ABSTRACT

Title of Document: DIVERSITY, INVASIBILITY, AND RESOURCE USE IN MARINE FOULING COMMUNITIES OF SAN FRANCISCO BAY.

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Invasive species threaten the biodiversity of estuaries worldwide. To examine the relationships between biodiversity, invasibility, and invasion success, I conducted field surveys and experiments in San Francisco Bay marine fouling communities, including 1) surveys to estimate alpha, gamma, and beta diversity of native, non-native and cryptogenic components of the community; 2) experiments to assess the influence of diversity and resource availability on short-term recruitment of novel non-indigenous species (NIS) into test communities and subsequent community development over time; and 3) an experiment to explore the role of facilitative interactions of NIS in the diversity-invasibility relationship. Surveys (10-24 sites) showed that non-native alpha diversity was significantly greater than native or cryptogenic alpha diversity, beta diversity was significantly greater for native and cryptogenic species than for NIS, and gamma diversity was similar for NIS and native species. These results indicate that native

species had high turn over from site to site while NIS were spread throughout the Bay. Experiments showed that on short time scales (2-4 weeks), the effect of initial diversity on the density of recruitment of NIS was significant and negative, with no effect of resource level (increased open space). Changes in community composition over time (2-24 weeks) also indicated significant inverse relationships between percent cover of NIS and diversity of the initial community with no evidence of a resource effect. Abundant NIS occupied less space in communities with higher initial diversity. However, the same NIS occupied (i.e., had invaded) all experimental communities regardless of starting diversity. Additional experiments revealed that recruitment to secondary substrates did not vary significantly with invasive species diversity or resource availability. When total recruitment to primary and secondary substrates were combined, there was no longer a significant relationship between diversity and recruitment. Analysis of secondary settlement patterns revealed that some NIS, such as *Bugula neritina*, were facilitating recruitment and settlement of additional NIS. In contrast, other species, such as *Clathria prolifera* and *Botryllus schlosseri*, inhibited secondary settlement of NIS. The influence of diversity and primary resource availability on secondary settlement did not appear to affect settlement on facilitative species, but reduced settlement on inhibitive species.

DIVERSITY, INVASIBILITY, AND RESOURCE USE IN MARINE FOULING COMMUNITIES OF SAN FRANCISCO BAY

By

Safra Altman

Dissertation submitted to the Faculty of the Graduate School of the
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Dedication

I dedicate this dissertation to the late Dr. Edna J. O'Connor (1943-2010), who was an inspiration of strength and persistence, and a true testament to the power of education and educators.

Acknowledgements

There are many people who have contributed to this work, in one way or another. Without the help and guidance of my committee and advisors, the depth and quality of this work would have greatly suffered. Thanks to my co-advisors Tuck Hines and Marjorie Reaka, who have managed to help steer me through this process. Greg Ruiz, who has, for all intents and purposes been an advisor as well, has been a mentor for over ten years, and I trust will continue to be a friend and colleague. Greg, Tuck and Marjorie have consistently given me the freedom and independence to develop myself as a scientist. The rest of my committee, Alexa Bely, Andy Baldwin and Karen Carlton have all provided valuable insight along the way. Karen was willing to join my committee in the later stages of the process, and I am grateful to her for her flexibility and willingness to step out of her field and indulge in the world of marine invertebrates. Matt Hare also served on my committee while he was a faculty member at University of Maryland, and I thank him for giving me the opportunity to try my hand at population genetics and build a foundation in that subject.

My family has been supportive of my graduate pursuits for many, many years, as I completed a master's degree and during the course of the PhD. I am grateful to all of them for their patience, and enthusiasm along the way. I am so lucky that I could commiserate with my sister Irit at every step, as we both completed PhD's in marine science. My sister Rachel provided relief and perspective, especially while I was completing field work and experiments in the Bay area. It is hard to compete with an older brother who writes statistics texts, which is why I am just grateful to be able to

ask him questions about statistics instead. My parents, Jeremy and Penny, instilled both the importance of education and the value of creativity early on, and have always been a source of strength.

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I spent many months at Richmond Marina Bay while completing my experiments. In addition to the hospitality of the Marina staff, the live-aboards on Dock F went out of their way to make the site a second home to me. From feeding me and my dog, to providing space for my equipment and taking me sailing, these folks really extended their community to include me. Special thanks to Brian and Vicky for popsicles, walks and conversation.

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To complete this work, I spent many hours at the microscope and at the dock, counting, scraping, glueing, etc. Stories and music from This American Life, The Moth, Pandora, and audio books kept me entertained and mildly sane. My intrepid dog Sydney was a faithful companion at my field sites, travelled cross country with me four times and reminded me daily that no matter what I thought I needed to do, I should probably go take a walk first.

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Dissertation Introduction

Biological Invasions

Non-indigenous species (NIS) have resulted in many ecological problems including the decline of commercially important species and alteration of ecosystems (Vitousek et al., 1996; Carlton, 1999). Species introduction can threaten native biodiversity, create challenges to managing biodiversity, and lead to an increase in biotic homogenization across localities (McKinney and Lockwood, 1999; Brooks et al., 2004; Olden et al., 2004; Smart et al., 2006). Second to habitat loss, introduced species are thought to be the most important factor in the decline of native species (Ruiz et al., 1997). The increased rate of bioinvasion is primarily due to intentional and unintentional human activity, and has affected terrestrial, aquatic and marine systems (Carlton, 1989; Everett, 2000; Pimentel et al., 2000; Mckinney and Lockwood, 1999). Historically, the study of species introduction has focused on terrestrial systems, while the study of coastal invasions began only 20-30 years ago (e.g., Carlton, 1989; Grosholz, 2002; Stewart and Hull, 1949; Beatley, 1966; Elton, 1958). Many stressors contribute to a heightened susceptibility to invasion in coastal waters including urbanization, eutrophication, exploitation of fisheries, and shipping. While coastal ecosystems currently represent one of the most invaded systems on the planet, the mechanisms that underlie these successful invasions are not well understood (Carlton, 1989; Grosholz, 2002; Cohen and Carlton, 1998; Carlton and Geller; 1993).

Understanding what makes an invasive species successful is an important step in developing a predictive science in regard to invasion mechanisms and in determining effective management strategies. Invasions biology, or the study of the processes, patterns, mechanisms and impacts of non-native species on the community they invade, is a relatively young discipline, and the issue of how to make it more effective in a predictive sense is at the forefront of ecology. To this end, the current dissertation examines the relationships between biodiversity, invasibility, and invasion success in marine fouling communities of San Francisco Bay, USA.

Species invasions of coastal marine systems in North America display an exponential rate of increase over the past two hundred years (Ruiz et al., 2000). When patterns of invasion were compared by coast (North American West, East, and Gulf coasts), the number of invasive species on record was consistently higher on the West coast of North America from 1850 onward (Ruiz et al., 2000). The primary vectors responsible for these species introductions were shipping and fisheries activities, with shipping playing an increasingly larger role in species transfer after 1850 (Ruiz et al., 2000). Aside from species transport in ships, via entrainment in ballast water, and on ship hulls, other vectors include fisheries and aquaculture activity, and the aquarium trade.

Biological Invasions in San Francisco Bay

San Francisco Bay is one of the most invaded estuarine systems in the world (Cohen and Carlton, 1998). Cohen and Carlton (1998) estimated that between 1851-1960, one new non-native species was able to establish in the estuary every 55 weeks. Between 1961-1995, the estimated rate increased so that one new species was able to

establish every 14 weeks (Cohen and Carlton, 1998). Non-native species in the bay can be found from most taxonomic groups including vertebrates and fish, invertebrates, vascular plants, algae, and microbial organisms. Of these groups, invertebrate species make up the largest percentage of established non-native species within San Francisco Bay. Generally, in bays and estuaries, fouling species make up a large proportion of the known invaders. In fact, over half of the known invasive marine invertebrates in North America are members of the fouling community (Ruiz et al., 2000; Ruiz et al., 2009). San Francisco Bay also follows this general pattern in which many of the non-native invertebrates within the bay are members of the marine fouling community.

Marine Fouling Community

Marine fouling communities, or hard substrate assemblages, provide an ideal system in which to study questions related to invasion dynamics, because they are ubiquitous in coastal regions and are good monitors of the local ecosystem (Ruiz et al., 2009). Fouling communities contain a diverse assemblage of species and native and non-native species within these communities often fill similar functional groups. Most of the sessile organisms are suspension or filter feeders. Invaders can have a direct effect on species biodiversity and species interaction within the fouling community, and an economic impact on fisheries as well as many other economically important activities and structures associated with shipping, recreation and navigation. Fouling communities can have an economic impact on coastal areas and on ships because they can overgrow and clog aquaculture and industrial equipment

(e.g. power plant intake pipes), as well as ship hulls. Monitoring invasions patterns in fouling communities also may highlight the relative impact of hull fouling and ballast water as vectors of invasive species.

Approximately 73% of the non-native species found within fouling communities in San Francisco Bay are tunicates (sea squirts), bryozoans and hydrozoans. Other common fouling community members include barnacles, bivalves, sponges and polychaete worms. Examples of some of these taxa can be seen in Figure 1. All of these organisms disperse as larvae that are in the plankton for hours to weeks until they settle, metamorphose and grow into sessile adults. As filter or suspension feeders, these species are competing for plankton in the water column for food, and space for settlement and growth. Tunicate, bryozoan and hydrozoan invaders tend to foul many different hard substrata, including submerged rock faces, as well as nets set up for bivalve aquaculture, pilings, docks, barges, vessels, buoys, and other structures.

To study fouling communities in a standardized fashion, PVC fouling panels were used throughout the studies presented in this dissertation. This method consists of deploying weighted PVC panels of a standard area and shape and allowing organisms to settle and grow on the panel surface *in situ*. This general method is commonly used in observational and experimental work worldwide. Specific details pertaining to panels used in the current studies are described in subsequent chapters. However, a general idea of the variety of panels used can be seen in Figure 2.

As described in detail in Chapters 1-3, this dissertation uses observational and experimental approaches to examine patterns of biodiversity, invasibility, and

invasion success. In Chapter 1, I describe a survey of biodiversity in San Francisco fouling communities. This survey was conducted in two years, using multiple sites to determine alpha (local), gamma (regional) and beta (turn-over) diversity of the native, non-native and cryptogenic components of the fouling community. Chapter 2 presents a series of experiments designed to assess the influence of initial community diversity and resource availability on the success of novel non-indigenous species (NIS). Success of novel NIS was measured on the basis of short term (up to 4 weeks) recruitment of new species into test communities as well as subsequent community development over a longer time interval (up to 6 months). In Chapter 3, I describe a similar experiment that focused on the role of facilitative and inhibitive interactions of NIS in the diversity-invasibility relationship.

A) Tunicata

Styela clava

Botryllus schlosseri

Ciona savignyi

B) Bryozoa

Bugula stolonifera

Bugula neritina

C) Porifera (Sponge)

Clathria prolifera

Figure 1. Examples of some common non-native fouling species found in San Francisco bay including A) solitary and colonial tunicates (sea squirts), B) two species of arborescent bryozoans, and C) a common non-native sponge.

A)

B)

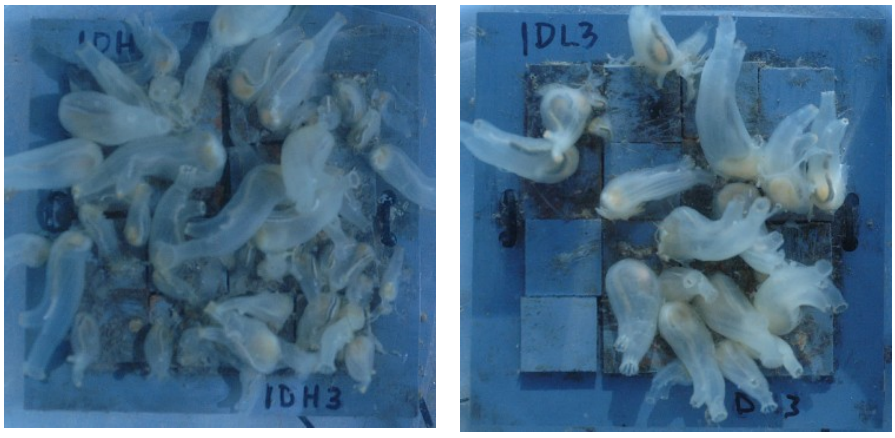


Figure 2. Examples of PVC panels used to create replicate fouling communities. A) An example of a wood block panel (l) designed to collect wood boring organisms and a standard PVC panel (r) used in surveys as described in Chapter 1. B) Examples of aggregate communities assembled with multiple small PVC squares as described in experiments in Chapters 2 and 3.

Chapter 1: Native and Non-indigenous Species: Alpha & Beta Diversity in the marine fouling community of San Francisco Bay

Abstract

Although non-indigenous species (NIS) often represent a threat to native biodiversity, there are few reports of NIS distribution and turnover in relation to native species distribution in the same site**.** Alpha and gamma diversity refer to the number of species or the variance in species identity at local and regional sites, respectively. Beta diversity is a measure of the regional variation in species composition among sites, or species turnover. These measures provide insight on ecosystem make up and function and can also be used to inform ecosystem management and the conservation of biodiversity. This study focused on quantifying the alpha, beta and gamma diversity of native, non-native and cryptogenic components of the marine fouling community in San Francisco Bay by surveying 10-24 sites in each of two years (2000, 2001). Regardless of year, non-native alpha diversity was significantly greater than native or cryptogenic alpha diversity. In contrast, beta diversity was significantly greater for native and cryptogenic species than for invasive species. Gamma diversity was highest for NIS, but native species also displayed comparable regional diversity. These results indicate that native species have high turn over from site to site and fewer native species are found within fouling communities in general across the bay. NIS are spread throughout the Bay and with little species turnover from site to site. Closer inspection of the species composition of NIS reveals a prevalence of tunicate and bryozoan species that are regionally over-distributed relative to native species

and are also widespread globally. These results indicate that biotic homogenization has likely occurred bay-wide. Homogenization can influence species spread and community resistance to future invasions, and can create a positive feedback loop for NIS establishment and success.

Introduction

Non-indigenous species (NIS) often represent a threat to native biodiversity, create challenges to managing biodiversity, and can lead to an increase in biotic homogenization across localities (McKinney and Lockwood, 1999; Brooks et al., 2004; Olden et al., 2004; Smart et al., 2006). Current literature regarding how biodiversity in the native community affects invasion success (on multiple scales including resource heterogeneity, space and time), has relied primarily on measures of species richness only (Levine and D'Antonio, 1999). Few studies incorporate other measures of diversity (e.g. Shannon –Weiner Index, Simpson Index), perhaps due to constraints presented by the available presence/absence data. Studies in which α-diversity (mean diversity within a community; species richness), β-diversity (species turnover or change in species composition from site to site; γ/α), and γ-diversity (cumulative landscape or regional diversity) are compared with respect to natives and invaders are rare. This is surprising considering that these metrics can be gathered easily from presence/absence data (but see Davies et al., 2005). Most studies conducted on small spatial scales have relied on α-diversity, while large-scale studies use γ-diversity to define native and invasive species diversity (Davies, 2005; Stohlgren et al., 2003; Lonsdale, 1999). Examining the patterns of α and β-diversity

for members of current native communities as well as NIS members would not only reveal patterns of local species turnover, but may expose inherent differences in how these two groups are distributed within a region. These differences could assess the degree of regional biotic homogenization, as well as decreases in native diversity and / or spread, and may relate to cascading effects of invasion success.

In examining community assemblage, α-diversity and β-diversity are often described as indicators of community complexity. However, in regard to distribution patterns of non-indigenous species, our current assessments of global diversity patterns contain a gap. To my knowledge, there have been no reports on the patterns of α, β and γ-diversity with respect to native and non-native species within the same marine community. Here I present data from surveys of marine fouling communities throughout San Francisco Bay, where invasive species are prevalent (Cohen and Carlton, 1995). I describe patterns of native and non-native α and β-diversity over space, and also look at species diversity change in marine fouling communities over multiple years within the estuary.

Marine fouling communities, or hard substrate assemblages, provide an ideal system in which to study questions related to invasion dynamics, because they are ubiquitous in coastal regions and are good monitors of the local ecosystem (Ruiz et al., 2009). Fouling organisms can be transported via boat hulls or ballast water and are thus closely linked to some of the major vectors of marine NIS transfer (Fofonoff et al., 2003a). Estuarine systems tend to have a higher absolute number of invasive species than their coastal counterparts (Wasson, et al., 2005, Ruiz et al., 2009). In bays and estuaries, fouling species make up a large proportion of the known invaders.

In fact, over half of the known invasive marine invertebrates in North America are members of the fouling community (Ruiz et al., 2009). The majority of these invaders are tunicates (sea squirts), bryozoans and hydrozoans. These organisms all disperse as larvae that are in the plankton for hours to days until they settle, metamorphose and grow into sessile adults. Most of the sessile fouling community members are suspension or filter feeders. Thus, these species are competing for the same resources: plankton in the water column for food and space for settlement and growth. Tunicate, bryozoan and hydrozoan invaders tend to foul many different hard substrata, including nets set up for bivalve aquaculture, as well as pilings, docks, barges, vessels, buoys, and other structures. Consequently, these invaders can have a direct effect not only on species biodiversity and species interaction within the fouling community, but an economic impact on fisheries as well as many other economically important activities and structures associated with shipping, recreation and navigation.

San Francisco Bay, California, is documented as having the greatest number of invasive species of any estuary in North America and arguably the world (Cohen and Carlton, 1998; Ruiz et al., 2000). The current study aims to distinguish patterns of diversity and community turnover within San Francisco Bay to determine: 1) whether non-native species within the fouling community are distributed in the same way over space, time and habitat as native species; and 2) what implications these findings have for biodiversity within bays and estuarine systems in general.

Materials and Methods

Surveys

This study was conducted in San Francisco Bay, California, USA in 2000 and 2001. In San Francisco Bay, many manmade structures including docks, piers, marinas, and pilings, provide ample hard substrate to support the fouling assemblage. Natural substrates, such as submerged rocks, also provide potential habitat for this community. Due to the extensive habitat available along the perimeter of the Bay, fouling assemblages have a wide distribution and could be sampled across many locations. Sites that had approximately the same physical parameters (salinity, temperature, dissolved oxygen) were used to explore spatial patterns of native and non-native species diversity within the hard substrate fouling community. In 2000, 10 sites that encompassed marinas, ports, piers and one bridge were used. In 2001, the total number of sites were increased to 24, in part to explore community differences that might arise due to type of site (marina, port, pier, bridge) (Figure 1).

Type of site may have an effect on diversity because of differences in water flow, proximity to commercial ship traffic, or proximity to recreational vessels. For example, marina sites differ from pier sites in that they have more frequent and sustained exposure to recreational vessels, potentially supporting a larger source of NIS. In addition, the physical structure of the marina can alter the water flow so that water is entrained within the site. In comparison, water flow is often greater around piers. Water flow could affect larval transport as well as larval attachment to hard substrate. Port sites experience increased commercial ship traffic, so these sites might

experience higher propagule pressure from NIS associated with ship ballast or hull fouling.

At each site, ten 14cm X 14cm X 0.25cm sanded, gray, Polyvinyl Chloride (PVC) settlement plates were deployed. Plates were deployed either from fixed, non-floating structures at approximately one meter below mean lower low water or from floating structures at approximately one meter below the water surface. At each site, settlement plates were distributed in a random fashion. In order to maintain orientation within the water column, each individual plate was weighted with a brick attached to the upward facing surface. Upon deployment, the downward facing surface (collecting surface) was bare and unobstructed, providing ample surface for invertebrate settlement. Panels were left in place underwater from late May-August during the highest period of recruitment into the fouling community. After approximately 3 months, panels were retrieved and transported from field sites to the laboratory in individual containers filled with seawater.

A subset of five panels per site was immediately analyzed using dissecting microscopy to collect replicate voucher specimens of all sessile invertebrate species present on the collecting surface. Vouchers were preserved in either buffered formalin or 75% ethanol depending on taxonomic group. Following live analysis, all panels were fixed in a 10% buffered formalin solution and preserved in 70% ethanol. Voucher specimens were also collected from five additional preserved panels per site in order to obtain a complete species list from ten replicate communities at each site. In cases in which panels were missing and could not be retrieved or analyzed, replication within site was reduced. This occurred in the following sites in 2001:

Coyote Point Marina (n=9), Corinthian Yacht Club (n=8), Oyster Point Marina (n=7), Jack London Square Marina (n=6), and Romberg Tiburon Center (n=6).

Taxonomic Identification

Species identification of voucher specimens was completed and/or verified by taxonomic experts. Species were assigned to three subsets: native, non-indigenous (NIS) and cryptogenic. NIS are defined here as species that were considered introduced by human activity, based in criteria outlined by Chapman and Carlton (1991; see also Ruiz et al., 2000). Cryptogenic species are those that are not demonstrably native or invasive (Carlton, 1996). Status assignments were based on those from the National Exotic Marine and Estuarine Species Information System (NEMESIS) database housed in the Smithsonian Environmental Research Center (http://invasions.si.edu/nemesis/). NEMESIS status designations were derived from an intensive analysis of historical accounts of species occurrence in each bay, coupled with information on known biogeographical species ranges throughout the world (Fofonoff et al., 2003b). Voucher specimens that were unidentifiable or were identified at a taxonomic level leading to an ambiguous status designation (i.e., unknown) were removed from the analyses. Unknown taxa refer to morphotypes that could not be identified to a taxonomic level that permitted a status designation (e.g, a hydrozoan identified to the family level in a hydrozoan family that contains native, non-indigenous and cryptogenic species). While specimen quality and preservation quality can hinder identification, in some cases, even age and size of the organism in question prevented identification to the species level.

Analyses focused on six taxonomic groups of sessile invertebrates that encompass the majority of species and biomass of the fouling community and contain the majority of invasive species within this system: Tunicata, Bryozoa, Hydrozoa, Serpulidae, Cirripedia and Bivalvia (Altman et al., 2004). In addition, Nudibranchia were also included as a representative of mobile taxa within the community. Other mobile species, such as crustaceans and polychaetes, were also present in communities but were not included in the current analyses.

Diversity Measures and Statistical Analyses

I calculated α-diversity (local), β-diversity (species turnover) and γ-diversity (cumulative regional diversity) using a multiplicative model in which $\alpha^* \beta = \gamma$ as was first defined by Whittaker (1960) (see below). Some recent work partitions diversity by using an additive approach in which $\alpha + \beta = \gamma$ (Lande, 1996; Veech et al., 2002; Crist et al., 2003). While the additive approach is advantageous in some cases, multiple studies recommend the multiplicative approach for 1) data sets that do not encompass multiple geographic regions and 2) analyses that are limited to presence/absence data with no associated abundance measures, because this approach allows the alpha and beta components to be independent (Jost, 2010; Ricotta, 2008; Legendre et al., 2005).

Specifically, α-diversity measures were calculated as the mean species richness per site based on the number of sessile species present on each panel surveyed at each site. To determine whether α diversity of natives, NIS and cryptogenic species differed within and between sites, 2 factor nested ANOVAs were

conducted with species status (native, NIS, cryptogenic) nested within site. In these analyses, α, the dependent variable, was analyzed as the number of species types present per panel, and 10 replicate panels were used per site with the exception of panels that were lost prior to retrieval. Multiple pairwise comparisons between species status designations (native, NIS, cryptogenic) were determined using the Bonferroni adjustment. To examine the effect of site type (marina, pier, port, bridge) on α-diversity, 2 factor nested ANOVAs were conducted with site nested within site type. Alpha diversity was again the dependent variable, and was analyzed as the number of species per panel. Bonferroni adjusted multiple pairwise comparisons were used to identify specific differences due to habitat type. Analyses were conducted separately for the 2000 and 2001 data. Additional one way ANOVAs were also performed on a site specific basis with species status as the main effect. In all cases, the data conformed to assumptions of homogeneity and normality and did not require transformation. All analyses were conducted using the SAS 9.1 analysis package.

Gamma diversity was measured as the cumulative number of species present at all sites surveyed. To calculate β-diversity, I used a modification of Whittaker's multiplicative model that was proposed by Kiflawi and Spencer (2004). This method of β-diversity calculation relies on the first-order jackknife estimate of species richness for the region ($\hat{\gamma}$) using the following equations (as described by Kiflawi and Spencer, 2004):

$$\beta = \frac{\hat{\gamma}}{\bar{\alpha}} - 1 \qquad (1)$$

where

$$\hat{\gamma} = \gamma_{obs} + u\left(\frac{N-1}{N}\right) \qquad (2)$$

and u is the number of unique species (i.e., those encountered in only one of the sampled panels), N is the total number of panels. This approach to calculating β-diversity makes it possible to produce a variance estimate for β-diversity and complete hypothesis testing to determine if two estimates of β differ. The variance in β is estimated by the formula:

$$Var[ln\beta] \approx \left[\frac{\hat{\gamma}}{\alpha(\hat{\gamma}-\alpha)}\right]^2 Var(\alpha) + \left(\frac{1}{\hat{\gamma}-\alpha}\right)^2 Var(\hat{\gamma}) \qquad (3)$$

To compute equation (3), the variance in α and $\hat{\gamma}$ were estimated using the following:

$$Var(\alpha) = \left[\sum_i^{\gamma obs} \hat{p_i}(1-\hat{p_i}) + 2\sum_i^{\gamma obs}\sum_{j>i}^{\gamma obs} Cov(I_i, I_j)\right]\frac{1}{N} \qquad (4)$$

$$Var(\hat{\gamma}) = \frac{N-1}{N}\sum_{s=1}^{\gamma obs}\left(s^2 f_s - \frac{u^2}{N}\right) \qquad (5)$$

where p_i is the observed incidence of species i ,Cov(I_i, Ij) is the covariance of species i and j's observed presence/absence, u is the number of unique species and f_s, is the number of panels that contain exactly s of the u unique species.

Finally, by using the odds ratio, Ho: $\beta_1/\beta_2 = 1$, the null hypothesis can be tested using

$$Z_\beta = \frac{\ln(\beta_1/\beta_2)}{\{Var[\ln(\beta_1)] + Var[\ln(\beta_2)]\}^{0.5}} \qquad (6)$$

Using the variance estimates and equations above, I tested the following null hypotheses in each year:

Ho_1: $\beta_{NIS}/\beta_{Native} = 1$,

Ho_2: $\beta_{NIS}/\beta_{cryptogenic} = 1$ and

Ho_3: $\beta_{Native}/\beta_{cryptogenic} = 1$.

As these are essentially pairwise comparisons, I used a Bonneferoni corrected p-value of 0.016 to indicate rejection of each null hypothesis.

Results

α-Diversity

In both 2000 and 2001, NIS α-diversity was greater than native α-diversity at almost every site (9 out of 10 sites in 2000, and 24 out of 24 sites in 2001). Specifically, in 2000, mean values of NIS α-diversity by site ranged from 3.7-8.1. In contrast, the range of mean α values for native and cryptogenic species were 0.5-4.1 and 0-2.5, respectively. Alpha diversity was significantly higher for non-indigenous taxa than for native or cryptogenic taxa at all sites except Berkeley (Figure 2; DF= 27, F= 47.3, P<0.001). In half of the sites (Coyote Point, Dumbarton Bridge, East Harbour Marina, Oakland, and San Leandro Marina), α-diversity of cryptogenic species did not differ significantly from native species.

In 2001, α-diversity in the fouling community followed similar patterns to 2000. Mean NIS α-diversity ranged from 4.51-15.14 while mean native and cryptogenic α-diversity was 0-5 and 0-4.33, respectively. As seen in 2000, overall α-diversity differed significantly among sites and was significantly higher for NIS than for native or cryptogenic species (Figure 3; DF=66, F=155.76, P<0.001). On a site by site basis, non-indigenous α-diversity was significantly higher than native and cryptogenic α-diversity; and α-diversity of native species did not differ significantly from cryptogenic α-diversity in all sites except South Hampton Shoal. In South Hampton Shoal, α-diversity of native and cryptogenic species did not differ significantly.

Analyses designed to identify differences in α-diversity due to site type revealed slight differences depending on year. In 2000, when 10 sites were studied, no significant differences were seen among any of the site types (bridge, marina, pier or

port; DF=6, F=0.46, p=0.72). In contrast, in 2001, when the number of sites was increased to 24, significant differences in α-diversity were found depending on site type (DF=19, F=4.48, p=0.015). Bonferroni pairwise comparisons revealed significant differences between marina sites and pier sites only (Figure 4; $\alpha_{marina} < \alpha_{pier}$, adjusted p=0.03), all other site types were not statistically different from one another.

γ-Diversity

Gamma diversity, which in this case describes overall fouling community diversity within the San Francisco Bay region based on our study sites, reflected similar patterns as seen in α-diversity measures. Total γ-diversity was 81 species and 104 species in 2000 and 2001, respectively. These values represent the total number of species found for the 7 taxonomic groups (tunicata, bryozoa, hydrozoa, serpulidae, cirripedia, bivalvia, and nudibranchia) reviewed in this study. When grouped according to species designation, γ-diversity was highest in the NIS portion of the community, followed by native γ-diversity; and cryptogenic taxa displayed the lowest γ-diversity (Figure 5). These patterns were found in both years.

β-Diversity

Beta diversity was lowest for non-indigenous taxa in both 2000 and 2001 when compared to native and cryptogenic taxa (Figure 6). Native *β*-diversity was roughly 2 - 5 times higher than NIS *β*-diversity, depending on year. Hypothesis tests revealed that these differences between native and NIS *β*-diversity were significant in each year (2000 survey, p<0.001; 2001 survey; p<0.001). Cryptogenic *β*-diversity

was also significantly higher than the non-indigenous β value in each year (2000 survey, $p<0.001$; 2001 survey; $p<0.001$).Cryptogenic β-diversity was higher than native β-diversity in 2000 and did not differ from native β-diversity in 2001 (2000 survey, $p<0.001$; 2001 survey, $p=0.18$).

Taxonomic Composition

In both survey years, species abundance varied among taxonomic groups of the fouling communities of San Francisco Bay. The highest numbers of distinctly different taxonomic records were found in the bryozoans, hydrozoans, and tunicates (56, 32 and 31 records, respectively; Table 1). There were 19 and 15 distinct taxonomic records of bivalves and nudibranchs, respectively, while cirripedia and serpulidae had the fewest morphotypes present of the seven taxonomic groups examined (5 and 6 records respectively; Table 1). As shown in Table 1, taxonomic records were binned by status groups (NIS, native, cryptogenic, unknown) to determine which species occurred most frequently to influence the α and β-diversity patterns observed. When examined by species status, 39 records of non-indigenous taxa, 37 records of native taxa, 29 records of cryptogenic taxa and 56 records of unknown taxa were seen in the fouling communities observed at all sites in both 2000 and 2001 (Table 1).

The frequency of occurrence of each taxon in a replicate community (i.e., settling plate) when compared to the total number of communities examined is displayed as a percentage in Table 1. As data were recorded on a presence/absence basis, this value does not represent the frequency of occurrence of a particular taxon

within each replicate community (an indication of dominance), but rather the percentage of replicate communities that contained a particular taxon as a community member. These data indicate that among the NIS present, tunicates and bryozoans were represented most frequently with pooled non-native tunicates and non-native bryozoans occurring respectively in 99.3-100% and 44.5-96.6% of the communities examined (Table 1; ranges refer to frequency of occurrence in 2000 and 2001 for each respective taxonomic group). On a species-specific level, several tunicate and bryozoan species occurred in more than half of the communities sampled. These species include the solitary tunicates *Molgula manhattensis* (68-69.1%) and *Ascidia zara (41-61.3%)*, the colonial tunicates *Botryllus schlosseri* (57.6-66%) and *Botrylloides violaceus (48-67.3%)*, and the upright bryozoan *Bugula stolonifera(37.8-71%)* (Table 1).

As expected with the high values of β-diversity seen in the native community indicating high species turnover, there were some native phyla that were found in a high proportion of communities samples (Bryozoa, 40.2-97.2%) but no individual native species that was found in more than 46% of the communities sampled. The native species that occurred most frequently as community members were the encrusting bryozoan *Smittoidea prolifica* (40-45.6%), the upright bryozoan *Bowerbankia aggregata* (19.8-33%), and the barnacle *Balanus crenatus* (18-39%; Table 1)**.** The majority of the native species (28 out of 37 distinct morphological records) occurred in less than 10% of the total number of replicate communities sampled.

With the exception of the bryozoans *Celloporella hyalina* (2.3-14%) and *Bowerbankia gracilis* (2.8-10%) and the hydrozoans *Obelia dichotoma* (0.5-18%) and *O. bidentata* (1.8-11%), cryptogenic taxa also were present in less than 10% of the communities studied (Table 1). Most of the taxa designated as 'unknown' did not occur across a high percentage of communities. However, the bivalve *Mytilus sp*. was present in 32-39.2% of the communities examined. In San Francisco Bay, *Mytilus sp* represents a *M. trossolus-galloprovinicialis* complex that includes individuals from native and non-native species, as well as their hybrids, and is thus designated as 'unknown' for our purposes (Suchanek, 1997; Wonham 2004).

Many taxa occurred in a similar percentage of communities from year to year. However, the percentage of communities containing several invasive tunicates (*Botrylloides violaceus, Ascidia zara, Ciona savignyi, C. intestinalis,* and *Diplosoma literianum*) increased markedly from 2000 to 2001. The bryozoans *Watersipora subtorquata* and *Bugula neritina* also increased in percentage from 2000 to 2001, while the incidence of several other bryozoan species (*Bugula stolonifera, Bowerbankia aggregata, Bowerbankia gracilis, Conopeum tennuissimum, C. osburni, Celloporella hyalina*) decreased.

Discussion

Although α and *β*-diversity are often used to determine how regional diversity is related to local community structure (Gering and Crist, 2002), the distinction between

native and non-native counterparts within communities is rarely, if ever, made. Most studies that focus on examining diversity patterns do not distinguish species origin (Condit et al., 2002; Kessler et al., 2009). When species origin or status is considered, the effect of the presence of a particular invasive species on overall α and β-diversity in a community has been examined (Piazzi and Balata, 2008), but the differences in diversity between native, non-native and cryptogenic species has not been addressed. In this study, species status was partitioned prior to examining diversity patterns to determine whether each group of species displayed different patterns of local diversity, global diversity and site to site turnover. Multiple years and multiple types of sites were also considered to determine the consistency of patterns found over time and in relation to habitat type.

Results show that NIS were ubiquitously spread across San Francisco Bay, regardless of location, type of site, or year. In contrast, native taxa, while usually present in the community, had low α-diversity and correspondingly high β-diversity indicating that there was high turnover of native species from site to site within the bay in both years. These results were not only consistent year to year, but also on a site to site basis with the exception of one site in each year. These patterns represent a fundamental difference in distribution between natives and non-natives across the bay itself.

Out of the 27 sites surveyed in the two years of this study, only two sites, Berkeley Marina and South Hampton Shoal, had communities in which α-diversity of NIS and natives did not differ. In both cases, NIS α-diversity was lower than most of the other sites studied and statistically equivalent to native α-diversity. South

Hampton Shoal was only surveyed one year and may represent a site with a unique diversity pattern. Berkeley Marina was surveyed in 2000 and 2001 and, despite the similarity in diversity seen in the marina in 2000, the communities conformed to the patterns seen throughout the bay in 2001 with the α-diversity of NIS being significantly different and greater than native α-diversity. The results for Berkeley Marina seem to indicate that under specific circumstances, certain sites may serve as a refuge for native diversity, but this role does not persist and is variable over time.

For the most part, α-diversity was not significantly different in communities that developed in or around marinas, ports, piers or bridges. In 2001, a difference was found in the α-diversity levels of marina communities and pier communities (Figure 4). While NIS diversity remained high for all sites, there was higher diversity in the native and cryptogenic communities in piers than in marinas. This was true even in cases like Berkeley in which the two site types (pier, marina) were close geographically but supported very different levels of native and cryptogenic taxa (with no natives observed in the marina). This suggests that the native and cryptogenic species are better able to persist and maintain space in the pier sites that are more exposed to higher water flow, than they are in the protected marinas. In comparison to pier sites, marinas tend to have more frequent and sustained exposure to recreational vessels, potentially supporting a larger source of NIS. Water flow within marinas is often low enough that water is entrained within the site. This in turn can influence the rate of fouling recruitment by limiting the dispersal of recruits out of the marina while simultaneously increasing the propagule pressure to hard substrate surfaces within the marina (Floerl and Inglis, 2003). This combination, in

contrast to the more exposed pier sites, likely contributed to the differences seen in native diversity in marinas vs. piers. Additional support for the effect of water flow on native and non-native species distribution is seen in fish assemblages in California streams, where native species tend to aggregate in sites with faster water flow while non-native species are negatively correlated with increased waterflow (Marchetti and Moyle, 2001; Moyle and Marchetti, 2006).

In terms of γ-diversity, this study supports previous documentation of the high level of invasive species diversity within San Francisco Bay (Cohen and Carlton, 1998; Ruiz et al., 2000) and shows that the fouling community is no exception to this trend. San Francisco remains one of the most highly invaded estuaries in the world and the fouling community within the bay is dominated by NIS. However, the number of native species observed was similar in magnitude to the number of NIS (43 vs. 37 recognized species, respectively). Thus, despite the low occurrence of native species in many sites within the Bay, the number of native species increases in aggregation when the entire system is observed. This is also an expected consequence of the high β-diversity or species turnover seen in native distribution.

The current analysis of α, β and γ-diversity specifically delineates NIS, native and cryptogenic species, without including specimens of 'unknown' status. Note that for the purposes of the present study, the unknown designation refers to samples that were either 1) too small to identify to species or 2) too damaged to identify to species. In contrast, the cryptogenic designation refers to specimens that were identified as species that are neither clearly native nor non-native based on historical accounts and global biogeography (Carlton, 1996; Foffonoff et al., 2003). Although unknown taxa

were removed from the analyses, their frequency of occurrence among all the communities studied is presented (Table 1). In many cases, the unknown genera that occurred at the highest frequency (>10%) in replicate communities (such as *Ascidia* sp., *Ciona* sp. and *Styela* sp.) probably represented NIS species. As a result, if we were able to classify these individual specimens and designate species status, the inclusion of the unknown species likely would strengthen our results. Thus, the current results represent a conservative and robust estimate of the patterns of α and *β*-diversity in the Bay.

On a species-specific basis, communities throughout the Bay frequently contained non-native colonial and solitary tunicates, encrusting and erect bryozoans, hydroids and barnacles. When natives were present, they were most commonly represented by species of bryozoan and barnacles. Common cryptogenic species included bryozoans and hydrozoans. While historical records of the San Francisco fouling community are sparse, Graham and Gay (1945) conducted a multi-year fouling survey of the estuary in Oakland, California in the 1940's. Their work described a fouling community that was dominated by the hydroid *Tubularia crocea*, the polychaete *Polydora ligni*, the barnacle *Balanus improvisus* (now *Amphibalanus improvises)*, and mytilid bivalves (Graham and Gay, 1945). All of the dominant species found in the 1940's were established non-native species or, in the case of *Mytilus sp.*, a mixture of native and non-native populations (Carlton and Zullo, 1969; Carlton, 1977; Cohen and Carlton, 1998, Carlton, 2007). This historical reference highlights two observations: (1) the mid 20th century fouling communities on record were also dominated by NIS;(2) the prevalent NIS in the system have shifted in the past 70 years from a community

dominated by hydroids, bryozoans, and barnacles to one dominated by tunicates, different bryozoans and different barnacles. This is also reflected in the high proportion of tunicate species that are NIS (68% compared to 50% or less for other groups). Coupled with increases in manmade substrate and available habitat as well as an increase in the speed and supply of transport mechanisms for NIS propagules, the community appears to have changed taxonomically. Whether the distribution of NIS throughout the Bay has changed since the mid 20th century is difficult to assess given the paucity of historic fouling community data. However, it is possible that the increase in non-native species in the system as well as their widely spread distribution has led to displacement and narrowing of the distribution of native species. The hypothesis that the presence or dominance of non-native species may have reduced the distribution of native species within the region deserves futher study.

The impact of freshwater in the San Francisco Bay region due to annual variation in seasonal rain and runoff can affect community composition and species richness depending on whether it is a dry (average Net Delta Outflow<20,000 cubic feet per second (cfs)), moderate (average Net Delta Outflow 30,000 cfs) or wet year (average Net Delta Outflow =77, 600cfs) (Chang, 2009). Net Delta Outflow is a measure of the total volume of fresh water that flows from the Sacramento-San Joaquin Delta into San Francisco Bay. The California Data Exchange Center of the United States Geological Survey (USGS) houses these data (USGS, 2009). Chang's (2009) work on fouling communities in San Francisco Bay suggests that community composition varies depending on freshwater input, and that overall species richness is higher in moderate years than in dry or wet years. According to the same methodology used by

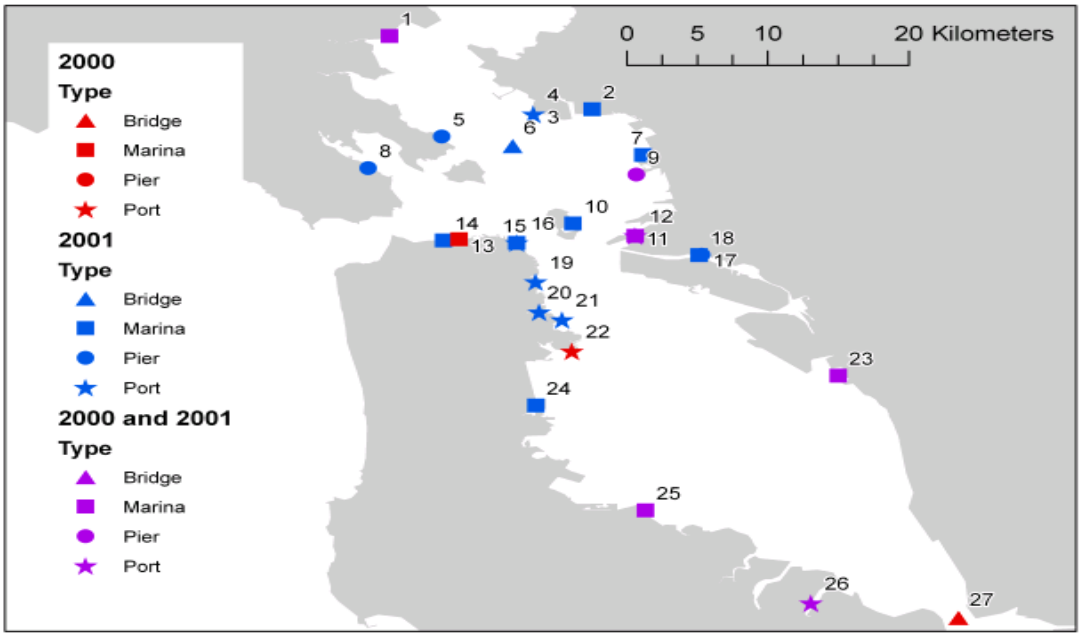
Chang (2009), I used daily average Net Delta Outflow from November to May of 1999 and 2000 to determine that the current study was conducted in a moderate year in 2000 and a dry year in 2001. However, in contrast to Chang's conclusions, the present data indicate higher species richness values in 2001, the dry year, than in 2000. This is the case for overall species richness, as well as native and NIS richness. Chang's data for moderate years follow a very wet year in which species richness was greatly depressed. That particular moderate year (2007) most likely represented a recovery period in which species richness was increasing relative to the low levels seen in the previous year and may not be comparable to the moderate year (2000) shown in the present study, which did not follow a year with markedly low salinity. Chang (2009) also observed that prevalence of *Ciona intestinalis* increased during dry years. In the present study, the increase in percent occurrence of *C. intestinalis* in the surveyed communities during the dry year (2001) seems to support Chang's results as well. Perhaps more relevant from the perspective of the α and *β*-diversity patterns that are the focus of this study, the consistency in α and *β*-diversity patterns for native and NIS from year to year did not seem to be affected by changes in freshwater regime.

Conclusions

This study demonstrates that established non-indigenous species are spread throughout fouling communities within San Francisco bay, contributing to biotic homogenization within and among sites. The high α-diversity coupled with low beta diversity found for NIS may be due to multiple introductions within the estuary combined with the opportunistic growth and spread of the NIS present. This two-year snapshot in which native diversity is rare and patchy reflects the different

distributions of native and non-native species within the Bay and highlights the degree of biotic homogenization that has already occurred in this community. Homogenization can influence species spread and community resistance to future invasions, creating a positive feedback loop for NIS establishment and success (Garcia-Ramos and Rodriguez, 2002). As taxonomic homogenization is often coupled with genetic and functional homogenization and can have impacts on multiple levels, identifying and quantifying these impacts is critical to determining the effect of NIS distribution on native populations (Olden et al., 2004). Though this work focuses on San Francisco Bay, given the widespread distribution of hull fouling NIS throughout estuaries and bays worldwide (Lambert, 2007; Cohen et al., 2005; Floerl and Inglis, 2005), I suspect that similar distributions of native and invasive species persist on a global scale.

Tables & Figures



ID	Type	Name
1	Marina	Loch Lomond
2	Marina	Richmond Marina Bay Yacht Haven
3	Port	Port of Richmond Terminal 1
4	Port	Port of Richmond Terminal 4
5	Pier	Romberg Tiburon Center
6	Bridge	South Hampton Shoal
7	Marina	Berkeley Marina
8	Pier	Sausalito Bay Model Pier
9	Pier	Berkeley Fishing Pier
10	Marina	Treasure Island Dock
11	Marina	Corinthian Yacht Club
12	Port	Port of Oakland
13	Marina	East Harbour Marina, Gas House Cove
14	Marina	San Francisco Marina

ID	Type	Name
15	Marina	Port of Redwood City Yacht Harbor
16	Port	Port of San Francisco Pier 23
17	Pier	Jack London Square Fishing Pier
18	Marina	Jack London Square Marina
19	Port	Port of SF Pier 50
20	Port	Port of SF Pier 80
21	Port	Port of SF Pier 96
22	Port	Hunters Point
23	Marina	San Leandro Marina
24	Marina	Oyster Pt Marina
25	Marina	Coyote Point Marina
26	Port	Port of Redwood City
27	Bridge	Dumbarton Swing (Railway) Bridge

Figure 1. Map of San Francisco Bay sites surveyed in 2000 and 2001.

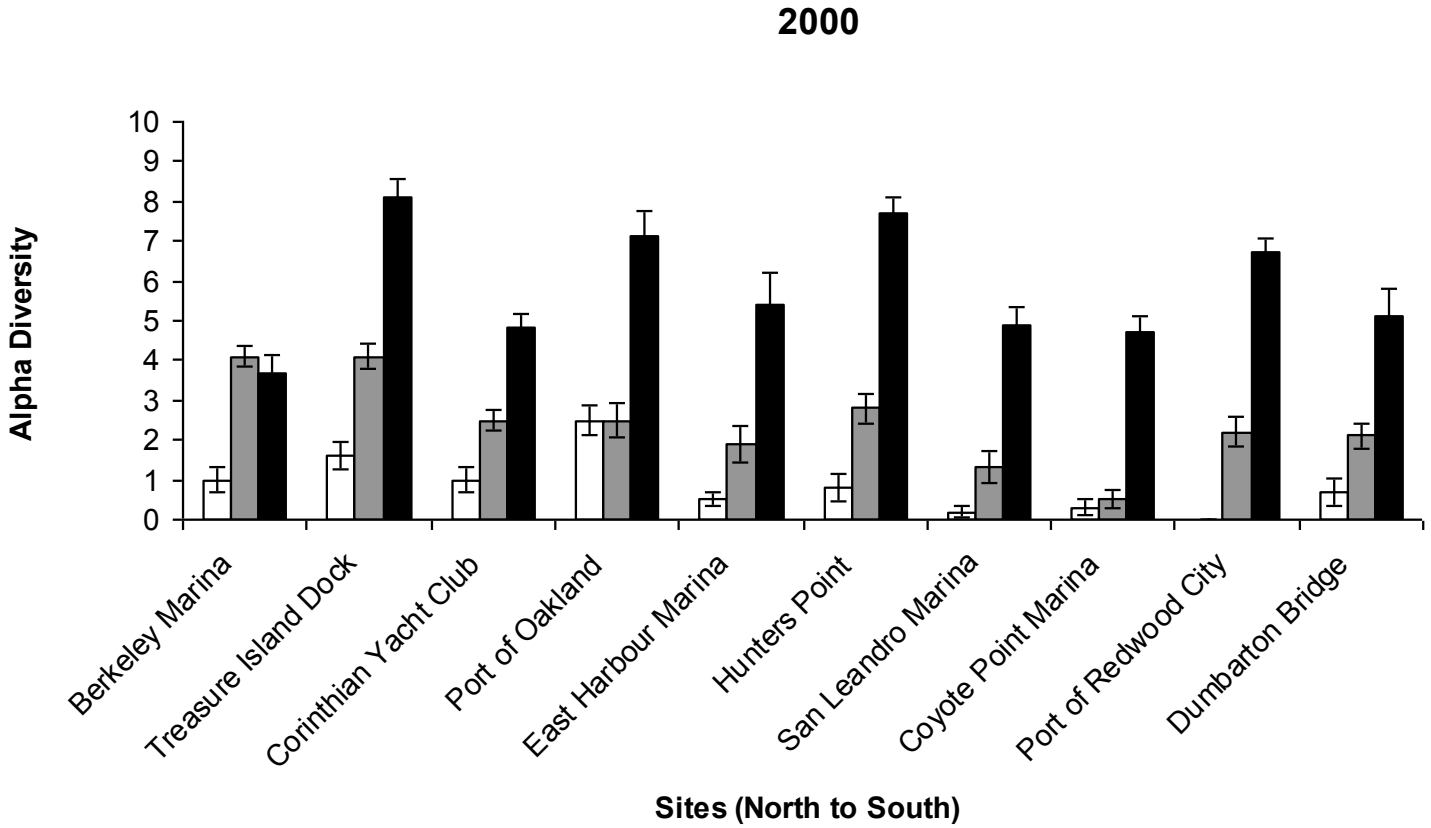


Figure 2. Alpha diversity of cryptogenic (white), native (gray) and non-indigenous (black) taxa in fouling communities collected throughout San Francisco Bay during the summer of 2000. Bars represent mean alpha value, error bars refer to +/- one standard error of the mean, n=10 for all sites.

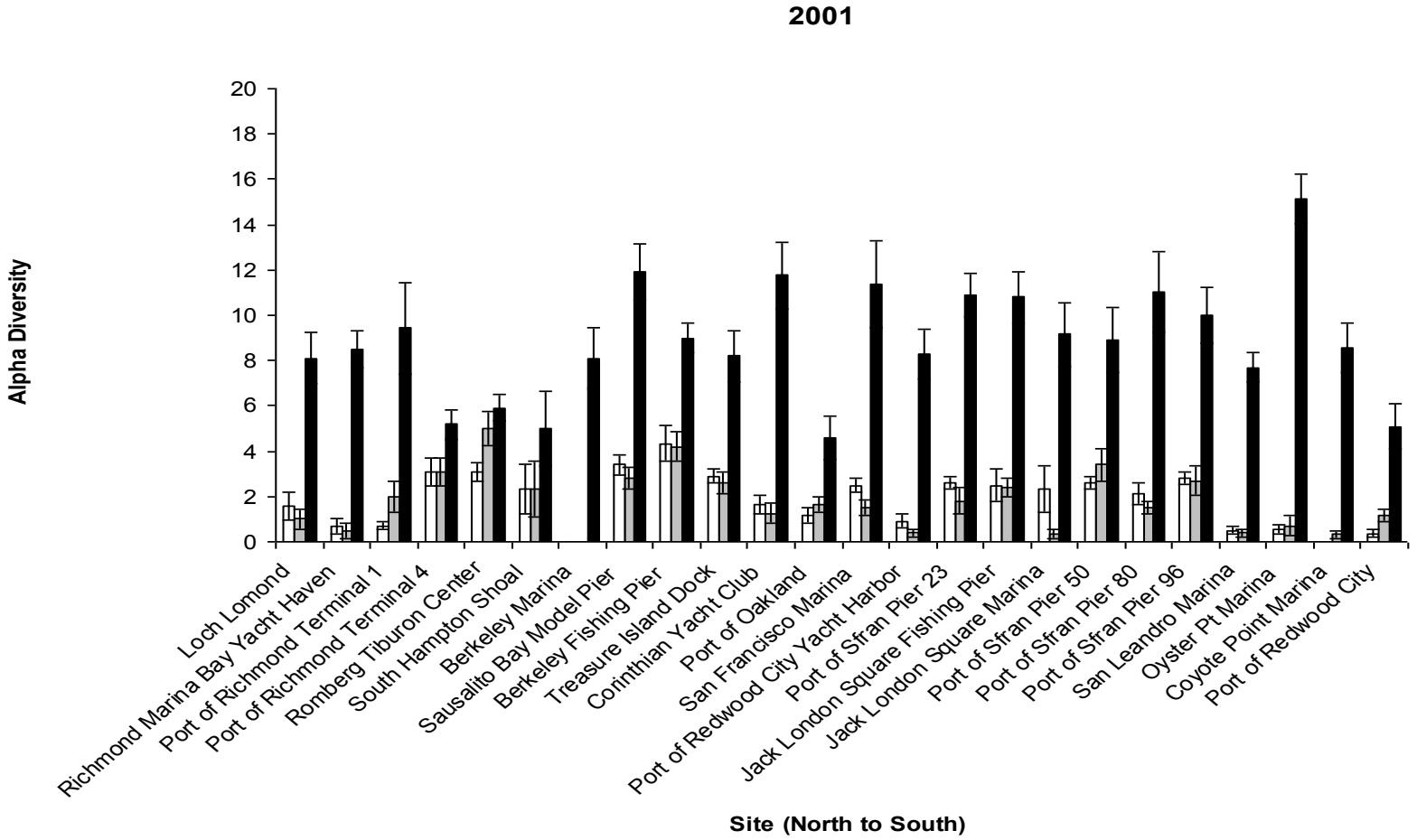


Figure 3. Alpha diversity of cryptogenic (white), native (gray) and non-indigenous (black) taxa in fouling communities collected throughout San Francisco Bay during the summer of 2001. Bars represent mean alpha value, error bars refer to +/- one standard error of the mean, n=10 for all sites except those in which panels were lost prior to retrieval ((Corinthian Yacht Club (n=8), Coyote Point Marina (n=9), Jack London Square Marina (n=6), Oyster Point Marina (n=7), and Romberg Tiburon Center (n=6)).

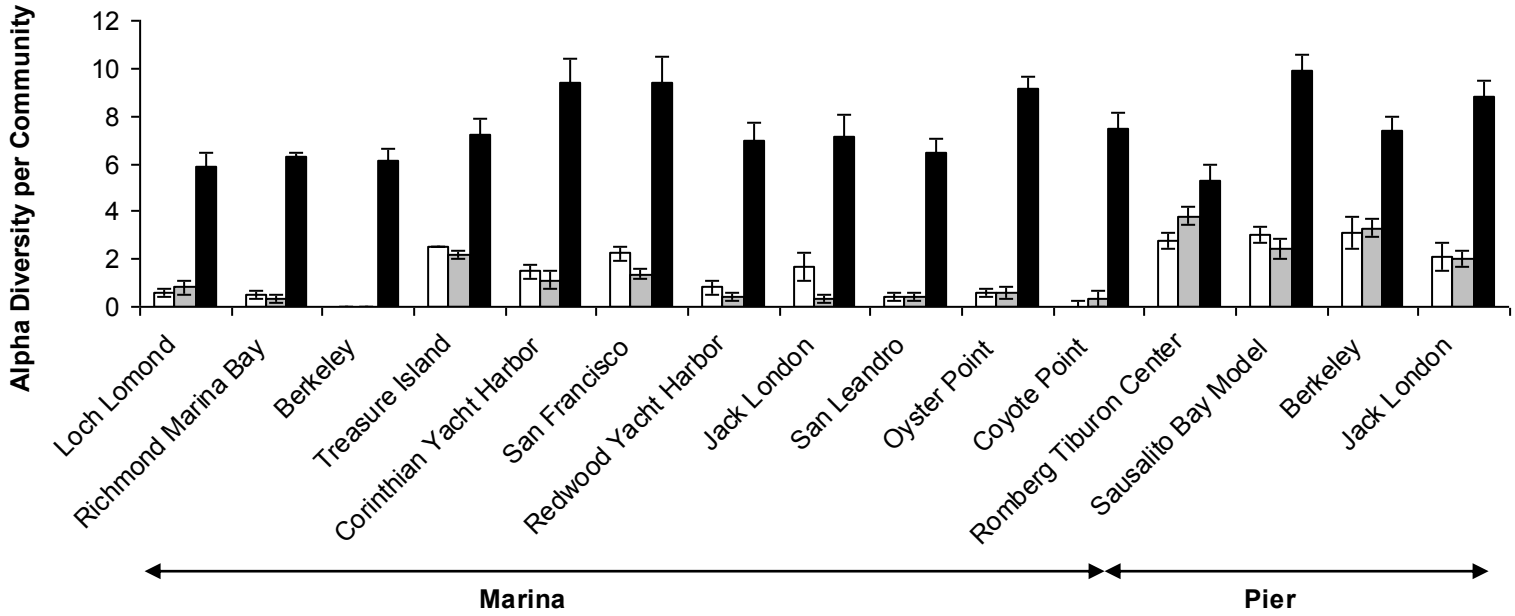


Figure 4. Alpha diversity of cryptogenic (white), native (gray) and non-indigenous (black) taxa in fouling communities collected at marina and pier sites in San Francisco Bay during the summer of 2001. Bonferroni pairwise comparisons revealed significant differences between marina and pier sites (adjusted p=0.03) Within each site type, site locations are arranged along the x axis from north to south. Bars represent mean alpha value, error bars refer to +/- one standard error of the mean, n=10 for all sites except those in which panels were lost prior to retrieval ((Corinthian Yacht Club (n=8), Coyote Point Marina (n=9), Jack London Square Marina (n=6), Oyster Point Marina (n=7), and Romberg Tiburon Center (n=6)).

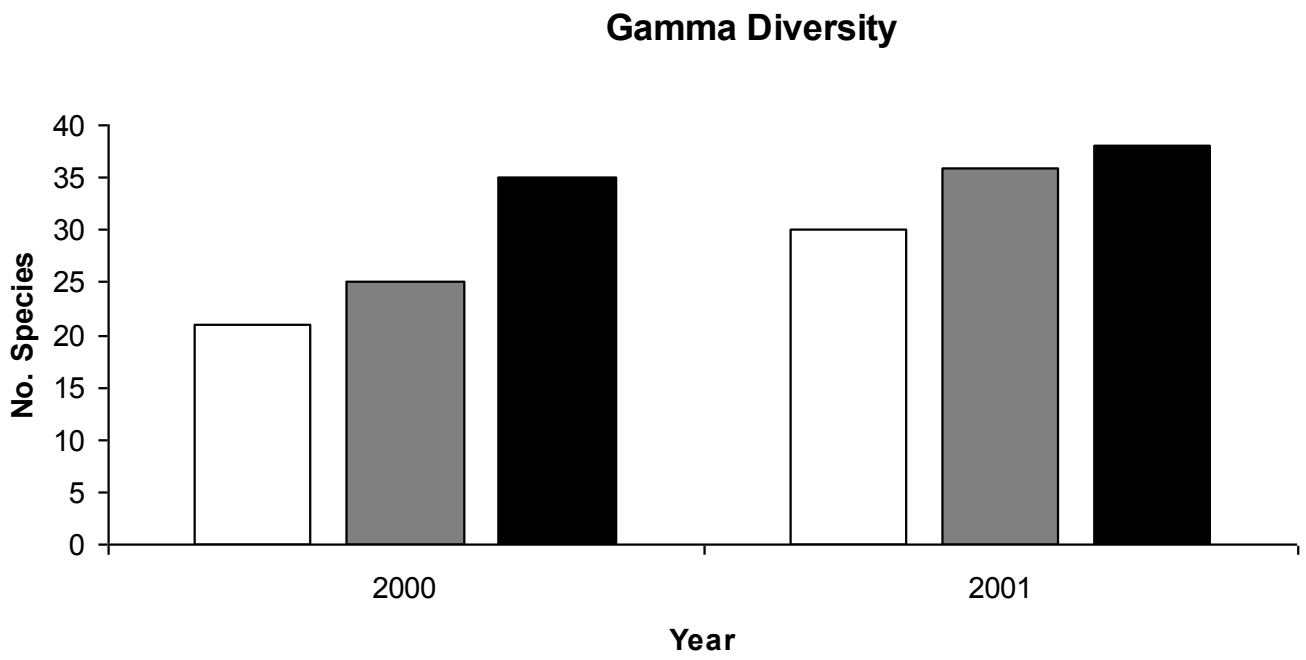


Figure 5. Gamma diversity of non-indigenous (black), native (gray) and cryptogenic (white) taxa fouling communities surveyed throughout San Francisco Bay during the summer of 2000 and 2001.

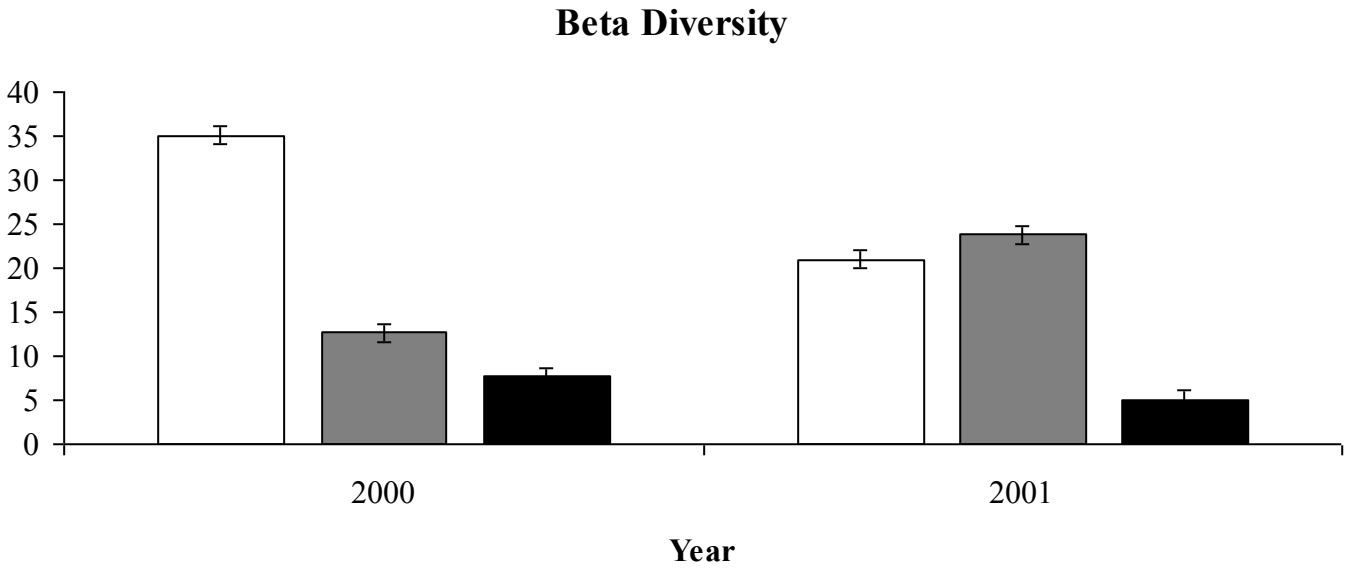


Figure 6. Beta diversity of non-indigenous (black), native (gray) and cryptogenic (white) taxa fouling communities surveyed throughout San Francisco Bay during the summer of 2000 and 2001. Error bars represent 95% confidence intervals.

Table 1. Comprehensive list of identified voucher specimens from fouling communities at all sites within San Francisco Bay. Status designations include nonindigenous species (NIS), native species (N), cryptogenic species (C) and specimens that were too immature or damaged to identify to species (U).

Taxa	Family	Genus	Species	Status	Percent occurrence of total replicates per year	
					2000	2001
Tunicata						
	Molgulidae	*Molgula*	*manhattensis*	NIS	68.0	69.1
	Styelidae	*Botryllus*	*schlosseri*	NIS	66.0	57.6
	Styelidae	*Botrylloides*	*violaceus*	NIS	48.0	67.3
	Ascidiidae	*Ascidia*	*zara*	NIS	41.0	61.3
	Cionidae	*Ciona*	*savignyi*	NIS	30.0	45.6
	Styelidae	*Styela*	*clava*	NIS	20.0	18.4
	Cionidae	*Ciona*	*intestinalis*	NIS	16.0	45.6
	Styelidae	*Styela*	*plicata*	NIS	12.0	4.1
	Didemnidae	*Didemnum*	*vexillum*	NIS	10.0	9.7
	Didemnidae	*Diplosoma*	*listerianum*	NIS	4.0	32.7
	Perophoridae	*Perophora*	*viridis*	NIS	1.0	0.0
	Styelidae	*Styela*	*canopus*	NIS	1.0	0.5
	Styelidae	*Polyandrocarpa*	*zorritensis*	NIS	0.0	0.5
	Didemnidae	*Didemnum*	*carnulentum*	N	9.0	14.3
	Clavelinidae	*Distaplia*	*occidentalis*	N	0.0	1.8
	Ascidiidae	*Ascidia*	*ceratodes*	N	0.0	0.5
	Ascidiidae	*Ascidia*	*callosa*	N	0.0	0.5
	Styelidae	*Styela*	*truncata*	N	0.0	0.5
	Molgulidae	*Molgula*	*retortiformis*	N	0.0	0.5
	Styelidae			U	6.0	15.2
	Ascidiidae	*Ascidia*	*sp.*	U	4.0	5.5
	Styelidae	*Styela*	*sp.*	U	4.0	17.5
	Didemnidae	*Didemnum*	*sp.*	U	0.0	6.0
	Didemnidae			U	0.0	2.8
	Molgulidae	*Molgula*	*sp.*	U	0.0	1.8
	Didemnidae	*Diplosoma*	*sp.*	U	0.0	1.4
	Ascidiidae			U	0.0	0.5
			Pooled Tunicata	NIS	99.3	100.0
			Pooled Tunicata	N	9.4	18.4
			Pooled Tunicata	C	0.0	0.0
Bryozoa						
	Bugulidae	*Bugula*	*stolonifera*	NIS	71.0	37.8
	Cryptosulidae	*Cryptosula*	*pallasiana*	NIS	35.0	33.2
	Nolellidae	*Anguinella*	*palmata*	NIS	26.0	26.7
	Schizoporellidae	*Schizoporella*	*japonica*	NIS	22.0	22.1
	Watersiporidae	*Watersipora*	*subtorquata*	NIS	14.0	41.5

Membraniporidae	*Conopeum*	*tenuissimum*	NIS	11.0	0.5
Schizoporellidae	*Schizoporella*	*variabilis*	NIS	9.0	2.8
Bugulidae	*Bugula*	*neritina*	NIS	8.0	54.4
Schizoporellidae	*Schizoporella*	*errata*	NIS	3.0	6.5
Buskiidae	*Buskia*	*serriata*	NIS	0.0	0.5
Mucronellidae	*Parasmittina*	*trispinosa*	NIS	0.0	0.5
Schizoporellidae	*Smittoidea*	*prolifica*	N	40.0	45.6
Vesicolariidae	*Bowerbankia*	*aggregata*	N	33.0	19.8
Bugulidae	*Bugula*	*californica*	N	23.0	19.4
Membraniporidae	*Conopeum*	*osburni*	N	21.0	2.3
Schizoporellidae	*Schizoporella*	*pseudoerrata*	N	19.0	18.0
Scrupocellariidae	*Scrupocellaria*	*diegensis*	N	11.0	8.3
Bugulidae	*Bugula*	*pacifica occidentalis*	N	6.0	9.2
Scrupocellariidae	*Tricellaria*	*catalinensis*	N	5.0	8.8
Alcyonidiidae	*Alcyonidium*	*mammillatum*	N	4.0	8.8
Bugulidae	*Bugula*	*longirostrata*	N	2.0	19.4
Bugulidae	*Caulibugula*	*ciliata*	N	2.0	0.9
Calycellidae	*Calycella*	*syringa*	N	2.0	0.0
Cribrilinidae	*Cribrilina*	*corbicula*	N	1.0	0.0
Nolellidae	*Nolella*	*stipata*	N	0.0	0.9
Crisiidae	*Crisia*	*occidentalis*	N	0.0	0.9
Celleporariidae	*Celleporaria*	*brunnea*	N	0.0	0.5
Hippothoidae	*Celleporella*	*hyalina*	C	14.0	2.3
Vesicolariidae	*Bowerbankia*	*gracilis*	C	10.0	2.8
Electridae	*Aspidelectra*	*melolontha*	C	3.0	0.0
Electridae	*Electra*	*anomala*	C	2.0	0.0
Microporellidae	*Fenestrulina*	*delicia*	C	2.0	12.9
Crisiidae	*Filicrisia*	*franciscana*	C	1.0	1.8
Electridae	*Electra*	*monostachys*	C	1.0	0.9
Membraniporidae	*Conopeum*	*reticulum*	C	1.0	0.5
Crisiidae			C	1.0	0.0
Vesicolariidae	*Bowerbankia*	*tertia*	C	1.0	0.0
Scruparidae	*Scruparia*	*ambigua*	C	0.0	2.3
Scrupocellariidae	*Tricellaria*	*sp.*	C	0.0	1.4
Alcyonidiidae	*Alcyonidium*	*polyoum*	C	0.0	0.5
Vesicolariidae	*Bowerbankia*	*sp.*	U	9.0	27.2
Schizoporellidae	*Schizoporella*	*sp.*	U	8.0	2.3
Alcyonidiidae	*Alcyonidium*	*sp.*	U	5.0	11.5
Bugulidae	*Bugula*	*sp.*	U	5.0	4.1
Schizoporellidae	*Smittoidea*	*sp.*	U	3.0	0.0
Membraniporidae	*Conopeum*	*sp.*	U	1.0	0.5
Electridae	*Electra*	*sp.*	U	1.0	0.5
Membraniporidae	*Sinoflustra*	*annae*	U	1.0	0.0
Membraniporidae			U	1.0	0.0
Scrupocellariidae	*Scrupocellaria*	*sp.*	U	1.0	0.0
Microporellidae	*Fenestruloides*	*sp.*	U	0.0	4.1
Smittinidae			U	0.0	0.9
Anomiidae			U	0.0	0.5

			Pooled Bryozoa	NIS	96.6	44.5
			Pooled Bryozoa	N	87.2	40.2
			Pooled Bryozoa	C	22.8	10.5
Cirripedia						
	Balanidae	*Amphibalanus*	*improvisus*	NIS	26.0	14.7
	Balanidae	*Amphibalanus*	*amphitrite*	NIS	1.0	3.2
	Balanidae	*Balanus*	*crenatus*	N	39.0	18.0
	Balanidae	*Balanus*	*sp.*	U	13.0	26.3
	Balanidae			U	1.0	1.8
			Pooled Cirripedia	NIS	32.2	18.4
			Pooled Cirripedia	N	42.3	20.3
			Pooled Cirripedia	C	0.0	0.0
Hydrozoa						
	Tubulariidae	*Pinauay*	*crocea*	NIS	19.0	19.8
	Bougainvilliidae	*Garveia*	*franciscana*	NIS	2.0	0.9
	Campanulariidae	*Laomedea*	*calceolifera*	NIS	1.0	0.0
	Bougainvilliidae	*Garveia*	*annulata*	N	4.0	2.8
	Plumulariidae	*Plumularia*	*lagenifera*	N	0.0	2.3
	Plumulariidae	*Plumularia*	*setacea*	N	0.0	2.8
	Campanulariidae	*Obelia*	*dichotoma*	C	18.0	0.5
	Campanulariidae	*Obelia*	*bidentata*	C	11.0	1.8
	Campanulariidae	*Clytia*	*hemisphaerica*	C	7.0	0.0
	Tubulariidae	*Pinauay*	*marina*	C	7.0	0.0
	Campanulariidae	*Clytia*	*gracilis*	C	3.0	0.0
	Tubulariidae	*Ectopleura*	*dumortierii*	C	2.0	1.4
	Campanulariidae	*Obelia*	*sp.*	C	2.0	0.9
	Campanulariidae	*Clytia*	*paulensis*	C	1.0	0.0
	Campanulariidae	*Gonothyraea*	*clarki*	C	1.0	0.0
	Campanulariidae	*Gonothyraea*	*loveni*	C	1.0	0.0
	Bougainvilliidae	*Bougainvillia*	*muscus*	C	0.0	0.5
	Campanulariidae	*Obelia*	*longissima*	C	0.0	1.4
	Campanulariidae	*Opercularella*	*lacerata*	C	0.0	0.9
	Eudendriidae	*Eudendrium*	*capillare*	C	0.0	0.9
	Eudendriidae	*Eudendrium*	*cochleatum*	C	0.0	0.9
	Halopteridiidae	*Halopteris*	*tenella*	C	0.0	0.9
	Tubulariidae	*Ectopleura*	*sp.*	U	10.0	10.6
	Tubulariidae			U	10.0	15.2
	Campanulariidae			U	3.0	1.4
	Athecata			U	1.0	0.9
	Bougainvilliidae			U	1.0	2.8
	Eudendriidae	*Eudendrium*	*sp.*	U	1.0	1.4
	Bougainvilliidae	*Garveia*	*sp.*	U	1.0	1.4
	Campanulariidae	*Gonothyraea*	*sp.*	U	1.0	0.0
	Bougainvilliidae	*Bougainvillia*	*sp.*	U	0.0	0.5

			Pooled Hydrozoa	NIS	21.5	16.6
			Pooled Hydrozoa	N	3.4	7.4
			Pooled Hydrozoa	C	33.6	24.9
Serpulidae						
	Serpulidae	*Ficopomatus*	*enigmaticus*	NIS	3.0	0.9
	Serpulidae	*Pseudochitinopoma*	*occidentalis*	N	2.0	2.8
	Serpulidae	*Hydroides*	*gracilis*	N	1.0	0.9
	Serpulidae	*Serpula*	*sp.*	C	0.0	0.5
	Serpulidae	*Pseudochitinopoma*	*sp.*	U	0.0	0.5
	Serpulidae	*Hydroides*	*sp.*	U	0.0	0.5
			Pooled Serpulidae	NIS	5.4	0.9
			Pooled Serpulidae	N	2.7	2.8
			Pooled Serpulidae	C	0.0	1.8
Bivalvia						
	Veneridae	*Venerupsis*	*philippinarum*	NIS	2.0	0.0
	Mytilidae	*Musculista*	*senhousia*	NIS	1.0	3.7
	Corbulidae	*Potamocorbula*	*amurensis*	NIS	1.0	0.0
	Calyptraeidae			NIS	0.0	1.4
	Ostreidae	*Ostrea*	*conchaphila*	N	4.0	12.4
	Hiatellidae	*Hiatella*	*arctica*	N	2.0	0.0
	Ostreidae	*Ostrea*	*sp.*	N	2.0	0.0
	Mytilidae	*Modiolus*	*sp.*	N	1.0	0.9
	Ostreidae			N	0.0	2.3
	Cardiidae	*Clinocardium*	*nuttallii*	N	0.0	0.5
	Veneridae	*Protothaca*	*sp.*	N	0.0	0.5
	Veneridae	*Pitar*	*columbianus*	N	0.0	0.5
	Lasaeidae	*Kellia*	*suborbicularis*	C	1.0	0.5
	Mactridae			C	0.0	0.5
	Chamidae	*Pseudochama*	*granti*	C	0.0	0.5
	Mytilidae	*Mytilus*	*sp.*	U	32.0	39.2
	Mytilidae			U	3.0	1.8
	Ungulinidae	*Diplodonta*	*sp.*	U	0.0	0.5
	Tellinidae	*Macoma*	*sp.*	U	0.0	0.9
			Pooled Bivalvia	NIS	2.7	5.5
			Pooled Bivalvia	N	5.4	17.5
			Pooled Bivalvia	C	0.7	2.3
Nudibranchia						
	Glaucidae	*Sakuraeolis*	*enosimensis*	NIS	6.0	2.3
	Tergipedidae	*Catriona*	*rickettsi*	NIS	3.0	0.5

	Eubranchidae	*Eubranchus*	*misakiensis*	NIS	2.0	0.0
	Tergipedidae	*Cuthona*	*albocrusta*	N	7.0	0.0
	Glaucidae	*Hermissenda*	*crassicornis*	N	1.0	1.4
	Onchidoridiidae	*Onchidoris*	*muricata*	N	0.0	1.4
	Onchidoridiidae	*Acanthodoris*	*brunnea*	N	0.0	0.9
	Polyceridae	*Polycera*	*hedgpethi*	N	0.0	0.9
	Onchidoridiidae	*Acanthodoris*	*lutea*	N	0.0	0.5
	Onchidoridiidae	*Acanthodoris*	*rhodoceras*	N	0.0	0.5
	Dironidae	*Dirona*	*picta*	C	1.0	0.0
	Onchidoridiidae	*Acanthodoris*	*sp.*	U	0.0	0.5
	Cumanotidae	*Cumanotus*	*sp.*	U	2.0	0.9
	Tergipedidae	*Cuthona*	*sp.*	U	1.0	0.5
	Gastropteridae	*Gastropteron*	*sp.*	U	1.0	0.0
			Pooled Nudibranchia	NIS	9.4	2.8
			Pooled Nudibranchia	N	6.0	6.9
			Pooled Nudibranchia	C	0.7	1.4

Chapter 2: The effect of diversity and resource availability on invasibility of novel non-native species

Abstract

Community diversity and resource availability are often used to explain the mechanisms driving successful invasions of non-native species. The diversity resistance hypothesis predicts that high diversity should lead to community resistance to invasion because limiting resources are more fully utilized within the community. However, theoretical and empirical studies have reported conflicting trends in which species richness relates negatively to invasion success in some cases, and positively in others. The current study explores the diversity-invasibility relationship in marine fouling communities of San Francisco Bay by experimentally assessing the influence of diversity and resource availability (open space) on both short-term recruitment of novel invasive species into test communities and subsequent community development over the course of multiple seasons. On short time scales (2-4 weeks), in experiments conducted in the fall of 2006 and the summer of 2007, the effect of initial diversity on the density of recruitment of novel non-indigenous species was significant and negative, with no effect of resource level (increased open space). In both 2006 and 2007, the recruitment of one or two species displayed a significant inverse relationship with community diversity (*Botrylloides violaceus* in the fall of 2006, *Ciona intestinalis* and *Bugula stolonifera* in the summer of 2007). Changes in community composition over time (up to 6 months) also indicated significant inverse relationships between percent cover of non-native species and diversity of the initial fouling community with no evidence of a resource effect. Abundant non-native species occupied less space in communities with higher

initial diversity. However, the same non-native species were present in (i.e., invaded) all experimental communities regardless of starting diversity. The significant effects of diversity on recruitment density and percent cover, combined with the lack of resource effects across both years, does not support the hypothesis that resource limitation is driving the effects of diversity. Resource use may be more complex and most likely includes primary as well as secondary substrate. Instead of resource limitation, the diversity-invasibility relationships seen in fouling communities could be driven by other factors such as larval behavior and settlement in response to the adults present in the community.

Introduction

Elton (1958) postulated that high community diversity should lead to resistance to invasion. He reasoned that simple, low diversity systems are unable to maintain "balance" and are more susceptible to "destructive oscillations" than more diverse communities. Several lines of evidence were presented in support of this hypothesis. Mathematical models of population dynamics predict that populations will fluctuate dramatically, and populations will not stabilize in simple systems (often one prey and one predator). Similar results have been seen in laboratory experiments using protozoa, with a single prey and a single predator. Another line of evidence was that island communities, which tend to have low diversity, also tend to be highly invaded (Elton, 1958). Cultivated land, that supports a reduced number of species, also tends to be susceptible to colonization by invasive species (Elton, 1958). In contrast high diversity systems such as undisturbed tropical rainforests, do not show these types of susceptibility to invasion

(Elton, 1958). Elton's final line of evidence in support of the resistance of diverse systems to invasions was that unlike treated orchards, orchards that are not treated with pesticides, and are consequently more diverse, are also more stable and less vulnerable to pest invasion than treated orchards.

The stability seen in highly diverse communities is interpreted to be a result of high competition leading to complete utilization of limiting resources. This decreases available resources for new species entering the community, making it more difficult for them to invade (Elton, 1958; Cronk and Fuller, 1995; Levine and D'Antonio, 2000). The diversity resistance hypothesis has been prevalent in the literature for several decades, and has been supported by theory (Case, 1990; Drake, 1990; Lockwood et al. 1997). More recently, empirical studies have examined the link between biodiversity and successful invasion to determine whether highly diverse communities are less susceptible to invasion (Weltzin et al., 2003; Stachowicz et al., 2002; Foster et al., 2002; Fargione and Tilman, 2005).

Theoretical and empirical studies in terrestrial systems, where the majority of this work has been done, have shown conflicting trends in which species richness relates negatively to invasion success in some cases, and positively in others (Elton, 1958; Usher, 1988; Case, 1990; Robinson et al., 1995). Negative relationships are reported from studies and models conducted at small spatial scales (Tilman 1997; Levine 2000, Naeem et al., 2000; Brown and Peet 2003) but positive relationships are seen at larger spatial scales (Lonsdale 1999, Stohlgren et al., 1999, 2003). In these studies, spatial scales ranged in order of magnitude from 100 cm^2 (small scale) to 4000 m^2 ("landscape" scale, Stohlgren et al. 1999, 2003). In sessile marine invertebrate communities, conflicting

results also have been seen in two studies that were both conducted on small scales (community sizes of ~100cm^2). One experimental study showed an inverse relationship between species richness and species invasion (Stachowicz et al., 1999), while another observational study showed a positive relationship (Dunstan and Johnson, 2004).

Recent theory suggests that the different trends may be dependent on the spatial scale used to define each community (Shea and Chesson, 2002). Shea and Chesson (2002) posit that, theoretically, a negative relationship between invasion success and species richness may be seen at local scales, while a positive relationship could be seen when a broader spatial scale is considered. Explanations for this shift in relationship include local factors such as niche partitioning and competitive exclusion acting at small scales, and extrinsic factors (e.g., propagule supply rate) or increased heterogeneity of abiotic factors acting at large spatial scales (Levine and D'Antonio, 1999; Shea and Chesson, 2002; Davies et al., 2005; Jewett et al., 2005). Thus, small scale, negative relationships may be driven by competitive interactions, while large scale positive relationships may reflect the effects of external factors that are more heterogeneous over large spatial scales and obscure competitive effects (Davies et al., 2005).

The current study aims to explore the diversity-invasibility relationship at the small scale in marine fouling communities in San Francisco Bay. These communities are dominated by non-native species with higher diversity than native species in the local system. Thus, this study uses invasive species to create communities of different diversity. Coupled with resource manipulation, the goal of the study is to assess the influence of diversity and resources on short term recruitment of novel non-native species

into the local community and subsequent development of the community over the course of multiple seasons.

Materials and Methods

Experimental Design

This experiment is designed to examine the effects of both diversity and resource availability on short-term community recruitment and longer-term community development. As San Francisco Bay fouling communities are predominantly made up of non-native species, replicate communities of different diversity levels were constructed using abundant non-native species, and the recruitment, settlement and community composition of novel non-native species was recorded over time. Experiments were conducted at Richmond Marina Bay, San Francisco Bay, CA (37°54'41"N – 122°21'05"W) and laboratory analyses were conducted at the Romberg Tiburon Center for Environmental Studies, San Francisco State University.

The experiment consisted of determining the success of novel species in response to two independent variables created in fouling communities on replicate fouling panels: diversity of community assemblages created at 4 levels (1-4 species); and resource availability (two levels of open space, the major limiting resource in these communities). For the purposes of this study, 'novel' species refer to any new non-native species that were not used to create initial community diversity treatments. Invasion success was measured by either the number of novel recruits that settled on primary space, or the percent cover of the novel species. The diversity-invasibility relationship described refers to the relationship between the dependent variable, invasion success, and the explanatory

variables, diversity and resource availability. Negative diversity-invasibilty relationships are those in which invasion success was inversely related to the explanatory variables. Methodological and analytical aspects are described in detail below.

To create fouling communities of different diversities, I used 2.5 X 2.5 cm PVC squares with monocultures of species and combined them into composite 10 X 10 cm panels of 16 squares each. Using different combinations of the small monospecific squares as well as blank 2.5 X 2.5 cm squares, I was able to control species diversity and available open space.

To create the 2.5 X 2.5 cm monocultures, the squares were submerged in the water column for several weeks to allow initial settlement. The tunicates *Ciona savignyi, Styela clava,* and *Botryllus schlosseri*. settled in high numbers on the squares. For several weeks, a weeding process was employed to remove non-target species and allow either one *C. savignyi*, one *S. clava* , or one colony of *B. schlosseri* to grow on the square.. Other species that did not settle on the squares but were abundant and amenable to artificial attachment were attached using Krazy Glue© epoxy, visually monitored for several weeks and gardened to remove other species. These species included the sponge *Clathria prolifera*, the bryozoans *Bugula stolonifera* and *B. neritina*, and the tunicates *S. clava* and *B. schlosseri*. The tunicates *S. clava* and *B. shlosseri* were attached using both methods (natural settlement and artificial attachment). Prior to assembling experimental communities, each square contained either one individual or one colony of the six species mentioned above.

Experimental species, i.e. species used to create initial experimental diversity, were chosen based on natural density during the month prior to experimentation and ease

of attachment to the panels. Although most invertebrate members of the fouling community are either filter feeders or suspension feeders, an effort was made to select species that represented a variety of growth forms or 'functional groups'. The species selected to create diversity treatments represent solitary tunicates (S. *clava, C. savignyi*), colonial tunicates (*B. schlosseri*), upright bryozoans (*B. neritina, B. stolonifera*) and a sponge (*C. prolifera*). All experimental species are non-native to San Francisco Bay.

Communities were assembled using combinations of 1-4 species by screwing sixteen of the monoculture squares into a PVC backboard to create a 10 X 10cm community of known diversity (following the methods of Stachowicz et al., 1999; Stachowicz et al., 2002). Diversity treatment 1 consisted of eight replicate monoculture communities for each species being used in the experiment. For higher levels of species richness (2-4), communities were assembled using different species combinations to control for differences associated with individual species effects on the results (as opposed to combined species effects) and avoid psuedoreplication. Four species combinations were randomly chosen at each diversity level and 8 replicates were used for a total of 32 replicate communities for diversity treatments 2 and 3 (Table 1). The highest diversity treatment (4) was not replicated with multiple species combinations due to limitations in species abundance and availability at the study site. This treatment was represented by one combination of four species with 8 replicate communities (see Table 1). The spatial location of each species within the assembled community was determined randomly.

In addition to diversity treatments, I also manipulated available space (the primary resource in the system) to test the effect of resource availability on the relationship

between diversity and novel invasion success. The resource treatment contained two levels, low and high, such that treatments initially contained 0 or 25% open space. Thus, for high resource treatments, assembled communities contained 4 blank 2.5 X 2.5cm squares while low resource treatments did not contain any blank space. Half of the replicates described above in the explanation of diversity treatments were assigned to the low resource treatment and half to the high resource treatment. Open space was randomly distributed across the panel area. Bare space was not maintained or manipulated in the communities after initial treatments were deployed. The percent bare space remaining in communities was recorded throughout the course of each experiment.

Once initial diversity and resource level were established in each replicate community, panels were attached to floating docks in the marina, deployed 1m below the water surface and removed for analysis purposes only. Replicate communities were grown *in situ* at the Richmond Marina Bay site. Two weeks and four weeks after communities were established they were analyzed in the laboratory using an overlaid grid to perform point count analysis (50 points) under a dissecting microscope to quantify bare space, novel species and native species space occupation. At each point, the species attached to the panel surface was identified. If the space was bare, this was also recorded. In addition to point count analyses, all new recruits that settled on all available primary substrate (the bare panel surface) in each community were enumerated and identified to the lowest taxonomic level possible. Recruitment was recorded for weeks 1-2 and weeks 3-4 of each experiment. Finally, communities were visually observed to identify rare species. To assess community development over a longer time scale, point counts were also conducted after three and six months. All panels were transported in individual, sealed bags filled with seawater from the site, and returned to the field in between sampling dates. Panels were removed from the field

for ~ 8 hour increments. Panels were kept in the laboratory in aerated coolers with water collected from the site. There were no obvious visual signs that transporting the panels or keeping them in the lab was negatively affecting the sessile invertebrates. The entire six month experiment was run in the Fall of 2006 (November 2006 – May 2007) and repeated in the Summer of 2007 (August 2007- February 2008) in order to explore effects due to seasonal variation.

Statistical Analysis

Short-term Recruitment

Factorial regression analyses were run to determine the interactive effects of community diversity level and resource availability on recruitment of novel non-indigenous species during weeks 1-2 and weeks 3-4. For each two-week period, the cumulative recruitment of novel non-indigenous species was treated as the dependent variable. Regressions were run using the following model where b_x represents regression coefficients:

Novel recruitment = $b_0 + b_1$Diversity + b_2Resource + b_3Diversity*Resource.

Each set of two weeks was analyzed separately using the general linear model (GLM) procedure in the SAS 9.1 analysis package. For analyses in which species recruitment was pooled, total novel recruitment was treated as a dependent variable and diversity, resource availability and their interaction were treated as fixed effects. Following analysis of pooled recruits, I ran regression analyses on all species with mean recruitment densities of at least 10 individuals per 100cm^2 community. For species-specific analyses, recruitment of the species in question was considered the dependent variable. Similar regression analyses were also run using the total species richness of novel recruits as the

dependent variable. Data that did not meet the requirements of normality or homogeneity of variance were transformed accordingly to meet model assumptions.

To determine whether differences seen in recruitment were due to species effects instead of diversity effects (when diversity treatments were found to be significant), I followed the methodology described by Wardle (2001). For all species or pooled groups (i.e. pooled novel non-indigenous recruits, total species richness of novel recruits) that showed a significant response in the analyses described above, a non-parametric Kruskal-Wallace one-way ANOVA was used to determine whether the change in abundance of the dependent variable was due to the experimental adults used in each monoculture treatment. Thus, ANOVAS were run on recruitment data for monoculture treatments only. If a significant difference was found within the monoculture treatment and this difference was only due to one experimental adult species used to set up the treatment, all combinations containing that species were removed from the entire season's recruitment data and an additional Kruskal Wallace ANOVA was run to determine whether the change in abundance of the dependent variable still varied significantly with increased diversity. If a significant difference was still found, these differences were interpreted to be a result of diversity and not a species effect.

Long-term Community Assemblage

To determine the effect of diversity and resource availability on subsequent community composition, I used the point count data (percent cover) to conduct multivariate analyses using the PRIMER-6 software package (Clarke and Gorley, 2006; Clarke, 1993). For all panels, points occupied by the species used to create the

communities (hereafter referred to as 'experimental species') were removed and remaining counts were standardized to the number of total points remaining per panel using the following equation:

$$Standardized\ Percent\ Cover = \left(\frac{Points_x}{Points_{total} - Points_{Experimental\ Species}}\right)100$$

where x refers to the species of interest.

This standardization was conducted in order to clearly evaluate the influence of novel species in each community. While this approach does not allow for interpretation of the increase or decline of experimental species, it does not change the interpretation of abundance and dominance of novel species in the system and ensures that community differences that are seen result from novel species themselves and not from differences in species that were used to set up the diversity treatments. The standardized data were square root transformed to prevent over-dominance of abundant species and under-dominance of the intermediately abundant species (Clarke and Warwick, 2001). Standardized, transformed data were used to create a Bray-Curtis similarity matrix for all panels in the Fall 2006 experiment and the Summer 2007 experiment.

Using the similarity matrices, analysis of similarity (ANOSIM) routines were conducted for each experiment. Specifically, for each experiment, a two-way crossed ANOSIM was run to examine the effects of sample time (2, 4, 12, 24 weeks) and resource availability (high, low) at each diversity level. In addition, two-way crossed ANOSIMs were run to examine diversity (1-4 species) and resource availability at each sampling time. In all cases, where significant differences were found at the $\alpha = 0.05$ level, Bonferroni corrected pairwise comparisons were used to compare levels of the treatment in question.

The Similarity Percentage Routine (SIMPER) was used to identify the species responsible for significant differences found in the ANOSIM routine. Once individual responsible species were identified, a non-parametric Kruskal-Wallace one-way ANOVA was used to determine whether that particular species' abundance changed with the diversity treatments at any given sample time. The resource treatments were not used as a factor in these analyses, since resource level had not been significant in previous tests. Instead, data were pooled for both resource levels and diversity was the only fixed factor included in these analyses. When a Kruskal-Wallace ANOVA indicated a significant difference between diversity treatments at a given sample time, Bonferroni corrected pairwise tests were conducted to identify which diversity treatments differed. While parametric tests (ANOVA) are also appropriate for this analysis, data from many individual species were not normally distributed and did not meet the requirements of the test even after transformation. Therefore, to maintain consistency for all of the species-specific analyses, I chose to present the non-parametric results even in cases in which parametric ANOVA would be entirely appropriate. In all cases in which parametric ANOVA were appropriate, there were no differences in the conclusions of the non-parametric analyses.

Finally, using the same methods described for the short term recruitment data, I tested for species effects in every group that was significantly affected by diversity (1-4 species) in the community assemblage data.

Results

Short-term Recruitment

Overall Recruitment

Results from factorial regression models show an overall negative diversity-invasibility relationship in which initial community diversity had an inverse effect on the recruitment of novel NIS in both years studied. This significant negative relationship was seen in the fall 2006 experiment after 2 and 4 weeks and in the summer 2007 experiments after 2 weeks (Table 2, Figure 1A, Figure 2A). No significant effect of resource treatments (i.e., amount of open space), or interactions between resource and diversity treatments on novel NIS recruitment density were found. While an overall decline in recruitment was seen, species-specific patterns of recruitment differed.

Species-specific Recruitment

In both experiments, recruitment patterns varied by species, and both negative and positive relationships between recruitment density and initial diversity of the recipient community were identified. In the fall 2006 experiment, there was a significant inverse relationship between recruitment density of *B. violaceus* and initial diversity. This species was predominantly responsible for the overall negative relationship seen in the first two weeks of the fall 2006 experiment (Figure 1B). There was no evidence that resource availability had an effect on *B. violaceus* recruitment and there were no significant interactions between initial diversity and resource level. While recruitment of *B.*

violaceus also decreased with diversity in the following two weeks, the relationship was no longer significant (Table 2). In contrast, recruitment of the bryozoan *B. neritina* increased significantly with initial diversity but was not affected by resource availability (Figure 1C, Table 2). This relationship was not apparent at four weeks.

There were four species that were dominant recruiters in the summer 2007 experiment: *C. intestinalis, C. savignyi, B. stolonifera, B. neritina.* The recruitment density of all four species decreased as initial diversity went up. Of the four dominant species, *C. intestinalis* and *B. stolonifera* displayed significant negative diversity-invasibility relationships after two weeks (Figure 2 B-C, Table 2). Increased resource availability did not have an effect on the density of recruitment and there were no significant interactions between diversity and resource treatments. However, further analyses confirm that the relationship between *C. intestinalis* recruitment and initial diversity of the community is, in fact, due to the presence of *S. clava* (See 'Species Effects' below).

Species Richness

The effect of diversity and resource availability on the species richness of NIS varied depending on year. In the fall 2006 experiment, species richness of NIS significantly increased with diversity and was unaffected by resource availability during the first two weeks (Figure 1D, Table 2). This result may indicate an unexpected facilitative effect of initial diversity on species richness. However, this pattern did not persist, and there was no relationship between species richness and initial diversity in the weeks following (Table 2). In contrast, a significant inverse relationship between the

species richness of NIS and initial diversity was observed in the summer 2007 experiment (Figure 2D, Table 2); as in year one, this effect was not evident after four weeks (Table 2).

Species Effects

I conducted additional analyses to ensure that the diversity-invasibility relationships described above were due to initial diversity treatments and not due to species-specific properties of the experimental adults used to create diversity treatments. To assess species effects, I conducted focused analyses on the pattern of recruitment density in monoculture communities (see Methods; Wardle, 2001).

Recruitment in the fall 2006 experiment was not affected by the presence of particular experimental species. Although there were significant differences in the number of novel NIS that recruited into monocultures, these differences were due to multiple species ($\chi^2 = 10.43$, DF = 3, p= 0.02). The presence of the sponge *C. prolifera* depressed recruitment of *B. violaceus* significantly ($\chi^2 = 11.75$, DF = 3, p= 0.008). However, when combinations containing this sponge were removed from all diversity treatment analyses, the recruitment of *B. violaceus* still significantly decreased with increasing diversity of the recipient community ($\chi^2 = 33.47$, DF = 3, p< 0.0001). The recruitment density of *B. neritina* did not vary among monoculture communities ($\chi^2 = 3.25$, DF = 3, p= 0.50). Species richness did not vary among monoculture communities either ($\chi^2 = 6.53$, DF = 3, p= 0.09).

With the exception of *C. intestinalis*, recruitment in the summer 2007 experiment was not affected by initial species treatment effects. The presence of *B. schlosseri*

depressed the recruitment density of both pooled novel NIS and *B. stolonifera* significantly (novel NIS recruitment: $\chi^2 = 21.78$, DF = 3, p= 0.0002; *B. stolonifera:* $\chi^2 = 16.01$, DF = 3, p= 0.003). When combinations containing this tunicate were removed from all diversity treatment analyses, the recruitment density of both novel NIS and *B. stolonifera* still significantly decreased with increasing diversity of the recipient community (novel NIS recruitment: $\chi^2 = 10.0$, DF = 3, p= 0.02; *B. stolonifera*: $\chi^2 = 9.3$, DF = 3, p= 0.03). *C. intestinalis* recruitment was significantly elevated in the presence of *S. clava* in monoculture treatments ($\chi^2 = 20.15$, DF = 3, p= 0.0005) and showed no significant difference in recruitment once diversity combinations that included *S. clava* were removed from analyses ($\chi^2 = 5.39$, DF = 3, p= 0.15). Therefore, the differences seen in *C. intestinalis* recruitment in the summer of 2007 were due to the presence of *S. clava* in the treatments and not due to diversity treatments per se. Species richness did not vary among monoculture communities ($\chi^2 = 6.53$, DF = 3, p= 0.09).

Long-term Community Assemblage

Compositional Changes Through Time

Two-way analysis of similarities (ANOSIM) of sample time and resource availability revealed that in both fall 2006 and summer 2007, community composition changed significantly through time at all levels of diversity treatments (Table 3). Pairwise comparisons of each sample time show that in most cases, communities changed significantly between all sample times. However, in the highest diversity treatment (4) during the summer 2007 experiment, community assemblage did not change between any period of time except 2 and 24 weeks. In contrast to temporal changes, no significant

differences were seen in community assemblage with respect to resource treatment (Table 3).

Diversity x Resource Availability

Results from two-way ANOSIM of sample diversity and resource availability show that across all time points (up to 6 months), there is a significant difference in community assemblage depending on the initial diversity of the community (diversity treatment, Table 4). This was the case in both years studied. Overall, the resource treatments did not have a significant effect on community assemblage in the fall 2006 experiment, but did have a significant global effect on communities observed in the summer 2007 experiment (Table 4). More detailed analysis of diversity and resource effects within each sample period revealed a significant effect of diversity on community assemblage at 2, 4, and 12 weeks during the Fall 2006 experiment and at 4 and 24 weeks during the Summer 2007 experiment (Table 4). Despite an overall resource effect in the summer 2007 experiment, no resource effect was seen within any individual sample time during either experiment (although resource was marginally significant at 12 weeks in 2006 and at 24 weeks in 2007) (Table 4).

Community Similarity & Percent Cover – 2006 Experiment

To determine which species were responsible for differences seen in community composition, the SIMPER procedure assessed the contribution of each species to the similarity or dissimilarity of treatment groups. In each set of experiments, a small number of conditions or species were responsible for almost all of the similarity seen between

communities. Specifically, in the fall 2006 experiment, once the effect of experimentally inserted species was removed, bare space contributed to most (79-98%) of the initial similarity between communities at every diversity level (Table 5). After 4 weeks, *B. violaceus* contributed up to 23% of the similarity in all diversity treatments except when 4 species were present. By 12 weeks, *C. intestinalis* contributed highly (25-45%) to community similarity at every diversity level, and, by 24 weeks, *C. savignyi* contributed 43-52% to the similarity of the community(Table 5). *Ascidia zara* also played a dominant role, contributing from about 11-23% and about 19-41% to community similarity in weeks 12 and 24, respectively (Table 5). In addition to the four species mentioned above, the following species also were contributed between approximately 3-10% to community similarity at various times: *B. schlosseri*, *S. clava*, sponge spp recruits (a complex of species that were too young to identify) and *Ciona spp*. recruits (a combination of *C. intestinalis* and *C. savignyi*; too young to identify to species) (Table 5). Thus, the majority of the species contributing to similarity in community composition were tunicates, and the same suite of species were important across all diversity treatments.

Once the species that contributed most to community similarity were identified, non-parametric ANOVAs were used to identify the effect of diversity on percent cover of specific species or conditions at each sample time. The percent of bare space was higher than the percent cover of any novel non-indigenous species during the first 12 weeks of the 2006 experiment, likely due to the low density of overall recruitment in the late fall and winter months (Figure 3A). In the first three sampling periods, significant differences were seen in the amount of bare space in a community depending on the diversity of the initial community. The direction of this pattern, however, was not consistent over time.

At 2 weeks, bare space decreased with increasing diversity while at 4 and 12 weeks bare space increased with increased initial diversity (Figure 3A).

Examination of the species that played important roles in community composition showed a variety of responses. The majority of species occupied less substrate in communities with initial diversities that were high. Percent cover of *C. intestinalis* varied widely depending on sampling time. In periods in which there was a significant effect of diversity on *C. intestinalis* coverage (4 and 12 weeks), the species covered less substrate when initial diversities were high (Figure 3B). The percent cover of *Styela clava* was very low at all sample times except 24 weeks. At 24 weeks, *S. clava* also covered less substrate when initial diversity was high (Figure 3 F). Colonial tunicates also played an important role in community assemblage across treatments. *Botrylloides violaceus* consistently occupied less space in communities with high initial diversity. Although this pattern was not significant at 24 weeks, it was significant at all other times (Figure 3 G). *B. schlosseri* covered less space than *B. violaceus*, was present at all sample times and showed significant, negative relationships between percent cover and diversity at 4 and 12 weeks (Figure 3 H).

One group, *Ciona* recruits, occupied more substrate when initial diversity was high (Figure 3 E). The significant effect of initial diversity on the percent cover of Ciona recruits was seen only at 12 weeks, and percent cover of *Ciona* recruits was generally fairly low. Given the timing of adult coverage of both *C. intestinalis* and *C. savignyi* at 12 and 24 weeks, it is likely that the majority of these recruits were *C. savigyni*.

Initial diversity had no effect on the percent cover of the remaining groups of species that were important contributors to community similarity. The percent cover of

both *C. savignyi* and *A. zara* increased from 0 to over 30% after 6 months (Figure 3 C-D). Although both species were important contributors to community similarity, with one exception, the amount of substrate they covered did not vary significantly with different initial diversities (Figure 3 C-D). The recruitment of sponge species (a complex of species that were too young to identify) never contributed more than 2% cover on average and showed no significant differences between diversity treatments at any sample time.

In summary, four species showed a negative relationship between percent cover and initial diversity. Only one group of recruits showed a positive relationship between percent cover and initial diversity. Finally, the percent cover of two species and one species complex were not affected by initial diversity. For most species, when significant differences were found, the difference in percent cover was between the lowest diversity treatments (monocultures or 1 and 2 species) and the rest of the diversity treatments (2, 3 and 4 or 3 and 4 species). The exception to this trend is seen in the *C. intestinalis* results for 2006 where percent cover in diversity treatments 1-3 were the same but differed from the lower percent cover of *C. intestinalis* in communities with an initial diversity of 4.

Community Similarity & Percent Cover – 2007 Experiment

SIMPER analyses of the summer 2007 experiment showed that at every diversity level and every sample time, *C. intestinalis* accounted for the largest proportion of the similarity (~36-92%) seen among communities (Table 6). With respect to other solitary tunicates, *C. savignyi* made moderate contributions to similarity at 2 weeks in the monoculture treatments (Diversity =1 species) and had an increased contribution to

community similarity at 24 weeks in diversity treatments with 2 and 4 species (Table 6). *Ascidia zara* was absent in early sampling periods but contributed about 12-36% to community similarity once the communities were 24 weeks old (Table 6).

Unlike the fall 2006 experiment, colonial tunicates did not play a dominant role in community composition. Upright bryozoans, however, did contribute to community composition in an important way. Both *Bugula neritina* and *B. stolonifera* were among the top contributors to the similarity of communities at 2 weeks in diversity treatments with 1-3 species (Table 6). As time passed, *B. neritina* remained an important contributor but *B. stolonifera* did not. In the highest diversity treatment (4 species), bryozoans were not dominant and did not contribute to community similarity (Table 6). Generally, there were fewer species contributing to community similarity in the treatment with highest initial diversity (4 species; Table 6).

As described for the 2006 experiment, non-parametric ANOVAs were used to identify the effects of diversity on species-specific differences in percent cover at each sample time. The percent cover of bare space was lower in the summer 2007 experiment than in the fall 2006 experiment but increased once the communities reached 24 weeks of age (February, when ambient recruitment was low; Figure 4A). In the summer 2007 experiment, the percent of bare space did not differ between diversity treatments at any time.

Of all of the solitary tunicates that played an important role in community composition in the fall 2006 experiment, *C. intestinalis, C. savignyi* and *A. zara*, also were important in the summer 2007 experiment. Percent cover of *C. intestinalis* varied depending on sampling time. In time periods where a significant difference was found in

C. intestinalis coverage (4 and 12 weeks), the species occupied less substrate when initial diversities were higher (Figure 4B). This negative pattern was seen at all time periods, but the effect of initial diversity on percent cover was not always significant. At all sample periods, the upright bryozoans *B. neritina* and *B. stolonifera* also covered significantly less substrate when initial diversities were higher (Figure 4E-F).

Although most species occupied less space when initial diversity was high, percent cover of *A. zara* showed the opposite pattern. The percent cover of *A. zara* was very low until the 24 week sampling interval, when it reached about 20% coverage and showed a significant increase in coverage with increased initial diversity (Figure 4C).

The effect of initial diversity on percent cover occupied by *Ciona savignyi* varied with sampling interval. At 2 weeks, *C. savignyi* covered significantly less substrate when initial diversities were higher (Figure 4D). However, at 24 weeks the species covered significantly more substrate when initial diversities were high (Figure 4D).

Coverage of sabellid polychaete tubes accounted for less than 5% of substratum space and did not differ with respect to diversity treatment at any time. Unlike the fall 2006 experiment, *S. clava, B. violaceus,* and *B. schlosseri* did not play dominant roles in community composition.

. Similar to the fall 2006 experiment, in the summer 2007 experiment, the majority of species, 4, occupied less substrate in communities with initial diversities that were high. One species was affected by initial diversity in the opposite way. One species showed positive and negative relationships between percent cover and initial diversity. Lastly, the percent cover of one group was not affected by initial diversity. For most species, when significant differences were found, the difference in percent cover was

between the lowest diversity treatments (monocultures or 1 and 2species) and the rest of the diversity treatments (2, 3 and 4 or 3 and 4 species).

Examination of potential species effects driving described community assemblage patterns (as opposed to diversity effects) showed that for the most part, species effects were not significant (Kruskal Wallis 1-way ANOVA). The percent cover of 9 out of 11 species did not show affects due to particular experimental species. There were a two notable exceptions as follows: in the 2006 experiment, the decrease in percent cover of *C. intestinalis* at 12 weeks was the result of a species effect of *S. clava* in the initial diversity combinations (χ^2 = 15.03, DF = 3, p =0.02) and in the 2007 experiment the percent cover of *B. neritina* at 4 and 12 weeks, respectively, was due to the presence of *B. schlosseri* (χ^2 = 17.74, DF = 3, p =0.0014; χ^2 = 15.02, DF = 3, p =0.005). However, this effect did not persist in subsequent sampling periods.

Discussion

Previous studies exploring the diversity resistance hypothesis from theoretical and empirical standpoints have resulted in conflicting conclusions (Fridley et al., 2007). Experimental work in the marine fouling community system also has shown variable results where the success of invading species is either positively or negatively associated with diversity of the recipient community (Stachowicz et al., 2002; Dunstan and Johnson, 2004). The drivers for the conflicting relationships seen are hypothesized to result from resource availability at small spatial scales, and heterogeneity at larger scales. The focus of the present study was to expand our knowledge of the diversity-invasibility

relationship on a small spatial scale by concentrating on resource use, seasonality and time scale.

Diversity

The results here indicate that generally, overall recruitment and community assembly are both affected significantly by diversity regardless of the amount of bare space present. On a short time scale of 2-4 weeks, novel non-indigenous recruitment consistently decreased as diversity of the recipient community increased. This was neither a result of resource limitation in terms of available primary space, nor species effects. This significant, negative relationship was found in both years studied, as recruitment was diminishing in the late fall and during the peak season of ambient recruitment . These results contrast with similar studies of marine fouling communities in which communities of different species richness were monitored or manipulated and where either no relationship was seen between non-native recruitment and community species richness (Stachowicz et al., 2002) or a positive relationship was reported (Dunstan and Johnson, 2004).

The recruitment relationships described in the current study were driven by one or two species, and on a species level there was also an example of a significant positive relationship between recruitment and diversity (e.g., *B. neritina* in Fall 2006). Thus, although an overall negative relationship is predicted from my results, depending on the dominant species recruiting, a positive relationship can sometimes occur.

The results indicated that many individual species did not show significant effects, and the ones that did were not consistent in their influence throughout the year. *Botrylloides violaceus*, for example, recruited in the summer months as well as the fall, but did not show a significant response to diversity in both seasons.

While recruitment patterns provide one indication of the diversity-invasibility relationship, novel species must establish themselves within the community and persist over time in order to be successful. On a longer time scale, the significant negative diversity-invasibility patterns were seen in the community assemblage data for communities between 0-6 months (Table 3). Overall, this relationship was persistent, although the species driving it changed through time.

In both seasons, all of the communities shifted and were dominated by a handful of species. In the fall 2006 experiment, the dominant species were all tunicates while in the summer 2007 experiment, a mix of solitary tunicates and bryozoans occupied most of the primary space. A swamping effect was seen in which dominant species that were recruiting at high densities settled in all of the communities, regardless of diversity level. The negative effects seen were therefore a measure of the negative affect of diversity on density of settlement, as opposed to species presence. For example, although the percent cover of the solitary tunicate *C. intestinalis* decreased significantly with diversity in the 2007 summer experiment, *C. intestinalis* also was an important presence in all of the diversity treatments at the time (Figure 3B, Table 6). While communities looked the same in terms of community composition, the amount of space occupied by novel species decreased with diversity. This outcome then affects how abundant each species is, but does not change which species persists in the community. Accordingly, estimates of the diversity-invasibility relationship that rely on presence/absence information would yield a different result than measurements that incorporate spatial coverage or density. This may contribute to the differences seen across studies and may lead to differences in the interpretation of invasion success. Identifying an invasion as successful due to the

presence of a non-native individual in a community is not necessarily equivalent to a successful invasion that is due to abundance or density. If a novel species is able to persist in a community and reproduce, it could be considered successful whether it was represented at high or low abundance. On a larger spatial scale, these small scale differences in space occupation may become less important, contributing to a similar effect as the proposed variation in resource heterogeneity as scale increases (Davies, 2005).

Open Space

The lack of a resource effect across the study combined with significant effects of diversity does not support the hypothesis that resource limitation is driving the diversity response (Stachowicz et al., 2002). If this were the case, in communities with ample primary space, no diversity effect would be expected. Instead, I saw no differences with respect to resource treatments except for an overall effect in the summer 2007 experiment that was not evident during individual time periods or at different diversity levels (Table 4).

Results from the current experiments and previous observational studies suggest that, unlike fouling communities in other locations (New England: Altman and Whitlatch, 2007; Bodega Bay, California: Stachowicz and Byrnes, 2006), the fouling communities in San Francisco Bay may have more fluctuations in limitation of primary spatial resources. Unpublished temporal data from San Francisco communities suggest that these communities are not saturated in terms of space (Ruiz, pers. comm.; Jewett, unpublished data). Panels that were deployed in quarterly intervals at five locations within the bay show a seasonal pattern of space availability where mean bare space fluctuated from 15%

to 40% across sites (Jewett et al., in prep.). In this survey, peak space availability was seen in communities deployed during the summer (May-August; 20-40% bare space) and winter (November-February; 32% bare space). In communities with varying exposure time in the water column, the average bare space was consistently ~20% in communities in San Francisco Bay regardless of the length of time the communities were allowed to develop (3,6,9,12,15, 18, 30 months; Jewett et al., in prep.). This suggests that communities are not saturated, even after two and a half years. As a result, primary space may have been limited only when initial resource levels were established in experimental treatments.

Despite the perception that most fouling communities are space limited, abundant primary space may be more common than has been previously thought. Studies exploring the impact of dissolved oxygen on NIS and native species in Chesapeake Bay fouling communities also showed high fluctuations in open space due to barnacle mortality (Jewett, 2005). Recent survey work by Grey (2009) suggests that fouling communities in Puget Sound are not space limited. In a nested spatial and temporal survey, space availability increased with native species richness at local scales of 0.0576 m^2 (Grey, 2009). In fact, in addition to an increase in open space in more diverse communities, Grey (2006) observed a decrease in non-native species cover, a similar result to what was found in the present study.

Diversity x Open Space

Possible explanations for significant negative diversity-invasibility relationships coupled with ample primary space include an increased complexity in settlement landscape in high diversity communities. As community diversity increases, and multiple

species are present, those species provide an increase in the physical complexity of the landscape. Larvae then need to navigate through this more complex landscape to settle on bare substrate in the system. Having multiple types of species present may change the flow regime in the community, as well as the distance larvae need to travel to reach primary space (Koehl and Hadfield, 2010). In addition, individual species are known to facilitate or inhibit settlement of other species (Lages et al., 2010; Grosberg, 1981). Having more species present may change the perceived quality of primary space on a species-specific basis and simultaneously provide secondary settlement substrate. This could lead to a dynamic in which there is an advantage to settling on primary substrate versus secondary substrate depending on community diversity and species identity. The role of secondary space will be addressed further in the subsequent chapter of this dissertation.

Finally, while the adult species used in the experiments were all filter or suspension feeders, having a more complex landscape of adults in the community may also result in higher and more complicated predation risk to larvae entering the community. A combination of multiple species may make a more complex settlement field with complex patterns of micro-turbulance, and thus pose a higher consumption threat. As most of the differences seen in the community composition data show that monocultures often have a different community signature than higher diversity treatments, this explanation seems plausible (Figure 2, 3; Table 4). Increasing the diversity from 1 to 2 or 2 to 3 species can have a strong effect on the magnitude of space occupation by a given species. The role of community productivity, competitive ability

(specifically in terms of feeding) and facilitative and inhibitive effects also may be important.

Another possible explanation for why no resource effect was seen is that the effect is not cumulative, but is seen only on an individual basis or for certain combinations of species. Multiple facilitative interactions coupled with inhibitive interactions between species would result in no overall, cumulative effect**.**

Conclusions

In terms of the diversity-invasibility debate, this study adds to the growing literature that provides evidence of a negative relationship at small spatial scales (Grey, 2009; Fargione and Tilman, 2005). My data suggest that this negative relationship can be found at multiple time scales, but is more complex than anticipated. I found that as communities age, the negative diversity-invasibility relationship persisted when percent cover of novel species was treated as the dependent variable. However, dominant species were found in all communities regardless of initial diversity. This suggests that diverse communities may be less susceptible to invasion success in terms of invader abundance, but not in terms of invader presence. This has broad implications with respect to management of the spread of invasive species, as it implies that competitively dominant species may be able to invade diverse communities at low densities, despite diversity resistance.

This study does not support the hypothesis that the decrease in invasion success in high diversity communities relates to low resource availability in the fouling community. Instead, significant negative relationships between recruitment density and initial species diversity and between percent cover and initial species diversity persisted in treatments

and communities that had ample settlement space. These results suggest that the marine fouling communities in San Francisco Bay are not limited by spatial resources, at least in terms of primary space. This may mean that resource limitation is more complicated and involves the influence of secondary substrate. The influence of secondary substrate is tied to the particular species that make up the community, and may mean that species-specific effects play a larger role in diversity-invasibility relationships than previously examined. On a broader level, this result highlights the importance of identifying the most influential resources in a community, and being aware of the resource complexity on multiple levels.

Tables & Figures

Table 1. Species combinations used in experiments. Each combination was replicated 4 times for the low resource treatment (0% bare space) and 4 times for the high diversity treatment (25% bare space).

Year	Diversity Treatment	Combination	Species
2006	1	A	*Styela clava*
	1	B	*Bugula stolonifera*
	1	C	*Clathria prolifera*
	1	D	*Botryllus schlosseri*
	2	A, B	*S.clava, B. stolonifera*
	2	C, D	*C. prolifera, B. schlosseri*
	2	A, D	*S. clava, B. schlosseri*
	2	B, C	*B. stolonifera, C. prolifera*
	3	A, C, D	*A clava, C. prolifera, B.schlosseri*
	3	B, C, D	*B. stolonifera, C. prolifera, B.schlosseri*
	3	A, B, C	*S. clava, B. stolonifera, C. prolifera*
	3	A, B, D	*S. clava, B. stolonifera, B. schlosseri*
	4	A, B, C, D	*S. clava, B. stolonifera, C. prolifera, B. schlosseri*
2007	1	A	*Styela clava*
	1	B	*Bugula neritina*
	1	C	*Clathria prolifera*
	1	D	*Botryllus schlosseri*
	1	E	*Ciona savignyi*
	2	B, D	*B. neritina, B. schlosseri*
	2	A, E	*S. clava, C. savignyi*
	2	C, D	*C. prolifera, B. schlosseri*
	2	A, B	*S. clava, B. neritina*
	3	B, C, E	*B. neritina, C. prolifera, C. savignyi*
	3	A, D, E	*S. clava, C. savignyi, B. schlosseri*
	3	A, B, C	*S. clava, B. neritina, C. prolifera*
	3	B, D, E	*B. neritina, C. savignyi, B. schlosseri*
	4	A, B, C, E	*S. clava, B. neritina, C. prolifera, C. savignyi*

Table 2. Results from regressions run on recruitment density data. Regression models used diversity, resource and their interaction as fixed effects. Recruitment density was measured cumulatively over 2 week periods during the first month of each experiment. In all cases, where a significant relationship was identified (bold p value), the relationship was due to a significant effect of diversity on recruitment. There was no evidence of resource effects or interactions.

Year	Sample Time	Dependent Variable	DF	F	P	R^2
Fall 2006	2 weeks	Novel NIS	3	5.23	**0.0021**	0.136
		Community Species Richness	3	4.04	**0.0093**	0.1087
		Botrylloides violaceus	3	27.98	**<0.0001**	0.456
		Bugula neritina	3	3.48	**0.0187**	0.0946
	4 weeks	Novel NIS	3	4.62	**0.005**	0.123
		Community Species Richness	3	0.43	0.7311	
		Botrylloides violaceus	3	12.64	**<0.0001**	0.277
		Bugula neritina	3	1.34	0.2669	
Summer 2007	2 weeks	Novel NIS	3	7.23	**0.0002**	0.1685
		Community Species Richness	3	7.75	**<0.0001**	0.1785
		Ciona intestinalis	3	3.17	**0.0273**	0.0816
		Bugula stolonifera	3	4.05	**0.008**	0.1043
	4 weeks	Novel NIS	3	1.35	0.2631	
		Community Species Richness	3	0.67	0.5737	
		Ciona intestinalis	3	0.57	0.6375	
		Bugula stolonifera	3	0.42	0.7388	

Table 3. Results of the two-way crossed analysis of similarities (ANOSIM) examining sample time and resource availability for the Fall 2006 and Summer 2007 experiments. Diversity level, indicated by number in the first and sixth columns, refers to initial community diversity. Significant p-values, in bold, refer to time periods in which communities were significantly different from one another in terms of species abundance. The Bonferroni corrected α=0.0083.

Fall 2006					Summer 2007				
Diversity Level	Factor		R	P	Diversity Level	Factor		R	P
1	Time	*Global ANOSIM*	0.690	**0.001**	1	Time	*Global ANOSIM*	0.17	**0.001**
		2 wks:4 wks	0.319	**0.001**			2 wks:4 wks	0.169	**0.001**
		2 wks:12 wks	0.909	**0.001**			2 wks:12 wks	0.225	**0.001**
		2 wks:24 wks	0.975	**0.001**			2 wks:24 wks	0.127	**0.001**
		4 wks:12 wks	0.539	**0.001**			4 wks:12 wks	0.047	0.032
		4 wks:24 wks	0.876	**0.001**			4 wks:24 wks	0.268	**0.001**
		12 wks:24 wks	0.784	**0.001**			12 wks:24 wks	0.21	**0.001**
	Resource	*Global ANOSIM*	-0.015	0.786		Resource	*Global ANOSIM*	0.025	0.061
2	Time	*Global ANOSIM*	0.714	**0.001**	2	Time	*Global ANOSIM*	0.354	**0.001**
		2 wks:4 wks	0.237	**0.001**			2 wks:4 wks	0.286	**0.001**
		2 wks:12 wks	0.928	**0.001**			2 wks:12 wks	0.31	**0.001**
		2 wks:24 wks	0.980	**0.001**			2 wks:24 wks	0.535	**0.001**
		4 wks:12 wks	0.614	**0.001**			4 wks:12 wks	0.063	0.01
		4 wks:24 wks	0.911	**0.001**			4 wks:24 wks	0.67	**0.001**
		12 wks:24 wks	0.870	**0.001**			12 wks:24 wks	0.377	**0.001**
	Resource	*Global ANOSIM*	0.025	0.096		Resource	*Global ANOSIM*	-0.014	0.757

3	Time	*Global ANOSIM*	0.700	**0.001**	3	Time	*Global ANOSIM*	0.253	**0.001**
		2 wks:4 wks	0.089	**0.005**			2 wks:4 wks	0.092	0.013
		2 wks:12 wks	0.907	**0.001**			2 wks:12 wks	0.208	**0.001**
		2 wks:24 wks	0.978	**0.001**			2 wks:24 wks	0.412	**0.001**
		4 wks:12 wks	0.712	**0.001**			4 wks:12 wks	0.09	**0.004**
		4 wks:24 wks	0.958	**0.001**			4 wks:24 wks	0.478	**0.001**
		12 wks:24 wks	0.869	**0.001**			12 wks:24 wks	0.343	**0.001**
	Resource	*Global ANOSIM*	-0.004	0.530		Resource	*Global ANOSIM*	0.027	0.096
4	Time	*Global ANOSIM*	0.768	**0.001**	4	Time	*Global ANOSIM*	0.342	**0.001**
		2 wks:4 wks	0.154	0.135			2 wks:4 wks	0.128	0.155
		2 wks:12 wks	0.828	**0.001**			2 wks:12 wks	0.289	0.024
		2 wks:24 wks	1.000	**0.002**			2 wks:24 wks	0.615	**0.004**
		4 wks:12 wks	0.813	**0.001**			4 wks:12 wks	0.083	0.224
		4 wks:24 wks	1.000	**0.002**			4 wks:24 wks	0.651	0.03
		12 wks:24 wks	0.964	**0.001**			12 wks:24 wks	0.391	0.019
	Resource	*Global ANOSIM*	-0.012	0.540		Resource	*Global ANOSIM*	0.07	0.219

Table 4. Results of the two-way crossed analysis of similarities (ANOSIM) examining diversity and resource treatments for the fall 2006 and summer 2007 experiments. Pairs of numbers in the third and eighth columns refer to the initial diversity of communities being compared. Significant p-values, in bold, refer to significant differences in species abundance between pairs of diversity treatments. The Bonferroni corrected α=0.0083.

Fall 2006					Summer 2007				
Time	**Factor**		**R**	**P**	**Time**	**Factor**		**R**	**P**
Overall	Diversity	*Global ANOSIM*	0.032	**0.002**	overall	Diversity	*Global ANOSIM*	0.023	**0.013**
		1:2	-0.008	0.943			1:2	0.027	**0.003**
		1:3	0.041	**0.001**			1:3	0.047	**0.002**
		1:4	0.075	0.045			1:4	0.02	0.366
		2:3	0.043	**0.001**			2:3	0.016	**0.026**
		2:4	0.091	**0.003**			2:4	-0.012	0.59
		3:4	0.017	0.298			3:4	-0.056	0.857
	Resource	*Global ANOSIM*	-0.006	0.841		Resource	*Global ANOSIM*	0.009	**0.041**
2 weeks	Diversity	*Global ANOSIM*	0.109	**0.001**	2 weeks	Diversity	*Global ANOSIM*	0.034	0.09
		1:2	-0.002	0.477					
		1:3	0.125	**0.002**		Resource	*Global ANOSIM*	0.019	0.17
		1:4	0.178	0.082					
		2:3	0.191	**0.001**					
		2:4	0.162	0.111					
		3:4	0.062	0.288					

	Resource	*Global ANOSIM*	-0.009	0.665					
4 weeks	Diversity	*Global ANOSIM*	0.175	**0.001**	4 weeks	Diversity	*Global ANOSIM*	0.052	**0.033**
		1:2	0.017	0.217			1:2	0.04	0.058
		1:3	0.293	**0.001**			1:3	0.065	**0.025**
		1:4	0.339	**0.001**			1:4	0.1	0.192
		2:3	0.224	**0.001**			2:3	0.041	0.063
		2:4	0.305	**0.007**			2:4	0.135	0.126
		3:4	-0.188	0.985			3:4	-0.045	0.633
	Resource	*Global ANOSIM*	0.019	0.187		Resource	*Global ANOSIM*	0.016	0.18
12 weeks	Diversity	*Global ANOSIM*	0.173	**0.001**	12 weeks	Diversity	*Global ANOSIM*	0.041	0.057
		1:2	0.022	0.191					
		1:3	0.157	**0.001**		Resource	*Global ANOSIM*	-0.014	0.798
		1:4	0.457	**0.001**					
		2:3	0.149	**0.001**					
		2:4	0.532	**0.001**					
		3:4	0.321	**0.006**					
	Resource	*Global ANOSIM*	0.035	0.071					
24 weeks	Diversity	*Global ANOSIM*	-0.028	0.862	24 weeks	Time	*Global ANOSIM*	0.071	**0.04**
							1:2	0.125	**0.01**

Resource	*Global ANOSIM*	-0.038	0.986		1:3	0.106	0.06
					1:4	0.098	0.175
					2:3	0.04	0.072
					2:4	-0.159	0.916
					3:4	-0.185	0.975
				Resource	*Global ANOSIM*	0.03	0.088

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Table 5. SIMPER (similarity percentage) results from the fall 2006 experiment showing which species made the greatest contribution to the similarity within each diversity treatment (1-4 species) over time. The first column, labeled diversity, refers to the number of species in the intial community. Note that average abundance corresponds to Bray-Curtis similarity matrix and should not be interpreted as percent cover.

Diversity	Time	Species	Average Abundance	Average Similarity	Average Similarity/SD	Contribution (%)
1						
	2 Weeks			77.14		
		Bare	9.29	65.39	5.67	84.78
		Botrylloides violaceus	2.39	10.23	1.12	13.26
						Total 98.04
	4 Weeks			64.52		
		Bare	7.86	38.95	3.97	60.37
		Botrylloides violaceus	3.54	14.52	1.91	22.51
		Botryllus schlosseri	1.69	3.48	0.66	5.4
		Ciona intestinalis	1.35	3.35	0.67	5.19
						Total 93.46
	12 Weeks			65.18		
		Ciona intestinalis	5.71	22.36	2.6	34.31
		Bare	4.32	14.53	1.75	22.29
		Botrylloides violaceus	3.56	13.64	2.77	20.93
		Ascidia zara	3.43	9.88	1.33	15.15
						Total 92.68
	24 Weeks			52.65		
		Ciona savignyi	5.76	23.54	1.53	44.72
		Ascidia zara	5.19	19.44	1.63	36.93
		Styela clava	1.78	3.41	0.5	6.47
		Botrylloides violaceus	1.45	2.26	0.54	4.3
						Total 92.41
2						
	2 Weeks			75.05		
		Bare	9.03	59.39	5.89	79.13
		Botrylloides violaceus	2.6	12.41	1.27	16.54
						Total 95.67
	4 Weeks			64.39		
		Bare	7.98	39.22	2.94	60.91
		Botrylloides violaceus	3.43	14.45	2.23	22.44
		Ciona intestinalis	1.6	3.89	0.7	6.04
		Botryllus schlosseri	1.33	2.69	0.55	4.18

					Total 93.56
	12 Weeks		68.06		
		Ciona intestinalis	5.46	21.53	4.16	31.64
		Bare	4.51	16.11	2.32	23.67
		Ascidia zara	3.82	13.05	1.98	19.17
		Botrylloides violaceus	3.42	11.41	1.62	16.76
						Total 91.24
	24 Weeks		56.12		
		Ciona savignyi	5.9	23.86	2	42.51
		Ascidia zara	4.81	19.17	3.15	34.15
		Styela clava	2.44	5.75	0.72	10.24
		Botrylloides violaceus	1.83	2.94	0.57	5.24
						Total 92.15
3						
	2 Weeks		77.48		
		Bare	9.57	74.25	7.44	95.84
						Total 95.84
	4 Weeks		68.16		
		Bare	9.18	59.67	4.52	87.54
		Botrylloides violaceus	1.29	3.62	0.61	5.3
						Total 92.85
	12 Weeks		66.81		
		Bare	6.15	25.08	3.68	37.53
		Ciona intestinalis	5.24	20.16	3.49	30.17
		Ascidia zara	2.89	7.64	1.18	11.43
		Botrylloides violaceus	2.24	6.74	1.35	10.09
		***Ciona* recruit**	1.47	3.47	0.77	5.19
						Total 94.41
	24 Weeks		56.03		
		Ciona savignyi	6.23	24.93	1.53	44.5
		Ascidia zara	5.07	21.13	2.97	37.72
		Botrylloides violaceus	1.28	2.17	0.61	3.88
		Bare	1.45	1.94	0.52	3.46
		Styela clava	1.15	1.9	0.5	3.38
						Total 92.95
4						
	2 Weeks		78.89		
		Bare	9.37	69.74	3.6	88.41

	Botryllus schlosseri	1.49	4.17	0.55	5.28 Total 93.69
4 Weeks			79.92		
	Bare	9.72	78.88	8.6	98.69 Total 98.69
12 Weeks			60.17		
	Bare	6.56	24.61	1.59	40.9
	Ciona intestinalis	3.69	14.73	2.82	24.48
	Ascidia zara	3.67	13.72	2.51	22.79
	Sponge spp.	1.15	3.99	0.9	6.63 Total 94.80
24 Weeks			68.81		
	Ciona savignyi	7.12	35.68	3.62	51.85
	Ascidia zara	5.93	28.09	4.33	40.83 Total 92.68

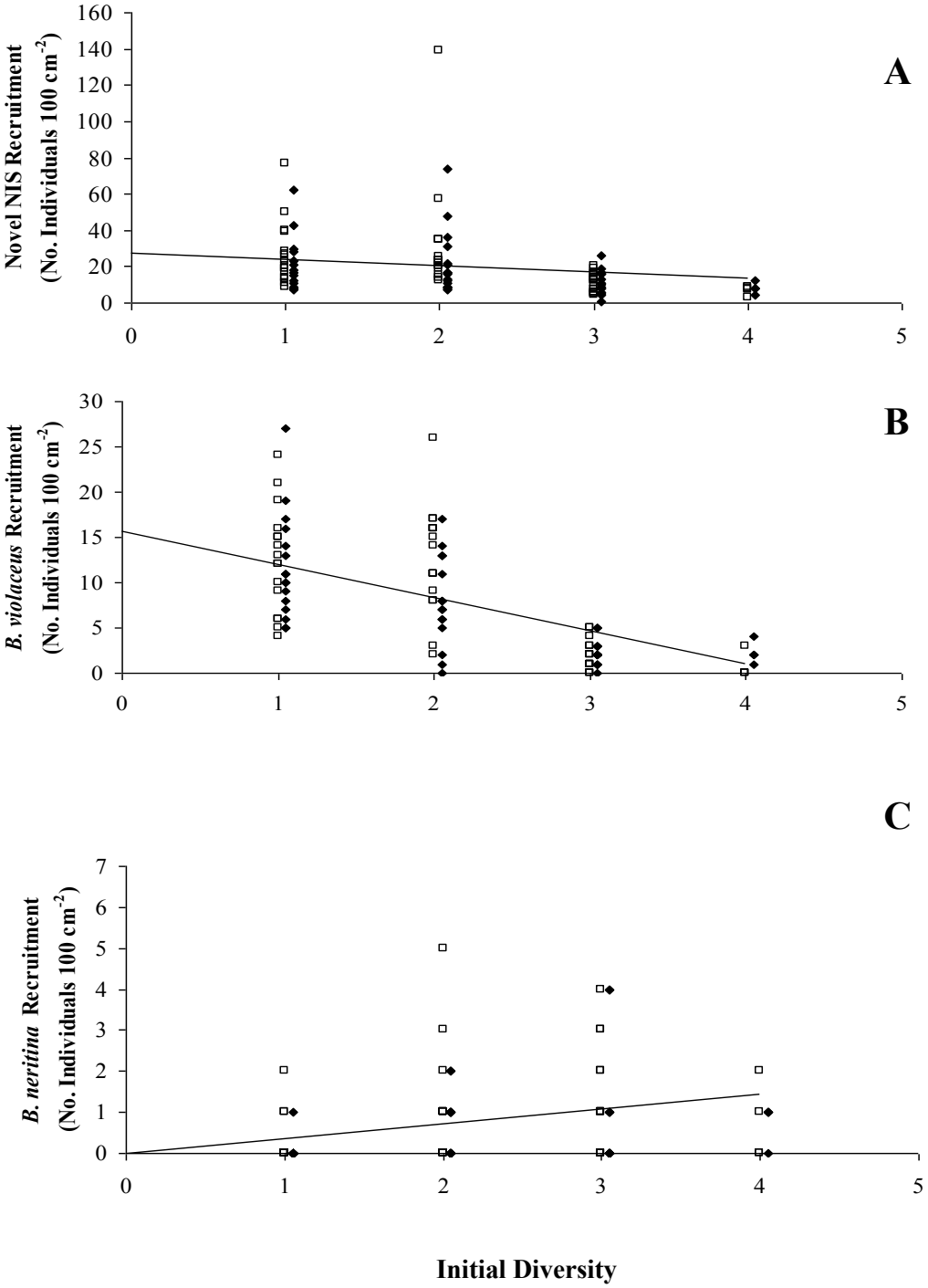
Table 6. SIMPER (similarity percentage) results from the Summer 2007 experiment showing which species made the greatest contribution to the similarity within each diversity treatment (1-4 species) over time. The first column, labeled diversity, refers to the number of species in the intial community. Note that average abundance corresponds to Bray-Curtis similarity matrix and should not be interpreted as percent cover.

Diversity	Time	Species	Average Abundance	Average Similarity	Average Similarity/SD	Contribution (%)
1						
	2 Weeks			45.05		
		Ciona intestinalis	5.76	22.41	1.16	49.74
		Bugula stolonifera	2.74	7.42	0.84	16.48
		Bugula neritina	2.5	6.61	0.89	14.66
		Bare	2.18	3.71	0.55	8.24
		Ciona savignyi	1.18	1.57	0.33	3.48
						Total 92.6
	4 Weeks			65.16		
		Ciona intestinalis	8.49	54.19	2.38	83.16
		Bugula neritina	2.74	7.94	0.81	12.19
						Total 93.35
	12 Weeks			63.08		
		Ciona intestinalis	8.47	50.12	2.16	79.45
		Bugula neritina	2.04	4.26	0.6	6.75
		Sabellid Polychaete Tube	1.52	4.1	0.66	6.5
						Total 92.69
	24 Weeks			50.37		
		Ciona intestinalis	5.95	21.1	1.33	41.88
		Bare	3.55	10	1.3	19.85
		Bugula neritina	2.75	7.83	1.26	15.54
		Ascidia zara	2.55	6.01	1.09	11.93
		Ciona savignyi	0.99	1.21	0.46	2.41
						Total 91.61
2						
	2 Weeks			58.26		
		Ciona intestinalis	7.51	38.6	2.74	66.26
		Bugula stolonifera	2.23	6.47	0.8	11.11
		Bugula neritina	2.23	5.43	0.7	9.31
		Bare	2.2	4.37	0.53	7.5
						Total 94.18
	4 Weeks			74.57		
		Ciona intestinalis	9.36	68.68	4.9	92.11

					Total 92.11
	12 Weeks		64.62		
		Ciona intestinalis	8.72	52.84	2.7	81.77
		Bare	1.65	4.36	0.8	6.74
		Sabellid Polychaete Tube	1.46	3.31	0.59	5.12
						Total 93.63
	24 Weeks		54.9		
		Ciona intestinalis	5.72	19.74	1.81	35.95
		Ascidia zara	4.42	14.37	1.84	26.18
		Bare	2.98	7.84	1.17	14.29
		Ciona savignyi	2.14	5.53	0.99	10.06
		Sabellid Polychaete Tube	1.24	2.2	0.54	4.01
						Total 90.49
3						
	2 Weeks		55.29		
		Ciona intestinalis	7.41	41.03	1.97	74.22
		Bare	3.07	7.8	0.69	14.11
		Bugula stolonifera	1.87	3.14	0.4	5.68
						Total 94.01
	4 Weeks		64.66		
		Ciona intestinalis	8.65	57.69	2.43	89.21
		Bugula neritina	1.44	2.35	0.43	3.63
						Total 92.84
	12 Weeks		62.21		
		Ciona intestinalis	8.29	45.1	2.93	72.49
		Sabellid Polychaete Tube	2.54	8.07	0.92	12.97
		Bare	2.15	5.75	0.82	9.24
						Total 94.7
	24 Weeks		48.45		
		Ciona intestinalis	5.28	17.07	1.43	35.22
		Ascidia zara	3.78	11.17	1.27	23.06
		Bare	3.54	10.71	1.18	22.11
		Filamentous Diatom	1.41	2.26	0.55	4.67
		Sabellid Polychaete Tube	1.28	1.73	0.39	3.56
		Bugula neritina	1.13	1.35	0.32	2.79

					Total 91.41
4					
	2 Weeks		52.04		
		Ciona intestinalis	7.67	45.61	1.41	87.63
		Bare	1.81	2.87	0.29	5.51
						Total 93.14
	4 Weeks		72.05		
		Ciona intestinalis	8.94	60.98	3.37	84.64
		Bare	2	7.3	0.94	10.13
						Total 94.77
	12 Weeks		67.94		
		Ciona intestinalis	8.64	48.04	5.11	70.72
		Bare	2.83	9.44	1.46	13.9
		Ascidia zara	1.55	4.9	0.96	7.22
						Total 91.83
	24 Weeks		62.63		
		Ciona intestinalis	6.28	25.23	2.46	40.27
		Ascidia zara	5.33	20.82	2.99	33.24
		Bare	2.73	8.63	1.56	13.77
		Ciona savignyi	2.07	4.49	0.92	7.17
						Total 94.45

Figure 1. Recruitment of novel non-indigenous species (A), *B. violaceus* (B), and *B. neritina* (C) into experimental communities after 2 weeks in the fall 2006 experiment. Panel D refers to species richness in experimental communities during the same time period. Open squares represent low resource treatments and closed diamonds represent high resource treatments. Lines represent significant regression equations.



D

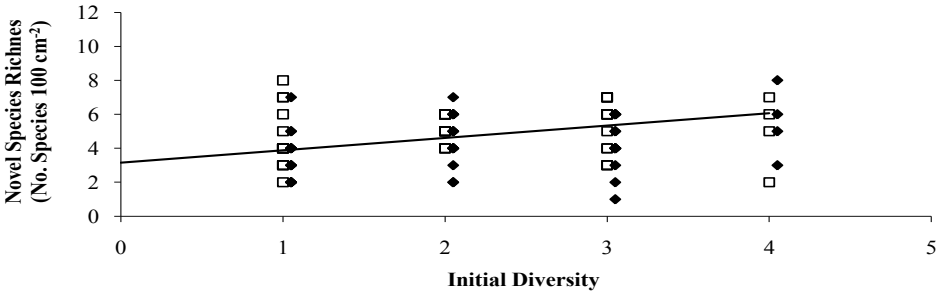
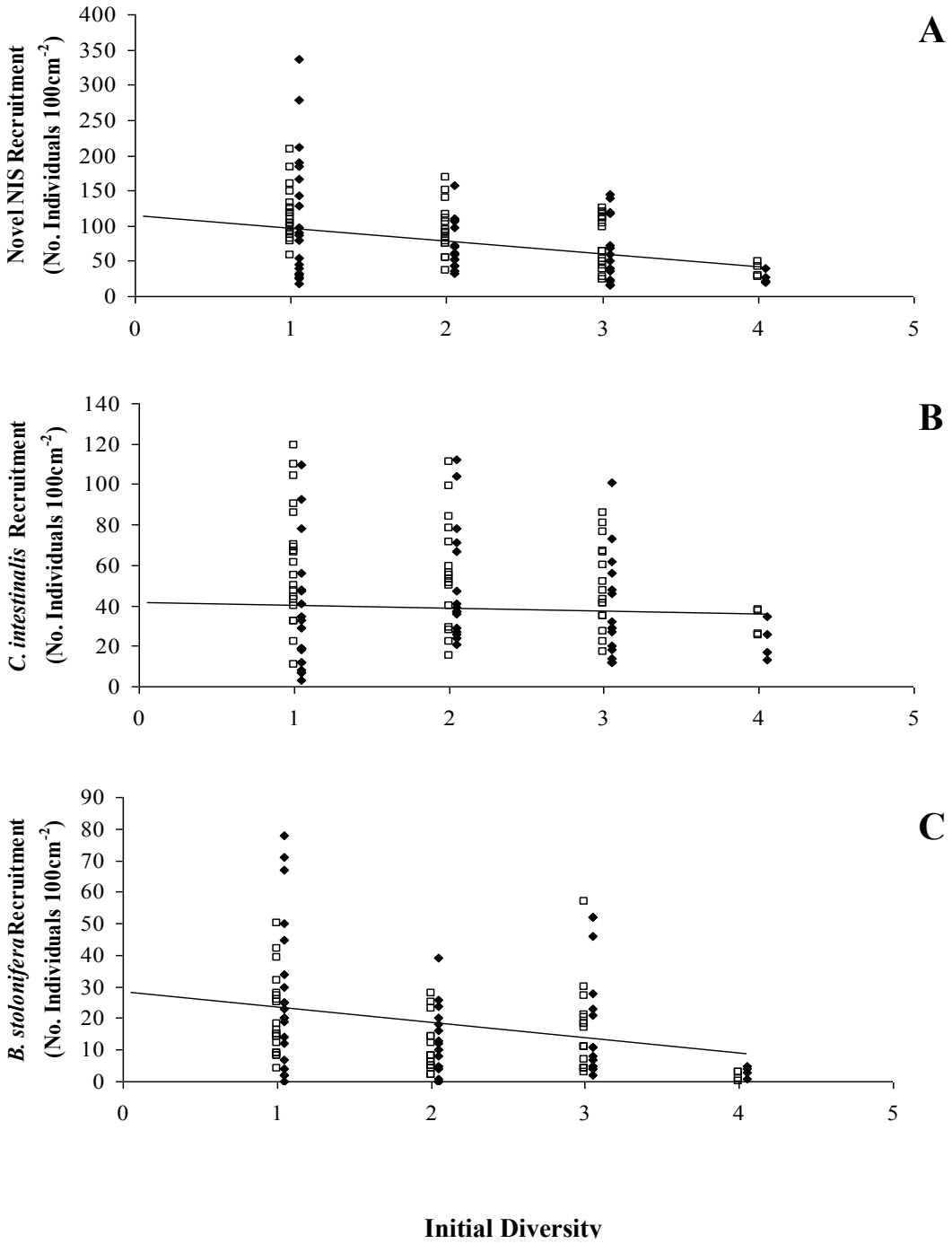

Novel Species Richnes
(No. Species 100 cm-2)
12
10
8
6
4
2
0
0
1
2
3
4
5
Initial Diversity

Figure 2. Recruitment of novel non-indigenous species (A), *C. intestinalis* (B), and *B. stolonifera* (C) into experimental communities after 2 weeks in the summer 2007 experiment. Panel D refers to species richness in experimental communities during the same time period. Open squares represent low resource treatments and closed diamonds represent high resource treatments Lines represent significant regression equations.



D

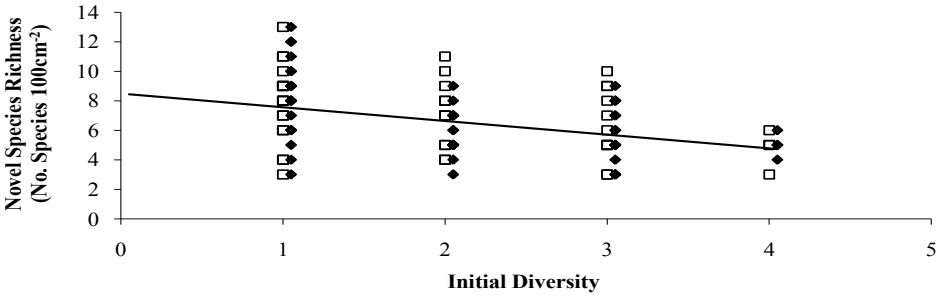
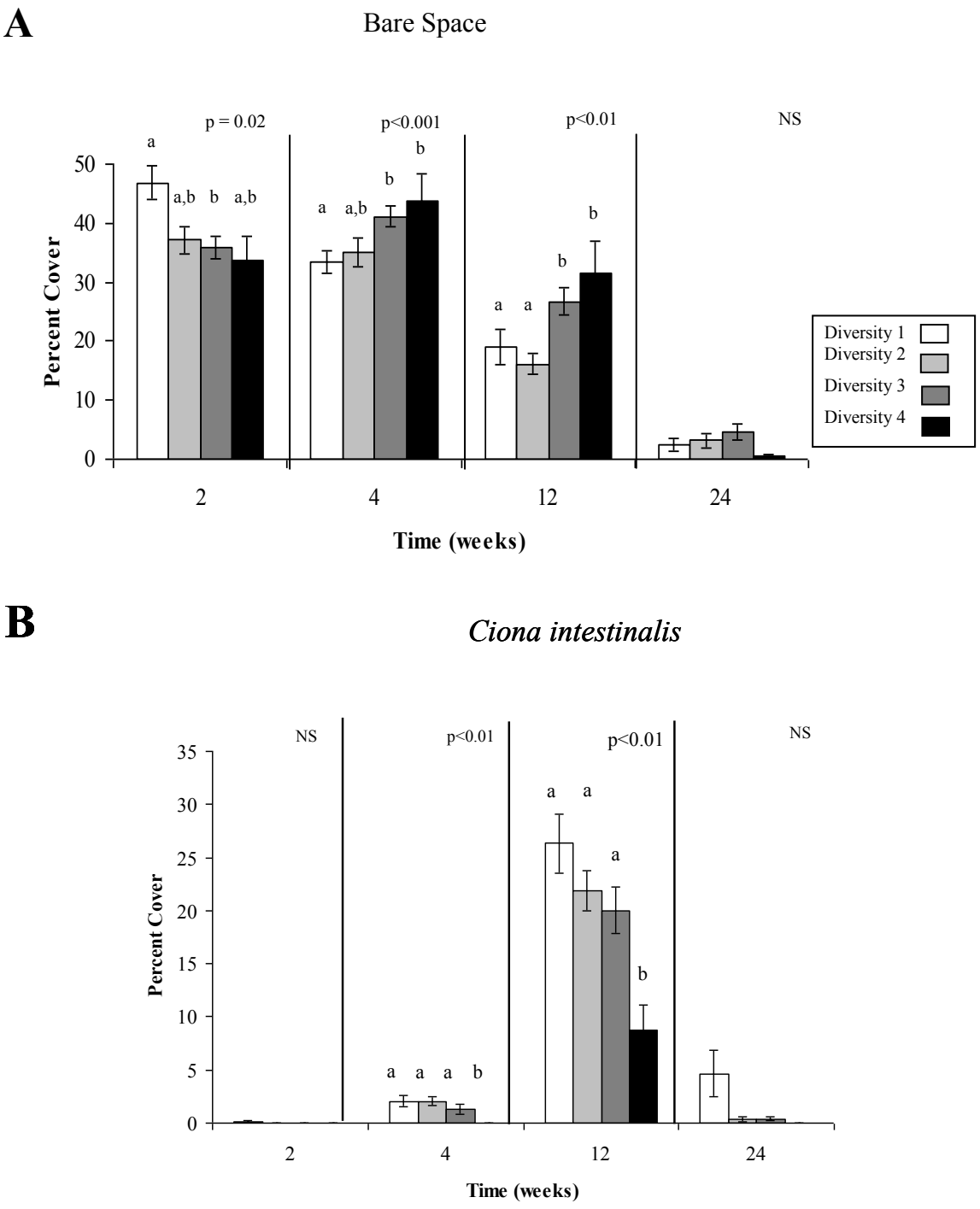
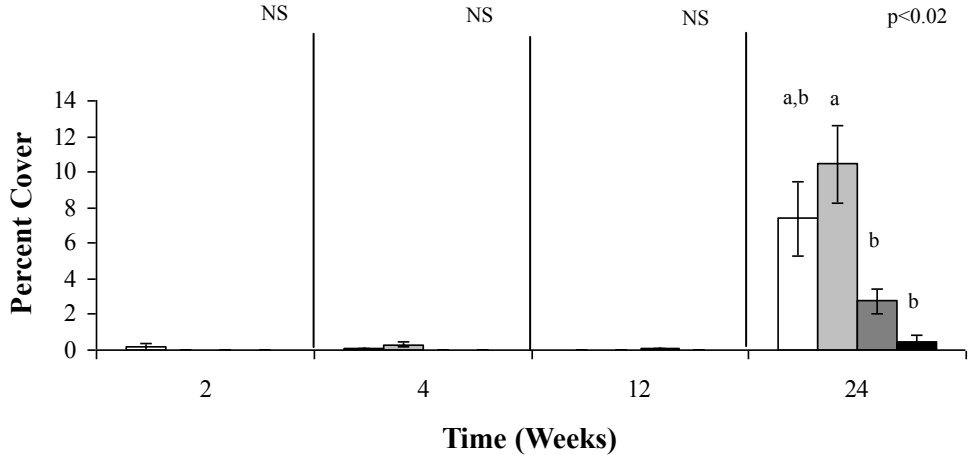

Novel Species Richness
(No. Species 100cm-2)
14
12
10
8
6
4
2
0
0
1
2
3
4
5
Initial Diversity

Figure 3. Change in community abundance through time in the fall 2006 experiment**.** Abundance is presented as percent cover of bare space (A), *C. intestinalis* (B), *S. clava* (C), *B. violaceus* (D), *B. schlosseri* (E), *Ciona spp.* recruits (F), *C. savignyi* (G), and *A. zara* (H). Each species is displayed through time and by diversity treatment. ANOVA analyses were run for each sampling time. Error bars = +/- 1 SE of the mean, NS = non significant ANOVA.



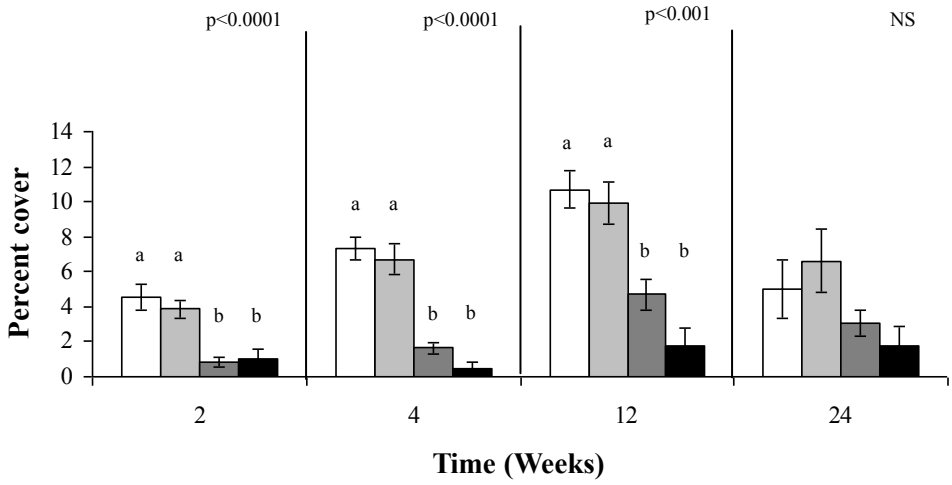
C

Styela clava



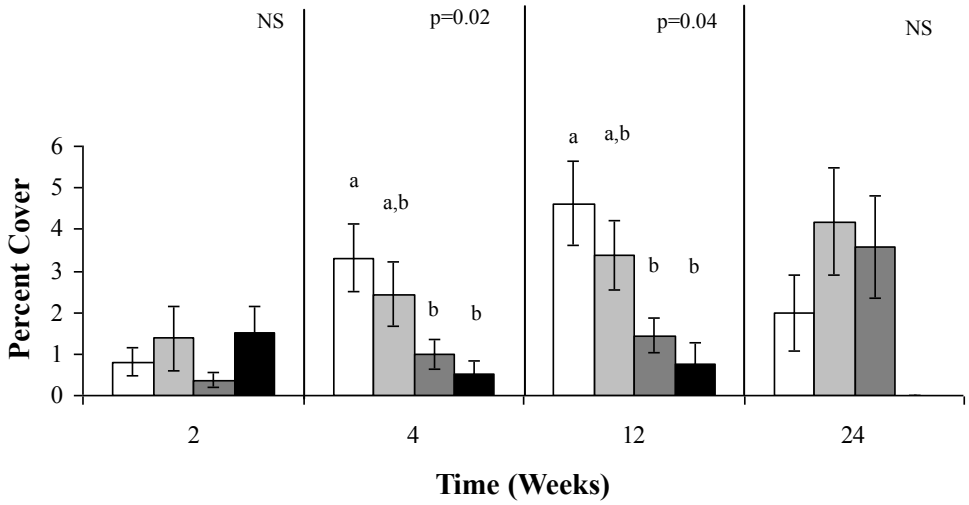
D

Botrylloides violaceus



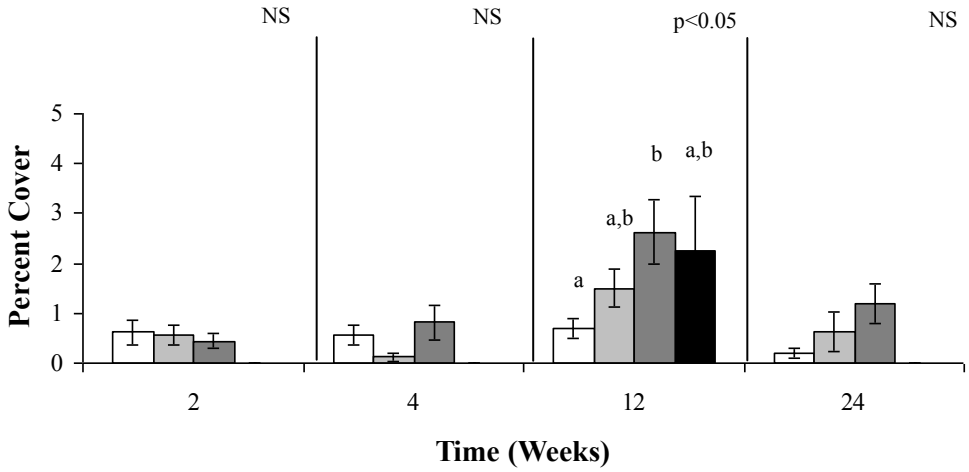
E

Botryllus schlosseri



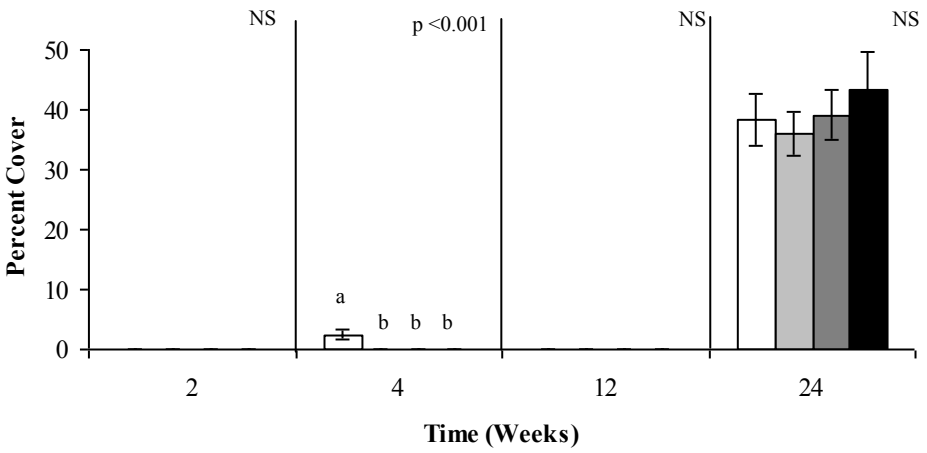
F

Ciona spp. recruit



G

Ciona savignyi



Ascidia zara

H

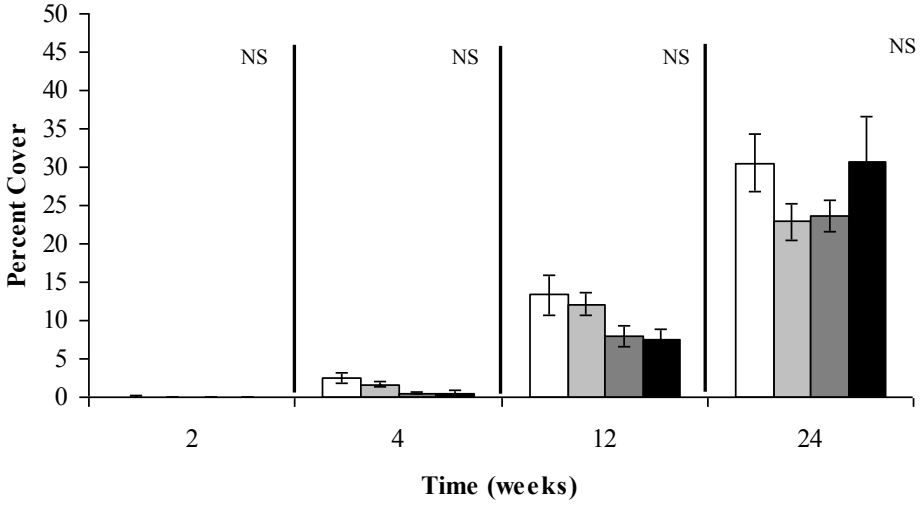
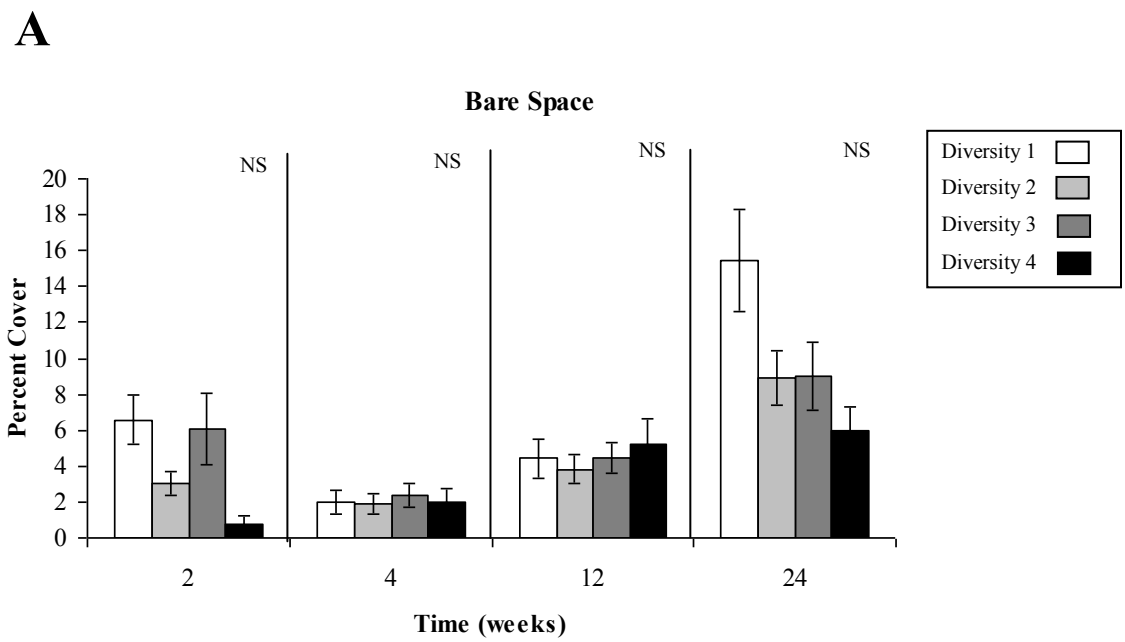
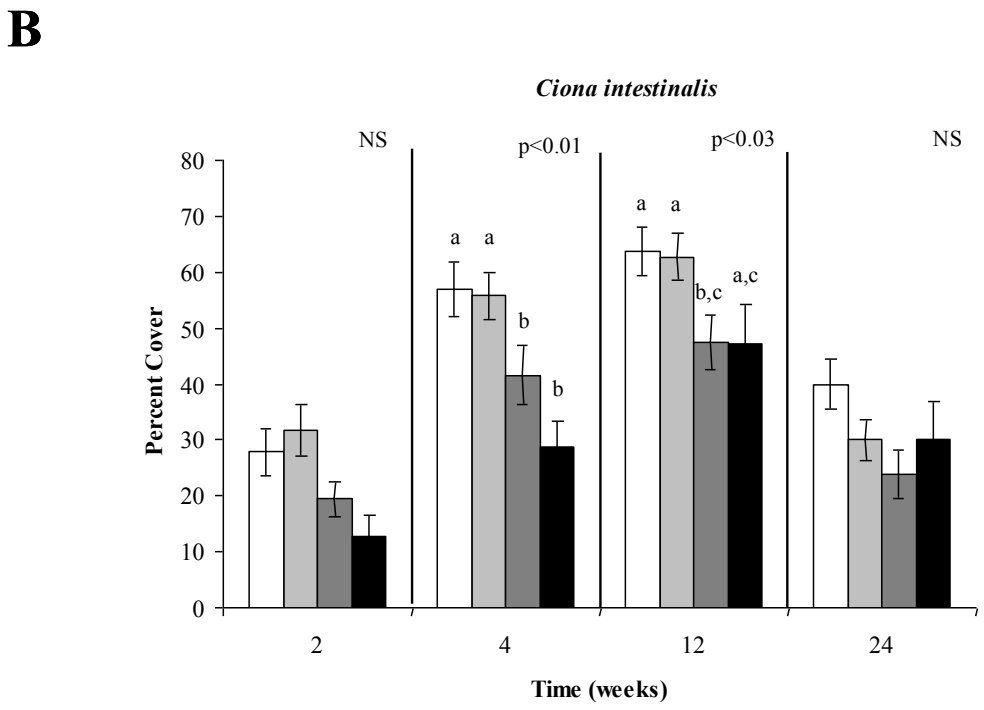
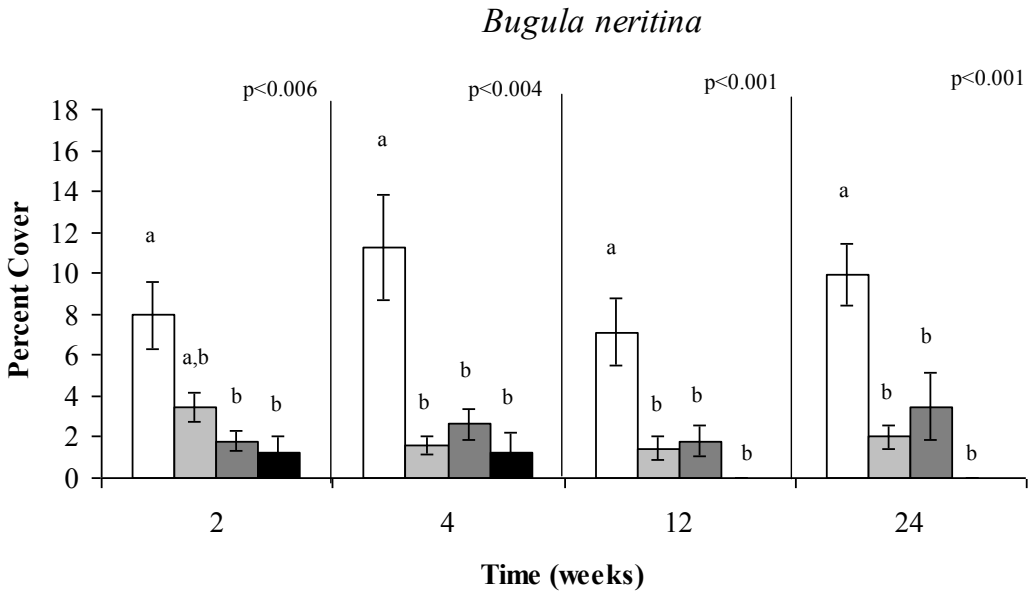


Figure 4. Change in community abundance through time in the summer 2007 experiment**.** Abundance is presented as percent cover of bare space (A), *C. intestinalis* (B), *B. neritina* (C), *B. stolonifera* (D), *A. zara* (E), and *C. savignyi* (F). Each species is displayed through time and by diversity treatment. ANOVA analyses were run for each sampling time. Error bars = +/- 1 SE of the mean, NS = non significant ANOVA.

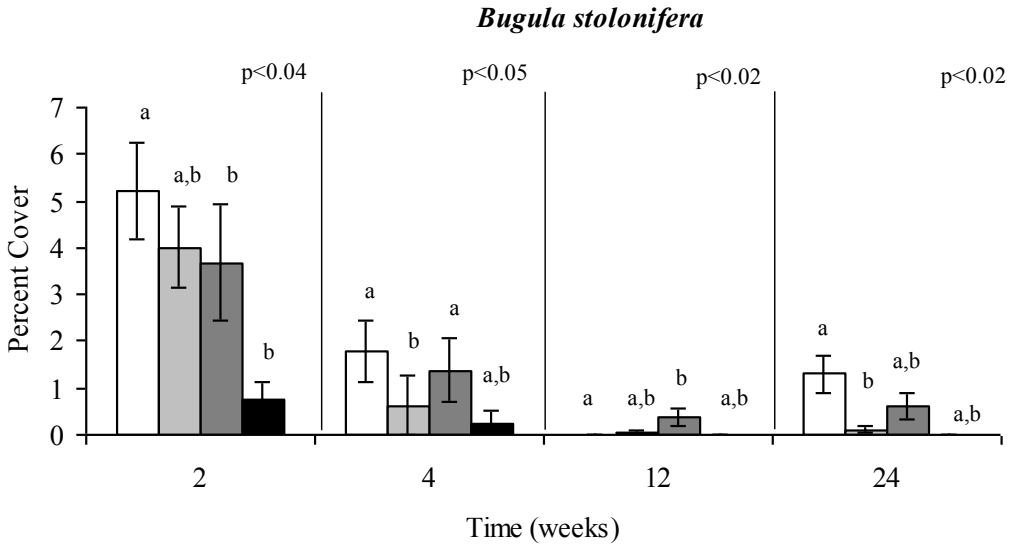




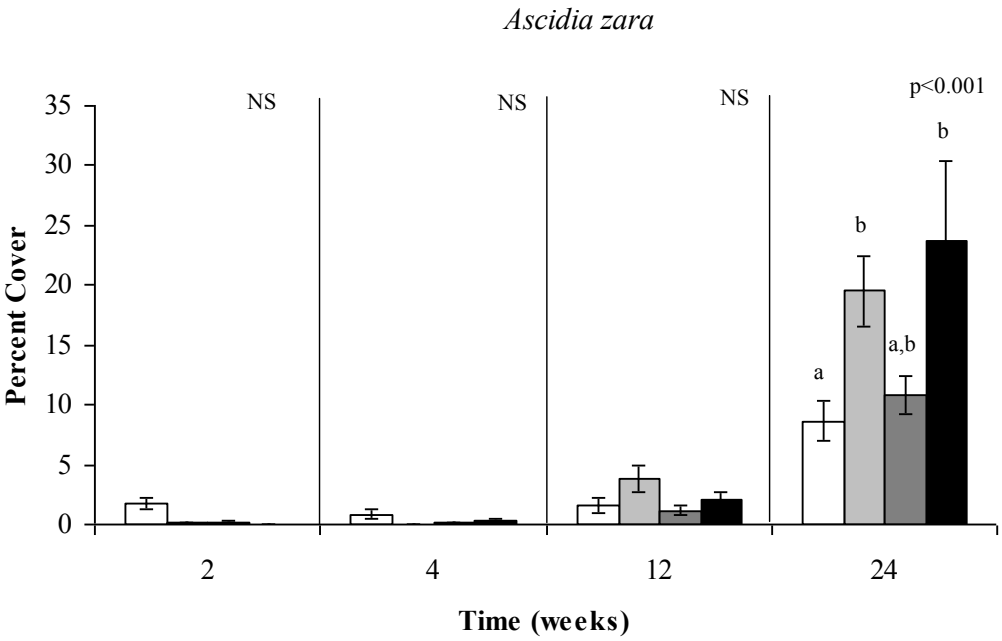
C


Bugula neritina
p<0.006
p<0.004
p<0.001
p<0.001
Percent Cover
Time (weeks)
2
4
12
24

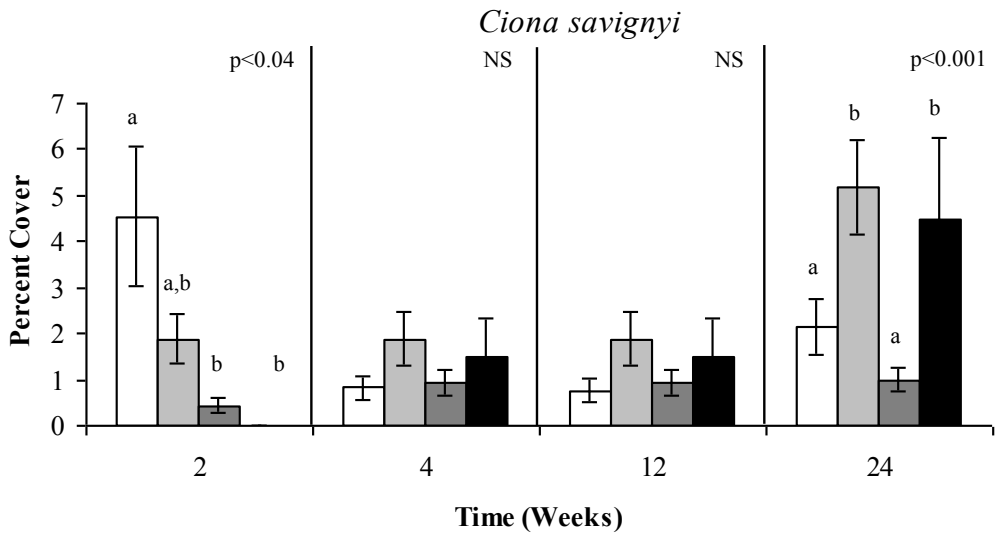
D


Bugula stolonifera
p<0.04
p<0.05
p<0.02
p<0.02
Percent Cover
Time (weeks)
2
4
12
24

E


Ascidia zara
NS
NS
NS
p<0.001
Percent Cover
35
30
25
20
15
10
5
0
a
b
a,b
b
2
4
12
24
Time (weeks)

F


Ciona savignyi
p<0.04
NS
NS
p<0.001
Percent Cover
7
6
5
4
3
2
1
0
a
a,b
b
b
a
b
a
b
2
4
12
24
Time (Weeks)

Chapter 3: The role of facilitation by invaders in the diversity-invasibility debate

Abstract

The relationship between species diversity and susceptibility to species' invasions in communities appears to vary with scale. Large scale patterns often show a positive relationship between diversity and invasibility, while small-scale patterns often show a negative relationship. This conflict has made it difficult to develop general explanatory mechanisms, theory and management strategies. Recent work in marine fouling communities at a small scale suggests a consistent negative relationship between novel non-indigenous species recruitment and diversity, with no effect of available spatial resources on invasions (Altman, Chapter 2). Instead of resource limitation driving the diversity-invasibility relationship in this marine fouling system, the relationships could be driven by propagule supply, and, importantly, larval behavior in response to the adults present in the community. Here I present results from a manipulative field experiment that explores the role of facilitative and inhibitive interactions of invasive species in the diversity-invasibility relationship. Diversity of non-native species and primary resource availability were manipulated, and recruitment to primary and secondary substrates was evaluated after two weeks. Results indicate that 1) Initial community diversity affected the number of recruits that settled onto primary space; 2) Initial community diversity did not affect the number of recruits that settled onto secondary substrate or the combination of primary and secondary subtrates; 3) Despite the fact that there was no effect of diversity on settlement to secondary substrate, certain individual species did facilitate or

inhibit secondary settlement, and 4) As initial community diversity increased, the facilitative and inhibitive properties of individual species were still important. The species that exhibited facilitative properties was the bryozoan *Bugula neritina*. The sponge *Clathria prolifera* and the tunicate *Botryllus schlosseri* both inhibited secondary settlement of non-native species. As the initial diversity of the community increased, *B. neritina* facilitated the settlement of a greater number of individual tunicates. In contrast, as initial diversity of the community increased, both *C. prolifera* and *B. schlosseri* inhibited the settlement of fewer individuals. These results highlight the importance of secondary substrate as a species-specific resource in this particular community, as well as the role of invasive species in facilitating or inhibiting additional invasion.

Introduction

Understanding what drives the success of non-indigenous species (NIS) has been challenging despite considerable research (Elton 1958; Vitousek et al., 1997; Levine and D'Antonio 1999; Tilman 1999; Millennium Ecosystem Assessment 2005). Theoretical and experimental work examining the relationship between species diversity and susceptibility to species' invasions in communities has revealed positive relationships at large scales (e.g., Lonsdale, 1999, Stohlgren et al.., 1999 2003; Sax et al.., 2002; Brown and Peet, 2003; Davies et al., 2005) and negative relationships at small scales (e.g., Knops et al., 1999; Stachowicz et al., 1999; Tilman, 1999; Kennedy et al., 2002). These conflicting results have made it difficult to develop generalities about the mechanisms driving diversity-invasibility relationships (Shea and Chesson, 2002; Fridley et al., 2007).

Recent work studying the diversity-invasibility relationship in marine fouling communities at a small scale suggests a consistent negative relationship between density of novel non-indigenous species recruitment and initial community diversity, with no effect of increased open space on invasion success (Altman, Chapter 2). Over a longer time scale (to 6 months), significant negative relationships between percent cover of several dominant species and the diversity of the initial fouling community continue to persist. I proposed that, in addition to or instead of resource limitation driving the diversity-invasibility relationship in this marine fouling system, the relationship could be driven by propagule supply and larval behavior in response to the adults present in the community. In marine fouling communities, sessile invertebrate larvae either attach and settle onto hard substrates such as rocks, docks, pilings, etc. (primary substrates), or onto the tunics, shells, and tests provided by other invertebrates growing within the community itself (secondary substrates). A focus on use of secondary resource at the community level has not yet been integrated into the literature and could provide insight on the role of facilitation in invasion success and the diversity-invasion relationship.

Facilitative interactions, as described by Bruno et al. (2003), refer to "positive interactions between organisms that benefit at least one of the participants and cause harm to neither". Recent models and observational studies suggest that facilitation can generate positive relationships between diversity and invasibility (Simberloff, 1986; Levine and D'Antonio, 1999; Richardson et al., 2000; Dunstan and Johnson, 2004; Stachowicz and Byrnes, 2006; Bulleri et al., 2008). Facilitation also critically influences community structure (Bertness and Callaway, 1994; Stachowicz, 2001; Bruno et al., 2003). Native species have been shown to facilitate the settlement or growth of other

natives and thus increase native diversity (Witman, 1985; Callaway, 1995; Hacker and Bertness, 1999) and also aid in the success of invasive species (Smith et al., 2004; Zabin and Altieri, 2007; Bulleri and Benedetti-Cecchi, 2008). The role of facilitation in resolving the conflicting results of diversity-invasibility studies (i.e., the "invasions paradox"; Fridley et al., 2007) is limited and has only begun to be explored (Bulleri et al., 2008; Altieri et al., 2010).

Inhibitive, or negative interactions between non-native species, also may be important in determining the impacts of diversity on invasibility. There are few studies that focus on the negative interactions between non-indigenous species (Simberloff and Von Holle, 1999). However, there is recent evidence that resource use by the European green crab, *Carcinus maenas*, is affected by negative interactions with the Asian shore crab, *Hemigrapsus sanguineus* (Griffen, et al., 2008). Terrestrial studies indicate that native plants, such as Lupine, can have inhibitive and facilitative impacts on different non-native plant species (Morris and Wood, 1989). How inhibition effects the diversity-invasibility relationship remains unknown.

Here I present results from a manipulative field experiment that explores the role of facilitative and inhibitive interactions of invasive species in the diversity-invasibility relationship. Marine fouling communities are diverse communities made of up sessile invertebrates such as barnacles, tunicates, bryozoans, and sponges. Though the limiting resource in the community is thought to be primary substrate on which the animals can settle and grow, there is often additional settlement onto the surface of adult organisms. Thus, adult organisms can provide additional substrate, facilitating further settlement. This also may play an important role in resource use (and limitation) and in community

structure and development. Marine fouling communities of San Francisco Bay are dominated by NIS (see Chapter 1). This study uses invasive species to create communities of different diversity and explores the roles of community diversity, primary resource availability, and secondary resource use to 1) determine how recruitment to secondary substrate changes the interpretation of the diversity-invasibility relationship, 2) identify invasive facilitators in the system, and 3) determine whether the nature and degree of facilitation changes with increased community diversity and primary resource availability.

Materials and Methods

Experimental Design

This experiment was designed to examine the effects of both diversity and resource availability on the recruitment of novel non-native species to primary substrate and secondary substrate. As San Francisco Bay fouling communities are predominantly made up of invasive species, replicate communities of different diversities were constructed using abundant invasive species. The recruitment of novel species to primary and secondary substrate was recorded after two weeks. Species collection, community assemblage and experimental deployment were conducted at Richmond Marina Bay, San Francisco Bay, CA (37°54'41"N – 122°21'05"W) and laboratory analyses were conducted at the Romberg Tiburon Center for Environmental Studies, San Francisco State University. Experiments were conducted in July of 2008.

Fouling communities of different diversities were assembled using the methodology described in Chapter 2 of this dissertation. Species selected to create communities of different species richness were as follows: Solitary tunicates *Styela clava* and *Ciona savignyi*, colonial tunicate *Botryllus schlosseri*, upright bryozoan *Bugula neritina,* and the sponge, *Clathria prolifera* (Table 1). All species are non-native to San Francisco Bay. Species were attached to 2.5 X 2.5 cm PVC squares as described in Chapter 2. Communities were assembled using combinations of 1-4 species by screwing sixteen 2.5 X 2.5cm monoculture squares into a PVC backboard to create a 10 X 10cm community of know diversity (following the methods of Stachowicz et al., 1999; Stachowicz et al., 2002). Each 10 X 10cm panel, or experimental community, was assigned to a diversity and a resource treatment as described below.

Diversity treatment 1 consisted of 8 replicate monoculture communities for each of the above species. For higher levels of species richness (2-4), communities were assembled using different species combinations to avoid problems associated with individual species effects on the results. Four species combinations were randomly chosen at each diversity level and 8 replicates were used for a total of 32 replicate communities for diversity treatments 2-4 (Table 1). The spatial location of each species within the community was established randomly through a random number table.

In addition to diversity treatments, I also manipulated available open space to test the effect of resource availability in the same manner as described in Chapter 2. The resource treatment contained two levels, low and high, such that treatments initially contained 0 or 25% open space. Thus, for high resource treatments, assembled communities contained 4 blank 2.5 X 2.5cm squares while low resource treatments did

not contain any blank space. Half of the replicates were randomly assigned to the low resource treatment and half to the high resource treatment. Open space was randomly distributed across the panel area. Bare space was not maintained or manipulated in the communities after initial treatments were deployed.

Once initial diversity and resource level were established in each replicate community, panels were attached to a floating dock, deployed 1m below the water surface and removed only for analysis purposes. Replicate communities were grown *in situ* at the Richmond Marina Bay site for two weeks in July of 2008. After two weeks, new recruits that settled on primary substrate (the bare panel surface) were enumerated and identified to the lowest taxonomic level possible.

Following recruitment analysis, all adult species that were used to create replicate communities were removed from the panel surface and preserved in a 10% buffered formalin solution and subsequently transferred to 70% EtOH. New recruits that settled on the surface of the adult specimens (secondary substrate) were identified and enumerated using dissecting microscopy. I did not determine the surface area of adult species and thus, quantification of secondary recruitment is in terms of number of individual recruits as opposed to density of recruits. Total secondary recruitment to each community was quantified in this way for a subset of half of the experimental communities. This subset consisted of 2 replicate communities from each species and resource combination such that for diversity levels 2-4, 16 community panels were analyzed for total recruitment to primary and secondary substrate. Of those 16 communities, 8 were from the high resource treatment and 8 were from the low resource treatment. As there were five

species representing the monoculture treatment, 20 panels were analyzed for recruitment to primary and secondary substrate.

An additional subset was analyzed from the remaining replicates in order to determine how secondary recruitment to individual species changed with diversity and resource treatments. This subset consisted of one representative specimen of each species from each of the remaining community panels. As some species were used more often than others to create the initial diversity combination, replication was not even between species and varied from 28-36 individuals as follows: *Styela clava*, n=36; *Bugula neritina*, n= 32; *Clathria prolifera*, n = 28; *Ciona savigyni*, n= 32; *Botryllus schlosseri*, n=36.

Statistical Analysis

Regression analyses were conducted to determine the relationship between 1) community diversity, 2) resource availability, and 3) recruitment of novel non-indigenous species to a) primary substrate, b) secondary substrate, and c) total substrate (primary + secondary). Each substrate grouping was analyzed separately using the general linear model (GLM) procedure in the SAS 9.1 analysis package for factorial regression models. Novel recruitment was treated as a dependent variable, while diversity, resource availability, and their interaction were treated as fixed effects. Recruitment was measured as 1) the density of individuals settling on primary substrate, 2) the number of individuals settling on secondary substrate, and 3) the number of individuals settling to total substrate. Data met the requirements of normality and homogeneity of variance and did not require transformation.

ANOVAs were used to assess differences between primary and secondary recruitment to the adult species used to create the communities. Recruitment and settlement of novel NIS, bryozoans, colonial tunicates, solitary tunicates and species richness were each used as dependent variables in separate analyses of recruitment into monoculture communities. Recruitment was measured as described above and, when referring to species richness, as the number of species settling to either primary or secondary substrate. When assessing differences between monocultures of different species, separate ANOVAs were used for settlement to primary space and secondary space. To assess differences in primary and secondary settlement within monocultures of the same species, t-tests were run.

Finally, ANOVAs determined whether or not secondary settlement onto each adult species changed in response to diversity and resource treatments. For these analyses, recruitment category (novel NIS, novel bryozoan, etc.) was treated as the dependent variable, and diversity, resource and their interaction were treated as random fixed effects. Bonferroni corrected multiple pairwise comparisons were used to identify treatment levels with significant influence. Again, data met the requirements of normality and homogeneity of variance and transformation was unnecessary.

Results

Overall Recruitment

After two weeks of deployment, the density of primary recruitment of novel NIS varied inversely with initial community diversity in the experimental communities ($F = 7.35$, $p < 0.0001$, Figure 1A). However, the density of primary recruitment of novel NIS

did not vary significantly with the amount of open primary space, and no significant interaction of open space with initial diversity was identified**.** In contrast, despite a negative trend, the number of novel non-indigenous individuals that recruited to secondary substrate did not vary significantly with diversity, with availability of primary substrate, or their interaction ($F = 0.74$, $p = 0.538$, Figure 1B). As adult surface area was not estimated, a standardized comparison of the density of settlement cannot be made. Note, however, that settlement onto secondary surfaces was at times twice as high as settlement onto primary substrate. When primary and secondary recruitment were combined, recruitment of the total number of novel non-indigenous individuals did not depend upon initial diversity or open space resource ($F = 1.04$, $p = 0.389$, Figure 1C).

Recruitment to Monocultures

Novel NIS

The density of novel NIS recruitment to primary substrate did not differ among monocultures of different species ($F = 4.06$, $p = 0.08$; Figure 2A). In contrast, the number of individuals that recruited to secondary substrate differed significantly depending which adult species was present in the monoculture ($F = 28.09$, $p = 0.001$; Figure 2B). Specifically, the highest secondary recruitment occurred on monocultures of the bryozoan *B. neritina*. Little secondary recruitment was seen on the surface of the sponge *C. prolifera,* the colonial tunicate *B. schlosseri*, or solitary tunicate *C. savignyi*. *Styela clava*, also a solitary tunicate, did provide habitable secondary surface and had elevated settlement, though this was not significantly different from settlement on the sponge or other tunicates (Figure 2B). T-tests between primary and secondary settlement within each type of monoculture revealed significant differences in settlement to *B. neritina*

communities (t = -8.8, p = 0.013, higher settlement on secondary substrate), C. *prolifera* communities (t =10.44, p = 0.009, lower settlement to secondary substrate) and *B. schlosseri* communities (t = 20.02, p = 0.003, lower settlement to secondary substrate) (Figure 2A-B).

Dominant Taxa

To examine these recruitment patterns further, I grouped novel recruitment into the following dominant taxa: bryozoans, colonial tunicates, and solitary tunicates. The density of recruitment of novel non-native bryozoans to primary space was low for all monoculture communities except those occupied by the sponge *C. prolifera* (Figure 3A). In this case, there was a significant increase in the density of bryozoan recruitment when compared to the other species (F = 21.69, p = 0.002, Figure 3A). When recruitment to secondary substrate was examined, individual non-native bryozoan colonies recruited to *B. neritina* monocultures in significantly higher numbers than monocultures made up of other species (F = 24.74, p = 0.002, Figure 3B). Recruitment to primary vs. secondary substrate was different in both the *C. prolifera* and *B. neritina* communities (t = 5.22, p = 0.03; t = -5.78, p = 003, respectively; Figure 3 A-B). The predominant bryozoan species recruiting into communities at this time was *B. stolonifera*, a conspecific to *B. neritina*.

The density of recruitment of novel non-indigenous colonial tunicates to primary substrate differed significantly among monoculture species (F = 7.56, p = 0.024, Figure 4A). Recruitment to the primary substrate occurred at a lower density in *C. savignyi* monocultures than other monocultures, and pairwise comparisons showed that this

reduced recruitment was significantly lower than recruitment in *C. prolifera* and *B. schlosseri* monocultures (Figure 4A).

The number of individual non-indigenous colonial tunicates that recruited to secondary substrate was also different depending on the monoculture ($F = 51.56$, $p = 0.0003$, Figure 4B). The number of colonies that recruited to *B. neritina* monocultures was at least twice as high as the colonial tunicate recruitment in any other type of monoculture (Figure 4B). Significant differences were found between primary and secondary settlement in *B. neritina* communities ($t = -6.06$, $p = 0.02$, higher settlement on secondary substrate), C. *prolifera* communities ($t = 11.22$, $p = 0.05$, lower settlement to secondary substrate) and *B. schlosseri* communities ($t = 10.84$, $p = 0.008$, lower settlement to secondary substrate) (Figure 4A-B). The pool of colonial tunicates that were recruiting during the course of the experiment was dominated by the didemnid *Diplosoma listerianum*. This species was likely responsible for differences in settlement of colonial tunicates to primary and secondary substrates.

The density of recruitment of solitary tunicates to primary space did not differ significantly among monoculture species ($F = 1.52$, $p = 0.325$, Figure 5A). The number of individual solitary tunicates that recruited to secondary substrate also did not differ significantly among monoculture species, although the number of individuals that settled on *B. neritina* and *S. clava* was higher than the number of individuals that settled on the other adult species that made up the monocultures ($F = 2.24$, $p = 0.20$, Figure 5B). In sponge communities, solitary tunicate settlement differed significantly between primary and secondary substrates ($t = 22.45$, $p = 0.03$, lower settlement to secondary substrate, Figure 5A-B). The dominant solitary tunicate recruiting during this experiment was *C.*

intestinalis, which showed the same patterns described for the group of non-indigenous solitary tunicates.

Species Richness

On primary substrate, novel species richness did not differ among any monoculture communities ($F = 1.23$, $p = 0.403$, Figure 6A). The number of species that settled on secondary substrate varied significantly among monocultures and was highest in *B. neritina* monocultures and *S. clava* monocultures ($F = 16.00$, $p = 0.005$, Figure 6B). In *S. clava* monocultures, the number of species thar recruited to secondary substrate was significantly higher than on primary substrate ($t = -6.71$, $p = 0.021$, Figure 6A-B).

Recruitment across Diversity Treatments

To examine whether secondary recruitment patterns seen in monocultures changed as a result of species richness or resource availability, an additional subset of individual adults from every treatment type was analyzed (as described in the methods) (Table 2). Novel recruitment of the number of individual non-native bryozoan and colonial tunicate colonies to the surface of the upright bryozoan *B. neritina* did not vary with community diversity or resource availability. However, the number of individual solitary tunicates that recruited to *B. neritina* was significantly higher than on other species due to an interaction between increased diversity and decreased resources (Table 2). The number of novel non-indigenous individuals that recruited to the solitary tunicate *S. clava* decreased significantly as diversity increased (Table 2). This is likely due to decreased recruitment of both the number of novel bryozoan colonies (predominantly *B. stolonifera*) and the number of individual solitary tunicates (predominantly *C.*

intestinalis) (Table 2). In contrast, the number of organisms that recruited to the surface of the solitary tunicate *C. savignyi* did not change with community diversity or resource availability. *Ciona savignyi* had low settlement on its tunic in general. The number of novel colonial tunicates that recruited to *B. schlosseri*, a colonial tunicate itself, was significantly influenced by primary resource availability, such that an increase in primary space was associated with an increase in settlement on its surface (Table 2). The same pattern also was seen with respect to the number of species settling on this host. The number of individuals that recruited to the sponge *C. prolifera* was extremely low in monocultures but increased significantly when community diversity increased and primary resources decreased. When the number of novel tunicate colonies that recruited to *C. prolifera* was examined, an inverse relationship between the amount of primary spatial resources and secondary settlement was seen (Table 2). The same inverse relationship was seen in the number of species that recruited to individual sponges (Table 2).

Discussion

There are a number of overall conclusions that can be drawn from the current study. First, initial community diversity affected the number of recruits that settled onto primary substrate. In contrast, initial community diversity did not affect the number of recruits that settled to secondary substrate or total substrate when recruitment of individuals to primary and secondary space was combined. Although diversity had no affect on secondary settlement, certain individual species facilitated or inhibited settlement to the surface of their bodies. As initial community diversity increased, the facilitative properties of individual species appeared to be strengthened while the

inhibitive properties appeared to weaken. These general conclusions are discussed in detail below.

The number of individuals that recruited to primary space were significantly affected by initial community diversity. That is, the density of recruitment of novel non-native species onto the primary substrate of experimental fouling communities showed a negative relationship with diversity, as was seen in previous years and seasons (as described in chapter 2). Consistent with experiments run in November 2006 and August 2007, this negative relationship was due to diversity. Primary resource availability, though expected to be ultimately responsible for the diversity effect, did not have an influence on recruitment to primary substrate. This may be due to other organisms in the community that could mask or alter the effects of resource limitation by providing secondary surfaces for settlement onto their tunics, tests and outer coverings. The current results indicate that the organisms that make up the community itself can influence the recruitment and settlement of novel species into the community.

In contrast to recruitment on primary substrate, the total number of novel recruits that settled to secondary substrate was not affected by initial community diversity. The number of individuals that recruited to secondary surfaces within the community was more variable than primary recruitment to open substrate and was, at times, much higher. When the number of individuals that recruited to secondary substrate was examined in isolation, a significant effect of diversity and resource availability on the number of recruits did not emerge. If larvae prefer to settle on primary substrate rather than secondary substrates, one might expect an increase in bare primary substrate to result in reduced settlement on secondary substrate. This was not seen. Instead, there was no effect

of primary resource availability on recruitment of individuals to primary or secondary surfaces. This suggests that larvae may not prefer primary substrate over secondary substrate. The high variance in the number of individuals that recruited to secondary substrates suggests a possible preference for settlement on other organisms, in some cases. This may be due to a number of factors including the quality of substrate provided, the 3-dimensional location within the community, or microturbulence due to feeding activities that affects the ease of navigating through the adult community to find a viable settlement location (Koehl and Hadfield, 2010). However, the high variation seen in the number of individuals that recruited to secondary substrate, especially among different monocultures, indicates that larval settlement on secondary surfaces is highly species-specific.

Similarly, when novel recruitment of individuals to primary and secondary substrates was considered as a combined cumulative measure of settlement, the negative relationship initially seen between density of recruitment of NIS and diversity was no longer significant. Incorporating the signal of secondary resource use was not only important, it changed the overall interpretation of the diversity-invasibility relationship seen in this system in multiple seasons. As there is conflicting evidence in support of the "invasion paradox", it is critical that appropriate factors and resources be considered in observations and analyses. Secondary substrate has, for the most part, been overlooked as an important resource in fouling community studies.

In the marine fouling studies that have addressed the diversity-invasibility hypothesis, primary substrate was the focus of resource use (Stachowicz et al., 1999; Stachowicz et al. 2002; Dunstan and Johnson, 2004). An additional observational study

reported by Stachowicz and Byrnes (2006) posited that, although a negative relationship was reported in their previous experimental data, a shift in community composition could lead to a shift in diversity-invasibility dynamics if 'structure-forming' species were present in the community to ease space limitation. If species within the community provide substrate that can support additional species (both native and non-native), then the effect of spatial limitation may not be as strong.

The present study is one of few that explore the effect of secondary settlement on diversity-invasion relationships. The role of secondary space often is ignored and should be more fully studied and incorporated into our perception of resource limitation in fouling communities. It is thought that the complete utilization of limiting resources by species within a community decreases available resources for new species entering the community, thus making it more difficult for them to invade (Elton, 1958; Cronk and Fuller, 1995 ; Levine and D'Antonio, 2000) If adult organisms (often invasive species themselves) provide ample settlement substrate for invading recruits as demonstrated here, then the availability of primary space may not be as important in determining overall community invasibility as the availability of both primary and secondary space combined.

This study demonstrates that certain individual species can facilitate or inhibit secondary settlement. In the present study, we see that including the effects of facilitation and inhibition through secondary settlement does, in fact, change the negative relationship to a non-significant one. Indeed, having facilitators in the system adds additional resources and can enhance inclusion of additional species through ecosystem engineering or facilitation cascades (Crooks, 2002; Altieri et al., 2010, respectively).

Studies of monocultures provide insight into which species may be facilitators and provide suitable substrate to other species in the system. Some species such as *B. neritina* and *S. clava* clearly provided substrate that was settled upon by non-native bryozoans and tunicates, while other species, such as the sponge *C. prolifera* and tunicates *B. schlosseri* and *C. savignyi*, did not.

Previous reports have shown both positive and negative interactions between members of the fouling community in which some species facilitate the settlement of additional species while others inhibit it (facilitation: Stebbing, 1972; Moyse and Hiu, 1981, Jensen and Morse, 1984, Wethey, 1984; inhibition: Grosberg, 1981; Kent and Day, 1983; Havenhand and Svane, 1989; Bingham and Young, 1991; Davis et al., 1992). These studies focused on interactions between common local species but did not focus on geographical origin of the species (i.e., native, non-native) or make a distinction between interactions of native or non-native species.

It is evident from the current study that non-native adult species can provide suitable substrate for other non-native species, facilitating further invasion. In particular, *B. neritina* supports settlement of a number of non-native bryozoans and tunicates, including *B. stolonifera*, *D. listerianum*, and *C. intestinalis*. Previous studies of *B. neritina* demonstrate its ability to facilitate settlement of serpulid polychaetes through chemical mediation (Bryan et al., 1998). As an arborescent bryozoan, *B. neritina's* branched structure may be an ideal surface for settlement, or may obscure larval navigation to primary substrate. An additional case of non-native bryozoans providing habitat for native and non-native species was recently described in non-native *Schizoporella errata* bryoliths in San Francisco Bay (Zabin et al., 2010), and the non-

native *Watersipora subtorquata* has been shown to be a foundation species for other bryozoans, amphipods and polychaetes in Queensland, Australia (Floerl et al., 2009). It is interesting and perhaps surprising that *B. neritina* is able to provide useful substrate, since it is not an encrusting bryozoan like the previous examples.

The solitary tunicate *S. clava* does not appear to support more secondary settlement than the other adult species examined. However, in monocultures, the number of species that settled on *S. clava* was higher than the species richness found on primary substrate alone, suggesting that this species may enhance invasive community diversity. Thus, this tunicate could attract non-indigenous species to the community, even though the density of these novel species may be low.

The rest of the tunicates used in this study did not facilitate secondary settlement. *Botryllus schlosseri* appears to inhibit settlement of other colonial tunicates. Other studies involving *B. schlosseri* indicate that settlement on this species is low (Osman and Whitlatch, 1995; Grosberg, 1981). While there are no previous studies describing settlement on *C. savignyi* tunics, my results demonstrate that this substrate is not ideal for settlement, but that primary and secondary substrates in *C. savignyi* monocultures were of the same relative quality. Low settlement to the surface of these tunicates may be due to chemical, mechanical or bacterial properties of their respective tunics (Wahl et al., 1994).

Sponges are known to protect themselves chemically and mechanically to deter predators and inhibit settlers (Turon, 1996; Bingham and Young, 1991), and larval tunicates have been shown to avoid settling on sponges of different species (Davis et al., 1991). It is not surprising, then, that little to no settlement occurred on the surface of *C. prolifera* throughout this study. The significant increase in settlement in primary space

compared to secondary space in sponge communities further suggests that larval bryozoans and tunicates avoided settlement on sponges and preferred to settle on bare space instead.

As additional species were added to the initial community, and diversity increased, the facilitative properties of individual species appeared to be strengthened while the inhibitive properties of other species appeared to weaken. Clear, species-specific patterns of both facilitation by *B. neritina* and inhibition by *C. prolifera* and *B. schlosseri* (with respect to colonial tunicates) were identified among monoculture communities. To determine whether these properties were maintained in higher diversity communities and with varied resources, I examined an additional subset of adults from all treatment combinations. For *B. neritina*, the most influential facilitator in this study, the number of species and number of individuals that settled did not change with diversity or resource availability except in solitary tunicates. Solitary tunicates did not actually show a significant increase in secondary settlement to *B. neritina* monocultures, but were affected by a significant interaction between diversity and resource availability, where secondary settlement to *B. neritina* increased as diversity increased and open primary space decreased. In other words, when bare primary space was limited and there were more adult species in the community, solitary tunicates were more likely to settle on the secondary substrate provided by the bryozoan than on the bare space. This result suggests that the faciliative properties of *B. neritina* were stronger in communities with high initial diversity.

Species that displayed inhibition included *C. prolifera* and *B. schlosseri.* Overall recruitment to the surface of the sponge was very low, although some significant

relationships between the number of individuals that recruited and initial community diversity and resource availability were found. As diversity increased and resources decreased, higher settlement was seen on the sponge surface. This result suggests that the inhibitive properties of *C. prolifera* were weaker in communities with high diversity and low resources. The increase in secondary settlement may be due to the fact that there was less primary space to settle upon, forcing larvae to settle on less ideal secondary substrates. Studies of toxicity in a different species of poecilosclerid sponge indicate a potential decrease in toxicity as sponges grow and age (Turon et al., 1996). As colonies of *C. prolifera* grow both laterally across primary substrate and in finger-like masses away from primary substrates, there may be some variability in toxicity within the physical structure of the sponge, changing the suitability of the secondary substrate it provides.

Initial community diversity only affected secondary settlement on the solitary tunicate *S. clava*. The number of overall non-indigenous individuals, non-native bryozoan colonies, and solitary tunicates that recruited to *S. clava* tunics varied inversely with diversity (although the effect on solitary tunicates was marginally significant). While *Styela clava* did support some settlement, analysis of monocultures suggested that it was not considered a facilitator. Thus, the suitability of the secondary substrate that an individual species provides can change with community diversity. However, since *S. clava* was not a significant facilitator of secondary substrate to begin with, this effect probably does not facilitate multiple invasions. In contrast, *C. savignyi* did not change in its ability to inhibit or facilitate recruitment and provides an example of a solitary tunicate with consistent properties despite community changes.

Conclusions

This study highlights the importance of the roles of facilitation and inhibition in regulating invasibility as a function of community diversity. Focusing on primary and secondary substrate as a resource in the fouling community changes the nature of the relationship seen between novel recruitment of non-native individuals and diversity from a significantly negative relationship to a non-significant one. This change is due to settlement onto adult species in the community that can act to facilitate or inhibit settlement and additional invasion. The species that was identified as a strong facilitator, *B. neritina*, was not affected in an inconsistent way by diversity or resource changes. In other words, this bryozoan continued to facilitate additional recruitment of non-indigenous individuals in low and high diversity communities and when spatial resources were low. The species that were strong inhibitors to settlement were less successful at inhibiting recruitment of individuals when diversity increased (*C. prolifera*) or resources decreased (*C. prolifera, B. schlosseri*). The combined effect of a strong facilitator and two weaker inhibitors in the system leads to a hypothesis of overall facilitation of new invasive recruits and a potential 'invasional meltdown' (*sensu* Simberloff and Von Holle, 1999). Other studies that also highlight the ability of NIS to facilitate the success of additional invasions include interactions between invasive bryozoans and other invertebrates (Zabin et al., 2010; Floerl et al., 2009), invasive bryozoans and kelp (Watanabe et al., 2010), macroalgae and epiphytic algae (Jones and Thornber, 2010), crabs and other invertebrates (Altieri et al., 2010) and fish and frogs (Adams et al., 2003). Recognizing the importance of secondary substrate or other overlooked resources that serve to facilitate additional invaders is critical to understanding relationships between

diversity and community invasibility. Future research should emphasize the role of secondary substrate and other overlooked resources over multiple time scales with a focus on how long term success of invaders is influenced.

Tables & Figures

Table 1. Species combinations used in experiment. Each combination was replicated 4 times for the low resource treatment (0% bare space) and 4 times for the high diversity treatment (25% bare space).

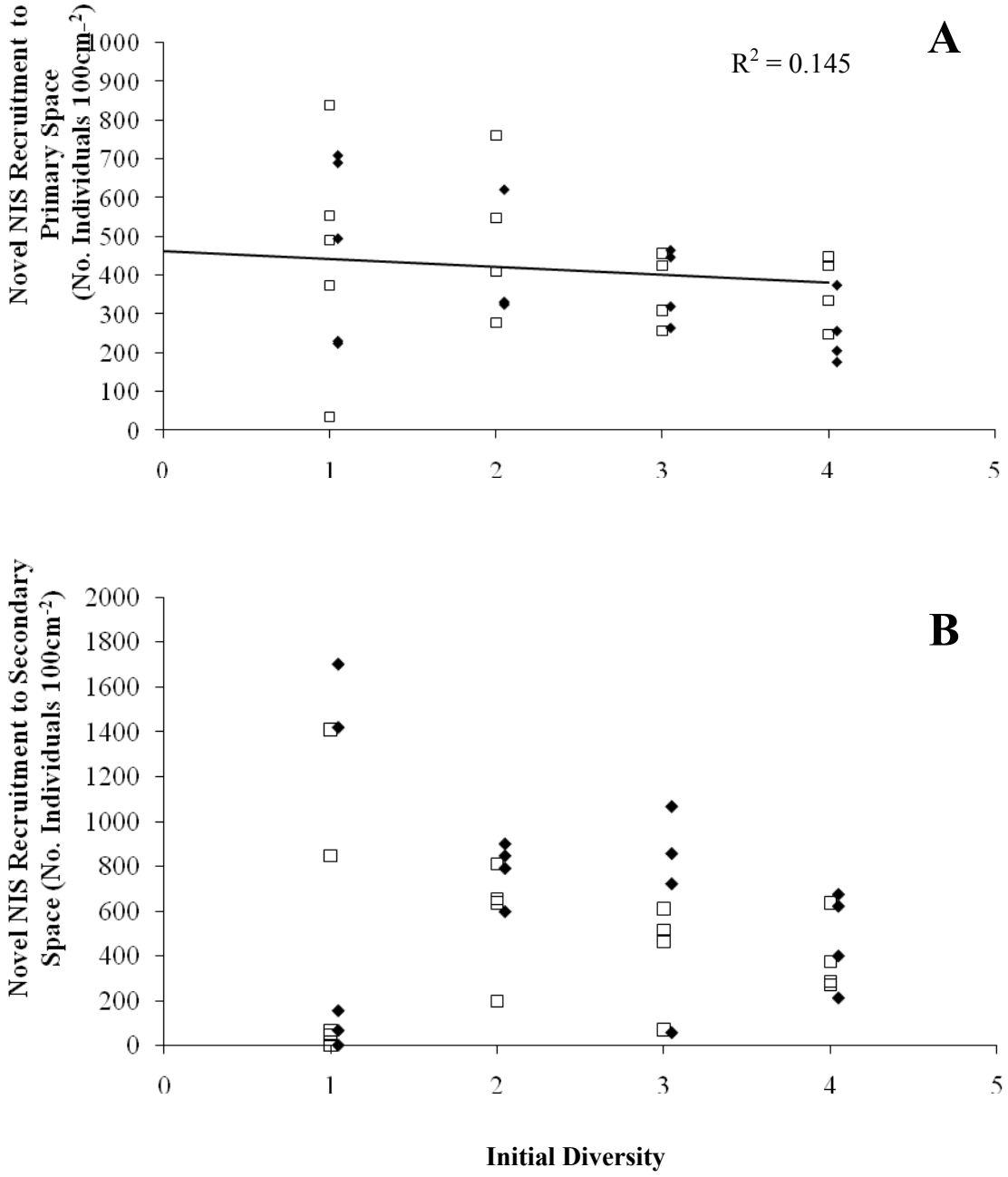
Year	Diversity Treatment	Combination	Species
2008	1	A	*Styela clava*
	1	B	*Bugula neritina*
	1	C	*Clathria prolifera*
	1	D	*Ciona savignyi*
	1	E	*Botryllus schlosseri*
	2	A, D	*S. clava, C. savignyi*
	2	B, C	*B. neritina, C. prolifera*
	2	B, E	*B. neritina, C. savignyi*
	2	A, E	*S. clava, B. schlosseri*
	3	A, B, D	*S. clava,, B. neritina, C. savignyi*
	3	C, D, E	*C. prolifera, C. savignyi, B. schlosseri,*
	3	A, B, E	*S. clava, B. neritina, B. schlosseri*
	3	A, C, E	*S. clava, C. prolifera, B. schlosseri*
	4	A, B, C, D	*S. clava, B. neritina, C. prolifera, C. savignyi*
	4	B, C, D, E	*B. neritina,, C. prolifera, C. savignyi, B. schlosseri*
	4	A, B, D, E	*S. clava, B. neritina, C. savignyi, B. schlosseri*
	4	A, C, D, E	*S. clava, C. prolifera, C. savignyi, B. schlosseri*

Table 2. Results from 2 way ANOVAs determining how recruitment to the surface of adult species is affected by community diversity and/or primary resource availability. Secondary substrate refers to adult species in question, recruitment group was treated as a dependent variable and diversity and resource as independent variables. Bold numbers refer to significant p values using alpha = 0.05.

Secondary Substrate	Recruitment		DF	MS	F	p
Bugula neritina						
	Novel NIS		3	1314.26	0.76	0.519
	Novel Bryozoan		3	1314.26	0.76	0.519
	Novel Colonial Tunicate		3	1358.24	2.26	0.0862
	Novel Solitary Tunicate		3	295.185	7.48	**0.0002**
		Diversity	1	101.589	2.58	0.112
		Resource	1	1.3947	0.04	0.8513
		Interaction	1	782.57	19.84	**<0.0001**
	Species Richness		3	6.601	1.98	0.1233
Styela clava						
	Novel NIS		3	8291.85	5.96	**0.0009**
		Diversity	1	23640.289	16.98	**<0.0001**
		Resource	1	822.48	0.59	0.4439
		Interaction	1	412.79	0.3	0.5873
	Novel Bryozoan		3	212.75	4.2	**0.0076**
		Diversity	1	610.27	12.06	**0.0008**
		Resource	1	20.83	0.41	0.523
		Interaction	1	7.14	0.14	0.708
	Novel Colonial Tunicate		3	54.13	1.19	0.317
	Novel Solitary Tunicate		3	146.11	2.51	0.0629
	Species Richness		3	5.495	1.48	0.2245
Ciona savigyni						
	Novel NIS		3	1.2702	1.84	0.1481
	Novel Bryozoan		3	0.261	1.04	0.3809
	Novel Colonial Tunicate		3	0.0299	0.57	0.639
	Novel Solitary Tunicate	No Solitary Tunicate Settlement				
	Species Richness		3	0.3292	1.08	0.3631
Botryllus schlosseri						
	Novel NIS		3	42.127	1.99	0.123
	Novel Bryozoan		3	1.988	2.01	0.1206
	Novel Colonial Tunicate		3	8.386	3.03	**0.035**
		Diversity	1	2.674	0.97	0.3288
		Resource	1	14.053	5.08	**0.0273**
		Interaction	1	8.43	3.05	0.0852
	Novel Solitary Tunicate		3	4.973	2.55	0.0625

	Species Richness		3	5.7487	3.65	**0.0167**
		Diversity	1	4.14	2.63	0.1096
		Resource	1	10.937	6.94	**0.0104**
		Interaction	1	2.169	1.38	0.2447
Clathria prolifera						
	Novel NIS		3	220.387	6.58	**0.0005**
		Diversity	1	172.05	5.14	**0.0263**
		Resource	1	272.58	8.17	**0.0055**
		Interaction	1	215.54	6.44	**0.0133**
	Novel Bryozoan		3	12.45	0.84	0.474
	Novel Colonial Tunicate		3	38.125	8.58	**<0.0001**
		Diversity	1	16.54	3.72	0.0575
		Resource	1	77.385	17.41	**<0.0001**
		Interaction	1	20.45	4.6	**0.0352**
	Novel Solitary Tunicate		3	1.257	0.81	0.4901
	Species Richness		3	16.274	6.84	**0.0004**
		Diversity	1	0.74225	0.31	0.5781
		Resource	1	36.184	15.21	**0.0002**
		Interaction	1	11.896	5	**0.0283**

Figure 1. Recruitment of novel non-indigenous species (NIS) to A) primary substrate, B) secondary substrate and C) primary and secondary substrates (total recruitment to community) over 2 weeks in July 2008. Initial diversity refers to manipulated diversity of the community at the beginning of the experiment. Open squares refer to high resource treatments (25% bare space) and closed diamonds refer to low resource treatments (0% bare space). Recruitment of NIS to primary space showed a significant negative relationship with diversity as indicated by regression line (A). Negative relationships were not significant for secondary or total recruitment (B, C). There were no differences seen between resource treatments



C

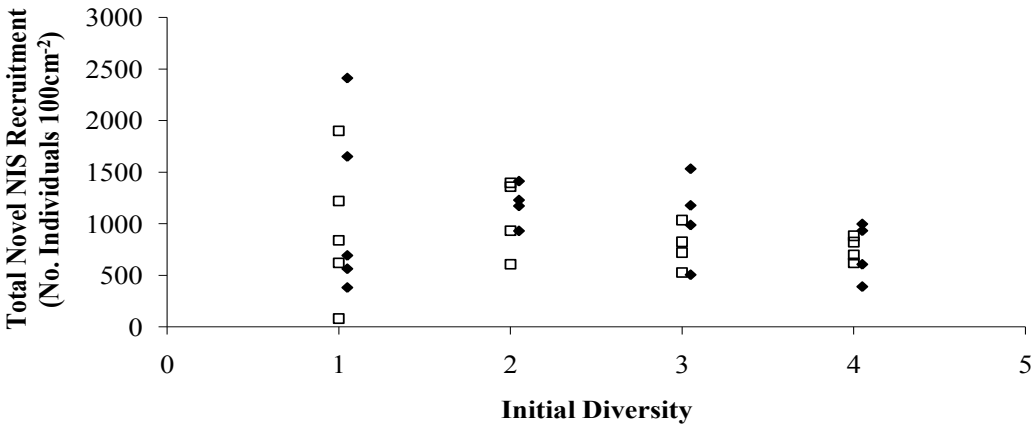

Total Novel NIS Recruitment (No. Individuals 100cm-2)
3000
2500
2000
1500
1000
500
0
0
1
2
3
4
5
Initial Diversity

Figure 2. Recruitment of novel NIS to primary substrate (A, above) and secondary substrate (B, below) in monoculture communities. Adult species used to create monocultures are identified by color/pattern of bar, while height of bar indicates the number of recruits that settled in each type of monoculture (mean +/- 1 SE). Within each panel (A, B), small letters refer to significant differences in recruitment between monocultures (from ANOVA analyses; no letters indicate no significant differences). Between each panel (A, B), asterisks refer to significant differences between recruitment to primary and secondary substrate in each monoculture community (from t-tests; no asterisk indicates no significant difference). Statistical analyses detailed in the text.

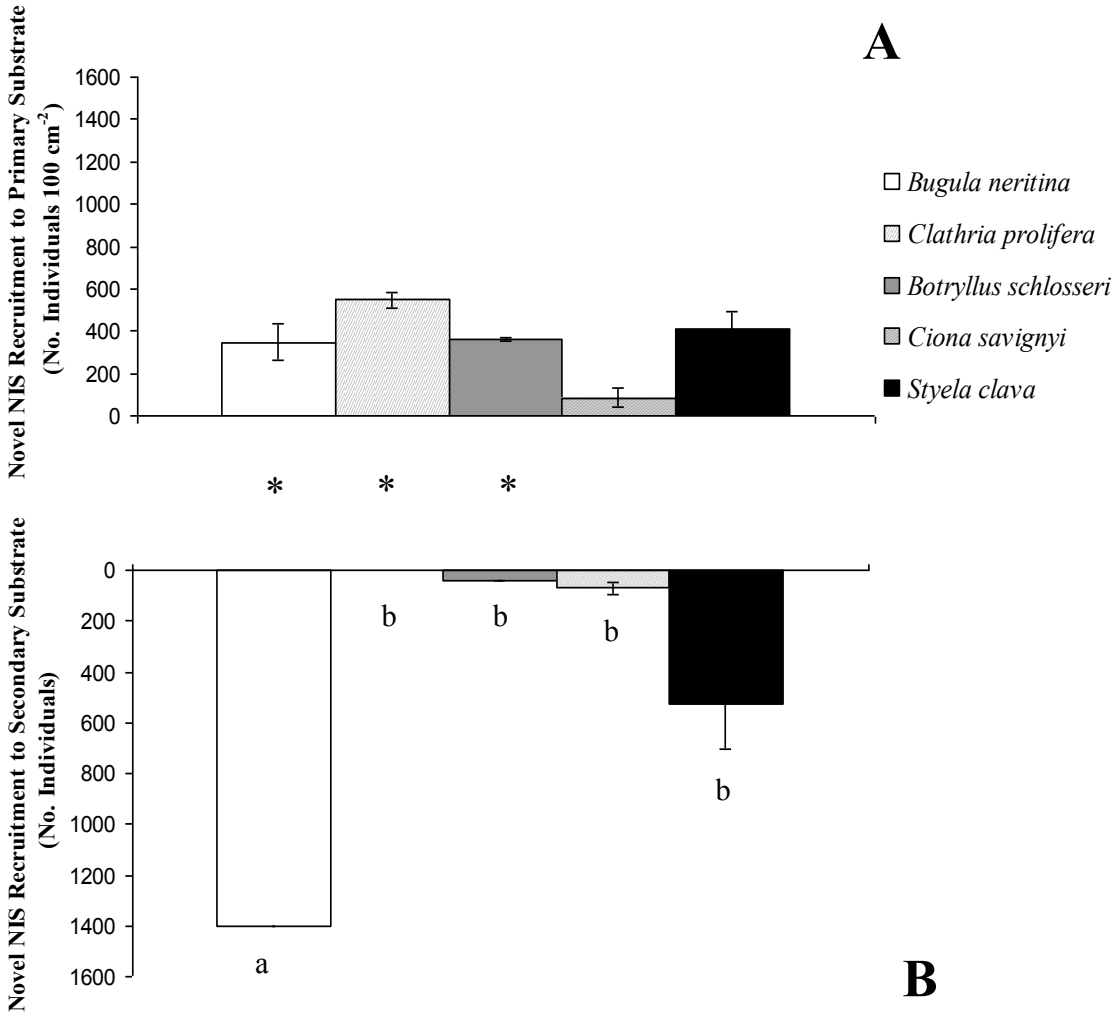


Figure 3. Recruitment of novel non-native bryozoans to primary substrate (A, above) and secondary substrate (B, below) in monoculture communities. Adult species used to create monocultures are identified by color/pattern of bar, while height of bar indicates the number of recruits that settled in each type of monoculture (mean +/- 1 SE). Within each panel (A, B), small letters refer to significant differences in recruitment between monocultures (from ANOVA analyses; no letters indicate no significant differences). Between each panel (A, B), asterisks refer to significant differences between recruitment to primary and secondary substrate in each monoculture community (from t-tests; no asterisk indicates no significant difference). Statistical analyses detailed in the text.

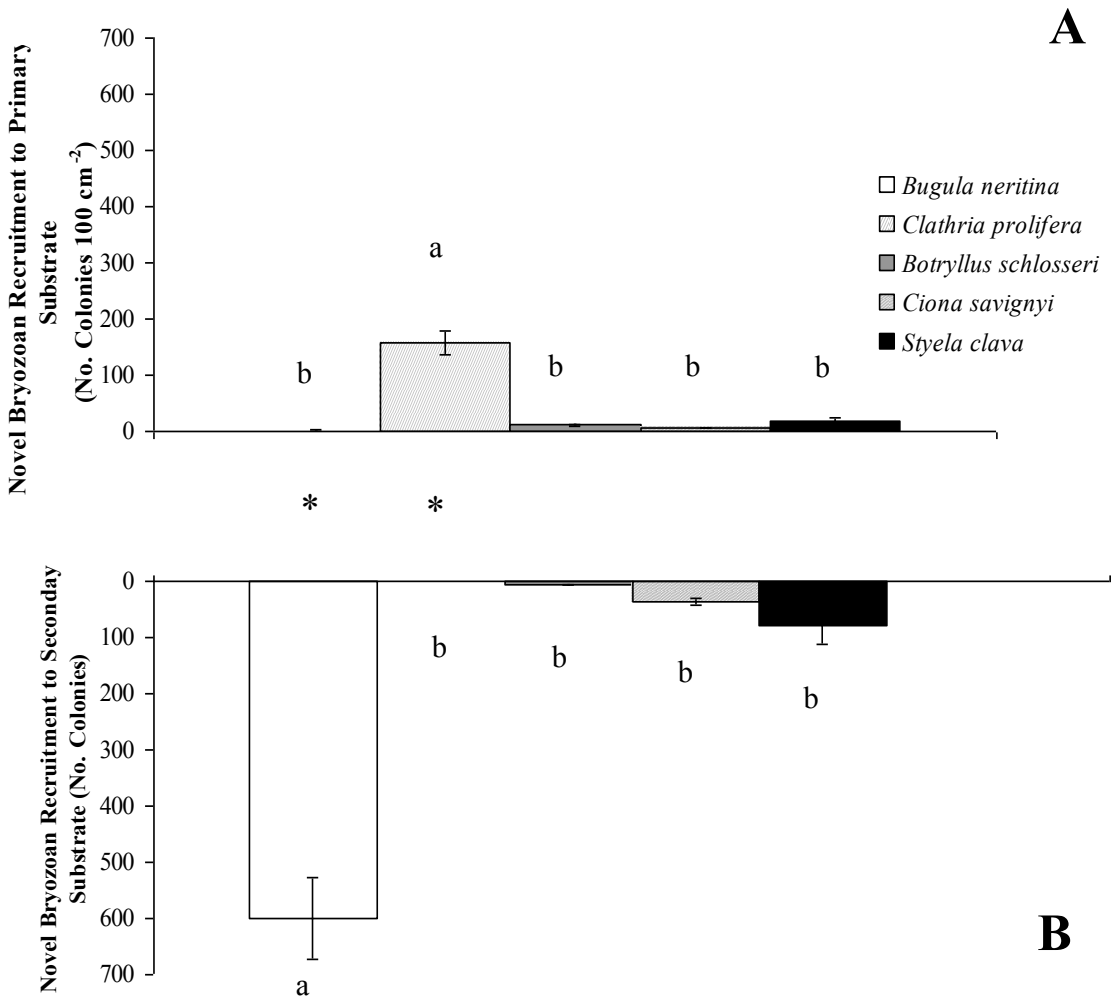


Figure 4. Recruitment of novel non-native colonial tunicates to primary substrate (A, above) and secondary substrate (B, below) in monoculture communities. Adult species used to create monocultures are identified by color/pattern of bar, while height of bar indicates the number of recruits that settled in each type of monoculture (mean +/- 1 SE). Within each panel (A, B), small letters refer to significant differences in recruitment between monocultures (from ANOVA analyses; no letters indicate no significant differences). Between each panel (A, B), asterisks refer to significant differences between recruitment to primary and secondary substrate in each monoculture community (from t-tests; no asterisk indicates no significant difference). Statistical analyses detailed in the text.

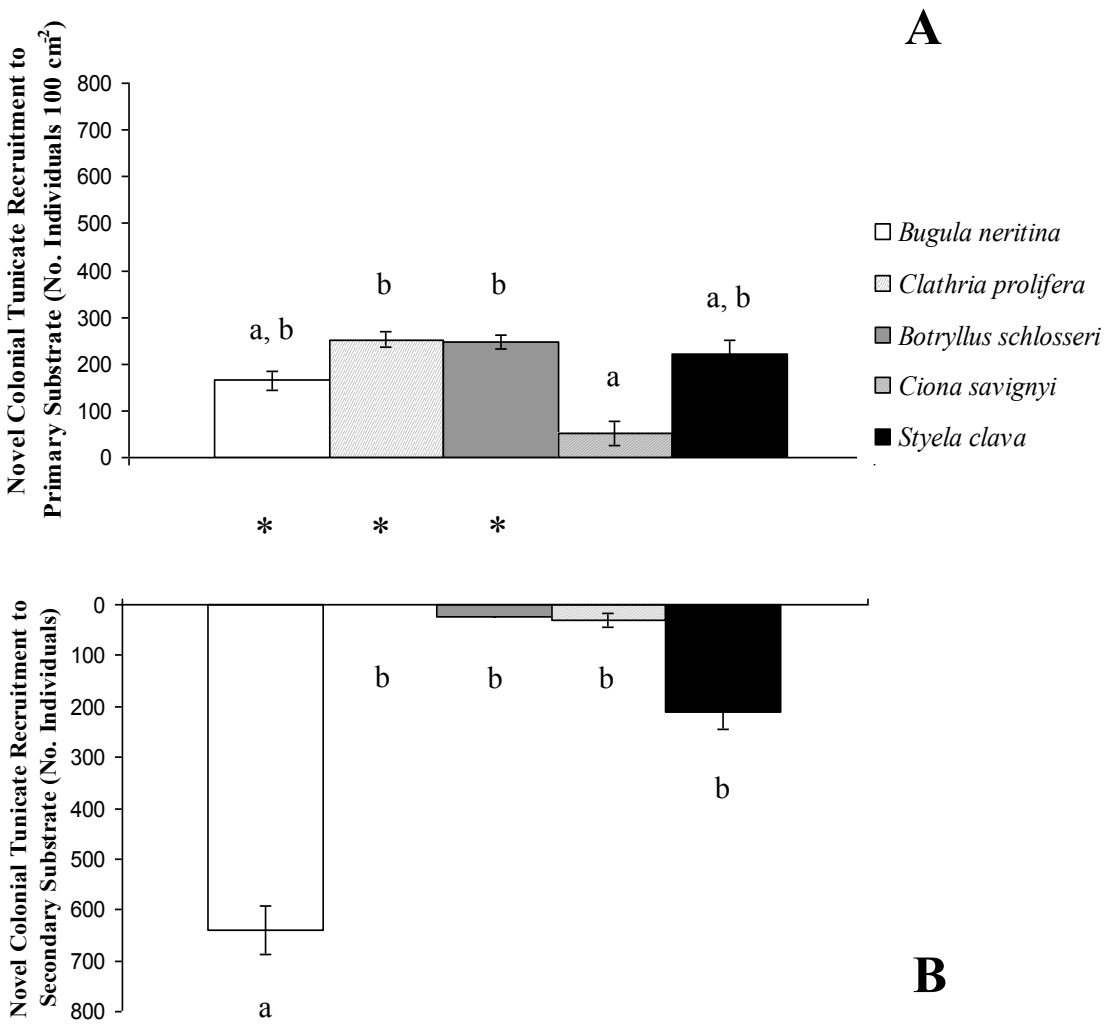


Figure 5. Recruitment of novel non-native solitary tunicates to primary substrate (A, above) and secondary substrate (B, below) in monoculture communities. Adult species used to create monocultures are identified by color/pattern of bar, while height of bar indicates the number of recruits that settled in each type of monoculture (mean +/- 1 SE). Within each panel (A, B), small letters refer to significant differences in recruitment between monocultures (from ANOVA analyses; no letters indicate no significant differences). Between each panel (A, B), asterisks refer to significant differences between recruitment to primary and secondary substrate in each monoculture community (from t-tests; no asterisk indicates no significant difference). Statistical analyses detailed in the text.

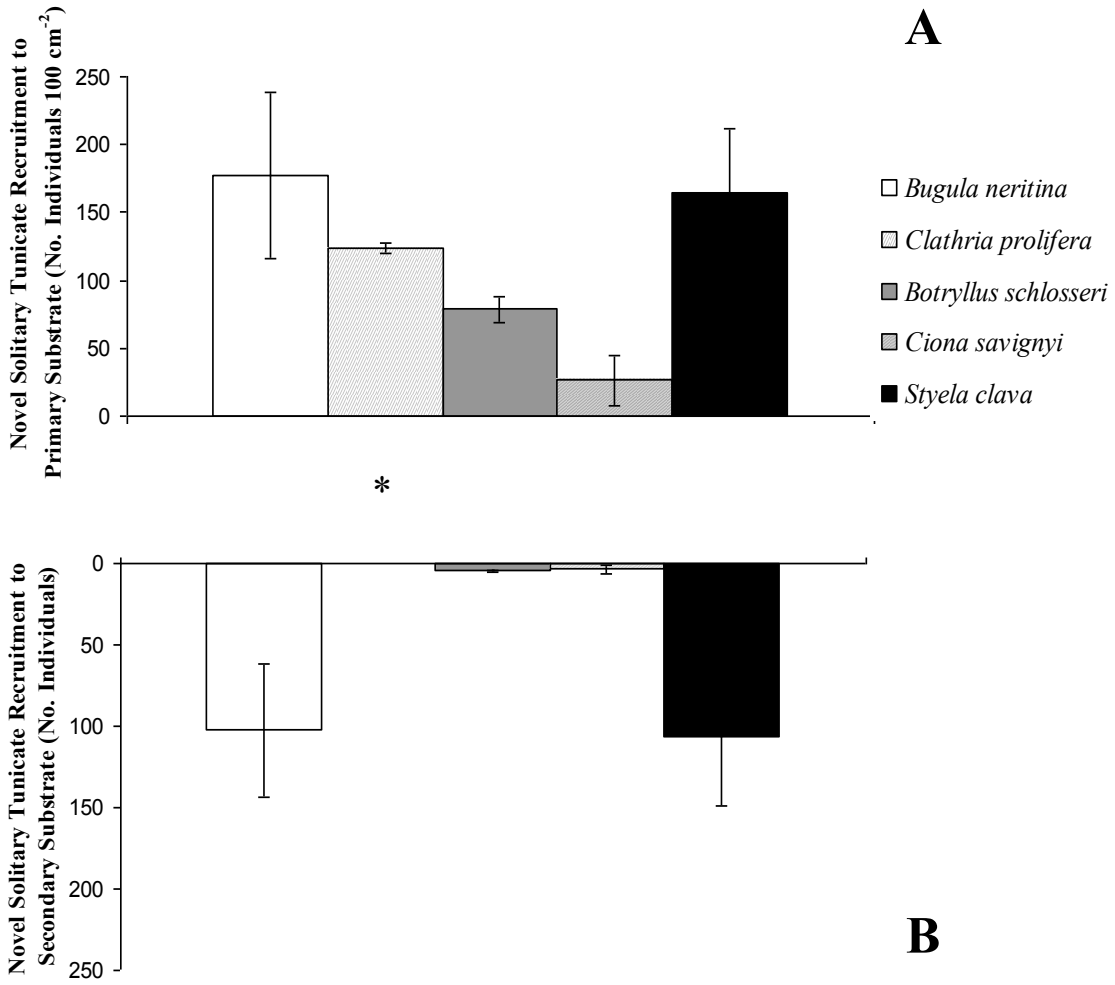
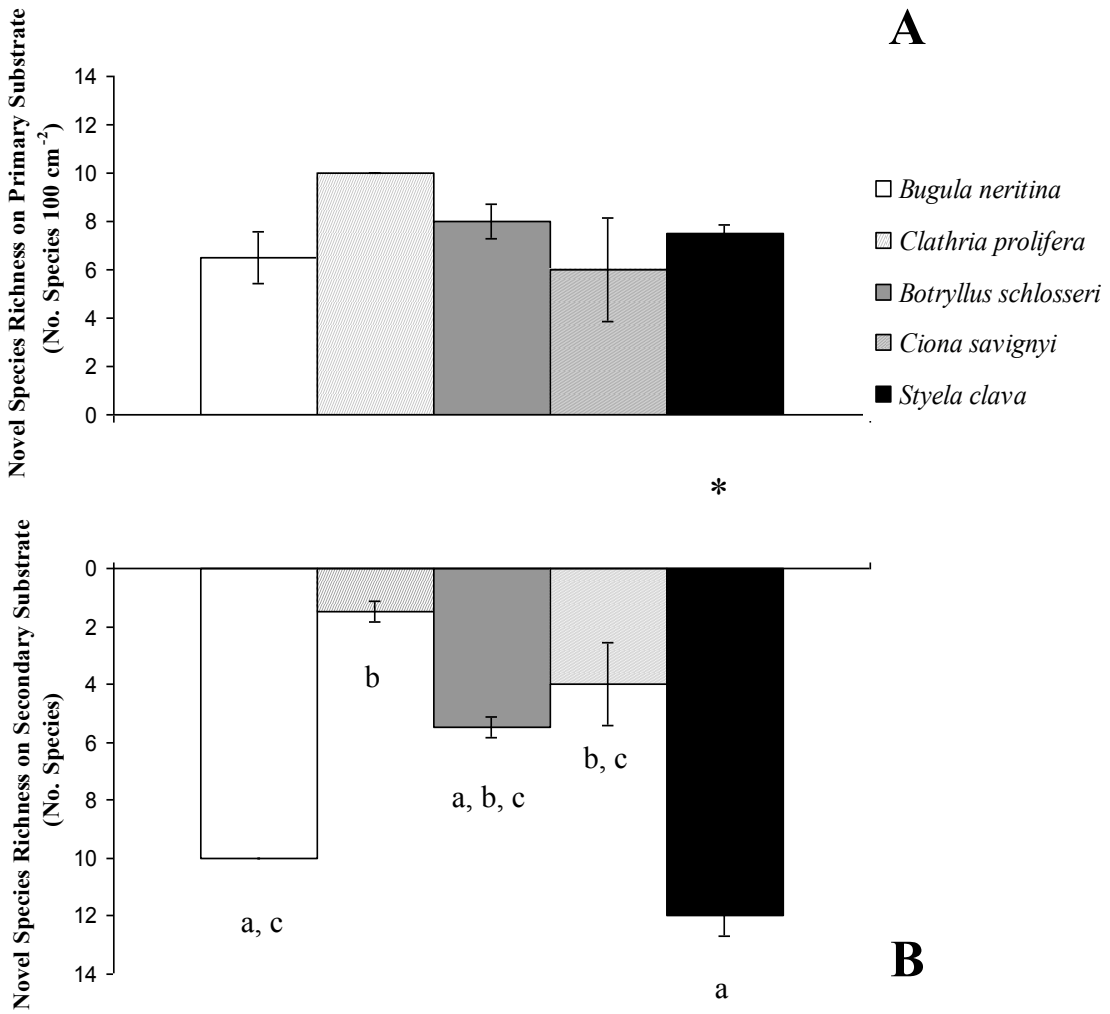


Figure 6. Novel non-native species richness found in primary substrate (A, above) and secondary substrate (B, below) in monoculture communities. Adult species used to create monocultures are identified by color/pattern of bar, while height of bar indicates the number of species that settled in each type of monoculture (mean +/- 1 SE). Within each panel (A, B), small letters refer to significant differences in species richness between monocultures (from ANOVA analyses; no letters indicate no significant differences). Between each panel (A, B), asterisks refer to significant differences in the number of species on primary and secondary substrate in each monoculture community (from t-tests; no asterisk indicates no significant difference). Statistical analyses detailed in the text.



Dissertation Conclusion

Overview

The present work has contributed to a better understanding of the patterns of biodiversity, and how biodiversity relates to invasibility and the success of non-native species within fouling communities of San Francisco Bay. Specifically, Chapter 1 focused on quantifying the α, β and gamma diversity of the native, non-native and cryptogenic components of the marine fouling community through surveys conducted in 2000 and 2001. Alpha and γ-diversity refer to the number of species at local and regional sites, respectively, while β-diversity is a measure of the regional variation in species composition among sites, or species turnover. Results from diversity surveys showed that non-native α-diversity was significantly greater than native or cryptogenic α-diversity. The opposite pattern was seen in measures of β-diversity, in which native and cryptogenic species had significantly greater β-diversity than NIS. Finally, γ-diversity was highest for NIS, but native species also displayed comparable regional diversity. These results indicate that native species have high turn over from site to site and fewer native species are found within individual fouling communities across the bay. In contrast, NIS are spread throughout the bay with little species turnover between sites, types of site, or years. These patterns represent a fundamental difference in distribution between natives and non-natives across the bay itself and indicate that biotic homogenization has likely occurred bay-wide.

In Chapter 2, I explored the diversity resistance hypothesis. This hypothesis predicts that high diversity should lead to community resistance to invasion because limiting resources are more fully utilized within the community. To test the validity of this hypothesis in marine fouling communities of San Francisco Bay, I ran experiments

that focused on the influence of diversity and resource availability (open space) on both short-term recruitment of novel invasive species into test communities and subsequent community development over the course of multiple seasons. On short time scales of 2-4 weeks, the effect of initial community diversity on the density of recruitment of novel non-indigenous species was significant and negative, with no effect of resource level (increased open space). In both 2006 and 2007, the recruitment of one or two species displayed a significant inverse relationship with community diversity (*Botrylloides violaceus* in the fall of 2006, *Ciona intestinalis* and *Bugula stolonifera* in the summer of 2007, Chapter 2). Changes in community composition over longer time scales of up to 6 months also indicated significant inverse relationships between percent cover of non-native species and diversity of the initial fouling community with no evidence of a resource effect. Abundant non-native species occupied less space in communities with higher initial diversity. However, the same suite of non-native species were present in (i.e., invaded) all experimental communities regardless of starting diversity. Despite significant results, the lack of resource effects across both studies does not support the hypothesis that resource limitation is driving the effects of diversity. Resource use may be more complex and most likely includes primary as well as secondary substrate.

In Chapter 3, I further explored the use of resources in the fouling community by focusing on primary and secondary resources. I conducted experiments in which the diversity of non-native species and primary resource availability were manipulated, and recruitment to primary and secondary substrates was evaluated. Although initial community diversity affected the number of recruits that settled onto primary space, initial community diversity did not affect the number of recruits that settled onto

secondary substrate or the combination of primary and secondary subtrates. Even though there was no affect of diversity on settlement to secondary substrate, certain individual species did facilitate or inhibit secondary settlement. As initial community diversity increased, the facilitative and inhibitive properties of individual species remained important. These results indicate that the influence of secondary substrate is tied to the particular species that make up the community, and may mean that species-specific effects play a larger role in diversity-invasibility relationships than previously examined. This study also highlights the role of non-native species in facilitating or inhibiting invasion of other non-natives.

When examined comprehensively, this dissertation reveals five key points pertaining to invasion patterns and dynamics in the marine fouling communities of San Francisco Bay:

1) There are many NIS present and they are spread throughout the bay, unlike their native counterparts which have more limited species distributions in the bay, such that NIS contribute to bay-wide homogenization of this community;
2) As diversity in the initial community increases, new NIS are less successful. This can be interpreted as an increased resistance to invasion due to increased initial community diversity;
3) Primary resource use does not appear to drive diversity-resistance patterns (as described in 2) and primary resources do not appear to be limited;
4) When the influence of secondary resources is also incorporated, there is no longer an increased resistance to invasion due to initial community diversity;

5) Specific adult species can facilitate or inhibit settlement by NIS through their provision of secondary substrate, and community diversity can affect the strength of facilitation or inhibition.

Management

With respect to management implications and recommendations, these general results present a community overrun with NIS that dominate fouling communities throughout the world. Thus, given the nature and spread of non-native fouling species within San Francisco bay and worldwide, the most influential management objective may be to focus on the vectors that initially bring new species from one estuarine system to another. While vector management of ballast water has a short history in the U.S., in less than two decades there has been great progress on ballast water management and regulation with respect to invasive species (United States Coast Guard, 2010). As a vector for invasive species transfer, hull fouling has not been emphasized in the U.S., but its importance is beginning to be recognized, and monitoring and regulatory efforts have begun in the state of California (Takata et. al., 2006). Successful management and reduction of the movement of species on the hulls of commercial vessels and recreational vessels would limit or prevent introduction of new fouling species.

Aside from vector management, there are also other management approaches that may be helpful in reducing invasion success. The current body of work demonstrated that communities with higher initial diversity were more resistant to invasion by novel species. Protecting diverse sites, especially sites that have higher numbers of native species or native individuals, or enhancing diversity by seeding sites with a diverse array of native species may also allow for this resistance. However, my results also indicated

that while novel NIS were less successful in communities with higher initial diversity, most common dominant species were present or had invaded treatments of all diversity levels. From a management perspective, this indicates that despite ecological resistance conferred by community diversity, dominant NIS could invade any community. This suggests instead that a targeted management strategy that focuses on removal of specific dominant species might be a more effective approach to disrupting NIS populations and reducing effects of biotic homogenization. A combined approach that promoted high diversity and removed dominant species such as *Ciona intestinalis, C. savignyi***,** and *Botrylloides violaceus* might enhance the effect of community resistance.

In addition to targeting common species, it would be useful to focus management efforts on non-native species that serve as facilitators for other non-natives. The current work identifies the bryozoan *Bugula neritina* as one such facilitator. In contrast, the sponge *Clathria prolifera* and the tunicate *Botryllus schlosseri* were identified as inhibitors to secondary settlement of novel NIS. Targeting the removal of *B. neritina* while allowing *C. prolifera* and *B. schlosseri* to remain in fouling communities might help diminish the effect of facilitation through settlement on secondary subtrates. Removal could be achieved through development of species-specific biocides, or through manual removal of specific species.

The volume and extent of artificial hard substrate that is present within San Francisco Bay most likely contributes to the success of the fouling community in general and to NIS in that community. This is in part because artificial hard substrates (such as those provided by piers, pilings, docks, and marinas, etc.) are more prevalent within the bay than natural hard substrates such as rock outcroppings. Limiting the construction of

artificial substrates, carefully designing them, and using natural substrates when possible could also benefit native species within the community. Limiting artificial substrates to high flow environments within the bay may also deter settlement of NIS, as lower non-native alpha diversities were seen in higher flow sites such as piers when compared to lower flow marinas (Chapter 1).

Future Studies

There are several areas of future work that would further inform the results presented in this dissertation. The current work focused on several taxonomic groups that are common in fouling communities. Including a broader array of taxonomic groups, mobile species and mobile predators would provide an even more comprehensive account of community dynamics, and may highlight differences between the success of mobile and sessile NIS. Although predators were not extensive in the study sites that were examined, predation can play an important role on community structure and development (Byrnes and Stachowicz, 2009). It would be interesting to identify the affect, if any, of predation on relationships between community diversity and invasion success. It should be noted, however, that in the experiments described in this dissertation, no attempt was made to remove predators from experimental communities.

A focused study on the differences in water flow within the bay and how this relates to native and non-native abundance or growth might elucidate how patterns associated with water flow affect success of NIS. It also would be useful to determine how common a negative association with high flow environments and NIS abundance is

in marine and aquatic systems, as there is evidence that non-native fish are less abundant in high flow sites as well (Moyle and Marchetti, 2006).

Incorporating the role of secondary substrate in fouling community studies in general would provide a more complete picture of fouling community dynamics. Many studies ignore the influence of secondary substrate completely, and its role as an overlooked resource is most likely important in determining species composition within a community, as well as the species turn-over within communities over time. The amount of secondary substrate within individual fouling communities was not calculated in the current study. Quantifying the amount of secondary substrate would provide a relative index of the amount of primary vs. secondary substrate availability and potentially a more realistic assessment of resource limitation within fouling communities.

A comprehensive understanding of diversity-invasibility relationships requires studying diversity patterns and effects in multiple systems. Even at a regional spatial scale, incorporating similar studies in other types of communities (e.g., soft sediment habitats, seagrass beds) would help determine common patterns with respect to community diversity and how diversity relates to invasion success. Results may also help to further validate the use of marine fouling communities as a model system for estuarine studies of this nature.

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