

Invasive prey indirectly increase predation on their native competitors

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Abstract. Ecological theory predicts that invasive prey can interact with native prey directly by competing for shared resources or indirectly by changing the abundance or behavior of shared native predators. However, both the study and management of invasive prey have historically overlooked indirect effects. In southern California estuaries, introduction of the Asian nest mussel *Arcuatula senhousia* has been linked to profound changes in native bivalve assemblages, but the mechanisms of these interactions remain unclear. We performed three field experiments to assess the mechanisms of competition between *Arcuatula* and native bivalves, and evaluated the potential for *Arcuatula* to indirectly mediate native predator–prey dynamics. We found that *Arcuatula* reduces the diversity, abundance, and size of native bivalve recruits by preemptively exploiting space in surface sediments. When paired with native shallow-dwelling clams (*Chione undatella* and *Laevicardium substriatum*), *Arcuatula* reduces adult survival through overgrowth competition. However, *Arcuatula* also attracts native predators, causing apparent competition by indirectly increasing predation of native clams, especially for poorly defended species. Therefore, invasive prey can indirectly increase predation rates on native competitors by changing the behavior of shared native predators, but the magnitude of apparent competition strongly depends on the vulnerability of natives to predation. Interestingly, our results indicate that the vulnerability of invasive prey to predation can greatly exacerbate impacts on their native competitors. Our findings suggest that consideration of both direct and indirect effects of invasive prey, as well as native predator–prey relationships, should lead to more effective invasive species management.

Key words: *apparent competition; Arcuatula (Musculista) senhousia; bivalves; competition; estuary; indirect interactions; invasive species; Mission Bay, California, USA; nonnative species; predation; recruitment; San Diego Bay, California, USA.*

INTRODUCTION

Competition for limited resources is a major process by which introduced species impact native populations, communities, and ecosystems (Ruiz et al. 1999, Shea and Chesson 2002, Grosholz 2005, Byers 2009), but ecological theory predicts that invading prey can also interact with their native competitors indirectly through shared native predators (Noonburg and Byers 2005). Nevertheless, indirect effects are relatively overlooked in invasive species science and management, even though they appear to be common and significant mechanisms of impact (Simberloff and Von Holle 1999, Prenter et al. 2004, Rodriguez 2006, White et al. 2006, Ricciardi et al. 2013) and can complicate eradication or restoration efforts (Zavaleta et al. 2001). Introduced prey have the potential to indirectly affect native predator–prey

systems in two primary ways: diminishing mortality of native prey by shifting predation pressure away from natives (Fairweather 1985, Rodriguez 2006) or enhancing mortality on natives by increasing predator abundance or foraging success (i.e., apparent competition; Holt 1977, Holt and Kotler 1987). However, few studies have tested the potential for invasive prey to indirectly mediate predation on their native competitors. Furthermore, the few experimental tests of invader-driven apparent competition have been focused on refuge-mediated effects in plant communities (Sessions and Kelly 2002, White et al. 2006, Dangremond et al. 2010, Orrock et al. 2010a, b).

Suspension-feeding bivalves are ubiquitous invaders of marine, estuarine, and freshwater ecosystems, and are excellent organisms for testing the direct and indirect effects of invasive prey. Once established, introduced bivalves often achieve numerical dominance relative to natives (Grosholz 2005, Ruesink et al. 2005) and compete with them by altering phytoplankton abundance or composition (Alpine and Cloern 1992), or modifying the physical or biogeochemical conditions of the substrate and water column (Sousa et al. 2009).

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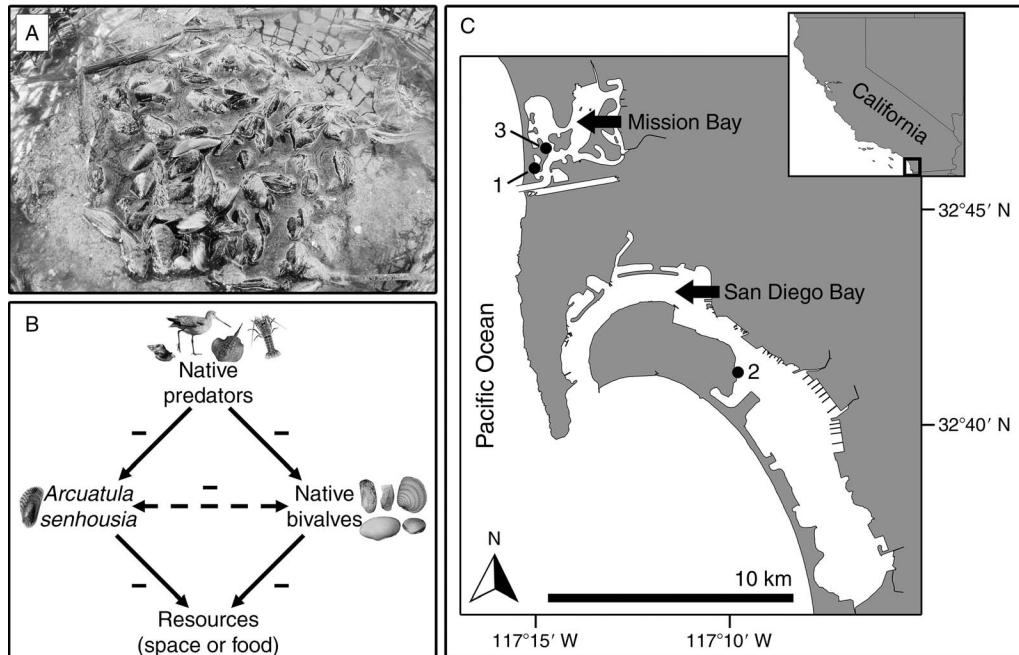


FIG. 1. (A) *Arcuatula senhousia* transforms the physical structure of surface sediments. The photo shows a high-density (8000 mussels/m²) plot from Experiment 1 exposed during low tide. (B) Hypothesized relationships between *Arcuatula* and native bivalves (photographs not to scale). Solid and dashed arrows indicate direct and indirect interactions, respectively. Introduced mussels and native bivalves may compete for surface-sediment space or waterborne food. In addition, a suite of native predators consumes both introduced and native bivalves, creating the potential for indirect effects. (C) Map of study sites in San Diego, California, USA. Site numbers correspond to experiments; Mariner's Cove (1), Coronado (2), and Ventura Cove (3). Photo credit: M. C. N. Castorani.

Invasive bivalves are also commonly prey for a wide range of native predators (Robinson and Wellborn 1988, Reusch 1998, Ruesink et al. 2005). However, most examinations of indirect interactions between introduced and native bivalves have been anecdotal or correlative (Crooks 1998, Grosholz 2005, Ruesink et al. 2005), and the few experimental field studies have found little or no support for predator-mediated competition (Byers 2005, Bidegain and Juanes 2013).

In southern California estuaries, introduction of the Asian nest mussel, *Arcuatula* (*Musculista*) *senhousia* (hereafter referred to as *Arcuatula*), has been implicated in profound changes to native bivalve assemblages over the past 50 years (Crooks 1998, 2001, Dexter and Crooks 2000). *Arcuatula* is a small (≤ 28 mm shell length; SL), fast-growing (Crooks 1996), and prolific shallow-burrowing mytilid (Fig. 1A, see Plate 1). The abundance of this invader is highly variable over space and time (Dexter and Crooks 2000, Cheng and Hovel 2010), but *Arcuatula* is commonly found in densities of thousands of adults/m² and sometimes exceeding 10 000 adults/m² (Dexter and Crooks 2000, Williams et al. 2005). At high densities, *Arcuatula* transforms the structure of surface sediments by producing dense, tangled webs of byssal "cocoon" (Crooks and Khim 1999). Evidence suggests that *Arcuatula* may reduce the growth and survival of clams in native (Uchida 1965) and introduced (Crooks 2001) ranges, but the mechanisms of this interaction

remain obscure. It is possible that *Arcuatula* competes with native bivalves by preempting or competitively exploiting benthic space (Peterson and Andre 1980). However, *Arcuatula* attracts a suite of native predators (Crooks and Khim 1999, Kushner and Hovel 2006) and is highly vulnerable to predation (Reusch 1998, Crooks 2002b, Kushner and Hovel 2006, Cheng and Hovel 2010). Therefore, *Arcuatula* might influence native bivalve assemblages indirectly by changing the abundance or behavior of shared consumers.

We tested the hypothesis that *Arcuatula* indirectly mediates predation on their native bivalve competitors (Fig. 1B). We first explored the strength and mechanisms of competition between *Arcuatula* and native bivalves by performing two experiments to quantify interactions with early and adult life-history stages, respectively. Then, in a third experiment, we assessed the effects of *Arcuatula* on native predators and the consequences for native bivalve survival.

METHODS

Study region and fauna

Our study took place in two estuaries in San Diego, California, USA (Fig. 1C): Mission Bay (32°46' N, 117°14' W) and San Diego Bay (32°43' N, 117°11' W). Both bays have typical Mediterranean seasonality in temperature (~ 14 – 25°C) and salinity (~ 32 – 36 practical salinity units; PSU), with winter freshwater inflow and

hypersalinity during long, dry summers (Largier et al. 1997).

Arcuatula was first observed in San Diego in the 1960s (MacDonald 1969) and is now the most abundant bivalve in intertidal and shallow subtidal soft sediments (Crooks 1998, 2001, Dexter and Crooks 2000). Less abundant, but relatively common native soft-sediment clams and cockles include *Chione* spp., *Laevicardium substriatum*, *Leukoma (Protothaca) staminea*, *Macoma nasuta*, and *Tagelus* spp. (Crooks 1998, 2001). Native bivalve predators are numerous and diverse, and include drilling gastropods, lobsters, crabs, fishes, and wading shorebirds (Reusch 1998, Crooks 2002b, Cheng and Hovel 2010).

Experiment 1: Competition effects on native bivalve recruitment

To evaluate the potential for preemptive competition by *Arcuatula* and quantify impacts on early life-history stages of native bivalves, we manipulated *Arcuatula* density and measured bivalve recruitment in an intertidal eelgrass (*Zostera marina*) meadow near the mouth of Mission Bay (Mariner's Cove; Fig. 1C). We first collected adult *Arcuatula* (SL = 27.1 ± 2.7 mm [mean \pm SD]) from several locations in Mission Bay and kept them in flow-through seawater aquaria at the San Diego State University Coastal and Marine Institute Laboratory until the experiment commenced (<3 weeks). In February 2012, we deployed 48 circular plots (15.24 cm diameter \times 5 cm high PVC rings with 1-mm mesh bottoms filled with sieved beach sand) in the eelgrass meadow by placing plots into shallow excavations from which eelgrass had been removed, so that plots were flush with the sediment surface. Plots were separated by no less than 1 m and were deployed at 0 m elevation relative to mean lower low water (MLLW). After establishing plots, we randomly applied a density treatment to each and carefully transplanted *Arcuatula* as they are found in nature (posterior end slightly protruding above the sediment surface) to create plots with 0, 5, 9, 18, 36, 73, or 146 mussels/plot ($n = 6$), corresponding to densities commonly observed in the region (approximately equivalent to 0, 250, 500, 1000, 2000, 4000, or 8000 mussels/m², respectively; Dexter and Crooks 2000, Williams et al. 2005). Pilot studies showed that even at high densities, transplanted mussels do not migrate out of PVC rings and rapidly (<1 h) reattach their byssal threads and resume feeding. Pilot studies also indicated that predation of *Arcuatula* would greatly compromise density manipulations. Therefore, we covered each plot with a galvanized-wire cage (25 cm diameter \times 30 cm height; 1.3-cm mesh), buried to a 15 cm depth. Once to twice per week, we gently scrubbed cages and checked them for predators (none were found). To control for artifacts of our design, we also created "true control" plots, consisting of excavations filled directly with sieved sediment but with no PVC rings or cages ($n = 5$).

After 11 weeks, we collected sediments from all plots, sieved sediments to retain all bivalves ≥ 1 mm, and preserved the contents of each plot in 95% ethanol. In the lab, we identified, counted, and measured all bivalves (SL to nearest millimeter). To correct for occasional, highly variable *Arcuatula* mortality ($42\% \pm 23\%$), we calculated *Arcuatula* density as the average between the start and end of the experiment. To generate conservative estimates of recruitment, we excluded unidentifiable specimens and did not measure the size of damaged individuals. We characterized bivalve recruit composition as species richness, species evenness, and Simpson's index of diversity (Simpson 1949).

To determine the effect of caging on all response variables, we compared caged and uncaged control plots (0 *Arcuatula*/m²) using two-tailed *t* tests in R 3.0.2 (R Development Core Team 2013) and calculated standardized effect sizes using Cohen's *d* ($(\bar{x}_1 - \bar{x}_2)/s_{\text{pooled}}$). To determine normality of the residuals for this test and other parametric analyses (in this experiment and Experiments 2 and 3), we used normal probability plots. To assess data linearity and homoscedasticity of the residuals, we visually examined the relationship between residuals and fitted values, and used the Brown-Forsythe test for equality of variances (Brown and Forsythe 1974). We tested for the effect of *Arcuatula* density on all response variables using separate ordinary least squares (OLS) linear regressions using R 3.0.2. When necessary to meet the assumptions of OLS regression, we log-transformed ($\ln[y + 1]$) recruitment data.

When nonlinearity or heteroscedasticity could not be resolved by transformations, we performed nonlinear regressions using JMP 10.0 (SAS Institute, Cary, North Carolina, USA). We selected the most parsimonious models (specified a priori; see Appendix A) based on comparisons of Akaike information criterion values corrected for sample size bias (AIC_c) to optimize goodness-of-fit but avoid model overfitting (Hurvich and Tsai 1989). We ranked models based on delta-AIC_c values (Δ_i), a measure of the strength of evidence of each model *i* relative to the best model (i.e., the model with the minimum AIC_c value; $\Delta_i = \text{AIC}_i - \text{AIC}_{\text{min}}$). We considered $\Delta_i < 2$ to indicate substantial model support, $4 < \Delta_i < 7$ to indicate considerably less support, and $\Delta_i > 10$ to indicate very low support (Burnham and Anderson 2002). We report nonlinear model comparisons as Δ_i and Akaike weights (w_i), the probability that model *i* is best among all *R* candidate models

$$w_i = e^{-\Delta_i/2} / \sum_{i=1}^R e^{-\Delta_i/2}.$$

We also report model comparisons as evidence ratios for the best model relative to each other model *i* (w_{max}/w_i , where w_{max} is the maximum Akaike weight from the best model), given the set of candidate models and data. We report model fit by pseudo-*R*²; $1 - (\text{residual sum-of-squares}/\text{corrected total sum-of-squares})$.

Experiment 2: Competition effects on adult native bivalves

To determine the potential for exploitative competition between *Arcuatula* and adult native bivalves, we tested the effect of *Arcuatula* density on the growth and survival of two native clam species, the egg cockle, *Laevicardium substriatum*, and the wavy venus, *Chione undatella*, in the absence of predators. These two native species inhabit surface sediments in intertidal and shallow subtidal areas at densities generally <10–20 clams/m and have similar distributions, feeding behaviors, and burrowing depths as *Arcuatula* (MacDonald 1969, Reusch and Williams 1999).

We collected adult native clams and *Arcuatula* from several sites in San Diego Bay and held them in captivity as described in *Experiment 1*. To determine native clam growth rates (change in SL), we measured initial SL to the nearest 0.1 mm (mean initial SL for *C. undatella* and *L. substriatum* were 23.0 ± 1.0 mm and 12.6 ± 0.2 mm, respectively). Then, in February 2005, we transplanted one clam to each of 120 square plots ($12.6 \times 12.6 \times 7$ cm PVC squares with 1-mm mesh bottoms filled with sieved beach sand; Appendix B), creating 60 plots with *C. undatella* and 60 plots with *L. substriatum* (clam species assigned randomly). Plots were deployed no less than 1 m apart on a shallow subtidal sandflat adjacent to an eelgrass bed in San Diego Bay (Coronado; Fig. 1C). Sixteen artificial eelgrass shoots were tied to each plot to simulate *Z. marina* habitat (Virnstein and Curran 1986), which allowed us to control the precise amount of habitat structure around bivalves. Each plot then was randomly assigned one of 10 *Arcuatula* densities: 0, 2, 4, 8, 12, 16, 24, 32, 56, or 80 mussels/plot, approximately equivalent to 0, 125, 250, 500, 750, 1000, 1500, 2000, 3500, or 5000 mussels/m², respectively ($n = 6$, except for the loss of 1 *C. undatella* plot and 3 *L. substriatum* plots due to storm damage). To prevent predation, we covered each plot with a galvanized-wire cage buried to a 10 cm depth. We gently scrubbed cages and checked them for predators weekly. Despite cages, small predatory mud crabs (*Lophopenopeus* spp.) were discovered within a few plots.

After 61–78 d (it was not feasible to sample all plots concurrently), we collected plots and identified each clam as (1) alive, (2) dead and not consumed (i.e., valves intact), or (3) preyed upon (i.e., dead with valve broken, crushed, or drilled and flesh absent, or missing). We assumed missing clams were taken and preyed upon by mobile predators (e.g., fishes, octopuses). We excluded from our calculations plots in which cages failed or otherwise exhibited evidence of predation. We used binomial logistic regressions in JMP 10.0 to test the effect of *Arcuatula* density on native clam survival (alive vs. dead; species analyzed separately). We rejected models not meeting the Hosmer and Lemeshow (1989) goodness-of-fit criteria. For ease of interpreting the ecological relevance of model results, we report the effects of *Arcuatula* density on parameter estimates and odds ratios in units of 1000 mussels/m².

For living clams, we measured SL (nearest 0.1 mm) and estimated the daily growth rate; (final SL – initial SL)/days in the field. Smaller bivalves grow faster than larger ones (Peterson 1982) and OLS regression revealed that native clam initial SL was highly negatively correlated with growth for both species (*L. substriatum*, $n = 23$, $P = 0.0017$, $R^2 = 38.0\%$; *C. undatella*, $n = 46$, $P < 0.0001$, $R^2 = 29.9\%$). Therefore, we used the residuals from these models as a measure of relative (i.e., size-specific) growth rate. We tested the effects of *Arcuatula* density on the relative growth rate of each native clam species separately using OLS regression in JMP 10.0. To correct for occasional, highly variable *Arcuatula* mortality ($26\% \pm 30\%$), we calculated *Arcuatula* density as the average between the start and end of the experiment.

Experiment 3: Indirect effects on native predator–prey dynamics

To test the potential for *Arcuatula* to indirectly affect native bivalves through shared native predators, we measured the effect of *Arcuatula* density on predator abundance and the proportional mortality of two native clam species. Although they occupy similar niches, *L. substriatum* and *C. undatella* differ greatly in their size and shell morphology. We hypothesized that the larger, thicker shelled, and more inflated *C. undatella* is less vulnerable to predation than the smaller, thinner shelled, and flatter *L. substriatum* (Peterson 1982, Reusch 1998) and, therefore, more resistant to predator-mediated impacts by *Arcuatula*.

We deployed 20 uncaged square artificial seagrass plots ($22.3 \times 22.3 \times 7$ cm and separated by 2 m; Appendix B) in June 2004, located approximately 1 m below MLLW in a shallow subtidal eelgrass meadow in Mission Bay (Ventura Cove; Fig. 1C). Plots were used to factorially manipulate native clam identity (*L. substriatum* or *C. undatella*; 8 clams/plot = 160 clams/m²) and *Arcuatula* density (0, 8, or 32 mussels/plot, approximately equivalent to 0, 160, or 640 mussels/m²) during two separate 5-d trials (for each trial, $n = 3$ plots per clam species per *Arcuatula* density treatment; treatments assigned randomly). Our highest *Arcuatula* density was modest relative to those in naturally occurring eelgrass meadows to avoid confounding our experiment with competition effects between *Arcuatula* and native clams. To determine the amount of native clam mortality not attributable to predation (e.g., competition, transplantation stress), for each trial we also created plots for two control treatments (one per native clam species) consisting of a caged artificial seagrass plot (cage similar to those used for Experiment 2) containing *L. substriatum* or *C. undatella* (160 clams/m²) and a high density of *Arcuatula* (640 mussels/m²).

After each trial, we collected all plots and counted the abundance of predators. We identified clams and mussels as alive, dead and not consumed, or preyed upon. We presumed missing clams were taken and consumed by mobile predators because we recovered

91–100% of clams in caged control plots. We used separate two-way analyses of variance (ANOVAs) in JMP 10.0 to test the effects of native species identity and *Arcuatula* density on (1) native clam total proportional mortality, (2) proportion of native clams consumed, and (3) the density of predators observed in plots at the end of the experiment. Where ANOVAs showed evidence of treatment effects ($P < 0.05$), we made post-hoc pairwise comparisons using Fisher's least significant difference test.

RESULTS

Experiment 1: Competition effects on native bivalve recruitment

Preemptive competition for space by *Arcuatula* reduced the diversity and evenness of native bivalve recruits and, for a few abundant taxa, altered recruit density and size. Recruits from 22 native bivalve taxa colonized our plots. *Arcuatula* density was uncorrelated with species richness ($P = 0.696$), inversely correlated with species evenness ($P = 0.00658$, $R^2 = 17.1\%$), and marginally inversely correlated with Simpson's diversity ($P = 0.0910$, $R^2 = 7.0\%$; Fig. 2). Patterns of diversity and evenness were driven primarily by variation in the recruitment of the single most abundant native, *Leukoma staminea*, which was strongly inversely correlated with species evenness ($P < 0.0001$, $R^2 = 68.8\%$), whereas the next most abundant taxa had much weaker associations (*Tresus nuttallii*, $P = 0.013$, $R^2 = 14.5\%$; *Donax gouldii*, $P = 0.150$).

The majority of taxa (17) were rare, having ≤ 19 individuals among all plots (Appendix C). We performed separate regression analyses of density and size for the six species that represented 95% of all bivalves (Fig. 3; Appendix D). Increasing *Arcuatula* density was matched by a saturating (logistic) increase in *L. staminea* density ($w_i = 0.84$, pseudo- $R^2 = 30.6\%$; Appendix A), an exponential decrease in *T. nuttallii* density ($w_i = 0.73$, pseudo- $R^2 = 32.8\%$; Appendix A), a linear decrease in *D. gouldii* density ($P = 0.034$, $R^2 = 10.8\%$), and no change in the density of *Chione* spp., *Cooperella subdiaphana*, or *Saxidomus nuttalli* (all $P > 0.126$).

Increasing *Arcuatula* density was correlated with a marginal linear decrease in the mean size (SL) of *L. staminea* recruits ($P = 0.098$, $R^2 = 6.9\%$) and an exponential decrease in the size of *T. nuttallii* recruits ($w_i = 0.95$, pseudo- $R^2 = 51.2\%$; Appendix A), while the size of the other four species were unaffected (all $P > 0.311$).

Comparisons of caged and uncaged control plots showed that cages had no effect on species richness ($P = 0.517$) or Simpson's diversity ($P = 0.142$), but caused a marginal decrease in evenness ($P = 0.070$). Recruitment was higher in caged than uncaged plots for *D. gouldii* (71 ± 21 vs. 24 ± 22 clams/m²; $t_9 = 3.55$, $P = 0.006$, $d = 2.14$) and *T. nuttallii* (231 ± 49 vs. 53 ± 45 clams/m²; $t_9 = 6.21$, $P < 0.001$, $d = 3.81$), marginally lower for *C. subdiaphana* (0 vs. 12 ± 11 clams/m²; $t_9 = 2.45$, $P =$

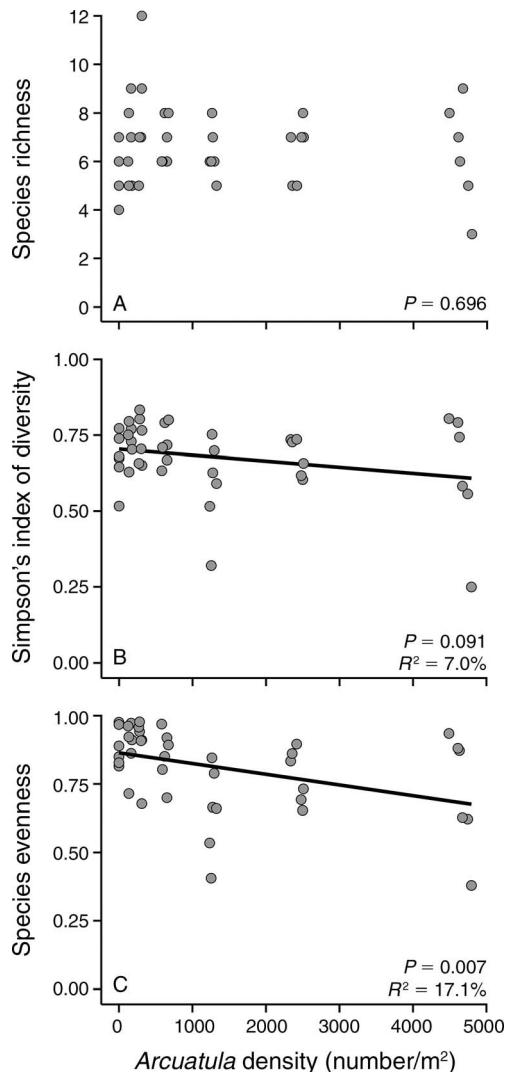


FIG. 2. Relationship between *A. senhousia* density and native bivalve (A) species richness, (B) Simpson's index of diversity, and (C) species evenness (Experiment 1).

0.071, $d = 1.45$), and no different for other species (all $P > 0.294$).

Experiment 2: Competition effects on adult native bivalves

When paired with shallow-dwelling native clams, *Arcuatula* strongly competed for surface sediment space and/or access to waterborne food, reducing adult native bivalve survival but not growth. In control plots (without *Arcuatula*), 100% of *Chione undatella* and 84% of *L. substriatum* survived. In experimental plots, survival of both native clams was inversely correlated with *Arcuatula* density (*C. undatella*, $P = 0.0309$; *L. substriatum*, $P = 0.0186$; Fig. 4 A, B; see Appendix E for parameter estimates). Each increase of 1000 *Arcuatula*/m² decreased the odds of survival by 1.64 (95% CI = 1.05–2.63) for *C. undatella* and 1.91 (95% CI = 1.18–3.54) for *L. substriatum*.

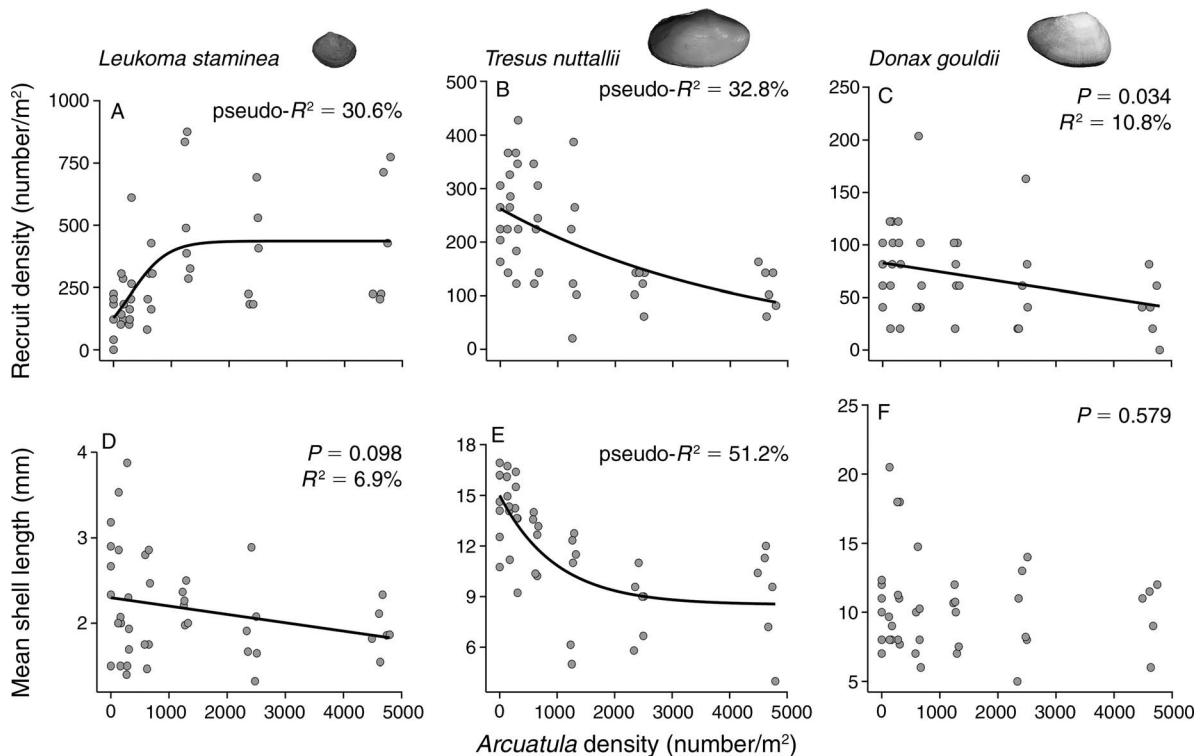


FIG. 3. Relationship between *A. senhousia* density and the (A–C) density and (D–F) size (mean shell length; mm) of native bivalve recruits for the three most abundant species (Experiment 1). See Appendix A for nonlinear regression functions and model comparisons. See Appendix D for plots of less abundant species (*Saxidomus nuttalli*, *Chione* spp., and *Cooperella subdiaphana*). Bivalve photographs not to scale. Photo credit: M. C. N. Castorani.

Arcuatula density was not correlated with the relative growth rate for either native clam species (*C. undatella*, $P = 0.216$; *L. substriatum*, $P = 0.813$; Fig. 4C, D). However, only one *L. substriatum* survived *Arcuatula* densities >2500 mussel/m², limiting the range of mussel densities available for growth analysis.

Experiment 3: Indirect effects on native predator–prey dynamics

Arcuatula indirectly increased the mortality of native clams, especially for poorly defended species with greater vulnerability to predation, by changing the behavior of native predators. There was no effect of trial number on response variables ($P > 0.2$) and we therefore pooled trials for analysis. In caged control plots, native clam survival was high (100% for *C. undatella* and 91% for *L. substriatum*). In uncaged plots, both total proportional mortality of native clams and the proportion of clams consumed were higher in plots with greater *Arcuatula* densities, and higher for *L. substriatum* than for *C. undatella* (Table 1; Fig. 5A, B). There was a trend ($P = 0.075$) for an interaction of clam species and *Arcuatula* density in explaining proportional consumption, with relatively greater predation of *L. substriatum* in the densest *Arcuatula* treatment (640 mussels/m²). Nearly all *Arcuatula* that remained in plots had drilled or crushed shells, indicating that native clams

were eaten along with *Arcuatula* as a result of predator aggregation.

Arcuatula density and native clam species had an interactive effect on the density of predators found within plots (Table 1; Fig. 5C). Predators aggregated in plots with highest densities of *Arcuatula* (640 mussels/m²). However, predators were more abundant in plots with *L. substriatum* than *C. undatella* at the highest density but not at lower densities. Several predators colonized uncaged plots: *Hypsoblennius gentilis* (blennies; $0.68\% \pm 0.46\%$ of total), *Lophopenopeus* spp. (mud crabs; $2.4\% \pm 1.7\%$), and gastropods (*Pteropurpura festiva*, $84.9\% \pm 4.8\%$; *Conus californicus*, $12.0\% \pm 5.7\%$). *Pteropurpura festiva* (see Plate 1) was responsible for the majority (71.5%) of bivalve consumption, as evidenced by conspicuous drill holes in bivalve shells, corroborating results from previous studies in San Diego estuaries (Reusch 1998, Kushner and Hovel 2006, Cheng and Hovel 2010). However, crabs and other mobile predators may have had effects on clam and mussel mortality disproportionate to their abundance in plots: $24.4\% \pm 3.1\%$ of bivalves went missing, which may have resulted from removal by mobile predators.

DISCUSSION

We have demonstrated that invasive prey can harm their native competitors through both direct and indirect

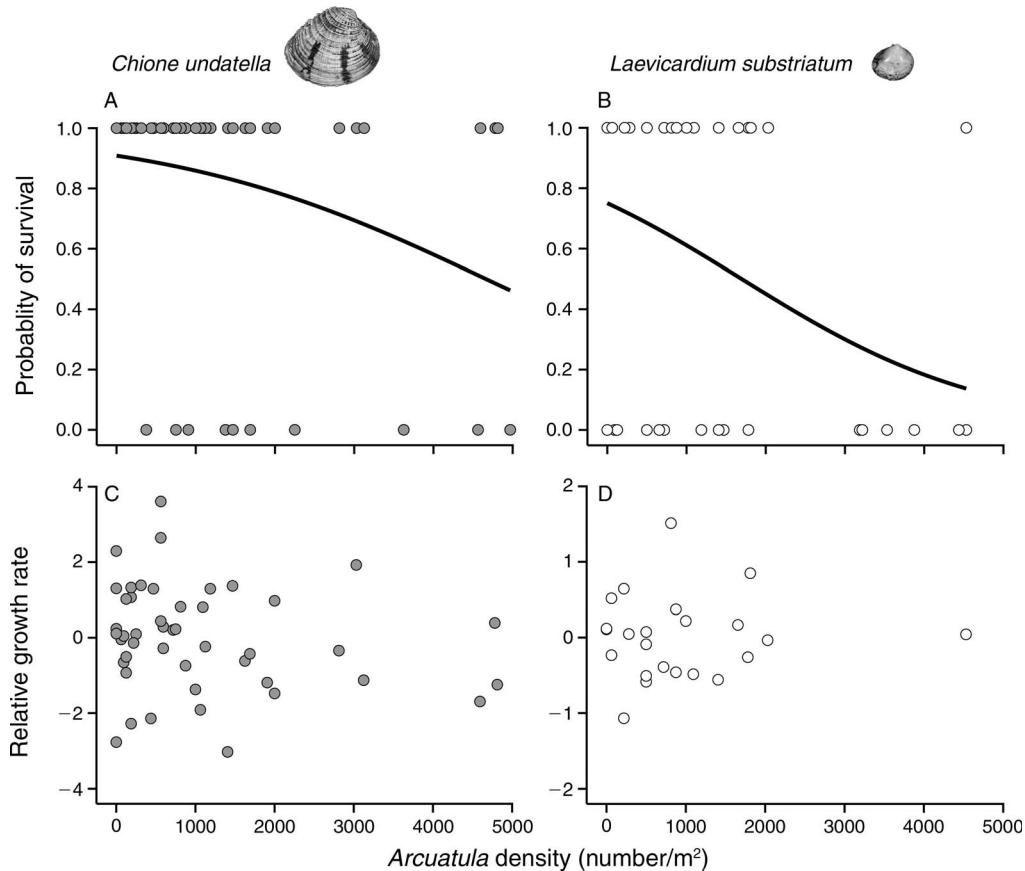


FIG. 4. Relationship between *A. senhousia* density and (A, B) the probability of survival and (C, D) relative growth rate of adult native clams, *Chione undatella* ($n = 46$) and *Laevicardium substriatum* ($n = 23$; Experiment 2). In (A) and (B), points are actual survival data and lines represent predicted survival from binomial logistic regression models. In (C) and (D), relative (i.e., size corrected) growth rate represents the residuals from a regression of shell growth on initial clam shell length. Bivalve photographs not to scale. Photo credit: M. C. N. Castorani.

interactions. Our findings highlight the important role that indirect effects play in nonnative species impacts (Prenter et al. 2004, Rodriguez 2006, White et al. 2006, Ricciardi et al. 2013). In our study, exploitative competition by an invasive mussel affected both juvenile and adult stages of native southern California bivalves. By preempting space, *Arcuatula* suppressed the density and size of recruits for a few abundant native taxa (Fig. 3), thereby reducing the diversity and evenness of overall

native recruitment (Fig. 2). Competition between *Arcuatula* and adults of two native clams resulted in decreased survival of both native species, suggesting overgrowth competition (Fig. 4). At very modest densities, *Arcuatula* also attracted native predators, indirectly increasing mortality of native clams, especially the poorly defended *L. substriatum* (Fig. 5). Our study illustrates that the vulnerability of invasive prey to predation can exacerbate impacts on their native competitors.

TABLE 1. Results of factorial ANOVAs testing for effects of *Arcuatula senhousia* density, native clam species (*Chione undatella* and *Laevicardium substriatum*), and their interaction on total proportional mortality, proportional consumption (i.e., mortality due to predation), and the density of predators within plots (Experiment 3).

Source of variation	Total proportional mortality				Proportion consumed				Predator density			
	df	MS	F	P	df	MS	F	P	df	MS	F	P
<i>Arcuatula</i> density	2	0.10	3.78	0.034	2	0.05	5.79	0.007	2	127.58	51.61	<0.001
Clam species	1	1.83	73.1	<0.001	1	0.10	11.1	0.002	1	12.25	4.96	0.034
<i>Arcuatula</i> density × clam species	2	0.04	1.57	0.224	2	0.03	2.82	0.075	2	18.58	7.52	0.002
Residual	30	0.03			30	0.01			30	2.47		

Notes: P values < 0.05 are shown in boldface type. MS indicates the mean squared deviation from the mean (i.e., the sample variance).

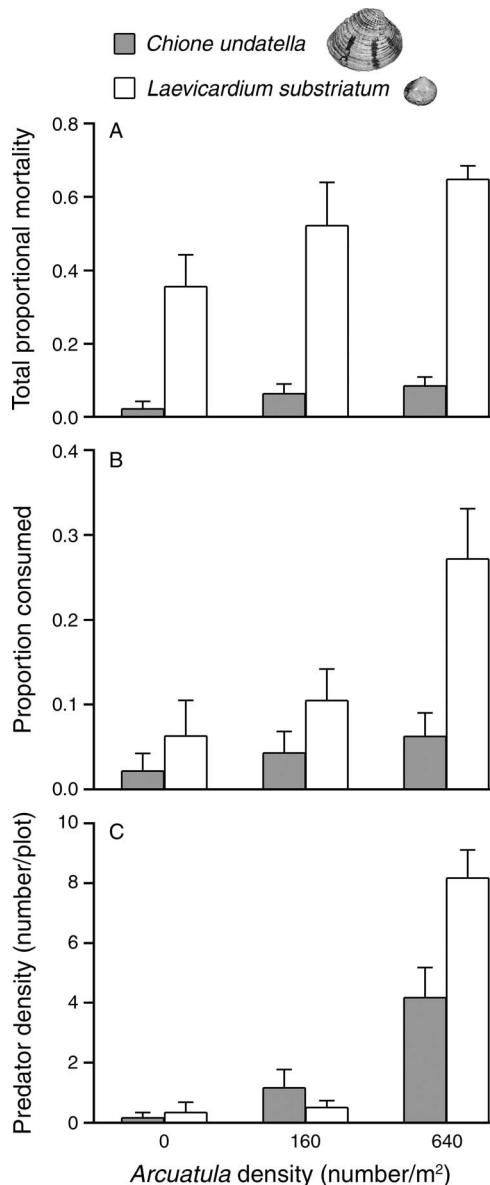


FIG. 5. Effects of *A. senhousia* density on (A) total proportional mortality of adult native clams (*C. undatella* and *L. substriatum*), (B) proportion of native clams consumed (i.e., proportional mortality due to predation), and (C) density of predators in plots (Experiment 3). Bivalve photographs not to scale. Values are means and SE. Photo credit: M. C. N. Castorani.

Preemptive competition and larval recruitment

Results from our first experiment add to a growing body of literature suggesting that introduced species can affect native communities by altering recruitment dynamics (e.g., Gribben and Wright 2006). Spatial and temporal variability in propagule recruitment is a major determinant of community structure (Tilman 1994), especially for sessile assemblages in benthic marine and estuarine ecosystems (Gaines and Roughgarden 1985).

We found that preemption of space by *Arcuatula* decreases the diversity and evenness, but not richness, of native bivalve recruits. Patterns of diversity and evenness were driven primarily by variation in recruitment of the most abundant native bivalve (*L. staminea*; compare Figs. 2 and 3A). For the three most abundant native taxa, *Arcuatula* altered recruit density and size, possibly by modifying habitat structure or reducing resources (e.g., access to food). Analogously, an introduced polychaete changes the recruitment of native sessile invertebrates by altering benthic habitat structure (Holloway and Keough 2002), and an invasive brown alga reduces recruitment of native giant kelp, *Macrocystis pyrifera*, by reducing light availability (Ambrose and Nelson 1982).

There are several pre- and post-settlement processes that could explain how *Arcuatula* alters the density and size of native bivalve recruits (Connell 1985). First, *Arcuatula* may have changed the behavior of native larvae by altering settlement cues (Woodin 1991). Second, *Arcuatula* may have modified the availability or suitability of habitat, an important mechanism of invader impacts on natives (Crooks 2002a). At moderate to high densities, *Arcuatula* monopolizes surface sediments and transforms benthic structure with a tangled web of byssal threads, thereby causing changes to infaunal communities (Crooks and Khim 1999). Third, it is possible that *Arcuatula* directly altered bivalve recruitment by filtering and ingesting native larvae (Davenport et al. 2000). Introduced oysters (*Crassostrea gigas*) more efficiently consume bivalve larvae of native species than of conspecifics (Troost et al. 2008); this is an interesting but unexplored possibility for *Arcuatula*.

Preemptive competition by *Arcuatula* altered recruitment density for the three most abundant native taxa. *Arcuatula* was correlated with a saturating increase in the density of Pacific littleneck clams, *L. staminea*, possibly by creating suitable interstitial habitat for these very small recruits (SL = 2.2 ± 0.6 cm). *Arcuatula* was also correlated with decreases in the densities of Pacific gaper clams, *T. nuttallii*, and California bean clams, *D. gouldii*. These two species were among the largest recruits and possibly competed with *Arcuatula* for space in surface sediments. *Donax gouldii* is a relatively mobile clam typically found in the swash zone of sandy beaches and it is possible that density reductions for this species were driven by larval settlement aversion or post-settlement emigration. *Arcuatula* also reduced the size of *L. staminea* and *T. nuttallii*, possibly by reducing near-bottom phytoplankton concentrations, interfering with feeding behavior, or confining interstitial space.

Densities of *T. nuttallii* and *D. gouldii* recruits were three to four times higher in caged than uncaged control plots, indicating that predation, in addition to competition with nonnatives, is a process important to the success of native bivalve early life-history stages. This observation implies a caveat to our assessment of the impacts of nonnative competition on native recruitment



PLATE 1. In southern California (USA) estuaries, introduction of the Asian nest mussel *Arcuatula senhousia* (left) has been linked to profound changes in native bivalve assemblages. Native predators, such as the drilling gastropod *Pteropurpura festiva* (right), consume both introduced and native bivalves, creating the potential for apparent competition. Photo credits: M. C. N. Castorani (left) and Douglas Mason (right).

because predator presence or lower bivalve densities might weaken interactions between *Arcuatula* and native bivalve recruits. In addition, caution should be taken when extending our findings to other regions, as the effects of *Arcuatula* on native bivalve recruitment likely vary among locations or differing oceanographic conditions.

Resource competition in soft sediments

Results from our second experiment support the idea that bivalves occupying similar depth zones compete for living space or access to the water column (Peterson and Andre 1980, Peterson 1982). We found that for each increase of 1000 *Arcuatula*/m², the odds of mortality increased by 64% for *C. undatella* and 91% for *L. substriatum*. We suspect that overgrowth by *Arcuatula* outcompetes shallow-burrowing native bivalves by modifying benthic habitat in ways that reduce surface sediment space, limit access to waterborne food, or restrict clam movement or feeding, leading to starvation or anoxia. While short-siphoned clams like *C. undatella* and *L. substriatum* may be unable to alleviate overgrowth competition with *Arcuatula* by surviving at deep burial depths, deep-dwelling species are probably unaffected as long as they can maintain siphon access to the water column, as has been shown for the benthic clam, *Macoma nasuta* (Crooks 2001). Still, *Arcuatula* may have significant impacts on early life-history stages of deep-burrowing bivalves, as our results indicate for *T. nuttallii* recruits. The negative effect of *Arcuatula* on native clam survival is in contrast to that of the invasive clam *Venerupis philippinarum*, which has no effect on the survival or growth of the functionally similar Eastern Pacific native *L. staminea* (Byers 2005).

Contrary to earlier work (Crooks 2001), we found no effect of *Arcuatula* on native clam growth. Competitive effects on growth are typically detected before effects on survival (Peterson 1982), but rapid mortality can

preclude the ability to measure growth effects. Furthermore, if growth suppression occurs only at high densities (over 5000 mussels/m²; Crooks 2001), low survival of native bivalves in our densest *Arcuatula* treatment (5000 mussels/m²) may have limited our ability to detect changes in growth.

Apparent competition between introduced and native prey

Most existing studies of apparent competition caused by nonnative prey involve refuge-mediated indirect effects (White et al. 2006), in which invasive prey indirectly increase consumption of native prey by providing a novel refuge for native consumers (Sessions and Kelly 2002, Dangremond et al. 2010, Orrock et al. 2010a, b). By contrast, results from our third experiment illustrate that even without creating refuge, invasive prey can change the behavior of shared predators and indirectly increase consumption rates on native competitors (Holt and Kotler 1987, Noonburg and Byers 2005). The most abundant and influential predator found in our experiment was the drilling gastropod *Pteropurpura festiva* (see Plate 1), an important predator of *Arcuatula* (Reusch 1998, Cheng and Hovel 2010) that sometimes aggregates in dense *Arcuatula* patches (Kushner and Hovel 2006). In a terrestrial analog, palatable invasive orchids indirectly harm co-occurring native orchids by attracting native flower-eating weevils (Recart et al. 2012). Thus, invasive prey can strongly impact natives even in the absence of enemy release (Keane and Crawley 2002).

Native predators can be important to reducing the success and impacts of invasive prey (Robinson and Wellborn 1988, Keane and Crawley 2002, Kimbro et al. 2013) and, in our study system, a suite of native predators (crustaceans, fishes, gastropods, shorebirds) consume *Arcuatula* and provide limited biotic resistance to invasion (Reusch 1998, Crooks 2002b, Cheng and

Hovel 2010). However, our findings suggest that the wide palatability and high vulnerability of *Arcuatula* may come at a cost to vulnerable native clams. Instead of being preferred by predators and thereby reducing predation on native prey (Fairweather 1985, Rodriguez 2006), *Arcuatula* increases predation on equally vulnerable native bivalves by attracting predators, even at very modest densities (640 mussels/m²). At higher invader densities, it is possible that predators could satiate on *Arcuatula*, facilitating native bivalves. However, results from our second experiment suggest that competition by *Arcuatula* would offset this potential positive effect. Furthermore, if native consumers are food limited, increases in their population size could still be detrimental to native bivalves (Holt 1977).

Interestingly, we found that the magnitude of apparent competition strongly depends on the vulnerability of natives to predation. Native predators consumed a higher proportion of smaller, thin shelled *L. substriatum* than the larger, thick shelled, and better-defended *C. undatella* (Peterson 1982, Reusch 1998). This pattern may explain why earlier experimental studies, which examined relatively well-defended native and invasive bivalves (*L. staminea*, *Ruditapes decussatus*, *V. philippinarum*), found no support for predator-mediated interactions (Byers 2005, Bidegain and Juanes 2013). When competition among native bivalves is strong, we suspect that apparent competition between poorly defended invasive and native bivalves could have positive indirect effects on less-vulnerable prey, such as well-defended (e.g., *Chione* spp.) or deep-dwelling species (Reusch 1998).

Implications for managing long-term changes to native bivalve assemblages

A central challenge in ecology and ecosystem management is generalizing the results of small-scale, short-term experiments to scales of space and time with greater relevance (Levin 1992, Thrush et al. 1997). Through a series of field manipulations, we have demonstrated that invasive prey interact with their native counterparts directly by competing with early and adult life-history stages, and indirectly by changing the behavior of shared native predators. However, the magnitudes of these effects are species specific, suggesting care in extrapolation to other taxa and systems. To determine the degree to which findings from our experiments translate to competition and predator-prey interactions at the landscape and ecosystem scales, further studies are needed that explicitly account for variation in these processes over space and time.

However, we can gain limited insight by comparing the results from our experiments with historical surveys. Introduction of *Arcuatula* to southern California in the 1960s was followed by several decades of change to native bivalve assemblages. In Mission Bay, populations of *Chione* spp., *Cryptomya californiensis* (softshell clams), *S. nuttalli* (butterclams), *Solen rostriformis*

(jack-knife clams), and *T. nuttallii* have decreased over the past 50 years (Crooks 1998, Dexter and Crooks 2000). Although many factors may have contributed to these declines, including dramatic habitat modification and overharvesting, the results of this study and Crooks' (2001) suggest that invasion by *Arcuatula* may have played an important role. Presently, *Arcuatula* is the most common and abundant bivalve in intertidal and shallow subtidal soft sediments in San Diego estuaries (Dexter and Crooks 2000, Crooks 2001; K. A. H., *personal observation*). Concomitant with declines in native bivalve populations and invasion of *Arcuatula*, eelgrass meadows have been degraded and fragmented in some areas of San Diego Bay and Mission Bay. This decrease in native habitat may enhance *Arcuatula* spread and impacts on native bivalves because expansive eelgrass meadows reduce *Arcuatula* growth, fecundity, and survival (Reusch and Williams 1999).

Managers are increasingly considering indirect effects in habitat restoration and mitigation, as well as invasive species management and eradication. Our findings indicate that the introduction of palatable invasive species should not necessarily be considered a low concern for management action. Balanced consideration of direct and indirect effects of invasive prey, as well as native predator-prey relationships, should lead to more effective management decisions with fewer unforeseen consequences.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–E are available online: <http://dx.doi.org/10.1890/14-1538.1.sm>