Evol Ecol (2013) 27:1117–1127
DOI 10.1007/s10682-013-9632-4

ORIGINAL PAPER

Complex consequences of increased density for reproductive output in an invasive freshwater snail

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Received: 20 November 2012 / Accepted: 3 February 2013 / Published online: 15 February 2013

Abstract Population density can have profound, often negative effects on fitness-related traits and population dynamics, and density dependence is of central importance to many prominent ecological and evolutionary hypotheses. Here, we used experimental manipulations of food, population density, and water conditioning to characterize the mechanisms underlying reproductive density-dependence in *Potamopyrgus antipodarum*. This New Zealand freshwater snail is a prominent model system for invasion biology, ecotoxicology, and the maintenance of sexual reproduction. We demonstrated that a primary source of negative density-dependence is food limitation, but surprisingly, we found that *P. antipodarum* reproductive output was much higher in high density versus low-density conditions when food was adequate. We then used manipulations of water environment to demonstrate that these positive effects of high density are likely caused by a waterborne substance produced by *P. antipodarum*. Altogether, these results indicate that there are strong and complex connections between food availability, density, and reproductive output in this important model system that could influence the dynamics of invasive populations, the costs and benefits of sex, and the approaches used for ecotoxicology studies.

Keywords Density dependence · Facilitation · Allee effect · Resource limitation · *Potamopyrgus antipodarum*

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Introduction

Density dependence is a common feature of plant and animal populations (reviewed in Turchin and Taylor 1992; Woiwod and Hanski 1992; Zeng et al. 1998; Sibly et al. 2005; Brook and Bradshaw 2006; Bonenfant et al. 2009), and density-dependent mechanisms are likely to often be an important determinant of population dynamics (Brook and Bradshaw 2006; Bonenfant et al. 2009). While food limitation is frequently a source of density dependence (e.g., Fowler 1987; Dillon 2000; Cross and Benke 2002; Sibly et al. 2005; Bonenfant et al. 2009), many other mechanisms can also cause or contribute to negative consequences of high density (e.g., access to water, e.g., Chamaillé-Jammes et al. 2007; physical interference, e.g., Baur and Baur 1990; chemical inhibition, e.g., Levy et al. 1973; increased risk of predation, e.g., Steele and Forrester 2005).

Here, we used experimental manipulations of food and population density to determine the mechanism(s) underlying previously documented severe negative effects of high population density on reproductive output in *Potamopyrgus antipodarum* (Neiman 2006). This freshwater New Zealand snail is often used to study the maintenance of sexual reproduction in natural populations because frequent coexistence between obligately sexual and obligately asexual individuals (Lively 1987, 1992) and multiple independent transitions to asexuality (Dybdahl and Lively 1995; Neiman and Lively 2004) allow for direct comparisons between sexuals and asexuals without introducing confounding effects of different source populations or genetic background.

A better understanding of the mechanisms underlying negative density-dependence for any model system used to study the evolution of sexual reproduction is especially important in light of a growing body of theory suggesting that density dependence can profoundly influence the maintenance of sex (e.g., Doncaster et al. 2000; Lively 2009; recently reviewed in Song et al. 2011). The rising interest in *P. antipodarum* as an ecotoxicology model system (e.g., Duft et al. 2007; Wagner and Oelhmann 2009; Stange and Oehlmann 2012) and as a potentially harmful invasive species in North American, European, and Australian freshwaters (recently reviewed in Alonso and Castro-Díez 2012) provides additional impetus to characterize the biology of this broadly interesting species.

An earlier study (Neiman 2006) found that there was a nearly twofold increase in the number of embryos brooded by female asexual *P. antipodarum* housed in low- versus high-density populations. All populations in Neiman (2006) received the same amount of food, meaning that it was impossible to determine whether the marked decrease in reproductive output in the high-density populations was due to lower per capita food versus other influences of living in high-density conditions. Here, we used a full-factorial approach to systematically vary food and population density and decouple their effects on reproduction in *P. antipodarum*.

This present study clearly identified food limitation as the primary source of negative density-dependence in *P. antipodarum*. However, we also found a strong positive effect of high population density ("facilitation") on reproductive output when food was adequate (also see Brenneis et al. 2010). One plausible explanation for this phenomenon is that the *P. antipodarum* in our study were influenced by waterborne substances produced by coexisting individuals. Such a mechanism was suggested by Cope and Winterbourn (2004), who found that growth in *Physa acuta*, another freshwater snail, increased when exposed to water conditioned by *P. antipodarum*. Facilitation via snail-produced waterborne substances has been documented in several other freshwater snail species (e.g., Thomas and Aram 1974; Kawata and Ishigami 1992; reviewed in Dillon 2000). With this in mind, we performed an additional study designed to identify whether such a mechanism might underlie the observed positive effect of high population density on reproduction in *P. antipodarum* under high-food conditions.

Materials and methods

Experiment 1a/b: decoupling the effects of density from the effects of food limitation

We conducted two identical experiments involving full-factorial manipulations of food and population density with two different asexual *P. antipodarum* lineages, Denmark B (Experiment 1a; July–August 2010) and Mapourika 75 (Experiment 1b; September–November 2010). Members of each lineage were descended from a single asexual female *P. antipodarum* originally sampled from a natural population in Lake Mapourika, New Zealand (Mapourika 75) and an invasive population in Denmark (Denmark B). We randomly selected 128 female *P. antipodarum* measuring between 2.25 and 4.00 mm in shell length from each lineage. We chose snails of this size because female *P. antipodarum* of this shell length typically achieve reproductive maturity within 2–3 months (Winterbourn 1970; Tibbets et al. 2010), meaning that we could use these *P. antipodarum* to study how our treatments affected reproductive output within the course of a 10-week experiment.

Each individual was randomly assigned to a low- versus high-food treatment and a low (two snails) versus high (six snails) density treatment, for a total of four treatment combinations (low food + low density, low food + high density, high food + low density, high food + high density). These population sizes were chosen based on other studies in which similar manipulations of *P. antipodarum* population density resulted in marked reduction in reproduction for the high-density treatment relative to the low-density treatment (e.g., Neiman 2006). We replicated each of the four treatment combinations eight times, for a total of 32 experimental populations for each of the two lineages.

Each replicate population was housed in an 800 ml plastic cup (11.5 cm diameter at the top rim, 9.5 cm diameter at the bottom, and 8 cm in height) containing 300 ml water. We used nail polish to mark each snail within each population with a unique (within population) color identifier on the back of its shell and then photographed each individual next to a ruler under a dissecting microscope. We then used ImageJ software to quantify initial shell length. All populations were fed dried *Spirulina* algae, a standard food source for laboratory *P. antipodarum* (e.g., Krist and Lively 1998; Tibbets et al. 2010), three times per week. Each low-food population received 0.008 mg dried *Spirulina*/snail and each high-food population received 0.023 mg *Spirulina*/snail. These food levels were chosen following a combination of previous studies of the influence of the amount of *Spirulina* provided to *P. antipodarum* (e.g., Krist et al. 2004) and our own pilot experiments. Snails were housed in a 16 °C room with a 16 h light/8 h dark cycle. We changed water and cleaned cups weekly in order to control for microorganism growth and waste build-up. Cups were arranged haphazardly with respect to treatment and were rearranged haphazardly after cleaning in order to control for any potential positional effects. We checked each cup for dead snails three times a week, replacing dead individuals with a similarly sized individual from the same lineage in order to maintain density within each population. These replacement individuals were not included in data analyses. We maintained each experiment for 10 weeks, following previous studies that evaluated how environmental conditions influence reproduction in female *P. antipodarum* (e.g., Neiman 2006). We then measured final shell length and dissected each individual in order to count the number of embryos (if any) she was brooding. These embryo number data were used as an estimate of reproductive output (e.g., Jokela et al. 1997; Wagner and Oelhmann 2009; Tibbets et al. 2010). Because it takes about 35 days for *P. antipodarum* embryos to develop and hatch (Gust et al. 2011), the 10-week duration of the experiment also meant that we focused solely on embryos produced during the course of the experiment.

Experiment 2: evaluation of the source of facilitation

We used female asexual *P. antipodarum* from the Denmark B lineage to begin to characterize the mechanism underlying the reproductive facilitation in high density/high-food environments observed in Experiment 1a/b. All but fifteen individuals exceeded the 2.5 mm shell length often used as a threshold to assume non-juvenile status (i.e., the potential for reproductive activity) in *P. antipodarum* (e.g., Negovetic and Jokela 2001; Tibbets et al. 2010). The remaining females were at least 2.0 mm in shell length and were thus likely within a few months of reproductive maturity (Winterbourn 1970), though the notably high morphological and size variation that characterizes *P. antipodarum* (e.g., Haase 2003) means that the use of a size threshold to assign juvenile versus non-juvenile status does carry some risk of error.

We haphazardly assigned each individual to one of six experimental population types that varied in population density and water conditioning. The high-density control populations contained six snails/population ("HDC"), and the low-density control populations contained three snails/population ("LDC"). The controls were not exposed to water conditioned by other snails, while the other four treatment combinations were exposed to water conditioned by the control *P. antipodarum*. These water-conditioning treatment types included high density (six snails) and low density (three snails) populations exposed to water from the low-density controls (hereafter "HDLW" and "LDLW", respectively) as well as high density (six snails; "HDHW") and low density (three snails; "LDHW") populations exposed to water from high-density controls. We replicated the controls ten times and the conditioned water treatments eight times, for a total of 52 experimental populations. Snails were housed and fed (high-food level) as described for experiment 1.

We checked for mortality three times per week and replaced dead individuals with individually marked Denmark B (>2.0 mm in shell length) in order to maintain population density. Data from these replacement snails were not included in statistical analyses. We removed all water and cleaned each cup once per week. At this time, water from the control populations was pooled into two containers (with high density and low-density control water pooled separately), and was then topped off with fresh water to account for evaporation from the previous week. The pooled control water was then distributed by 300 ml portions to the cups making up the conditioned-water treatment populations. We maintained the snails under experimental conditions for 10 weeks, after which we measured final shell length and counted the number of brooded embryos contained by each female.

Statistical analyses

For both experiments, we began by using individual female embryo counts to calculate the mean embryo number per female per population. We used these population means for all subsequent analyses in order to control for non-independence of individuals that were housed together within cups. We next used Shapiro–Wilk tests to evaluate whether the embryo count data from each experiment met the normal distribution requirement of parametric statistical analyses. In both cases, the datasets departed significantly from a normal distribution (Experiment 1: Shapiro–Wilk test statistic $= 0.789$, $df = 64$, $p < 0.0001$; Experiment 2: Shapiro–Wilk test statistic $= 0.895$, $df = 52$, $p < 0.0001$), so we used non-parametric approaches for all analyses. All statistical analyses were implemented with IBM SPSS Statistics v. 19 unless otherwise indicated.

Experiment 1a/b

Because positive shell length-fecundity relationships have been reported in female *P. antipodarum* (e.g., Tibbets et al. 2010; McKenzie et al. 2013), we first used Spearman's correlations to establish whether we needed to control for final shell length. Embryo number and final shell length were not significantly correlated across all 64 populations (Spearman's $\rho = 0.075$, $p = 0.555$), across the 45 populations that produced embryos (Spearman's $\rho = 0.038$, $p = 0.805$), or across the 32 populations represented by each lineage (Denmark B: Spearman's $\rho = -0.183$, $p = 0.316$; Mapourika 75: Spearman's $\rho = 0.257$, $p = 0.155$). Because we did not detect significant shell-length fecundity correlations, we used uncorrected embryo count data for all analyses of reproductive output.

We first used a Mann–Whitney *U* test to evaluate whether there was a significant effect of lineage (Denmark B vs. Mapourika 75) on mean embryo production. Since this analysis outcome was not significant ($p = 0.47$), we pooled embryo data across lineages. We then used Mann–Whitney *U* tests to determine whether there were significant effects of the population density and food treatments on mean embryo production. We also used Mann–Whitney *U* tests within each level of the food and density treatments to determine how food and density influenced embryo production within each treatment level of the other factor.

We then repeated these Mann–Whitney *U* analyses with a dataset including only populations in which at least one female had produced embryos. We also used Fisher's exact tests (http://graphpad.com/quickcalcs/contingency1.cfm) to compare the number of populations in which at least one female produced embryos to the number of populations where no females produced any embryos both across and within the density and food treatments. These analyses allowed us to evaluate how the treatments influenced the presence of reproductive activity as well as embryo output in females that were actually reproducing.

Experiment 2

We first used Spearman's correlations to determine whether the independent variable of final shell length and the dependent variable of embryo output were significantly associated in order to control (if necessary) for effects of size on fecundity. This relationship was not significant either across all populations ($N = 52$, Spearman's $\rho = 0.075$, $p = 0.595$) or across the 46 populations that produced embryos ($N = 46$, Spearman's $\rho = 0.171$, $p = 0.256$), so we used the uncorrected embryo data for all subsequent analyses. We then used Kruskal–Wallis tests (water conditioning) and Mann–Whitney *U* tests (density) to determine whether there were significant effects of the population density and water conditioning treatments on mean embryo production. We also used Mann–Whitney *U* tests to determine how density and water conditioning influenced embryo production within each treatment level of the other factor.

Results

Experiment 1a/b

There was a large main effect of food treatment on embryo production, with females in the high-food treatment producing $\sim 20\times$ more embryos than females in the low-food treatment (Mann–Whitney *U*, $p < 0.0001$; Fig. 1). Significantly more populations contained at least one brooding female in the high food (28 of 32 populations) versus the low-food

treatment (15 of 32 populations) (Fisher's exact test, $p = 0.0054$), consistent with previous reports that food-stressed female *P. antipodarum* often produce no offspring (Jokela et al. 1999). Within density treatments, females in the high-food treatment produced significantly more embryos than low-food females under both high density (Mann–Whitney U, $p < 0.0001$) and low density ($p = 0.003$) conditions. These results suggest that reproduction in asexual female *P. antipodarum* in the low-food treatment was food limited.

The difference in embryo production between the low and high-food treatments was much more marked under high-density conditions. Here, females in the low-food treatment produced nearly 50-fold fewer embryos than females in the high-food treatment. In contrast, there was only an eight-fold decrease in embryo production for females in the low density/low-food treatment combination relative to females experiencing low density/high-food conditions. Populations in the high food/high-density treatment combination were also significantly more likely to contain at least one brooding female than populations experiencing low food/high-density conditions (Fisher's exact test, $p = 0.0177$), but there was no difference between the number of populations with and without brooding females across food treatments in the low-density populations ($p = 0.1489$).

There was not a significant main effect of density on embryo number across the two food levels (Mann–Whitney U, $p = 0.069$) or within the low-food treatment (Mann–Whitney U, $p = 0.718$) (Fig. 1). However, females in the high-food treatment produced significantly more embryos ($\sim 2\times$) in high density versus low-density conditions

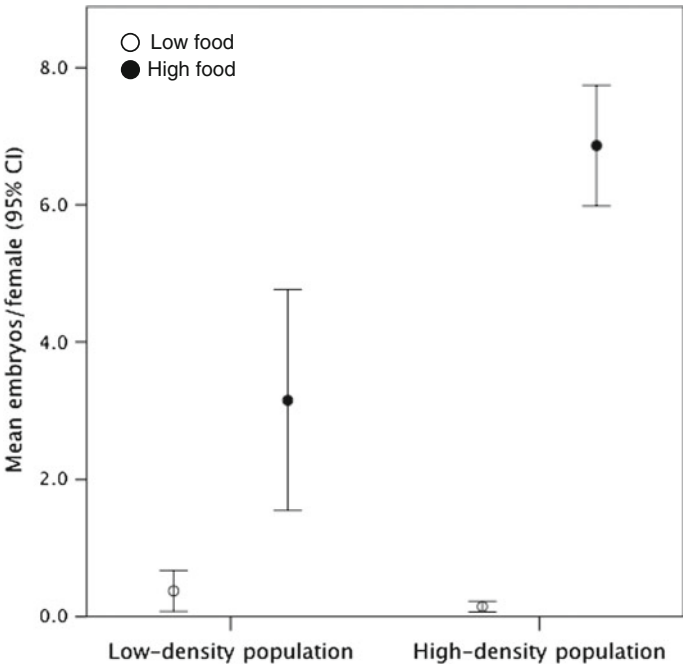

Fig. 1 Mean embryo production per female per population across the population density and food treatments in Experiment 1a/b. Female *P. antipodarum* produced significantly fewer embryos under low food versus high-food conditions across and within both density levels. While there was not a significant main effect of density, there was significantly lower embryo production in females in the low-density treatment versus the high-density treatment under high-food conditions. In contrast, there was no significant effect of density level on embryo production for females in the low-food treatment

(Mann–Whitney $U, p = 0.001$). There was not a significant effect of density on the number of populations containing at least one brooding female across both food levels (Fisher's exact test, $p = 0.094$) or within either the high food ($p = 0.1012$) or low food ($p = 0.4795$) treatments.

Experiment 2

Reproductive output was very sensitive to water conditioning (Kruskal–Wallis, $p = 0.001$) but not to density per se (Mann–Whitney U, $p = 0.084$). Mann–Whitney U tests within and across treatment levels indicated that these results were driven by significantly higher reproduction ($\sim$3–4$\times$) in treatments experiencing high-density water environments (HDC, HDHW, LDHW) relative to treatments experiencing low-density water environments (LDC, HDLW, LDLW) ($p \leq 0.031$ for all pairwise comparisons). There were no significant differences in reproduction among treatments experiencing the same type of water environments (low-density water environment: $p \geq 0.559$; high-density water environment: $p \geq 0.526$). These results are summarized in Fig. 2.

Discussion

We showed that (1) reproductive output in asexual female *P. antipodarum* is markedly depressed when food was limited, regardless of density, (2) reproductive output increases at high density when food is adequate, and (3), the increased reproductive output that occurs under high-density conditions can be generated by exposure to water from high-density populations. Taken together, these results demonstrate that reproduction in the two different *P. antipodarum* lineages that we studied is very sensitive to resource availability and population density.

One novel conclusion from these experiments is that documented reductions in fitness-related traits like growth and reproduction in female asexual *P. antipodarum* under high-density conditions (Cope and Winterbourn 2004; Richards and Shinn 2004; Neiman 2006) are likely due to food limitation rather than other potential consequences of high density such as chemical inhibition or physical interference (e.g., Cameron and Carter 1979; Dan and Bailey 1982; reviewed in Dillon 2000). Food limitation has also been implicated as an important source of negative density-dependence in several other gastropod species (e.g., Baur and Baur 1990; Cross and Benke 2002) as well as in a comprehensive review of the sources of population regulation in freshwater mollusks (Dillon 2000).

Surprisingly, reproductive output in *P. antipodarum* was notably higher under high-density conditions when food was adequate. Increased reproduction by female asexual *P. antipodarum* at high population density was also reported by Brenneis et al. (2010), though the source of this effect was not identified. An intriguing potential explanation for the mechanism underlying these positive effects of high density was provided by Cope and Winterbourn (2004), who found that *Physa acuta* (another freshwater snail) grew more rapidly when housed in water conditioned by *P. antipodarum*. Cope and Winterbourn suggested that relatively high concentrations of water-soluble substances produced by *P. antipodarum* might be responsible for the positive effect of *P. antipodarum* on growth in *Physa acuta*.

The results of Experiment 2 are consistent with this possibility, demonstrating that snails housed in low density/high-food populations but exposed to water conditioned by high-density populations produced as many embryos as snails actually housed in high

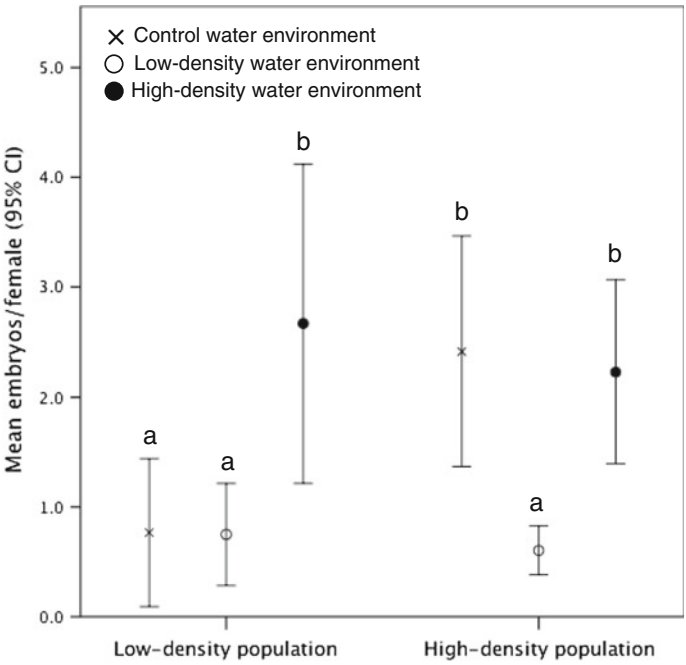

Fig. 2 Mean embryo production per female per population across the population density and water conditioning treatments used in Experiment 2. There was a significant main effect of water conditioning on embryo production as well as a significant water conditioning by density interaction, but no significant main effect of density. *Shared letters* denote treatments that were not significantly different (Mann–Whitney *U* test, $p \geq= 0.53$); *different letters* indicate significant differences at $p \leq= 0.031$

density/high-food conditions. While we cannot exclude effects of unmeasured factors correlated with the water-conditioning treatments (e.g., higher microorganism loads in water inhabited by more snails), these results do provide the most direct evidence to date of water-mediated conspecific reproductive facilitation in *P. antipodarum*. They also allow us to rule out other potential explanations for positive density-dependence such as social interactions (e.g., Vernon 1995), and point instead towards a positive density-fecundity connection that is mediated by increased concentration and/or exposure to a yet-to-be-identified substance produced by *P. antipodarum*.

Evidence for chemically mediated facilitation in snails was first reported by Thomas et al. (1975) in a study aimed at identifying the mechanisms underlying observed positive effects of high conspecific density on growth and reproduction in *Biomphalaria glabrata*, a freshwater pulmonate snail (also see review by Thomas 1982). A similar phenomenon was implicated by Kawata (1993) with respect to positive conspecific effects on growth rate in another freshwater snail, *Physa acuta*. Since then, chemical facilitation has been documented in laboratory cultures of multiple other snail species as well as in natural snail populations (reviewed in Dillon 2000). Regardless of the mechanism involved, the fact that a nuisance invasive species like *P. antipodarum* is so sensitive to conspecific density is particularly intriguing given the recent suggestion that negative density-dependence could be exploited for conservation and biological control purposes (Tobin et al. 2011). The sensitivity of reproduction in *P. antipodarum* to density is also an important consideration when it comes to the many ecotoxicology studies that use measures of *P. antipodarum*

reproductive output to illuminate the biological consequences of various pollutants and contaminants (e.g., Jacobsen and Forbes 1997; Jensen et al. 2001; Wagner and Oelhmann 2009).

Whether these observed connections between food, density, and reproduction can be applied to invasion biology or illuminate phenomena observed in *P. antipodarum* such as dramatic fluctuations in density of invasive populations in Australia and Europe (Dorgelo 1987; Schreiber et al. 1998) and increased reproductive output when exposed to plastic-derived estrogen-like compounds (Wagner and Oelhmann 2009) awaits determination of (1) the extent to which our results are generalizable to other *P. antipodarum* lineages and (2), whether and how density dependence influences *P. antipodarum* physiology, population dynamics, and lifetime fitness. The next steps addressing these possibilities could include repeating these experiments with other lineages, evaluating whether the increased reproductive output we observed in *P. antipodarum* housed in high-density conditions generates tradeoffs with other important traits, quantifying population growth rate in experimental populations where density is controlled, and identifying the substances involved in facilitation. A promising direction of future enquiry with respect to the latter point is suggested by the recent documentation of increased expression of genes in estrogen-exposed *P. antipodarum* that are already known to be hormone responsive in vertebrates (Stange and Oehlmann 2012).

In light of hypothesized links between density dependence and the selective advantage associated with sexual reproduction (e.g., Young 1981; Doncaster et al. 2000; Lively 2009), the complex connections between density and reproductive output that we observed may also be relevant to understanding the costs and benefits of sex in this important natural model system for the evolution of sexual reproduction. Future studies should focus on addressing whether sexual and asexual *P. antipodarum* experience different relationships between density and fitness-related traits and how the relatedness of coexisting individuals and genetic diversity of populations affects response to population density.

Acknowledgments We thank Curt Lively and Britt Koskella for snail donations, Katelyn Larkin, Andy Thompson, Claire Tucci, and other members of the Neiman lab for help with snail maintenance and data collection, Bennett Brown, Steve Hendrix, and Joel Sharbrough for helpful discussions, and Andrew Forbes, Steve Hendrix, Hang Lim, Dorota Paczesniak, and Joel Sharbrough for comments on an earlier version of the manuscript. We also acknowledge John Endler, F. Xavier Picó, Martin Haase, and an anonymous reviewer for very constructive criticism and suggestions that much improved the manuscript. This research was funded by the Secondary Student Training Program at the University of Iowa, the Iowa Center for Research by Undergraduates, and by the Research Council of Norway.

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