

Relative effects of environment and direct species interactions on the population growth rate of an exotic ascidian

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Abstract The success of exotic species can be influenced by both the abiotic environment and species interactions. Many studies have demonstrated significant effects of either type of factor on aspects of exotic success, but few have considered their relative effects on population growth rate, a more holistic measure of success. To quantify the relative effects of environment and direct competition on an exotic ascidian, *Botrylloides violaceus*, I manipulated direct contact interactions at four sites with different abiotic environments and tracked individual colonies over 3 years. I tested site and contact treatment effects on survival, growth and fecundity, and then conducted a life table response experiment on a periodic, size-structured population matrix model to test their effects on population growth rate. Both site and contact interaction were important to explaining variation in survival and growth. Contact interactions decreased the survival and growth of larger colonies but unexpectedly increased the survival of small colonies at some sites, which led to relatively weaker and spatially variable effects on overall population growth rates. Site effects on population growth rates were an order of magnitude larger than contact effects, and site variation in winter vital rates made the largest contributions to

changes in population growth rate. The results of this study suggest that the abiotic environment plays a larger role in the success of *B. violaceus*. Thus, environmental variables, such as temperature and salinity, could be used to predict this exotic species' success under different environmental scenarios, including global climate change.

Keywords *Botrylloides violaceus* · Competition · Exotic species · Life table response experiment · Matrix model

Introduction

Invasions of non-native species can cause significant ecological and economic damage (Pimentel et al. 2001) and are considered a major threat to biodiversity and ecosystem function (Vitousek et al. 1996). To effectively manage these exotic species, we must understand the factors that influence their success in new habitats. To invade a new habitat, exotic species must sustain positive population growth rates under new abiotic and biotic conditions. It is well known that abiotic variables such as temperature can influence individual vital rates (survival, growth, fecundity) that in turn determine population growth rates. However, environmental niche models, which map expected exotic distribution based on abiotic variables, have received criticism because they neglect potentially important biotic interactions (Peterson 2003). Negative biotic interactions such as predation and competition can hinder the establishment or growth of exotics, while positive interactions can facilitate their success. While many studies have found significant effects of biotic interactions on the survival or growth of exotic species (Levine et al. 2004), few have integrated abiotic variable and biotic interactions over entire life histories. Thus, we still lack an

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understanding of the relative importance of abiotic versus biotic effects in determining exotic species success.

Demographic models that consider entire life histories, such as population matrix models, can be valuable tools for understanding how different factors influence population growth rate, thereby providing an important link between empirical, theoretical and applied ecology (Benton and Grant 1999; Sibley and Hone 2002). Matrix models are prevalent in invasion studies, where they have been used to understand spatial or temporal variability in population dynamics (Werner and Caswell 1977; Parker 2000; Koop and Horvitz 2005; Dudas et al. 2007), to compare exotic and native demography (Marco and Paez 2000), to develop management strategies (Shea and Kelly 1998; Buhle et al. 2005) and to project invasion speed (Neubert and Caswell 2000). Yet few studies to date have explicitly considered the effects of biotic interactions, which are widely considered to be important determinants of invasive species success (Bruno et al. 2005; Mitchell et al. 2006). Here, I investigated the relative influence of abiotic environment and direct-contact interactions on population growth rate of a common exotic ascidian, *Botrylloides violaceus*, using a combination of field experiments and demographic analysis. This approach enabled me to tease apart the important drivers of *B. violaceus* success and to generate predictions under new abiotic and biotic scenarios.

B. violaceus is a colonial ascidian that has colonized many temperate marine fouling communities world-wide. Space competition, in the form of direct-contact overgrowth and indirect exploitation of space, have been shown to have important effects on the demography of sessile invertebrates (Connell 1961; Dayton 1971; Jackson 1977). Survival, growth and reproduction of these organisms are also known to be influenced by spatial and seasonal variation in the abiotic variables such as temperature and salinity (Newell and Bayne 1973; Leichter and Witman 1997; Pechenik et al. 2000; Stachowicz et al. 2002; McCarthy et al. 2007; Epelbaum et al. 2009). Despite these known effects, biotic interactions and abiotic variables are rarely considered together in these communities, so the extent to which declining biodiversity or climate change will influence exotic species success in these habitats is still unclear. To understand how the effect of direct-contact interactions and the abiotic environment affect the population growth of *B. violaceus*, I first conducted a neighbor-removal experiment at four sites with different abiotic environments and tracked individual survival, growth and fecundity rates. Regression techniques were used to determine the effects of each treatment on these vital rates. I then determined treatment effects on population growth rates using a size-based matrix model and life table response experiment (LTRE) analysis. LTRE is an analytical method that partitions population growth rate

variation among treatments by considering both the magnitude of the treatment effect on a vital rate and the sensitivity of population growth to this vital rate.

LTRE studies have been previously applied to many terrestrial exotic plants. For example, they have been used to compare the demography of invasive and noninvasive plants in different abiotic environments (Burns 2008), to understand the effects of burning regimes on the demography of knapweed *Centaurea maculosa* (Emery and Gross 2005) and tussock grass *Molinia caerulea* (Jacquemyn et al. 2005). To the best of my knowledge, however, this is the first report of a manipulative LTRE conducted on an exotic marine species, and the only one to consider both abiotic and biotic factors. Applying this method to other exotic species could help to understand the relative effects of the abiotic environment and biotic interactions. Such knowledge could also be used to develop invasive species management plans and to predict exotic spread under different biotic (e.g., declining biodiversity) or abiotic (e.g., global warming) scenarios.

Materials and methods

Study system

Botrylloides violaceus is a colonial ascidian, widely-believed to be native to Japan (Lambert and Sanamyan 2001), that is now found worldwide in coastal temperate habitats. The exact time of introduction to the study sites is not known, but it was first reported on the US west coast in the late 1970s (Lambert and Sanamyan 2001) and was present in all Washington marinas surveyed to date (Grey 2009). *B. violaceus* reproduces asexually via budding of zooids within a common tunic and sexually via internal fertilization to produce short-lived tadpole larvae (Berrill 1947; Saito et al. 1981; Mukai et al. 1987). Natural dispersal distance for this species is short (<5 m) so long-distance dispersal is most likely achieved via hull-fouling or aquaculture (Lambert 2005).

B. violaceus has colonized many marine fouling communities, which are assemblages of sessile marine invertebrates that occupy hard substrata. Space competition, seasonal recruitment and predation are all common features of fouling communities (Mook 1976; Sutherland and Karlson 1977; Stachowicz et al. 1999; Nydam and Stachowicz 2007; Dias et al. 2008).

Experiment

To determine the effects of site, direct-contact treatment and their interaction on *B. violaceus* vital rates, I tracked individual colonies within a full-factorial experimental

design (4 sites \times 2 competition levels). Four sites in coastal Washington (Appendix A in Electronic Supplementary Material; Makah: 48°22'05"N, 124°36'42"W; Wayne: 48°03'43"N, 123°02'18"W; Lopez: 48°30'55"N, 122°54'56"W; and Pleasant 47°39'42"N, 122°54'56"W) were chosen because they had similar substrates (floating concrete docks) and established *B. violaceus* populations, but varied in abiotic variables such as temperature and salinity. *B. violaceus* population densities were highest at Wayne (94.4 ind m^{-2}) followed by Pleasant (51.2 ind m^{-2}), Makah (22.4 ind m^{-2}) and Lopez (8.2 ind m^{-2}) (Grey, unpublished data). Two of these abiotic variables were measured during for this study: temperature was recorded at hourly intervals using HOBO® (Onset Computer, Pocasset, MA, USA) temperature loggers deployed \sim 0.5 m deep, and surface salinity (10 cm depth) was measured with a light refractometer at each site at each census (every 2–3 weeks from May to September and once in December from 2005 to 2007). The abiotic data (Appendix B in Electronic Supplementary Material) show that Pleasant was the warmest and least saline site, while Makah was slightly cooler and more saline than Lopez and Wayne.

Colonies were grown on 13 cm \times 13 cm sanded acrylic plates that were deployed horizontally underneath docks (\sim 75 cm below the surface) so that they hung face-down with their backs against the bottom of the dock. At each site, plates were deployed on six racks, which consisted of six plates spaced 10 cm apart. The racks were placed within 60 cm of other racks on the outermost dock. Colonies were grown under one of two treatments: no interaction or direct-contact interaction. One to four colonies were present on a plate and treatments were alternated among neighboring plates. To achieve a treatment with no interaction, I removed both conspecific and heterospecific individuals from colony edges every 2–3 weeks during the summers (May–September, between 7 and 9 censuses per year) from 2005 to 2007. Occasionally, contact did occur via settlement and growth of competitors during the census dates. If more than 5% of colony was in touch with a competitor, the colony was removed from the experiment. For the direct-contact interaction treatment, conspecific and heterospecific individuals were allowed to settle naturally and grow into contact with *B. violaceus* colonies. Due to chance, some colonies in the contact treatment did not experience much competition, so only those with $>15\%$ of their edges in contact with competitors were classified as contact interactions. Mean percent contact did not vary amongst sites (one-way ANOVA, $P = 0.593$), and was roughly 50% of the colony perimeter at all sites. Ten of the 18 competitor species were present at all sites, so there were some site-specific species (Appendix C in Electronic

Supplementary Material). Colony growth and survival was tracked by digital photographs and colony area was measured with ImageJ software (<http://rsbweb.nih.gov/ij/>).

Fecundity measurements were destructive because colonies had to be dissected to count larvae, so I limited sampling to test for contact and site effects, but not their interaction. To test for contact interaction effects on fecundity, I selected seven colonies from each treatment at one site (Wayne) in the middle of reproductive season (8 July 2008), measured colony area and counted the number of brooding larvae per zooid under a light microscope. To test for site effects on fecundity, I collected 6–9 colonies from three sites (Wayne, Pleasant, Lopez) from 8 to 11 July 2008, preserved them in 90% EtOH and then measured them for area and number of brooded larvae.

Statistical analyses

Effects of rack and colony identity over time on daily growth rate were tested using a repeated-measures ANOVA. Since they were found to be insignificant (Appendix D in Electronic Supplementary Material; rack $P = 0.195$, colony identity $P = 0.850$, colony identity \times date = 0.915), they were not included in further analysis.

To determine which parameters need to be included in an accurate model of *B. violaceus* dynamics, I used Akaike model selection criterion (AIC) to select the statistical model which best described the survival and growth data (Akaike 1974). AIC model selection facilitated the transition from raw data, which was a time-series with varying between-census intervals, to matrix model parameters for the LTRE analysis and ensured that I did not make the matrix models unnecessarily complex given the data. For survival and growth rates, summer and winter data were analyzed separately because preliminary analysis indicated these rates varied significantly amongst seasons. Between-census intervals varied, and this was incorporated directly into the survival model and indirectly into the growth model by scaling next colony area to a 2-week expectation $\{\ln(\text{area}_2) = \ln(\text{area}_1) + [\ln(\text{area}_2) - \ln(\text{area}_1)]/14/\text{interval}(d)\}$ prior to analysis. For survival analysis, a logistic regression was used with census interval, colony area, site and contact treatment and all interactions of the latter three as potential factors. For the growth analysis, I used a linear regression model and considered previous colony area, site, contact treatment and all possible interactions as factors. For fecundity, an ANCOVA was used to test treatment effects on the fecundity–area relationship. All statistical analyses were conducted using the R Programming language (<http://www.R-project.org/>).

Population matrix model and treatment contributions to λ

After determining how each treatment influenced size-specific vital rates, I needed a population model to translate these effects into overall population growth. To model *B. violaceus* population dynamics, I chose a periodic, size-based transition matrix (A , Eq. 1) with two seasons (Summer, Winter) and three size classes (Recruit <0.25 cm², Medium 0.25–6.0 cm², Large >6.0 cm²) (Fig. 1).

$$A = \begin{pmatrix} s_{RPRR} & s_{MPMR} + f_M & f_L \\ s_{RPRM} & s_{MPMM} & s_{LPML} \\ s_{RPRL} & s_{MPML} & s_{LP LL} \end{pmatrix} \times \begin{pmatrix} s_{R.wPRR.w} & s_{M.wPMR.w} & 0 \\ s_{R.wPRM.w} & s_{M.wPMM.w} & s_{L.wPLM.w} \\ 0 & s_{M.wPML.w} & s_{L.wPLL.w} \end{pmatrix} \quad (1)$$

Two seasons were chosen because season was found to significantly affect survival and growth, and because *B. violaceus* reproduces during the summer only, when temperatures become greater than ~10°C. Three size classes were chosen size because survival, growth and reproduction were found to significantly vary with size. The recruit size class included colonies too small to reproduce, while the medium size was chosen to capture significant size-related variation in vital rates (see “Results”). Survival probabilities for each size-class were calculated as the mean of the survival probability curve from the best fit model (at 14-day intervals) between the minimum and maximum size of each class. Fourteen-day transition probabilities were calculated directly from life-tables. To estimate larval recruitment, size-class fecundities were derived from the fecundity regression multiplied by larval survival rate. Larval survival rate was not explicitly estimated in this study, so a value similar to published estimates of colonial ascidian larval survival (Stoner 1990) was used (larval survival = 0.4). Varying larval survival rates from 0.2 to 0.8 was found to change population growth rate estimates, but did not significantly alter LTRE results.

The goal of this experiment was to understand how environment and direct-contact interactions affect overall success of *B. violaceus*, so I chose population growth rate (λ) as the response variable. For each treatment, the dominant eigenvalue of its transition matrix provided an estimate of λ . To estimate the confidence intervals for λ , I randomly re-sampled with replacement from the original dataset 10,000 times, re-calculated vital rates from the new survival model and life-table, and then determined λ for each re-sampled parameter set.

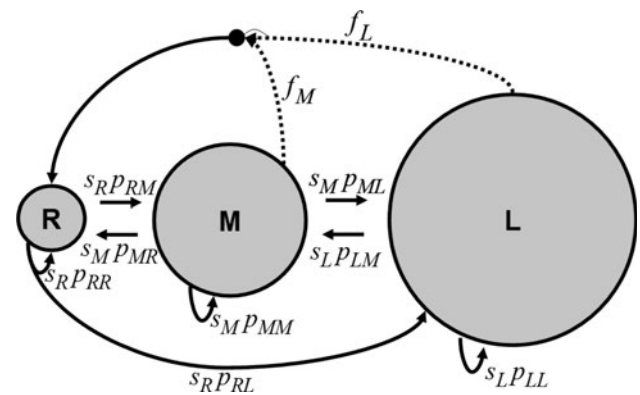


Fig. 1 Schematic diagram of the *Botrylloides violaceus* life cycle (not drawn to scale). *R* recruit size class (<0.25 cm²), *M* medium size class (0.25 cm² → 6.0 cm²), *L* large size class (>6.0 cm²), s_X survival of size class *X*, p_{XY} probability of transitioning from size class *X* to size class *Y*, where the subscripts refer to classes *R*, *M*, and *L*, solid arrow size class transition, dashed arrow sexual reproduction

To quantify the effects of each treatment on λ , I created a mean transition matrix $A^{(\cdot)}$ from pooled data, considered observed λ s as a linear function of the experimental treatments:

$$\lambda^{(ij)} = \lambda^{(\cdot)} + \alpha^{(i)} + \beta^{(j)} + \alpha\beta^{(ij)} \quad (2)$$

where $\alpha^{(i)}$ represents the effect of contact treatment *i*, $\beta^{(j)}$ represents the effect of site treatment *j* and $\alpha\beta^{(ij)}$ represents the interaction effect of contact treatment *i* and site treatment *j*. I then conducted a two-way fixed-effect LTRE (Caswell 2001), where treatment effects were analytically determined as:

$$\hat{\alpha}^{(i)} = \lambda^{(i)} - \lambda^{(\cdot)} \quad (3.1)$$

$$\hat{\beta}^{(j)} = \lambda^{(j)} - \lambda^{(\cdot)} \quad (3.2)$$

$$(\hat{\alpha}\hat{\beta}) = \lambda^{(ij)} - \hat{\alpha}^{(i)} - \hat{\beta}^{(j)} - \lambda^{(\cdot)} \quad (3.3)$$

where $\alpha^{(i)}$ = Contact effect *i*, $\beta^{(j)}$ = Site effect *j*, and $\alpha\beta^{(ij)}$ = Interaction effect *ij*.

The above equations determined treatment effects on λ , but gave no insight into what size-specific vital rates contributed the most to these effects. To pinpoint the vital rate effects that caused the largest changes in λ , I used decomposition analysis according to Caswell 2001. Assuming a first-order, linear relationship between a change in λ and a change in vital rate, the contribution of each treatment effects can be decomposed as follows:

$$\tilde{\alpha}^{(i)} = \sum_n \left(v_n^{(i)} - v_n^{(\cdot)} \right) \frac{\partial \lambda}{\partial v_n} \bigg|_{\frac{1}{2}(A^{(i)} + A^{(\cdot)})} \quad (4.1)$$

$$\tilde{\beta}^{(j)} = \sum_n \left(v_n^{(j)} - v_n^{(\cdot)} \right) \frac{\partial \lambda}{\partial v_n} \bigg|_{\frac{1}{2}(A^{(j)} + A^{(\cdot)})} \quad (4.2)$$

Table 1 Survival model selection for *Botrylloides violaceus*

Model parameters	<i>k</i>	ΔAIC
(a) Summer survival		
Area × site × contact – area:site:contact	15	
Area × site × contact – contact:site – area:site:contact	12	0.95
Area × contact + site	9	3.47
Area × site × contact	18	4.54
Area + site + contact	8	6.33
Area × site + contact	11	6.36
Area + site × contact	11	6.73
Area × contact	6	9.47
Area + contact	5	12.97
Area + site	7	15.61
Area × site	10	16.20
Area	3	19.93
Contact	3	176.03
Site	5	176.16
(b) Winter survival		
Area × site	9	
Area + site	6	4.31
Area	3	16.97
Site	5	20.22

Results of summer (a) and winter (b) survival model selection. Logistic regression was used to model survival probability as a function of census interval (not shown) plus colony area (area), contact (contact), site (site). All possible subsets of the full-factorial model were fit to the data, with “×” denoting full-factorial interactions, “:” denoting interaction terms and “+” denoting additive terms. Total number of parameters is given in column *k*. Models are sorted by their AIC value, from lowest (best) to highest (worst), with the ΔAIC column presenting the differences between the each model's AIC and the lowest AIC value

$$(\tilde{\alpha}\tilde{\beta})^{(ij)} = \sum_n \left(v_n^{(ij)} - v_n^{(\cdot\cdot)} \right) \frac{\partial \lambda}{\partial v_n} \bigg|_{\frac{1}{2}(A^{(ij)} + A^{(\cdot\cdot)})} - \tilde{\alpha}^{(i)} - \tilde{\beta}^{(j)} \quad (4.3)$$

where $v_n^{(ij)} - v_n^{(\cdot\cdot)}$ represents the difference between treatment and reference vital rates and $\partial \lambda / \partial v_n$ represents the sensitivity of λ to vital rate v_n calculated from a matrix halfway between the mean treatment matrix $A^{(i\cdot)}$ and the reference $A^{(\cdot\cdot)}$. In other words, an effect's contribution to λ is equal to its effect on vital rates multiplied by the sensitivity of λ to those vital rates.

Variation in survival, growth and fecundity of *B. violaceus* over a wide range of temperatures (5–25°C) and salinities (14–38 ppt) has been already estimated in a laboratory setting (Epelbaum et al. 2009). To test whether these known abiotic effects were detectable in the field, I conducted two analyses. First, I used regression to test the relationship between daily growth rate ($\Delta \log \text{area day}^{-1}$) and temperature (°C) and salinity (ppt) over all sites and dates. Then, to

focus on the relationship between abiotic variables and important vital rates, I correlated average summer and winter temperatures (°C) and salinities (ppt) at each site with the two most important vital rates of those seasons (i.e. those which contributed the most to changes in λ).

Results

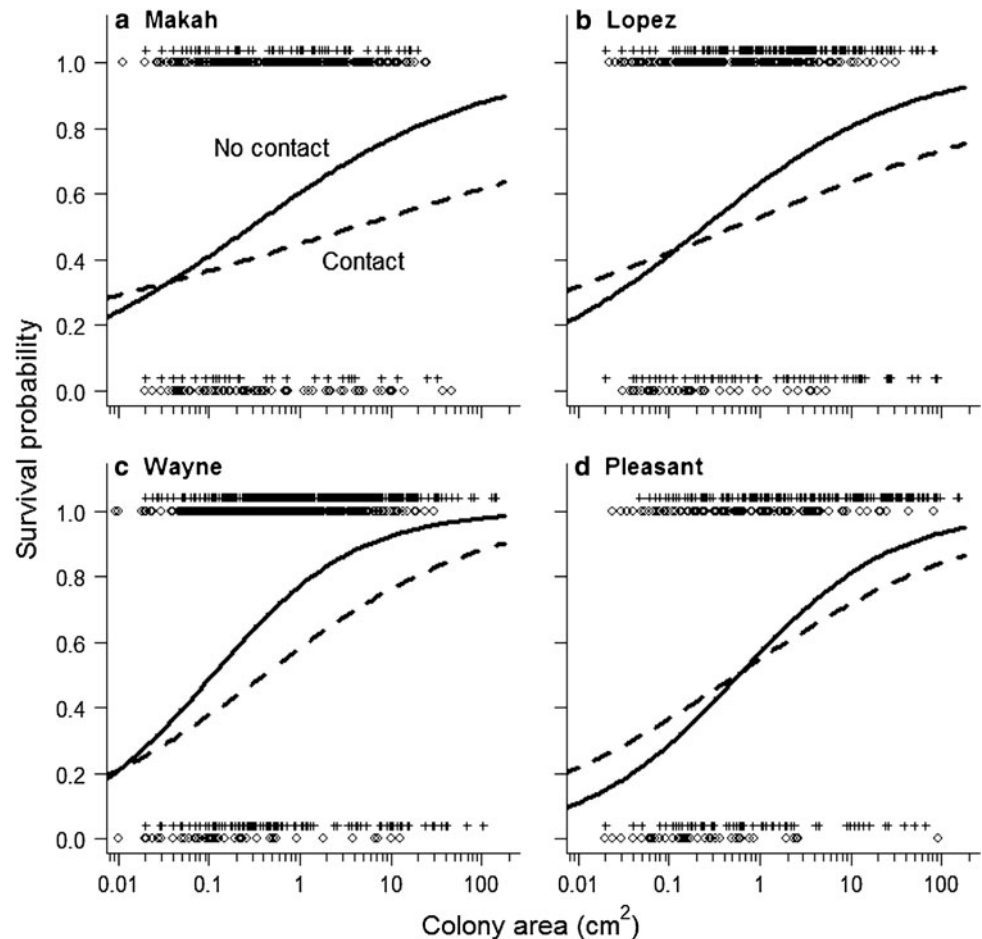
Treatment effects on vital rates

Overall, >3,000 colony transitions were observed over all sites and years (1,813 contact, 1,550 no contact). The best model describing summer survival probability included colony area, site, contact treatment and all interactions except the area × site × contact (Table 1a), although a similar model without the contact × site interaction had an ΔAIC value <3, so can be considered comparable (Burnham and Anderson 2002). Survival probability increased with colony area (Fig. 2), which is typical for colonial invertebrates. The effect of contact interaction on summer survival varied with colony area: it decreased the survival probability of larger colonies but unexpectedly increased the survival probability of very small colonies at three sites (Makah, Lopez and Pleasant). I tested this surprising result more explicitly with a logistic regression using just recruit class data. This post-hoc test revealed that direct-contact only significantly increased recruit survival at Pleasant (coefficient = 0.823, $P = 0.036$), and its effect was insignificant at Makah, Lopez and Wayne.

Site effects on survival also varied with size, with survival probability increasing with size most rapidly at Pleasant. For winter survival, the best model included colony area, site and their interaction (Table 1b) and winter survival probability increased with size (Fig. 4a), although not as rapidly as in the summer. Contact effects on winter survival could not be estimated because the contact treatments were not imposed during this season. Again, Pleasant exhibited a drastically different winter survival-area curve, with small colonies having a relatively low survival probability but very large colonies having the highest survival probability among sites.

I found that growth data were best fit by a model including colony area, site, contact and all interactions for the summer (Table 2a) and by a model including area, site and their interaction during the winter (Table 2b). As with winter survival, contact effects on winter growth could not be determined because the treatments were not imposed during this season. Contact and site effects were only slightly different during the summer (Fig. 3), but during the winter, site had a larger effect on growth curves (Fig. 4b). The number of larvae increased with colony area as expected (Appendix E in Electronic Supplementary

Fig. 2 The predicted curve of summer survival probability by colony area for *Botrylloides violaceus* with no contact (solid line, open circles) and with contact (dashed line, crosses) within each site: **a** Makah, **b** Lopez, **c** Wayne, and **d** Pleasant. For each plot, raw survival (1 = survive, 0 = died) is plotted by colony area (cm^2). Prediction curves were calculated from the best survival model (Table 1a). Contact data (crosses) are placed slightly above no contact data (open circles) for readability



Material), and neither site nor contact treatment significantly influenced this relationship (Table 3).

Life table response experiment result

Because treatment effects on survival and growth interacted with each other and colony area, individual treatment effects were inconsistent across *B. violaceus*' life history. LTRE analysis was therefore useful for translating these complex results into overall effects on λ , and for identifying where in the life history these effects made the largest contributions to λ . Vital rates estimates used LTRE analysis were derived directly from the experimental data and are available in Appendix F in Electronic Supplementary Material. Estimates of treatment λ s based on the model were highly variable (Fig. 5): Lopez and Wayne exhibited positive growth rates ($\lambda > 1$), while mean λ estimates for Makah and Pleasant were negative ($\lambda < 1$) but not significantly so (95% CIs overlapped 1). Site treatments had the largest effects (absolute values range from 0.272 to 0.545; Table 4) and explained more variance in λ than did contact treatment (absolute value = 0.038; Table 4). The effect of

contact was slightly negative overall (−0.038; Table 4), but actually positive at Pleasant (Fig. 5), although confidence intervals show that the effect of direct contact treatment was not significant at any site.

Consistent with differences in λ , differences in matrix model parameters were relatively larger amongst sites than amongst contact treatments (Figs. 6 and 7; site differences range −0.44 to 0.44, contact differences range −0.031 to 0.031). While differences were fairly evenly spread amongst vital rates, larger contributions to λ tended to occur in the winter, and winter recruit survival ($s_{R,w}$) and winter growth to medium ($p_{RM,w}$) were the largest contributors to λ (Fig. 7). Contact treatment effects on summer medium colony growth (p_{ML}) made the most significant species interaction contributions to λ (range −0.027 to 0.027; Fig. 6), but the magnitude of these contributions were just ~10% of the largest contributions made by site differences (range −0.277 to 0.256; Fig. 7).

The contact treatment was only imposed during the summer season, potentially underestimating the effect of direct interactions on λ if it was important in the winter. I thus also estimated winter vital rates with a contact effect

Table 2 Growth model selection for *Botrylloides violaceus*

Model parameters	<i>k</i>	ΔAIC
(a) Summer growth		
Area × site × contact	18	
Area × site × contact – area:site:contact	15	3.33
Area × site × contact – area:site:contact – contact:site	12	6.83
Area × site + contact	11	13.64
Area × contact + site	9	18.90
Area + site × contact	11	32.36
Area + site + contact	8	38.14
Area × site	10	59.82
Area + site	7	93.22
Area × contact	6	260.68
Area + contact	5	268.57
Area	3	281.84
Site	5	3013.44
Contact	3	3092.92
(b) Winter growth		
Area × site	9	
Area + site	6	49.05
Area	3	86.25
Site	5	569.41

Results of summer (a) and winter (b) growth model selection. Linear regression was used to model next colony size as a function of previous colony size (area), contact (contact), and site (site). All possible subsets of the full-factorial model were fit to the data, with “×” denoting full-factorial interactions, “:” denoting interaction terms and “+” denoting additive terms. Models are sorted by their AIC value, from lowest (best) to highest (worst), with ΔAIC column presenting the differences between the each model’s AIC and the lowest AIC value

proportional to its summer effect, and used LTRE on these new transition matrices (Appendix G in Electronic Supplementary Material). This did enhance the Contact × Site interaction effects (range −0.251 to 0.189; Table G1), but did not alter the differences in contact and no-contact λ s within sites (Contact effects range −0.038 to 0.038; Table G1). Thus, my conclusion that the site in which a *B. violaceus* population resided made a greater contribution (Site effect range −0.502 to 0.545; Table G1) to λ than did contact treatment remained unchanged. Also, similar to the previous LTRE, Contact effects were variable among sites: for Makah and Wayne, the contact λ became smaller with respect to the no-contact λ , and for Lopez and Pleasant, the contact λ became larger with respect to the no-contact λ . Again, however, confidence intervals overlapped so that contact treatment did not significantly vary within any site (Fig. G1). In summary, incorporating contact effects in the winter increased direct-contacts effect on λ within each

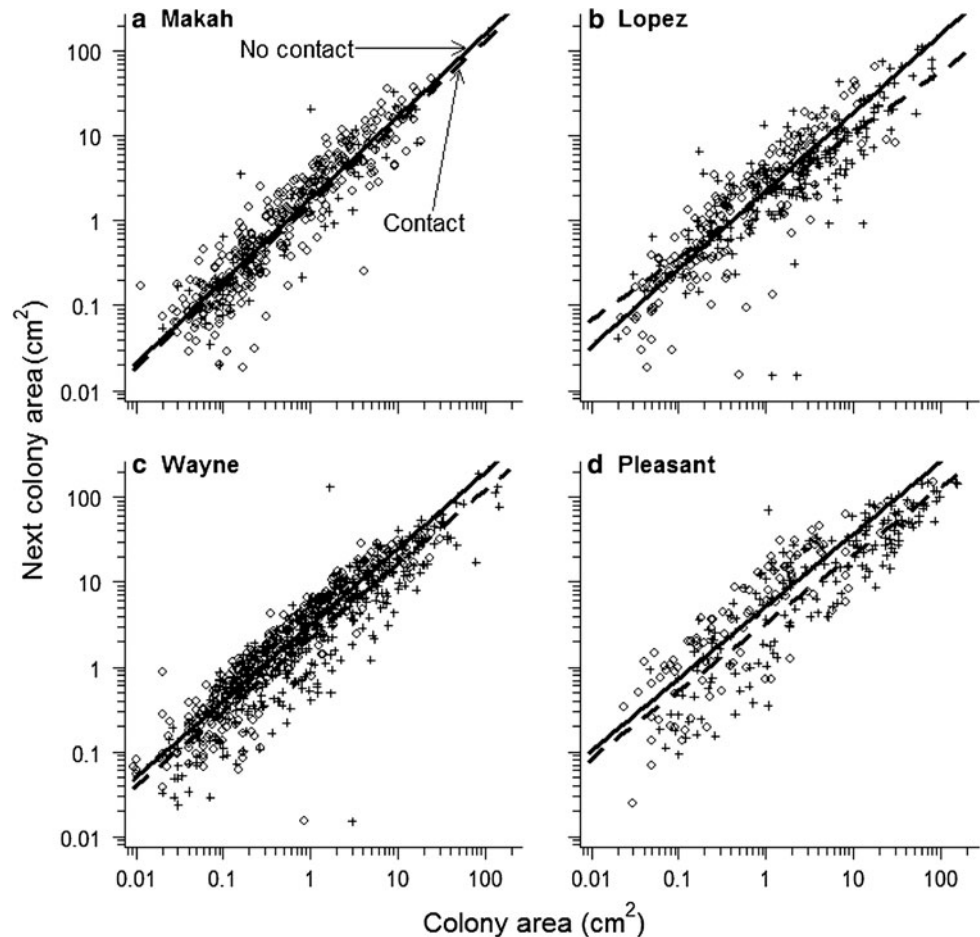
site, but it did not increase this factor’s relative explanatory power across sites.

Given the significance of site effects on λ and the observation that temperature and salinity varied greatly among sites, I first tested the relationship between daily growth rate and temperature and salinity among all sites and dates (Appendix H, Table H1 in Electronic Supplementary Material). As expected from previous laboratory studies, daily growth rate increased with mean temperature ($P < 0.001$) and mean salinity ($P = 0.005$) and there was a significant temperature × salinity interaction ($P = 0.001$). I then focused on the relationship between abiotic variables and the most important vital rates in each season (Appendix H, Fig. H1 in Electronic Supplementary Material). For summer vital rates, the two most important vital rates were recruit and medium growth (Fig. 7). Medium growth rates correlated positively with mean site temperature ($r = 0.999$, $p < 0.001$) and negatively with mean site salinity ($r = -0.99$, $P = 0.014$), but recruit growth, surprisingly, did not correlate significantly with either variable (temperature: $r = 0.79$, $P = 0.22$; salinity: $r = -0.75$, $P = 0.25$). During the winter, where vital rates contributed even more strongly to λ , recruit survival and recruit growth were the most important (Fig. 7) and both correlated positively with winter salinity (recruit survival: $r = 0.99$, $P = 0.006$; recruit growth: $r = 0.95$, $P = 0.047$), and marginally negatively with winter temperature (recruit survival: $r = -0.95$, $P = 0.053$; recruit growth: $r = -0.91$, $P = 0.086$). While only weakly correlative, these latter results are consistent with those of Epelbaum et al. (2009), who measured *B. violaceus* growth and survival across a wider range of temperatures and salinities in the laboratory. Overall, these two analyses suggest that temperature and salinity may have explanatory power in determining the success of *B. violaceus* in dock fouling communities.

Discussion

Abiotic variables and biotic interactions can influence the success of exotic species, but few studies have investigated their relative effects on population growth rate. Here, I found that both site and direct contact interactions were important in explaining variation in survival and growth of the exotic *B. violaceus*. However, site effects were an order of magnitude larger than contact effects. Therefore, environmental niche models may be sufficient to predict the distribution of this exotic species in fouling communities. This finding does not reject strong interference effects of particular species (see Dias et al. 2008), it only suggests that these strong interactions were not naturally common enough to make a large impact on population growth. This

Fig. 3 The predicted summer growth curves by colony area for *Botrylloides violaceus* with no contact (solid line, open circles) and with contact (dashed line, crosses) within each site: **a** Makah, **b** Lopez, **c** Wayne and **d** Pleasant. For each plot, next colony area (cm^2) is plotted by previous colony area (cm^2). Prediction curves were calculated from the best growth model (Table 2a)



finding of weak interference effects is consistent with coexistence theory, which predicts that successful exotic species should suffer little from interference competition (Amarasekare 2002).

Though effects of direct-contact interactions on λ were relatively weak and not significant at any sites, it is interesting that the direction of these effects were site-dependent: at three sites, Makah, Wayne and Lopez, λ was lower in contact treatments, but at the fourth site, Pleasant, λ was actually higher in contact treatments. This suggests possible facilitation, via increasing recruit survival, of an exotic species by resident species, an interaction that is often overlooked (Bruno et al. 2005). It also demonstrates that biotic interactions can quantitatively and qualitatively change across life history stage or abiotic environments, adding another example to a growing list of geographically variable species interactions (Thompson 1988; Travis 1996; Sanford et al. 2003; Mönkkönen et al. 2004; Pennings and Silliman 2005).

This experiment demonstrates that site had a relatively large effect on population growth rate and, and because

colonies were grown in the absence of other species during the experiment, this effect can be attributed to abiotic variables such as temperature, salinity, water flow, food availability. In natural populations, however, two other negative biotic interactions, predation and indirect exploitation competition, could be influencing *B. violaceus* population growth and here I consider their potential magnitude. Predation on exotics is generally thought to be weaker in novel ranges (Keane and Crawley 2002), although this does not require that predators have small effects on exotic success. Indeed, they have been found to inhibit exotic success in a variety of systems (see Carlson et al. 2009 for examples). In this system, grazing by chitons and echinoderms was observed, but a predator-exclusion experiment found that these large grazers did not have a significant effect on *B. violaceus* abundance or recruitment (Grey 2010). Similarly, Osman and Whitlatch found that, in New England, USA, *B. violaceus* colonies >1 week old were not affected by predation (1996). However, there is still little known about micro-predation and diseases in colonial ascidians, and if these varied by

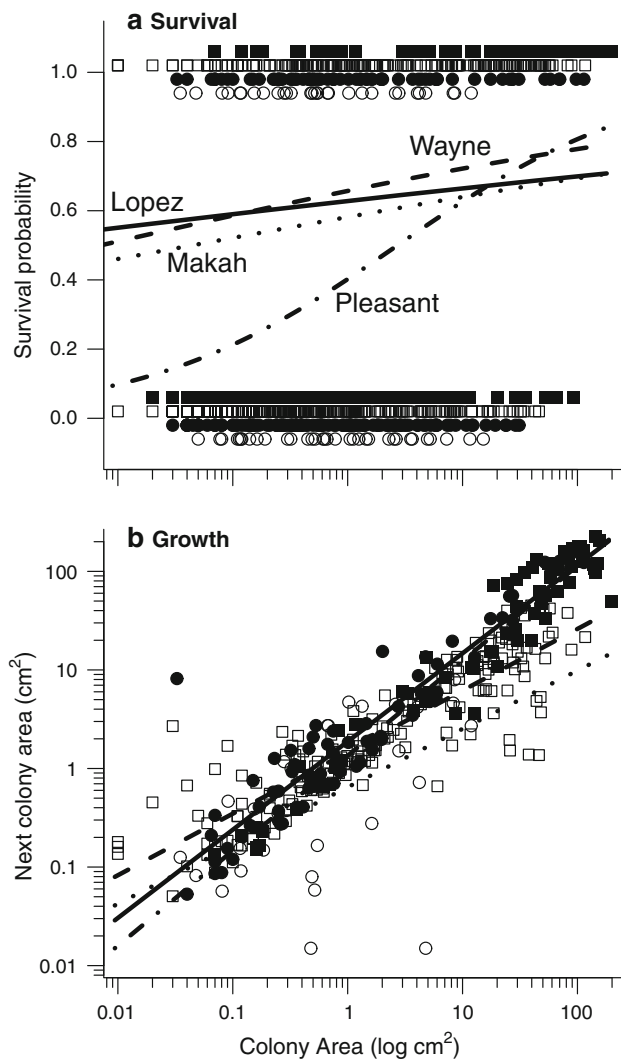


Fig. 4 **a** Raw survival and **b** growth of *Botryllodes violaceus* for the winter season with predicted curves for each site from best fit models (Tables 1b and 2b): Makah (dotted lines, open circles), Lopez (solid lines, solid circles), Wayne (dashed line, open squares), Pleasant (dashed-dotted line, solid squares)

site or season they could potentially affect population growth rates.

Indirect competition via resource exploitation is widely considered to inhibit exotic invasions and is frequently invoked in the diversity–resistance theory, which posits that more diverse communities will more fully utilize resources and thereby inhibit invasions (Elton 1958). In this system, the limiting resource is space (Paine 1974; Buss 1990), so exploitation competition could reduce λ by lowering either the colony growth rate or the colonization rate of larvae. Established colonies were observed to readily overgrow other species during

Table 3 Fecundity analysis of covariance

	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i> value	<i>Pr</i> (> <i>F</i>)
(a) Contact experiment					
Area	1	14,010.47	14,010.47	13.46	0.003**
Contact	1	323.85	323.85	0.31	0.587
Residuals	13	13,535.12	1,041.16		
(b) Site experiment					
Area	1	6,453.50	6,453.50	4.09	0.059
Site	2	5,654.95	2,827.48	1.79	0.196
Residuals	17	26,799.36	1,576.43		

Analysis of covariance tables for (a) contact and (b) site effects on the larvae–area relationship. Separate data were used for each experiment

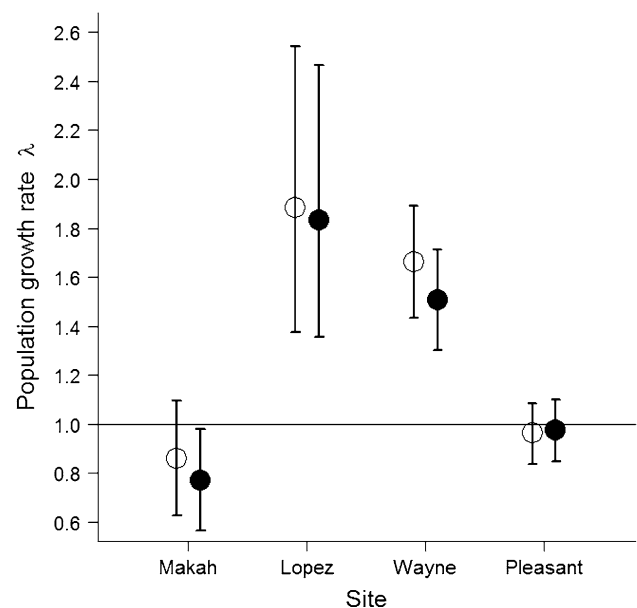


Fig. 5 Population growth rate (λ) under no contact (open circles) and contact (solid circles) treatments are plotted by site with bootstrapped 95% confidence intervals. The solid black line represents stable population growth ($\lambda = 1$)

the course of this experiment, so it is unlikely that resource exploitation strongly reduced colony growth rates. However, competitors could prevent the colonization of larvae, and a parameter related to this (fecundity) had high elasticity (Appendix I in Electronic Supplementary Material). The extent to which competition interacts with colonization rate is the subject of future study (Grey, in preparation).

Species interactions may not have explained variation in population growth rate well, and temperature and salinity appear to be better predictors of *B. violaceus* success. A laboratory study of *B. violaceus* found that

Table 4 Factorial LTRE

Treatment	Effect
No contact (N)	0.038
Contact (C)	−0.038
Site	
Makah	−0.502
Lopez	0.545
Wayne	0.272
Pleasant	−0.352
N × Makah	0.008
C × Makah	−0.008
N × Lopez	−0.013
C × Lopez	0.015
N × Wayne	0.038
C × Wayne	−0.039
N × Pleasant	−0.048
C × Pleasant	0.045

The effect of each contact treatment, each site treatment and their interactions on the population growth rate λ , which were determined analytically according to Eq. 2

colony growth and survival rates varied over a range of temperatures and salinities (Epelbaum et al. 2009), and this study found similar relationships between vital rates and temperature and salinity in the field. These relationships could help us predict *B. violaceus* success in a new range or under different climate change scenarios. For instance, nearly all climate change models predict warmer ocean temperatures and most predict increased precipitation in this study region (Scavia et al. 2002). Warmer ocean temperatures should enhance the population growth rate of *B. violaceus*. However, if increasing precipitation leads to decreasing near-shore salinities, this could have a negative effect on *B. violaceus* λ . As climate predictions are further refined regionally, they will provide a means of connecting climate change with specific environmental variables, such as temperature and salinity, that are suggested here to be important to the success of the exotic *B. violaceus* in Washington fouling communities.

Fig. 6 **a, b** Vital rate differences and **c, d** contributions to λ , by **a, c** no contact (*open bars*) and **b, d** contact treatments (*solid bars*). Summer vital rates are s_R Recruit survival, p_{RR} Recruit–Recruit growth, p_{RM} Recruit–Medium growth, p_{RL} Recruit–Large growth, s_M Medium colony survival, p_{MR} Medium–Recruit growth, p_{MM} Medium–Medium growth, p_{ML} Medium–Large growth, s_L Large Colony survival, p_{LM} Large–Medium growth and p_{LL} Large–Large growth

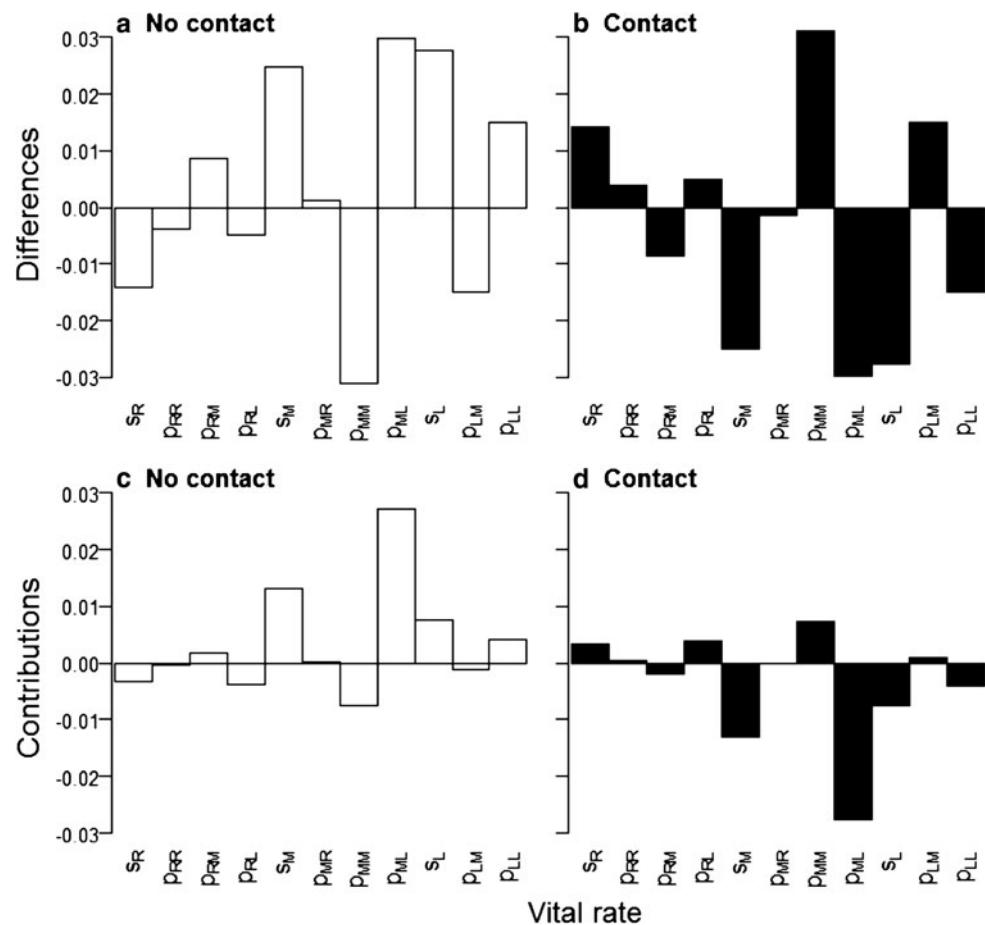
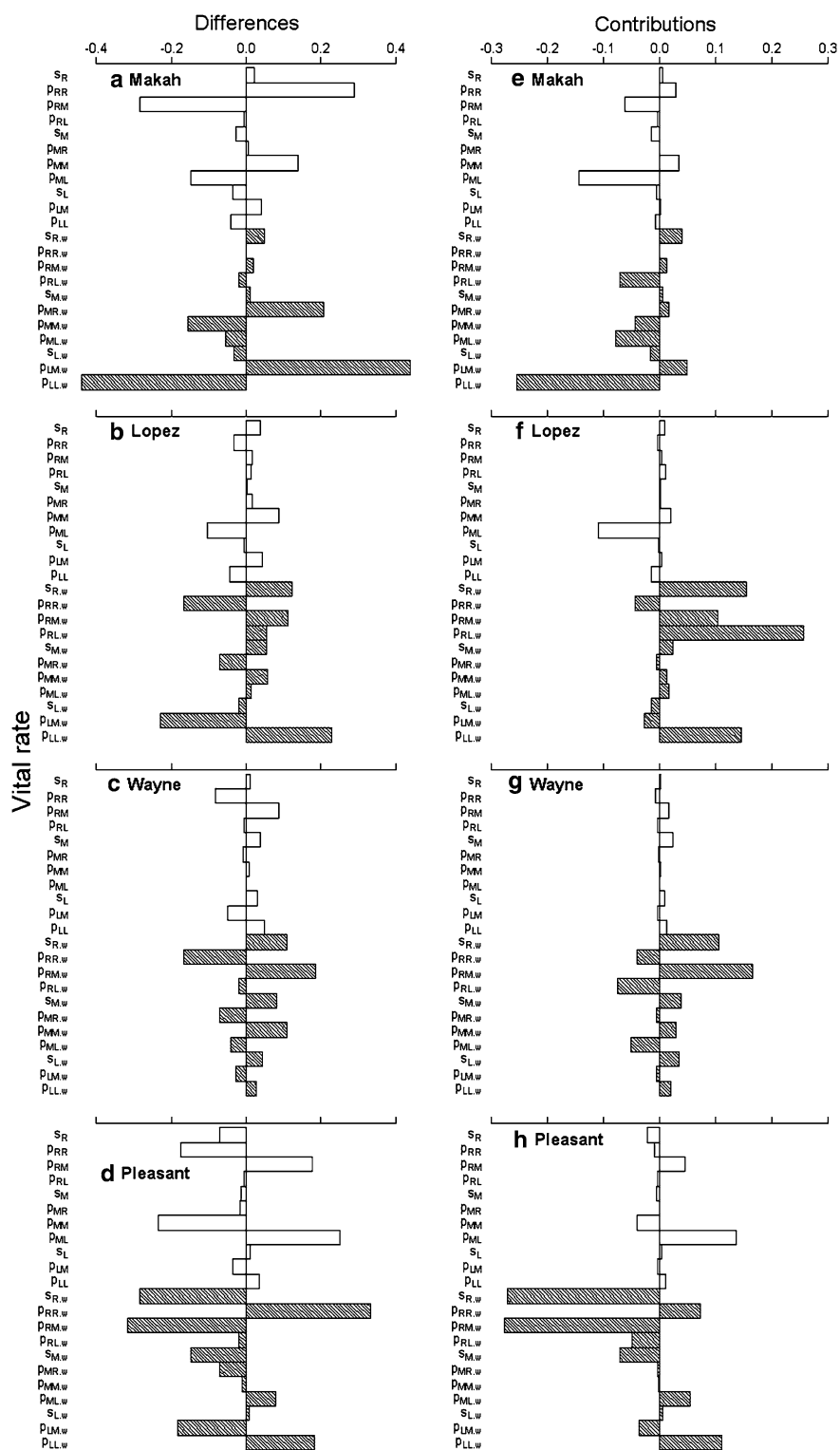


Fig. 7



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