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Quantifying geographic variation in physiological performance to address the absence of invading species[1]

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Abstract: An estuarine snail (*Batillaria attramentaria*), introduced to northern California marshes, is displacing a native confamilial mudsnail (*Cerithidea californica*) through superior competition for shared, limiting food resources. *Batillaria*, however, is absent from similar marsh habitats in southern California. I tested whether regional-scale variation in relative performance (growth) of the snails may have influenced *Batillaria*'s invasion pattern. I quantified growth using RNA:DNA ratios (a growth index that I ground-truthed with direct growth measurements) for snails collected throughout their entire collective North American distribution. *Batillaria* exhibited a high growth rate that was more than double *Cerithidea*'s growth rate in sympatric populations. A broad-scale relationship of species' growth rates against latitude projected an amply adequate growth rate for *Batillaria* in southern California where it is presently absent. Furthermore, growth rates of *Cerithidea* did not increase in southern California, suggesting that *Batillaria* would maintain its dramatic relative performance advantage. Thus, even if resources are limiting at southern latitudes, biotic resistance through competition with *Cerithidea* does not explain *Batillaria*'s absence. Among alternative, untested hypotheses for *Batillaria*'s absence, insufficient propagule inoculation has strongest support. Because transplant experiments with nonindigenous species are unethical, examination of species' performance over geographic scales provides a powerful alternative approach for invasion studies.
Keywords: estuaries, exotic species, exploitative competition, invasibility, latitudinal gradients, macroecology, nonindigenous species, RNA:DNA ratios.

Résumé : Un escargot estuarien (*Batillaria attramentaria*), introduit dans les marais du nord de la Californie, est en compétion avec un escargot indigène (*Cerithidea californica*) pour le partage de ressources alimentaires limitées. Or, *B. attramentaria* est toujours absent des marais du sud de la Californie. J'ai donc cherché à savoir si des variations régionales de la performance relative (croissance) des escargots peuvent avoir influencé son patron d'invasion. J'ai évalué la croissance d'escargots récoltés dans l'ensemble de leur aire de répartition nord-américaine en utilisant les rapports ARN:ADN (un indice de croissance que j'ai validé avec des mesures directes de croissance). Le taux de croissance de *B. attramentaria* est plus de deux fois supérieur à celui de *C. californica* dans les populations sympatriques. Il est possible de déterminer le taux de croissance qu'aurait *B. attramentaria* dans le sud de la Californie à l'aide d'une relation à grande échelle, du taux de croissance de l'espèce en fonction de la latitude. Le taux de croissance de *C. californica* n'augmente pas dans le sud de la Californie, ce qui suggère que *B. attramentaria* pourrait maintenir son avantage dans cette région. Par conséquent, même si les ressources sont limitées dans le sud, la compétition de *C. californica* ne peut expliquer l'absence de *B. attramentaria*. Parmi les hypothèses alternatives pouvant expliquer son absence, celle d'un apport insuffisant d'individus serait très plausible. Comme il serait contraire à l'éthique d'introduire une espèce d'escargot pour tester cette hypothèse, l'examen du succès des espèces à une grande échelle géographique constitue une approche alternative pour l'étude des invasions.
Mots-clés : compétition, espèce exotique, espèce non indigène, estuaire, gradient latitudinal, macroécologie, susceptibilité à l'envahissement, rapport ARN:ADN.

Nomenclature : Haldeman, 1840; Sowerby, 1855.

Introduction

Intrinsic characteristics of invading species and their recipient environments are often presumed to interact to determine the effectiveness and extent of invasion (Simberloff, 1985; Crawley, 1987; Huston, 1994; Thebaud *et al.,* 1996). This assessment has in part led to the general conclusion that most species introductions are highly case- or site-specific (Drake *et al.,* 1989). In practice, however, to determine the impact of an exotic species, data from a single site are often projected uniformly throughout the range of the invasion for lack of broad-scale empirical studies (Parker *et al.,* 1999). Although this approach is clearly better than having no data at all, such extrapolations from data that are not spatially replicated to generalize an invader's performance throughout the entire extent of its invasion are technically pseudoreplicated.

Here, I combine quantifying invader performance at multiple sites with another powerful methodological approach that is rarely, if ever, the focus of nonindigenous species studies — to examine mechanisms that underlie the absence of nonindigenous species at specific sites. One reason this approach may not be utilized in invasion studies is that transplant experiments, which directly test a species' performance in novel environments

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(*i.e.,* where it is presently absent), are not an ethical methodology when working with nonindigenous species. Instead, I quantify the relative performance of competing native and nonindigenous species throughout the majority of their existing geographic ranges (*i.e.,* the natural range for the native species and non-native range for the invader) and project the trend of the nonindigenous species' performance onto areas where it has not already invaded. Hence, I can test whether poor relative performance of a nonindigenous species may explain its absence from otherwise suitable habitat, and potentially illuminate the degree of variability in biotic resistance to invasion by the native species. Although several studies have addressed nonindigenous species' performance on small, regional scales (Thebaud *et al.,* 1996; Blossey & Schat, 1997; Hutchinson & Vankat, 1997), few have simultaneously examined the relative performance of interacting native species that may influence the success of the invasion (Milberg, Lamont & Perez-Fernandez, 1999; Gotelli & Arnett, 2000; Radford & Cousens, 2000).

The potamidid mudsnail *Cerithidea californica* inhabits salt marshes along the Pacific coast from Bahía San Quintín (Baja California) (T. Huspeni, K. Lafferty, pers. comm.) to Tomales Bay (Marin Co., California) (McLean, 1978; Abbott & Haderlie, 1980; Byers, 1999). It is one of the few macrofaunal intertidal grazers in salt marshes across this range. A confamilial and ecologically similar Japanese mudsnail, *Batillaria attramentaria* ([*B. cumingi*] J. McLean, pers. comm.), was introduced with imports of the Pacific oyster *Crassostrea gigas* in the early 1900s to several bays in northern California and northern Washington (Byers, 1999). Because *Batillaria*, like *Cerithidea*, lays eggs that attach to the mud surface and develop directly (Whitlatch, 1972; Yamada & Sankurathri, 1977; Adachi & Wada, 1999), the species has remained confined within bays to which it was introduced with *C. gigas* plantings. Over the decades since its introduction, *Batillaria* has become abundant in several northern California bays where *C. gigas* was planted liberally, and is apparently replacing *Cerithidea* in several areas where the two snails co-occur (Byers, 1999; 2000a). *Batillaria* has not established in southern California marshes, though there are records of a small number of plantings of *C. gigas* in southern marshes (Barrett, 1963; Byers, 1999) and at least one apparent interception of *Batillaria* in an incoming oyster shipment to a southern bay (Byers, 1999).

Previous work in northern California (*i.e.,* Bolinas Lagoon and Tomales Bay, Figure 1), areas of sympatry for these two snails, demonstrated that the species compete exploitatively for their shared food resource (epipelic diatoms) (Whitlatch, 1972; Whitlatch & Obrebski, 1980; Byers, 2000a). Due to an enhanced resource conversion efficiency, *Batillaria* increases its tissue mass at a rate 2-5 times faster and supports higher population densities than *Cerithidea* (Byers, 2000a). Because of similar size–fecundity responses between the species (Byers & Goldwasser, 2001), the effect of *Batillaria*'s growth advantage leads to superior rates of egg production and faster population growth. The Lotka-Volterra equations describing two species competing for a single resource under equilibrium conditions demonstrate that *Batillaria* persists on a lower equilibrium level of the shared resource (R*) and will consequently exclude *Cerithidea* (Byers, 2000a). *Batillaria* also appears better able to tolerate the most common disturbance events in the area (flooding and hypoxia) (Byers, 2000a,b).

Although *Batillaria*'s resource conversion efficiency and consequent growth rate are much greater than *Cerithidea*'s, the competitive exclusion of *Cerithidea* takes many years. In northern California where resources are limiting, *Batillaria* affects *Cerithidea* by decreasing its growth (and thus its size-associated birth rates) and has no direct effect on death rates. This means of competitive effect, in combination with the snails' longevity (10 y), produces a demographic lag in competitive exclusion. Even if *Cerithidea*'s reproduction is fairing badly due to competition, adults are not being killed by the interaction and by continuing to survive, prolong coexistence. Byers and Goldwasser (2001) demonstrate that empirical measurements of *Batillaria*'s advantage in exploitative competition result in *Cerithidea*'s exclusion 55-70 y after *Batillaria*'s introduction.

Outside of northern California, however, gradients in physical factors that correlate with latitude (*e.g.,* temperature, diets, tidal regimes) may affect the relative performance of the two species and help explain the spatial pattern of *Batillaria's* invasions. Specifically, the majority of successful *Batillaria* invasions have occurred at the northern

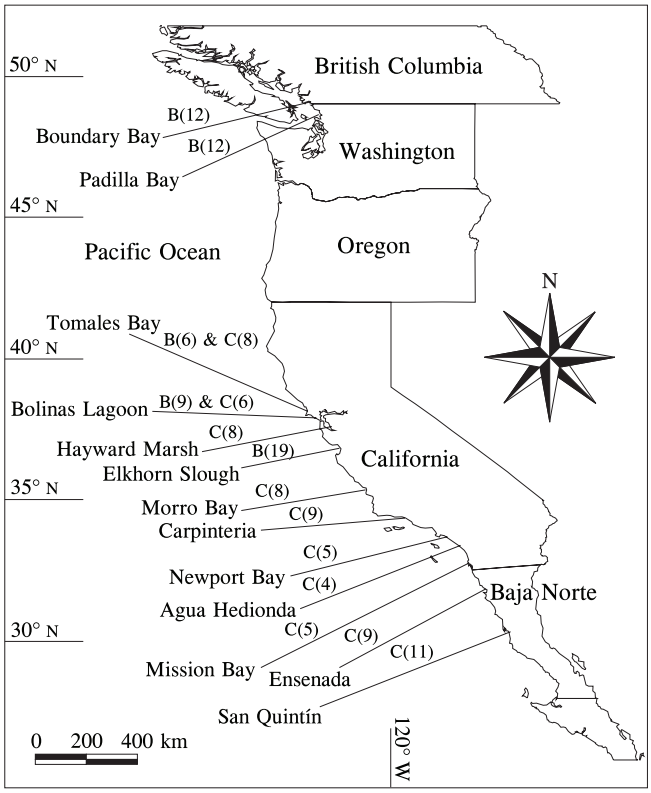

FIGURE 1. Sampled locations along the Pacific coast of North America representing nearly the entire geographic ranges of the native snail *Cerithidea californica* and the non-native snail *Batillaria attramentaria*. Symbols relate to which species were collected at each site: B = *B. attramentaria*; C = *C. californica*. In parentheses is the number of each species sampled at each site.

limit of *Cerithidea*'s range, where conditions may be less favourable to *Cerithidea* than in more southerly parts of its range. If edges of a species' range reflect a transition from favourable to unfavourable conditions (Caughley *et al.,* 1988; Brown, Mehlman & Stevens, 1995), individuals inhabiting the edge of the range may be more susceptible to removal forces, *e.g.,* competition, predation, and sudden abiotic fluctuations (Stohlgren, 1993; Thomas, 1994; Geroudet, 1995). This theory predicts not only that *Cerithidea* will perform better in the south, but that its performance may peak in central areas of its distributional range.

This study addresses two fundamental issues: 1) How does growth of each species vary with latitude? Specifically, could projection of poor physiological performance with latitude explain *Batillaria*'s absence from more southerly latitudes? 2) Does *Cerithidea*'s relative performance vary throughout its range, increasing toward the centre of its distribution? And, is the variation in *Cerithidea*'s geographic-scale performance sufficient to suggest that (if resources were limiting) a heightened competitive ability could explain *Batillaria*'s absence in southern California? Answers to these questions should demonstrate how spatial variability in either species' per-for-mance may influence *Batillaria*'s success within its non-native range. In general, understanding the spatial variation in species' relative performance should help determine whether broad-scale patterns of species' performance can improve predictions of invasion outcomes at the scale of individual sites. Such insight could focus efforts to reduce an invader's spread upon these more vulnerable areas.

Methods

SAMPLE COLLECTION

In 1997, I sampled *Cerithidea californica* and *Batillaria attramentaria* throughout the majority of their geographic ranges on the Pacific coast of North America (Figure 1). Snails were sampled from south to north within a 27-d period in late summer, the height of the primary growing season of the snails (McDermott, 1996; Byers, 2000a). A few additional snails from Elkhorn Slough and Bolinas Lagoon were collected at the end of the south-to-north sampling. Since both species reside on open mud surfaces almost exclusively (*Cerithidea*) or predominantly (*Batillaria*) (McDermott, 1996; J. E. Byers, pers. observ.), at all sample locations I selected an area of marsh with a mud substrate in the upper intertidal zone [> 1 m above mean lower low water (MLLW)]. I haphazardly collected ~ 12-20 of each of the two species. To examine density-dependent influences on growth of the sampled snails, I measured snail densities over a ~ 30-m^2 area surrounding my collection area by haphazardly placing a 0.05-m^2 quadrat 3-7 times depending on the variability in density. Given the generally limited mobility of these species (J. E. Byers, unpubl. data) I confined the density measurements to this localized spatial scale where density could potentially affect the growth of the collected snails. I measured the snails with calipers to the nearest 0.1 mm, cracked them open with a hammer, and examined them under a dissecting scope to determine the sex and to check for trematode parasites in the gonad. I excised the foot of each snail and removed the operculum on a sterilized polyethylene cutting board, placed the tissue in a cryogenic vial, and flash-froze the sample in liquid nitrogen. In the laboratory, tissue samples were removed from liquid nitrogen and stored at –80 °C until ready for use.

QUANTIFICATION OF GROWTH RATES AND RNA:DNA RATIOS

To examine both species' relative performance throughout their ranges, I quantified nucleic acids in foot tissue to construct ratios of RNA to DNA. Ratios of RNA/DNA relate the amount of protein synthesis standardized by the number of cells in a sample and have been repeatedly demonstrated to be a reliable index of short-term growth (Bulow, 1970; Buckley, 1984; Clemmesen, 1989; Foster *et al.,* 1993; Juinio & Cobb, 1994; Moss, 1994; Dahlhoff & Menge, 1996). To control for potential influences of size on growth, for these analyses I used individuals of standardized size (17-25 mm in length) (mean size ± SD; *Cerithidea*: 20.44 ± 2.15 mm; *Batillaria*: 20.87 ± 1.98 mm) that had been found to be free of parasites. The final number of snails of each species used from each site varied ($n_{mean} = 9$, $n_{median} = 8$, $4 \leq n \leq 19$).

The experimental protocol I used for quantifying nucleic acids largely follows the product instructions for PicoGreen® DNA and RiboGreen™ RNA quantification kits (Molecular Probes, 1996). Tissue was ground until completely dissolved in TE buffer solution (25 ml of 200 mM Tris-HCl, 20 mM EDTA, pH 7.5 in 500 ml DEPC-treated water) at a 1:80 ratio in homogenization tubes kept in crushed ice for 5 min. The sample was then sonicated 30 s, shaken on a Vortex mixer, and extracted into three vials; these were then diluted with precise amounts of DEPC-treated water. For DNA quantification, I added 12 µL of RNase to one vial and incubated it 10 min in a water bath at 37 °C (DNA was quantified with only one vial because DNA readings were very stable, exhibiting low variability during trial runs). For RNA quantification, a buffer salt and 20-µL DNase were added to the two remaining vials and incubated 20 min. After incubation, 1,000 µL of the appropriate photoreactive dye was added to each vial in the dark, kept 5 min at room temperature, transferred into crystal cuvettes, and read on a spectrofluorometer (Perkin Elmer LS-50, Wellesley, Massachusetts, USA) (excitation wavelength 480 nm, emission wavelength 520 nm). Due to moderate variability in fluorometer readings between days, even on samples from the same location, calibration curves constructed daily with nucleic acid standards were scaled to a fixed calibration curve constructed on the middle day of analyses to maintain appropriate scaling throughout the procedure.

To translate RNA:DNA ratios into meaningful measurements of snail growth rates and enable interspecific comparison of species' performance, I quantified RNA:DNA ratios and tissue growth in the same individually marked snails from Bolinas Lagoon. I haphazardly collected many snails of each species over a range of sizes that I measured and individually marked with Testor's enamel and placed back into the field within 0.1-m^2 open-topped, 2-mm mesh enclosure pens at ambient densities.

This enclosure pen design has been shown to have negligible influence on snail growth rates (Byers, 2000a). To establish the initial tissue mass of these marked snails I retained a random subsample of 50 snails of each species, for which I measured the external dimensions and extracted, dried, and weighed the tissue. For each species I regressed dry tissue mass against shell width (both $R^2 > 0.94$). Upon collection of the marked snails 60 d later, I similarly quantified the empirical relationships between external measurements and final dry tissue mass using > 100 snails of each species. A subset of the marked snails was measured externally and, instead of having their tissue dried and weighed, had their tissue sacrificed to the nucleic acid protocol. However, using the relationships of external shell dimensions and tissue mass quantified for the same cohort I could accurately calculate individual growth of dry tissue as estimated final dry tissue mass minus estimated initial dry tissue mass. I then regressed the change in dry tissue mass against RNA:DNA ratios to ground the ratios in empirical measurements of snail growth, permitting translation of ratios into tissue growth across all sites. This translation uses a commonly demonstrated linear relationship between RNA:DNA ratios and growth rates within a species (Bulow, 1970; Buckley, 1984; Buckley *et al.,* 1984; Foster *et al.,* 1993; Juinio & Cobb, 1994; Moss, 1994).

STATISTICAL ANALYSES

RNA:DNA ratios for each species were tested with Bartlett's test for homogeneity of variances (Zar, 1996) and found to be homoscedastic. Also, ratios for each species within and among sites were tested for normality and did not differ from a normal distribution. Although snails at each location were collected haphazardly and thus were roughly equal in the number of males and females, I used ANOVA to examine the effect of gender and site on RNA:DNA ratios for each species to determine whether gender was a factor to be controlled in analyses. For *Cerithidea* six sites that had fewer than three representatives per gender were excluded from this analysis. For *Batillaria* one site with a single female was excluded. As no differences were found (Table I), data for both sexes were pooled and all sites were incorporated for subsequent analyses.

To determine whether RNA:DNA ratios varied significantly between locations, I tested the effect of site on ratios with a one-way ANOVA for each species. RNA:DNA ratios measured at each site were then converted to dry tissue growth using the quantified relationship between RNA:DNA ratios and dry tissue growth established for snails in Bolinas Lagoon.

TABLE I. ANOVA results of test for sex and site differences in RNA:DNA ratios for each snail species.

	Cerithidea			*Batillaria*		
Source	df	*F*	*P*	df	*F*	*P*
Sex	1	0.26	0.61	1	1.04	0.31
Site	4	2.25	0.086	3	4.60	0.007
Sex × Site	4	1.53	0.22	3	0.73	0.54
Error	31			44		

To investigate a potential latitudinal trend in each species' performance, I regressed average growth against latitude for each species. To examine whether local snail density would significantly enhance the fit of these regressions, I used multiple regression to examine the effects of both snail density and latitude on each species' growth. Snail densities were usually intraspecific; however, I used combined *Batillaria* and *Cerithidea* densities where they co-occurred. Next, to determine if there was a unimodal (humped) pattern to *Cerithidea*'s performance across its geographic range, I tested the fit of a second-degree polynomial to *Cerithidea*'s growth data as a function of latitude. For purposes of this exploratory analysis only, the San Quintín population (the southernmost sample point) was treated as an outlier because of its high value and its high influence on the shape of the regression.

Finally, I used ANCOVA to test for differences between the species in their average growth rates by latitude, with species as the fixed factor and latitude the covariate (SAS 8.02, Proc glm, Type II SS).

Results

Gender did not significantly affect RNA:DNA ratios for either species (Table I). Due to very similar mean values for the sexes, the power to detect a significant difference was low (*Cerithidea*: 1 - β = 0.13, *Batillaria*: 1 - β = 0.17). However, at least one other study has corroborated that growth of adult *Cerithidea* is not sex dependent (Sousa, 1983). After pooling data for both sexes and incorporating data from sites that had been excluded from the sex analyses, *Batillaria*'s RNA:DNA ratios varied significantly across sites, and for *Cerithidea* the effect of site was nearly significant (*Batillaria*: $F = 3.76$, df = 4, 53; $P = 0.009$; *Cerithidea*: $F = 1.80$, df = 9, 63; $P = 0.085$). Although not formally significant, *Cerithidea*'s ratios did exhibit moderate variation between sites, with a 38% difference between its highest and lowest sites.

The relation between RNA:DNA ratios and dry tissue growth in grams (G) for each species in Bolinas Lagoon was: $G_{Batillaria} = 0.0026 * (\text{RNA:DNA}) + 0.0103$ ($n = 9$, $R^2 = 0.34$); $G_{Cerithidea} = 0.0022 * (\text{RNA:DNA}) - 0.0016$ ($n = 6$, $R^2 = 0.56$). These equations were used to translate measured RNA:DNA ratios into growth rates. The effect of latitude on average growth per location was not significant for either species (*Cerithidea*: $n = 10$, $R^2 = 0.058$, $P = 0.50$; *Batillaria*: $n = 5$, $R^2 = 0.21$, $P = 0.43$). For *Cerithidea* the low fit appeared to have been due to a non-linear response of growth with latitude. However, after excluding San Quintín (the southernmost site) as an outlier, a second-degree (unimodal) polynomial improved the fit only slightly ($R^2 = 0.074$, $P = 0.79$). Multiple regression that examined the response of snail growth to snail density, in addition to latitude, did not alter the significance of latitude on growth for either species, and in the case of *Cerithidea* did not improve the fit (*Cerithidea* $R^2 = 0.10$, $P = 0.69$; *Batillaria* $R^2 = 0.60$, $P = 0.40$). For *Batillaria* the non-significant *P*-value despite its high R^2 value was likely due to low power stemming from the low number of sites with *Batillaria* populations ($n = 5$).

Over the extant ranges of each species, *Batillaria* grew considerably faster than *Cerithidea*. *Batillaria*, for

example, grew nearly two and a quarter times faster than *Cerithidea* in Bolinas Lagoon (*Batillaria*: 0.027 ± 0.0062 g dry tissue mass/60 d (mean ± SD), *Cerithidea*: 0.012 ± 0.0022 g dry tissue mass/60 d) (Figure 2). The slopes of the lines comparing the average relative performance of the two species with latitude were not significantly different (ANCOVA: species latitude $F = 1.36$, $P > 0.27$). Subsequent removal of this interaction term from the ANCOVA analysis allowed isolation of the effects of species and latitude on growth rates, which demonstrated a significant effect of species on growth rates (Table II).

Discussion

Batillaria performs superiorly to *Cerithidea* in areas of sympatry. Barring any dramatic discontinuity in the quantified geographic trend, extrapolation of *Batillaria*'s performance to southern allopatric *Cerithidea* populations indicates *Batillaria* should grow well and retain a strong performance advantage over *Cerithidea* (Figure 2). Furthermore, if the snails' food resource remains limiting, faster growth should continue to reflect competitive dominance because it indicates better use of shared resources; thus, the growth of one species necessarily occurs at the other's expense (Byers, 2000a). Individual growth rates should in turn affect relative rates of population growth of the competitors due to the similar relationships between size and fecundity in these species (Byers & Goldwasser, 2001). If resources are not limiting at southern latitudes (and competition was thus reduced or absent), *Cerithidea* would provide weak to no biotic resistance, further underscoring that *Batillaria*'s amply adequate growth rate fails to explain its absence. Thus, poor physiological performance (growth) by *Batillaria* and resistance by native *Cerithidea* through exploitative competitive can be eliminated as viable explanations for *Batillaria*'s absence in southern California.

While this study falsified one hypothesis to explain *Batillaria*'s absence, it is possible to speculate on several alternative hypotheses that may still explain its absence. First, although *Batillaria* has a large geographic distribution in its native habitat, extending into tropical waters as far south as Hong Kong (22°N) (*N.B.*, *B. attramentaria* = *B. cumingi* in Asia) (Wells, 1983), abiotic factors may differ sufficiently between northern and southern California marshes to alter relative survival rates. *Batillaria* may be particularly sensitive to such differences since the source of their introduced populations was largely the northern areas of its native range, which had the most extensive oyster exportation (Barrett, 1963). Factors unaccounted for by this study, *e.g.,* habitat encroachment or eutrophication, could influence *Batillaria*'s performance (or presence/absence) and would likely be higher in the more urbanized marshes of southern California. However, all studies to date indicate *Batillaria* does at least as well, if not better than, *Cerithidea* in handling such disturbances (Carlton, 1993; Byers, 1999; 2000b).

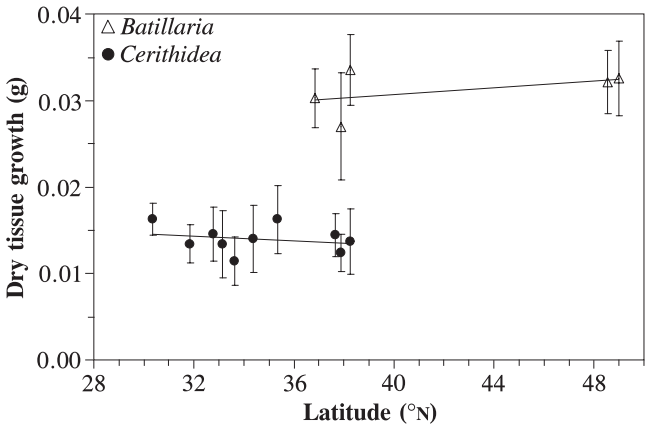

FIGURE 2. Dry tissue growth (computed through RNA:DNA ratios) over 60 d for 17- to 25-mm *Cerithidea californica* (circles) and *Batillaria attramentaria* (triangles) as a function of latitude. Error bars represent one standard deviation (SD).

Second, changes in predator composition, prey selectivity, or relative rates of predation could differentially impact *Batillaria* in southern California marshes. Measured predation rates on the snails however are small (Stenzel, Huber & Page, 1976; Sousa, 1993; J. Byers, pers. observ.), and the known predators (shorecrabs and wetland birds, particularly the willet [*Catoptrophorus semipalmatus*]) are distributed throughout northern and southern sites. Changes in the suite of trematode parasites that infect and castrate the snails are unlikely and furthermore would have little influence on *Batillaria*'s invasion of southern California. In North America, *Batillaria* is only infected with a single highly host-specific parasite that is itself a non-native species (*Cercaria batillariae*) from *Batillaria*'s native habitat; none of the 18 trematode species known to infect *Cerithidea* infects *Batillaria* (Torchin, Byers & Huspeni, in press). Additionally, trematodes seemingly exert minimal control over *Batillaria'*s population growth. For example, in Padilla Bay, Washington, *Batillaria* is highly infected (80%) (Torchin, Byers & Huspeni, in press) yet persists at one of its highest measured densities. Most importantly, a mathematical model of *Batillaria*'s invasion demonstrated that even a large differential in parasite infection rates between the snail species would have little influence on the outcome of *Batillaria*'s invasion or the speed of its displacement of *Cerithidea* (Byers & Goldwasser, 2001).

Finally, *Batillaria*'s absence in southern areas may be explained by a lack of sufficient propagule inoculation, a factor suspected to differ at least moderately between northern and southern sites. Plantings of *Batillaria*'s transport vector, *C. gigas*, were far more extensive in northern than southern California, where plantings were short-term trials that were deemed unsuccessful and discontinued quickly (Barrett, 1963; Byers, 1999). Marshes in the middle of *Batillaria*'s non-native range (Oregon

TABLE II. ANCOVA results testing the effect of species on average dry tissue growth rates at each latitude. The interaction term was not significant and therefore excluded from this analysis.

Source	df	*F*	*P*
Species	1	125.0	< 0.0001
Latitude	1	0.50	0.49
Error	12		

and southern Washington), and even San Francisco Bay near its present southern limit, received intermediate levels of *C. gigas* plantings (Galtsoff, 1932; Barrett, 1963; Byers, 1999). These sites also lack *Batillaria* populations, although the relationship of *Batillaria*'s performance with latitude suggests that the invader would do well there. Consistent with this hypothesis, if intermediate frequencies and quantities of *C. gigas* introductions were insufficient to introduce or establish *Batillaria* populations in these areas, it seems plausible that much smaller numbers of Pacific oyster imports in southern California would fail to establish *Batillaria*. If indeed insufficient propagule inoculation explains *Batillaria*'s absence, all marshes across the latitude studied here (*i.e.,* in Oregon as well as southern California) are vulnerable to *Batillaria* invasion. The conspicuous absence of *Batillaria* in San Francisco Bay despite its presence in several marshes immediately to either side and despite the many different microenvironments within it underscores not only its vulnerability to *Batillaria* invasion, but also the difficulty of the snail dispersing even a few km on its own, let alone into southern California. With multiple *Batillaria* populations only tens to hundreds of kilometres away from marshes where the snail is presently absent, the risk of *Batillaria*'s introduction through human-mediated transport may be especially great. Examination of these alternative hypotheses remains a topic ripe for further research.

While the fairly sizable variation in RNA:DNA ratios measured across sites could reflect real variation, it is likely that at least some was due to procedural noise. For example, similar-sized conspecifics of each species in Bolinas Lagoon that had similar growth rates exhibited variation up to ~35% in their ratios. Some authors have demonstrated even larger variation in ratios (Clemmesen, 1994; Bergeron, 1997; Esteves *et al.,* 2000). However, despite the large variability in ratios within sites, *Batillaria* exhibited significant differences in growth across sites that may have derived in part from its larger geographic distribution, which likely encompassed more environmental heterogeneity. Also, variation in *Batillaria* across sites could stem from its possible establishment in North America through multiple independent introductions, which potentially increases genetic differences. In this study, the difference in growth between the species was still large enough to detect significant differences. However, the resolution necessary to examine relative performance differences between species may not always be attainable through RNA:DNA ratios, particularly in cases where the species' growth rates are more similar.

Although growth of each species varied significantly (or nearly so) among sites, it did not vary systematically with latitude, especially for *Cerithidea*. Although *Cerithidea*'s performance was highest at the centre of its range (Morro Bay, 35° 20' N, 120° 50' W) (Figure 2), there was no distinct humped-shaped pattern to its performance with latitude. The lack of strong latitudinal variation in growth rates of either species may reflect that potentially influential variables like marsh water temperature do not vary with latitude nearly to the same extent as temperatures on the outer coast. The lack of a trend also may reflect the timing of my sampling to coincide with peak growth. Factors such as a shorter growing season at higher latitude do affect annualized growth rates of *Batillaria* (Whitlatch, 1974; Yamada, 1982), implying that latitudinal trends (*e.g.,* a decrease in growth at the northern end) would be apparent at other times of year when seasonal differences are more pronounced across latitude. Snail density on a local scale likewise had little effect, at least on *Cerithidea*'s growth, perhaps due to low variance in *Cerithidea*'s density in the areas sampled (CV = 49%, compared to 84% for *Batillaria*).

In summary, the invader in this system appears to perform superiorly across its entire introduced range and is predicted to do similarly well among several suitable sites where it has not yet been introduced. However, in other biological invasions where species are more evenly matched, examination of geographic gradients in species' performance may reveal variation sufficient to allow invaders to perform well in some areas and poorly in others, especially compared to potential competitors. Quantifying large-scale patterns of variability may therefore help identify sites that are most vulnerable to invasion and help explain not only why an invading species prospers where it occurs, but also whether it could prosper where it is presently absent. Thus, while invasion success may be site-specific, analysis of species' performance over a geographic scale can enable predictions of invasibility by illuminating patterns apparent over larger spatial scales.

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