Multivariate trade-offs, succession, and phenological differentiation in a guild of colonial invertebrates

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Abstract. For competing species limited by one or few resources, diversity is thought to be maintained by trade-offs that allow niche differentiation without resource partitioning. However, few studies have quantified multiple key traits for each species in a guild and shown that trade-offs among these traits apply across the guild. Here we document strong bivariate and multivariate relationships among growth rate, fecundity, longevity, and overgrowth ability for six co-occurring colonial invertebrates. We find that all four of these traits are constrained to a single “fast–slow” niche axis that mechanistically relates life history variation to a colonization–competition trade-off. The location of species on this axis strongly predicts the timing of their peak abundance during succession. We also find that species closer to each other on the fast–slow axis are more likely to differ in reproductive phenology, suggesting a secondary dimension of niche differentiation for otherwise similar species.

Key words: coexistence; colonization–competition; fast–slow continuum; fouling community; life history; marine; multivariate trade-off; storage effect.

INTRODUCTION

A perennial challenge in ecology is to explain the maintenance of species diversity in systems with one or few limiting resources (Hutchinson 1961, Fargione and Tilman 2002). An abundance of plausible coexistence mechanisms have been proposed, each with some supporting evidence, and the current task is to determine which and how many mechanisms operate in particular communities (Fargione and Tilman 2002). Variation in life history strategy is thought to be a common way in which species differentiate niches without using different resources. This basic idea underlies a broad range of interrelated ecological concepts, such as the causes of succession, coexistence via a colonization-competition trade-off, coexistence mediated by disturbance, and competition in fluctuating environments, (e.g., Sousa 1979, Tilman 1994, Rees et al. 2001, Angert et al. 2009).

In order to understand the effects of life history variation on coexistence, it is necessary to quantify, across competitors, the relationships among life history traits and competitive interactions. However, few studies have directly measured competitive ability and a suite of life history traits for each species in a guild and shown that trade-offs among these traits apply across the guild (e.g., Tilman 1990, Pacala et al. 1996). This kind of species-specific mechanistic approach can be powerful, because it facilitates the integration of coexistence models with field data, and allows insights into which traits show trade-offs and how multiple coexistence mechanisms combine to jointly structure communities (Schoener 1986, Tilman 1990, Fargione and Tilman 2002). Furthermore, when these trait relationships are quantified for a community, the patterns can then be compared to intraspecific genetic variation and macroevolutionary trends, to gain a more unified understanding of the evolutionary processes that structure communities.

Competition and coexistence have been well-studied in hard-substrate marine communities, especially among sessile species for which space is often limiting (e.g., Sousa 1979, Sebens 1986). In many communities, natural or experimental disturbances are followed by a fairly predictable successional sequence, in which quickly arriving species are replaced by later arrivals which outgrow (e.g., Paine and Levin 1981) or outlive (e.g., Sousa 1979) them. For these communities, it is thought that spatial patchiness in disturbance or other sources of mortality leads to coexistence via a mosaic of patches at different stages of succession. The role of life history trade-offs is evident in this model of coexistence, because traits such as fecundity and longevity relate directly to the dynamics of space occupation. Our goal in this study is to discern and quantify the life history and competitive traits that underlie successional patterns. This will allow for a mechanistic understanding of how succession works, but more importantly this will allow for the benefits of a mechanistic approach to coexistence.

The community we describe here is comprised of six colonial invertebrates that compete for space. For each species we measure growth rate, fecundity, overgrowth ability, and mortality (from causes other than overgrowth). These four traits are primary determinants of species’ abilities to colonize free space (growth and fecundity), preempt occupied space from colonization

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(mortality/longevity), and capture occupied space (overgrowth). Because faster growth, greater fecundity, greater longevity, and better overgrowth ability may all plausibly involve a cost in resources, it is unlikely that any single “superspecies” exists that maximizes all of these traits simultaneously (Tilman 1982). However, within this general constraint the bivariate and multivariate relationships between traits could take many forms. Bivariate comparisons in many tree communities have shown that growth under high light is positively correlated with mortality under low light (e.g., Pacala et al. 1996, Poorter et al. 2008). Several studies have also shown that colonization rate, which is presumably affected by fecundity, growth rate, and dispersal ability, can trade-off with the ability to compete under resource limitation (sessile invertebrates, Sebens 1986; grassland plants, Tilman 1994; microcosm protists, Cadotte et al. 2006). Here we test for bivariate relationships among four key life history traits simultaneously. In addition, we quantify the multivariate structure of these traits, because in general there is little understanding of the number of niche dimensions necessary to explain coexistence in diverse communities. For example, Pacala et al. (1996) found for eight tree species that growth under high light, survival under low light, shade cast, and dispersal ability all varied along a single axis of colonization ability vs. shade tolerance. More studies are needed that use similar comparisons to assess the niche dimensionality of competitive communities.

In addition to the traits described above, we also quantify seasonal patterns of reproduction for the six species. In general, for organisms with high juvenile mortality from competition, but less competitive mortality as adults, temporal differences in recruitment can enhance coexistence via the storage effect (Chesson and Warner 1981). Recruitment phenology may therefore act as an additional source of niche differentiation, especially among species that have similar life history traits (e.g., Angert et al. 2009). Here we combine analyses of life history variation and recruitment variability to explore the potential effects of both of these factors on coexistence in this system. An analysis of the interactive effects of these factors on community dynamics is the subject of ongoing modeling work.

**Methods**

**Natural history.**—The sessile epibenthic invertebrate community in Bodega Harbor, California, USA is composed primarily of ascidians, bryozoans, mussels, barnacles, sea anemones, and sponges. In this study, we focus on six dominant colonial species: the five ascidians *Botrylloides diegensis*, *Botrylloides violaceus*, *Botryllus schlosseri*, *Didemnum vexillum*, and *Diplosoma listerianum*; and the bryozoan *Watersipora subtorquata*. All of these species except *Botrylloides diegensis* are considered to be nonnative (Van Name 1945, Ruiz et al. 2000, Bullard et al. 2007), and all six currently have a range that includes harbors around the globe. We chose these species because they are dominant space holders (together comprising up to 100% of local cover) and form a functional group of modular organisms that grow along hard surfaces (natural and anthropogenic) through asexual addition of new modules called zooids. All of these species brood larvae that likely disperse for a period lasting from minutes to several hours, at which point the larvae settle on unoccupied space and metamorphose. Metamorphosed individuals quickly spread asexually into available space by growing additional zooids. When heterospecific colonies come into contact, growth may cease or one colony may grow up onto the other, causing partial mortality and capturing occupied space. Space is freed by mortality, and mortality in this system appears to be caused by a combination of senescence and predation. The mortality rates we describe below appear to be dominated by senescence, consistent with the observation that consumer species with strong effects in this system (chitons and urchins) are at relatively low abundance in the harbor (Byrnes and Stachowicz 2009).

**Growth rate.**—We measured individual intrinsic growth rates during September–October 2008. This is a seasonal period of high growth in this system and likely represents peak growth rates. We deployed PVC panels at Spud Point Marina, face-down at 1 m depth, and allowed settlers to accumulate for three weeks. We then weeded the panels to a density of one to four colonies per 100-cm² panel, and followed colonies weekly for three to four weeks, with photographs taken in the field. Because growing colonies were at very low density they were able to colonize neighboring space unhindered. We used the photographs to estimate the exponential growth rate of colonies of each species; details of statistical estimation are in the Appendix A.

**Mortality.**—We used two approaches to estimate mortality for our six species. Here we are measuring mortality not due to overgrowth, which is estimated separately. For the species *Botryllus schlosseri*, *Botrylloides diegensis*, *Botrylloides violaceus*, and *Diplosoma listerianum*, in nearly all instances of mortality we observed, the entire colony would simultaneously degrade and eventually disappear over the course of one to two weeks. This likely represents mortality due to senescence, as described by Rinkevich et al. (1992) for *Botryllus schlosseri*. Other possible sources of mortality include disease, predation, disturbance, or intermittent abiotic stress; however, we did not observe any signs of mortality from these causes. For these four species we also observed that the age of death was relatively consistent within each species. We therefore treated each colony as an individual and estimated age-specific mortality probabilities using survival analysis.

For the species *Didemnum vexillum* and *Watersipora subtorquata*, colonies exhibited only partial mortality while the remainder of the colony continued to grow. For both these species, older parts of the colony appeared to die sooner. As for the other four species,
the source of mortality in most cases was probably senescence (as indicated by the presence of decaying tissue), although other causes are possible. For these species experiencing partial mortality, we estimated mortality rate in terms of the proportion of occupied space lost per unit time. We describe the details of the statistical estimation of mortality in the Appendix A.

**Overgrowth ability.**—Overgrowth was quantified by observing interactions between colonies in the field from July to November 2008. We followed interacting colonies over time with biweekly photographs. For each pairwise interaction during an interval, we measured the amount of space formerly occupied by one colony that was captured by another colony. This could result from the second colony growing on top of the first, or from the first colony retreating and the second advancing. If neither colony advanced into the other’s territory, we labeled this as a standoff, which is common among colonial ascidians (Schmidt and Warner 1986). We also measured the initial size of each colony and the length of border initially shared by those colonies. We used this data to rank species according to overgrowth ability; details are given in Appendices A and D.

**Fecundity.**—Estimating per capita fecundity in the field for ascidians and bryozoans is difficult, because colonies can produce eggs and release larvae for many weeks. We therefore estimated fecundity indirectly, by comparing the rate of larval settlement of a species to its abundance in the community. This approach is justifiable for these species because the duration of the larval period is short enough that the harbor should be an approximately closed system (e.g., Jackson 1986). Disadvantages of this method include a lack of accounting for mortality during dispersal, early postsettlement mortality, and the ontogenetic changes in colony reproduction as a function of age and size. However, the advantage of this method is that all of these components of reproduction and early life history are integrated to give a single metric of the ability of each species to produce successful settlers, as a function of the amount of space occupied. We describe the details of fecundity estimation in the Appendix A.

**Temporal patterns.**—We quantified larval settlement from 2006 to 2008 with PVC panels deployed regularly at two-week intervals. During each interval, we deployed four to eight panels face-down at 1 m depth, at each of two sites separated by ~500 m. After two weeks, we brought the panels to the lab and counted all settlers with a dissecting microscope. Temporal patterns were highly correlated between the two sites for all species, so we are confident that the patterns reported here represent temporal variation that is largely spatially consistent. We describe our methods for pairwise interspecific comparisons of settlement patterns in the Appendix A.

**RESULTS**

**Parameter estimates.**—In the absence of competitors, exponential growth rates of the six species range from 0.068 to 0.18 day⁻¹ (Fig. 1, Appendix B). These rates correspond to a doubling time for colony size ranging from 3.8 to 10.2 days. For the four species with whole-colony mortality, expected lifespan ranged from 56 to 109 days (Fig. 1, Appendix B). For the two species with partial mortality, *Didemnum vexillum* and *Watersipora subtorquata*, the proportional mortality rates were 0.002 and 0.003 day⁻¹, respectively (Fig. 1, Appendix B). These rates correspond to an expected lifespan for a unit of the colony of 500 and 331 days. Fecundities ranged from 3.6 × 10⁻⁵ to 4.4 × 10⁻⁵ settlers per cm² per fraction of space occupied (Fig. 1, Appendix B).

Overgrowth interactions were essentially hierarchical (Appendix D). In 12 of the pairwise interactions, one species was a clear dominant and overgrew the other in at least 50% of encounters. In three of the pairwise interactions, the species were evenly matched and no species won 50% of the time. These pairs include *B. diegensis* vs. *Watersipora*, *Watersipora* vs. *B. violaceus*, and *B. violaceus* vs. *B. schlosseri* (Appendix D). These “ties” were all pairs of species adjacent to one another in our ranking. We also compared the rate of overgrowth for each encounter to the expected rate of growth of the “winner” into free space. On average, overgrowth rate was substantially less than expected growth rate into free space (Appendix D). Furthermore, overgrowth rate was significantly related to the difference in overgrowth rank of the two species (*P* < 0.001; see Appendix D for details). For encounters in which a high ranking species overgrew a low ranking species, overgrowth rate approached the rate expected into free space. Overgrowth rate decreased for similarly ranked species, and declined to near zero for the rare encounters in which a lower ranked species succeeded in overgrowing a higher ranked species.

**Bivariate and multivariate trait relationships.**—We found significant correlations among four of the six bivariate trait relationships (results of all statistical analyses are on Fig. 1). Species with high growth rates tend to have high mortality rates (Fig. 1A); species with high growth rates tend to have high fecundity rates (Fig. 1C); species with high fecundity rates tend to have high mortality rates (Fig. 1B); and species with high fecundity rates tend to have low overgrowth ability (Fig. 1E). In addition there are nonsignificant trends (at *α* = 0.05) for species with high overgrowth ability to have low mortality rates (*P* = 0.065; Fig. 1F), and for species with high overgrowth ability to have low growth rates into free space (*P* = 0.14; Fig. 1D). All of these relationships are qualitatively unchanged if the one bryozoan is removed from the analysis (*Watersipora subtorquata*; K. F. Edwards, *unpublished data*), although visual inspection (open circle on Fig. 1) suggests it may be less constrained to these relationships than the ascidians.

We performed a principal components analysis on the four traits to quantify multivariate patterns. We found that a single principal component explained 87% of the variation among traits. Consistent with the bivariate relationships, this axis associates high growth rate, high
fecundity, high mortality rate, and low overgrowth ability (loadings for these traits, quantified as in Fig. 1, are $-0.50$, $-0.51$, $-0.51$, and $-0.48$, respectively), leading to a single axis of variation that describes a continuum from fast to slow life histories. Furthermore, the placement of species along this axis strongly predicts the timing of peak abundance during succession (Fig. 2A, B), with species with high growth, fecundity, and mortality rates and low overgrowth ability being serially replaced by those with greater overgrowth ability but lower growth and fecundity.

**Temporal patterns in recruitment.**—Settlement varied seasonally for all species in the community, with the majority of settlement occurring from May to mid-November (Fig. 2C). Within this overall seasonal trend, settlement could fluctuate greatly over two to four weeks, and species often exhibited distinct patterns. The median correlation between species was 0.47 and pairwise patterns were significantly different in 23 of 45 cases (Appendix C). We also found that the distance between a pair of species on the life history continuum (Fig. 2C) was negatively correlated with the number of years in which those species had significantly different recruitment patterns (Appendix C; Pearson $r = -0.58$, $P = 0.025$, df = 13). In other words, species with similar life history traits were more likely to show divergent seasonal phenologies.

**Discussion**

**Life history variation and coexistence.**—Our results show that strong relationships between primary life history and competitive traits structure this community. Growth rate is positively correlated with mortality rate; fecundity is positively correlated with mortality rate; growth rate is positively correlated with fecundity; and fecundity is negatively correlated with overgrowth ability (Fig. 1). A multivariate analysis shows that these traits are arrayed primarily along a single axis, forming a “fast–slow” continuum that associates high growth rate and fecundity with high mortality rate and low overgrowth ability. The position of species along this axis strongly predicts the timing of species’ peak abundances during succession (Fig. 2B). In addition, temporal patterns of settlement often differ between species (Fig. 2C, Appendix C), and species with similar life history traits are more likely to show different settlement patterns. A summary of these trait relationships is given in Fig. 2C.

These results yield a mechanistic understanding of how life history variation translates into the successional processes that are thought to maintain diversity in spatially structured communities. When patches of space are freed by mortality, the species with greatest fecundity
and growth rate (Diplosoma; Fig. 2) is the first to dominate, and is eventually replaced by a series of species in which later dominants can both overgrow and outlive earlier dominants. This multivariate trade-off axis is therefore a specific example of a colonization-competition trade-off, which is thought to maintain diversity for a variety of organisms, such as marine invertebrates and macroalgae (Sousa 1979, Paine and Levin 1981, Sebens 1986), terrestrial plants (Tilman 1994), lichens (Crowley et al. 2005), and ants (Stanton et al. 2002).

One interesting question for future research is whether the underlying trait differences in other communities show multivariate patterns similar to those reported here. This is likely to be true for other benthic marine communities, in which early successional species often appear to have a large number of propagules that grow quickly, while late successional species are more resistant to various sources of mortality, and have some advantage in direct competition (e.g., Sousa 1979, Paine and Levin 1981, Berlow 1997). Our results, in combination with earlier data from communities of prairie plants (Tilman 1990) and temperate trees (Pacala et al. 1996), suggest that entire suites of competitive traits tend to be organized along a single trade-off axis. It may therefore be the case that the number of niche dimensions necessary to understand coexistence is much less than is implied by the vast number of traits in which competitors differ.

Our results also show one way to synthesize the approximate regularity of successional sequences with the fact that recruitment fluctuation can lead to stochasticity in species' abundances during succession (e.g., Sutherland 1974, Berlow 1997). Recruitment

FIG. 2. Succession and the principal axis of trait variation. (A) Succession on cleared substrate from July 2008 to March 2009. The abundance of each species is standardized by its summed abundance over all measurements. Lines are spline interpolated to aid visualization. (B) Midpoint of successional abundance vs. position on the main axis of trait variation (Pearson r = 0.89, P = 0.019). (C) A summary plot showing species' positions along the two “niche axes”: the fast–slow trait axis and the temporal distribution of settlement (in 2006). Settlement variation is plotted using a kernel density estimator.
fluctuation, in addition to causing stochasticity in succession, may act as a source of temporal niche differentiation (Chesson and Warner 1981; Appendix C, Fig. 2C), and our results suggest that this effect may be most important for species that are otherwise very similar. Preliminary analyses of a model parameterized with the data presented here indicate that recruitment fluctuation has a particularly beneficial effect on coexistence among the three botryllid ascidians, for which stand-offs are common in overgrowth interactions (Appendix D). For example, Botrylloides diegensis and B. violaceus occupy nearly identical positions on the multivariate axis that describes growth, fecundity, mortality and overgrowth ability, but have statistically distinct seasonal patterns of recruitment in all three years (Appendix C, Fig. 2C). These recruitment differences have a substantial positive effect on coexistence in simulated competition between this pair (K. F. Edwards and J. J. Stachowicz, unpublished data). Conversely, for species that are very distinct on the multivariate axis (e.g., Diplosoma and Didemnum), there is stronger overlap in patterns of recruitment. Although further work is needed, it appears that phenology may be an orthogonal niche axis to that described by life history trade-offs, potentially increasing the number of species that can coexist in seasonal communities.

Life history evolution and community structure.—The trait relationships we have described ultimately derive from species’ life history evolution in response to their environment, including interspecific competitors. It is noteworthy that large-scale interspecific life history comparisons have shown patterns similar to those reported here, in a variety of taxa. For example, fecundity is inversely correlated with longevity in birds (Ricklefs 2000), mammals (Gaillard et al. 1989), and rotifers (Kirk 1997). Furthermore, multiple life history traits are often organized primarily along a single “fast–slow” continuum (Saether 1987). Our results show that the fast–slow life history continuum can translate from large-scale species differences to local community structure (Fig. 2). We have also shown that overgrowth ability falls onto the same axis, implying that ability in interference competition is entrained in the same selective pressures or functional constraints that affect more general life history traits.

The physiological or morphological underpinnings of life history variation in this community are unknown, but we note that species at the slow end of the continuum appear to be physically denser. For example, at either end of the continuum are two didemnid ascidians: at the “fast” end, Diplosoma has a low density of zooids per colony area and a thin, gelatinous tunic, whereas Didemnum, at the “slow” end, has a higher density of zooids and a thicker, more robust tunic that includes calcareous spicules. This suggests that greater investment in existing tissue is related to longevity and overgrowth ability, while greater investment in new tissue or propagules is related to rapid colonization of free space.

An interesting challenge for future work is to understand the mechanistic basis of overgrowth ability, and how that trait is functionally related to the other life history traits. A thorough understanding of the coupling between life history evolution and interspecific competition will require an analysis of what generates the clustering of many traits along a single axis, a long-standing question in life history theory (Ricklefs 2000). For example, fecundity and growth rate are positively correlated, although the two traits may use the same resources and would therefore be expected to be negatively correlated. Intraspecific studies of the ascidian Botryllus schlosseri have found both positive and negative genetic correlations between fecundity and growth rate, in different populations (Grosberg 1988, Yund et al. 1997). These results suggest that colonial ascidians are not functionally constrained so that fecundity and growth rate positively covary. Instead, correlational selection may cause the alignment of multiple traits along a single axis in this community (Ricklefs 2000). For example, high growth rate may be most advantageous when coupled with the production of many larvae that colonize patches of temporarily free space.

Finally, we note that the guild of species we have described is recently assembled and lives primarily in anthropogenic habitats. One species (B. diegensis) has likely colonized these habitats from natural subtidal communities, while the others were probably transported on boat hulls, with most arriving within the past forty years (cf. Boyd 1972). The recent assembly of this community, and the co-occurrence of these species in many harbors globally (Ruiz et al. 2000, Piola and Johnston 2008) suggests that these species are in a sense pre-adapted to coexist via the mechanisms we have described, rather than arriving at different strategies via in situ coevolution (Janzen 1985). Assembly has been driven by anthropogenic transport among similar environments, and it is likely that the resulting communities are comprised of species that perform well under anthropogenic conditions while having sufficient mutual niche differentiation.

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Literature Cited


APPENDIX A

Quantitative methods (Ecological Archives E091-220-A1).

APPENDIX B

Life history parameters (Ecological Archives E091-220-A2).

APPENDIX C

Pairwise comparisons of settlement patterns (Ecological Archives E091-220-A3).

APPENDIX D

Overgrowth interactions (Ecological Archives E091-220-A4).