscience* **57**: 561–572.

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.

Lande, R. & Arnold, S.J. 1983. The measurement of selection on correlated characters. *Evolution* **37**: 1210–1226.

Lange, R., Monro, K. & J Marshall, D. 2016. Environment-dependent variation in selection on life history across small spatial scales. *Evolution* **70**: 2404–2410.

Marshall, D.J. & Keough, M.J. 2004. Variable effects of larval size on post-metamorphic performance in the field. *Mar. Ecol. Prog. Ser.* **279**: 73–80.

Marshall, D.J. & Keough, M.J. 2009. Does interspecific competition affect offspring provisioning. *Ecology* **90**: 487–495.

Marshall, D.J. & Monro, K. 2013. Interspecific competition alters nonlinear selection on offspring size in the field. *Evolution* **67**: 328–337.

Monk, C.D. 1966. An ecological significance of evergreenness. *Ecology* **47**: 504–505.

Okamura, B. 1984. The effects of ambient flow velocity, colony size, and upstream colonies on the feeding success of Bryozoa. I. Bugula stolonifera Ryland, an arborescent species. *J. Exp. Mar. Biol. Ecol.* **83**: 179–193.

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. *J. Exp. Mar. Biol. Ecol.* **89**: 69–80.

Okamura, B. 1988. The influence of neighbors on the feeding of an epifaunal bryozoan. *J. Exp. Mar. Biol. Ecol.* **120**: 105–123.

Okamura, B. 1990. Particle size, flow velocity, and suspension-feeding by the erect bryozoans Bugula neritina and B. stolonifera. *Mar. Biol.* **105**: 33–38.

Palumbi, S.R. & Jackson, J. 1983. Aging in modular organisms: ecology of zooid senescence in Steginoporella sp. (Bryozoa; Cheilostomata). *Biol. Bull.* **164**: 267–278.

Parker, G.A. & Begon, M. 1986. Optimal egg size and clutch size: effects of environment and maternal phenotype. *Am. Nat.* **128**: 573–592.

Pedersen, B. & Tuomi, J. 1995. Hierarchical selection and fitness in modular and clonal organisms. *Oikos* **73**: 167–180.

Petralia, R.S., Mattson, M.P. & Yao, P.J. 2014. Aging and longevity in the simplest animals and the quest for immortality. *Ageing Res. Rev.* **16**: 66–82.

Pratt, M.C. 2008. Living where the flow is right: how flow affects feeding in bryozoans. *Integr. Comp. Biol.* **48**: 808–822.

Rinkevich, B. 2017. 11 Senescence in modular animals. In: *The Evolution of Senescence in the Tree of Life* (R.P. Shefferson, O.R. Jones, R. Salguero-Gómez, eds), pp. 220. Cambridge University Press, Cambridge.

Rinkevich, B., Lauzon, R.J., Brown, B. & Weissman, I.L. 1992. Evidence for a programmed life span in a colonial protochordate. *Proc. Natl. Acad. Sci.* **89**: 3546–3550.

Seiwa, K. & Kikuzawa, K. 1991. Phenology of tree seedlings in relation to seed size. *Can. J. Bot.* **69**: 532–538.

Seiwa, K. & Kikuzawa, K. 1996. Importance of seed size for the establishment of seedlings of five deciduous broad-leaved tree species. *Plant Ecol.* **123**: 51–64.

Silva, J.F., Kana, T.M. & Solbrig, O.T. 1982. Shoot demography in new England populations of Maianthemum canadense desf. *Oecologia* **52**: 181–186.

Smart, C.M. 1994. Gene expression during leaf senescence. *New Phytol.* **126**: 419–448.

Svanfeldt, K., Monro, K. & Marshall, D.J. 2016. Dispersal duration mediates selection on offspring size. *Oikos* **126**: 480–487.

Svanfeldt, K., Monro, K. & Marshall, D.J. 2017. Field manipulations of resources mediate the transition from intraspecific competition to facilitation. *J. Anim. Ecol.* **86**: 654–661.

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.

Terashima, I., Araya, T., Miyazawa, S.-I., Sone, K. & Yano, S. 2005. Construction and maintenance of the optimal photosynthetic systems of the leaf, herbaceous plant and tree: an eco-developmental treatise. *Ann. Bot.* **95**: 507–519.

Thomas, H. 1994. Aging in the plant and animal kingdoms–the role of cell death. *Rev. Clin. Gerontol.* **4**: 5–20.

Thomas, H. & Stoddart, J.L. 1980. Leaf senescence. *Annu. Rev. Plant Biol.* **31**: 83–111.

Tuomi, J. & Vuorisalo, T. 1989. What are the units of selection in modular organisms? *Oikos* **54**: 227–233.

Watkinson, A. & White, J. 1986. Some life-history consequences of modular construction in plants. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **313**: 31–51.

Watson, M.A. 1984. Developmental constraints: effect on population growth and patterns of resource allocation in a clonal plant. *Am. Nat.* **123**: 411–426.

Winkler, E. & Fischer, M. 1999. Two fitness measures for clonal plants and the importance of spatial aspects. *Plant Ecol.* **141**: 191–199.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F. *et al.* 2004. The worldwide leaf economics spectrum. *Nature* **428**: 821–827.