

Life-History Differences among Coral Reef Sponges Promote Mutualism or Exploitation of Mutualism by Influencing Partner Fidelity Feedback

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ABSTRACT: Mutualism can be favored over exploitation of mutualism when interests of potential heterospecific partners are aligned so that individual organisms are beneficial to each others' continued growth, survival, and reproduction, that is, when exploitation of a particular partner individual is costly. A coral reef sponge system is particularly amenable to field experiments probing how costs of exploitation can be influenced by life-history characteristics. Pairwise associations among three of the sponge species are mutually beneficial. A fourth species, *Desmapsamma anchorata*, exploits these mutualisms. *Desmapsamma* also differs from the other species by growing faster, fragmenting more readily, and suffering higher mortality rates. Evaluating costs and benefits of association in the context of the complex life histories of these asexually fragmenting sponges shows costs of exploitation to be high for the mutualistic species but very low for this essentially weedy species. Although it benefits from association more than the mutualist species, by relying on their superior tensile strength and extensibility to reduce damage by physical disturbance, exploitation is favored because each individual host is of only ephemeral use. These sponges illustrate how life-history differences can influence the duration of association between individuals and, thus, the role of partner fidelity in promoting mutualism.

Keywords: sponges, mutualism, partner fidelity, asexual fragmentation, weed strategies, exploitation.

Why some species participate in mutualisms while other species exploit mutualisms remains one of the more intriguing questions about interspecific interactions (e.g.,

overviews in Bronstein 1994, 2001*b*; Herre et al. 1999; Hoeksema and Bruna 2000; Stanton 2003; Thomson 2003; Sachs et al. 2004; Sachs and Simms 2006). Exploitation is promoted if there are conflicts of interest between potentially mutualistic partner species, whereas mutualism is promoted by factors that align interests. Several authors of recent theory and review articles have evaluated what specific factors might favor mutualism over exploitation of mutualism. For example, Herre et al. (1999) focused attention on how mutualism is promoted by vertical transmission of symbionts, a single symbiont genotype within a host, and population spatial structures that facilitate repeated interactions among potential mutualists and minimize other options. Hoeksema and Bruna (2000) showed that partner interests can align when benefits are symmetrical to the partners, partner species differ in their resource preferences, and successful transmission of a symbiont depends on a long-lived host. Likewise, Yu (2001) stressed the importance of reliable reassembly and the original benefit-donor (or its offspring) receiving the reciprocated benefit. Finally, a model by Foster and Wenseleers (2006) identified high benefit-to-cost ratios for heterospecific interactions, high within-species relatedness, and high between-species fidelity as helping mutualisms withstand the threat of exploitation.

In common among many of these mutualism-promoting factors is that they align interests of species by increasing how beneficial an individual (or clone or colony) of one species is to the continued survival, growth, and reproduction of a particular individual of the partner species. If fitness benefits are gained as long as the association is maintained, an exploiter risks damaging itself if it damages its partner, favoring mutualism without need for special sanctions against exploiters (i.e., "passive retaliation" in the sense of Bull and Rice [1991]). This has been referred to as "partner fidelity" by Bull and Rice (1991) and Sachs et al. (2004) and as "community of interest" by Leigh (2001) and has played a prominent role in discussions of

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parasite or pathogen virulence (e.g., Lewontin 1970; May and Anderson 1983, 1990; Leigh and Rowell 1995).

As pointed out by Bronstein (2001*b*), mutualisms that persist despite a lack of special sanctions against exploiters are only puzzling if exploitation confers benefits, and mutualism extracts costs. Determining whether mutualism (both heterospecific partners benefit from their interaction) or exploitation (in this case, a species-level characteristic, with one partner species accepting benefits but failing to provide benefits) is the superior strategy in any given example therefore hinges on appropriate evaluation of benefits and costs of interaction. Ideally, this involves monitoring individuals throughout their life cycles, but following individual mutualists is often difficult because one partner is very small or lives deeply embedded in the other, or individuals are constantly moving and otherwise thwarting repeated observations, or the partners cannot be dissociated for experimental comparisons because the association is obligate. For clonal organisms, monitoring individuals throughout their lives is further stymied by asexual propagation, complicating definitions of generation time and even of individuals. Nevertheless, the key roles of “directed reciprocity” (Sachs et al. 2004) via partner fidelity and partner choice in promoting mutualism cannot be tested empirically without following the dynamics of association between particular individuals to see whether they are, in fact, loyal to each other or whether they deploy sanctions adaptively. This requirement has spurred creative and elegant experimental approaches in which associated individuals, colonies, or clones have been followed through key portions of their life cycles (e.g., Kiers et al. 2003; Poulsen et al. 2003; Sachs and Bull 2005; Edwards et al. 2006; Sachs and Wilcox 2006; Simms et al. 2006; Mikheyev et al. 2007).

A set of mutualisms among coral reef sponge species is highly amenable to experimental manipulation in the field, offering a chance to explore the hypothesis that life histories that increase opportunities for long-term partner fidelity favor mutualism, whereas life histories that result in more ephemeral associations favor exploitation. The sponge associations are facultative, allowing comparisons of solo individuals with associated individuals, and participating individuals are continuously associated with each other and immobile. All participants are large sponges that are readily subdivided, allowing both genotype and size to be controlled in experiments and for growth and mortality to be measured in the field. The specific system involves three Caribbean species of large erect, branching coral reef sponges (*Iotrochota birotulata* [Higgin], *Amphimedon compressa* Duchassaing & Michelotti, and *Aplysina fulva* [Pallas]) for which growth and survival are improved by living adherent to a heterospecific sponge of these same three species (Wulff 1997). Individuals of a

fourth species (*Desmapsamma anchorata* [Carter]) can overgrow—and sometimes appear to smother—sponges of the three mutualistic species. The proximate aim of this study was to test the hypothesis that this fourth species is an exploiter, gaining by adhering to sponges of other species as if it were participating in the mutualism but failing to reciprocate and even causing harm.

Of more general interest to the theory of mutualism and its exploitation is the question of why a particular species plays the role of exploiter in an otherwise mutualistic system. Circumstances under which partner fidelity feedback might be expected to break down include different generation times of partner species, horizontal rather than vertical transmission of symbionts, and partners not being a limiting resource (e.g., Sachs et al. 2004). Although these seem to be heterogeneous circumstances, all of them directly influence the costs and benefits of continuing to maintain an association with a particular individual of the partner species. If the duration of the fitness benefit that partner individuals can provide influences development of mutualism versus exploitation, the exploiting species should be the one with the least potential for long-term gain from maintaining an association. Thus, I tested the series of hypotheses that (a) the fourth sponge species benefits from associating with the three mutualistic species and (b) fails to reciprocate but (c) avoids negative repercussions from harming associated sponges because its life-history characteristics result in relatively ephemeral associations with individuals of the mutualistic species.

Complex life cycles of these sponge species, in which asexual fragmentation, partial mortality, and indeterminate growth figure prominently, prompted design of a variety of experiments comparing associated versus solo individuals of the same genotype at different life-cycle stages. Life-cycle stages were defined by sizes of individuals, with established individuals distinguished from detached fragments. Transitions among stages are accomplished by growth, fragmentation, reattachment, and partial mortality (fig. 1), as has been discussed and depicted by Hughes (fig. 2, 1984), Jackson and Hughes (fig. 1, 1985), Caswell (fig. 6.7, 1985), and Gaino et al. (fig. 6, 1995). Experiments were monitored long enough (2–25 months) to quantify transition rates among life-cycle stages. Measurements of growth, mortality, susceptibility to fragmentation, and reattachment provided a life-history context for interpreting costs and benefits of association.

Study System: The Sponge Mutualisms

Sponges are among the most diverse and abundant sessile animals on coral reefs and in many other marine ecosys-

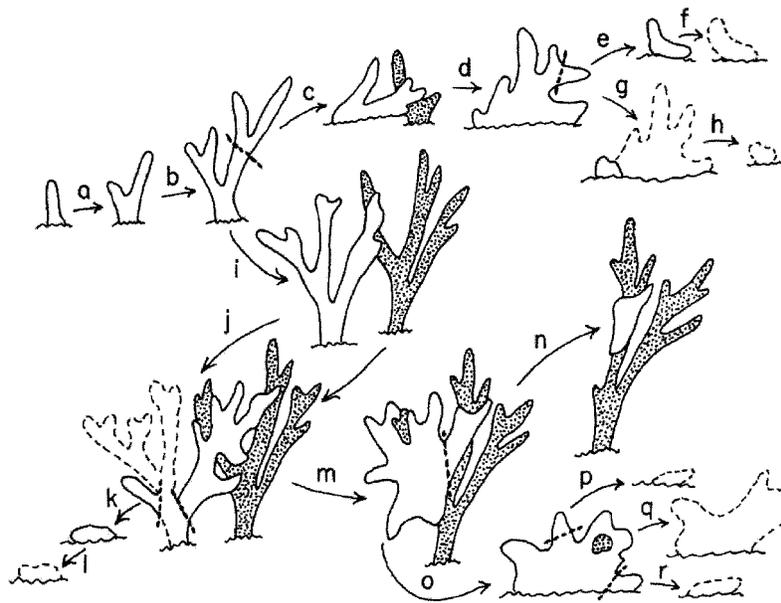


Figure 1: Summary of a typical life cycle of *Desmapsamma anchorata*, illustrated as a series of snapshots in time of the increasingly more fragmented pieces of a single genotype. Arrows indicate the passage of time (1–3 months) for transitions between stages, which are mediated by various combinations of growth (a–d, i, j, m), breakage (b, d, k, o, p, r), reattachment and growth of asexual fragments (c, e, k, o), death of fragments (f, h, l, p–r), partial mortality of established individuals by pieces breaking off and dying (j, k), attachment to neighboring heterospecific sponges (c, i, n), relinquishing its grip on all but a heterospecific sponge (m, n), and overgrowth of heterospecific neighbors that can cause their breakage or death (d, o). *Desmapsamma anchorata* is indicated by absence of shading; a different species (e.g., *Iotrochota birotulata*) is stippled; heavy, dotted straight lines indicate fragment generation by breakage; light dashed lines indicate mortality (quickly followed by complete disintegration) of the included portion.

tems (e.g., Diaz and Rützler 2001; Wulff 2001). Some of their success may be related to mutualistic associations with many types of organisms (review in Wulff 2006a), including heterospecific sponges. Although associations in which sponges of different species grow over or adhere to each other would reasonably be expected to be intensely competitive, since sponges are efficient filter feeders that pull water in through pores on their surfaces; the possibility of mutual benefit for participating sponge species was pointed out by Sarà (1970) and by Rützler (1970), working in the Mediterranean and Adriatic seas 37 years ago, and confirmed more recently by Sim (1997), Wulff (1997), and Wilcox et al. (2002).

The mechanism for increased survival of the coral reef sponges *Iotrochota birotulata*, *Amphimedon compressa*, and *Aplysina fulva* when they adhere to each other depends on differences among these species in their abilities to resist a variety of environmental hazards, including predators, storms, pathogens, and sediment (Wulff 1997). For example, if neighboring individuals of *Aplysina* and *Amphimedon* adhere to each other, and the base of the *Aplysina* is devoured by a sea star, the remainder of the sponge is held erect, in growth position and protected from further

sea star predation, by its attachment to the *Amphimedon*, which is unpalatable to sea stars (Wulff 1995b, 1997). In turn, if the base of the *Amphimedon* is broken by a storm wave, the sponge evades the dangers of being unattached (with a substantial 70% rate mortality per year in this habitat; Wulff 1985b) by its attachment to *Aplysina*, which better resists breakage by storm waves (Wulff 1995a, 1997).

Mutualism was experimentally analyzed for only these three species, but other sponge species commonly adhere to these species in stable associations (Wulff 1997) and may participate in these mutualisms. Sponges have been demonstrated to discourage adherence by other conspecific (e.g., Van de Vyver 1970; Hildemann et al. 1980; Kaye and Ortiz 1981; Bigger et al. 1983; Wulff 1986) and, in one case, heterospecific individuals (e.g., Thacker et al. 1998), but in order to participate in these mutualisms, sponges must allow heterospecific sponges to adhere to them. This opens the possibility that species that cause harm may also adhere. Observations of the common reef sponge *Desmapsamma anchorata* growing over other sponges to the point that they were smothered suggested that it could be exploiting these mutualisms.

Material and Methods

Distribution and Abundance Patterns and Study Site Description

The study site was on a coral reef in the lee of Guigalatupo Island, San Blas Islands, Republic of Panama (map in Wulff 1995*b*). The substratum, at 2.8–3.5 m below mean low water, is carbonate sand, coral rubble, and corals in the genera *Diploria*, *Agaricia*, and *Montastraea*. Sponges covered about 20% of the bottom and dominated this community in species diversity and biomass. The most abundant (by volume) were *Iotrochota birotulata*, *Amphimedon compressa*, *Aplysina fulva*, *Desmapsamma anchorata*, *Mycale laevis* (Carter), *Niphates erecta* Duchassaing & Michelotti, *Callyspongia vaginalis* (Lamarck), *Lissodendoryx colombiensis* Zea & van Soest, *Verongula rigida* (Esper), and several *Ircinia* species. This part of the Guigalatupo reef is slightly deeper and more protected than the site of previously described experiments (e.g., Wulff 1991, 1995*a*, 1997, 2006*b*). Experiments and observations were made between 1982 and 2000. Initially, *D. anchorata* had appeared to be a fourth mutualistic species, and it was included in investigations of the mutualisms (Wulff 1997) until consistently different results sparked design of a complementary set of experiments and observations.

All *D. anchorata* individuals in a 10 × 10-m area within the study site were measured in all dimensions for calculation of volume by approximation to appropriate conglomerations of geometric solids. Each individual was described with respect to attachment (to another sponge or sponges, to sponge and solid carbonate, or to solid carbonate only) and health (undamaged or recently damaged).

Growth, Survival, and Susceptibility to Fragmentation

Growth rates of 50 unmanipulated *D. anchorata* individuals in a range of initial sizes (2.5–340.4 cm³) were determined by making measurements from which volumes could be calculated, at time = 0, 9, and 22 months. For additional measures of growth and survival, on individuals standardized by initial size, shape, substratum type, and orientation, 35 *D. anchorata* branch pieces 10 cm long were cut from their parent sponges. These pieces were attached with small nylon cable ties to pieces of clean coral rubble gripped by stainless steel stakes (method described for the other three species in Wulff 1991). The stakes were inserted into the reef so sponges could maintain normal growth position on natural carbonate substrata, and sponges were monitored for survival and growth at 3, 5, and 15 months.

To evaluate susceptibility to fragmentation, *D. anchorata* branches ($n = 25$) 0.8–2.8 cm wide were cut to 8 cm long,

and each was stretched to the breaking point (as described in Wulff 1997). Extension before breaking and the force applied at breaking (i.e., breaking stress and strain) were recorded.

Experiment 1: Fragment Dispersal, Reattachment, and Survival, Alone and in Heterospecific Pairs

Branches were cut to 8 cm long, generating fragments of (a) *D. anchorata*, (b) *I. birotulata*, (c) *A. compressa*, and (d) *A. fulva* alone, as well as pairs (bound together lengthwise by a small cable tie with the loose end clipped off) of (e) *I. birotulata* with *D. anchorata*, (f) *A. compressa* with *D. anchorata*, and (g) *A. fulva* with *D. anchorata*. Sample size was 32 for *D. anchorata* alone and 16 for each of the other types. These 112 fragments were tagged with small cable ties and released at eight marked sites in the midst of the sponge community from which they were derived. Their dispersal, reattachment, and survival were monitored at intervals for 2 months.

Experiment 2: Growth, Survival, and Competitive Interactions of Size-Matched Individuals in Conspecific versus Heterospecific Pairs

To compare growth and survival of size-matched individuals in conspecific versus heterospecific pairs, *D. anchorata* branches were cut to 8 cm and grown on stakes with either another *D. anchorata* individual or an 8-cm-long individual of *I. birotulata*, *A. compressa*, or *A. fulva*. These 56 *D. anchorata* individuals and 42 individuals of the other three species (14 individuals in each combination) were monitored at 5, 12, and 25 months.

*Experiment 3: Growth and Survival of *D. anchorata* on Solid Carbonate versus Heterospecific Sponges*

Desmapsamma anchorata branches, cut to 4 cm long, were attached to branches of individuals of *I. birotulata*, *A. compressa*, and *A. fulva* with small cable ties, creating associations in which the *D. anchorata* individuals were very small relative to individuals of the other species. The control for each experimental sponge was a branch piece of the same genotype (cut from the same large “parent” sponge individual) and initial size that was attached with cable ties to coral rubble on a stake. Experimental and control sponges were as close to the same height above the substratum as possible, to minimize water flow differences. This experiment was done twice, with 14 same-genotype pairs attached to each of the other three sponge species and to coral rubble each time (a total of 168 *D. anchorata* individuals) and each time monitored every few weeks for 14 weeks and at 6 months. Measurements of all

dimensions of each sponge were converted into volumes by approximation to geometric solids.

To determine whether *D. anchorata* affects the growth of sponges to which it adheres, the branch width and the distance on the host sponge branch from the cable tie holding the *D. anchorata* to the tip of the branch were measured at time = 0 and after 14 weeks. The same measurements were made using as reference point a cable tie placed a similar distance down an unencumbered branch of the host sponge.

Experiment 4: Association of Small D. anchorata with Large Heterospecific Sponges and of Large D. anchorata with Small Heterospecific Sponges

Natural development of associations between *D. anchorata* and other species was mimicked by exchanging branch pieces between neighboring conspecific or heterospecific sponge individuals. Branch pieces 4 cm long were cut from each sponge and attached to a branch of the neighboring sponge with a small cable tie, again producing size-disparate heterospecific associations, including large *D. anchorata* individuals with very small individuals of the other species and vice versa. Eight replicates of each combination of *D. anchorata* with *I. birotulata*, *A. compressa*, *A. fulva*, *N. erecta*, and *C. vaginalis* and other *D. anchorata* (i.e., a total of 48 *D. anchorata* branch pieces and eight branch pieces of each of the other five sponge species) were monitored at 3, 9, and 17 months.

Results

Distribution and Abundance Patterns

A total of 157 *Desmapsamma anchorata* individuals, ranging in size from $<0.1 \text{ cm}^3$ to 660.5 cm^3 , and with a total combined volume of $11,280 \text{ cm}^3$, were living in the censused 100 m^2 . In this area, 54% of *D. anchorata* individuals (61% of the total volume) were growing solely on heterospecific sponges of seven species (frequency of adherence is given as percent of a total of 125): *Aplysina fulva* (52%), *Amphimedon compressa* (20%), *Irochota birotulata* (13.6%), *Callyspongia vaginalis* (9.6%), *Mycale laevis* (2.4%), *Niphates erecta* (1.6%), and *Lissodendoryx colombiensis* (0.8%). Frequency of adherence to sponges of particular species appeared to reflect relative abundance and growth form, but this was not studied in detail. *Desmapsamma anchorata* individuals growing on other sponges were often so large that 30.4% of them were attached to more than one other sponge.

Only 35% of the individuals were attached solely to solid carbonate substrata (11% were on both sponges and car-

bonate), and these were disproportionately the smaller individuals ($<50 \text{ cm}^3$; G-test, $P < .01$; fig. 2). Recent damage (by breakage) was evident on 20% of the individuals on carbonate substrata, but on only 1.2% of the individuals growing on other sponges.

Growth, Survival, and Susceptibility to Fragmentation

By 9 months, only eight of the unmanipulated 50 individuals survived (fig. 3A), and three of those had decreased in size. Although most of the 50 individuals were attached to solid carbonate substrata at time = 0, all eight survivors were attached solely to heterospecific sponges. By 22 months, only one individual survived, and it had decreased to $<1 \text{ cm}^3$.

The small, size-standardized (10 cm long) *D. anchorata* also survived poorly, with mortality at 45% by 5 months and 100% by 15 months (fig. 3B). For the three mutualist species, detachment from experimental substrata is best described as loss because all or part of a detached individual can sometimes be found nearby, and survival is 30% for loose fragments during the year after detachment in this habitat (Wulff 1985b). However, *D. anchorata* individuals that were not on their original substrata were never found, so their loss is equivalent to mortality.

Net size change reflects partial mortality (generally, breakage followed by mortality of the fragments; fig. 1) as well as growth, so growth rate over long periods is best estimated by maximum size increases. Specific growth rates (i.e., standardized by initial size) of the three un-

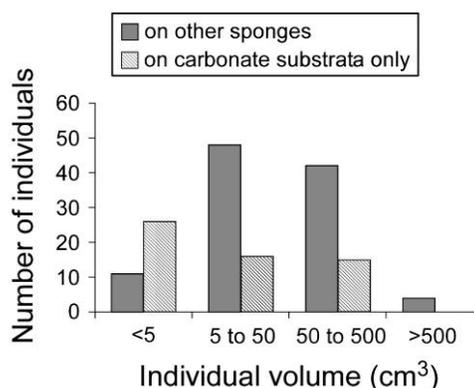


Figure 2: Natural abundance of *Desmapsamma anchorata* on other sponges versus solid carbonate substrata. Size frequency distribution of 157 individuals living on other sponges (and sometimes on carbonate substrata as well) or on solid carbonate substrate only (i.e., coral skeletons) in a $10 \times 10\text{-m}$ area of shallow reef, San Blas, Panama, in May 1998. Note that the size categories increase by orders of magnitude.

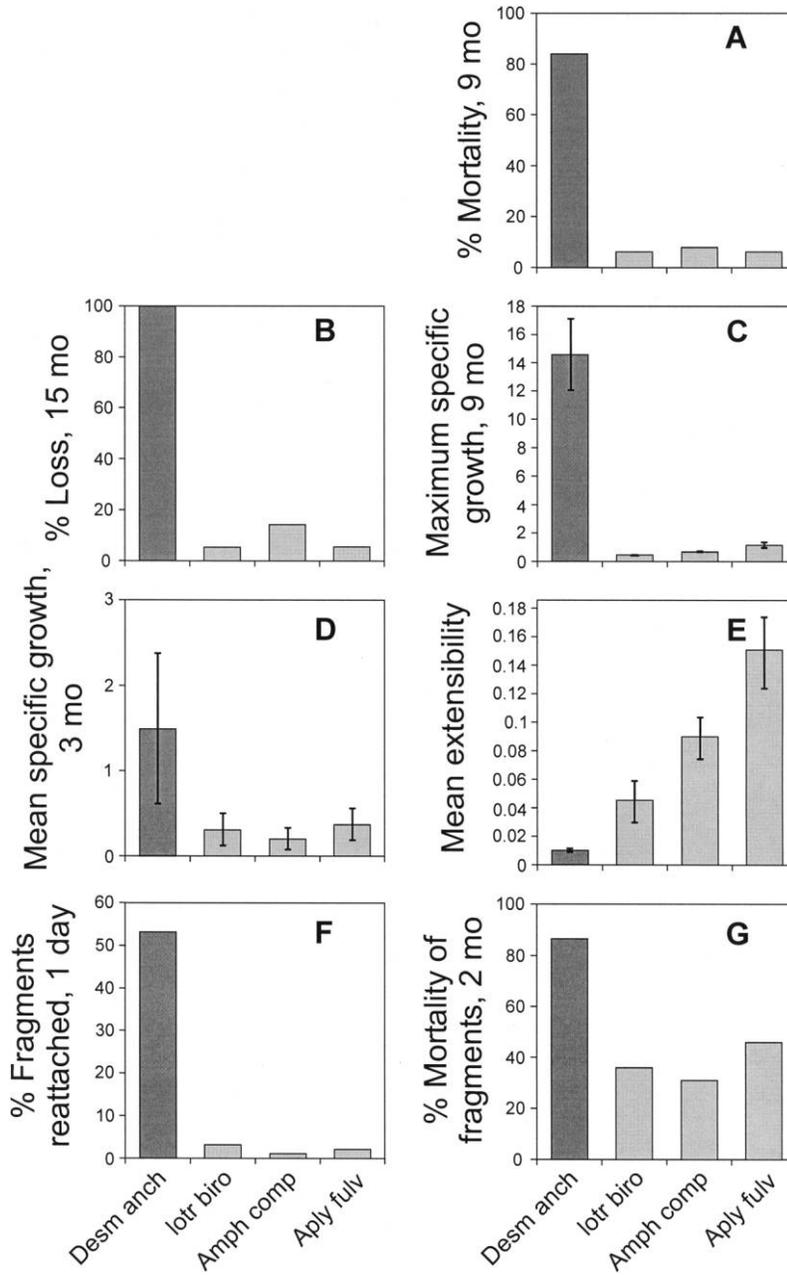


Figure 3: Characteristics influencing life histories of *Desmamma anchorata* (*Desm anch* in the figure) compared with those of *Iotrochota birotulata* (*Iotr biro*), *Amphimedon compressa* (*Amph comp*), and *Aplysina fulva* (*Aply fulv*). A, Mortality of unmanipulated individuals of a wide range of sizes, after 9 months ($n = 50$ for each species). B, Percent of size-standardized (10 cm long) individuals lost from carbonate substrata after 15 months ($n = 35$ for each species). Loss is equivalent to mortality for *D. anchorata*. (Data for the other species are from Wulff 1991.) C, Maximum specific growth rate as a mean of the three individuals of each species that grew most rapidly ($n = 50$ initially, for each species). Bars represent standard errors of the means. (Data for *I. birotulata*, *A. compressa*, and *A. fulva* are from Wulff 1990.) D, Mean specific growth rate after 3 months for individuals cut to 10 cm long and attached to stable carbonate substrata. Bars represent standard errors of the means. E, Mean extensibility (i.e., resistance to breakage by storm waves) for 25 individuals of each species. (Data for *I. birotulata*, *A. compressa*, and *A. fulva* are from Wulff 1997.) Bars represent standard errors of the means. F, Percent of experimentally generated fragments that reattached within 1 day ($n = 16$ for each species). G, Percent mortality of experimentally generated fragments after 2 months ($n = 16$ for each species).

manipulated individuals that increased the most in 9 months were 10.2, 12.7, and 20.8 (fig. 3C). Mean specific growth rate of the sponges cut to a standard initial size was calculated at 3 months to minimize confounding of growth rates with partial mortality. Growth was rapid and variable (fig. 3D; mean specific growth = 1.5, SE = 0.88).

Desmapsamma anchorata branches began to break as soon as tension was applied. In 25 trials, the maximum extensibility (extension/original length at breaking) measured was 0.012 (fig. 3E). The maximum tensile strength (force/area at breaking) measured was 0.19 MPa.

Experiment 1: Fragment Dispersal, Reattachment, and Survival, Alone and in Heterospecific Pairs

Within 1 day, 53% of the experimentally generated *D. anchorata* fragments reattached to solid carbonate substrata, contrasting with 2% reattachment of the fragments of the other three species (fig. 3F). By 2 months, all surviving fragments of all species had reattached.

Survival after 2 months was 66.7% for fragments of *I. birotulata*, *A. compressa*, and *A. fulva* (data for these three species are combined for brevity in fig. 4A and corroborate 65.3% survival after 7 weeks for fragments of these species in an earlier experiment; $n = 100$ for each species; Wulff 1985b). In contrast, survival of *D. anchorata* fragments on their own was a meager 13% (fig. 3G). Combination with *D. anchorata* did not affect survival of the other three species (fig. 4A) but boosted survival of *D. anchorata* significantly, from 13% to 39% (G -test, $P < .001$). Partial mortality (generally, breakage followed by mortality of the fragments) affected 86.7% of surviving *D. anchorata* fragments (length decreased to a mean of 6 cm, SE = 1.3), but no fragments of the other three species were damaged. *Desmapsamma anchorata* fragments dispersed as far as 3.4 m in the first 2 weeks.

Experiment 2: Growth, Survival, and Competitive Interactions of Size-Matched Sponges in Conspecific versus Heterospecific Pairs

Desmapsamma anchorata individuals paired with size-matched sponges of the other three species survived better over the course of 25 months than those paired with other *D. anchorata* (difference significant by the G -test, $P < .025$; fig. 4B). This graph illustrates only loss of entire individuals, but when the substantial partial mortality is taken into account, the difference in survival between *D. anchorata* paired with heterospecific versus conspecific sponges is more disparate: the size of most conspecifically

paired individuals surviving to 25 months had diminished to $<0.5 \text{ cm}^3$.

Heterospecific partners of *D. anchorata* survived better than did *D. anchorata*, with 71.4% of the *I. birotulata*, *A. compressa*, and *A. fulva* that were paired with *D. anchorata* still alive at 25 months (data combined for the three mutualist species). These three species survived significantly better paired with each other (88% survival of individuals in all three pairwise combinations), however, than paired with *D. anchorata* (88% vs. 71.4%; G -test, $P < .025$; fig. 4B). The drop in survival when paired with *D. anchorata* began only after 12 months (fig. 4B), when surviving *D. anchorata* individuals had grown large enough to overwhelm the individuals of the three mutualist species with which they were paired.

As the experiment progressed, a greater proportion of the surviving *D. anchorata* individuals relinquished their grips on their carbonate substrata and attached solely to the heterospecific sponges with which they were paired. By 12 months, 33% of the 30 surviving *D. anchorata* were attached solely to sponges of other species, and after 25 months, this proportion increased to 47% of the 15 survivors. *Desmapsamma anchorata* individuals that switched their attachment from stabilized coral rubble to a heterospecific sponge survived significantly better (7/10 vs. 8/20; G -test, $P < .01$).

Experiment 3: Growth and Mortality of *D. anchorata* on Solid Substrata versus Heterospecific Sponges

Small *D. anchorata* fragments that were attached to branches of larger individuals of the other three sponge species grew much larger than those of the same genotypes and initial sizes that were attached to stable solid carbonate (fig. 5), a mean increase of $+11.3 \text{ cm}^3$ for those on sponges and a mean decrease of -1.2 cm^3 for those on stable solid carbonate during 14 weeks (net sizes significantly different by Wilcoxon signed-rank test at $P < .005$). Growth was extremely rapid, with individuals on other sponges increasing as much as five to 10 times their initial sizes. Net size change reflected partial mortality as well as growth, with partial mortality dramatically overbalancing growth for most sponges on solid carbonate.

In the first run, low survival (53.4%) resulted from three-spot damselfish *Eupomacentrus planifrons* biting (and spitting out) sponges that were inadvertently placed near their territories until they were gone. Damselfish territories were avoided in the second run, and survival at 14 weeks of *D. anchorata* on heterospecific sponges was 90%. Many (69.6%) of the *D. anchorata* surviving on coral rubble after 14 weeks had decreased in size to $<2 \text{ cm}^3$, and survival to 6 months was 0% (fig. 4C). In contrast, survival

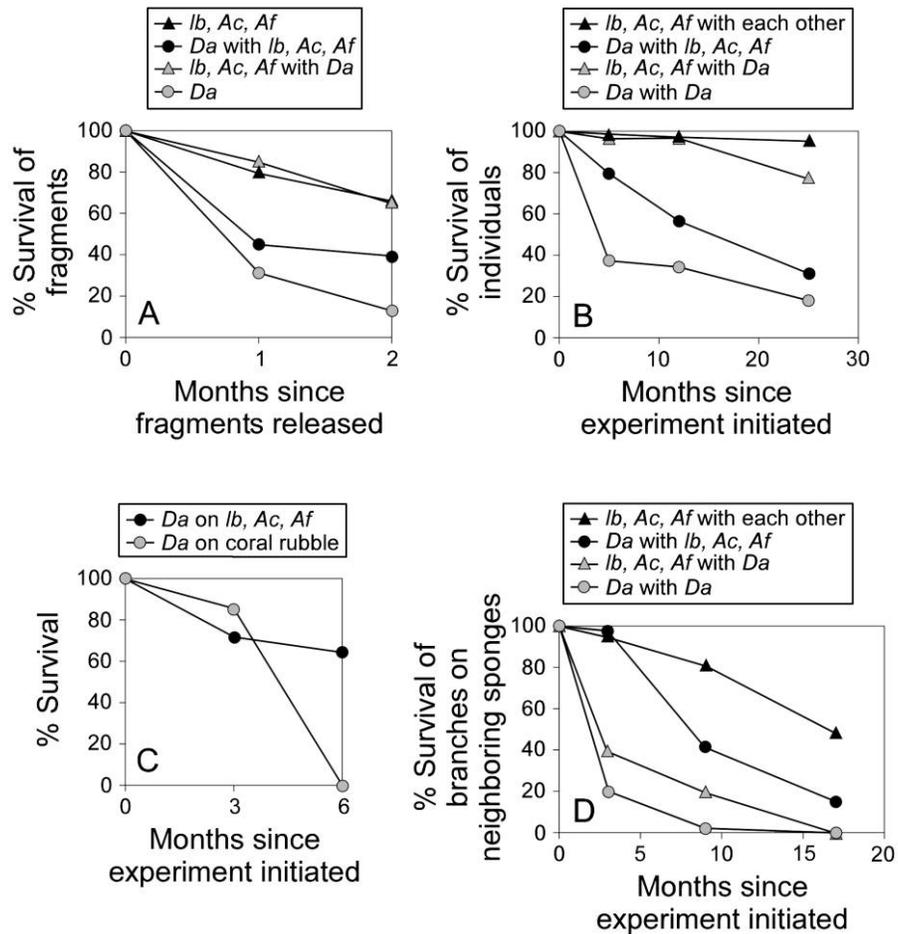


Figure 4: Comparisons of survival dynamics of *Iotrochota birotulata* (*Da* in the figure), *Amphimedon compressa* (*Ac*), *Aplysina fulva* (*Af*), and *Desmapsamma anchorata* (*Da*) in a variety of heterospecific associations and alone. In each graph, the data for the first three species are combined. **A**, Survival of fragments of *I. birotulata*, *A. compressa*, *A. fulva*, and *D. anchorata* alone and in heterospecific pairs. Differences in survival at 2 months are significant (G -test, $P < .001$) for comparisons of *D. anchorata* alone versus in heterospecific pairs and for *D. anchorata* alone versus the other three species alone. **B**, Loss rates from carbonate substrata of sponges grown in conspecific and heterospecific pairs among *I. birotulata*, *A. compressa*, *A. fulva*, and *D. anchorata*. Sponges were cut to 8 cm and were grown on carbonate rubble on stable stakes. A total of 56 *D. anchorata* individuals and 42 individuals of the other three species were included in the experiments (14 individuals of each species were involved in each combination). Proportions of individuals surviving after 25 months were significantly different by the G -test ($P < .05$) for comparisons of (1) *I. birotulata*, *A. compressa*, and *A. fulva* paired with each other versus with *D. anchorata*; (2) for *D. anchorata* grown with other *D. anchorata* versus *D. anchorata* paired with the other three species, and (3) for all *D. anchorata* versus all individuals of the other three species. (Data for heterospecific pairs of all pairwise combinations among *I. birotulata*, *A. compressa*, and *A. fulva* can be found in Wulff 1997; all three combinations are pooled for this graph.) **C**, Survival of genotype and size-controlled branch pieces (4 cm long initially) of *D. anchorata* on stable carbonate substrata versus on branches of heterospecific sponges. **D**, Survival of 4-cm-long branch fragments of *D. anchorata*, *I. birotulata*, *A. compressa*, and *A. fulva* on branches of large neighboring heterospecific or conspecific sponges. (Data for *I. birotulata*, *A. compressa*, and *A. fulva* on branches of these three species are from Wulff 1997.)

to 6 months of individuals attached to branches of other sponges was 64.3%. Of those survivors, 57% had grown to completely surround the host branch, and 29% had spread to also grow on another host branch.

Host sponge growth was not influenced by *D. anchorata* during the first 14 weeks. Branch widths did not change,

and of the 57 cases in which pairwise comparisons were possible, length increases of the control and host branches were within 3 mm of each other in 24 cases; the host branch had grown longer in 17 cases, and the control branch had grown longer in 16 cases. By 6 months, however, *D. anchorata* was influencing survival of host

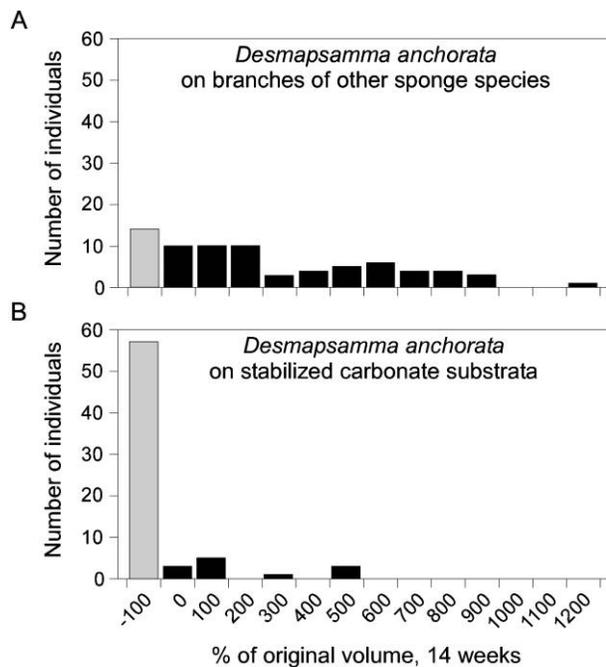


Figure 5: Genotype-controlled comparison of growth and partial mortality of *Desmapsamma anchorata* on (A) the branches of sponges of three other species ($n = 84$, i.e., 28 for each of the three host species) versus (B) stabilized carbonate substrata ($n = 84$). Frequency distributions of sizes (in terms of percent of original volume) of *D. anchorata* individuals grown on coral rubble versus on branches of three other sponge species (*Iotrochota birotilata*, *Amphimedon compressa*, and *Aplysina fulva*) for 14 weeks. Black bars represent individuals that increased in size, and gray bars represent individuals that decreased in size. Sample size was 28 *D. anchorata* individuals grown on each of the three host species, in paired comparisons with 28 *D. anchorata* individuals of the same genotypes and initial sizes, grown on coral rubble attached to stable stakes (i.e., a total of 186 *D. anchorata* individuals).

branches: no unencumbered branches broke, but host branches had broken, or were breaking, under 21% of surviving *D. anchorata*.

Experiment 4: Association of Small D. anchorata with Large Heterospecific Sponges and of Large D. anchorata with Small Heterospecific Sponges

After 3 months, most *D. anchorata* branch pieces transferred onto adjacent large individuals of other species were thriving (fig. 4D), with increases up to 10.3 times the original size. By contrast, most branch pieces of the other three species transferred to large adjacent *D. anchorata* were faring poorly, with 30% fallen onto the substratum due to disintegration of the large *D. anchorata* individuals,

15% with $<1 \text{ cm}^2$ of their surface still exposed, and 15% completely smothered to death by *D. anchorata*.

At 9 months, mortality of parent *D. anchorata* sponges (and consequent loss of hosts for branch pieces of the other five species) was high (58.3%), and half of the survivors were reduced to small fragments. By contrast, all parent sponges of the other five species survived.

After 17 months, only 15% of the original *D. anchorata* branches on heterospecific hosts survived. Variation in size of the few remaining sponges reflected various combinations of fast growth and heavy partial mortality, with two of the surviving *D. anchorata* branches increasing to 110.5 and 254.4 cm^3 (41 times the original size) but all others decreasing to $<36 \text{ cm}^3$. Mortality of parent *D. anchorata* was 100%, so branch pieces growing on heterospecific neighbors were the only surviving representatives of those genotypes.

Discussion

Benefits and Costs to Desmapsamma anchorata of Association with Other Sponge Species

Desmapsamma anchorata benefits substantially from association with other sponge species. Survival and net growth were significantly higher for *D. anchorata* attached to heterospecific sponges rather than carbonate substrata, in a variety of situations. *Desmapsamma anchorata* on branches of other sponge species increased in size (mean of $+11.3 \text{ cm}^3$), while those on carbonate substrata decreased (mean of -1.2 cm^3), and survival to 6 months was 64.3% on sponges versus 0% on carbonate. Small *D. anchorata* branch pieces attached to neighboring heterospecific sponges were the only surviving portions of the parent sponges by 17 months, even though the parent sponges had been orders of magnitude larger at the start. The only unmanipulated *D. anchorata* individuals surviving after 9 months were those attached solely to heterospecific sponges, and survival was significantly increased for experimentally paired individuals that switched their attachment from carbonate rubble to their heterospecific sponge partner. In addition, *D. anchorata* fragments survived significantly better when paired with fragments of the other three species. The great benefits conferred on *D. anchorata* by association with the other three species are reflected in the disproportionate natural distribution of large *D. anchorata* individuals on sponges of other species instead of on carbonate substrata and the greater incidence of recent damage to *D. anchorata* individuals on carbonate substrata. No costs of association were identified for *D. anchorata*, even by this variety of experimental situations.

Differences in net size change between solo and associated *D. anchorata* are due to the heavy partial mortality

suffered by individuals on solid substrata. Maximum growth rates on solid substrata, as well as mean growth rates over a short period (minimizing influence of partial mortality), were very high (fig. 3C, 3D). However, *D. anchorata* has little inherent resistance to fragmentation, and so branches that grow quickly during periods of calm water are readily broken by episodic moderate water motion, and storms can fragment entire *Desmapsamma* individuals to the point of pulverization. By adhering to the mutualist species, *D. anchorata* diminishes damage by making use of its superior tensile strength and extensibility. Greater tensile strength (i.e., breaking stress, the force per unit cross-sectional area at breakage) of the mutualist species—with maximum tensile strengths of 0.46, 0.32, and 0.45 MPa for *Iotrochota birotulata*, *Amphimedon compressa*, and *Aplysina fulva*, respectively (Wulff 1997), versus 0.19 MPa for *D. anchorata*—allow *Desmapsamma* adhere to one of these species to be supported without the expense of making its own strong skeleton, just as vines and lianas use trunks of trees to deploy their leaves high in the canopy without the expense of manufacturing their own structural support (e.g., Darwin 1875; Putz 1984) and hydrozoan corals of *Millepora* spp. grow over neighboring gorgonians to gain feeding advantages of large erect morphology while greatly diminishing their own carbonate skeleton production expenses (Wahle 1980). The other important biomechanical difference between the mutualist and exploiter sponge species is extensibility (i.e., breaking strain, the ratio of maximum extended length to length before applying force). The three mutualist species reduce their susceptibility to fragmentation by being extensible to greater (*A. fulva*) or lesser (*I. birotulata*) extents, stretching when pulled by waves instead of immediately breaking (fig. 3E). When a host sponge avoids breakage by stretching with vigorous water flow, an adherent *D. anchorata* is essentially buffered from feeling the full force of the moving water.

An Exploiter of Mutualisms among Sponge Species

Growth and survival of individuals of *I. birotulata*, *A. compressa*, and *A. fulva* are increased by attachment to heterospecific sponges, and among these three species the benefit is mutual (Wulff 1997). Although associations of these mutualistic species with each other and with *D. anchorata* look very similar (cf. fig. 1 here with fig. 7 in Wulff 1997), associating with *D. anchorata* can be costly. Survival for 25 months of sponges of the three mutualistic species was significantly less when paired with *D. anchorata* (71.4%) than with each other (88%), and the even greater differences in partial mortality indicate that survival differences would have been much greater if the experiment had been longer. By 6 months, more than half of the initially very small *D. anchorata* attached to branches of

the other three species had grown to completely surround the host branches, and 21% of the host branches were broken or breaking where tissue was smothered by overgrowth. After only 3 months, 30% of the branch pieces of the three mutualistic species that were attached to a neighboring large *D. anchorata* were completely or nearly smothered to death by their host, and by 17 months, the mortality of the large *D. anchorata* individuals to which branch pieces of the other species were attached was 100%.

Probing these associations with a variety of experiments and monitoring the experiments for sufficient time to quantify life-history stage transitions (mediated by growth, partial mortality, fragmentation, and fragment reattachment) revealed that effects of association were negative when *D. anchorata* individuals were larger than associated heterospecific individuals at the start of the experiment (e.g., fig. 4D), or when initially smaller or same-sized *D. anchorata* grew to be large (e.g., fig. 4B). Thus, although small *D. anchorata* may not affect sponges to which they adhere, and high mortality rates preclude many of them from ever getting large, *D. anchorata* grows so much faster than the other species that surviving individuals can quickly become large enough to overwhelm associated sponges of the mutualistic species.

Consequences of a Weedy Life History

Differences in life history and other ecological attributes of *I. birotulata*, *A. compressa*, and *A. fulva* play key roles in the mutually beneficial effects of adhering to each other (Wulff 1997). For example, *A. fulva* is less readily fragmented, but fragment survival is poor; *A. compressa* grows relatively slowly but is immune to sea star predation; and *I. birotulata* breaks easily, but its fragments reattach quickly. Associated heterospecific sponges survive better than solo individuals because their combined characteristics resist more environmental hazards.

Although life histories of the three mutualist species differ clearly if they are compared only with each other, they cluster tightly when the very different *D. anchorata* is added to the comparison (fig. 3). It grows and reattaches much more quickly, but these traits are counterbalanced by a high rate of mortality, extreme susceptibility to fragmentation, and poor survival of fragments. High growth rates are linked to high mortality by the minimal investment this species makes in its own structural support. When *D. anchorata* adheres to an individual of one of the mutualist species, it gains from their superior biomechanical characteristics; however, even with such a boost to its survival and net growth (e.g., figs. 4, 5), *D. anchorata* survives poorly compared with the other species. The essentially weedy nature of this species is corroborated by community dynamics in a slightly shallower plot on the

Guigalatupo reef. Five full censuses over 14 years revealed that 20 of the original 39 sponge species vanished from the plot, and three species colonized (Wulff 2006b). *Desmapsamma anchorata* was the only species that vanished for a census period and was represented again in a subsequent census period. Thus, all of the measured characteristics of *D. anchorata* indicate relatively ephemeral occupation of any particular site (summarized and illustrated by fig. 1).

Very rapid growth and regeneration rates and extreme variation in net growth of *D. anchorata* were also measured in Colombia by Aerts (1999). Observations of contact points between *D. anchorata* and corals indicated that this species could be an aggressive competitor for space (Aerts 1999). However, high mortality and dependence on more extensible organisms for support can render gains in coverage of corals and other solid substrata ephemeral. Corroborating substratum distribution patterns documented in the San Blas Islands, Aerts and van Soest (1997) reported more *D. anchorata* on algae, sponges, and gorgonians than on corals in Colombia; and in Puerto Rico this has been studied on gorgonians as well (e.g., E. McClean, personal communication). If data from Caribbean Panama are representative of better survival on upright extensible substrata versus solid substrata, recent reports of invasion of the Pacific by this sponge species (Calcinai et al. 2004), apparently in association with the gorgonian *Carijoa riisei*, may be of more concern than local increases on solid substrata of Caribbean reefs, even if they are very rapid.

Life-History Differences Shift the Balance of Costs and Benefits of Exploitation

Exploitation of potentially mutualistic partners does not necessarily benefit its practitioners more than mutualism would (e.g., Bronstein 2001b). Partner fidelity feedback favors mutualism because the cost of exploitation can be high when survival, growth, or reproductive advantages depend on the continued good condition of a particular partner individual. The three mutualistic sponge species remain true to their branching habit when adherent to each other (examples in fig. 7 in Wulff 1997), resulting in minimal coverage of each other's surfaces. As *D. anchorata* individuals grow larger, however, they tend to cover the surface of host sponges (e.g., fig. 1). While this improves their grip, it also blocks the covered sponge's access to the water column. Although sponges can reorganize their internal canal systems to maintain water flow if part of their surface is blocked (e.g., Hartman and Reischwig 1973), when too much surface is blocked, they are smothered and they die (e.g., Reischwig 1973; Sutherland 1980; Wulff 2005). Sponge skeletons rapidly disintegrate once the tissue dies (e.g., Wulff 2006c).

For the three mutualistic sponge species, neither partner gains by overgrowing the other, because support is lost where smothered portions die and disintegrate. Greater advantage is achieved by maintaining the long-term association, which can continue for many years (Wulff 1997). By contrast, for an individual of a weedy, ephemeral species, the long-term maintenance of the health and structural integrity of a partner individual may be irrelevant. For the exploiter, *D. anchorata*, a short-term advantage is compatible with its rapid life cycle.

Janzen's (1975) work on ants and acacias in Central America provides a strikingly parallel example. Ants of the species *Pseudomyrmex nigropilosa* inhabit swollen thorn acacia trees but do not benefit their hosts. Why this species exploits this common mutualism while three other sympatric *Pseudomyrmex* species reciprocate by protecting their hosts becomes evident when life histories of the ants are compared. Whereas the mutualistic ant species produce alates of both sexes after 2 years, when they have achieved colony sizes of >1,200 workers, the parasitic ant species in only 2 months gains the colony size of 20 that it needs to produce alate reproductives of both sexes (Janzen 1975). A colony of the mutualistic ants that fails to care for its host tree loses a home before completing the life-cycle stage for which that host is required, but a particular acacia tree has no long-term value for a colony of the exploiter ant species, which quickly moves on to fresh hosts. Thus, in both the sponge and ant examples, differences among otherwise similar species in characters influencing life histories shift the ultimate balance of costs and benefits to favor mutualism or exploitation via partner fidelity feedback.

Life Cycles of Interacting Individuals

Continuous association, clonality, and vertical transmission are among the factors identified as promoting mutualism by recent theory articles (e.g., Herre et al. 1999; Hoeksema and Bruna 2000; Yu 2001; Sachs et al. 2004; Foster and Wenseleers 2006). These same factors were identified by a literature survey showing a strongly positive association of clonality and mutualism in 316 orders representing 16 invertebrate phyla (Wulff 1985a). Impetus for this survey was a verbal model that was based in part on the increased possibility in clonal organisms for vertical transmission of symbionts and (when both partners are clonal) tandem proliferation of associations, that is, simultaneous vertical transmission of both partners (Wulff 1985a).

Associations of *D. anchorata* with heterospecific sponges are continuous and—because sponges are clonal—can also proliferate in tandem, but they are not benevolent. Curiously, *D. anchorata* benefits from associating with het-

erospecific sponges much more than the demonstrated mutualists do, and with no apparent costs to *D. anchorata*. A simple cost-benefit analysis might suggest that *D. anchorata* has the most to gain from aiding heterospecific partner individuals, favoring mutualism. It was only by explicitly including multiple life-cycle stages in experiments that the high cost incurred by other species from associating with *D. anchorata*, if this exploiter is large or has a chance to grow large, was revealed. In addition, it was only by monitoring experiments over periods long enough to include transitions among life-cycle stages that the ephemeral nature of the association of a particular *D. anchorata* individual with a particular heterospecific sponge individual was discovered.

Recent advances in theory of mutualisms and their exploiters include explicit predictions of how costs and benefits balance under different conditions, resulting in classification schemes for mutualisms and mutualism-promoting factors (e.g., Bull and Rice 1991; Bronstein 2001*b*; Sachs et al. 2004; Foster and Wenseleers 2006). A great advantage of these developments is that attention is focused clearly on mechanisms of interaction and on dynamics of association between individual organisms (as has been advocated especially eloquently by Janzen [1985] and Bronstein [2001*a*]). In particular, predictions emerging from theory involving partner fidelity feedback and partner choice (e.g., Sachs et al. 2004; Foster and Wenseleers 2006) cannot be tested empirically without following individual organisms to determine whether they actually maintain fidelity to a particular partner or direct sanctions at potential exploiters. As pointed out by Bull and Rice (1991), partner fidelity feedback is likely to be limited to life-cycle stages for which a heterospecific partner is useful, and so succumbing to the temptation to focus on only an obvious or most readily studied life stage may risk misinterpretation. Explicit comparisons among otherwise similar species may be able to pinpoint why a particular species plays the role of exploiter in an otherwise mutualistic system, but the key differences may not be evident until costs and benefits of association are evaluated in the context of entire life cycles of interacting individuals.

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enduring creative contributions of the visionary Italian evolutionary and sponge biologist Michele Sarà.

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