

Does size predict demographic fate? Modular demography and constraints on growth determine response to decreases in size

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Abstract. The modular construction of many plants and animals defies conventional approaches to the study of life histories and population dynamics. An important complication of modular construction is that individuals can rapidly decrease in size when some modules are removed or die or when an individual fragments. Most attempts to describe life histories and population dynamics of modular organisms classify individuals according to their size. This approach relies on the fundamental assumption that fragmentation and module loss have no consequences for an individual apart from a simple decrease in size. Here we experimentally test this assumption.

Using a modular marine invertebrate, the encrusting bryozoan *Watersipora subtorquata*, as a model species, we manipulated colony size and then assessed performance against three potential explanatory models based on size, age, and damage. In a second experiment we disrupted the internal modular demography of colonies to determine whether the performance of a fragment is influenced by the type of modules that remain. Finally, we investigated how constraints on growth in modular organisms uniquely influence growth after module loss. We found that single-state variables such as size or age do not describe performance in our species. Internal constraints substantially reduce growth after a decrease in size, and the age of modules that remain determines the timing of reproductive onset and fecundity. A knowledge of the size history of individuals, including any decreases in size, is necessary to accurately describe life histories and population dynamics in this modular organism. Our results have major consequences for established methods for modeling the demography of modular organisms.

Key words: bryozoan; demography; fragmentation; life history; modular demography; modular organism; module loss; partial mortality; state variable; *Watersipora subtorquata*.

INTRODUCTION

Compared with unitary organisms, the modular construction of many plants and animals adds significant complexity to their life histories and population dynamics (Jackson et al. 1985, Harper et al. 1986, Stearns 1992, Hughes 2005). Each module (including polyps in corals, zooids in ascidians and bryozoans, and leaves and inflorescences in plants) within an “individual” has the potential to feed and reproduce, and because no module is indispensable, individuals can survive drastic decreases in size through module death and fragmentation (Hughes and Jackson 1980, Highsmith 1982). Most descriptions of the life histories and population dynamics of modular organisms classify individuals according to their size (Harper 1977, Hughes 1984, Kirkpatrick 1984, Caswell 1985, 1988, Harper et al. 1986). This is because size, rather than ontogeny, is considered the principal determinant of performance in modular organisms for two reasons. First, the ability of

modular organisms to fragment and survive module loss means that the age and size of an individual are not correlated, and second, size confers substantial benefits for growth, survivorship, and fecundity (Hughes 1984, Watkinson and White 1986, Raymundo and Maypa 2004).

Life-history models based on size rely on the fundamental and often untested assumption that an individual's history has no effect on performance. This assumption persists even though a history of module loss has the potential to generate large differences among individuals of equivalent size (Hughes 1984). For example, an individual may reach a certain size through uninterrupted growth from a larva or seed or instead may be a fragment of a formerly large individual. If an individual's history affects its subsequent capacity to survive and grow, then size alone will not accurately reflect or predict performance (Hughes 1984).

One consequence of surviving large decreases in size is that an individual's age and size become decoupled such that same-sized individuals may be very different ages (Hughes and Jackson 1980). Because of the strong influence of size on demographic rates, it has often been assumed that an individual's age is unimportant.

Manuscript received 21 September 2008; accepted 25 September 2008. Corresponding Editor: A. M. Ellison.

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However, there is some empirical evidence from plants and corals to suggest that an individual's age can also affect demographic rates (Lacey 1986, Hughes and Connell 1987, Lopez et al. 2001) so age and size may interact to determine performance.

Losing modules can have further important consequences apart from a simple decrease in size. Module loss often occurs as a consequence of predation, competition, or disturbance that causes damage to an individual that needs to be repaired. Regeneration after damage requires that resources be diverted from growth or reproduction (Rinkevich 1996, Zakai et al. 2000), but damage can also increase growth and induce reproduction in some taxa (Paige and Whitham 1987, Harvell and Helling 1993, Sanchez and Lasker 2004). Further, the modules within an individual are of different ages and may be specialized for defense, reproduction, or structural support, but module loss can disrupt this internal modular demography such that only a biased subset of modules remains (Hughes 1984, Harvell 1991). The effects of damage and changes in modular demography can create potentially large differences among individuals that are independent of both size and age.

Fragmentation and module loss, therefore, have the potential to substantially influence demographic rates in ways not considered by current models, but the assumption that module loss has no effect apart from a simple decrease in size is poorly tested. While many studies have determined the effects of module loss due to herbivory, disturbance, or defoliation, very few have explicitly compared individuals of equivalent size but with different size histories. Most work on modular organisms has been done on plants and reef corals, but tests of these ideas are difficult in these longer-lived taxa because of their relatively slow growth and reproduction (Hughes et al. 1992). Shorter-lived species provide a tractable alternative for detailed experimental studies on the consequences of modularity, but studies on these taxa are rare. Here we examine the consequences of module loss that causes a rapid decrease in size in a modular organism. We use a short-lived, sessile marine invertebrate, the bryozoan *Watersipora subtorquata*, as a model species. In the first experiment we investigated the consequences of being reduced to a small fragment from the edge of a large colony. We assessed colony performance against three explanatory models: (1) if size predicts performance, then a fragment should perform according to its current size; (2) if age predicts performance, then a fragment should perform like the colony from which it was derived; or (3) if damage predicts performance, then a fragment will perform like a damaged colony that has not changed in size. In our second experiment we disrupted the internal modular demography of colonies to determine whether the performance of a fragment is influenced by the type of modules that remain after module loss. Observations from the first two experiments indicated that regenera-

tion after module loss is directional, occurring only along a short section of a fragment's margin. In a final experiment we investigated this growth constraint further to determine whether colonies of different sizes but with equal lengths of growing margin have a similar potential for growth.

METHODS

Study species

Watersipora subtorquata is an encrusting bryozoan found in sessile marine communities worldwide and is an invasive species in Australia (Hewitt et al. 2004). Colonies of this species are composed of unspecialized (isomorphic) modules (called "zooids") with a calcium carbonate exoskeleton. The lateral and end walls of each zooid are fused with adjacent zooids to form an encrusting sheet that radiates out from the founding zooid (ancestrula; Fig. 1). Undifferentiated buds at the margins of the colony form a "growing edge." When growth is uninterrupted, colonies become circular; however, circular colonies are rare and *W. subtorquata* is known to fragment frequently, forming individuals of irregular size and shape (S. P. Hart, *personal observation*; M. J. Keough, *unpublished data*; Fig. 1a). Individual zooids survive for approximately three weeks during which time they contribute to colony growth and reproduce; unlike some other bryozoans, there is no polypide cycling in *W. subtorquata*. Zooids brood embryos internally. The bryozoa are an extraordinarily diverse group. *Watersipora subtorquata* belongs to the largest group of all living bryozoans (order Cheilostomata, suborder Ascophora) and exhibits a growth form (encrusting/foliose) that is common to many species. Unlike most bryozoans in this group, *W. subtorquata* lacks specialized zooids.

General methods

Experiments were done at Breakwater Pier in Williamstown, a temperate location at the northern end of Port Phillip Bay in southern Australia (37°51' S, 144°54' E). We allowed *W. subtorquata* to settle naturally onto 20 × 20 cm roughened, gray, PVC settlement plates suspended horizontally, 2 m below the low water mark. Four settlement plates were attached to the underside of 60 × 60 cm gray, PVC backing plates with stainless steel bolts. Each experiment was done on a single backing plate. Throughout the experiments, other sessile organisms were removed from settlement plates and some *W. subtorquata* colonies were also removed to prevent colonies overgrowing. We maintained several colonies on each settlement plate until they reached sizes sufficient for each experiment to begin.

To manipulate and measure colonies during the experiments, we removed individual settlement plates from a backing plate and kept them in a small container of cool seawater. We created fragments using a scalpel to remove zooids from intact colonies to leave only the

desired fragment(s). We measured colony size and colony perimeter by tracing each colony onto an overhead projector transparency with a permanent marker. We scanned each colony trace and then measured the digitized image using SigmaScan Pro 5 (SPSS, Chicago, Illinois, USA). When present, *W. subtorquata* embryos are visible as spherical pink structures behind the frontal wall of individual zooids. To determine reproductive status and fecundity we counted the embryos in each colony using a dissecting microscope.

Experiment 1: effects of colony size, colony age, and damage

The aim of this experiment was to test the performance of a colony against explanatory models based on size, age, and damage. To do this we created fragments from the edge of large colonies and compared their performance to unfragmented colonies that were the same size or age or had the same amount of damage.

The experiment had four treatments (Fig. 1b). (1) Fragments were created from colonies 27–38 mm in diameter. Zooids were removed to leave a fragment 8–12 mm in diameter at the original colony edge. A fragment's perimeter included a portion of the parent colony's original edge equal to one-quarter of the fragment's total perimeter. (2) Large control colonies were the same size (27–38 mm in diameter) and age as the fragments' parent colonies. (3) Small control colonies were the same size as fragments (8–12 mm in diameter) but reached this size through uninterrupted growth from a larva. (4) Small damaged colonies were created by removing 1–2 mm of edge tissue from three-quarters of the perimeter of a small colony (8–12 mm diameter). Small damaged colonies therefore retained one-quarter of their perimeter as undamaged edge, which mimicked the level of damage to a fragment (also one-quarter undamaged edge). Comparisons between fragments and small control colonies test the model based on current size. Comparisons between fragments and large control colonies test the model based on age. Comparisons between fragments and small damaged colonies test the model based on damage incurred by a colony during fragmentation.

The experiment began on 11 January 2001. Large and small colonies were randomly assigned to undamaged and damaged treatments. We measured colony size and fecundity weekly for three weeks. *Watersipora subtorquata* colonies of different sizes have different absolute growth because larger colonies have more perimeter from which can be budded more zooids. To directly compare treatments we calculated relative growth to account for differences in colony size. We did this by dividing the change in colony area by the perimeter of each colony at the beginning of each week ($(\text{area at time } 2 - \text{area at time } 1) / (\text{perimeter at time } 1)$). This calculation estimates a colony's linear edge extension and is used to reflect the constraints on growth imposed by *W.*

subtorquata's encrusting, two-dimensional growth form, in which the primary responsibility for growth is with the zooids near the perimeter of the colony. Similarly, we standardized fecundity to embryos per unit live colony area.

Experiment 2: effects of modular demography

Watersipora subtorquata has within-colony age structure. In unfragmented colonies the youngest zooids are near the colony margin and old zooids are in the colony center. The aim of this experiment was to determine whether the performance of a fragment is influenced by the age of the modules that remain after module loss. The experiment had two treatments (Fig. 1c): (1) old fragments were created near the center of the parent colony and were therefore composed of old zooids; and (2) young fragments were created at the edge of the parent colony and were composed of young zooids. Old fragments cannot have an intact growing edge at the time of fragmentation because they come from the center of a colony. Therefore, we removed the remaining intact edge from young fragments so that we could directly compare them with old fragments.

Fragments were created in pairs with each old–young pair coming from the same colony. This allowed us to isolate the effects of zooid age from the confounding effects of colony age. Fragments were 8 mm in diameter and were created from colonies of equal age and equal size (25 mm diameter). We measured live colony size and fecundity weekly for three weeks.

Experiment 3: effects of size and growth constraints

In the first two experiments, regeneration and growth in fragments were highly directional, occurring only in the direction of the original growing margin (i.e., distally; Fig. 1, Appendix A). This result suggests a possible constraint on growth in response to module loss. Because naturally created fragments of *W. subtorquata* vary in shape as well as size, this growth constraint may have a strong influence on growth potential after module loss.

The first aim of this experiment was to determine the extent to which the length of growing margin of a colony determines growth. We did this by keeping the size (i.e., number of zooids) of fragments constant, but varying the length of their growing margin. This part of the experiment had two treatments (Fig. 1d): (1) square fragments were 8×8 mm and were created by removing the zooids at the edge of a large colony to leave a square fragment at the original colony edge; and (2) thin, rectangular fragments were 4×16 mm and were created by removing zooids to leave a thin rectangular fragment at the original colony edge. Thin rectangular fragments were composed of the same number of zooids as square fragments, but had twice the length of growing edge (16 mm compared to 8 mm).

The second aim of this experiment was to determine whether fragments with equal lengths of growing edge

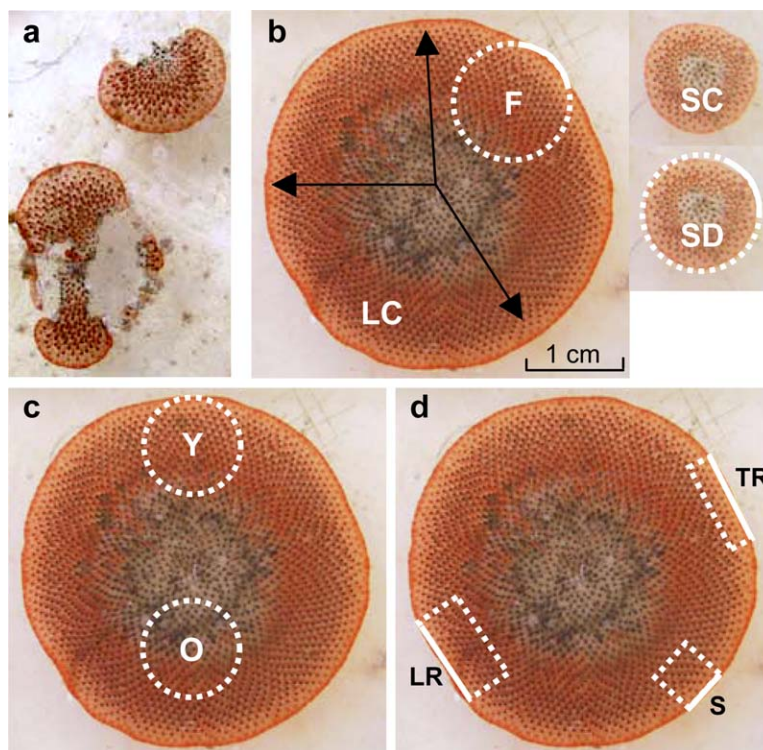


FIG. 1. (a) Naturally occurring fragments in *Watersipora subtorquata*, an encrusting bryozoan. (b) Treatments in experiment 1: fragment from a large colony, F; large control, LC; small control, SC; and small, damaged, SD. Arrows indicate proximal distal direction of growth in unfragmented colonies. (c) Treatments in experiment 2: fragment composed of young zooids from the edge of a large colony, Y; and fragment composed of old zooids from near the center of a large colony, O. (d) Treatments in experiment 3: square fragment, S; thin, rectangular fragment, TR; and large, rectangular fragment, LR. Solid white lines indicate undamaged edges; stippled white lines indicate damaged edges. Experiments were done at Breakwater Pier in Williamstown, a temperate location at the northern end of Port Phillip Bay in southern Australia.

but different numbers of zooids (i.e., different size) have different abilities to grow. This required a third treatment (Fig. 1d): (3) large rectangular fragments were 8×16 mm and had the same length of growing edge but twice the number of zooids than thin rectangular fragments.

Fragments in each of the three treatments came from the same colonies. After two weeks we measured colony size. We calculated growth and growth per unit size to determine the extent to which all zooids are contributing to growth in a colony.

Statistical analyses

We used one-way ANOVA and repeated-measures ANOVA (RM ANOVA) to analyze our results. Treatment was a fixed factor in all analyses and time was a fixed, repeated factor in RM ANOVA. Where separate treatments came from the same colony (experiments 2 and 3), colony was a blocking factor. In experiment 3 we used planned comparisons to compare specific treatments. Statistical analyses were performed using SYSTAT 11 (SPSS), and statistical significance levels were set at $\alpha = 0.05$.

RESULTS

Experiment 1: effects of colony size, colony age, and damage

The growth of fragments could not be described by the three explanatory models based on current size, history, or damage. Growth of fragments was lower than the other treatments throughout the experiment (Fig. 1a; Appendix B: Table B1). Averaged over the duration of the experiment, fragments grew 76% less than large controls, 51% less than small controls, and 32% less than small, damaged colonies. When growth was adjusted for size, fragments still performed poorly, particularly in the first two weeks after fragmentation (Fig. 2b; Appendix B: Table B1). There was a significant time \times treatment interaction in this analysis that occurred because the growth of fragments and small, damaged colonies increased over time relative to the small and large control colonies, i.e., there was some recovery in relative growth in fragments and small, damaged colonies, even though absolute growth remained low (Fig. 2a, b). There was little difference in relative growth between the small and large control colonies throughout the experiment.

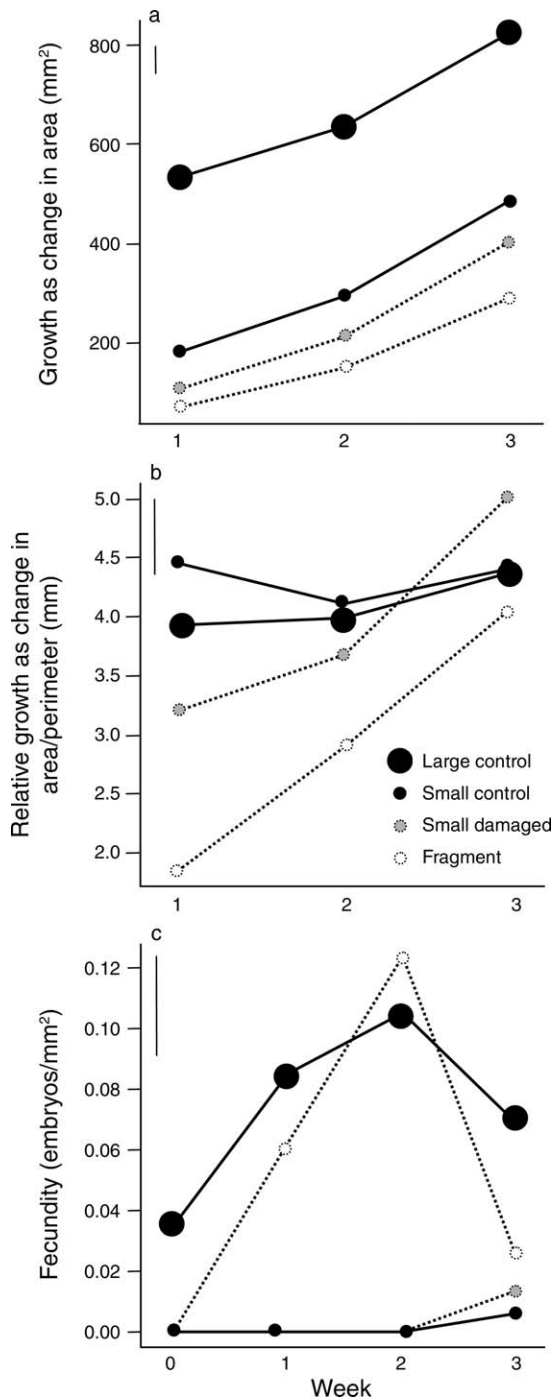


FIG. 2. (a) Growth, (b) relative growth, and (c) fecundity of *Watersipora subtorquata* colonies in experiment 1; measurements were made weekly for three weeks. Relative growth is calculated as the change in area (measured in mm²) divided by initial perimeter (measured in mm). Error bars appear in the top left corner of each plot and equal the root mean square of the within-subjects term in the repeated-measures (RM) ANOVA.

The pattern of reproduction in fragments was most similar to large control colonies (Fig. 2c). Fragments began reproducing earlier (week one) and therefore at a much smaller size than small control and small, damaged colonies (Fig. 2c). Indeed, small control and small, damaged colonies did not become reproductive until the end of the experiment. Large control colonies were reproductive for the duration of the experiment. An RM ANOVA indicated a significant time \times treatment interaction (Appendix B: Table B1). The interaction occurred because fragments had similar fecundity to large control colonies during weeks one and two, but not at the beginning and end of the experiment. In particular, the fecundity of fragments decreased markedly in the third week of the experiment to be more similar to the small, damaged and small control treatments.

Experiment 2: effects of modular demography

Fragments composed of modules of different ages had very different capacities for growth and reproduction (Fig. 3; Appendices A and B: Table B2). Young fragments grew whereas old fragments did not (Fig. 3a). Old fragments actually decreased in size because partial mortality (i.e., zooid senescence) occurred at a higher rate than growth. In contrast, young fragments were able to quickly regenerate a growing edge and then continued to increase in size for the rest of the experiment (Fig. 4a).

Repeated-measures ANOVA on fecundity indicated a complex time \times treatment interaction (Fig. 3b; Appendix B: Table B2). Old fragments were reproductive at the beginning of the experiment but their fecundity declined through time. In contrast, young fragments did not become reproductive until week one but then had a net increase in fecundity through time. The decline in fecundity in old fragments coincided with the death of the zooids of which these fragments were composed.

Experiment 3: effects of size and growth constraints

Fragments that differed in size and shape with respect to the length of their growing margin showed different capacities for growth (Fig. 4a; Appendix B: Table B3). The thin rectangular fragment grew substantially more than the square fragment despite both these treatments being the same size. Growth of large, rectangular fragments and thin, rectangular fragments was similar despite the large, rectangular fragments being twice the size of the thin, rectangular fragments. Both the thin, rectangular fragments and large, rectangular colonies grew significantly more than square colonies. In all treatments, most growth occurred from the distal growing edge (Appendix C).

We also compared growth adjusted according to initial colony size (Fig. 4b; Appendix B: Table B3). In this comparison, thin, rectangular fragments grew more per unit size than the other two treatments. Large,

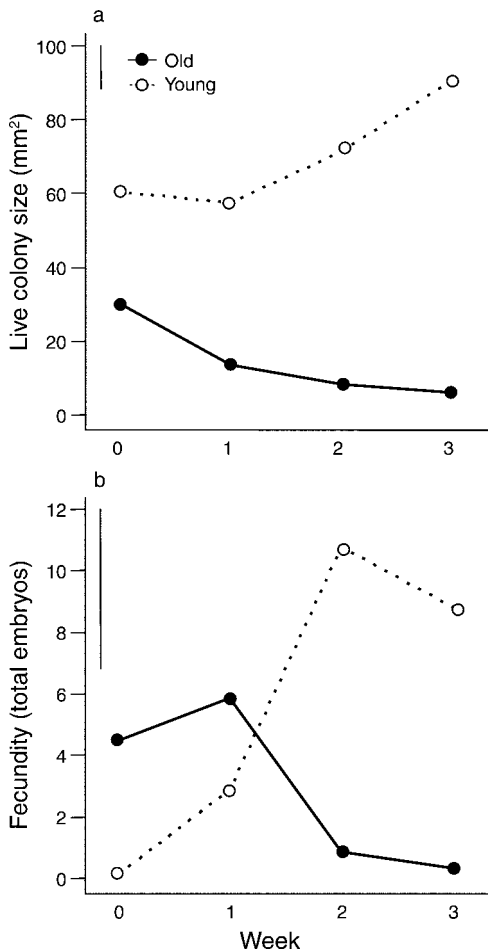


FIG. 3. (a) Growth and (b) fecundity of colonies composed of young and old zooids. Error bars appear in the top left corner of the plots and equal the root mean square of the within-subjects term in the repeated-measures (RM) ANOVA.

rectangular fragments and square fragments had similar levels of growth per unit size.

DISCUSSION

Module loss in *W. subtorquata* has broad consequences for a colony that are independent of a simple decrease in size. A decrease in size in *W. subtorquata* results in lower growth and fecundity compared with large colonies of equivalent age that have not decreased in size, and lower growth and higher fecundity than equivalent-sized individuals (Fig. 2). While many studies have investigated the effect of damage, defoliation, fragmentation, and module loss in a range of modular taxa, our study is unique in that it compares individuals of equivalent size (and age) but with different size histories. Our results show that single-state variables such as size are poor predictors of demographic fate in *W. subtorquata* because a history of module loss alters growth and reproduction so that individuals that are the

same size but have different size histories have different demographic fates.

Flexible growth and form and an ability to reallocate resources according to changing demands are assumed to be primary advantages of modularity (Oren et al. 2001, Sanchez and Lasker 2004). However, *W. subtorquata* did not demonstrate such flexibility in response to a decrease in size. Many modular taxa divert resources to regeneration and growth at the expense of reproduction after damage (Henry and Hart 2005, Brody et al. 2007), and many taxa can partially compensate for a decrease in size (Strauss and Agrawal 1999, Haukioja and Koricheva 2000, Stowe et al. 2000, Tiffin 2000). Although *W. subtorquata* did recover its relative growth (Fig. 2b), colonies did not fully compensate for a decrease in size; absolute growth and reproduction remained lower than in unfragmented colonies. While some plants fully compensate for a decrease in size (Paige and Whitham 1987), what is clear from our results and most other studies is that there are limits on the ability of individuals to respond to module

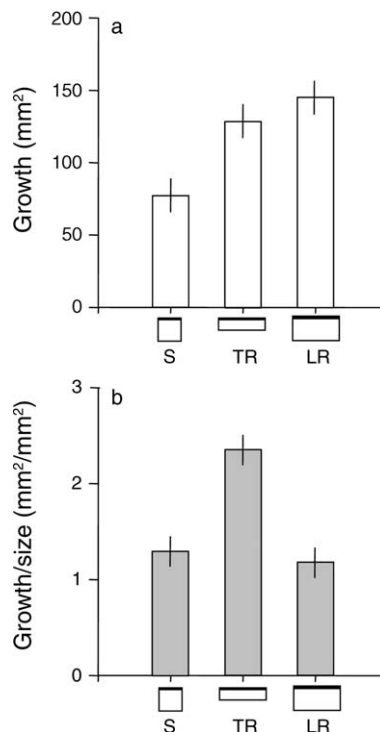


FIG. 4. (a) Growth and (b) growth per unit live area (mean \pm SE) of colonies that differ in their size and/or length of growing margin. Boxes on the x-axis are a schematic representation of the three fragment types in this experiment, showing their relative dimensions, including the length of intact growing margin (thicker line). From left to right on each plot these fragment types are: square (S); thin rectangle (TR); and large rectangle (LR). Square and thin rectangular fragments are the same size but have different lengths of growing margin. Large rectangular fragments are twice the size of thin rectangular fragments, but these two treatments have the same length of growing margin.

loss (Bigger and Marvier 1998, Hawkes and Sullivan 2001). These limits depend on levels of integration within an individual and constraints on resource transport and allocation among modules (Marquis 1992).

Growth in most modular organisms relies on highly localized growing regions such as meristems in plants, growing tips in branching corals and arborescent bryozoans, and growing margins in sheet-like corals, bryozoans, and ascidians. Removal of modules changes the location and activity of these growing regions, which disrupts normal patterns of growth (Doak 1991, Strauss and Agrawal 1999, Tiffin 2000, Sanchez and Lasker 2004). In *W. subtorquata* and other encrusting bryozoans, growth normally occurs adjacent to young zooids along the entire margin of a colony (Fig. 1). Fragmentation creates new colony margins, but *W. subtorquata* is only capable of substantial regeneration at or near the original growing edge (Fig. 4, Appendices A and C). Some plants, corals, and bryozoans can respond to a decrease in size by initiating growth in new locations (e.g., axillary meristems in plants) or by increasing growth in unaffected areas (Paige and Whitham 1987, Harvell and Helling 1993, Sanchez and Lasker 2004). However, *W. subtorquata* does not respond to the loss of growing regions by growing from new margins or by increasing growth through the original margin (Fig. 4). Despite differences in the details of their response to a decrease in size, what is consistent among these taxa is that the growth of an individual is not dependent solely on current size. Growth in *W. subtorquata* and in other modular taxa may be better described by the number and size of actively growing regions, rather than individual size per se (also see Stowe et al. 2000).

Most studies of reproduction in modular organisms emphasize the age or size dependence of reproduction (Law 1983, Lacey 1986, Klinkhamer et al. 1992, Kapela and Lasker 1999, Childs et al. 2003, Burd et al. 2006). Our results are a clear departure from these studies because the reproductive characteristics of *W. subtorquata* are not determined by colony size or age. In our second experiment, fragments composed of old zooids were reproductive at the time of fragmentation but their fecundity declined as zooids senesced (and were not replaced), whereas fragments composed of young zooids were not initially reproductive but their fecundity increased over time (Fig. 3b). These results indicate that zooids become reproductive as they age so that the reproductive characteristics of an individual are determined at the module level. Because fragments are derived from larger, older colonies, they are more likely to contain older modules and therefore become reproductive earlier and at smaller sizes than unfragmented individuals of equivalent size (Fig. 2c). The pattern of reproduction has strong consequences for the manner in which an individual is likely to respond to a decrease in size. Many modular taxa delay reproduction and/or have reduced fecundity in response to a decrease in size

(Lennartsson et al. 1997, Bone and Keough 2005, Henry and Hart 2005, Brathen and Junttila 2006), but this did not occur in *W. subtorquata*.

There is a strong effect of modular demography on the growth, reproduction, and survival of individuals after a decrease in size (Fig. 3). Our results support the suggestion by Hughes (1984) that the response of an individual to module loss will depend critically on the type of modules that remain. Zooids in *W. subtorquata* are isomorphic and so modular demography influences performance as a consequence of the aging of zooids. In many species of bryozoan, zooids delay senescence and instead go through several cycles of degeneration and regeneration known as polypide cycling, and this is likely to further complicate the effects seen in *W. subtorquata*. Modules deteriorate with age in other bryozoans and in corals and plants (Meesters and Bak 1995, Bayer and Todd 1997, Munne-Bosch 2007) and so similar effects to those seen in *W. subtorquata* may be expected in these taxa. However, in many modular organisms individual modules are specialized for support, growth, reproduction, and defense, and so the effects of modular demography in many taxa could be far greater than our results suggest. The nature of these effects will vary depending on the configuration of the modules that remain, but the influence of modular demography has the potential to generate enormous variability in demographic rates among individuals of similar age and size.

Consequences for population demographics of modular organisms

Established methods to describe population demography of modular organisms rely on the choice of an appropriate state variable, which should be an accurate predictor of an individual's demographic fate (Law 1983, Caswell 2001). These models typically use simple state descriptors such as size or age (Caswell 2001). In *W. subtorquata*, however, models based purely on size will consistently overestimate state transition probabilities and, counterintuitively, underestimate the reproductive contribution of smaller colonies to population persistence. A further, major consequence of our findings is that field-derived, empirical estimates of demographic fates based on size will not actually measure the true size dependence of demographic fates, but will also include the complicating influence of fragmentation. Such measurements may be useful for population projections if fragmentation rates are the same among populations or constant through time. However, variable fragmentation rates (caused by disturbance, for example) will cause time-invariant projection matrices to overestimate population growth rates and final population sizes (e.g., Boyce et al. 2006). More complex population demographic models allow classification of individuals by more than one state variable (Linacre and Keough 2003, Pfister and Wang 2005, Ellner and Rees 2006). Even these more complex

models, however, would treat all fragments as having the same demographic properties. In *W. subtorquata*, all fragments are not equal; demographic differences between old and young fragments and between fragments of different shapes are substantial. These differences appear large enough to significantly affect population trajectories and so would need to be incorporated into any demographic model.

Module loss in *W. subtorquata* has large effects apart from a simple decrease in size, and there are strong indications that this is also likely in other modular taxa. The implications of our results pose several problems for existing demographic models that are not easily resolved. To understand the inaccuracy of existing models and to improve our understanding of the demography of modular organisms, future models will require estimates of the rate and consequences of module loss in the field. In the meantime, it is clear that standard approaches for modeling demography of modular organisms need to be applied carefully.

ACKNOWLEDGMENTS

We thank P. Hart, K. Hutson, T. Ng, D. Marshall, and the Keough laboratory for their valuable assistance in the field. This manuscript was improved substantially through discussions and helpful comments from K. Monro, S. Burgess, D. Marshall, J. Carey, and L. Morris, as well as one anonymous reviewer. This work was funded by an Australian Research Council grant to M. J. Keough.

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APPENDIX A

The effect of modular demography (module age) on growth showing unidirectional growth in young fragments and limited regeneration in old fragments (*Ecological Archives* E090-114-A1).

APPENDIX B

Repeated-measures (RM) ANOVA comparing growth, relative growth, and fecundity among colonies in experiment 1, RM ANOVA comparing size and fecundity of young and old fragments in experiment 2, and ANOVA comparing growth of colonies that differ in their size and length of growing margin followed by planned contrasts in experiment 3 (*Ecological Archives* E090-114-A2).

APPENDIX C

Effects of size and distal-edge length on growth in *Watersipora subtorquata* (*Ecological Archives* E090-114-A3).