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LETTER

Short and long term consequences of increases in exotic species richness on water filtration by marine invertebrates

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Abstract

Although recent research has considered the consequences of global declines in the number of species, less attention has focused on the aggregate effects of regional increases in species richness as a result of human-mediated introductions. Here we examine several potential ecosystem consequences of increasing exotic species diversity of suspension feeding marine invertebrates. First, we experimentally manipulated native and non-native suspension feeder richness and measured its effect on short-term phytoplankton clearance rates. Multispecies communities all performed similarly, regardless of whether they were dominated by natives, exotics, or an even mix of the two. Individual species varied considerably in filtration rates, but non-native species often filtered less than the most similar native. Second, we determined potential changes in integrated function over time by comparing seasonal patterns of recruitment as a proxy for the ability to quickly recover filtration capacity after a disturbance. We found that exotic species have complementary seasonal phenologies both to native species and each other. Our results suggest that the consequences of local increases in species richness due to invasions may be manifest over long (annual to interannual) time scales, even when short term changes in ecosystem function are negligible.

Keywords

Biodiversity, ecosystem function, filtration, fouling communities, invasions, phenology.

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INTRODUCTION

The past decade has witnessed an explosion of research addressing the consequences of global declines in biodiversity for ecosystem function (Hooper *et al.* 2005; Spehn *et al.* 2005; Cardinale *et al.* 2006; Worm *et al.* 2006; Stachowicz *et al.* 2007). At regional spatial scales (e.g. islands, watersheds, estuaries), however, species diversity is increasing due to invasions of new species exceeding extinctions of local biota (Sax *et al.* 2002; Sax & Gaines 2003). The strong relationship between local and regional richness in many systems (Witman *et al.* 2004; Harrison & Cornell 2008) suggests that increases in local richness could result, though few data are available to rigorously assess this. Nonetheless, with the exception of pest biocontrol (Parker *et al.* 2006) most experiments investigating relationships between biodiversity and ecosystem function have considered the consequences of *decreases* in native species richness (Hooper *et al.* 2005; Spehn *et al.* 2005; Duffy *et al.* 2007). It is not clear whether these results can be extrapolated to predict the consequences of *increases* in local species richness, particularly when the species being added are from different biogeographic regions with different evolutionary histories. Similarly, we have little idea of whether increasing exotic species richness will affect ecosystem function any more than the impact of a single dominant invasive species. Lastly, understanding how exotic species as a group might differ from the native species that are being lost will be important for understanding how net changes in exotic species diversity will affect ecosystem functioning.

In coastal marine ecosystems, extinctions of native species happen at high trophic levels whereas invasions consist mostly of suspension feeders and other lower trophic level consumers (Duffy 2002; Lotze *et al.* 2005; Byrnes *et al.* 2007; Bruno & Cardinale 2008). These suspension feeders include a diverse array of taxa from a wide variety of phyla and can have large ecosystem-wide effects. For example, seasonal phytoplankton blooms and larval recruitment have been dramatically altered due to a single invasive filter feeder (e.g. the Asian Clam *Potamocorbula amuernsis* in San Francisco Bay, Alpine & Cloern 1992; Kimmerer *et al.* 1994). This type of large change in community filtration rates alters the biomass or composition of the plankton available at the base of the food chain for fish (Kimmerer 2002) as well as both nutrient and organic matter deposition into the sediment (Newell 2004). We do not know, however, whether introductions of multiple exotic suspension feeders act additively, antagonistically, or synergistically in their effects on ecosystem functioning.

Increases in exotic filter feeder diversity could increase or decrease water filtration capacity of the benthic assemblage over short temporal scales in a variety of ways. Diversity might enhance depletion of phytoplankton via complementarity among species in diet (Cucci *et al.* 1989; Lesser *et al.* 1992; Demott 1995; Tamburri & Zimmer- Faust 1996) or in their use of different flow regimes (Leichter & Witman 1997; Wildish & Kristmanson 1997). Diversity could also enhance filtration via facilitation, either from increased food delivery to the benthos due to turbulence caused by biogenic substrate complexity (Cardinale *et al.* 2002), or increases in total community biomass due to secondary settlement and species layering. In addition, increases in exotic species diversity might correlate with the establishment of a particularly efficient or high biomass filter feeder (i.e. the sampling effect *sensu* Huston 1997). Conversely, if a species with low filtration rates is competitively dominant, total filtration capacity could be decreased.

Increases in exotic species diversity can also alter filtration over longer time scales by changing integrated annual function. Increases in species diversity have been shown to often have their greatest impact on longer temporal scales (Cardinale *et al.* 2007; Stachowicz *et al.* 2008a). One mechanism behind this pattern is temporal complementarity (e.g. Stachowicz *et al.* 2002a), with species differing in phenologies maximizing function at different times of year. We might expect this of exotic species, as one prevalent strategy of successful invaders is to exploit a vacant temporal niche for settlement and growth (Crawley 1989; Stachowicz & Tilman 2005). Particularly in an environment in which disturbances periodically open free space, if exotic species recruit at a time of year that native species do not, they could increase consistency of community filtration by ensuring newly opened space is filled with consumers more quickly than by vegetative regrowth around a cleared patch alone.

We examined the short and long-term consequences of increased exotic species diversity in the highly invaded 'fouling' communities – assemblages of marine invertebrates living on docks, pier pilings and other hard substrates in bays and estuaries. Our study areas have seen an increase in the number of suspension feeding species over the past few decades at both the dock and quadrat scale, with no extinctions (for comparison, see data in Boyd 1973; Stachowicz & Byrnes 2006). We first examined the effects of native and exotic species individually and in combination on the instantaneous ecosystem processes of filtration in 24 h-long experiments. This allowed us to directly contrast the effects of increasing native species richness, exotic species richness, and both in combination. We then determined the potential for temporal complementarity between native and exotic species to increase the constancy of filtration over annual timescales by examining a 5-year record of invertebrate settlement. Together, these analyses allowed us to evaluate both the potential short and long-term consequences of increases in exotic species diversity to estuarine marine fouling communities on the interaction between these communities and the water column.

METHODS

Study system

Our study focused on the marine invertebrate epifaunal communities of Spud Point Harbor and Mason's Marina, Bodega Bay, CA, USA (38°19′41.60″N 123° 3′23.11″W). On these docks, exotic species comprise roughly half of the species and up to 100% of the spatial cover (Stachowicz & Byrnes 2006). Native and exotic species comprise a wide range of taxa (ascidians, bivalves, bryozoans and hydroids) with a variety of different suspension feeding mechanisms. In similar communities in the Western Atlantic, native species often have complementary phenologies of both recruitment (Sutherland & Karlson 1977; Stachowicz & Byrnes 2006) and mortality (Stachowicz *et al.* 2002a), but we do not know if exotics follow similar patterns. In addition, fouling communities on floating docks in Northern California are subject to natural and human caused disturbances that create open space throughout the year (Nydam & Stachowicz 2007). This community is not unusual in these aspects compared to other fouling communities or to communities in other ecosystems in highly seasonal environments.

Mesocosm experiment

In order to determine how increases in non-native species diversity (here we use richness and diversity interchangeably) altered instantaneous filtration rates on a time scale of hours, we constructed assemblages varying in native and non-native filter feeder diversity in closed mesocosms and measured filtration over 24 h. We selected species so that native and exotic species came from similar functional and morphological groups: solitary ascidians (*Ascidia ceratodes* v. the exotic *Ciona intestinalis*), colonial botryllid ascidians

(*Botrylloides diegensis* v. the exotic *B. violaceous*), colonial aplousobranch ascidians (*Distaplia occidentalis* v. the exotic *Didemnum vexillum*), and mussels (*Mytilus californianus* v. the exotic *M. galloprovincialis*). We also included the exotic colonial bryozoan *Watersipora subtorquata*, as it is a space holding dominant that forms three-dimensional 'heads' with no native analogue (Stachowicz & Byrnes 2006).

In order to examine the effects of increases in diversity due to exotic species introductions vs. increases in diversity *per se*, we conducted a replacement design experiment (i.e. monoculture and polyculture treatments with equal density of individuals), but varied the ratio of native to exotic species in our polyculture treatments. Treatments consisted of all nine species in monoculture, a four species native only polyculture, a four species native-exotic mixture (in each replicate we chose two native species and two non-native species at random), a five species all exotic polyculture, and a nine species polyculture. In all treatments total space covered by suspension feeders was held roughly constant (replacement design), as space, not biomass, is saturated on the hard substrates these animals occupy. A single unit of space, roughly the size of one solitary ascidian or mussel, was 50 cm^2. All assemblages were comprised of 9 units divided equally among species. Colonial species were cut or broken to fill a round 50 cm^2 template and allowed to recover for several hours before being placed in chambers. For treatments in which the number of species was not divisible into nine, one 'unit' of a single species, chosen at random, was either added or subtracted to ensure constant space occupancy across all assemblages. Dry biomass (excluding shells) was included as a covariate in all analyses.

We temporally blocked the experiment in order to increase replication of each treatment for a total of two trials (i.e. $n = 6$ replicates per treatment over both trials). At the start of each trial, every 44 cm × 30 cm × 19 cm mesocosm was filled with 5 L of seawater. During trial 1, raw seawater was taken directly from the docks where animals were collected and used immediately in experiments. For trial 2, we incubated seawater from the docks with 10 pellets of commercial Osmocote$^{\text{TM}}$ (Scotts Miracle-Gro Company, Marysville, OH) for 2 weeks to boost initial chlorophyll levels in order to allow us to estimate changes in chlorophyll with higher resolution. This boosted initial *in vivo* chlorophyll for trial 2 to 1.33 ± 0.08 μg L^{-1} from 0.348 ± 0.03 μg L^{-1} for trial 1. Average *in vivo* chlorophyll from 2006–2008 on the docks was 0.51 μg L^{-1} but ranged from 0–2.267 μg L^{-1}, so total chl in both trials was well within the natural range of variation (C. J. Sorte, unpublished data). Mesocosms in both trials were aerated to prevent oxygen depletion. This created a slow non-directional flow in boxes. We felt that this type of flow environment was appropriate after preliminary dye experiments revealed that water movement close to filter feeders on docks was slow, variable and dominated by diffusive rather than laminar flow (J. Byrnes, personal observation).

To determine the effects of treatment on filtration rate we measured *in vivo* chlorophyll using a Turner Designs Aquafluor Handheld Fluorometer at 0, 4, 8, and 24 h after adding filter feeders. During trial 2 we also measured chlorophyll at 1 h. As initial chlorophyll levels varied both within and between trials, we standardized measurements to proportion change in chlorophyll. While *in vivo* chlorophyll measurements can be affected by ambient conditions, and hence are not always a measure of absolute planktonic biomass, they do provide good information on the relative condition of the plankton (Loftus & Seliger 1975). We therefore analysed the proportional change of *in vivo* chlorophyll rather than absolute change in order to account for any variation in measurement due to differing conditions between mesocosms and trials. We log(x + 1) transformed the data, and performed a repeated measure MANCOVA with treatment, trial, their interaction, and mass as independent variables using *R* (R Core Development Team 2008). The transformation of the data allowed us to account for the fact that proportion change in chlorophyll could not fall below-1 as well as minimizing the heterogeneous variance created by having a minimum possible value. Data on proportion change had no similar upper bound, as plankton could increase more than 100%. As time interacted with treatment (see Results), we then analysed the data at each time point separately with effects of trial, treatment, their interaction, and mass as a covariate. We used generalized linear models with a gamma error and a log link on proportion change + 1 data due to the bounds on our response data, the increasing error with increasing mean, and the fact that our data was continuous. Linear models with log (x + 1) transformations resulted in excessively large residuals at high and low predicted values. The data from 1-h samples during trial 2 were analysed separately using a generalized linear model.

We evaluated the following specific hypotheses regarding differences between native and exotic communities using a series of general linear hypothesis tests (Hothorn *et al.* 2008) for each time step. We compared: (i) the native only polyculture v. the all nine species (native + exotic) polyculture to test whether shifting the assemblage from one composed of only natives to a mixture of natives and exotics without extinction of natives alters filtration; (ii) we compared the native only polyculture v. the mixed (native + exotic) four species polyculture to test whether any effect of shifting the community in comparison 1 was due to increasing the number of species; (iii) we compared the native only polyculture v. the exotic species only polyculture to test whether there were any inherent differences between native and exotic dominated communities; (iv) we compared pairs of similar native and exotic species (*Ascidia* v. *Ciona*, *Botrylloides diegensis* v. *B. violaceous*, *Distaplia* v. *Didemnum*, *Mytilus callifornianus* v. *M. galloprovincialis*) to test whether exotic species filtered water any differently than their most similar native species. We made these comparisons for each trial separately due to a treatment × trial interaction (see below). As these were not orthogonal hypotheses, we corrected for multiple hypothesis testing by adjusting *P*-values at each time step using the False Discovery Rate (Verhoeven *et al.* 2005).

In trial 2, we also used flow cytometry to evaluate whether particular species and mixtures differed in their rates of removal of specific particle types (Cucci *et al.* 1989; Lesser *et al.* 1992) in order to test the mechanism of complementarity. These results did not differ qualitatively from the *in vivo* chlorophyll results presented here for any particle type, nor was any complementarity indicated. These results and more detailed methods are presented in Supplementary Materials A.

Temporal consistency and settlement complementarity

We recognize that our laboratory experiments were relatively short in temporal duration and that conditions were fairly homogeneous. However, they do provide a test of whether certain mechanisms (e.g. complementarity in preferred particle sizes) operate. Other mechanisms, especially those involving population level responses need to be addressed over longer time scales (Cardinale *et al.* 2007; Stachowicz *et al.* 2008b). As it proved not possible to measure filtration in manipulated communities over longer time periods, we used seasonal phenologies of each species as a proxy to assess consistency of filtration over the course of a year. Docks are subject to a wide variety of disturbances. In addition to patches being cleared by regular chaffing from boats, patches of organisms may be removed by consumers (Nydam & Stachowicz 2007) or through sloughing of species forming the base layer of a patch due to natural senescence (Stachowicz *et al.* 2002a). While vegetative growth may slowly restore lost function to these bare patches, colonization, even by a species with a low filtration rate, will more quickly restore some measure of lost function. If a bare patch is created during a time of year when there are no species recruiting and the patch is not small enough to be rapidly closed by vegetative growth from surrounding adults, the filtration capacity of that area will be lost.

We examined the importance of temporal complementarity in recruitment phenology between native and exotic species in order to determine whether exotic species diversity increased the resilience of community cover from disturbance thus would help regain some measure of lost function after a disturbance. For these analyses, we used a 5-year record of invertebrate settlement from Spud Point Harbor and Mason's Marina. From January of 2003 through December of 2007, we deployed 4–8 100 cm^2 roughened grey Polyvinyl Chloride (PVC) panels for a period of approximately 2 weeks at each site. Settlers of all metazoan species were identified to species and counted. Because submersion dates varied slightly over the course of the record, we calculated average daily settlement for each species by dividing the number of recruits by duration of exposure. This variation in exposure time did not alter estimates of daily settlement rates (P. Reynolds, unpublished data).

To quantify the effects of exotic species diversity on temporal consistency in settlement, we used our recruitment records to simulate total recruitment in assemblages of native plus all possible combinations of exotic species and then examined the temporal coefficient of variation (Gaston & McArdle 1994) in settlement over the course of the year for each assemblage. For each combination of exotic species at each level of exotic species richness, S, we used our empirical data to calculate the number of native + exotic settlers for each sampling date over the course of a year. We then calculated the temporal coefficient of variation (CV) for that year with that combination of exotic species. We then plotted the mean temporal CV of settlement against exotic species richness for each year. This method of simulating all possible invasion histories and extrapolating from settlement records assumes that recruitment within these systems is a function of abiotic, rather than biotic, factors. While competition can influence the magnitude of recruitment events, previous analyses (Stachowicz *et al.* 2002b) have shown that a large proportion of variation in timing of recruitment within a species can be attributed to variation in abiotic conditions.

To quantify the relative importance of complementarity between exotics and natives in determining the number of sampling intervals with high settlement rates as well as the relative importance of complementarity between exotic species, we first looked at differences in the seasonality of native and exotic species settlement. To examine the role of exotic richness *per se*, we then modified the methods of Stachowicz & Byrnes (2006) to simulate all possible invasion histories as in the CV analysis and assessed the number of sampling periods in which settlement exceeded five settlers per plate per day. While this threshold was somewhat arbitrary, it translated to at least one settler per square cm within 20 days, not counting vegetative growth of newly arrived individuals, which would lead to 100% cover of a plate within roughly one month (K. Edwards, unpublished data). Our results also appeared robust to changes in the threshold (Supplementary Materials B). For simulated species combinations, we plotted the following three metrics as a function of exotic species richness: (i) the average number of days above the settlement threshold for all combinations; (ii) the average number of days above our settlement threshold for the exotic species that, in combination with native species, had the greatest number of sampling periods above the threshold; and (iii) the average number of days above our settlement threshold for the exotic species that, alone, had the highest number of days above the settlement threshold. A comparison of the first two curves revealed the relative importance of temporal complementarity between exotic species. A comparison of the last two curves revealed the relative importance of complementarity between natives and the dominant exotic species.

RESULTS

Mesocosm experiment

We found that the proportion of *in vivo* chlorophyll remaining was altered by treatment, trial, and their interaction (Table 1). As chlorophyll was depleted over time, the effect of trial and treatment were both altered (Table 1), with some differences manifest early in the experiment, particularly during trial 2, while others only materialized after 8 or 24 h. Mass had no effect as a covariate. Two general trends emerged regarding polycultures that were consistent across both time and trial. First, chlorophyll was rapidly depleted in all polycultures. Secondly, native only polycultures did not differ from either nine species polycultures or four species native-exotic mixtures in either trial or at any point in time ($p_{\text{adj}} > 0.05$, Table 2, Fig. 1).

When comparing similar native and exotic species, natives caused a greater change in chlorophyll than exotics in two of four cases (Fig. 2). Most notable was the relatively low filtration rates of *Botrylloides violaceous* and *Didemnum vexillum* relative to similar natives. During trial 1, chlorophyll depletion was lower in tanks with *B. violaceous* than in those of its native congener at all points in time (Table 2, Fig. 2a). After 24 h, depletion was less in *D. vexillum* treatments than in treatments with a similar native colonial ascidian (*Distaplia*). During trial two this was not the case, and chlorophyll rarely differed between similar pairs rarely across all times, with the exception of *B. violaceous* at 4 h (Table 2, Fig. 2b). In most treatments chlorophyll declined to virtually undetectable levels within 4 h, with some recovery and growth by 24 h in the case of trial 1 (Fig. 2a). In trial 2, mussels were largely able to clear the water by 1 h, faster than any other treatment, but most other species were able to filter comparable amounts by 4 h (Fig. 2b).

Temporal variation and settlement complementarity

Increasing exotic species diversity decreased the temporal CV in settlement (Fig. 3, Fig. S4), implying that natives and exotics have complementary recruitment patterns. In some years exotic species had settlement patterns that were complementary to natives (2003, 2004; Fig. 4, Fig. S5). In other years, they merely augmented native settlement (2007). In some years, they did both (2005, 2006). In general, though, exotic species tended to settle in the late summer and early fall while native settlement peaked in the late spring and early summer. This varied across years, and multiple species led to multiple settlement peaks for each species type. Settlement magnitude also differed markedly between years, but this was not necessarily correlated with the degree to which natives and exotics exhibited different settlement patterns.

In most years, not only did complementarity between native and exotic species as a group lead to more days above a given settlement threshold but complementarity among exotic species increased the number of periods of high settlement (Fig. 5, Fig. S6, Supplementary Materials B). The exotic species with the highest average settlement rate (i.e. the 'best-performing' species) alone rarely determined the number of days above a threshold by itself, indicating the importance of complementarity between natives and exotics in general (Fig. 5a, c, d). However, in some years (e.g. 2004) the number of periods above the threshold was similar regardless of whether the single best-performing exotic species or all exotic species were combined with the native species (Fig. 5b) indicating the importance of a single dominant exotic species. Together, these results indicate that increasing exotic species richness on average increased

	Wilk's lambda	Approximate *F*	Numerator DF	Denominator DF	Pr (≥ *F*)
Treatment	0.282	10.785	13	55	< 0.0001
Trial	0.579	39.985	1	55	< 0.0001
Mass	0.981	1.067	1	55	0.306
Treatment:trial	0.648	2.301	13	55	0.016
Time	0.338	52.932	2	54	< 0.0001
Treatment:time	0.327	3.11	26	108	< 0.0001
Trial:time	0.478	29.431	2	54	< 0.0001
Mass:time	0.949	1.456	2	54	0.242
Treatment:trial:time	0.654	0.984	26	108	0.495

Table 1 MANOVA table for the effect of treatment and trial on proportion change of *in vivo* chlorophyll during mesocosm filtration experiment. Time, treatment, trial and their interactions are all categorical variables. Mass is a continuous covariate

Table 2 Contrast tables for proportion change of *in vivo* chlorophyll during mesocosm filtration experiment. Generalized Linear hypothesis tests for change of *in vivo* chlorophyll trial 1, trial 2. Contrasts are broken up by hour, and the results each come from an generalized linear model fit for each hour with trial, treatment and their interaction included as categorical variables and mass as a continuous covariate. Within each hour, contrasts are broken up by trial due to the trial × treatment interaction. Note, estimated differences and error are on a log scale, and coefficient sign reflects the contrast matrix rather than whether the exotic or native species had a higher filtration rate. See Fig. 2 to visualize the differences. Differences that are significantly different from zero at the $P < 0.05$ level after correction for multiple hypothesis testing are in bold

	Estimate	Standard error	*Z*-value	*P*-value
1 h, trial 2				
Mono v. poly	3.567	3.009	1.185	0.726
Native v. exotic	−0.613	0.525	−1.166	0.726
Native v. mixed	−0.345	0.509	−0.678	0.726
Native v. high	−0.441	0.531	−0.831	0.726
Ciona v. Ascidia	*−0.340*	*0.560*	*−0.607*	*0.726*
Botrylloides violaceous v. *Botrylloides diegensis*	−0.514	0.486	−1.059	0.726
Didemnum v. *Distaplia*	−0.225	0.534	−0.421	0.77
Mytilus californianus v. *Mytilus galloprovincialis*	−0.072	0.553	−0.13	0.896
4 h				
Native v. exotic trial 1	0.585	0.432	1.353	0.617
Native v. mixed trial 1	0.212	0.365	0.58	0.872
Native v. high trial 1	−0.177	0.368	−0.481	0.872
Ciona v. *Ascidia* trial 1	0.140	0.350	0.4	0.872
B. viol* v. *B. dieg trial 1	**−0.971**	**0.350**	**−2.772**	**0.039**
Didemnum v. *Distaplia* trial 1	0.662	0.352	1.878	0.282
M. calif v. *M. gallo* trial 1	0.088	0.799	0.11	0.912
Native v. exotic trial 2	0.335	0.363	0.921	0.714
Native v. mixed trial 2	−0.116	0.358	−0.322	0.872
Native v. high trial 2	0.165	0.365	0.453	0.872
Ciona v. *Ascidia* trial 2	−0.439	0.374	−1.173	0.674
B. viol* v. *B. dieg trial 2	**−1.185**	**0.35126**	**−3.375**	**0.010**
Didemnum v. *Distaplia* trial 2	−0.087	0.36603	−0.237	0.875
M. calif v. *M. gallo* trial 2	−0.388	0.37186	−1.043	0.693
8 h				
Native v. exotic trial 1	0.221	0.512	0.433	0.825
Native v. mixed trial 1	0.209	0.432	0.484	0.825
Native v. high trial 1	−1.139	0.436	−2.613	0.063
Ciona v. *Ascidia* trial 1	−0.634	0.415	−1.527	0.355
B. viol* v. *B. dieg trial 1	**−1.697**	**0.415**	**−4.09**	**< 0.001**
Didemnum v. *Distaplia* trial 1	1.029	0.418	2.463	0.064
M. calif v. *M. gallo* trial 1	0.356	0.947	0.376	0.825
Native v. exotic trial 2	0.547	0.430	1.27	0.408
Native v. mixed trial 2	0.078	0.425	0.184	0.920
Native v. high trial 2	0.036	0.432	0.084	0.933
Ciona v. *Ascidia* trial 2	−0.568	0.443	−1.281	0.408
B. viol v. *B. dieg* trial 2	−0.237	0.416	−0.568	0.825
Didemnum v. *Distaplia* trial 2	0.235	0.434	0.542	0.825
M. calif v. *M. gallo* trial 2	−0.814	0.441	−1.848	0.226
24 h				
Native v. exotic trial 1	0.201	0.51899	0.387	0.909
Native v. mixed trial 1	−0.542	0.43828	−1.237	0.626
Native v. high trial 1	0.090	0.44184	0.205	0.909
Ciona v. *Ascidia* trial 1	0.416	0.42086	0.988	0.646
B. viol* v. *B. dieg trial 1	**−1.330**	**0.42063**	**−3.162**	**0.022**
***Didemnum* v. *Distaplia* trial 1**	**1.252**	**0.42345**	**2.957**	**0.022**
M. calif v. *M. gallo* trial 1	1.373	0.95986	1.43	0.626
Native v. exotic trial 2	0.520	0.43639	1.191	0.626
Native v. mixed trial 2	−0.085	0.43045	−0.196	0.909
Native v. high trial 2	0.039	0.43847	0.087	0.931
Ciona v. *Ascidia* trial 2	0.273	0.44962	0.607	0.846
B. viol v. *B. dieg* trial 2	−0.467	0.42195	−1.107	0.626
Didemnum v. *Distaplia* trial 2	0.391	0.43969	0.888	0.655
M. calif v. *M. gallo* trial 2	−0.113	0.44668	−0.25	0.909

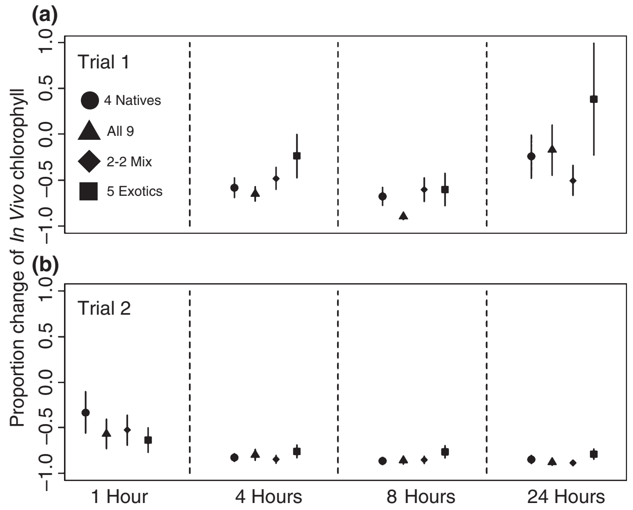

Figure 1 Change in proportion of chlorophyll over time during mesocosm filtration experiment for all treatments with more than one species. Figure is separated into results from (a) trial 1 and (b) trial 2 for ease of visualizing the trial × treatment interaction. Negative values indication net filtration while positive values indicate net growth of phytoplankton. There are no differences between any of these treatments and the four natives alone treatment at any point in time.

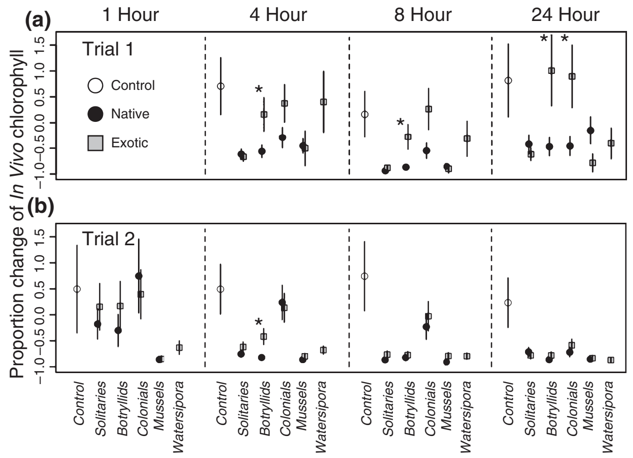

Figure 2 Change in proportion of chlorophyll over time during mesocosm filtration experiment for all treatments with only one species. Figure is separated into results from (a) trial 1 and (b) trial 2 for ease of visualizing the trial × treatment interaction. Negative values indication net filtration while positive values indicate net growth of phytoplankton. A * indicates a difference between an exotic species and its most similar native species. Note the decreased net filtration in *Botrylloides violaceous* and *Didemnum* treatments during trial 1.

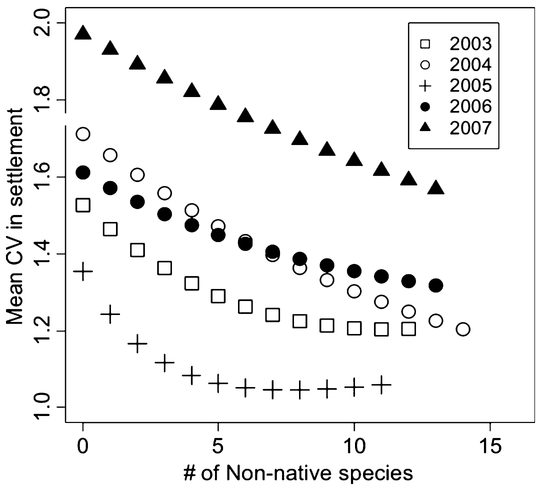

Figure 3 Mean temporal coefficient of variation in recruitment for all combinations of exotic species at a particular level of diversity plus natives. Data are from simulations using settler counts from the Spud Point Marina. Different symbols represent results for different years (open squares: 2003, open circles: 2004, crosses: 2005, closed circles: 2006, closed triangles: 2007).

the consistency of annual settlement (no. of weeks above the settlement threshold) via temporal complementarity, likely leading to more constant space coverage and decreasing the loss of water filtration capacity due to disturbance over time. These results were qualitatively the same for an additional site, Mason's Marina (Figs S4–S6).

DISCUSSION

The main effect of increasing exotic species filter feeder diversity appears to be at longer temporal scales, enhancing consistency of filtration over time rather than instantaneous rates. Our results predict that temporal complementarity, rather than strict instantaneous resource use complementarity, will drive how filtration will change with changing species richness as a result of invasion. This finding supports those of recent case studies (Stachowicz *et al.* 2008b) and meta-analysis (Cardinale *et al.* 2007) that the effects of diversity and complementarity are stronger over longer time scales. In the short term, our results also show that the function of exotic and native communities appears to be largely similar. If certain invaders are able to dominate space, however, the effect on filtration is more unpredictable as some exotic species filtered at a slower rate than comparable natives.

In our short-term experiment, increasing the diversity of exotic species did not alter filtration rates relative to a comparable diverse native community of the same density (Fig. 1). In contrast, if an exotic species was able to dominate space (i.e. our monoculture treatments) filtration rates were either the same or lower than those of either a similar native species, or a high diversity mixture of native

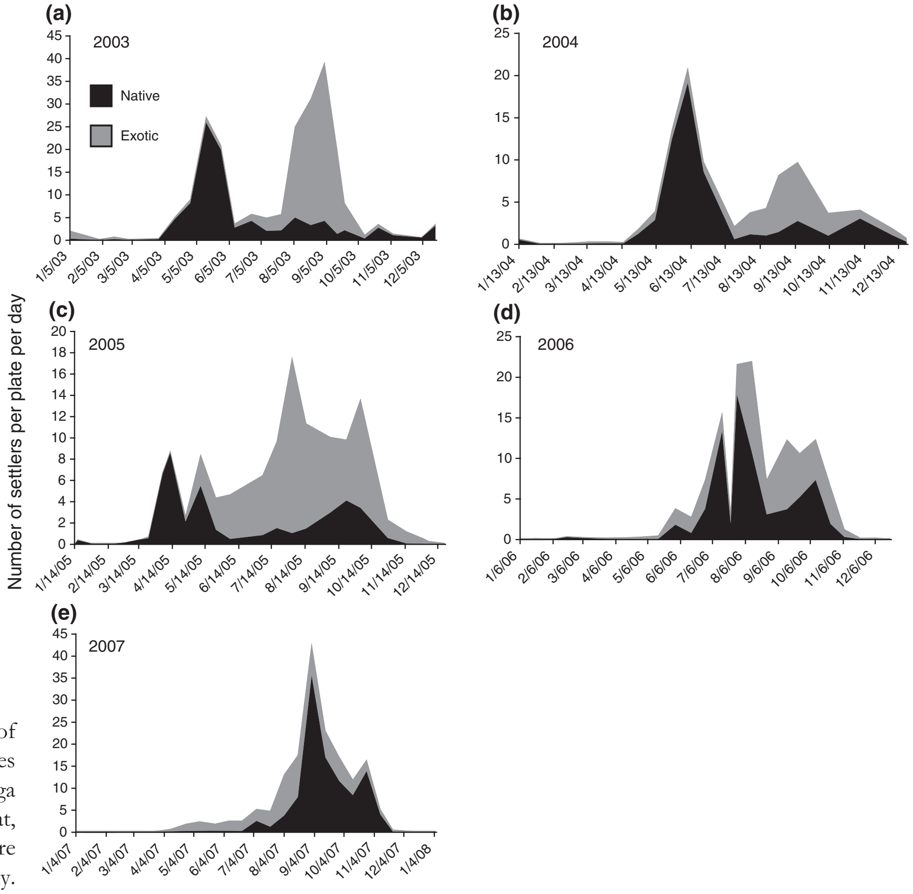

Figure 4 Stacked plots showing patterns of native (black) and non-native (grey) species settlement at Spud Point Marina, Bodega Bay, CA, USA in 2003–2007. Note that, while in some years peaks of settlement are distinct, in others they overlap considerably.

species (Fig. 2). Additionally, while in our trials *M. galloprovincialis* filtered at a rate no different than its native congener, in other experiments on even shorter time scales (15 min) this exotic mussel filtered plankton more slowly than its native congener (Shinen 2007). Replacement of native by exotic species within a functional group could thus decrease community filtration, though consequences of replacements of species with those from other functional groups are more difficult to predict. Our experimental design assumed that species invasions lead to evenly mixed polycultures. This is not always the case, however, and even in high richness areas, a single exotic species can dominate nearly 100% of the space. When evenness is low, regardless of richness, the competitive dominant can determine the rate of ecosystem processes (Altieri *et al.* 2009). This suggests that comparisons between monocultures of competitively dominant invaders and diverse native communities may have greater relevance for changes in short-term function due to invasions.

It is possible that we have underestimated the short-term effects of diversity due to the laboratory nature of our experiments, as we saw little evidence of complementarity. While flow cytometry (Supplementary Materials A) showed that two types of cells dominated the water in trial 2, there was no qualitative difference in patterns of filtration between these two cell types. We do not have comparable results for trial 1. We suspect that differences between trials were likely due to differences in planktonic community composition between trials 1 and 2. Ageing water with nutrients likely shifted composition to larger types of plankton (e.g. diatoms Stibor *et al.* 2004), with trial 1 potentially being closer to field conditions with a greater diversity of cell types. We also note that the homogeneity of our mesocosms may have caused us to underestimate other diversity effects (e.g. due to differences among species in response to flow, low richness of phytoplankton community, etc.) that may act in the field. In addition some, but not all, treatments were able to deplete the entire volume of water within 4–8 h, reducing our ability to differentiate more long-term effects. These types of underestimations may be common in short-term controlled laboratory studies in general (Stachowicz *et al.* 2008a). Measuring filtration on manipulated assemblages in the field was not possible in this system.

Field data on recruitment demonstrated that increases in exotic species richness could have an effect on integrated

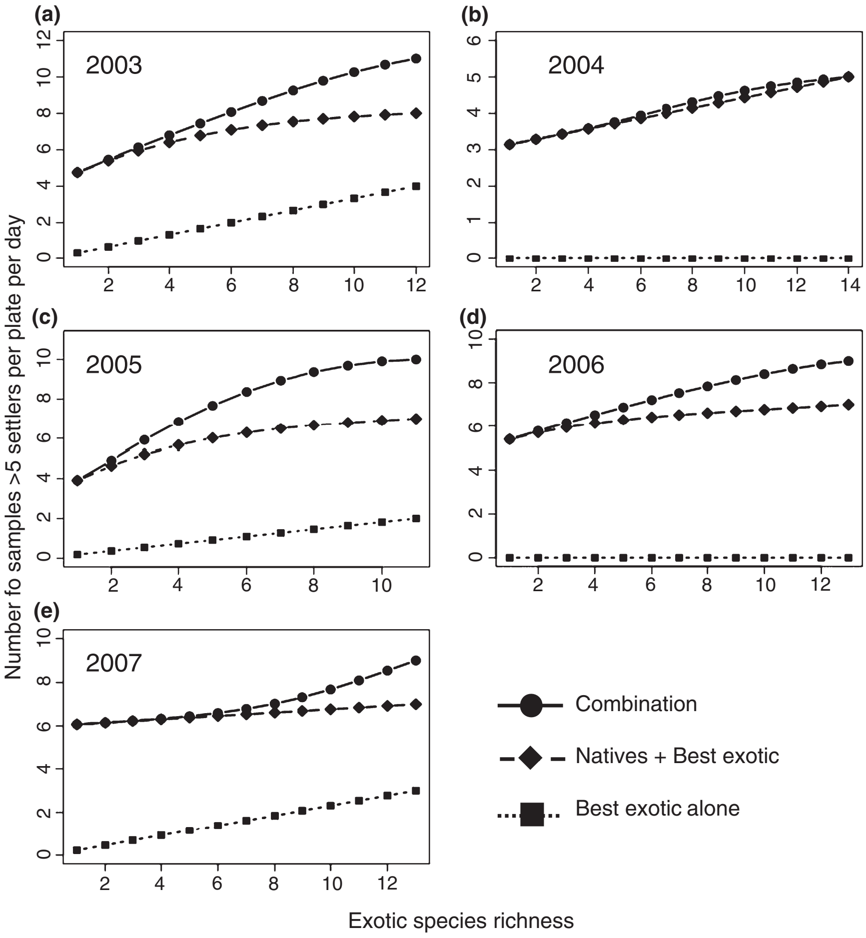

Figure 5 The number of days where invertebrate settlement is above a threshold of five settlers per 100 cm^2 per day from simulations of different community composition using data from Spud Point Marina in 2003–2007. Simulation results are averaged for each level of exotic species richness. Simulations used every possible combination of exotic invertebrates. We then calculated the number of days above the settlement threshold three different ways: (i) total settlement of the simulated exotic community added to the total settlement of all natives (Circles); (ii) settlement of the invertebrate from that simulation with the highest number of days above the threshold added to the settlement of all natives (Diamonds); (iii) Settlement of the exotic invertebrate from that simulation with the highest number of days above the threshold alone, without natives (Squares). The number of days above the settlement threshold for native species alone is equivalent to the number of days above a threshold of the natives + the average best exotic species (Diamonds) at an exotic species richness of 1, as in all cases the number of days above a threshold for the best exotic species alone at a richness of 1 was 0.

function over time by decreasing variability in settlement and allowing cleared patches to be quickly recolonized during more times of year. Complementary phenologies of both mortality and recruitment can alter the availability of free resources and reduce species invasions (Stachowicz *et al.* 2002a; Stachowicz & Byrnes 2006). This suggests that successful exotic species should have complementary recruitment phenologies to natives. It also suggests that as multiple species invade a community, successful new invaders will have different temporal niches than already established exotic species (Crawley 1989; Stachowicz & Tilman 2005). Our results support both of these conclusions. This phenomena raises the possibility that exotic species may generally alter integrated function over time. Even in situations where the immediate impact of exotic species appears negligible, if exotics differ in phenology both from extant natives and each other, increases in exotic species diversity may change net function over large temporal and spatial scales. This change may be subtle, and not noticeable from short-term observations and experiments. This increase in function over time may lead to increased resource capture at lower trophic levels while higher trophic levels are subjected to increased probability of extinction due to human impacts (Byrnes *et al.* 2007).

It is tempting to consider that the loss of ecological function in communities due to local extinctions might be buffered by local increases in diversity due to invasions. However, the mismatch in the trophic level of extinctions and invasions (Lotze *et al.* 2005; Byrnes *et al.* 2007; Bruno & Cardinale 2008) suggests that this is unlikely to be the case. Increases in filtration over time at lower trophic levels coupled with decreases in the diversity of invertebrate-consuming predators might act synergistically to alter the distribution of biomass and energy within marine food webs. Indeed, our results suggest that, particularly over large temporal scales, increasing suspension feeder richness may lead to increases in the amount and decreases in the temporal variability of energy entering at the base of marine food webs. Therefore, changes in trophic skew of diversity may well translate to changes in trophic skew of biomass. Future work on realistic biodiversity change scenarios must incorporate not only the changes wrought by extinction, but consider how interactions with changes in diversity due to invasions may influence the functions provided by natural ecosystems.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Change in proportion of cell type 1 (A) and 2 (B) during trial 2 of the mesocosm filtration experiment for all treatments with more than one species. Negative values indication net filtration while positive values indicate net growth of phytoplankton. A *indicates differences between a polyculture and the native only polyculture. During trial 1 for both cell types, all polycultures that include exotic species removed a greater proportion of cells.

Figure S2 Change in proportion of cell type 1 (A) and 2 (B) during trial 2 of the mesocosm filtration experiment for all treatments with only one species. Negative values indication net filtration while positive values indicate net growth of phytoplankton. A *indicated a difference between an exotic species and its most similar native species. Note the decreased ner filtration in *Botrylloides violaceous* and *Didemnum* for both cell types.

Figure S3 The number of days where invertebrate settlement is above a threshold of 10 settlers per day from simulations of different community composition using data from 2003–2007. Circles represent the average of simulated communities of all natives along with all possible combinations of exotic species at different levels of diversity. Diamonds represent the average of simulated communities with all natives together with the exotic invertebrate with the highest number of days above the settlement threshold. Squares represent that best exotic invertebrate alone.

Figure S4 Mean temporal coefficient of variation in recruitment for all combinations of exotic species at a particular level of diversity plus natives. Data are from simulations using settler counts from the Mason's Marina. Different symbols represent results for different years (open squares: 2003, open circles: 2004, crosses: 2005, closed circles: 2006, closed triangles: 2007).

Figure S5 Stacked plots showing patterns of native (black) and non-native (grey) species settlement at Mason's Marina, Bodega Bay, CA, USA in 2003–2007. Note that, while in some years peaks of settlement are distinct, in others they overlap by a large amount.

Figure S6 The number of days where invertebrate settlement is above a threshold of five settlers per day from simulations of different community composition using data from Mason's Marina in 2003–2007. Simulation results are averaged for each level of exotic species richness. Simulations used every possible combination of exotic invertebrates. We then calculated the number of days above the settlement threshold three different ways: (i) total settlement of the simulated exotic community added to the total settlement of all natives (Circles); (ii) settlement of the invertebrate from that simulation with the highest number of days above the threshold added to the settlement of all natives (Diamonds); and (iii) settlement of the exotic invertebrate from that simulation with the highest number of days above the threshold alone, without natives (Squares). The number of days above the settlement threshold for native species alone is equivalent to the number of days above a threshold of the natives + the average best exotic species (Diamonds) at an exotic species richness of 1, as in all cases the number of days above a threshold for the best exotic species alone at a richness of 1 was 0.

Table S1 MANOVA table for the effect of treatment on proportion change in cell type 1 and 2 (B) during trial 2 of the mesocosm filtration experiment.

Table S2 Contrast tables for proportion change in cell type 1 (A) and 2 (B) during trial 2 of the mesocosm filtration experiment. Contrasts are broken up by hour. Within each hour, contrasts are broken up by trial due to the trial × treatment interaction. Note, estimated differences and error are on a log scale.

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